Sampling bias obscures biodiversity patterns, reveals data gaps in priority conservation areas: a call for improved documentation

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ABSTRACT

- 19 Where and how species are sampled can shape biodiversity knowledge, spatial patterns, and
- 20 data-driven conservation. In many Global South biodiversity hotspots, sampling remains
- 21 uneven, and available data often lack the synthesis needed to assess region-wide gaps for
- 22 effective conservation planning and priority-setting. This shortfall is common within
- conserved areas and key biodiversity areas (hereafter 'priority conservation areas' or PCAs).
- We demonstrate this case in the Philippines, one of the most biodiverse countries in the
- world, where longstanding biodiversity research and growing policy momentum support
- 26 efforts to expand coverage of conserved areas. Drawing on over a century of species
- 27 occurrence records made digitally accessible, we compiled and manually curated these data
- 28 to assemble and analyze information on Philippine amphibians and squamate reptiles from
- 29 multiple sources, assessing the spatial distribution of observed diversity in relation to PCAs.
- 30 Results reveal strong spatial biases, with preserved specimens comprising the majority of
- 31 records and largely shaping observed diversity patterns. Citizen-science data complement
- 32 already well-sampled regions, while records from peer-reviewed literature contribute
- valuable documentation in poorly sampled areas. PCAs are proportionally well-sampled,
- 34 although gaps and biases remain. Sampling effort and observed diversity were higher in
- 35 larger PCAs, but this positive area effect diminishes with increasing topographic relief,
- highlighting large mountain ranges as persistent blind spots in biodiversity documentation.
- Notably, some areas of higher diversity occur outside established PCAs. We discuss
- 38 implications of these biases and propose enabling mechanisms to improve primary
- 39 biodiversity data collection. This study affirms the importance of integrating digitally
- 40 accessible biodiversity data from multiple sources in revealing sampling gaps and biases,
- 41 guiding future studies towards poorly sampled areas and informing conservation priorities.
- 43 **Keywords:** Philippines, biodiversity data, knowledge shortfalls, protected areas, mountains,
- 44 macroecology

INTRODUCTION

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Biodiversity data remain unevenly distributed across taxonomic groups and geographic regions, with pronounced biases against global biodiversity hotspots (Hortal et al., 2015; Hughes et al., 2021; Moura & Jetz, 2021; Ondo et al., 2024; Ball et al., 2025). Several factors contribute to these biases, including limited research capacity (Barber et al., 2014; Zhang et al., 2023), preferential focus on certain taxonomic groups (Titley et al., 2017; Moura & Jetz, 2021; Ondo et al., 2024) and charismatic taxa (Troudet et al., 2017; Guénard et al., 2025), ease of site accessibility (Oliveira et al., 2016; Mandeville et al., 2022; Penhacek et al., 2025), and prevailing tendency to conduct research in areas of special interest (Sastre & Lobo, 2009; Mentges et al., 2021). As a result, many regions and their wildlife remain poorly sampled—and where data exist, they are often not digitally accessible or fall into "biodiversity blind spots", obscuring biodiversity patterns (Ball et al., 2025). These sampling biases can hinder robust macroecological analyses and obstruct evidence-based conservation planning (Jetz et al., 2012; Engemann et al., 2015; Santini et al., 2021; Diniz-Filho et al., 2023; Hughes et al., 2024), particularly at national scales where most conservation policies and management actions are implemented (Grattarola et al., 2020; Perino et al., 2021, Soberón, 2022). Therefore, identifying where biodiversity data exist, for which taxa, and to what extent is essential for proactively addressing these biases and strengthening the knowledge base needed for effective conservation.

Challenges in biodiversity data availability are persistent even within global biodiversity hotspots, like the Philippines, where gaps and biases in data coverage skew biodiversity knowledge toward certain regions and taxonomic groups (Berba & Matias, 2022; Meneses et al., 2024; Pitogo, 2025). As a megadiverse and biogeographically unique country threatened by habitat loss (Brown et al., 2013; Huais et al., 2025), the Philippines urgently requires robust and data-informed conservation strategies. However, limited availability and discoverability of biodiversity data, and a lack of information on how these data are spatially distributed, constrains efforts to evaluate sampling completeness and to guide national biodiversity strategies and research priorities (Soberón & Peterson, 2009; Soberón, 2022). The need for synthesized biodiversity data to inform conservation planning is especially urgent, as biodiversity loss and the global momentum under the Kunming-Montreal Global Biodiversity Framework (CBD, 2022; Orr et al., 2022) have prompted policy responses to expand protected areas (PAs) and recognition of other effective area-based conservation measures (OECMs), now covering approximately 15% of the Philippines' land area (ASEAN Centre for Biodiversity, 2023). This expansion not only demands effective management grounded in ecologically representative, well-connected, and equitably governed networks of PAs and OECMs (CBD, 2022) but also must deliver measurable, positive outcomes for biodiversity (Maxwell et al., 2020). A critical first step towards achieving such outcomes is to strengthen biodiversity data by improving sampling coverage and accessibility (Soberón & Peterson 2009; Mallari et al., 2013; Jetz et al., 2019; Grattarola et al., 2020; Hochkirch et al., 2021; Soberón, 2022; Urbano et al., 2023).

A key step toward ensuring that biodiversity knowledge of a particular area is sufficient to support conservation strategies is to assess where biodiversity data are spatially distributed

90 and how these patterns align with conserved areas (PAs and OECMs) and key biodiversity 91 areas (collectively referred to herein as 'priority conservation areas' or PCAs). Such an approach remains lacking for the Philippines despite long-standing efforts to document 92 93 wildlife in this megadiverse, global biodiversity hotspot (Brown et al., 2001; Heaney, 2001; Pelser et al., 2011; Heaney et al., 2016; Tanalgo & Hughes, 2018; Allen, 2020; Gamalo et al., 94 95 2021; Berba & Matias, 2022; Meneses et al., 2024; delos Angeles et al., 2025; Fernandez et 96 al., 2025; Balisco & Liao 2025; Pitogo, 2025). While data deficiencies affect many 97 taxonomic groups, some are better represented due to sustained research and collection 98 efforts. Herpetofauna offer a compelling case for such analysis in the Philippines: the group 99 has benefited from over a century of active and sustained research effort (Brown et al., 2001; 100 Meneses et al., 2024). In fact, recent years have seen an acceleration of engagement in 101 amphibian and reptile studies, with increasing numbers of researchers, broader types of 102 investigations, and expanding publication output (Meneses et al., 2024), all suggesting that herpetofauna are a particularly timely and relevant group for such work and that data 103 104 availability will likely continue to grow. Endemic herpetofauna are also relatively well-105 sampled genetically, with voucher specimens housed in museum collections (Pitogo, 2025); 106 and curated occurrence records are available in substantial volume across peer-reviewed 107 literature (Diesmos et al., 2015; Leviton et al., 2018). Moreover, reptiles have been shown to 108 serve as effective surrogates for broader vertebrate biodiversity patterns in KBAs across the 109 country (Fidelino et al., 2025). Herpetofauna thus provide a valuable lens to evaluate spatial patterns in biodiversity data for improving country-wide biodiversity documentation and 110 111 ensuring that conservation efforts are grounded in the best available evidence.

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Leveraging species data on Philippine herpetofauna spanning ~125 years (1900s–2025) made digitally accessible, we compiled, manually curated, and analyzed occurrence records to conduct country-wide spatial assessments of observed diversity of amphibians and squamate reptiles using multiple data sources. Specifically, we ask: (1) How is observed herpetofaunal diversity spatially distributed across the Philippines, and how well do these distribution patterns coincide with PCAs? (2) Which PCAs, and which types, are more thoroughly sampled? and (3) How do observed biodiversity patterns differ across datasets derived from museum collections, citizen-science platforms, and peer-reviewed literature? Our findings offer novel, long-overdue insights into spatial distribution of biodiversity data in the Philippines, particularly in relation to PCAs. Drawing from our results, we propose and discuss enabling mechanisms to improve primary biodiversity data collection, strengthening the knowledge base necessary in assessing management effectiveness for area-based conservation measures needed in the country (Mallari et al., 2016; Struebig et al., 2025). By identifying key data shortfalls and sampling biases, this study contributes to the growing body of empirical evidence underscoring the critical role of integrating digitally accessible biodiversity data from multiple sources. Such data are essential not only for revealing spatial and taxonomic gaps to guide future studies towards poorly sampled areas but also for enabling evidence-informed conservation in one of the world's most important biodiversity hotspots.

MATERIALS & METHODS

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Data assembly and curation

All georeferenced occurrence records for amphibians and squamate reptiles from the Philippines were downloaded from the Global Biodiversity Information Facility (GBIF) on 31 January 2025 (amphibians) and 07 February 2025 (squamate reptiles). To reduce data duplication, we initially excluded records categorized as material citations and retained only human-observation records from iNaturalist and HerpWatch Pilipinas. These were then merged with expert-curated species occurrence data from the literature: amphibians from Diesmos et al., (2015) and snakes from Leviton et al., (2018). To avoid overlap between GBIF records and these curated datasets, only GBIF records dated post-publication—2015 onwards for amphibians and 2018 onwards for snakes—were retained. For lizards, all GBIF records were included. Additionally, duplicate field numbers from Sam Noble Oklahoma Museum of Natural History and Father Saturnino Urios University-Biodiversity Informatics and Research Center that corresponded to catalogued specimens from the University of Kansas Natural History Museum (KU) were excluded, with only KU records retained. Finally, we incorporated verifiable occurrence records of non-museum-catalogued specimens from peer-reviewed literature compiled by Meneses et al., (2024), along with a few additional entries. For consistency in categorization, all museum records were treated as "preserved specimen" records; iNaturalist and HerpWatch Pilipinas as "citizen science" records; and data from peer-reviewed literature as "material citation" records.

After initial clean-up, we recovered 471 nominal and candidate species of terrestrial amphibians and squamate reptiles that have digitally accessible occurrence records. Occurrence records for each species were then manually curated using currently accepted taxonomic treatments and synonyms. Each species' occurrence records were mapped in QGIS 3.4 Madeira (QGIS Development Team, 2018) to assess spatial accuracy of each point. Records falling outside the known geographic range of a species and lacking verifiable documentation were excluded. In cases where a formerly widespread species had been taxonomically split, historical records were reassigned to currently accepted species name based on updated diagnostic and distributional information in taxonomic studies. For species with unclear taxonomic or geographic boundaries, only records supported by verifiable data (e.g., curated vouchered specimens, occurrences within known distribution supported by peer-reviewed literature) were retained. Since expert-curated distributional literature for Philippine lizards is lacking, we adopted an additional measure by comparing our preliminary range estimates with the Global Assessment of Reptile Distributions (Roll et al., 2017; Caetano et al., 2022). This conservative step was taken to minimize potential overestimation of species diversity metrics.

Records not identified to the species level were excluded unless a species name or a placeholder name (e.g., sp. + island name, sp. + number) could be confidently assigned without the risk of double-counting (e.g., when only a single species from a genus is known to occur in the area). Given that the frog genus *Platymantis* remains taxonomically unresolved (Brown et al., 2015), a conservative approach that accounts for this uncertainty

- was adopted by including records of candidate species occurring in areas with no known range overlap with closely related congeners. This strategy minimizes the risk of double-counting should these populations ultimately represent a single species, while also retaining valuable data that would otherwise be discarded. This decision was informed by phylogenetic evidence, following Brown et al., (2015).
- All records lacking locality information were discarded. Additionally, records with coordinates at 16.45°N, 120.55°E and 13°N, 122°E from GBIF were excluded, as the associated locality descriptions did not match the expected geographic locations. These coordinates appear to be generalized placeholders rather than accurate site data.

Statistical analyses

Mapping herpetological diversity across the Philippines

Occurrence records for amphibians and squamate reptiles were used to generate a presence—absence matrix (PAM) at a 10-km grid resolution across the Philippines, using prepare_base_pam function from the R package biosurvey (Nuñez-Penichet et al., 2022). Separate PAMs were created for (1) all data types, (2) preserved-specimen records, (3) citizen-science records, and (4) material-citation records. For each PAM, alpha diversity (species richness) was calculated per 10-km grid cell, and the results were visualized as spatial maps using QGIS 3.4 Madeira. The resulting maps of herpetological diversity were overlaid with shapefiles of PCAs to assess spatial overlap between species richness and coverage area. Shapefiles for PCAs were obtained from the World Database on Protected Areas (www.protectedplanet.net).

To assess whether species richness classes were evenly represented across grid cells, a chi-square goodness-of-fit test was conducted using the chisq.test function in R version 4.3.1 (R Core Team, 2023). Richness values were grouped into nine discrete classes, and the observed frequency of cells in each class was compared to a uniform distribution, under the assumption that all classes were equally likely. Expected counts were computed by dividing the total number of grid cells by the number of richness classes. All expected frequencies exceeded 5, meeting assumptions of the chi-square test.

Predictors of herpetological diversity across priority conservation areas

To quantify species occurrence records and diversity within PCAs, we spatially intersected occurrence points with PCA boundaries using "Join Attributes by Location" tool in QGIS 3.4 Madeira (input: occurrence points; join layer: PCA polygons; predicate: intersects). The resulting dataset was exported as a CSV file and processed in R statistical software, where records without PCA matches were excluded. Data were grouped by PCA to calculate the number of occurrence records and unique species per PCA. PCAs without intersecting occurrences were retained with zero counts. Polygon area (in km²) was calculated using expanse function in the terra package (Hijmans, 2024). Only terrestrial PCAs were included in the analysis, comprising 207 CAs and 109 KBAs.

- Topographic relief for each PCA was extracted using a Digital Elevation Model (DEM) of
- the Philippines downloaded from the CGIAR Consortium for Spatial Information
- 227 (https://srtm.csi.cgiar.org/). This DEM, provided in Arc/Info Grid format, was clipped to the
- spatial extents of each PCA. Clipping was performed using QGIS' 'Clip Raster by Mask
- 229 Layer' tool, with DEM as the input raster and PCA polygon shapefiles as the mask layer. The
- 230 resulting clipped DEM layers contained elevation data exclusively within each PCA
- boundary. Subsequently, minimum and maximum elevation values were calculated for each
- 232 PCA polygon using the 'Zonal Statistics' tool in QGIS. The difference between these values
- was used to quantify topographic relief (in meters) of each PCA.

To investigate potential drivers of species diversity across PCAs, we fitted generalized linear models with a negative binomial error distribution to account for overdispersion (dispersion parameter < 1, compared to >5 in the Poisson models) and improve model fit (AIC > 1000 for Poisson, but < 1000 for negative binomial models). The response variable was the total number of species recorded per PCA. Fixed predictors included total area (km²), occurrence density (number of occurrence records per km²), and topographic relief (m). Total area and topographic relief served as proxies for landscape features, based on hypotheses that larger areas and those spanning broader elevational gradients —by virtue of having heterogenous habitat—support higher biodiversity (Ricklefs & Lovette, 1999: Gotelli, 2008). Occurrence density was used as a proxy for sampling effort, since species diversity per grid cell increased with occurrence points. Predictor variables were transformed based on their distribution to improve model fit: area and occurrence density were log₁₀-transformed due to strong right skew, and topographic relief was square-root-transformed due to moderate right skew. All predictors were then mean-centered and scaled to facilitate model convergence and interpretation of coefficients.

Because PCAs differ in their underlying species pools due to historical biogeographic structuring or other evolutionary processes, we initially included the Pleistocene Aggregate Island Complex (PAIC; see Brown et al., 2013) as a random effect for potential non-independence in species diversity. However, PAIC explained less than 1% of the variance and did not improve model performance, so it was excluded from the final model. We then fitted a fully factorial model with negative binomial error and performed stepwise model selection based on Akaike Information Criterion (AIC), using the stepAIC function in the R package MASS (Venables & Ripley, 2002; Table S1–S2). Residual diagnostics using DHARMa indicated quantile deviations for the occurrence density predictor, likely attributable to an excess of zero values reflecting undersampling, rather than model misspecification. Tests of overdispersion and residual uniformity did not indicate violations of model assumptions.

In addition to modeling species diversity, total occurrence records per PCA were modeled as a function of total area, topographic relief, and PAIC as fixed predictors, using a negative binomial error distribution. A two-way interaction between total area and topographic relief improved model fit and was retained in the final model, as supported by model selection based on AIC (Table S3–S4). DHARMa diagnostics indicated no major violations of model assumptions, although quantile deviations were observed for the total area predictor. These

deviations likely reflect an exponential increase in predicted values and a widening spread of residuals at higher area values, where fewer PCAs occur and variability is greater (Figure S3). This sampling effort model aimed to determine whether species-poor areas are genuinely less diverse or simply poorly sampled.

Generalized linear models were fitted using the glmmTMB package (Brooks et al., 2017). Overdispersion was initially assessed using a custom R function that calculates the ratio of the sum of squared Pearson residuals to residual degrees of freedom, with values >1.5 considered indicative of overdispersion requiring correction (Zuur et al., 2009). Model diagnostics for final models were conducted using the DHARMa package (Hartig, 2024). Simulated residuals were generated with the simulateResiduals function (plot = TRUE), and goodness-of-fit tests on scaled residuals were done using testZeroInflation, testUniformity, and testDispersion functions. Residuals were also plotted against each fixed predictor using plotResiduals to check for non-random patterns. Variance inflation factors (VIFs) for all predictors, calculated using the R package performance (Lüdecke et al., 2021), were generally within acceptable limits (all VIFs < 5). However, moderate collinearity was observed in KBA species diversity model for the interaction between occurrence density and area (VIF = 6.42), as well as for topographic relief (VIF = 5.34). All diagnostic outputs and residual plots are provided in Figures S1–S4.

As a complement to model-based inference, bivariate relationships between the response variable and continuous predictors were visually examined. These relationships were plotted using locally estimated scatterplot smoothing (LOESS) with 95% confidence intervals, implemented via the ggplot2 package. Predictor variables were transformed to match model specifications, and point colors were used to reflect the values of interacting variables with significant effects, unless otherwise stated, aiding interpretation of interaction patterns. For descriptive purposes, Pearson correlation coefficients were calculated for each plot, with significance assessed at $\alpha = 0.05$ using the cor.test function. All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2023) and documented in the attached Supplementary Material.

RESULTS

Spatial distribution of herpetofaunal diversity in the Philippines

Spatial distribution of observed herpetofaunal diversity in the Philippines is non-uniform and fragmented, with unequal national-scale coverage that varies considerably across islands (Figure 1A). The distribution of species richness classes significantly deviated from a uniform expectation ($\chi^2(8) = 15,843$, p < 0.001), indicating uneven observed species richness across the archipelago. Some richness classes were overrepresented, while others were underrepresented relative to expectations if all classes were equally likely. Nationally, only ~2% (n = 87) of the 10-km² grids have more than 41 observed species—roughly 50% of maximum richness recorded in any grid—while 31% (n = 1,370) have between 1 and 40 species, and 66.7% (n = 2,914) have zero recorded species.

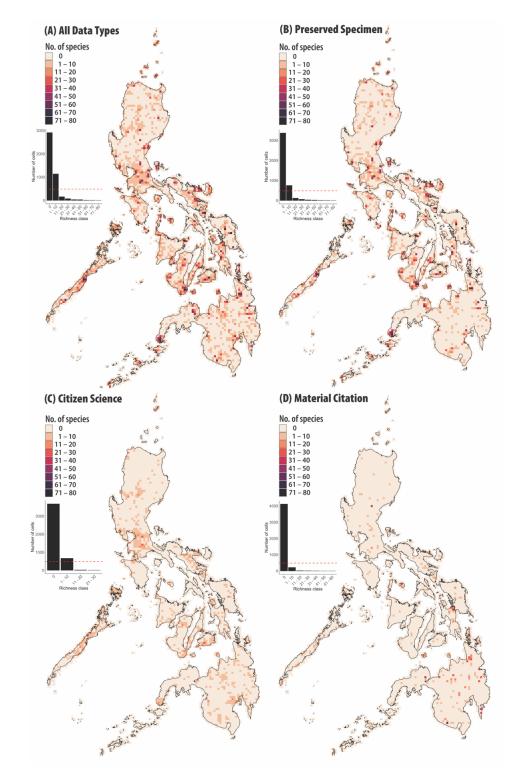


Figure 1. Spatial distribution of observed amphibian and squamate reptile diversity for (A) all data types; (B) preserved-specimen records; (C) citizen-science records; and (D) material-citation records. Species richness is calculated per 10-km² grid cell across the Philippines. Inset bar graph shows frequency distribution of grid cells across species richness classes for each dataset. Dashed red line indicates expected frequency for each class under a uniform distribution, as used in chi-square goodness-of-fit tests.

 Different data sources provide complementary insights into herpetofaunal diversity. The majority of occurrence records came from preserved specimens (n = 70,112), followed by citizen science contributions (n = 3,735) and material citations (n = 2,344), while 37 points were unclassified. Both preserved-specimen and citizen-science data represent individual occurrences, while material citations typically reflect species-level records, as published species inventory studies usually report presence by species rather than by individuals. All three data types significantly deviated from a uniform expectation ($\chi^2(8) = 20,186-30,610, p < 0.001$). Because preserved specimens account for 92% of all records, spatial richness patterns largely mirror those derived from the combined dataset (Figure 1B). Citizen science data generally contribute 1–10 species per grid, with a few grids reaching up to 30 species, and tend to complement regions already covered by specimen-based surveys (Figure 1C). Material citation data are concentrated in fewer areas, consistent with the targeted, site-specific nature of biotic inventories (Figure 1D).

Priority conservation areas were proportionally well-sampled, although distribution of herpetofaunal diversity is uneven and concentrated in few areas (Figure 2). Of the 76,228 curated occurrence records, 21,210 (27.8%) fell within CAs and 23,058 (30.2%) within KBAs—proportions that are disproportionately high relative to the Philippine land area occupied by these designations (12–15% for CAs and 6.72% for KBAs). Overlaying species richness with PCA boundaries shows that whereas some high-richness grid cells lie within PCAs, many large sites include cells with sparse or no records. Notably, 52.7% of 207 CAs and 20.2% of 109 KBAs contain grid cells with zero species records, and an additional 22.4% of CAs and 29.4% of KBAs contain only up to 10 recorded species. At the same time, several well-sampled areas with high observed diversity (>40 recorded species) occur outside established CAs but within forested areas, many of which partially overlap with KBAs (Figure S5).

Well-surveyed sites, those with >40 recorded species, make up 8.8% of CAs and 18.3% of KBAs (Figure 2). Particularly species-rich locations (>60 species) include Samar Island Natural Park, Pasonanca Natural Park, Mt. Malindang Natural Park, Mt. Makiling Forest Reserve, and PP1636 (unnamed wildlife sanctuary in southcentral Luzon). These sites have been extensively surveyed, with data available in public repositories like GBIF, though many records remain absent from, or not reported in, peer-reviewed literature (but see Nuneza et al., 2010; Gonzalez et al., 2020). Other well-documented areas combine strong specimen representation in collections with published data: Cuernos de Negros (Brown & Alcala 1961, 1970), Aurora Memorial National Park (Brown et al., 2000; Siler et al., 2011), Mt. Busa–Kimba (Brown, 2015; Pitogo et al., 2021), Mt. Guiting-Guiting (Siler et al., 2012; Meneses et al., 2022), Mt. Hilong-hilong (Plaza et al., 2015; Sanguila et al., 2016), Pantabangan-Caranglan Watershed Reservation (Gojo-Cruz et al., 2018), and Victoria-Anepahan Ranges (Supsup et al., 2020). The 40-species cut-off, however, is used here solely as a reference point for discussion and should not be interpreted as a true threshold of diversity, since observed values remain influenced by sampling limitations and potential biases.

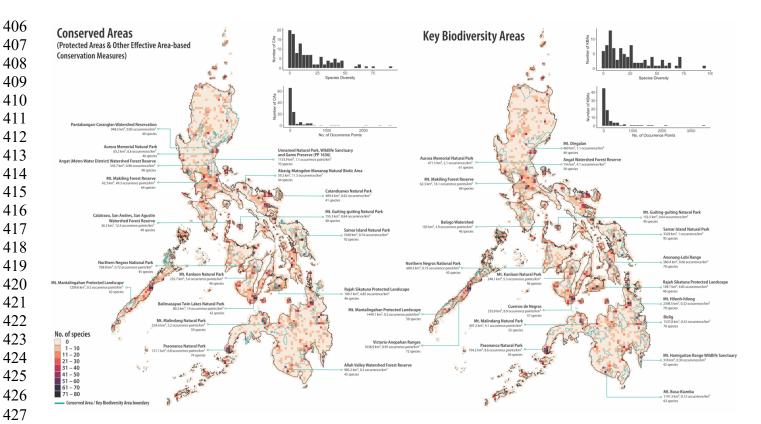


Figure 2. Relative locations of well-sampled (≥40 species) conserved areas and key biodiversity areas across the Philippines. Total area, occurrence point density, and number of species are included for each area. Base map shows spatial distribution of observed amphibian and squamate reptile diversity for all data types. Inset histogram shows frequency distribution of priority conservation areas by species richness and number of occurrence records.

Predictors of species diversity across conservation areas

Species diversity in PCAs was best explained by models that included total area, occurrence density, and their interactions with topographic relief, although the structure of these relationships varied. For CAs, the top-ranked model included total area, occurrence density, topographic relief, and an interaction between area and topographic relief (AIC = 875.8; Table S1). Both total area (1.9556 \pm 0.1894 SE, z = 10.326, p < 0.01) and occurrence density (1.4503 \pm 0.1496 SE, z = 9.696, p < 0.01) were strong positive predictors of species diversity (Table 1).

Results from model-based inference aligned with patterns observed in scatterplots, which showed moderate positive correlations between species diversity and total area (Pearson's r = 0.51, p < 0.05; Figure 3A), and a steep but variable trend for occurrence density (r = 0.53, p < 0.05), particularly at higher values (Figure 3B). A slightly weaker positive correlation was

found between species diversity and topographic relief, with an initial increase that flattened at broader elevational ranges (r = 0.41, p < 0.05; Figure 3C).

Table 1. Coefficient estimates from generalized linear models (negative binomial) relating species diversity to total area, occurrence density, and topographic relief for priority conservation areas in the Philippines. Total area and occurrence density were log-transformed, and topographic relief was square-root-transformed; all predictors were scaled and mean-centered. Significance assessed at $\alpha = 0.05(*)$.

| Predictors | Estimate ± SE | z-value | p-value |
|---|----------------------|---------|---------|
| Conserved Areas | | | |
| Intercept | 0.6405 ± 0.1423 | 4.502 | <0.01* |
| Total Area | 1.9556 ± 0.1894 | 10.326 | <0.01* |
| Occurrence Density | 1.4503 ± 0.1496 | 9.696 | <0.01* |
| Topographic Relief | 0.0021 ± 0.1645 | 0.013 | 0.989 |
| Area * Topographic Relief | -0.2322 ± 0.1430 | -1.624 | 0.104 |
| Key Biodiversity Areas | | | |
| Intercept | 2.8210 ± 0.1279 | 22.049 | <0.01* |
| Total Area | 0.8974 ± 0.1553 | 5.780 | <0.01* |
| Occurrence Density | 1.3127 ± 0.1868 | 7.027 | <0.01* |
| Topographic relief | 0.2019 ± 0.1435 | 1.407 | 0.1593 |
| Area * Occurrence Density | 0.5501 ± 0.2188 | 2.514 | 0.0119* |
| Area * Topographic Relief | -0.4243 ± 0.1439 | -2.948 | 0.0032* |
| Occurrence Density * Topographic Relief | -0.5392 ± 0.2362 | -2.283 | 0.0225* |

For KBAs, the best-supported model additionally included interactions between topographic relief and both total area and occurrence density (AIC = 779.2; Table S2). Occurrence density (1.3127 ± 0.1868 SE, z = 7.027, p < 0.01) was a stronger predictor than total area (0.8974 ± 0.1553 SE, z = 5.780, p < 0.01), and their interaction was positive (0.5501 ± 0.2188 SE, z = 2.514, p = 0.0119) (Table 1). Topographic relief had no significant main effect on species diversity, but its interactions with total area (-0.4243 ± 0.1439 SE, z = -2.948, p = 0.0032) and occurrence density (-0.5392 ± 0.2362 SE, z = -2.283, p = 0.0225) were both significant and negative. These results suggest that topographic relief may modulate influence of area and sampling effort on observed species diversity in KBAs.

Similar patterns emerged in the scatterplots: species diversity generally increased with total area, though the relationship flattened at intermediate values before rising again (r = 0.31, p < 0.05; Figure 3D). A steep initial increase was also observed with occurrence density, followed by greater variability at higher densities (r = 0.46, p < 0.05; Figure 3E). The association between topographic relief and species diversity was also weak but positive (r = 0.30, p < 0.05; Figure 3F), resembling the pattern observed in CAs.

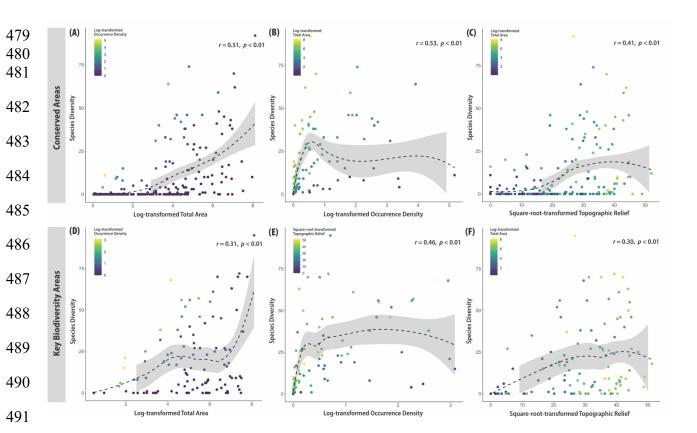


Figure 3. Scatterplots showing species diversity in relation to total area, occurrence density, and topographic relief for conserved areas (top panels) and key biodiversity areas (bottom panels). Dashed line represents LOESS-smoothed trend, with grey shaded area indicating 95% confidence interval. Each point represents a priority conservation area; colors denote interacting variables with significant effects or inclusion in the best-fit generalized linear models. No interactions were significant in the top panels, although area \times topographic relief interaction was retained in the best model. Y-axis is fixed at a lower limit of 0 for better visualization. Pearson correlation coefficients (r) and p-values are shown; significance is based on $\alpha = 0.05$.

Predictors of sampling effort across conservation areas

Sampling effort in PCAs was best explained by models that included total area, topographic relief, their interaction, and biogeographic subregion (PAIC) as a categorical predictor (AIC = 1348.4 for CAs; AIC = 1172.9 for KBAs; Tables S3–S4). In CAs, both total area (1.1765 \pm 0.3709 SE, z = 3.172, p = 0.0015) and topographic relief (1.2525 \pm 0.3938 SE, z = 3.181, p = 0.0015) were strong positive predictors of sampling effort (Table 2). However, their interaction had a significant negative effect (–0.6413 \pm 0.2683 SE, z = -2.390, p = 0.0168), suggesting that the combined influence of total area and topographic relief on sampling density may diminish at high values. Sampling effort was highest in Luzon, the reference level, among all PAICs. No other PAIC differed significantly from Luzon, except West Visayas, which exhibited comparably higher sampling effort (3.3097 \pm 0.8625 SE, z = 3.827, p < 0.01).

In KBAs, the same model structure identified a strong positive effect of the intercept (Luzon) and weak individual effects of total area and topographic relief (Table 2). Although total area $(0.3027 \pm 0.2802 \text{ SE}, z = 1.080, p = 0.2801)$ and topographic relief $(0.4453 \pm 0.2790 \text{ SE}, z = 1.596, p = 0.1105)$ were not individually significant, the interaction term showed a marginally significant negative effect $(-0.3679 \pm 0.1937 \text{ SE}, z = -1.899, p = 0.0576)$. Luzon, the reference level, had the highest sampling effort among PAICs. Only the Sulu Island Group had significantly lower sampling effort compared to Luzon $(-4.7948 \pm 1.5603 \text{ SE}, z = -3.073, p = 0.0021)$, possibly reflecting logistical challenges or reduced field access in this region.

Table 2. Coefficient estimates from generalized linear models (negative binomial) relating number of occurrence records to total area and topographic relief for priority conservation areas in the Philippines. Total area was log-transformed and topographic relief was square-root-transformed; continuous predictors were scaled and mean-centered. Significance assessed at $\alpha = 0.05(*)$. PAIC = Pleistocene Aggregate Island Complexes. Reference level for PAIC is Luzon.

| Predictors | Estimate \pm SE | z-value | p-value | | |
|----------------------------|----------------------|---------|----------|--|--|
| Conserved Areas | | | | | |
| Intercept | 3.3381 ± 0.3142 | 10.62 | < 0.01 * | | |
| Total Area | 1.1765 ± 0.3709 | 3.172 | 0.0015 * | | |
| Topographic Relief | 1.2525 ± 0.3938 | 3.181 | 0.0015 * | | |
| PAIC: Mindanao | 0.1343 ± 0.4606 | 0.292 | 0.7706 | | |
| PAIC: Mindoro | 0.5381 ± 1.5006 | 0.359 | 0.72 | | |
| PAIC: Palawan | 0.4310 ± 1.0143 | 0.425 | 0.6709 | | |
| PAIC: Romblon Island Group | 1.9644 ± 1.9589 | 1.003 | 0.3160 | | |
| PAIC: Sulu Island Group | 0.4890 ± 2.8422 | 0.172 | 0.8634 | | |
| PAIC: West Visayas | 3.3097 ± 0.8625 | 3.837 | 0.0001 * | | |
| Area * Topographic Relief | -0.6413 ± 0.2683 | -2.390 | 0.017 * | | |
| Key Biodiversity Areas | | | | | |
| Intercept | 4.9874 ± 0.3419 | 14.59 | < 0.01 * | | |
| Total Area | 0.3027 ± 0.2802 | 1.080 | 0.28 | | |
| Topographic Relief | 0.4453 ± 0.2790 | 1.596 | 0.1105 | | |
| PAIC: Mindanao | 0.3802 ± 0.4864 | 0.782 | 0.4345 | | |
| PAIC: Mindoro | -0.7675 ± 0.7252 | -1.058 | 0.29 | | |
| PAIC: Palawan | 0.4971 ± 0.8467 | 0.587 | 0.5571 | | |
| PAIC: Romblon Island Group | 0.5533 ± 1.1229 | 0.493 | 0.6222 | | |
| PAIC: Sulu Island Group | -4.7948 ± 1.5603 | -3.073 | 0.0021 * | | |
| PAIC: West Visayas | 1.1147 ± 0.5995 | 1.859 | 0.0630 | | |
| Area * Topographic Relief | -0.3679 ± 0.1937 | -1.899 | 0.0576 | | |

These model-based findings were broadly consistent with scatterplot analyses. Among CAs, weak positive correlations were observed between sampling effort and both total area (r = 0.32, p < 0.05; Figure 4A) and topographic relief (r = 0.27, p < 0.05; Figure 4B). For KBAs, correlations were weaker (r = 0.24 for total area, Figure 4C; and r = 0.19 for topographic relief, Figure 4D; both p < 0.05), likely reflecting influence of zero values or sampling gaps across several sites.

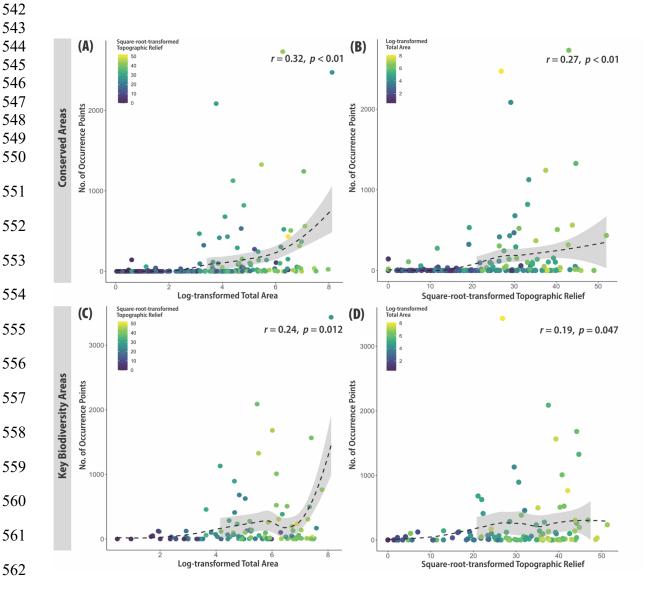


Figure 4. Scatterplots showing number of occurrence points in relation to total area and topographic relief for conserved areas (top panels) and key biodiversity areas (bottom panels). Dashed line represents LOESS-smoothed trend, with grey shaded area indicating 95% confidence interval. Each point represents a priority conservation area; colors indicate interacting variables with significant effects. Y-axis is fixed at a lower limit of 0 for better visualization. Pearson correlation coefficients (r) and p-values are shown; significance at $\alpha = 0.05$.

DISCUSSION

Uneven spatial diversity pattern reflects sampling biases

Sustained biodiversity documentation across the Philippines has enabled spatial mapping of observed species diversity of amphibians and squamate reptiles, revealing stark patterns of sampling biases. More than two-thirds of grid cells contain either zero or only 1–10 documented species, while comparatively fewer cells (~2%) exhibit higher species diversity levels. This pronounced disparity reflects persistent spatial biases in biodiversity knowledge. Observed species diversity patterns likely indicate where sampling has been more intensive, rather than accurately representing underlying ecological or biogeographic factors—a pattern that is persistent across many biodiversity-rich areas globally (Azovsky, 2011; Engemann et al., 2015; Grattarola et al., 2020; Hughes et al., 2024). Addressing these biases is critical not only for improving knowledge of Philippine biodiversity but also for ensuring that conservation policy, priority-setting, and management decisions rest on a more complete and representative knowledge base.

A recent comprehensive review of Philippine herpetology revealed substantial geographic gaps in field sampling across the archipelago (see Meneses et al., 2024 for a detailed discussion). Our findings broadly align with these observations but offer additional fine-scale information by integrating curated species point data and grid-based species richness estimates. This approach not only identifies where sampling has occurred but also quantifies its intensity, demonstrating that higher diversity values are associated with well-sampled sites. Notably, we found that a disproportionate share of documented herpetological diversity is concentrated in a few intensively surveyed areas—mostly in Luzon, the largest island, and in West Visayas, comprising most central islands—where collection efforts in recent decades have been more intense (Brown et al., 2001, 2012; Meneses et al., 2024). High-resolution data of this kind are critical for accurately representing spatial patterns of sampling effort, thereby guiding resources and research efforts towards poorly explored regions. Furthermore, by incorporating species point data from different sources, we recovered diversity data in areas that would otherwise appear as knowledge gaps, such as the Sulu Archipelago in the south (Meneses et al., 2024); although sampling effort is still disproportionately lower in this region. As such, given that biodiversity data in the Philippines are fragmented, reliance on selective or incomplete datasets for any synthesis studies can introduce substantial bias (Pitogo et al., 2025).

Priority conservation areas (PCAs) are relatively well-sampled in proportion to their total area, yet herpetofaunal knowledge across them remains limited and uneven. Despite these gains, many PCAs still lack species records altogether or may have data that are not accessible in digital form. Where species data are lacking in PCAs, they are however available outside delineated boundaries, which may suggest persistent issues associated with sampling within PCAs, including permitting and other bureaucratic processes (particularly for legislated protected areas), logistical access, and security constraints (Sanguila et al., 2016; Brown et al., 2020; Meneses et al., 2024; see Figure 5). Although well-surveyed sites include some of the country's known PCAs, vast portions of other mountain ranges and

many smaller islands remain poorly sampled or lack species data that are readily accessible for broader scientific and conservation use. Expanding targeted field-based surveys beyond established PCAs—and ensuring that resulting data are made publicly and digitally available for mobilization—remains urgently needed to support conservation initiatives grounded in accurate, comprehensive biodiversity knowledge (Di Minin & Toivonen 2015; Grattarola et al., 2020).

Sampling biases skew knowledge toward large conservation areas

Documenting biodiversity is critical in areas where such information can directly inform protection and management decisions. Conserved areas remain central to efforts aimed at safeguarding biodiversity across genetic, species, and ecosystem levels (Watson, 2014; Jonas et al., 2021). Complementing these, KBAs, though lacking formal protection or management, are identified as priority sites for future conservation efforts (Eken et al., 2004). Thus, biodiversity data support monitoring and adaptive management within CAs and guiding prioritization and investment in KBAs. However, digitally accessible records for Philippine herpetofauna show strong uneven documentation: some sites are well-surveyed, others poorly sampled, and many contain no (digitally accessible) records. These disparities mask true biodiversity patterns and pose significant challenges for efficient, evidence-based conservation planning (Hoffman, 2022).

Observed species diversity and sampling effort for herpetofauna were generally higher in larger PCAs. However, this relationship weakens with increasing topographic relief. Our results suggest that although larger areas tend to receive more sampling effort (and have higher observed diversity), this effect weakens in high mountainous areas. The significant negative interaction between topographic relief and total area on observed diversity contrasts with hypothesis that topographic complexity, by virtue of hosting diverse habitat types, should support higher species diversity (Ricklefs & Lovette, 1999; Gotelli, 2008; Engemann et al., 2015; Tenorio et al., 2023), an inconsistency that likely reflects sampling limitations. Mountainous areas in the Philippines, despite their potential for high species richness, are often poorly sampled likely due to logistical constraints, along with other factors (Pitogo & Saavedra 2023; see Figure 5). This hypothesis is especially supported by our results, which recovered significant negative interaction effects between topographic relief and sampling effort. These challenges systematically bias biodiversity knowledge away from topographically complex areas, which are some of the most ecologically critical and conservation-relevant regions in the country (Heaney, 2004; Brown et al., 2013).

Data limitations are not confined to large mountain ranges. Smaller conservation areas, particularly those in island environments, also suffer from substantial biodiversity knowledge gaps (also see Fidelino et al., 2025). Although this pattern was not statistically prominent in our model-based inference, it was evident in our exploratory data analyses and visualizations (e.g., small-sized, low-topographic-relief PCAs in Figures 3–4). Many small island conservation areas in the Philippines remain poorly sampled despite yielding newly discovered species and harboring unique, range-restricted taxa (McGuire & Alcala, 2000; Allen et al., 2004; Heaney et al., 2006; Brown et al., 2011; Oliveros et al., 2011; Siler et al.,

2012; Reyes et al., 2017; Barley et al., 2020; Clores et al., 2021; Supsup et al., 2021). These systems face disproportionate threats from climate-driven sea-level rise, extreme weather events, invasive species, and habitat loss (Russell & Kueffer, 2019), yet lack the baseline biodiversity data for adaptive management. Targeted surveys are urgently needed in these areas to document species presence and build taxonomic and ecological knowledge base required for effective conservation in islands (Borges et al., 2016). Without action, island ecosystems risk becoming critical blind spots in the country's conservation efforts.

Data gaps and biases persist, but diverse sources can address them

The majority of digitally accessible knowledge on Philippine herpetofauna comes from natural history collections. These collections represent over a century of fieldwork that has shaped taxonomic and systematics knowledge, increasing herpetofaunal diversity estimates in the country (Brown et al., 2001; Meneses et al., 2024). As such, specimen-associated data serve as a vital resource for improving knowledge on biodiversity patterns (Ball et al., 2025; Blades et al., 2025). They also support large-scale ecological studies, which depend on spatially referenced records to examine broad biodiversity trends and guide conservation planning (Jetz et al., 2012; Heberling et al., 2021; Orr et al., 2022). Although many regions remain underrepresented in biodiversity data, it is noteworthy that areas with limited contemporary surveys—as mentioned earlier, Sulu Archipelago, where fieldwork has been limited (Meneses et al., 2024)—still hold valuable records preserved through historical collections.

In areas where specimens are lacking, citizen science provides a valuable complementary data stream to help address distributional biases. Online biodiversity platforms (Amano et al., 2016; Della Rocha et al., 2024; Mason et al., 2025) and social media (Barve, 2014; Chowdhurry et al., 2023; Tabeta & Bejar, 2025) have become particularly useful where museum records are absent or limited. Although still emerging in Philippine herpetology (but see Madera, 2019; Acuña et al., 2021), citizen-science contributions are already well established in other taxonomic groups. For example, active birding communities regularly contribute to platforms like eBird (Sullivan et al., 2014) and collaborate with researchers and biodiversity managers to inform site-level conservation efforts in the Philippines (e.g., Pitogo et al., 2024). Another notable initiative is Co's Digital Flora of the Philippines (Barcelona et al., 2013), where citizen scientists and taxonomists work together to maintain a real-time overview of Philippine flora. At least 54% of the country's vascular plant species have been photo-documented, many with associated geographic coordinates (Pelser et al., 2011 onwards). These examples show that citizen-science contributions to observed diversity may be more pronounced in taxonomic groups with active, organized communities driving such efforts. Despite challenges related to data quality and metadata completeness, carefully curated citizen-science records can enhance biodiversity knowledge, particularly in remote or poorly sampled regions (Amano et al., 2016; Pernat et al., 2024).

Another important yet often overlooked source of biodiversity data comes from formal surveys that do not involve specimen collection and eventual deposition in natural history museums (e.g., Binaday et al., 2017; Gojo-Cruz et al., 2018; Pitogo et al., 2021; Maglangit et

al., 2022; Decena et al., 2023). And if there are such records, they are often not digitized and published in publicly accessible domains, especially when deposited in university-based museums. Many in-country scientists conduct fieldwork that reports valuable records published in peer-reviewed journals, yet these data are rarely archived in open-access databases such as GBIF (Beck et al., 2013). Such studies frequently document species in poorly sampled areas in the Philippines, providing crucial complementary information (Meneses et al., 2024). Although valuable for expanding species distribution knowledge, many of these studies do not provide specific geographic coordinates of areas sampled, which are limited in their use for geospatial research; thus, submission of spatial occurrences to online databases like GBIF is highly encouraged (Hochkirch et al., 2021). In addition, a wealth of biodiversity data remains locked in grey literature—government reports, university theses, and project documents—that are not digitally accessible but are often used in sitelevel management. Incorporating these sources into public repositories and ensuring they are properly curated would improve national biodiversity coverage (Cadotte et al., 2025).

Disparate biodiversity data types underscores the need for standardized archiving practices (Wieczorek et al., 2012; Ball-Damerow et al., 2019; Marques et al., 2024) and greater adherence to best-practice guidelines in dealing with big data (Costello et al., 2014; Hughes et al., 2024). Although these varied data streams help fill distributional gaps, they often differ in quality, accessibility, and curation. These differences are especially true for non-specimen-based data, which typically lack the standardized metadata associated with museum specimens. To maximize their scientific utility, we recommend that non-specimen-based records be accompanied by metadata, including GPS coordinates (including uncertainty), observation date and time, natural history notes, among others. Robust metadata not only enhances credibility and utility of individual records but also facilitates their integration into broader ecological, biogeographic, and conservation research (Jetz et al., 2012).

Scaling biodiversity documentation to meet conservation targets

The Kunming-Montreal Global Biodiversity Framework, adopted in 2022, sets an ambitious goal: to protect 30% of the world's terrestrial and marine ecosystems by 2030, building on the earlier Aichi Target 11 (Robinson et al., 2024). Achieving this target requires more than simply expanding protected area coverage; it also demands effective management that delivers measurable benefits for biodiversity (CBD, 2022). These outcomes depend on robust, accurate biodiversity data, particularly within PCAs (Mallari et al., 2013; Buckland & Johnston, 2017; Wenk et al., 2024). However, our results show that persistent data gaps and biases, especially in large mountainous and island conservation areas, continue to shape observed biodiversity data patterns. Although many PCAs with apparent data gaps may in fact hold biodiversity data, their lack of digital accessibility limits inclusion in national-scale assessments of sampling effort. This limitation hinders resource allocation for improved documentation, reduces opportunities for external vetting and expert curation of data, and impedes integration into broader datasets that inform national conservation planning (Ball-Damerow et al., 2019; Grattarola et al., 2020; Orr et al., 2022).

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Addressing the challenge of insufficient biodiversity documentation requires developing and implementing enabling mechanisms to overcome constraints in site-level primary data collection, which comprises the majority—if not all—of available biodiversity data (Figure 5). This includes prioritizing biodiversity documentation within national conservation policies and planning frameworks (e.g., Philippine Biodiversity Strategy and Action Plan, PBSAP 2024–2040) to strengthen institutional support for field-based activities, especially within PCAs (Soberón, 2022). For example, streamlining research permitting processes, fully aligned with Indigenous Peoples' rights and national access and benefit-sharing policies, can reduce bureaucratic barriers to ethical and standardized data collection (Britz et al., 2020; Horckirch et al., 2021). Engaging Indigenous Peoples and local communities as collaborators, and supporting culturally appropriate awareness and communication initiatives, can further foster equitable partnerships and mutual knowledge exchange (Dawson et al., 2024). Financial mechanisms within PAs, such as the Integrated Protected Area Fund, can be leveraged to support student-led and locally collaborative field research. Local or subnational government policies and support mechanisms are also critical for ensuring logistical coordination, safe access, and community involvement in fieldwork.

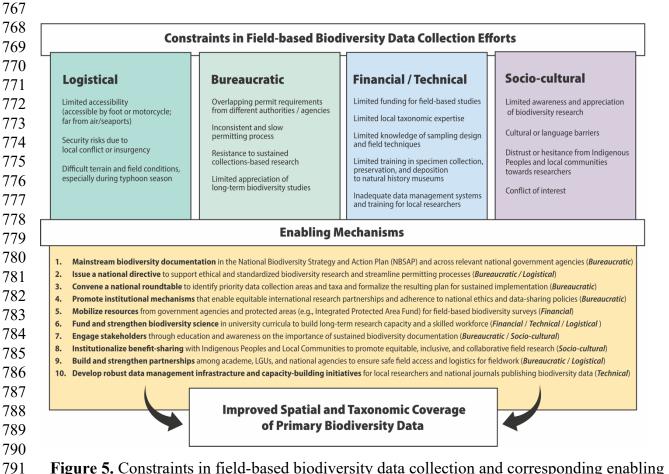


Figure 5. Constraints in field-based biodiversity data collection and corresponding enabling mechanisms to improve primary biodiversity data coverage. Each mechanism primarily addresses one or more constraint types (italicized text).

Beyond site-level interventions, targeted national funding for species discovery and taxonomic capacity-building can incentivize early-career researchers to pursue field-based work (Britz et al., 2020; Abrahamse et al., 2021). These efforts should be complemented by investments in biodiversity science within university curricula (Soberón & Peterson, 2004), ensuring students are trained in both theory and practice. Addressing the limited data management capacity among local researchers is also critical for promoting effective datasharing, enhancing the verifiability and utility of biodiversity studies. Comprehensive training programs and standardized data systems can help overcome this barrier, ensuring the production of high-quality, accessible datasets. At the same time, the increasing diversity of data contributors underscores the need for a streamlined and curated national biodiversity data infrastructure (Güntsch et al., 2025). Such a platform should ensure that biodiversity data, especially those generated from PCAs, are digitally and publicly accessible, enabling diverse stakeholders to collectively contribute to and benefit from biodiversity knowledge. Ultimately, these in-country initiatives must be paired with stronger domestic and international institutional mechanisms, such as equitable collaboration standards and datasharing agreements, to ensure that non-monetary benefits from biological resource use are meaningfully shared with local collaborators and inform national policy and conservation planning (Collela et al., 2023).

Finally, scaling biodiversity documentation beyond existing PCAs can guide the identification of new priority sites for protected area establishment. Our findings show that several well-sampled, high-diversity areas remain outside current PCAs, many overlapping with only partially protected KBAs, underscoring opportunities to align future CA expansion with empirically documented biodiversity patterns. The updated national biodiversity strategy and action plan (PBSAP 2024–2040) targets protecting 24% of terrestrial areas through CAs (DENR-BMB, 2025), yet only ~15% are currently protected. Prioritizing wellsampled, high-diversity areas for protection will be critical to achieving this goal. Our results, however, only focus on herpetofauna and similar data gaps and biases likely affect many taxonomic groups in the Philippines (Berba & Matias, 2022; Pitogo, 2025), reinforcing the need for broader, inclusive biodiversity documentation. Building a robust and representative biodiversity knowledge base—well-curated and aligned with FAIR (findable, accessible, interoperable, reusable) and CARE (collective benefit, authority to control, responsibility, ethics) principles—will require sustained collaboration among scientists, conservation practitioners, and institutions, and critically, with Indigenous Peoples and local communities (Jetz et al., 2012; Schmeller et al., 2017; Carroll et al., 2021). Strengthening such collective and inclusive efforts is essential for transforming biodiversity knowledge into tangible conservation outcomes and ensuring the Philippines meets its national and global biodiversity commitments.

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Table S1. Stepwise model selection using AIC for species richness as a function of area, occurrence density, and topographic relief (species diversity model for conserved areas). The starting model included all main effects and their three-way interaction. The final model retained only two main effects and one two-way interaction.

| Step | Model Terms | Action | Df | AIC |
|------|---------------------------------|-------------------------|----|--------|
| 0 | log Area × log Occurrence × | Start model | | 877.56 |
| | sqrt_Topo_Relief | | | |
| 1 | log_Area + log_Occurrence + | Dropped 3-way | 1 | 876.73 |
| | sqrt_Topo_Relief + | interaction | | |
| | log_Area:log_Occurrence + | | | |
| | log_Area:sqrt_Topo_Relief + | | | |
| | log_Occurrence:sqrt_Topo_Relief | | | |
| 2 | Same as above but without | Dropped 2-way | 1 | 876.49 |
| | log_Occurrence:sqrt_Topo_Relief | interaction: | | |
| | | log_Occurrence × | | |
| | | sqrt Topo Relief | | |
| 3 | log_Area + log_Occurrence + | Dropped 2-way | 1 | 875.77 |
| | sqrt_Topo_Relief + | interaction: log_Area × | | |
| | log_Area:sqrt_Topo_Relief | log_Occurrence | | |
| 4 | Same as above | Final model (no change | _ | 875.77 |
| | | improves AIC) | | |

Table S2. Stepwise model selection using AIC for species richness as a function of area, occurrence density, and topographic relief (species diversity model for key biodiversity areas). The starting model included all main effects and their three-way interaction. The final model retained all main effects and two-way interactions, excluding the three-way interaction.

| Step | Model Terms | Action | Df | AIC |
|------|---------------------------------|-----------------|----|--------|
| 0 | log_Area × log_Occurrence × | Start model | _ | 780.98 |
| | sqrt Topo Relief | | | |
| 1 | log_Area + log_Occurrence + | Dropped 3-way | 1 | 779.22 |
| | sqrt_Topo_Relief + | interaction | | |
| | log_Area:log_Occurrence + | | | |
| | log_Area:sqrt_Topo_Relief+ | | | |
| | log_Occurrence:sqrt_Topo_Relief | | | |
| 2 | Same as above | Final model (no | _ | 779.22 |
| | | change improves | | |
| | | AIC) | | |

Table S3. Stepwise model selection using AIC for occurrence count as a function of area, topographic relief, and biogeographic subregion or PAIC (sampling effort model for conserved areas). The starting model included a two-way interaction between area and relief, and an additive effect of PAIC level.

| Step | Model Terms | Action | Df | AIC |
|------|-------------------------|---------------------------------|----|---------|
| 0 | log_Area × | Start model | | 1348.35 |
| | sqrt_Topo_Relief + PAIC | | | |
| 1 | log_Area + | Dropped interaction: log_Area × | 1 | 1351.50 |
| | sqrt_Topo_Relief + PAIC | sqrt_Topo_Relief | | |
| 2 | log_Area + | Dropped PAIC | 6 | 1354.20 |
| | sqrt_Topo_Relief | | | |

Table S4. Stepwise model selection using AIC for occurrence count as a function of area, topographic relief, and biogeographic subregion or PAIC (sampling effort model for key biodiversity areas). The starting model included a two-way interaction between area and relief, and an additive effect of PAIC level.

| Step | Model Terms | Action | Df | AIC |
|------|-------------------------------|-------------------------------|----|---------|
| Step | NIOUCI I CI IIIS | Action | וע | AIC |
| 0 | log_Area × sqrt_Topo_Relief + | Start model | | 1172.87 |
| | PAIC | | | |
| 1 | log_Area × sqrt_Topo_Relief | Dropped PAIC | 6 | 1173.30 |
| 2 | log_Area + sqrt_Topo_Relief + | Dropped interaction: log_Area | 1 | 1174.20 |
| | PAIC | × sqrt Topo Relief | | |

Figure S1. Model diagnostic results from DHARMa for the best-fit species diversity model for conserved areas (Species Diversity ~ log_Area + log_Occurrence + sqrt_Topo_Relief + log_Area:sqrt_Topo_Relief). Upper-right panel shows a Q-Q plot used to detect deviations from the expected distribution, along with tests for distribution (Kolmogorov-Smirnov), dispersion, and outliers. Additional panels show scaled residuals plotted against predicted values and each predictor. Simulation outliers, data points falling outside the range of simulated values, are highlighted as red stars. Red line indicates statistically significant deviations from model expectations. DHARMa zero-inflation test is also included.

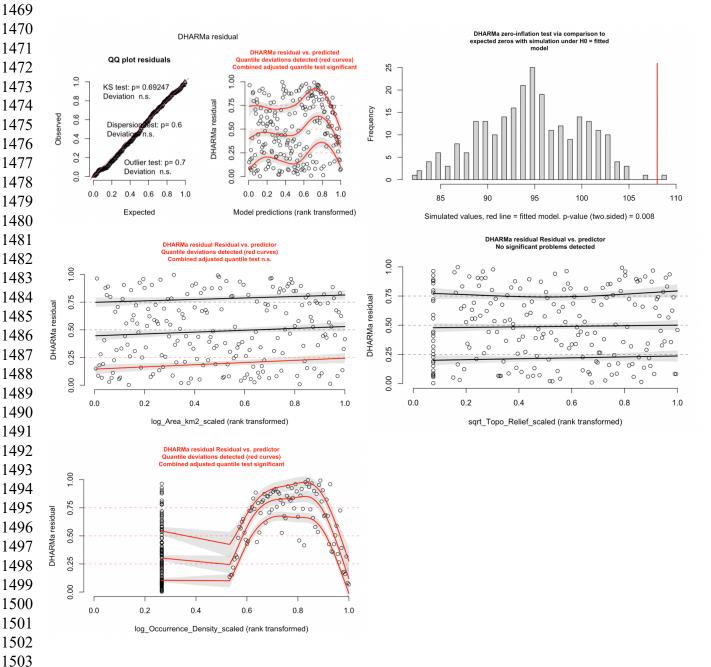


Figure S2. Model diagnostic results from DHARMa for the best-fit species diversity model for key biodiversity areas (Species Diversity ~ log_Area + log_Occurrence + sqrt_Topo_Relief + log_Area:log_Occurrence + log_Area:sqrt_Topo_Relief + log_Occurrence:sqrt_Topo_Relief). Upper-right panel shows a Q-Q plot used to detect deviations from the expected distribution, along with tests for distribution (Kolmogorov–Smirnov), dispersion, and outliers. Additional panels show scaled residuals plotted against predicted values and each predictor. Simulation outliers, data points falling outside the range of simulated values, are highlighted as red stars. Red line indicates statistically significant deviations from model expectations. DHARMa zero-inflation test is also included.

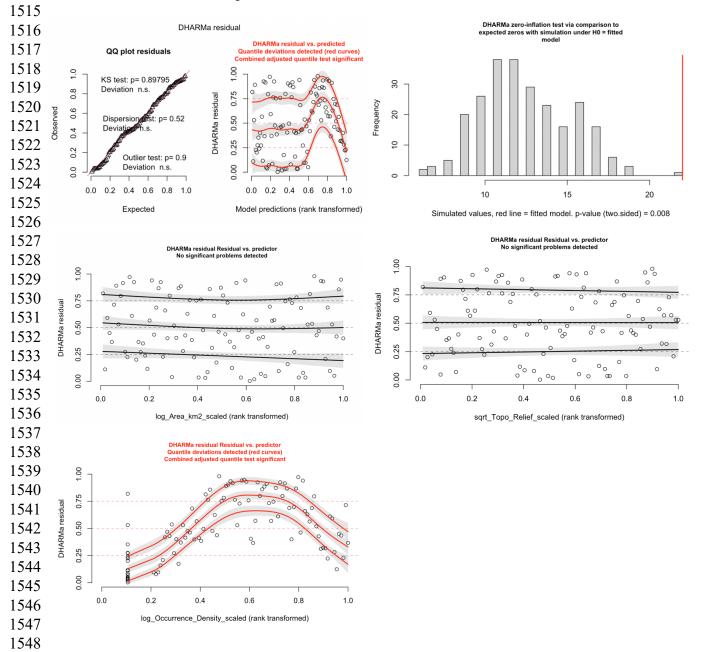


Figure S3. Model diagnostic results from DHARMa for the best-fit sampling effort model for conserved areas (No. of Occurrence Records ~ log_Area × sqrt_Topo_Relief + PAIC). Upper-right panel shows a Q–Q plot used to detect deviations from the expected distribution, along with tests for distribution (Kolmogorov–Smirnov), dispersion, and outliers. Additional panels show scaled residuals plotted against predicted values and each predictor. Simulation outliers, data points falling outside the range of simulated values, are highlighted as red stars. Red line indicates statistically significant deviations from model expectations. DHARMa zero-inflation test is also included.

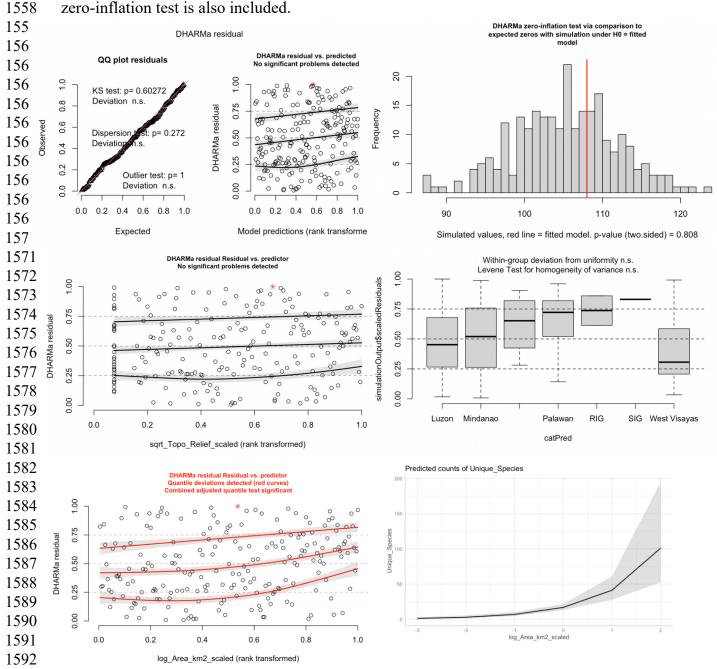


Figure S4. Model diagnostic results from DHARMa for the best-fit sampling effort model for key biodiversity areas (No. of Occurrence Records ~ log_Area × sqrt_Topo_Relief + PAIC). Upper-right panel shows a Q–Q plot used to detect deviations from the expected distribution, along with tests for distribution (Kolmogorov–Smirnov), dispersion, and outliers. Additional panels show scaled residuals plotted against predicted values and each predictor. Simulation outliers, data points falling outside the range of simulated values, are highlighted as red stars. Red line indicates statistically significant deviations from model expectations. DHARMa zero-inflation test is also included.

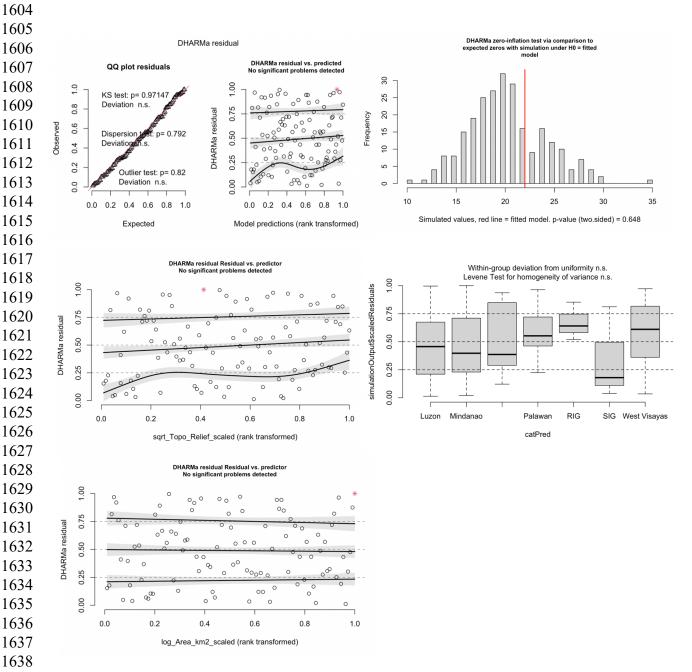


Figure S5. Map of the Philippines showing (A) overlap between forest cover, priority conservation areas (PCAs), and key biodiversity areas (KBAs), and (B) distribution of observed amphibian and squamate reptile diversity across all data types outside PCAs and KBAs, highlighting that many well-sampled sites with higher observed diversity lie beyond established conservation areas.

