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Sampling completeness changes perceptions of continental scale climate–species richness relationships in odonates

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Sampling completeness changes perceptions of continental scale climate–species richness relationships in odonates

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Abstract

Aim: Insects are one of the least studied taxa, with most species lacking basic ecological and biogeographical information. This problem is particularly acute in the tropics, where low sampling effort hampers accurate estimates of species richness at scale and potentially confounds efforts to identify the drivers of biogeographical gradients. Here, we evaluate the quality of the data on the distribution and diversity of odonate species in the Neotropics, while also examining the influence of sampling completeness on climate–richness relationships using a comprehensive database of odonates.

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Location: The Neotropics.

Taxon: Odonata.

Methods: Using 56,535 records collected from 1970 to 2021, we assess whether climate–species richness models vary under different scenarios of survey completeness.

Results: Our survey compilation revealed that most Neotropical diversity of Odonata likely remains unknown. Only 1% of the one-degree cells covering the Neotropics held reliable information on odonate species richness, with particularly severe gaps in the Caribbean, Central America, northeastern Brazil and northern Chile. Temperature, precipitation and potential evapotranspiration exert consistent effects on Odonata richness across the entire Neotropics, regardless the level of survey completeness. Whereas seasonality-related variables are less important predictors of species richness at the biogeographical scale.

Main Conclusions: By highlighting areas where inventories are more reliable and identifying regions that require increased data collection efforts and mobilization, our assessment offers a roadmap for improving the reliability of odonate inventories in the Neotropics. Furthermore, our findings underscore the importance of accounting for varying levels of survey completeness in macroecological models to reveal robust climate–species richness relationships. Simultaneously, they highlight strong climatic predictors of species richness, irrespective of survey effort intensity. These predictors provide a solid foundation for modelling and predicting odonate species richness in the Neotropics.

KEYWORDS
damselflies, dragonflies, Meso-America, sensitivity analysis, South America, spatial bias, species richness, survey completeness

1 | INTRODUCTION

Assessing biological diversity is an essential component of ecological and biogeographical studies and for designing effective strategies for species conservation (Magurran & Dornelas, 2010). However, our knowledge of species distributions is highly deficient (known as the Wallacean Shortfall), especially at large spatial scales, leading to incomplete and/or distorted representations of biodiversity patterns (Hortal et al., 2008, 2015). Distributional data are typically derived from surveys, which often fail to record all of species present in a given area (Maldonado et al., 2015) and do not encompass the full range of environmental conditions associated with species (Lobo et al., 2007). Moreover, the reliability of distributional data decays with time due to the dynamics of natural systems such as species turnover and local extinctions driven by environmental changes (Tessarolo et al., 2017). These issues generate biased estimates of species richness (Rocha-Ortega et al., 2021) that can severely hamper the identification of the biogeographic patterns such as climate–species richness relationships (Nori et al., 2023).

Biogeographers use sophisticated statistical models to identify the factors that explain the distribution and variation of species richness across geographic regions or environmental gradients (Guisan et al., 2006). These models typically use species distribution data extracted from atlases, standardized field surveys or opportunistic occurrence records conducted across different regions or habitats. Data are integrated and aggregated to a given spatial resolution and statistically related to environmental variables of interest, such as the climate (Ackerly et al., 2010). However, if survey effort is uneven or incomplete, the resulting estimates of species richness may not accurately reflect the true richness of the region or habitat. This could lead to incorrect identification of the factors that underlie species richness, or even to a complete failure to identify some environmental drivers (Yang et al., 2013).

To circumvent biases in biogeographical models in the face of patchy coverage and incompleteness of biodiversity surveys (in space and time), one can explicitly consider data-driven uncertainty. In this context, sensitivity analyses can be useful for evaluating the reliability of biogeographical models of species richness derived from spatially biased inventories with uneven levels of completeness (Brose et al., 2003). The advantage of this methodology is that it evaluates how sensitive model outputs are to changes in some model components, for example, sample size, estimated values of climatic predictors, and reliability of the samples.

Given the current rates of environmental change, quantifying spatio-temporal coverage and completeness of biodiversity surveys emerge as an urgent task for poorly studied taxa and regions such as insects in the Neotropics. Neotropical biodiversity remains poorly studied yet is increasingly threatened by human actions (Almond et al., 2022). Neotropical freshwater invertebrates are particularly understudied compared to their terrestrial and marine counterparts (Sundar et al., 2020). One such freshwater taxon is the Odonata (dragonflies and damselflies). These are among the most conspicuous and aesthetically appealing freshwater invertebrates. They are distributed on all continents (with exception of Antarctica), with highest levels of diversity typically occurring in tropical forests (Kalkman et al., 2008; Sandall et al., 2022). Odonata have a complex life cycle: As larvae, they spend their life in freshwater habitats (with a few species inhabiting brackish waters and semi-terrestrial habitats), and as adults use a wide range of terrestrial habitats (Kalkman et al., 2008).

Odonata are relatively well-studied in the Western Palearctic (e.g., Kalkman et al., 2022) and the Nearctic (e.g., Abbott et al., 2022) but are poorly known in the Neotropics. They are thought to be over 1700 known species of neotropical odonates (von Ellenrieder, 2009), though the actual number is almost certainly higher (Ortega-Salas et al., 2022). Specifically, there are large number of specimens in museum collections awaiting description (Paulson, 2004), and many areas such as the vast and remote forests of southwest Amazonia remain poorly surveyed (Bota-Sierra et al., 2015). Consequently, the current spatial pattern of Neotropical Odonata species richness is highly congruent with the location of well-surveyed areas, such as the Brazilian Southeastern region (e.g., De Marco & Vianna, 2005).

Here, we aim to evaluate the distribution and diversity of odonate species in the Neotropics, while also examining the impact of survey completeness on our ability to predict the relationship between climate and species richness.

2 | MATERIALS AND METHODS

2.1 | Data sources

We compiled species occurrence records for odonates in the Neotropical region and transition zones (i.e., the Mexican transition zone, which represents the overlap between the Nearctic and Neotropical regions, and the South American Transition zone which represents the overlap between the Neotropical and Andean regions; Morrone, 2014) from the following sources: (i) Global Biodiversity Information Facility—GBIF (GBIF, 2021); (ii) SpeciesLink network (https://specieslink.net/), (iii) an updated version of occurrence records compiled and organized by De Marco and Vianna (2005) and by von Ellenrieder (2009); and (iv) published and unpublished data collected by authors of this study. These occurrence records include both standardized surveys that follow predefined sampling protocols, and opportunistic occurrence records. We applied a protocol to exclude records with potential errors, so that we excluded records with: (i) georeferencing errors (including geographic coordinates assigned to country or province centroids, geographic coordinates that falls outside the limits of Neotropics); (ii) invalid date of collection (missing or incorrect); and (iii) invalid species names (e.g., nonexistent species name, identification to a taxonomic level higher than the species, such as genus, family or higher ranks), based on the World Odonata List, which contains the updated list of Odonata species (Paulson et al., 2022). We also checked for synonyms and replaced them with valid species names. We then integrated the different sources of data, and excluded duplicated records. This procedure removes records from different data sources, but with identical unique combinations of species name, date of collection and geographical coordinates (Stropp et al., 2016). In addition, we only considered records from 1970 onwards, the time period for which climate data was available (see below). The reliability of geographical coordinates was examined with the 'CoordinateCleaner' library for the R software (Zizka et al., 2019). The odonate occurrence database for the Neotropics and transition zones is available in the Appendix S1.

2.2 | Survey completeness

The comprehensive biodiversity database used in this study includes both standardized surveys and opportunistic occurrence records that may contain unknown levels of error and biases that affect result reliability. However, by compiling all these occurrences comprehensively, it becomes possible to estimate survey effort. We used the 'KnowB' function from the KnowBR package (Lobo et al., 2018). This allowed us to estimate sampling effort success across the Neotropics and ensure comparability of Odonata surveys across geographical sampling units (SUs) for the entire period (1970–2021) and different decades. Within 'KnowB' function, we defined SUs as one-degree grid cells. We acknowledge the limitations associated with the use of projections based on geographic degrees (i.e., lat-long). Unlike equal-area projections, they are characterized by uneven cell sizes (where grid cells become wider with decreasing latitude). However, Budic et al. (2016) study on the impact of geographic projections on species distribution modelling revealed that, even in the presence of some distortion in model estimates due to uneven cell sizes in degree-based projections, outside the poles this distortion can be considered negligible, as it does not significantly influence statistical analyses or conclusions related to species occurrence.

We used a coarse spatial resolution adequate to describe species richness–climate relationships, which allows also to include occurrence records with low precision of geographic coordinates (e.g., geographical coordinates with just one decimal place). Then, we calculated species accumulation curves for each SU within the Neotropics. These curves depict the cumulative increase in the observed species richness as new records are added for each SU. Subsequently, we fitted these curves to the Clench function (Clench, 1979) and used the extrapolated asymptotic value obtained to calculate survey completeness percentage. This percentage represents the proportion of observed species richness relative to the total number of species expected in each individual SU (Lobo et al., 2018). It allows distinguishing between well-sampled (i.e., with high percentages of completeness) from poorly sampled (i.e., with low completeness percentages) SUs across the Neotropics. Out of the four available functions in KnowBR, we chose to adjust accumulation curves to the Clench function because it produces better results at coarser spatial resolutions (Hortal et al., 2004), such as the 1-degree cells used in our study. To perform these analyses, it is advisable to establish a minimum ratio between the number of records and the number of species (Lobo et al., 2018), because small numbers of records can lead to artificially high completeness percentages (Stropp et al., 2016). For instance, a cell with only four records of two species could return an inventory completeness of 68%, which is not realistic. Therefore, following the results obtained from KnowBR, we filtered out grid cells with fewer than 15 unique records to prevent misleading inventory completeness results due to small numbers of records. This threshold represents the lower limit of the average number of odonate individuals sampled in a fieldwork day during the breeding season in the Neotropics (based on personal observations).

To assess survey effort at the country level, we calculated the ratio between the number of records and observed species richness (R/S ratio; Lobo et al., 2018). A ratio of 1 indicates that each new record corresponds to a new species. Conversely, higher values of this ratio indicate a substantial number of records are required to identify each new species, indicating a more intensive survey effort.

2.3 | Climatic predictors

To evaluate the relationship between climate and odonate species richness in the Neotropics, we selected climate-related predictors commonly associated with the geographic diversity gradients and the distribution of species from this group (Table 1). We extracted (i) temperature seasonality, (ii) maximum temperature of warmest month, referred hereafter as temperature, (iii) precipitation seasonality and (iv) precipitation of the wettest quarter, referred hereafter as precipitation from the WordClim 2 database (Fick & Hijmans, 2017) at a resolution of 10-min cells, which provides climate data representing averages for the period from 1970 to 2000. The inherent temporal autocorrelation within climate conditions enables the utilization of this data set for the analysis of biodiversity gradients up until at least the 2010s. During this period, climatic conditions experienced disruptions or changes on a smaller scale when compared to the more recent climatic shifts, specifically those prevailing in the 2020s. We obtained (v) Aridity and (vi) Potential Evapotranspiration (PET) from Global Aridity Index and Potential Evapotranspiration Climate Database v3 at 30 arc seconds resolution. Aridity indicates the availability of moisture in the environment (i.e., the lower the aridity index value, the drier is the environment),

TABLE 1 Climate-related predictors used in the present study.

Predictor	Unity	Source	Influence on Odonata
Temperature seasonality	°C	WordClim database (Fick & Hijmans, 2017)	Seasonality can impact odonate species richness at larger scales, leading to poor species communities. The mechanism behind this is that climate stability increases specialization over time and promotes speciation (Brasil et al., 2019; Currie, 1991)
Maximum temperature of warmest month, referred hereafter as temperature	°C	WordClim database (Fick & Hijmans, 2017)	Temperature is responsible for a significant increase in Odonata richness from the poles towards the equator (Kalkman et al., 2008). Warmer regions are expected to exhibit higher species richness due to several factors such as increased physiological processes and shorter generation times (Hassall & Thompson, 2008), higher mutation rates and therefore higher speciation rates (Rohde, 1992)
Precipitation seasonality	mm	WordClim database (Fick & Hijmans, 2017)	Seasonality can impact species richness at larger scales, leading to poor species communities. The mechanism behind this is that climate stability increases specialization over time and promotes speciation (Brasil et al., 2019; Currie, 1991)
Precipitation of the wettest quarter, referred hereafter as precipitation	mm	WordClim database (Fick & Hijmans, 2017)	Aquatic habitats are more abundant in areas of high precipitation, enhancing the colonization and persistence of odonates by providing suitable environments for their development and reproduction (Beatty et al., 2022)
Global Aridity Index, referred hereafter as moisture availability	-	Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Zomer et al., 2022)	Odonata spend part of their life cycle in freshwater. Therefore, water availability is essential for their survival and reproduction. The limited water availability in arid environments leads to poor species communities (Clausnitzer et al., 2012)
Potential evapotranspiration (PET)	mm	Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Zomer et al., 2022)	PET measures the energy input of an area. As this energy availability rises, population densities increase, making populations less susceptible to extinction (Evans et al., 2005; Keil et al., 2008)

and is referred hereafter as moisture availability, while PET provides a measure of the atmosphere's ability to remove water through evapotranspiration (Zomer et al., 2022). All spatial layers of climatic predictors were resampled to one-degree resolution to improve the detection of large-scale spatial patterns. Before conducting multiple regression and stepwise selection, we performed Spearman correlations to test for multicollinearity between the six climatic predictors. We observed that the correlations between these predictors were low or moderate, with absolute values of rho<=0.72.

2.4 | Multiple regressions and stepwise selection

We assessed whether climate–species richness relationships vary under different scenarios of inventory completeness. To do this, we first extracted the output of survey completeness analyses for all grid cells at one-degree resolution ($N=449$). Subsequently, we divided this data set into nine subsets based on increasing completeness thresholds, ranging from 0% to 80% (i.e., 0% represents the entire data set, while 10% corresponds to completeness ≥10%, 20% means completeness ≥20%, and so forth). For each of these nine subsets, we ran Generalized Linear Models (GLMs) with Poisson distribution, with the observed species richness as the response variable. In this step, we used a stepwise selection that generates all possible models and finds the best models through the sample-size corrected Akaike Information criteria (AICc; Burnham & Anderson, 2002). We obtained Akaike weights of each model—the relative likelihood of a model divided by the sum of relative likelihoods of all models (i.e., the probability that the model is the best one)—and estimated predictor importance as the sum of Akaike weights of the models in which the predictor appears. Because AIC-weights are standardized to sum to 1 within the set of candidate models, the total Akaike weights for each predictor can vary between 0 and 1. A strong predictor will have a total Akaike weight close to 1 (Torgersen & Close, 2004). In total, we selected 64 models based on all possible combinations of predictors for each subset, out of a total of 576 models across the nine subsets. We performed GLMs using the 'glm' function, a part of the core R package 'stats' (R Core Team, 2022). For stepwise selection, we used the MuMIn package (Bartoń, 2022).

All data preparation, cleaning, compilation and analyses were performed in R environment (R Core Team, 2022; version 4.2.0).

3 | RESULTS

3.1 | Quality of Odonata records

We compiled a total of 162,820 records of species occurrence for a total of 1819 taxon names in the Neotropical region. The first step of the data filtering process (i.e., the exclusion of records with missing information on collection date, georeferencing errors, and invalid taxon name) excluded 9% (15,464) of the initial records. The exclusion of duplicates eliminated 53% of the remaining records (77,714). Lastly, the temporal filtering led to an exclusion of 19% of the remaining unique records (13,107). Our final data set contained 56,535 records of 1602 species names, collected in 36 countries in the period from 1970 to 2021. This represents 35% of the initial database records and 88% of the initial taxon names.

3.2 | Spatial and temporal coverage of inventories

The observed number of odonate species increases towards the equator and decreases at higher latitudes (Figure 1). Brazil exhibits the greatest observed species richness in the Neotropics (785 species), followed by Colombia and Peru (416 and 392 species, respectively). Conversely, the Caribbean islands of Saint Vincent and the Grenadines, Cayman, and Grenada exhibit the lowest observed species richness, with only two species recorded for the former and one species for the latter two (Figure 1).

The distribution of Odonata species records in the Neotropical region is highly spatially clustered. Less than half of the 2417 one-degree cells ranging from northern Mexico to Patagonia have one or more records (1053 cells, ~43%). Out of a total of 1053 cells, only 449 contained at least 15 unique records for which we used survey completeness estimates (Appendix S2). The estimates of survey completeness ranged from 4.05% to 94.59% with a median of 50.55% and an interquartile range (IQR) of 34.31%. The largest number of records was registered in the Mexican state of Veracruz ($N=2547$ records). Brazil also showed a comparatively high number of records in the state of Pará, in the Brazilian Amazonia, and in the central region of the country. This contrasts with the poor completeness values for vast regions of the Neotropics, from which a west–east fringe, extending from the southern borders of the Amazon to the northeast of Brazil and as well as northern Chile, Central America and the Caribbean, stands out (Figure 2).

In the last five decades (1970–2021), the number of species records shows a ninefold increase, and the number of well-sampled locations (completeness >80%) has increased 15 times (Appendix S3–S7). The spatial coverage of Neotropical Odonata surveys through time shows that the largest increase in Odonata records occurred in the 2000s. From this period onwards, there was an increase in the spatial coverage of records and survey completeness, particularly for Argentina, Brazil and Colombia. Conversely, regions that had a significant survey coverage in previous decades, such as Venezuela, showed a remarkable decrease in the acquisition of new records more recently (Figure 3). Overall, both spatial coverage and survey quality increased over time. In the 1970s, only 7% (6 out of 79) surveyed cells met the criteria to be considered well-surveyed at a completeness >80% threshold. While about 34% (89 out 260) of surveyed cells sampled in the last decade were considered well-surveyed according to the same criterion (Appendix S3–S7).

Observed species richness is positively and significantly correlated with total number of records within the cells (Spearman rank correlation coefficient, rho$=0.90$; $p<0.001$; Figure 2a,b).

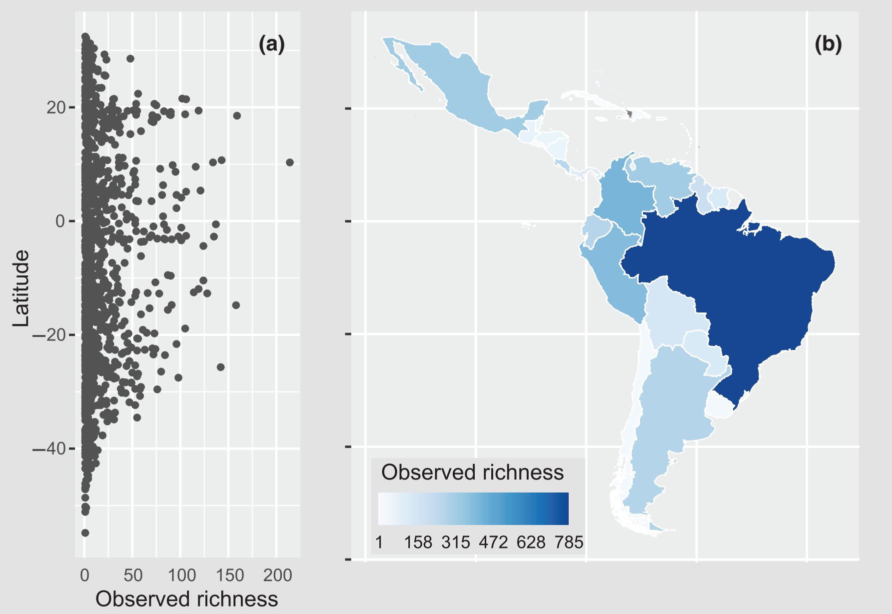

FIGURE 1 Observed species richness of odonates in the Neotropics: (a) along the latitudinal gradient comprised by our dataset; and (b) at country level. Notably, the number of observed species comprising our dataset remains underrepresented in some countries, such as Caribbean nations, Chile, and Uruguay.

The highest species richness was recorded in the north of Costa Rica (918 records of 214 species), while the second highest species richness was recorded in the Mexican state of Veracruz (2547 records of 159 species). The third highest species richness and the highest sampling effort were observed nearby Nova Xavantina municipality, Mato Grosso, Brazil, placed at the ecotone between Cerrado and Amazonia biomes (959 records and 158 species). The correlation between observed and expected species richness increased with increasing completeness thresholds. While correlation was comparatively low for the entire data set (rs = 0.687), it reached extremely high values with thresholds over 40% (rs > 0.95; Figure 4).

Our analysis also reveals a robust correlation between observed species richness and the total number of records (rho = 0.95; $p < 0.001$) at the country level. The ratio between the number of records and the observed species richness (R/S ratio) exceeded 10 only for Argentina, Puerto Rico, Brazil and Mexico. Notably, in Caribbean countries, the R/S ratio consistently stands at 1, indicating that each new record corresponds to a new species. Across most of the region, the R/S ratio per country remains below 10 (Appendix S8), underscoring the need to intensify survey efforts in most neotropical countries.

3.3 | Effect of inventory completeness on climate–species richness models

Our set of predictors for stepwise selection—moisture availability, temperature seasonality, temperature, precipitation seasonality, precipitation and potential evapotranspiration—produced 64 species richness models in combination for each completeness threshold. On average, the explanatory power of the models increased with higher survey completeness, as measured by Adjusted R^2 (Table 2).

Our sensitivity analysis revealed that climate–species richness relationships vary with the level of inventory completeness. Specifically, temperature exhibits a consistent increasing pattern, with higher standardized coefficients at greater completeness thresholds. Similarly, the importance of precipitation and PET remained consistent across all thresholds, highlighting that these climate predictors are strong predictors of odonate species richness in the Neotropics. In contrast, the importance of predictors associated with seasonality varied considerably across different survey completeness thresholds (Figure 5). Together, these findings underscore the importance of carefully considering the impact of sampling effort when interpreting climate–species richness relationships.

4 | DISCUSSION

Distributional information about Neotropical Odonata is strongly biased towards a few well-sampled regions. Species records and observed species richness values are positively correlated, which means that the number of species increases with sampling effort. Additionally, the relationship between observed species richness and climate is sensitive to sample coverage. At highest survey completeness, seasonality-related predictors become more important, while the importance of moisture availability decreases. Note also that the increase in survey completeness resulted in

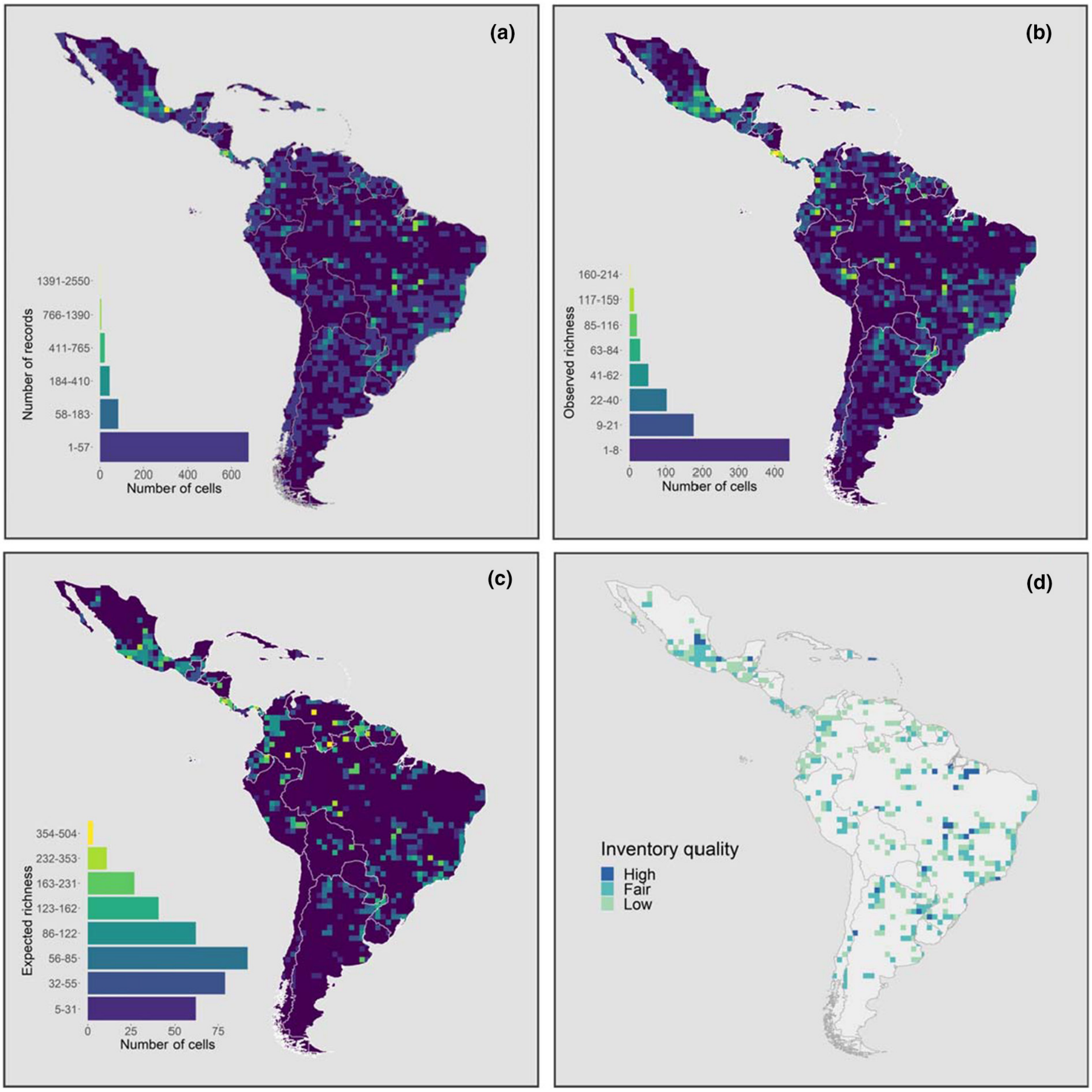

FIGURE 2 Distribution of Odonata information and species richness in the Neotropical region. Maps show: (a) the distribution of the occurrence records selected after applying different quality filters (see Section 2); (b) observed species richness; and (c) expected species richness; and (d) survey quality at different completeness thresholds: Low <50%; 50% <Fair <80%; High >80%.

better adjusted models (i.e., with higher Adjusted R^2). One key finding revealed by the sensitivity analysis is that the importance of temperature, precipitation and PET remains consistent across all levels of survey completeness. This suggests that these climatic variables are robust and essential for understanding variations in species richness, regardless of how intensive or limited the sampling effort may be.

As obligate aquatic organisms in their juvenile stage, the presence of freshwater has a great influence on odonate distribution (Abbott et al., 2022). Thus, areas with significant rainfall, such as the tropical rainforests of South America, often host more odonate species (Kalkman et al., 2008). Likewise, temperature is a universal driver of odonates' distribution (Pinkert et al., 2022; Tillyard, 1917). This finding is consistent with Sandall et al.'s (2022) global assessment of odonate species richness, showing that the warmer tropical areas closer to the Equator host a higher number of species compared to colder temperate zones. This suggests the existence of a latitudinal gradient of odonate Neotropical diversity (Spearman rho = −0.17, $p < 0.001$). Our findings also align with studies conducted in several biogeographic realms. For instance, large-scale odonate diversity is primarily driven by temperature in the Western Palearctic (Pinkert et al., 2018) and the Afrotropics (Pinkert et al., 2020). The distribution of odonates in the boreal ecosystems of British Columbia, in Canada, is structured by a temperature gradient, ranging from cold-adapted species in one gradient extremes to warm-adapted species on the opposed extreme (Cerini et al., 2021). In addition, some studies carried out in the Amazon suggest that temperature drives both local species richness (Alves-Martins, Brasil, et al., 2019) and species distributions (Alves-Martins, Calatayud, et al., 2019).

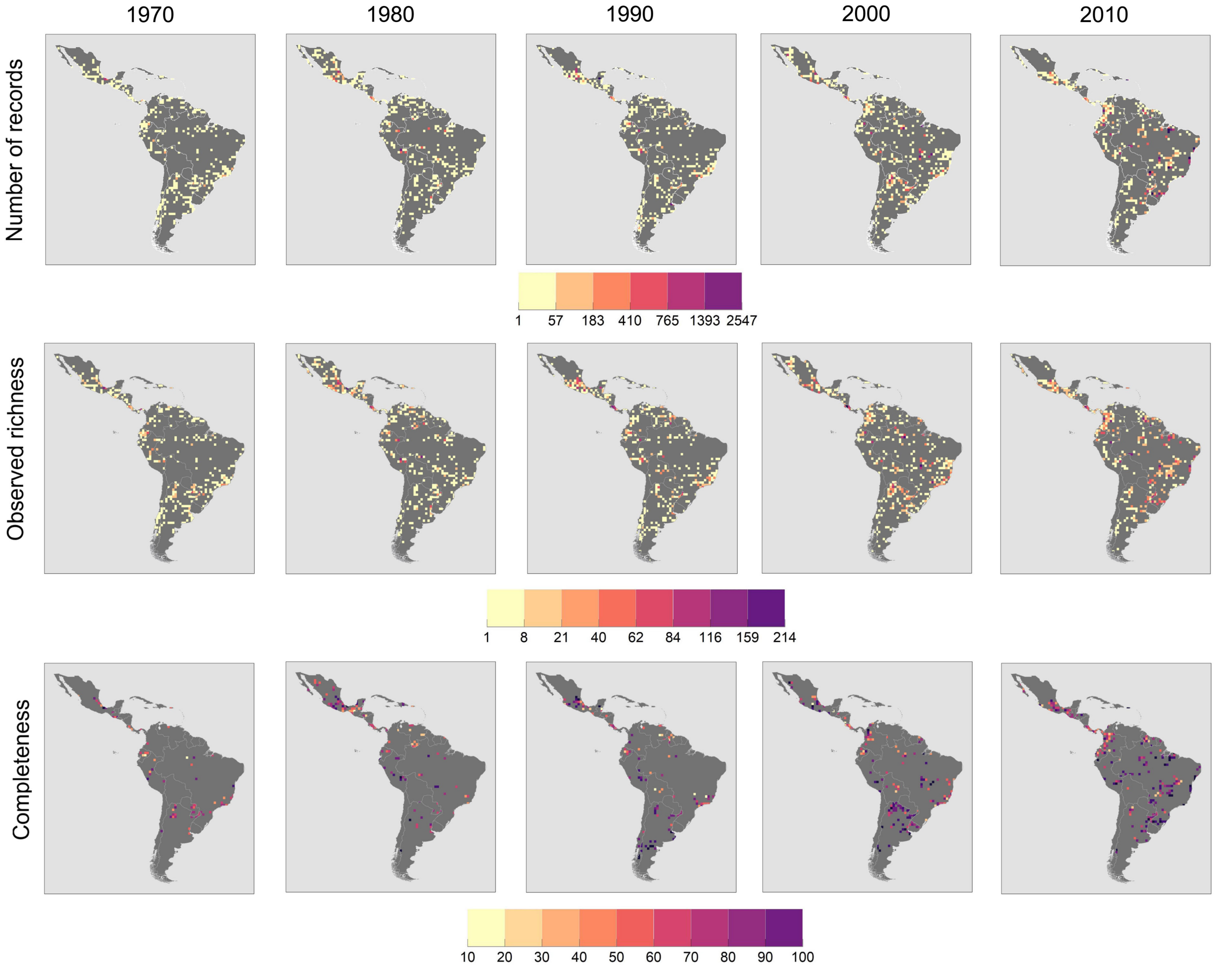

FIGURE 3 Spatial coverage of Odonata surveys over time in the Neotropics. Maps show the distribution of number of records (upper panel), observed species richness (middle panel) and survey completeness by decade at one-degree resolution (lower panel). In the maps of survey completeness (lower panel), we depict only those grid cells with a minimum sample size of 15 unique records, because smaller numbers of records may present artifactually high percentages of completeness (see Section 2).

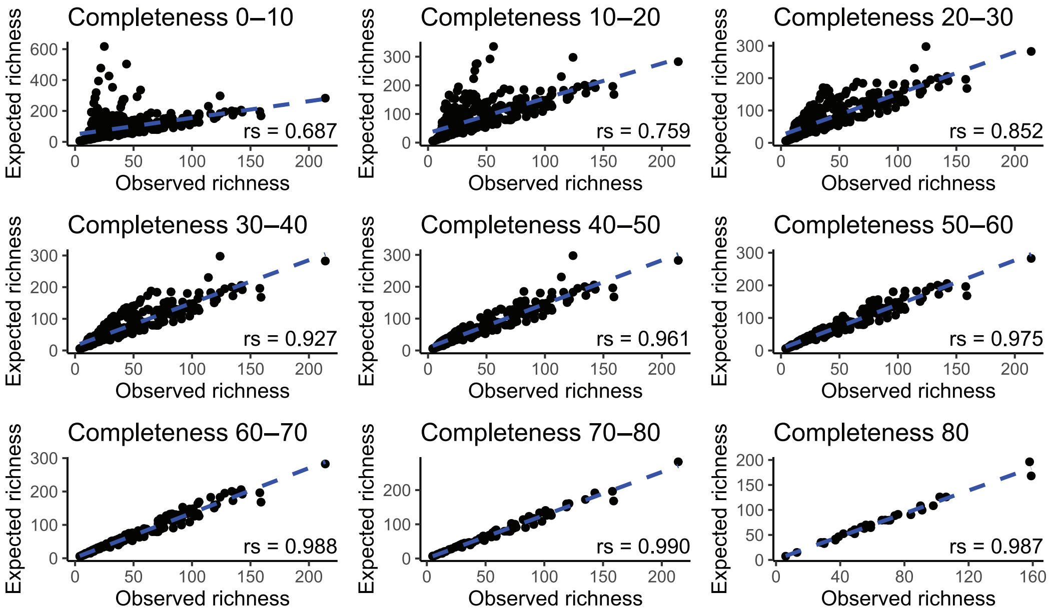

FIGURE 4 Spearman correlation (rho) between Observed and Expected Odonata species richness for different completeness thresholds. All correlations were significant at a $p < 0.001$ level.

TABLE 2 Spearman correlation (rho) between observed and expected richness for different completeness thresholds. *N* indicates the number of observations, i.e., number of one-decimal degree cell with a minimum sample size of 15 unique records. "All" refers to the full range of completeness values (including values lower than 10%). All correlations were significant at a $p < 0.001$ level.

		Models' summary	Best model			Standardized coefficients ± standard errors					
T	N	Adj. R^2	Adj. R^2	AICc	AICc weight	Moist	PET	Temp S	Temp	Prec S	Prec
All	449	0.06 ± 0.02	0.09	10544.20	0.35	0.005 ± 0.0005	0.001 ± 0.0004	0.001 ± 0.0004	0.002 ± 0.0003	0.001 ± 0.0003	0.004 ± 0.0004
10	434	0.07 ± 0.03	0.09	10245.50	0.41	0.004 ± 0.0004	0.001 ± 0.0004		0.002 ± 0.0003		0.004 ± 0.0004
20	400	0.08 ± 0.03	0.11	9525.67	0.58	0.005 ± 0.0004	0.002 ± 0.0004	0.001 ± 0.0004	0.002 ± 0.0003		0.005 ± 0.0004
30	351	0.10 ± 0.04	0.14	8467.29	0.53	0.006 ± 0.0004	0.003 ± 0.0004		0.002 ± 0.0003		0.005 ± 0.0004
40	296	0.11 ± 0.05	0.16	7396.94	0.49	0.006 ± 0.0004	0.004 ± 0.0004		0.001 ± 0.0003		0.004 ± 0.0004
50	227	0.12 ± 0.05	0.18	5576.54	0.40	0.007 ± 0.0005	0.006 ± 0.0004	−0.001 ± 0.0004	0.001 ± 0.0003		0.003 ± 0.0004
60	163	0.17 ± 0.07	0.25	3985.40	0.54	0.007 ± 0.0005	0.006 ± 0.0004		0.002 ± 0.0004	−0.001 ± 0.0003	0.004 ± 0.0004
70	89	0.19 ± 0.07	0.27	2048.22	0.48	0.008 ± 0.0007	0.005 ± 0.0006		0.003 ± 0.0005		0.002 ± 0.0005
80	33	0.13 ± 0.08	0.29	558.78	0.68		−0.004 ± 0.001	0.013 ± 0.001	0.012 ± 0.001	0.006 ± 0.001	0.006 ± 0.001

Our study also serves to identify gaps in Odonata species richness patterns. These are particularly pronounced for some parts of Brazil, eastern Colombia and northern Chile. Although nearly half of the cells that make up the Neotropical region have at least one occurrence record, most reflect low or fair survey completeness (Oliveira et al., 2016, 2019). As it is the case for other animal taxa (Oliver et al., 2021), studies of neotropical odonates have increased in the last decade (Miguel et al., 2017), with many focussed on the description of new species (e.g., Lozano & Rodrigues, 2018), local and regional diversity patterns (Bota-Sierra et al., 2021; Dalzochio et al., 2011; del Palacio et al., 2022) and species inventories (Koroiva et al., 2020; Muzón et al., 2014; Rodrigues & Roque, 2017). Despite these efforts, our findings indicate that distributional knowledge of Neotropical odonates is still insufficient to effectively perceive biodiversity patterns. This knowledge gap is driven by a number of factors including: (i) the large size of countries such as Brazil and Argentina, making systematic collection almost impossible given the limited resources available, (ii) practical difficulties to gain access to certain regions (e.g., Amazon; Stropp et al., 2020), (iii) a low scientific investment (Bolaños-Villegas et al., 2020); (iv) unstable/violent socio-political conditions in unexplored yet biodiversity rich areas (McNeely, 2003); and, (v) the lack of national systematic biodiversity assessments and conservation planning (Ferrer-Paris et al., 2013).

Predictably, the greatest sampling efforts were near research centres where established odonatologists work (e.g., Mexico, Puerto Rico, Brazil and Argentina). This confirms the well-known relationship between areas with scientific infrastructure/specialists and good biodiversity inventories (Meyer, 2016). High species richness (>100 species) and fair survey completeness in some areas (e.g., cells in Costa Rica, México, Brazilian Amazon and southeastern Brazil; 0.50 <survey completeness <0.80), indicate that odonate observed species richness is widely underestimated in many Neotropical ecosystems. Moreover, this is the case even in ecosystems that have been strongly impacted by human actions such as the Cerrado and the Atlantic Forest biomes of Brazil.

In the case of Brazil, our results are partially consistent with previous findings indicating the highest occurrence of records and species richness for Southeastern Brazil (De Marco & Vianna, 2005). We were able to add new occurrence records to the Brazilian Amazon. In this respect, there was a considerable increase (two-to-five times higher) in the overall number of occurrence records per cell, and in the overall observed species richness. The increase in the number of records in recent decades is partly due to the increase in the number of universities, research centres and permanent researchers (through the Brazilian Program to Support Restructuring and Expansion Plans of Federal Universities), particularly in the eastern Amazon, in central and southern Brazil. Yet, despite the quantitative increase in sampling effort and higher values of observed species richness, there are still considerable knowledge gaps in Brazil. This is the case, for example, for the Caatinga and the Amazon—two of the poorest Brazilian states, with low levels of scientific investment and lack of infrastructure. Furthermore, the Caatinga of northeast Brazil is a semi-arid biome that probably attracts less attention from

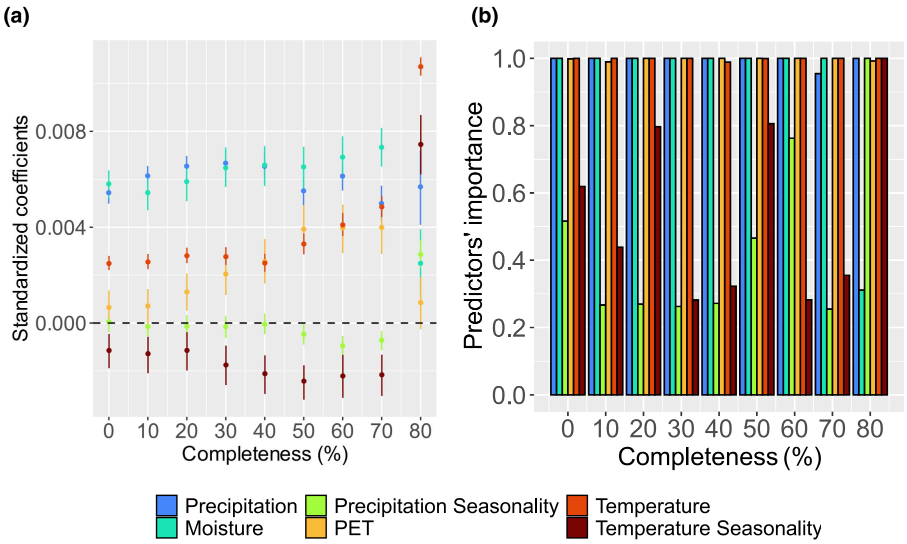

FIGURE 5 Climate–species richness models for each completeness threshold. (a) Mean standardized coefficients and their 95% confidence intervals derived from 64 models; and (b) Predictors' importance (i.e., the sum of AIC weights for the models of Odonata species richness in the Neotropical region in which the predictor appears) for different levels of survey completeness. A strong predictor will have a total Akaike (AIC) weight close to 1.

the scientific community than humid forest ecosystems (Santos et al., 2011). In the case of Amazon, data deficiency is probably related to low accessibility (Stropp et al., 2020). Moreover, sampling biodiversity in remote areas often requires considerable financial investment.

Our inventory of Neotropical odonates comprises 1602 species, 319 species less that the latest assessment by Sandall et al. (2022). At the national level, we also noted a lower number of recorded species compared to their assessment. Notably, Brazil, the country with the highest odonate species richness in both evaluations, recorded 864 species in their assessment, compared with 785 species in ours. These discrepancies likely arise from differences in data compilation approaches. Our compilation heavily relies on occurrence records, gathered from databases organized by De Marco and Vianna (2005) and von Ellenrieder (2009), along with the data collected by all the authors of this study, and the records available at GBIF. In contrast, Sandall et al. (2022) employed an approach based on combining published checklists and occurrence records. They also used an interpolation method based on the occurrence of species in neighbouring countries to estimate the potential presence of species in data-poor countries. This latter combination of methods is likely to provide larger regional checklists, but is not appropriate for representing the distribution of these species, nor the relationships between diversity and climate (see Hortal, 2008 for a discussion on the differences between these kinds of data).

5 | CONCLUDING REMARKS

We provide the most comprehensive assessment of odonate distribution and sampling effort to date in the Neotropics, which comprises nearly 25% of the world's Odonata biodiversity (sensu Paulson et al., 2022). Our compilation reveals that most Neotropical diversity of Odonata likely remains unknown. A close inspection of this compilation reveals that the observed species richness is highly conditioned by sampling effort, with reliable distributional information restricted to a few well-sampled locations. Despite this, our results clearly show that temperature, precipitation and PET are consistent drivers of Odonata, exerting positive effects on Odonata richness in the Neotropics (except for PET at the 80% survey completeness threshold, where the limited number of observations might be hindering robust estimations). This is consistent with other studies conducted in the Palearctic and Nearctic, which found that broad-scale species richness of odonates (Keil et al., 2008; Pinkert et al., 2017), butterflies (Hawkins et al., 2003; Hawkins & Porter, 2003) and dung beetles (Calatayud et al., 2016; Pessôa et al., 2021) is predominantly shaped by the availability of energy and water in the environment.

Our findings offer a roadmap for improving the reliability of odonate inventories in the Neotropics. Our assessment highlights areas where inventories are more reliable and identify regions requiring intensified data collection efforts and mobilization. Nonetheless, the sensitivity analysis emphasizes the reliability of temperature, precipitation, and PET as predictors of the variations in species richness, regardless of survey effort intensity. This provides additional evidence that both water and energy are crucial for shaping broad scale insect species richness. Furthermore, our results also suggest that these predictors offer a robust baseline for modelling and predicting odonate species richness in the Neotropics, potentially serving as a reference to guide effective conservation strategies in the region and gain insights into the responses of Neotropical odonates to climate change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting our study results are available in the Supporting information. We confirm that the data will be deposited in Dryad or other public repository after acceptance of the paper and will be publicly available at the time of publication.

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BIOSKETCH

Fernanda Alves-Martins is an ecologist with broad interest in macroecology, community ecology and conservation. In her research, Fernanda integrates and analyses data from field surveys, global biodiversity databases and environmental information to understand the relationships of biodiversity with its environment, and to explore how the impacts of global change on biodiversity can be predicted and mitigated.

Author Contributions: FA-M, JH and PDM conceived the ideas, with JS, LJ, JML and RJL. LJ, PDM, LSB, VRSF, RCB, AC-A, EFM-E, SD, DSV, AC-R, ADP, AR, AAC-S, ABSF, BOR, BS, CAB-S, CCM-P, DSV, DA-S, EP, EG-S, FOR, FL, FGC, FAAL, FPR, HO-S, HV, IS-V, JM, JCS, JM-F, JSB, JLSP, JMBO-J, KD-S, KGF, LBC, LAP-G, MER, MSD, MR-O, NVE, NH, PP, PR, RTM, RG-F, RK, TBM, TPM, UGN and WRA conducted the fieldwork and collected the data. FA-M processed the data with assistance from JM-A, JS, VRSF, RCB. FA-M led the writing with assistance from JH, JS and RJL. All authors discussed results, made edits to the manuscript, and approved its final version.

SUPPORTING INFORMATION

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

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