The Western Amazonian Richness Gradient for Squamate Reptiles: Are There Really Fewer Snakes and Lizards in Southwestern Amazonian Lowlands?

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Abstract: The lowland rainforests of the Amazon basin harbor some of the most species-rich reptile communities on Earth. However, there is considerable heterogeneity among climatically-similar sites across the Amazon basin, and faunal surveys for southwestern Amazonia in particular have revealed lower species diversity relative to sites in the northwestern and central Amazon. Here, we report a herpetofaunal inventory for Los Amigos Biological Station (LABS), a lowland site located in the Madre de Dios watershed of southern Peru. By combining active search and passive trapping methods with prior records for the site, we provide a comprehensive species list for squamate reptiles from LABS. We also estimate an "expected" list for LABS by tabulating additional taxa known from the regional species pool that we consider to have a high probability of detection with further sampling. The LABS total of 60 snake and 26 lizard taxa is perhaps the highest for any single site in the southern Amazon. Our estimate of the regional species pool for LABS suggests that the southwestern Amazonian lowlands harbor at least 25% fewer species of snakes relative to the western equatorial Amazon, a diversity reduction that is consistent with patterns observed in several other taxonomic groups. We discuss potential causes of this western Amazonian richness gradient and comment on the relationship between spatial diversity patterns in squamates and other taxa in the Amazon basin.

Keywords: species richness; diversity gradient; community structure; reptiles; neotropics; Amazon; rainforest; lizard; snake

1. Introduction

Perhaps most the fundamental challenge in biogeography is to explain why species richness varies across the surface of the Earth. Regardless of spatial grain of sampling, the most prominent biodiversity pattern on our planet is the extent to which the number of species differs between sites. The most famous example of this pattern is the latitudinal diversity gradient, whereby species richness peaks in the tropics and decreases with latitude as one moves towards increasingly temperate or polar regions. Importantly, species richness can vary substantially even among climatically-matched sites, for reasons that remain difficult to explain [1]. For example, species richness of rainforest trees is far higher in the Neotropics and southeast Asian tropics than in climatically-matched sites from the African tropics [2]. Similarly, the number of broadly-sympatric lizard taxa in the spinifex deserts of arid Australia greatly exceeds the number of lizard species that occur in any other region on Earth, including both climatically-matched desert regions and wet tropical regions alike [3–6].

Australian lizards aside, the Amazon basin and eastern Andes represent the most biodiverse region on Earth for the majority of terrestrial organisms [7,8]. The rainforests of western Amazonia are

characterized by extreme species richness, and represent one of the largest remaining wilderness areas on the planet. In spite of their high overall diversity, sites within the Amazon can vary substantially in species richness. Pitman et al. [9] observed that tree species richness at area-matched lowland sites varied along a gradient from north to south across the western Amazon. At Yasuni National Park, in the Ecuadorian Amazon (1° S), standardized survey plots (1 ha [hectare]) contain an average of 239 species, versus 174 species for sites in the Madre de Dios watershed of southern Peru (12° S). Pitman et al. [9] explored several possible explanations for this western Amazonian richness gradient, including the influence of biotic and abiotic differences between regions, concluding that regional climatic factors play an important role in mediating differences in species richness.

Squamate reptiles (lizards and snakes) show an intriguing pattern of species richness variation across the Amazon basin, and especially along a north-to-south gradient that extends from eastern Ecuador to southeastern Peru (Figure 1). Although snakes are phylogenetically nested within squamates, we nonetheless use the word "lizard" throughout this article to refer to all squamates that are not snakes, owing to major differences in ecology, abundance, and detectability between snakes and non-snake squamates [10]. Species lists for sites from the northwest Amazon (e.g., Rio Amazonas and Rio Napo of Peru and Ecuador) are markedly higher than those for the southwestern Amazonian lowlands, and include a number of genera that are not represented in the south [11]. More recently, estimates of species richness from reconstructed geographic ranges and museum samples suggest that richness of snakes in particular is considerably higher in the northwestern Amazon (= western equatorial Amazon) relative to the south [12–14]. A casual inspection of published species lists would suggest that sites in southern Peru harbor fewer species of both snakes and lizards relative to sites approximately 1000–1500 km further north. For example, 48–52 species of snakes and 24 species of lizards are known from Cusco Amazonico [15], an intensively-studied site along the Madre de Dios River in southern Peru. In contrast, approximately 94 species of squamates are known from a similar-sized area in the Ecuadorian Amazon [7,16]. These and other results [11,15] imply that alpha diversity for squamates in the northern Amazon is 30% higher relative than communities in the south, a ratio that approaches that observed for tree assemblages from the same regions [9].

However, it is challenging to draw general conclusions about variation in species richness and turnover in community composition for Amazonian squamate reptiles. These difficulties emerge for at least three reasons. First, the geographic scale of sampling for published squamate inventories is highly variable. The lack of standardization has necessitated that researchers perform biogeographic comparisons on communities that differ by three to four orders of magnitude in spatial extent (e.g., 300 ha to 4,500,000 ha; [11]). Second, squamate reptiles—and especially snakes—are notoriously difficult to sample; many species have detectabilities so low as to render them effectively invisible in the communities where they occur [10,17,18]. Finally, there is no single standardized protocol for sampling rainforest squamate communities: The low detectabilities of many species lead researchers to adopt a variety of methods for sampling communities, towards the goal of providing the most complete species list for an area. For these reasons, there remains a tremendous amount of uncertainty in community composition across Amazonian squamate communities.

Here, we report a comprehensive list of squamate taxa from a targeted sampling of a lowland rainforest site from southeastern Peru. From 2001–2018, we used a variety of methods to survey approximately 10 km^2 (1000 ha) of primary and secondary forest at Los Amigos Biological Station (hereafter, LABS) in the Madre de Dios region of southeastern Peru. We provide lists of those species documented explicitly at LABS, as well as an expanded list that includes other taxa from the region whose occurrence at LABS is highly probable with further sampling. Our work builds on previous surveys and compilations for this general region [19–21], and provides one of the most thorough and spatially-explicit inventories of squamates for a single Amazonian site. We contrast species richness at LABS to other Amazonian sites, and we compare these results to patterns documented for trees, lianas, birds, and other taxa. Our ultimate goal is to determine whether a true north-to-south gradient in species richness exists for squamate reptile communities in the western Amazon basin.
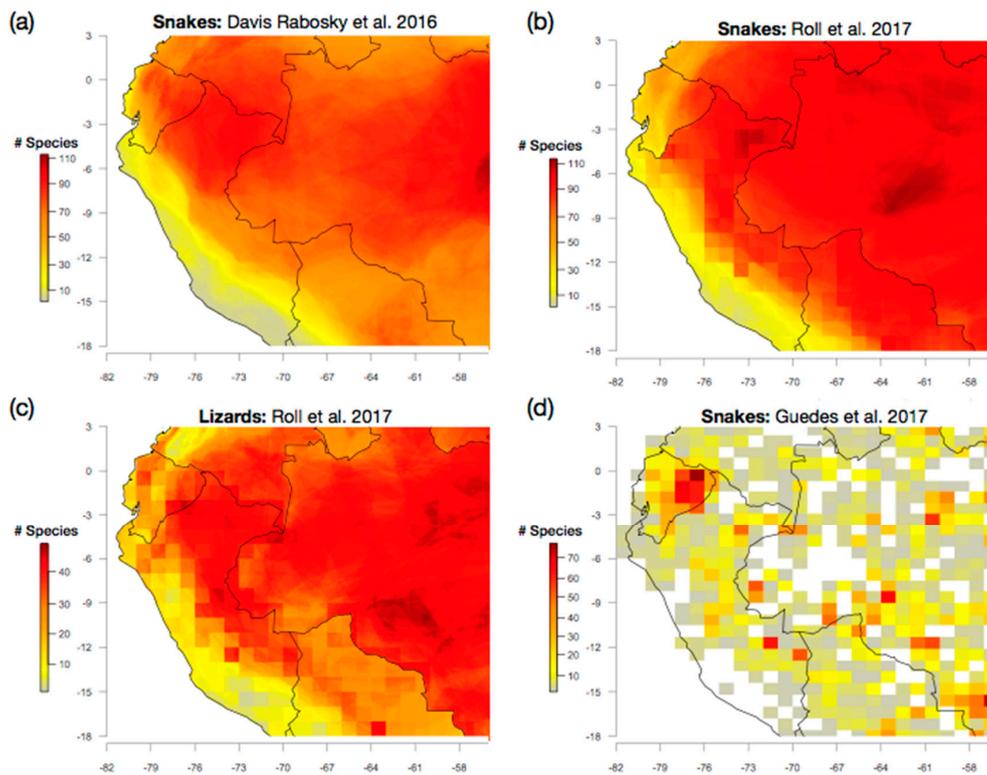
Figure 1. Species richness for squamate reptiles in the western Amazon basin as inferred from range reconstructions and primary occurrence data. Estimates of snake (**a**,**b**) and lizard (**c**) species richness from published range maps [13,14] suggests higher diversity in the western equatorial Amazon (northern Peru, Ecuador) relative to southern Peru. (**d**) Snake species richness from georeferenced museum occurrence data [12] is consistent with higher richness in the Ecuadorian Amazon relative to southern Peru. Results in (**d**) are heavily affected by biases in sampling and data availability; the data compilation included proportionately fewer occurrence records maintained by Peruvian institutions. Both (**a**,**b**) imply that some sites in the north contain 20–30 more species of snakes than sites from southern Peru.

2. Materials and Methods

2.1. Study Site

Research was performed at Los Amigos Biological Station (LABS; 12°34′07′′S, 70°05′57′′W, 250 m elev; also known as CICRA in previous literature), located in Manu province, Madre de Dios region, southeast Peru. In addition, we carried out field surveys at Centro de Monitoreo 1 (CM1; 12°34′17′′ S, 70°04′29′′ W), located ca. 3.5 km east from LABS, and Centro de Monitoreo 2 (CM2; 12°26′57′′ S, 70°15′06′′ W, 260 m), located ca. 25 km northwest from LABS. The annual rainfall recorded at LABS ranges between 2700 and 3000 mm [22]. The dry season (June–September) has markedly lower rainfall and is slightly cooler than the wet season. The mean annual temperature ranges between 21 °C and 26 °C (N. Pitman, pers. comm.). Most of our surveys took place in four forest types: mature floodplain forest (hereafter referred to as floodplain forest), terra firme forest, bamboo forest dominated by two native woody bamboo species (*Guadua sarcocarpa* and *G. weberbaueri*), and palm swamp dominated by a native palm (*Mauritia flexuosa*). We also surveyed other terrestrial habitats including secondary forest, riparian forest, clearings, and river banks; and various types of aquatic habitats including oxbow lakes, streams, permanent ponds (e.g., "Pozo Don Pedro"), seasonal ponds, and other wetlands (e.g., small swamps dominated by other palm species). Further details regarding primary forest types and aquatic habitats is available in earlier references [20,21,23–25].

2.2. Data Collection

From 2001 to 2018, we surveyed reptile and amphibian communities at LABS using a variety of sampling techniques. Survey methodologies included (1) leaf-litter plot surveys, (2) nocturnal visual encounter surveys, (3) passive trapping using pitfall traps and funnel traps, and (4) a variety of active and targeted search strategies to increase encounter probabilities for specific taxa and/or within particular microhabitats. Leaf-litter sampling protocols used at this location have been described previously [20] and involved exhaustive search through randomly-selected 100 m^2 or 25 m^2 square plots by teams of trained observers at night. Nocturnal visual encounter surveys were performed by actively search for reptiles and amphibians along the official LABS trail network (trail surveys), and by searching along 50 m or 100 m transects (transect surveys) that we established away from major trails [20]. Both trail and transect surveys typically involved groups of 2–3 researchers, but survey procedures differed, with trail surveys conducted at a more rapid walking pace (mean pace: 0.36 km/hr) relative to transect surveys (mean pace: 0.10 km/hr). Use of vertebrate animals was approved by the Animal Care and Use Committee of the University of Michigan (protocol PRO00008306).

In general, fieldwork from 2001–2015 emphasized transect surveys and leaf-litter plot surveys, and work from 2016–2018 was focused primarily on trail surveys and passive trapping. However, pitfall trapping and trail surveys occurred prior to 2016, and some transect/leaf-litter sampling occurred between 2016–2018. From 2016–2018, we conducted approximately 340 km and 14,500 min of nocturnal trail surveys. We also performed at least 32.5 km and 20,500 min of transect surveys (~650 transects), along with approximately 375 leaf-litter plot surveys.

Preliminary surveys with drift fences and pitfall traps took place in the dry seasons of 2005 and 2006. In four forest types (floodplain forest, terra firme forest, bamboo forest, and palm swamp), we set up three arrays of drift fences and pitfall traps. Each array had three fences of 5 m each in length. We used plastic sheets for making the fences and we buried each fence 10 cm in the ground, leaving at least 50 cm of fence above ground. We used four 19 L plastic buckets as pitfall traps, following a lineal construction design. The opening of each bucket was flush with the ground surface. The arrays remained in the same location up to four weeks, and were checked at least once per day.

From 2016–2018, we established a regular grid of pitfall and funnel traps in multiple habitats; sites were surveyed in March–April 2016, November–December 2016, November–December 2017, and November–December 2018. Each trapline involved either three pitfall traps or four funnel traps. Funnel trap [26] dimensions were 18 cm × 18 cm × 79 cm, and were purchased from Terrestrial Ecosystems (Mt Claremont, Australia). Traps were connected by 12 m of plastic drift fencing. All traps were checked at least once per day. From 2016–2018, we conducted a total of 9181 trap-days of funnel trap sampling, and 6670 trap-days of pitfall sampling. Many records were also obtained through opportunistic sampling, particularly medium-to-large diurnal snakes that were most commonly encountered on trails while researchers checked traps or performed other activities.

In general, we collected multiple voucher specimens per species, to facilitate taxonomic work, to generate a permanent and curated record of squamate biodiversity for LABS and to enable us to create and curate community resources that can only be provided by physical specimens (e.g., samples of venom, Duvernoy's gland, glandular skin, and internal parasites). Multiple tissue types were taken from all vouchered animals and preserved in RNAlater. All vouchered specimens were deposited in the herpetological collections at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM; Lima, Peru), or in the University of Michigan Museum of Zoology (UMMZ). Records for several species were obtained through opportunistic sampling by researchers or visitors to LABS who were unaffiliated with our research group. In these cases, we required that the records be accompanied by photographs and specific sublocality information.

2.3. Data Tabulation and Analysis

We compiled three lists of squamate reptiles for LABS. First, we consider only the set of species documented explicitly by our group from the immediate vicinity of the LABS station. The area of this

survey region is approximately 10 km^2, and thus provides a useful "local scale" counterpart to other spatially explicit, localized surveys in Amazonia (e.g., surveys at Cusco Amazonica, Peru; Tiputini Biological Station, Ecuador; Reserva Ducke, Brazil). The second list includes all species documented from the Los Amigos conservation concession, including parts of the reserve or its buffer zone that were located across the Rio Los Amigos (CM1) or some distance upriver from LABS (CM2). Finally, we generated an expected list that included all species known from lowland Amazonian rainforest with documented occurrences in the broader Los Amigos / Madre de Dios region; this includes all species known from other lowland sites within roughly 150 km of LABS, and which we consider to have a high likelihood of detection with continued work at the site. Where possible, we used recent taxonomic works to update the identifications of many specimens in our dataset (e.g., *Erythrolamprus*; [27]).

We analyzed the tempo of species accumulation through time for our 2016–2018 fieldwork, where much of our efforts were focused on squamate sampling, and where we believe we had a reasonably consistent sampling effort from day-to-day. We used randomized sampling from the full set of survey days from 2016–2018 (112 days) to generate an expected species accumulation curve as a function of survey effort. Using nonlinear regression, we fitted a simple hyperbolic model for species accumulation through time (equation 2 in [28]), and used it to predict both the total richness of the LABS squamate fauna and to estimate the effort required to achieve a comprehensive inventory. In this model [28], the estimated species richness is given by $S(n) = S_{max} n/(B + n)$, where B and S_{max} are fitted constants, and n is the number of samples. Here, a sample is equated to a "survey day", and S_{max} is the asymptotic richness as n becomes large.

For comparative purposes, we also compiled data on squamate richness from a number of previous studies. Where possible, we updated records from those previous lists to reflect recent taxonomic changes. However, we did not attempt to comprehensively address taxonomic changes to species lists, because most taxonomic changes involved updates to specific epithets, and thus had little impact on either the total or generic species richness at a given site. We also obtained estimates of species richness at the local-to-regional scale for a range of other taxa (e.g., trees, birds, lianas), focusing in particular on northern and southern lowland sites in the western Amazon basin. This generally involved comparing sites from the Rio Napo drainage (Yasuní, Tiputini) to those from southern Peru (Madre de Dios watershed). These and other locations discussed in text are shown in Figure 2.
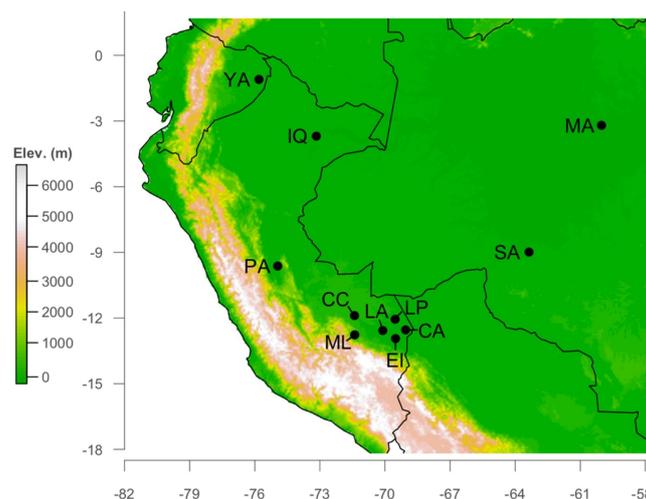
Figure 2. Localities in the western and central Amazon basin discussed in this article. YA: Yasuní National Park and Tiputini Biodiversity Station; IQ: Iquitos (Loreto, Peru); PA: Panguana Biological Station; CC: Cocha Cashu Biological Station; LA: Los Amigos Biological Station (LABS); ML: Manu Learning Centre; EI: Explorer's Inn; CA: Cusco Amazónico; LP: Las Piedras Biological Station; SA: Samuel Hydroelectric Project (Rondônia, Brazil); MA: Manaus, Brazil. All localities are lowland rainforest sites that receive approximately 2200–3200 mm of precipitation annually, although southern sites are markedly more seasonal than those in the north.

3. Results

The documented squamate fauna from LABS includes at least 26 species of lizards and 60 species of snakes (Appendix A: Table A1), an increase of 19 species relative to the most recently-published list for the site [16]. Several additional snake and lizard species are known from the Los Amigos Conservation Concession and are shown in Table A1 (LABS-R). Finally, the expected Los Amigos (LABS-X) list includes taxa that are known from geographically-nearby and climatically-similar sites in southern Peru and includes a total of 36 lizard and 68 snake taxa (Table A1: LABS-X). For the LABS-X list, we did not include taxa known only from foothill sites in the region (e.g., *Dipsas pavonina*; [16]). We also did not include taxa whose nearest documented occurrences are in adjacent regions of Brazil (e.g., *Bothrocophias hyoprora*; [29]). Table A1 provides, where available, representative catalog numbers for several reference specimens deposited in the herpetological collections at the UMMZ and MUSM. For the 2016–2018 survey period, mean numbers of captures per day ranged from 0–12 (snakes) and 0–19 (lizards), with resulting in averages of 2.9 (snakes) and 3.6 (lizards) species per day. The number of species detected per day throughout this survey period is shown in Figure 3. Overall, capture rates fluctuate through time and show considerable temporal autocorrelation, as expected if capture rates are responding to temporally-correlated drivers (e.g., weather; lunar cycle). The empirical species accumulation curve for our 2016–2018 work is shown in Figure 4. Expected richness as a function of the number of survey-days is shown in Figure 5. The fitted hyperbolic function provided a good fit to the overall tempo of species accumulation as a function of sampling (Figure 5), and the predicted maximum richness is 58 and 28 species of snakes and lizards, respectively. For lizards, the total reported species richness from LABS is similar to the predicted richness as extrapolated from the species accumulation curve (N = 26 versus N = 27 species; Figure 4). For snakes, the observed total is slightly higher than the predicted total, but somewhat lower than the number recorded during the 2016–2018 sampling period (N = 49 species). Using the fitted accumulation curve (Figure 5) and assuming a homogeneous sampling process, we estimate that an additional 260 days of sampling (e.g., more than twice the sampling effort already expended) would be needed to record 95% of the predicted snake richness in this system.
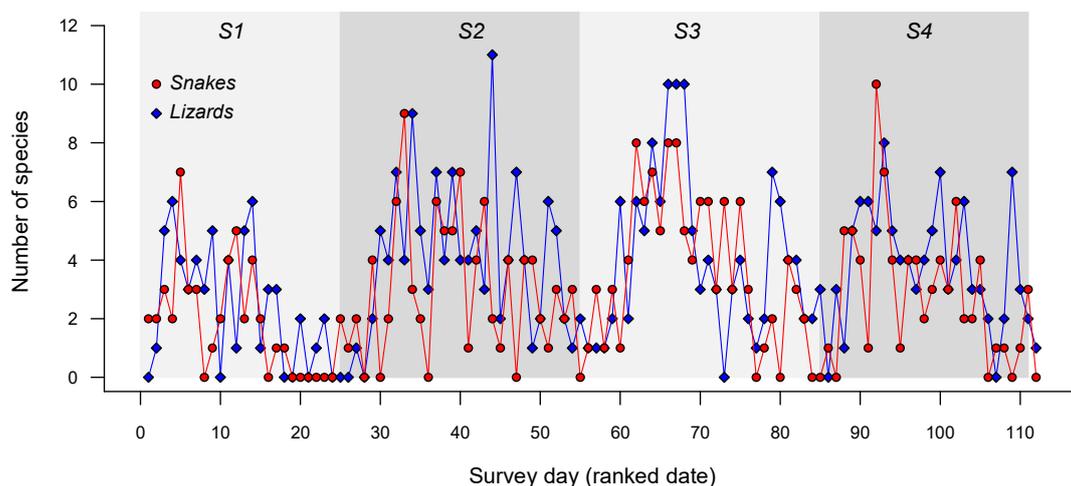
Figure 3. Numbers of species of snakes and lizards detected per sampling day during 2016–2018 fieldwork. Sampling periods: S1, March–April 2016; S2, November–December 2016; S3, November–December 2017; S4, November–December 2018.
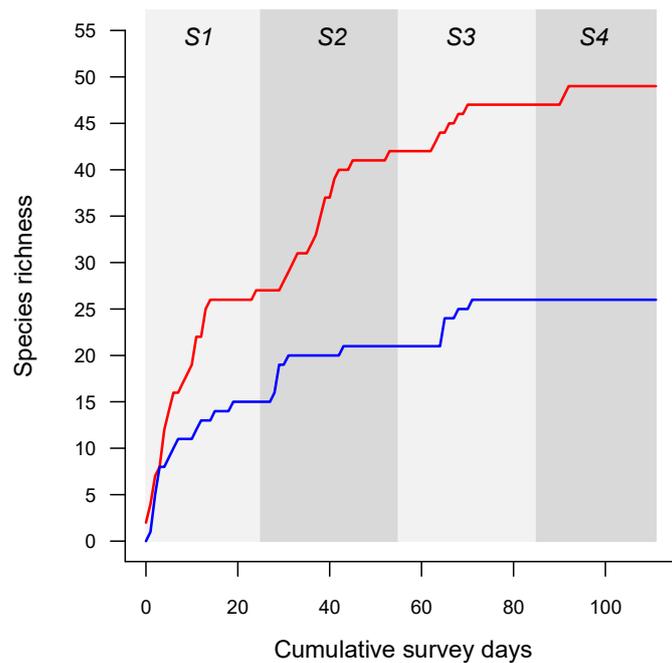
Figure 4. Cumulative numbers of species of snakes (red) and lizards (blue) during 2016–2018 fieldwork at Los Amigos Biological Station (LABS). Sampling periods: S1, March–April 2016; S2, November–December 2016; S3, November–December 2017; S4, November–December 2018.
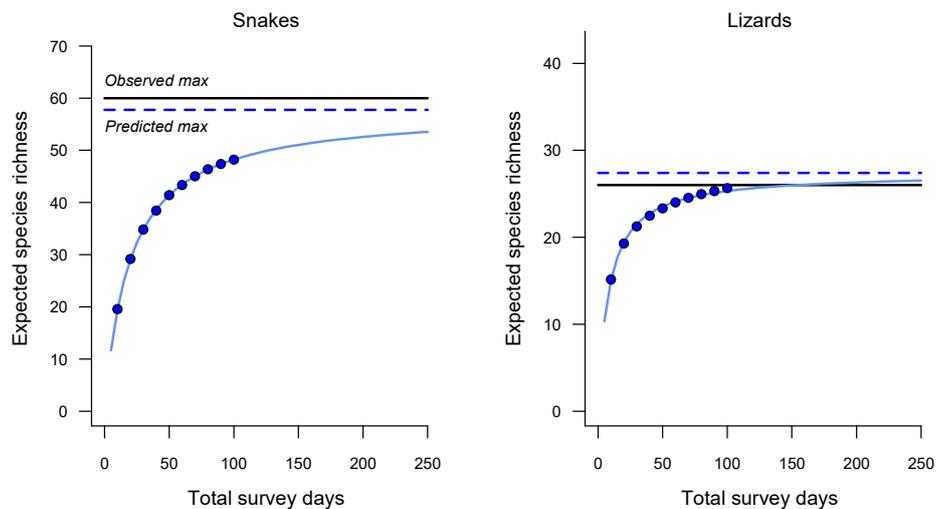
Figure 5. Expected species accumulation curves as a function of survey days for snakes (**left**) and lizards (**right**), using survey data from 2016–2018. Points show mean species richness as a function of survey days obtained from resampling the observed data; underlying blue line corresponds to fitted hyperbolic function [30]. Observed maximum (solid horizontal line) is the total number of species documented from LABS (N = 60), and predicted max (blue dashed line) is the expectation from the resampled survey data.

4. Discussion

With at least 60 species of snakes and 26 species of lizards documented, the squamate reptile diversity at LABS is the highest local-scale diversity reported for the southwestern Amazon basin. These numbers are comparable to those reported for Tiputini Biodiversity Station (Table 1), which is claimed to hold the global alpha diversity record for reptiles [7]. These numbers are based on broadly-comparable sampling regions; as defined here, the LABS total includes species detected in

an area of approximately 10 km² in the vicinity of the main research facilities, versus 6.5 km² for Tiputini. However, the comparisons offered in Table 1 do not address gross discrepancies in survey effort and should nonetheless be treated provisionally. LABS has been the subject of considerable long-term research, and we expect that the site has been more intensively surveyed than Tiputini. The "regional" list for LABS (LABS-X, Table A1) includes 68 snake species and 36 lizard species, and is thus considerably richer than faunas typically reported for the southwestern Amazon basin (Table 1 [11,15]).

Nonetheless, it is clear that the snake fauna of central/northwestern Amazonia is richer than for LABS and other southwestern sites. At least 89 species of snakes are known from the Iquitos region [31], which represents a 29% increase in richness relative to the LABS regional list (Table A1: LABS-X). The regional list for Iquitos encompasses a large spatial scale [31], but it is unlikely that the discrepancies in snake richness between these regions can be explained as an artifact of scale. For example, the Iquitos region includes multiple genera of snakes and lizards that have not been reported from the lowlands of southern Peru (e.g., *Arthrosaura*, *Bothrocophias*, *Iguana*, *Loxopholis*, *Thamnodynastes*), and several other genera are considerably more species-rich in the Iquitos region (e.g., *Amerotyphlops*, *Atractus*, *Helicops*, *Micrurus*, *Erythrolamprus*). Given the high richness of the Iquitos region overall, we predict that lowland sites in the Ecuadorian Amazon (Tiputini, Yasuní; Table 1) are more diverse than reported previously [7]. Southern Peru has been subject to greater sampling effort, and the discrepancies between local-scale tabulations for southern and northern sites (Table 1) seem likely to increase with additional sampling in the Rio Napo basin and adjacent regions.

Table 1. Species richness for lizards and snakes for selected sites in the western Amazon basin. Localities are shown in Figure 2. LABS, LABS-R, and LABS-X are documented and estimated richness totals for Los Amigos Biological Station, as in Table A1.

Locality	Scale	Latitude	Precipitation	Snakes	Lizards	Reference
Manu Learning Center (MLC) [1]	local	−12.8	3000	40	21	[16]
Los Amigos: LABS	local	−12.6	2600	60	27	This paper
Los Amigos: LABS-R	regional	−12.6	2600	62	28	This paper
Los Amigos: LABS-X	regional	−12.6	2600	68	36	This paper
Cusco Amazonico (CA)	local	−12.5	2400	52	28	[15,32]
Tambopata (EI)	local	−12.8	2500	50	26	[32]
Cocha Cashu	local	−11.9	2500	32	25	[16]
Panguana	local	−9.6	2500	44	27	[33]
Yasuni [2]	regional	−0.6	3100	78	33	[7]
Tiputini	local	−0.6	3100	63	31	[7]
Iquitos [3]	regional	−3.7	2900	89	39	[11]

[1] Higher elevation than other sites (500 m, vs 220–280 for others), presumably accounting for higher precipitation. [2] Bass et al. (2010) list does not include several taxa that are almost certainly present: *Ameiva ameiva*, *Epictia diaplocia*, and *Xenopholis scalaris*; listed totals include these taxa. [3] Added *Epictia diaplocia* to Iquitos list; vouchered specimens known from region [34].

4.1. A Western Amazonian Richness Gradient: Does It Exist?

For squamate reptiles, and especially for snakes, our results imply that there is a clear gradient in species richness from north to south in the western Amazon basin. Results parallel those found in a wide variety of taxa, including trees, vascular epiphytes, lianas, and frogs (Table 2). For example, regardless of spatial scale, tropical tree communities in Yasuní contain roughly 40–50% more species than sites at Cocha Cashu or LABS [9]. The causes of this western Amazonian richness gradient remain poorly understood. Pitman et al. [9] noted several structural differences between northern (Yasuní) and southern (Cocha Cashu) tree communities, including tree density, average height, leaf

size, and seed size. Furthermore, a number of macroecological descriptors differ between these communities, with species from northern Amazonian sites having smaller geographic and altitudinal ranges. Interestingly, more mobile taxa—birds and primates in particular—show no evidence for increased diversity in the north: Communities from Cocha Cashu and Los Amigos have effectively the same diversity as those from Yasuní, Tiputini, and the Iquitos region (Table 2).

Table 2. Species richness for different taxonomic groups in lowland rainforest in the northern equatorial Amazon (Loreto, Peru; Ecuador) and the southwestern Amazon (southern Peru, northwestern Bolivia). Diversity inflation is the proportional increase in species richness at northern sites relative to southern sites.

Taxon	Richness (North)	Richness (South)	Diversity Inflation (%)	Scale	Reference
Trees	239	174	40	local	[9]
Trees	1017	693	50	regional [1]	[9]
Trees	1356	1004	40	regional [2]	[9]
Vascular epiphytes [3]	313	152	110	regional	[35,36]
Lianas	203	115	80	local	[37]; Burnham, pers comm
Birds	550–600	550–600	0	regional	[7,38,39]
Snakes	90	68	30	regional	This study
Lizards	39	36	10	regional	This study
Frogs	141	100	40	regional	[7,32]
Primates	12–14	12–14	0	regional	[7,40–42]

[1] Directly estimated from plot data. [2] Estimated from regional compendia of tree diversity. [3] Estimated from surveys at Parque Nacional Madidi, northern Bolivia (border with Peru)

Pitman et al. [9] reviewed several candidate mechanisms for the western Amazonian richness gradient in trees. They considered it unlikely that higher tree richness in the north could be attributed to greater disturbance, increased biogeographic mixing, and intraspecific density-dependence (e.g., Janzen-Connell effects). Nonetheless, they noted that modern climate could play an important role in facilitating higher northern richness, because northern sites are simultaneously wetter and less seasonal than southern sites. Relative to the north, the southern Amazon is characterized by a greatly exacerbated dry season, with little precipitation during the months of June, July, and August. One possibility is that the generally wetter year-round climate in the north facilitates the persistence of water-limited taxa in the understory [9]; this model might also explain why amphibian diversity is substantially higher in the north (Table 2). However, it is unclear how water availability per se contributes to higher squamate richness; lizards in particular have diversity patterns that are effectively decoupled from annual precipitation, and exceptionally diverse assemblages can be found in regions with both high (e.g., Amazonia) and low (arid Australia) rainfall.

At present, many putative ecological drivers of the richness gradient for squamate reptiles cannot be assessed, because we lack basic information on population structure and dynamics for nearly all species of Amazonian squamates. For starters, we are not aware of any comparative data on the relative density of squamates at northern and southern sites. In addition, "local" communities (Table 1) might not be comparable in some ways. Some fraction of taxa within a particular local assemblage might be transient or otherwise non-coexisting species, maintained by mass effects that occur over larger spatial and temporal scales. Because we have so little information about the processes that generate local assemblages, it is all the more difficult to understand how those processes might vary in space. Furthermore, the lack of standardization in sampling methodology and scale makes it difficult to compare species abundance distributions among sites. We suggest that future studies should also consider historical explanations for the richness gradient, in addition to contemporary ecological

processes. The history of landscape-level change in the Amazon basin remains controversial [43,44], but it is nonetheless possible that expansion and contraction of savannah habitats in southwestern Amazonia might have resulted in the loss of some species that have not yet recolonized the region. Some widespread Amazonian taxa (e.g., *Iguana iguana*, *Bothrocophias hyoprora*, *Bothrops taeniautus*) apparently fail to occur in suitable habitat in southern Peru, even as they occur at similar latitudes and similarly seasonal climates in Brazil [29,45].

One site from the south-central Brazilian Amazon, "Samuel", purportedly hosts perhaps the highest snake diversity in the entire Amazon basin [11,46], despite a moderately southern latitude (–8.9) and marked seasonality in rainfall. At first glance, the high richness reported for Samuel would appear to reject local climatic explanations for the north-to-south richness gradient for squamates. However, this site cannot be compared to others listed in Table 1, for several reasons. First, the total richness frequently reported for Samuel (92+ species) is in fact a richness estimate for the Brazilian state of Rondonia [47]. The list includes the results of surveys through two major neotropical biomes (lowland Amazonian rainforest and cerrado) and with a survey area that greatly exceeds 100,000 km^2. A total of 68 snake species were reported from the principal survey in the vicinity of Samuel hydroelectric project (near Porto Velho, Brazil), with a survey area of roughly 200 km^2 [47]. Sampling intensity for this site was considerably greater than for nearly any other comparable site in the Amazon, and involved 1507 individual snake captures. Hence, we view the Samuel richness totals as comparable to the regional estimates for the Los Amigos snake fauna (68 species; Tables 1 and 2) and markedly lower than the regional snake fauna for the northwestern and equatorial western Amazon.

4.2. Taxonomic Issues

The taxonomy of many neotropical squamates is in flux: cryptic species appear to be present in many groups [48–51], and truly new species remain to be formally described. We present a species list for LABS with the caveat that nomenclatural boundaries for some taxa are likely to change in the near future. Any future use of the list presented here in a management context should exercise caution with respect to names assigned to particular taxa. For this reason, we have provided a list of vouchered specimens from LABS that can be cross-referenced by future studies. Potentially problematic groups include the following snake genera: (1) *Chironius*, including the relationship between *C. carinatus* and *C. exoletus* in southern Peru (listed as *C. exoletus/carinatus* in Table A1) as well the potential for cryptic diversity in several other taxa [48,52]; (2) all species in the genus *Erythrolamprus* (= *Liophis*), which appears to consist of five species at LABS, but where—in light of recent taxonomic work [27]—the connections between the taxa we list and *Erythrolamprus/Liophis* taxa reported for other Amazonian sites is unclear; (3) *Atractus*, a megadiverse snake genus that contains at least three species at LABS, but which is in need of comprehensive revision for southern Amazonia; species of this genus are frequently misidentified in both museum and field collections [53,54].

5. Conclusions

We have presented a taxonomic inventory of squamate reptiles for a well-sampled lowland rainforest site in southern Peru. Our results provide further support for the existence of a western Amazonian richness gradient, whereby species richness for some groups of plants and animals declines as one moves from the northwestern Amazon basin (Rio Amazonas, Peru; Ecuadorian Amazon) to the southwest (southern Peru). Further studies of this gradient (Table 2) can provide insights into the evolutionary and ecological processes that have shaped Amazonian biodiversity more generally. However, numerous challenges remain, especially for groups such as squamate reptiles, which are difficult and costly to sample. For example, de Fraga et al. [17] estimate the cost of finding a single snake in the Amazon to be approximately $120, a number that accords well with our own field costs. Martins and Oliveira [55], in one of the most comprehensive ecological studies of Amazonian snakes, estimated that approximately 3.25 h of survey effort were required per individual snake capture. To obtain a reasonably comprehensive taxonomic inventory of reptiles at any single site in the

Amazon is a daunting task, requiring many thousands of person-days of field time. Consequently, our understanding of the ecology of tropical reptile communities lags far behind that of many other taxa. Despite numerous human impacts on Amazonian forest communities, it is not yet possible to develop conservation and management strategies for most squamate reptile taxa, owing to the lack of basic information on the distribution and abundance of species.

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Appendix A

Table A1. Squamate reptiles of Los Amigos Biological Station (LABS) and adjacent Los Amigos Conservation Concession. LABS column includes only those species documented explicitly from the vicinity of the biological station. LABS-R denotes the full list of documented occurrences from the Los Amigos Conservation Concession, including LABS, CM1, and CM2. LABS-X is the documented and expected regional list for LABS and includes taxa not yet documented from Los Amigos, but which are likely to be detected with further sampling. MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima, Peru); UMMZ: University of Michigan Museum of Zoology; RAB: Rabosky Lab field series (formal accession pending; all specimens to be assigned UMMZ catalog numbers).

Clade	Species	LABS	LABS-R	LABS-X	Material Examined
Amphisbaenidae (lizard)	*Amphisbaena alba*			X [1]	
	Amphisbaena fuliginosa	X	X	X	
Anguidae (lizard)	*Diploglossus fasciatus*			X [2]	
Gekkota (lizard)	*Gonatodes hasemani*	X	X	X	RAB 2799, MUSM 38982

Table A1. *Cont.*

Clade	Species	LABS	LABS-R	LABS-X	Material Examined
	Gonatodes humeralis	X	X	X	RAB 3434, MUSM 38984
	Pseudogonatodes guianensis	X	X	X	RAB 2508, MUSM 39869
	Thecadactylus solimoensis	X	X	X	RAB 3277, MUSM 39869
Scincidae (lizard)	*Copeoglossum nigropunctatum*		X	X	
	Exila nigropalmata	X	X	X [3]	RAB 3514, MUSM 39156
	Varzea altamazonica		X	X	
Teioidea (lizard)	*Alopoglossus angulatus*	X	X	X	UMMZ 246710, MUSM 36813
	Ameiva ameiva	X	X	X	RAB 2924, MUSM 39781
	Bachia dorbignyi	X	X	X	RAB 3497, MUSM 39788
	Bachia trisanale	X	X	X [3]	RAB 3469, MUSM 38919
	Cercosaura argulus	X	X	X	RAB 2701, MUSM 38930
	Cercosaura bassleri	X	X	X	UMMZ 245038, MUSM 38937
	Cercosaura eigenmanni	X	X	X	UMMZ 246735, MUSM 36933
	Dracaena guianensis			X [1]	
	Iphisa elegans	X	X	X [3]	RAB 2931, MUSM 39020
	Kentropyx altamazonica			X [1,2]	
	Kentropyx pelviceps	X	X	X	UMMZ 246751, MUSM 37269
	Potamites ecpleopus			X [1,2]	
	Ptychoglossus brevifrontalis	X	X	X	UMMZ 246762, MUSM 39120
	Tupinambis teguixin	X	X	X	RAB 3430
Iguania (lizard)	*Anolis fuscoauratus*	X	X	X	RAB 2868, MUSM 36859
	Anolis ortonii	X	X	X	UMMZ 248371
	Anolis punctatus	X	X	X	RAB 2537, MUSM 39782
	Anolis tandai	X	X	X	RAB 2660, MUSM 38909
	Enyalioides palpebralis	X	X	X	MUSM 38981
	Plica plica	X	X	X	RAB 2704, MUSM 39860

Table A1. *Cont.*

Clade	Species	LABS	LABS-R	LABS-X	Material Examined
	Plica umbra	X	X	X	RAB 2682, MUSM 39099
	Polychrus liogaster			X [1]	
	Stenocercus fimbriatus			X [1,2]	
	Stenocercus roseiventris			X [1,2]	
	Uracentron azureum	X	X	X	
	Uracentron flaviceps	X	X	X	MUSM 39154
Typhlopidae (snake)	*Amerotyphlops reticulatus*	X	X	X	UMMZ 248453, MUSM 36160
Leptotyphlopidae (snake)	*Epictia diaplocia*	X	X	X	RAB 2932, MUSM 39046
Aniliidae (snake)	*Anilius scytale*	X	X	X [3]	RAB 2499, MUSM 36848
Boidae (snake)	*Boa constrictor*	X	X	X	
	Corallus batesii	X	X	X	
	Corallus hortulanus	X	X	X	UMMZ 248448, MUSM 36965
	Epicrates cenchria	X	X	X	RAB 2903, MUSM 37120
	Eunectes murinus	X	X	X	RAB 3417
Colubrinae (snake)	*Chironius carinatus / exoletus*	X	X	X [3]	UMMZ 246087, MUSM 38943
	Chironius fuscus	X	X	X	UMMZ 245047, MUSM 36957
	Chironius multiventris	X	X	X	UMMZ 245049, MUSM 36962
	Chironius scurrulus			X [1,7]	
	Chironius sp.	X	X	X [3,7]	UMMZ 248360
	Dendrophidion dendrophis	X	X	X	MUSM 36979
	Drymarchon corais	X	X	X [3]	RAB 2739, MUSM 36145
	Drymobius rhombifer	X	X	X [3]	UMMZ 245052, MUSM 39824
	Drymoluber dichrous	X	X	X	UMMZ 246799, MUSM 38977
	Leptophis ahaetulla	X	X	X	UMMZ 246823, MUSM 37345
	Oxybelis aeneus			X [1]	
	Oxybelis fulgidus			X [1]	
	Phrynonax poecilonotus	X	X	X [3]	RAB 3532, MUSM 39115
	Rhinobothryum lentiginosum	X	X	X	
	Spilotes pullatus	X	X	X	

Table A1. *Cont.*

Clade	Species	LABS	LABS-R	LABS-X	Material Examined
	Spilotes sulphureus			X [1]	
	Tantilla melanocephala	X	X	X [3]	UMMZ 246845, MUSM 39145
Dipsadinae (snake)	*Apostolepis nigroterminata*	X	X	X [3]	RAB 3393, MUSM 39783
	Atractus elaps	X	X	X [3]	RAB 3414, MUSM 39784
	Atractus major			X [1]	
	Atractus snethlageae	X	X	X [4]	RAB 2666, MUSM 35703
	Atractus sp.	X	X	X [3]	RAB 2924, MUSM 38913
	Clelia clelia	X	X	X	
	Dipsas catesbyi	X	X	X	RAB 2802, MUSM 38970
	Dipsas indica	X	X	X [3]	RAB 3561, MUSM 38973
	Drepanoides anomalus	X	X	X	RAB 3408, MUSM 38974
	Erythrolampus dorsocorallinus [6]	X	X	X [3]	MUSM 36049
	Erythrolampus oligolepis [6]	X	X	X [3]	RAB 3411, MUSM 39049
	Erythrolampus reginae [6]	X	X	X	RAB 3436, MUSM 39837
	Erythrolampus sp.	X	X	X	RAB 2711
	Erythrolampus taeniogaster [6]	X	X	X	
	Helicops angulatus	X	X	X	UMMZ 245053, MUSM 38989
	Helicops leopardinus	X	X	X	
	Helicops polylepis		X	X	
	Hydrops triangularis	X	X	X [3]	RAB 3500, MUSM 38992
	Imantodes cenchoa	X	X	X	UMMZ 246814, MUSM 35857
	Imantodes lentiferus	X	X	X	RAB 2900, MUSM 39834
	Leptodeira annulata	X	X	X	UMMZ 246822, MUSM 39043
	Oxyrhopus formosus	X	X	X	UMMZ 248365, MUSM 39077
	Oxyrhopus melanogenys	X	X	X	UMMZ 246832, MUSM 39855
	Oxyrhopus petolarius	X	X	X	UMMZ 245072, MUSM 39081
	Philodryas argentea			X	

Table A1. *Cont.*

Clade	Species	LABS	LABS-R	LABS-X	Material Examined
	Philodryas viridissima		X	X	
	Pseudoboa coronata			X	
	Pseudoeryx plicatilis	X	X	X	MUSM 24359
	Siphlophis cervinus	X	X	X [3]	MUSM 39141
	Siphlophis compressus	X	X	X	MUSM 39142
	Taeniophallus brevirostris	X	X	X [3]	RAB 2462, MUSM 39143
	Taeniophallus occipitalis	X	X	X	RAB 3391, MUSM 37708
	Xenodon rhabdocephalus	X	X	X [3]	UMMZ 246850, MUSM 39158
	Xenodon severus	X	X	X	RAB 2712
	Xenopholis scalaris	X	X	X	UMMZ 245077, MUSM 39889
Elapidae (snake)	*Micrurus annellatus*	X	X	X	UMMZ 248451, MUSM 39056
	Micrurus hemprichii	X	X	X [3,5]	
	Micrurus lemniscatus	X	X	X	UMMZ 248456, MUSM 39057
	Micrurus obscurus	X	X	X	UMMZ 248458, MUSM 39846
	Micrurus surinamensis	X	X	X [3]	UMMZ 246861, MUSM 37353
Viperidae (snake)	*Bothrops atrox*	X	X	X	RAB 2814, MUSM 35721
	Bothrops bilineatus	X	X	X	UMMZ 246865, MUSM 36919
	Bothrops brazili	X	X	X	MUSM 36922
	Lachesis muta	X	X	X	UMMZ 248454, MUSM 36149

[1] Known from multiple lowland sites in Departatmento de Madre de Dios, Peru [15,19,32]. [2] Known from adjacent Rio Las Piedras watershed; Margarita Medina-Müller and Emma Hume, pers. comm. [3] New LABS records documented as part of this study; compare to Whitworth et al. [16]. [4] *Atractus cf. flammigerus* previously (listed as A. flammigerus in [16]). [5] T. Paine, submitted manuscript; photographed. [6] Taxonomy given here follows recent revision of *Erythrolamprus / Liophis* [27]. [7] Reference [16] lists *Chironius cf. scurrulus* for Los Amigos, which we provisionally interpret as *Chironius sp.* based on more recently collected material.

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