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Country-level checklists and occurrences for the world's Odonata (dragonflies and damselflies)

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Abstract

Aim: Biogeographical inference and assessments of species' threat status and trends depend on comprehensive information on the current geographical distribution of species. Even country-level presences remain poorly known for many insect species and consistent global overviews for those species are missing. Here we integrate information from literature checklists, point occurrences, and identify potential species range gaps to provide a database of country-level checklists of dragonfly and damselfly species and a useful baseline for global biogeographical assessment and for assessing remaining gaps in taxonomic and spatial knowledge.

Location: Global.

Taxon: Odonata (damselflies and dragonflies).

Methods: Our database of checklist information contains country-level species distribution information from 491 literature sources, with a focus on checklist data from 1990 to 2021 to reflect the present taxonomic and country boundaries. Additionally, we apply a novel method to interpolate potential species–country combinations missing from the literature and point data by generating a list of species present in >50% of the surrounding countries.

Results: Of the 6,322 globally recognized odonate species, taxonomically harmonized literature checklist records and quality-controlled point occurrence data address 6,076 and 4,170 species, respectively. Our compilation provides a total of 31,569 unique species–country combinations, with 23,239 uniquely provided by literature checklist and 2,031 point occurrence data, respectively.

Main Conclusions: This odonate country checklist dataset provides a resource for scientists and conservation practitioners to examine questions related to baseline odonate species richness, distributions, regional conservation, and gaps in taxonomic and spatial data coverage. The combined literature and point occurrence country-level information provide the most comprehensive data available to date on the global distribution of Odonata. Our results show that checklist and point occurrences are concordant in well-studied regions and that literature data are of complementary value in tropical and species-rich countries.

KEYWORDS

arthropods, biodiversity assessment, GADM, GBIF, insect, Map of Life, odonates, range map, species richness

1 | INTRODUCTION

Insects make up one of the most diverse taxonomic groups on the planet and are critical to many ecosystem functions, but assessments of their global distribution patterns lag behind many of their vertebrate counterparts (Diniz-Filho et al., 2010). Closing information gaps for insect groups is particularly urgent given the documented declines of insect populations (Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019), requiring focused attention within global biodiversity research and planning (Wagner et al., 2021). As aquatic insects, odonates face pressures related to changes to water bodies and precipitation patterns (Hassall, 2015, Nagy et al., 2019, Rocha-Ortega et al., 2020). The distributional implications of these changes remain opaque for many regions and species (Clausnitzer et al., 2009; Termaat et al., 2019). More comprehensive information of odonate distributions is therefore needed to support progress in both basic and applied understanding and assessment of this group. Ideally, such information would address a particular taxon comprehensively at global extent and over defined spatial units, supporting the development of Species Distribution Essential Biodiversity Variables (Jetz et al., 2019).

A range of different data types support broad-scale species distribution insights including point occurrences, expert range maps, local inventories and regional checklists (Guralnick et al., 2007; Hurlbert & White, 2005; Jetz et al., 2012; Meyer et al., 2015). Among regional occurrence characterizations, country-level checklists can offer a particularly effective source for capturing basic distributions over global extent. Nations are the geographical units over which initial status assessments for particular taxonomic groups are commonly conducted, for example, as part of national biodiversity inventories, assessments and reporting. Interpretation and analysis of country occurrence information is complicated by the variability in size and shape, as nations do not represent uniform spatial units. Nevertheless, these data can provide greater coverage and detail than other sources such as point records and often remain the first or only available comprehensive information for a region. Regional species lists have, therefore, already been used to document specimen collections over time, assess biogeographical patterns, identify habitat associations, and establish sampling and conservation priorities (e.g. Kipping, 2011; O'Neill & Paulson, 2001; von Ellenrieder et al., 2017).

A reliable assessment of species distributions and range sizes at global extent typically requires the integration of different data sources and types (Jetz et al., 2012). This is especially important for taxa with limited data availability (Beck et al., 2013), to ensure sufficient accuracy to enable robust ecological and conservation analyses (i.e. Gaston & Fuller, 2009; Hurlbert & Jetz, 2007; Elith & Leathwick, 2009). Here, regional species checklists play an important role as they can offer an initial coarse-grained estimate and often enable a more straightforward assessment of quality and reproducibility (Reyserhove et al., 2020). To arrive at distributional estimates while limiting the rate of false absences, interpolations and model-based extrapolations are often used. Methods to assess and account for distributional data bias and gaps have leveraged combinations of multiple survey scales to infer species rarity (Leroy et al., 2013). To smooth out the gaps in these spatial data, interpolation methods using smoothing splines, kriging or spatial autocorrelation of environmental covariates are frequently used (Colwell et al., 2004). At coarse scales of species documentation, such as checklists, interpolating using a ruleset across spatial gaps can identify areas with greater taxonomic richness yet to be detected but likely missing.

Among insects, Odonata are one of the oldest lineages of winged insects and are important predators in aquatic systems throughout their complex life cycles (Bybee et al., 2016; Stoks & Cordoba-Aguilar, 2012). The lack of global range, larval diagnostics and natural history information at the species level have hindered broad study of biogeography and macroecological patterns, despite the charisma and size of the group. Pressures from invasive freshwater taxa, climate instability and habitat degradation require increased examination of odonate distributions (e.g. Hassall, 2015; Hassall & Thompson, 2008; Samways & Taylor, 2004). Odonates have taxonomically been well-resolved through morphological, genetic and genomic efforts (Bybee et al., 2008; Dijkstra et al., 2013, 2014; Rehn, 2003). Higher phylogenetic relationships are becoming increasingly well-resolved (Bybee et al., 2021), adding to the potential for further inference. With 6,322 recognized species, the group is small enough to become a study system for global macroevolutionary, ecological and conservation analyses, similar to the sort supported by tetrapod classes. However, doing so requires at least a basic global inference of odonate species' geographical distribution.

Important initial progress towards evaluating global odonate distributions has been made by the odonates IUCN Species Survival Commission (SSC) specialist working group and their work on assessing attributes informing species' threat status in support of conservation (Clausnitzer et al., 2009). Experts have developed significant initial documentation of global patterns of dragonfly and damselfly diversity at the scale (spatial resolution) of continents or bioregions (Kalkman et al., 2008, 2018). The active community on Odonata Central houses updated checklist and seasonality information, primarily for North America (Abbott, 2006–2021). Additionally, multiple regional species checklists have been comprehensively compiled for the Americas (Paulson, 2021a, 2021b), including some with state-level detail (e.g. Biggs, 2021; Paulson, 2009, 2011). Additionally, expert work has produced critical species lists and checklists for Africa in particular (e.g. Clausnitzer & Dijkstra, 2005; Dijkstra & Clausnitzer, 2004; Kipping et al., 2017). In recent years, additional emphasis on regions of high odonate species discovery potential in Asia has led to checklists in Bangladesh, Bhutan, India, Nepal, Pakistan, Papua New Guinea and Sri Lanka (e.g. Kalkman et al., 2020; Orr & Kalkman, 2015).

Historically, checklists have been generated for the dragonflies and damselflies to document species presence over time at a range of spatial scales, from local parks to the national level. The basis for these lists is often a combination of literature references, historically collected specimens and sampling or field documentation. The specimen and occurrence basis for these checklist assessments are represented in point occurrence data repositories and natural history collections, leading to a high degree of overlap and support between checklists published in the literature and those composed by occurrence data. Checklist updates can be used to identify changes in species composition over time, including the addition of new species, or to assist planning of additional surveying. Odonate checklists have been used for identification of habitat associations, establishment of community assemblages or as a basis for site occupancy modelling (e.g. Dolný et al., 2021; Kéry et al., 2010).

Here, we present a global database of country-level checklists of odonate species to promote global change biology and conservation analysis of the dragonflies and damselflies. For continuity with current country boundaries, the observed checklist dataset primarily addresses the 1990–2021 timeframe, supplemented by species description distribution information for taxa not present in any checklists, and is the first comprehensive capture of odonate country-level occurrences. The Odonata country checklist database includes data from literature sources and point occurrence data, harmonized to a single master taxonomy. While only one step of the many needed to fully address odonate geographical distributions globally, we expect this data resources to support a range of analyses and application in ecology, biogeography, evolution and conservation.

2 | MATERIALS AND METHODS

2.1 | Taxonomic compilation and harmonization

Raw species names used in the country checklists were collated into a master taxonomy for global odonate names. The master taxonomy dataset was generated using a parent–child numbering scheme to match raw (child) names and synonyms to valid (parent) dragonfly and damselfly names with authorship and description year. Synonyms were identified by literature search and harmonized against the May 2021 version of a taxonomically comprehensive accepted name authority, known as the 'World Odonata List' (Paulson et al., 2021; Paulson & Schorr, 2021). Verified sources of taxonomic information and phylogenetic classification make up the basis of this taxonomic authority, which is updated frequently by expert odonatologists (Bridges, 1993; Davies & Tobin, 1984; Davies & Tobin 1985; Dijkstra et al., 2013, 2014; Garrison, 1991; Tsuda, 1991). Doubtful species, subspecies and orthographic variants represented in raw checklist data sources were also incorporated into our master taxonomy if they could be identified as synonyms of the valid species of Paulson and Schorr (2021). All original name combinations in the country checklist dataset were harmonized to the valid species name before being compiled into the odonate country checklist database. Working names, generic-level identifications or references to undescribed species concepts were not incorporated into our dataset, as they could not be validated against the master taxonomy. In total, in this study, the global taxonomy of extant Odonata included 6322 valid species in 965 genera (Table S3). This master taxonomy of valid names and synonyms included a total of 12,516 odonate species names in 46 supported families, the Synthemistidae family complex and 1 *incertae sedis* family grouping that is currently unresolved (Bybee et al., 2021). Spatial and taxonomic data cleaning and harmonization were carried out in R 4.0.2 (R Core Team, 2020). The R packages 'dplyr' version 1.0.2 and 'tidyr' version 1.1.2 were used for cleaning and harmonizing the checklist species to the master taxonomy (Wickham, 2020; Wickham et al., 2020).

2.2 | Country checklist literature search and combination

We took a three-pronged approach to searching the literature for potential country checklist sources. First we conducted a literature search, cross-referenced between multiple published lists for single countries or regions and searched online for additional checklist sources to fill taxonomic or regional gaps, including those published by regional odonate societies. Second, we contacted odonate experts worldwide, including those who had previously published checklists or diversity assessments for a country to identify additional sources or checklist updates. Finally, we searched Google Scholar for the terms: 'checklist', 'Odonata', 'dragonflies', 'list', 'dragonfly', 'species' in combination with the country name(s), to create the most comprehensive lists of species present in each country. Checklist search results were restricted to sources from 1990 to 2021 to improve country name and boundary accuracy, recent species ranges and taxonomic accuracy. Critical species or regional lists within countries were incorporated into the dataset where full country checklists have not been published. Critical species lists, rather than complete country inventories, were the primary data type encountered for African countries. Subsequently, the Odonata Database of Africa version 1 (ODA) was used to generate checklists for African countries for which no explicit country checklist data could be retrieved (Clausnitzer et al., 2012). The ODA database includes specimen records, observations, literature checklists and survey data validated by expert odonatologists in the IUCN SSC Dragonfly Specialty Group and is the most comprehensive taxonomic and spatial source for African Odonata country information. If a country checklist published in the last 30 years indicates that it is building upon a specific previously published checklist authority, the older checklist was also included as a data source for that country if the cumulative checklist is not provided in the more recent source. Whenever possible, multiple checklist references provided confirmation and comprehensive coverage of each country.

To standardize the administrative units present in checklists, we used v. 3.6 of the Database of Global Administrative Area (GADM), which provides high spatial resolution boundaries of countries and territories and employs standardized alpha codes to delineate country divisions (Global Administrative Areas, 2012). This also enabled the separation of dependent island territories from their mainland sovereign countries in the data to make the analyses more biogeographically informative. Countries and territories (referred to as 'countries' in this study) were incorporated into the dataset using their GADM ISO3 codes. Checklist country names were converted to ISO3 codes using the R package 'GADMTools' before the checklist synonyms were matched to the valid species names and aggregated by ISO3 country (Decorps, 2021).

2.3 | Data inclusion criteria

To assess the expected diversity and coverage of odonate species in each country, we assembled a database of species checklist data for each country. We included checklist sources in the database that were generated or updated after 1990 and referenced odonate species and the country in which they were observed, in the form of peer-reviewed publications, country-level occurrence databases or regional checklists created by odonatological societies. Lists of species to fill spatial or taxonomic gaps, including those compiled by odonatological societies, results of regional biodiversity surveys, regional atlases or taxonomic experts, were identified by Google search. For valid odonate species that did not appear in any published checklists, we examined the taxonomic descriptions of these species to find information establishing country presence. In the case of countries with referenced updated versions of lists, taxonomic experts were contacted to incorporate more recent data into the country dataset.

2.4 | Literature data summary

Of the countries recognized in the GADM, 238 have one or more valid species identified in a checklist (from either literature or occurrence sources). After taxonomic harmonization of raw species names of records from literature, the number of country-level odonate species ranged from 1 to 828. At the country level, we found a total of 6,027 valid odonate species represented in literature checklist data. For four countries (Liechtenstein, Monaco, San Marino and Tokelau), no species checklist could be found in the literature, but the countries are represented by occurrence data. Seven countries (Antarctica, Bouvet Island, Falkland Islands/Malvinas, Greenland, Heard & McDonald Islands, South Georgia and South Sandwich Islands, and Svalbard and Jan Mayen) had zero odonate species present from either literature or occurrence data sources, expectedly due to their climates (arctic) or habitats being unsuitable for dragonfly or damselfly populations.

2.5 | Occurrence data summary

We downloaded georeferenced occurrence data for all Odonata available in GBIF (10.15468/dl.tc7q68) on July 8, 2021. We also accessed the updated occurrence data of ODA, the database of African Dragonflies and Damselflies Online, which was not included in the GBIF data (Clausnitzer et al., 2012; Odonata Database of Africa, 2021; accessed on June 17, 2020). Following downloads of these point occurrence data, the associated raw species names were incorporated into the master taxonomy to account for all synonyms, matched to the valid parent synonym through comparison of authors and publication years and examination of descriptions as necessary. Fuzzy matches of spelling of genus, species, subspecies or author were conducted manually to incorporate orthographic variants. These occurrence data were linked and harmonized to the master taxonomy using the R 'dplyr' package to confirm matches to the master taxonomy of valid names and join new species names before linkage using the parent–child linked numbering scheme. We converted the raw country names represented in occurrence data to the ISO3 country codes using the package 'countrycode' (Arel-Bundock et al., 2018). To increase the accuracy of occurrence records, we cleaned the data by removing duplicate records, inaccurately georeferenced localities (represented by zeroes or institutional localities), non-terrestrial localities (not intersecting with landmask of the Global Land One-kilometre base elevation [GLOBE] layer) (GLOBE Task Team and others, 1999; Karger et al., 2017a, 2017b). Country area was calculated with functions of the R package 'rgdal' (Bivand et al., 2018). Localities of occurrence records were compared with the country information from literature and all points more than 1000 km away from the border of a country from the literature checklist were excluded. Subsequently, if 50% and more records were excluded during this step, we adopted additional criteria to reasonably extend the literature-based checklist. Specifically, for each species, we calculated the number of records per country and the number of countries in which it occurred. Subsequently, those countries and occurrence records were added, for which the number of records per country was equal to, or greater, than the total number of countries for the species. We decided to use this relative rather than an absolute criterion, since the latter would exclude species with fewer records with a higher probability than species with many records. Note that 4539 records were removed during the checklist-based cleaning, the reconsideration of well-supported records retained the most crucial and uniquely available information (45 records of 12 of the 14 otherwise missing species). The low number of records that were found outside literature checklist countries indicates a rather high quality of spatially cleaned occurrence records for Odonata. Scripts and documentation for the checklist-based cleaning can be

TABLE 1 Odonata occurrence filtering steps and number of removed records

Step	Criteria	Initial # records	# records change	% records change[a]	Initial # species	# species change	% species change[a]
(1) Harmonizing species names[b]	Only species with names matching taxonomic backbone	6,939,020	−191,074	−28.0	5733	−487	−8.5
(2) Removing duplicates	Only unique coordinate-species-year combinations	6,747,946	−3,252,049	−46.9	5246	−994	−17.3
(3) Removing non-terrestrial records	Only records intersecting with project landmask	3,495,897	−20,219	−3.0	4252	−37	−6.0
(4) Removing coordinate placeholders and spatial outliers[c]	Records not equal/zeros/centroids/GBIF headquarters/outliers	3,475,678	−13,861	−2.0	4215	−31	−5.0
(5) Removing occurrences not supported by checklist	Only records <1000 km away from countries in checklist	3,461,817	−4184	−1.0	4184	−14	−2.0
(6) Addition of well-supported records[d]	Only species with > = 50% records outside country, #species–country combinations > = #countries	3,457,633	+45	+0.0	4170	+12	+2.0

[a]Relative to data at step 1.

[b]The decrease in species number in this step is due to synonymic species lumping.

[c]Cleaning steps were done using functions of the R package 'coordinatecleaner'. The number of records flagged in each inherent cleaning step were: (0/85/283/10,199/35/48,745).

[d]If, for example, four of eight records are outside checklist country, three in BRA and one in PIC, only BRA is added retroactively because as the number of species–BRA combinations is more or equal to the total number of countries in the subset (i.e. 3/2).

found at Map of Life (2021) from Pinkert et al. (2022). A summary of the records at each step of data cleaning is shown in Table 1.

2.6 | Country interpolation

To reduce the false absence rate from gaps in checklist data, we added likely missed species in undersampled countries through an interpolation procedure that uses as a basis the country-level presences provided by the union of the checklist and point occurrence data. For a species to be considered potentially present (and thus interpolated) in a country, we generated a dataset of species that are observed in bordering countries whose total land border length is greater than 50% of the total focal country border. We conducted this interpolation using the R 'dplyr' package to create a series of datasets of potential country additions and filter them by border length. At the species level, we consider these interpolated countries as those that have a high potential for additional species observances in checklists.

For each observed country, we identified all countries sharing land borders with it and then calculated the proportion of the land border that each bordering country represented (Central Intelligence Agency, 2021a, 2021b). We generated the list of potential country additions for each species by aggregating the combination of countries observed in the literature and occurrence checklists as the prior known range for the species. For each species, we then created an interpolated checklist of countries whose border was >50% of observed countries (Table S4). A visual representation of the workflow is found in Figure 1.

3 | RESULTS

3.1 | Database

We compiled a total of 23,239 and 17,063 species–country combinations from published checklists and cleaned point occurrence records addressing 6,076 and 4,170 species, respectively. In removing duplicate species–country combinations, these data resulted in a total of 25,270 unique species–country combinations, of which 60% of species–country combinations overlap between the literature and occurrence sources, 32% are represented only by published literature records and 8% only by point occurrence records (Figure 2). From the literature-based checklist data, over 96% of valid odonate species are represented in the database (6,076 species). The point occurrence-based checklist data support the literature with additional country-level data and represents over 65% of valid species. Two-thirds (4,008 species) of valid odonate species were supported by both literature and point occurrence data. From the union of these two data types, nearly 99% of valid odonate species are known from one or more country (6,238 species). Data sources for northern latitudes established full odonate absence for multiple countries, as indicated in Data S3 (Borisov et al., 2014).

The interpolation procedure identified an additional 6,299 likely species–country records. For 2,794 valid species, we identified one or more country in which the species had not been documented as present but could potentially be distributed as a result of the interpolation method (Table S4). These interpolated records represent at least one new country presence for 44% of valid odonate species. A full summary of combined species richness from the literature checklists, occurrence data and interpolation was created using the 'tidyverse', 'data.table' version 1.14.0 and 'janitor' version 2.1.0 packages and is available in Table S2 (Dowle & Srinivasan, 2021; Firke, 2021; Wickham et al., 2019, 2020). A detailed description and the R code for the country interpolation workflow are available on GitHub (DOI: 10.5281/zenodo.5889004).

3.2 | Support from literature, point occurrence and interpolation sources

We assessed the relative unique contributions of the source categories to the overall country checklist data. We found that cumulative literature and point occurrences indicate that estimated odonate country-level species richness is well represented in the literature for North America, Europe and much of Africa (combination of Figure 2a,c). Country data uniquely established from point occurrences have a relatively lower contribution to the comprehensive species richness map than that of literature checklist data (Figure 2b). Point occurrence data contribute over half of the estimated species richness in southeast Asia, parts of South America and the north central region of Africa (Figure 2b). Areas with higher amounts of community-collected or digitized specimen data, including Europe, Australia and North America, have the greatest concordance of species–country combinations in literature checklists and that of publicly available point occurrence data (Figure 2c). The odonate species with the greatest representation in both the checklist and occurrence data is *Pantala flavescens* (Fabricius, 1798), which is found in 190 countries in the union of literature checklist and occurrence countries and 209 in the comprehensive union of literature checklist, occurrence and interpolated countries (Table S2).

Through our method of summing border length of surrounding country presences, we identified countries in Africa, Europe, Asia and South America that have potential to include additional odonate species to their checklists through interpolation (Figure 2d). A summary of the summed proportions of neighbouring countries relative to each country interpolated for each species is shown in Table S4. Resultant comprehensive maps of literature checklist, occurrence and interpolated sources for select species are found in Figure S1.

3.3 | Species richness patterns

At the biogeographical realm level, highest areas of species richness are within the Neotropical and Indomalayan realms (Figure 3a). The Neotropical realm includes nearly one-third of the known species richness globally, with nearly 2000 species known. The total union of country-level information from literature, occurrence and interpolated checklist data indicates a peak country-level richness of 864 species in Brazil. China, as the country of second highest richness, has 818 known species. The next species-rich tropical countries have just over half as much odonate species diversity. Patterns of high species diversity in southeast Asian and the American countries are consistent at the genus level and family level (Figure 3a). An estimation of generic richness from the resultant union of country-level point occurrence data, literature checklist and interpolation sources indicates a similar richness pattern to that of the species level (Figure 3b). South central African countries additionally show relatively high species richness, but less so at the genus level. Family diversity at the country level also shows lower richness in North America and Africa relative to species and genus richness patterns (Figure 3c). The high endemism of tropical regions is withheld in richness patterns at the multiple taxonomic ranks examined in this study.

3.4 | Data records

Country checklists of odonate species are provided as a data table of raw literature checklist data by source, hosted on Map of Life (Table S1, DOI: 10.48600/mol-b8as-vh75). Additional data tables with species-level country count by literature or point occurrence source (Table S2) and a country-level count of species from literature and point occurrence sources, as well as the union of species from these two types of sources (Table S3). The raw list of interpolated species–country combinations and the proportions of neighbouring countries that these species are present in Table S4. The raw species, country, source and interpolation dataset are hosted on Map of Life (Table S5).

3.5 | Technical validation

We provide reference information for each type of source as part of the published database, including peer-reviewed published checklist, professional/amateur odonate society, personal communication and country interpolation. While we were able to find data for checklists for nearly all countries in the GADM, there are taxonomic and spatial gaps in the data, namely for long ago or recently described species that do not appear in checklists or regions that have not been comprehensively sampled or documented. Interpolated species–country combinations can be validated by additional surveys, point occurrences and updates to checklists. References were verified by taxonomic harmonization, ISO3 country matching and source collation at the country level.

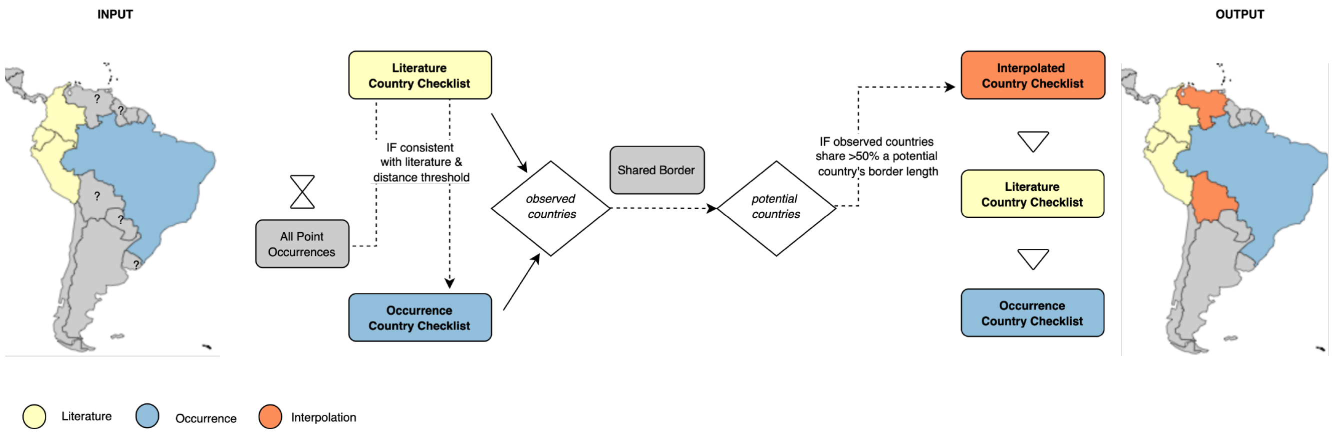

FIGURE 1 Workflow for establishing species-level odonate country checklists and interpolating potential species–country gaps in the checklist database. Data were combined from the literature and occurrence datasets to identify bordering countries in which a species may be missing in the checklist dataset. Overall proportion of species presence in bordering countries was calculated by summing the total land border length and dividing by the total border length of a potential country

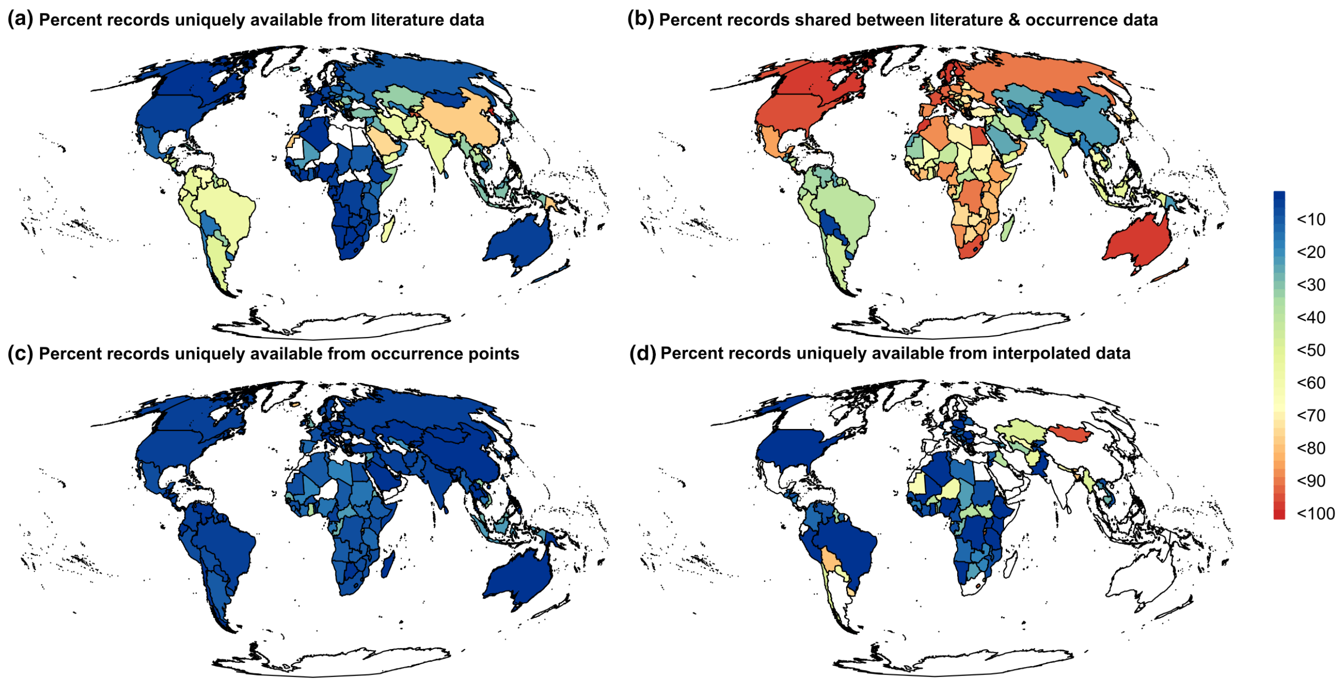

FIGURE 2 Percent of country-level odonate species observations: (a) uniquely available from literature data, (b) uniquely available from occurrence records, (c) available in both literature and occurrence sources, and (d) identified by interpolation at the national level. Maps are shown in a Mollweide equal-area projection. Colour class intervals are scaled to equally wide value ranges

4 | DISCUSSION

4.1 | Data quality and validity

This dataset represents the first comprehensive, time-stamped and transparently sourced dataset of odonate species checklists at the country level. The methods for collating country-level data using synonyms and valid names harmonized to a unified taxonomic backbone enable us to generate the most taxonomically and spatially comprehensive dataset of checklist data. The combined literature, occurrence and interpolated dataset provides for each species the most inclusive prediction of country-level species richness that can be confirmed with additional distributional data (Table S2). The comprehensive documentation of source information for species names and country-level information provides a dataset that can be harmonized with updated taxonomy in the future. Our country-level results for ~99% of the currently valid odonate species indicate that we have coverage of both long-established and recently described species, providing the greatest taxonomic coverage of any published global odonate macroecological dataset.

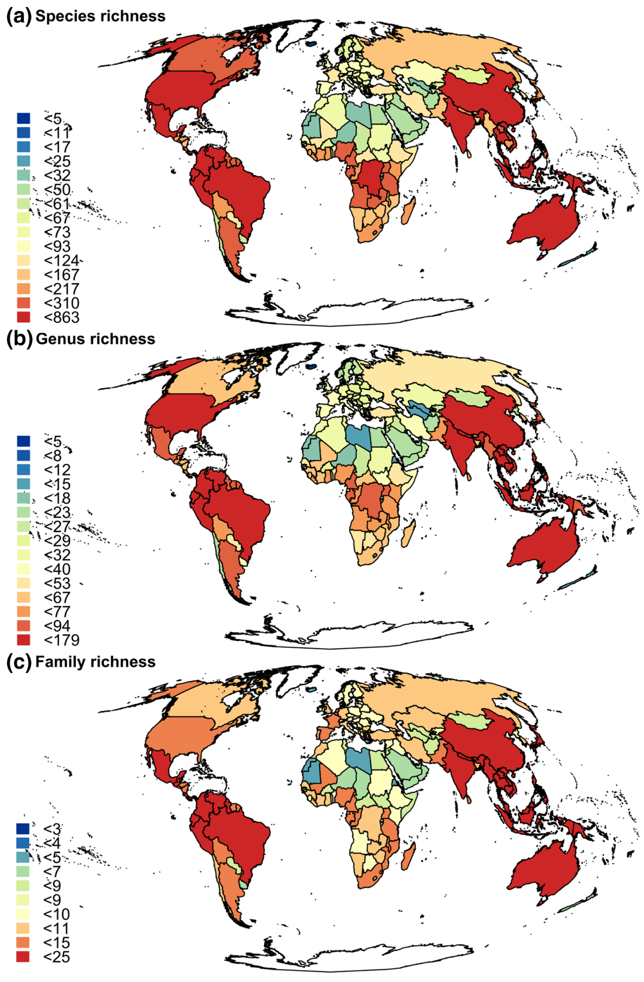

FIGURE 3 Geographical patterns of Odonata richness across different taxonomic levels. Data use the combined country-level occurrence data (union of all three source types). The maps are shown in a Mollweide equal-area projection. Colour class intervals are scaled to equal frequencies (quantiles). Note that across all taxonomic ranks, the richness of Odonata appears to follow a gradient of decreasing diversity from the equator to the poles

Comprehensive analyses of the systematics of odonate diversity have emphasized sampling the breadth of family level (e.g. Bybee et al., 2021; Dijkstra et al., 2013) or regionally at the genus level or species level, typically with more of a diagnostic focus (e.g. Dijkstra & Schröter, 2020; Garrison et al., 2006; Dijkstra & Lewington, 2006). Through our approach of harmonizing raw species names to a valid taxonomic backbone, we recognize that there will always be synonym name combinations that may be undetectable and missed in our checklist data search. Checklists inherently rely on maintenance of comprehensive lists of taxa through the efforts of experts with varying capacities and resources over time (Garnett et al., 2020). The valid species that are missing from our analysis primarily represent very recently described species, species currently classified as 'doubtful', or those that were described originally in the early part of the twentieth century, which have minimal description data to examine.

Despite their charismatic and ecological allure, global distribution studies of dragonflies and damselflies are limited in their spatial and taxonomic scope. While recent assessments of the knowledge of the order have suggested that it is well known at the species level, difficulties in reconciling the odonate phylogenetic backbone have impeded comprehensive distributional analyses (e.g. Bybee et al., 2016; Dijkstra et al., 2013). Macroecological studies of odonate species distribution to date have been primarily regional in scope, and those with the greatest taxonomic and spatial coverage have focused on North America (Paulson & Dunkle, 2012), Europe (Hassall, 2015; Keil et al., 2008) and Africa (Pinkert et al., 2020). Difficulties in estimating species distributions in the home range and migratory traits of in dragonflies and damselflies further complicate accurate range predictions (May, 2013; Outomuro & Johansson, 2019). Some individual species occurrences or checklist presences may represent vagrants, migrants or range shifts but are incorporated into checklists, data repositories or range maps. Transparency in spatial source information as well as taxonomic data enable checklists to be updated and individual species records or spatial gaps poised for further investigation (Reyserhove et al., 2020). Additionally, while global in intent and standardized in listing criteria, the data provided by the IUCN Red Lists undergo expert-reviewed updates in both taxonomy and checklist data at varying times, obscuring the age and source of checklist data. Reduction in checklist bias requires both transparency in sourcing and clarity in evaluation; the required time and resources to achieve both can be prohibitive (e.g. McBride et al., 2012). The presented checklist database is transparent in taxonomy and raw data sourcing, methods of inclusion of country-level data into checklists, follows open-data and FAIR standards, and aims to be a basis for nomenclatural and spatial data changes (Wilkinson et al., 2016).

4.2 | Spatial and biogeographical patterns

The origin of Odonata is probably a warm-adapted species from the Carboniferous (May, 1991). However, nowadays Odonata species are found on every continent of the world, except for Antarctica (Tillyard, 1917). In line with the long-standing hypothesis that thermal adaptations shaped the distribution of clades (Tillyard, 1917), a previous estimate at the biogeographical realm level (Kalkman et al., 2008) and a study on the phylogenetic diversity of European Odonata (Pinkert et al., 2018) indicated that the tropics have a larger proportion of families and genera than temperate regions of the world. Our results support this general pattern, with the number of species, genera and families decreasing from the equator to the poles (Spearman's ϱ of richness against absolute latitude: −0.30, −0.26 and −0.16, respectively; all $p < 0.05$). A marked exception to this overall trend is the United States having a disproportionately high number of clades for its latitudinal position. Similar, biogeographical idiosyncrasies of North American Odonata compared with, for instance European ones, found also in several other taxa (Hewitt, 2000), seem to result from the latitudinal orientation of the main mountain ranges that allowed species to cope with glacial fluctuations by shifting the ranges unhindered by strong dispersal barriers (Pinkert et al., 2017). Thus, in North America, a higher proportion of tropical clades appears to have survived in southern refugia and re-colonized previously glaciated areas when temperatures began to rise during the interglacials. Tropical regions apparently do not only harbour more, but also older families (Bybee et al., 2021). Our study adds further support to the hypothesis that only a few closely related lineages of Odonata have been able to colonize temperate climates (Pinkert et al., 2018), while the majority and the older lineages retained their initial tropical niche, likely because of constraints to the evolution of thermal adaptations (Pinkert & Zeuss, 2018).

4.3 | Limitations and extensions

The role of a checklist is to document the species known from a region in their current taxonomic status. Checklists of species can only show the presently observed taxonomic richness. They are limited by regional comprehensiveness, and regular updates are needed to account for changing taxonomy, newly present species and species range shifts. Additionally, the inclusion of different types of evidence (i.e. specimens and observations), documentation and sampling effort vary between checklists, making it difficult to assess the errors of commission and omission. The country checklist dataset presented in this paper, hosted on the Map of Life website, enables transparency in identifying original references and will be available to incorporate new sources of country checklists on the website via expert submission or Map of Life data curation. Updates and edits to the checklist data can be proposed via the general website contact form on Map of Life or directly to the contact information associated with the dataset (Map of Life, 2022). The addition of species to any richness estimate can be biased by detection and sampling, a general effect demonstrated in plants and animals (e.g. Beck & Schwanghart, 2010; Jarzyna & Jetz, 2016; Qian et al., 2018). Traits related to emergence detection in odonates are known to influence species inventories (Bried et al., 2015). To confirm country presences projected by country interpolation, we recognize that additional field sampling would be needed for verification. While we present all raw interpolated species–country combinations based on a 50% border sharing threshold, we recommend additional discretion in outright accepting interpolations in countries with extreme area or habitat differences. Despite greater confidence in interpolations above a 60% threshold, countries interpolated from the 50% to 60% threshold range (e.g. Mongolia, Bhutan, Bolivia) need greater scrutiny before acceptance of these species as missing from checklists. Climatic conditions in Mongolia pose an additional arid and hot barrier to addition of more dragonfly and damselfly diversity to the country's checklist (Hu et al., 2015).

Our results of high observed diversity and country interpolation in the tropics, particularly in southeast Asia, support the likelihood of additional species detections and checklist additions in the future. South central African countries additionally show patterns of high species richness per country, but less so at the genus level, likely as a result of a high number of recent generic synonymies and species descriptions (i.e. Dijkstra et al., 2015). Our results reflect the recent updates to the global family-level classification (Bybee et al., 2021), but any generic revisions or species descriptions will influence the stability of the global odonate richness patterns over time.

4.4 | Applications for conservation

Country-level checklists are relevant for regional, national and intergovernmental agencies to determine responsibilities, conservation risks and establish targets. Definition of protected areas and prioritization relies on up-to-date documentation of species presence, phylogenetic diversity and additional associated information, such as functional traits. Species checklists aid in identification of country-level taxonomic stewardship for national funding and resource allocation (Oliver et al., 2021). Odonata rely on freshwater habitats in all life stages, and the interconnectedness of water bodies requires a concerted effort between nations to identify and address regional habitat risks and resulting distributional implications. As one example set of potential future uses, our global dataset provides a baseline with which to examine the effect of global change and invasions on the distribution and richness of odonate taxa. Our comprehensive and comparative approach to understanding species presence in checklist data can enable identification of habitat overlap between countries through the use of species checklists.

The global diversity patterns of dragonflies and damselflies can be used to identify taxonomic and spatial shortfalls in a time of increased biodiversity point data and has implications for freshwater habitat management and conservation. Leveraging the literature checklists of expeditions and collection assessments and integrating the vast amounts of point occurrence data offer a helpfully comprehensive picture of the country-level diversity of a charismatic group of insects. Using these known country presences, it is possible to identify potential countries that could be a part of species ranges. Examination of emergent patterns in taxonomic and spatial data coverage at the country level can lead to identification of regions needing additional sampling and data incorporation to improve the resolution of regional diversity patterns. While our dataset represents individual present species in each country, incorporating population data at the regional scale is necessary for investigating global trends in odonate abundance or declines. Our dataset provides a time-stamped and transparent source for baseline global richness for the dragonflies and damselflies that can be built upon for macroecological and macroevolutionary analysis. The results from our integration of literature and point occurrence data to generate comprehensive country checklists improve previous global estimations of species richness, highlighting the gaps and synergies of these two data types in the global picture of odonate diversity.

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DATA AVAILABILITY STATEMENT

All data contributions to the manuscript are included in the supplementary material, and updated odonate maps and country checklist data are directly available on Map of Life at DOI: 10.48600/mol-b8as-vh75. Scripts from this study are available for download at DOI: 10.5281/zenodo.5889003. The occurrence data cleaning script is available on Map of Life and associated with DOI: 10.48600/mol-1sr2-nh14.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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