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RESEARCH ARTICLE

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Anticipating where are unknown aquatic insects in Europe to improve biodiversity conservation

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Abstract

Aim: Understanding biodiversity patterns is crucial for prioritizing future conservation efforts and reducing the current rates of biodiversity loss. However, a large proportion of species remain undescribed (i.e. unknown biodiversity), hindering our ability to conduct this task. This phenomenon, known as the 'Linnean shortfall', is especially relevant in highly diverse, yet endangered, taxonomic groups, such as insects. Here we explore the distributions of recently described freshwater insect species in Europe to (1) infer the potential location of unknown biodiversity hotspots and (2) determine the variables that can anticipate the distribution of unknown biodiversity.

Location: The European continent, including western Russia, Cyprus and Turkey.

Methods: Georeferenced information of all sites where new aquatic insect species were described across Europe from 2000 to 2020 was compiled. In order to understand the observed spatial patterns in richness of recently described species, spatial units were defined (level 6 of HydroBASINS) and associated with a combination of a set of socioeconomic, environmental and sampling effort descriptors. A zero-inflated Poisson regression approach was used to model the richness of newly described species within each spatial unit.

Results: Nine hundred and sixty-six recently described species were found: 398 Diptera, 362 Trichoptera, 105 Coleoptera, 66 Plecoptera, 28 Ephemeroptera, 3 Neuroptera, 2 Lepidoptera and 2 Odonata. The Mediterranean Basin was the region with the highest number of recently described species (74%). The richness of recently described species per spatial unit across Europe was highest at mid-elevation areas (between 400 and 1000 m), latitudes between 40 and 50° and in areas with yearly average precipitation levels of 500–1000 mm, a medium intensity of sampling effort and low population density. The percentage of protected areas in each study unit was not significantly related to the richness of recently described species. In fact, 70% of the species were found outside protected areas.

Main conclusions: The results highlight the urgent need to concentrate conservation efforts in freshwater ecosystems located at mid-altitude areas and out of protected areas across the Mediterranean Basin. The highest number of newly described species in those areas indicates that further monitoring efforts are required to ensure the aquatic biodiversity is adequately known and managed within a context of growing human impacts in freshwater ecosystems.

KEYWORDS
aquatic ecosystems, biodiversity loss, conservation priorities, protected areas, species distribution, vulnerability

1 | INTRODUCTION

Knowing where species occur is vital for setting priorities for biodiversity and ecosystem conservation (Whittaker et al., 2005). Incomplete or biased information on the distribution of biodiversity limits our capacity to effectively prioritize where conservation efforts should be allocated (Hermoso, Kennard, & Linke, 2015; Meyer et al., 2015), and thus to maintain healthy ecosystems and the services they provide (Cardinale et al., 2012; Hermoso, Filipe, et al., 2015). This is an urgent task, as climate change and other anthropogenic impacts, such as habitat loss and degradation, are causing an unprecedented biodiversity loss, and many species could likely disappear even before they are collected, identified and formally described (Costello, 2015).

Even though our knowledge about the number of current species is growing, the vast majority of species are not formally described yet, at least for some lineages (i.e. 'Linnean shortfall', Brown & Lomolino, 1998). Also, for many described species, there are several knowledge gaps related to their geographical distribution (i.e. 'Wallace shortfall', Lomolino, 2004), biology or ecological requirements (Bini et al., 2006; Hortal et al., 2015).

Improving the information on the distribution of biodiversity is especially urgent in the case of freshwater ecosystems as they are particularly affected by global change, even more than their terrestrial or marine counterparts (Hermoso et al., 2012; Reid et al., 2019; WWF, 2020). Compared with terrestrial invertebrates, freshwater species have smaller geographic ranges, lower dispersal abilities and higher endemism levels (Dudgeon et al., 2006). Moreover, freshwater ecosystems are very sensitive to human disturbances, mainly because they are not only receivers of disturbances (e.g. pollution or biological invasions) but also transmitters, meaning that disturbances effects are transported downstream to the whole drainage basin (Conti et al., 2014; Dudgeon et al., 2006).

Insects represent a big proportion of the world's total biodiversity and are key to ecosystem functioning because they control and maintain vital processes such as pollination, pest control and decomposition (Losey & Vaughan, 2006; Noriega et al., 2018; Schuldt & Assmann, 2010). However, around 80% of the expected insect species are formally undescribed by science (Stork, 2018) and, moreover, many other species are declining at an alarming rate (Cardoso et al., 2020; Wagner, 2020). Although taxonomists continue to describe new species, even in regions where taxonomic studies are abundant, incomplete taxonomic knowledge and declining trends are of particular concern for aquatic insects, as they occupy many trophic niches and are found in almost all freshwater ecosystems (Fenoglio et al., 2014; Múrria et al., 2018). Finally, the ecology, evolutionary biology and taxonomy remain poorly known for many groups of aquatic insects, especially for those with different larval (mostly aquatic) and adult (mostly terrestrial) habitat requirements (Dijkstra et al., 2014; Tierno de Figueroa et al., 2013).

Several reasons, including factors related to the scarce taxonomical studies, the lack of experts, low sampling efforts or the limited research funding (but see Meyer et al., 2015) may explain why in most countries there is still a large proportion of insect species to be described (Fontaine et al., 2012). To find new species, taxonomists commonly survey regions that are already known for having a high biodiversity, leaving regions that are expected to be poor in species un-explored (Sánchez-Fernández et al., 2022; Sánchez-Fernández, Lobo, et al., 2008; Sastre & Lobo, 2009). For example, protected areas and pristine regions tend to be more explored than areas impacted by human activities (Sastre & Lobo, 2009). Society preferences also affect the priorities in research investments and, therefore, funds are commonly devoted to studying charismatic species such as birds or mammals, while insects (less charismatic) remain largely under-studied (Troudet et al., 2017). Lepidoptera (Macrolepidoptera), Orthoptera and Odonata are exceptions, with more species listed as conservation concern than other insects, probably because of their size and vivid colouring (Leandro et al., 2017). Medically important groups, such as mosquitoes or black flies (Diptera), are also well-studied insects.

Here, the aim was to explore the distribution of recently described aquatic insect species in Europe to (1) infer the location of unknown biodiversity hotspots and (2) determine the variables that explain their distribution. It was assumed that areas where more species have been described in the last 20 years could be indicative that more species await to be described. Therefore, the results should indicate areas where more monitoring effort is still required, as their biodiversity could be higher than what we currently know. The first hypothesis was that unknown biodiversity hotspots would be found in southern Europe, that is, the Mediterranean Basin, a freshwater biodiversity hotspot (Tierno de Figueroa et al., 2013). The second hypothesis was that the location of the unknown biodiversity hotspots could be anticipated by a combination of socioeconomic, environmental and sampling effort variables. For instance, areas with less investment in research should have fewer descriptions in the time period studied than other areas, since the funds dedicated to research are low. Similarly, areas with high environmental variability (e.g. landscape heterogeneity) would show the highest number of recently described species because they harbour more habitat types (Nichols et al., 1998). Regarding sampling effort, regions that have been sampled more intensively would have more complete taxonomic inventories than other regions, and therefore the probability of new species descriptions is low. Knowing where unknown biodiversity hotspots are located will help anticipate where conservation actions need to be implemented before unknown species are lost by direct and indirect human impacts.

2 | METHODS

2.1 | Study area

The study focused on the European continent, including western Russia, Cyprus and Turkey (Figure 1), and comprised an extension of 11,324,000 km^2 across several bioclimatic regions from the Mediterranean to the Polar Artic. Despite being part of Europe, the Macaronesian islands were not included given their unique biogeographical history. For the whole study area, the level 6 of HydroBASINS (Lehner & Grill, 2013) was used as a spatial unit for summarizing the spatial information and carrying out statistical analyses. HydroBASINS portrays the watershed boundaries and sub-basin delineations at a global scale (Lehner & Grill, 2013) using the Pfafstetter coding system. The level 6 was selected because larger or smaller scales of spatial units were impractical, the former would dissipate environmental and socioeconomic factors, and the latter could have increased the number of spatial units with no data. This resulted in a total of 1381 spatial units (Figure 1).

2.2 | Species data

A database with information on species of aquatic insects described between 2000 and 2020 was compiled (see Table S1 in the supplementary materials). Subspecies or species groups were discarded. The list of monophyletic freshwater lineages in Múrria et al. (2018) was used to select the target taxonomic groups (orders and families). A first search on new described species was conducted in taxonomic and biodiversity web pages, including the Taxa and Autecology Database for Freshwater Organisms (freshwaterecology.info), the Index to Organisms Names (organismnames.com/query.htm), PESI (eu-nomen.eu) and the Barcode of Life Data System (boldsystems.org). A second search was focused on specialized journals (e.g. Aquatic Insects, Braueria, Graellsia, Zookeys, Zootaxa) and order-specific web portals, such as Ephemeroptera of the world (insecta.bio.spbu.ru/z/Eph-spp/index.htm), Trichoptera World Checklist (entweb.sites.clemson.edu/database/trichopt/index.php), Systema Dipterorum (diptera.org), the Chironomid home page (chironomidae.net), DragonflyPix (Odonata; dragonflypix.com/checklist_en.html) and the Plecoptera species file (Plecoptera.SpeciesFile.org). The scientific names, locality where the species was first recorded and authorship of all species described between 2000 and 2020 were retrieved from the original manuscript. In particular, the geographical coordinates of the holotype locality were preferably used, even when paratypes or other specimens were collected in other places that were usually close. When the coordinates were not available in the original manuscript, corresponding authors were contacted to get details on the locality and coordinates were retrieved using Google Maps. In addition, to ensure that all recently described species were included in the study, the database was reviewed, corrected and expanded by taxonomic experts (see details

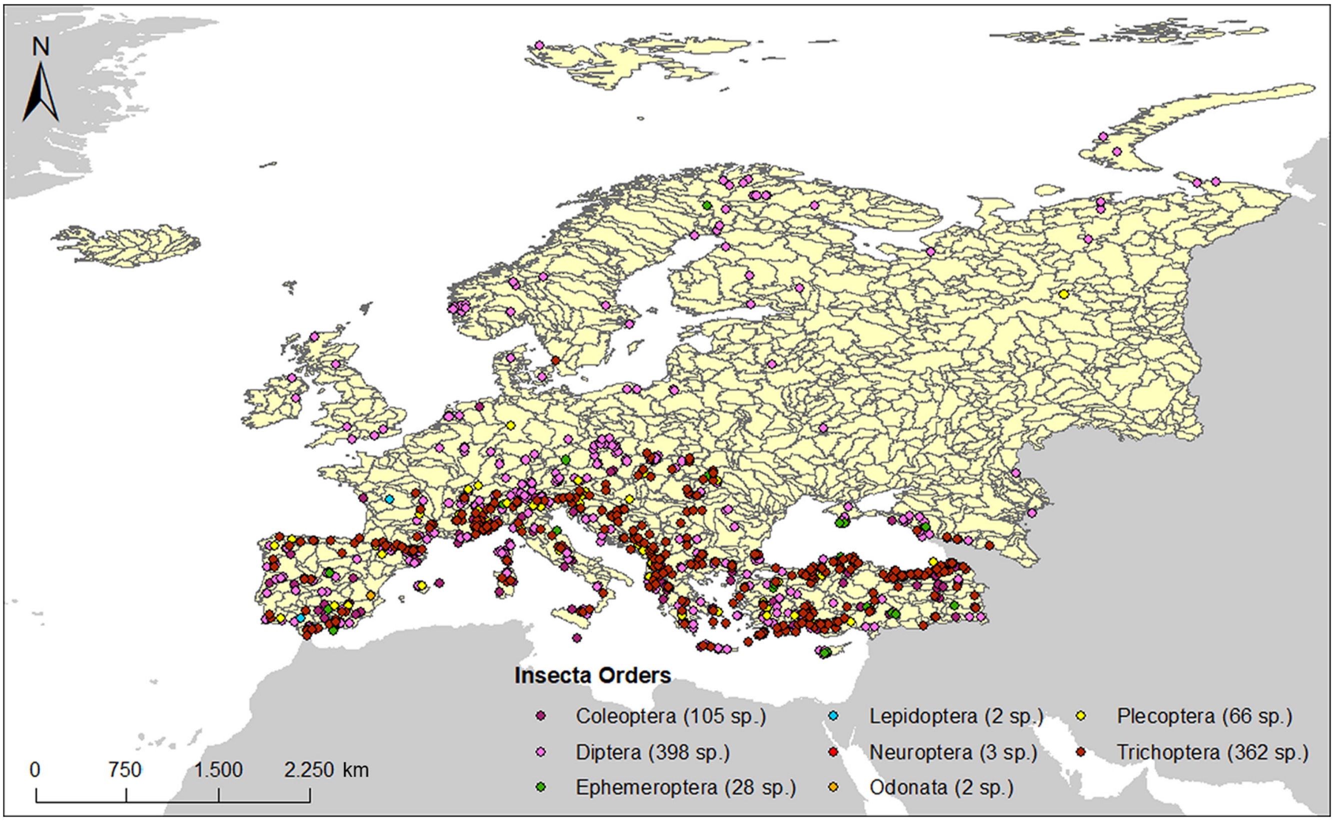

FIGURE 1 Map showing the extent of this study and the spatial units considered by the level 6 of HydroBASINS (Lehner & Grill, 2013) and all of the recently described species (2000–2020) of aquatic insects in Europe separated by taxonomic orders.

TABLE 1 Used data from the Global Biodiversity Information Facility (GBIF).

Order	Families
Coleoptera	Dryopidae, Dytiscidae, Elmidae, Gyrinidae, Haliplidae, Helophoridae, Hydraenidae, Hydrochidae, Hydrophilidae, Hydroscaphidae, Hygrobiidae, Noteridae, Sphaeriusidae
Diptera	Athericidae, Blephariceridae, Ceratopogonidae, Chironomidae, Culicidae, Dixidae, Dolichopodidae, Empididae, Ephydridae, Limoniidae, Muscidae, Psychodidae, Ptychopteridae, Rhagionidae, Scatophagidae, Sciomyzidae, Simuliidae, Stratiomyidae, Syrphidae, Tabanidae, Thaumaleidae, Tipulidae
Ephemeroptera	Ameletidae, Baetidae, Caenidae, Ephemerellidae, Ephemeridae, Heptageniidae, Isonychiidae, Leptophlebiidae, Metretopodidae, Neoephemeridae, Oligoneuriidae, Palingeniidae, Polymitarcyidae, Potamanthidae, Prosopistomatidae, Siphlonuridae
Hemiptera	Aphelocheriridae, Corixidae, Gerridae, Hydrometridae, Mesoveliidae, Naucoridae, Nepidae, Notonectidae, Pleidae, Veliidae
Lepidoptera	Crambidae
Megaloptera	Sialidae
Neuroptera	Osmylidae, Sisyridae, Nevrorthidae
Odonata	Lestidae, Calopterygidae, Euphaeidae, Platycnemididae, Coenagrionidae, Aeshnidae, Gomphidae, Cordulegastridae, Macromiidae, Corduliidae, Libellulidae
Plecoptera	Capniidae, Chloroperlidae, Leuctridae, Nemouridae, Perlidae, Perlodidae, Taeniopterygidae
Trichoptera	Apataniidae, Beraeidae, Brachycentridae, Calamoceratidae, Dipseudopsidae, Ecnomidae, Glossosomatidae, Goeridae, Helicophidae, Helicopsychidae, Hydropsychidae, Hydroptilidae, Lepidostomatidae, Leptoceridae, Limnephilidae, Limnophilidae, Molannidae, Odontoceridae, Philopotamidae, Phryganeidae, Polycentropodidae, Psychomyiidae, Rhyacophilidae, Sericostomatidae, Thremmatidae, Uenoidae

in Table S1): Marcos A. González, Füsun Sipahiler and Wolfram Graf for Trichoptera, Andrés Millán and David Sánchez-Fernández for Coleoptera and Hemiptera, José Manuel Tierno de Figueroa and Dávid Murányi for Plecoptera, Wolfram Mey for Lepidoptera, Tomáš Derka for Ephemeroptera, Marija Ivković for Diptera and Joel Moubayed for Chironomidae (Diptera).

2.3 | Potential explanatory variables

A preliminary list of socioeconomic, environmental, sampling effort and local variables that could potentially explain the distribution of recently described species such as elevation, temperature, precipitation or extent of ice sheets at the last glacial maximum, was compiled (see Table S2 in the supplementary materials). Environmental and socioeconomic data came from HydroBASINS, the European Tertiary Education Register (ETER) project (eter-project.com) and Eurostat (ec.europa.eu/eurostat), while environmental variables were retrieved from HydroBASINS (hydrosheds.org/page/hydrobasins; see Table S2 in the supplementary materials). Sampling effort was inferred from the number of species records currently available at the Global Biodiversity Information Facility (GBIF) by counting all records for the taxa included in the analyses (gbif.org) (Table 1) in each spatial unit (i. e. level 6 of HydroBASINS). The references for each downloaded data can be found at Table S3 in the supplementary material. The GBIF datasets included some fossil families such as Perlariopseidae (Plecoptera) that were disregarded. The final list of socioeconomic, environmental, sampling effort, environmental and spatial variables is found in Table 2.

In the case of predictive variables obtained from HydroBASINS (elevation, geographic coordinates, precipitation, temperature, population density and percentage of protected area), the variable values were already calculated at the resolution of our spatial units (level 6 in our case) in the polygonal layer. The data coming from GBIF and ETER Project (sampling effort and number of universities respectively), were georeferenced so it was possible to link each occurrence with the corresponding study unit using the *Spatial Join* tool in ArcMap. Regarding the researchers, education and R&D data from Eurostat, the values for each of these variables were averaged across the studied period at the NUTS2 level. Then they were translated into the network of spatial units, averaging across all NUTS2 that fell within each HydroBASINS polygon. The dependent variable, that is, the number of described species from 2000 to 2020 per spatial unit, was calculated as the counts of the species described at each sampling unit.

2.4 | Statistical analysis

Multicollinearity between pairs of predictive variables can lead to errors when estimating the effects of predictors in the model (Alin, 2010). Therefore, a correlation matrix with all pairwise combinations of the predictive variables was checked. In those pairs with an R-square value over 0.6, only one variable was randomly selected and kept to assure that only independent variables were used in the modelling procedure. All these independent variables covered different ranges and magnitudes and were accordingly scaled. Since elevation and species richness tended to have a quadratic relationship because species richness peaks at mid-elevations (Sanders & Rahbek, 2012), models considering the elevation as a quadratic term were tested.

A Shapiro–Wilk normality test on the dependent variable (i.e. the number of described species from 2000 to 2020 per spatial unit) showed that data were not compatible with a normal distribution (*p*-value <2.2e-16), likely because most of the spatial units did not have species described from 2000 to 2020.

A zero-inflated Poisson regression approach was used to model the richness of recently described species within each spatial unit (dependent variable) in front of a combination of potential explanatory variables (predictive variables). This approach assumes that the excess zeros are generated by separated processes from the richness values and zeros can be modelled independently (Long, 1997). This approach was chosen given the distribution of our data, that contains a disproportionate number of spatial units with no new descriptions and highly skewed towards lower richness values. The zero-inflated Poisson model has two components: a Poisson counts model for the units with at least one observed new species, and a logit model for predicting excess zeros. In the logit model, all spatial units with at least a newly described species are considered as 'presence', while all the remaining units with no new species described as 'absences'. Therefore, the first component of the model informs about the importance of each predictive variable at explaining the observed richness of new descriptions, while the second component informs about the probability of finding new species (Long, 1997). The zero-inflated Poisson regression models were ran using all individual non-correlated predictive variables and also all their possible combinations. The Akaike information criterion (AIC) was used to determine which combination of predictive variables better fit the distribution of the richness of described insect species between 2000 and 2020. Following this criteria, the lowest AIC models were considered the most adequate to explain the data since they had more statistical support (Burnham & Anderson, 2002). In addition, all models with an AIC increase equal to or less than seven units in relation to the model with the lowest AIC value were considered statistically significant (Burnham & Anderson, 2002; Hermoso et al., 2011).

The three orders with the highest number of species described between 2000 and 2020 (i.e. Diptera, Trichoptera and Coleoptera) were also analysed separately. The main reason for this additional analysis was because of the differential ecological features of these groups. For instance, Diptera and Coleoptera can tolerate a wide range of environmental conditions, whereas most Trichoptera require clean, cool and well-oxygenated waters (Resh & Cardé, 2009). Furthermore, an important number of Diptera and Coleoptera are found in the ecotone between land and inland waters, a habitat known for its rich biodiversity and sensitivity to environmental

TABLE 2 Socioeconomic (SE), environmental (E), sampling effort (S) and spatial (SP) variables selected after checking for multicollinearity of a longer list of potential variables (Table S2 in the supplementary material). In italics, variables used after checking for correlation.

Variable	Meaning	Units	Rationale	Source
Species per spatial unit according to GBIF^{S}	*Number of recorded species' occurrences for each spatial unit based on the data provided by GBIF*	*Number of species per country*	*Countries with more species could potentially have more species to be described*	*GBIF*
Researchers^{S}	*Number of researchers per spatial unit*	*Count*	*More naturalists going to the field to collect specimens, more chances to describe new species*	*Eurostat*
Elevation (DEM)^{E}	*Height above sea level*	*m*	*Remote areas (such as those in higher elevation) have more chances to host undescribed species.* *High is above 1000 m, mid between 400 and 1000 m, and low below 400 m*	*HydroBASINS*
Geographic coordinates of each spatial unit^{SP}	*Latitude and longitude of the centroid of each spatial unit*	*Decimal degrees*	*Some latitudes or longitudes may harbour more species than others (e.g. south vs north)*	*HydroBASINS*
Precipitation^{E}	*Annual average precipitation*	*mm*	*Precipitation levels play a big role in species distributions. Higher precipitation levels can increase nutrient availability, increasing insect populations*	*HydroBASINS*
Temperature^{E}	Annual air temperature average	°C	Temperature ranges play a big role in species distribution. Higher temperatures lead to shorter life cycles and, therefore, more evolutionary capacity (higher temperature means more mutation frequency), favouring speciation	HydroBASINS
Population density^{SE}	*Population per spatial unit*	*People per km*^{2}	*Higher population densities, more impacts on freshwater ecosystems and less chances to discover new species (probably already extinct)*	*HydroBASINS*
Percentage of protected areas^{E}	*Areas under protection figures*	*km*^{2}	*Protected areas could also protect undiscovered species*	*HydroBASINS*
Number of universities per country$^{S, SE}$	*University institutions in each country*	*Universities per country*	*More universities per country should lead into more researchers working on taxonomy*	*ETER Project*
Expenditure on education (EU)^{SE}	Resources dedicated towards education amongst the EU members	Euros	More money dedicated on education could increase the number of experts dedicated to taxonomy	Eurostat
Research and development expenditure (EU)^{SE}	Money intended for R&D projects	Euros	Countries that assign more money on R&D projects might invest also more on taxonomy	Eurostat

Note: Due to difficulties obtaining socioeconomic data from Russia, some spatial units had NA values in the socioeconomic variables (R&D expenditure, education expenditure and the number of researchers) that could invalidate the models, this is why these NA values were replaced by the mean of values for that variable.Links to source webpages: ETER Project eter-project.com; Eurostat http://ec.europa.eu/eurostat/data/database; GBIF gbif.org; HydroBASINS hydrosheds.org/products/hydrobasins.

changes (Ribera, 2000; Tachet et al., 2002; Resh & Cardé, 2009; Millán et al., 2014). The models for each individual order were carried out following the same process as for all orders together explained above.

The spatial analyses were conducted using ArcGIS (Environmental Systems Research Institute (ESRI), 2017) and the statistical analyses using the R programming language (R Core Team, 2021). The Hmisc package (Harrell Jr., 2021) was applied for the correlations between explanatory variables, and the pscl package (Jackman, 2020) to run the zero-inflated Poisson models. All graphics were presented using the ggplot2 package (Wickham, 2016).

3 | RESULTS

3.1 | Species database

The initial database included 1003 species described between 2000 and 2020. However, 37 species were discarded because the geographical coordinates of the holotype could not be obtained.

Therefore, final database included 966 recently described species, belonging to Diptera (398 sp.), Trichoptera (362 sp.), Coleoptera (105 sp.), Plecoptera (66 sp.), Ephemeroptera (28 sp.), Neuroptera (3 sp.), Lepidoptera (2 sp.) and Odonata (2 sp.) (Figure 1). No new species of Hemiptera (Heteroptera) or Megaloptera (Sialidae family) were described. The highest number of recently described species was found around the Mediterranean Basin (Figure 2), with Turkey being the country with most recent descriptions (220 sp.), followed by France (110 sp.), Italy (104 sp.) and Spain (100 sp.). In contrast, a small number of recently described species were recorded in northern and central Europe, mostly Diptera (Figure 3 and Figure S2).

3.2 | Variables influencing the distribution of recently described species

From the 45 tested models (individual models, additive model with all pairs of non-correlated variables and two-way additive models with all possible combinations of non-correlated variables), the one with the lowest AIC was the additive model with all non-correlated variables (see Table S4 in the supplementary materials for all the remaining models). The Poisson count component of the models explaining the distribution pattern of richness of recently described species, showed that the two variables with the highest weight were elevation and number of universities, that is, higher values for elevation/number of universities are associated with higher number of descriptions (Table 3), where a big part of the descriptions peak at mid-elevation areas (400–1000 m; Figure 4). Latitude, the number of GBIF occurrences and longitude also had a significant effect explaining the dependent variable, although less important than the previous two variables, as shown by their lower standardized regression coefficients (Table 3). When looking at the logistic portion of the models, exploring the probability of finding new species, regardless of richness, elevation and the number of GBIF records were the variables with higher standardized regression coefficients, indicating that lower probability of not finding new species at higher elevations and areas with already a large number of GBIF records. Results for the individual orders were somewhat similar to the ones obtained considering all orders together (see Tables S5 and S6 in the supplementary materials). In all three cases, the only model with enough statistical support was also the additive model with all non-correlated variables (Table S6). For Diptera, the number of universities was the variable with higher standardized regression coefficients and, therefore, the most important at explaining the distribution of the new descriptions of Diptera. In this case the possibility of finding new species

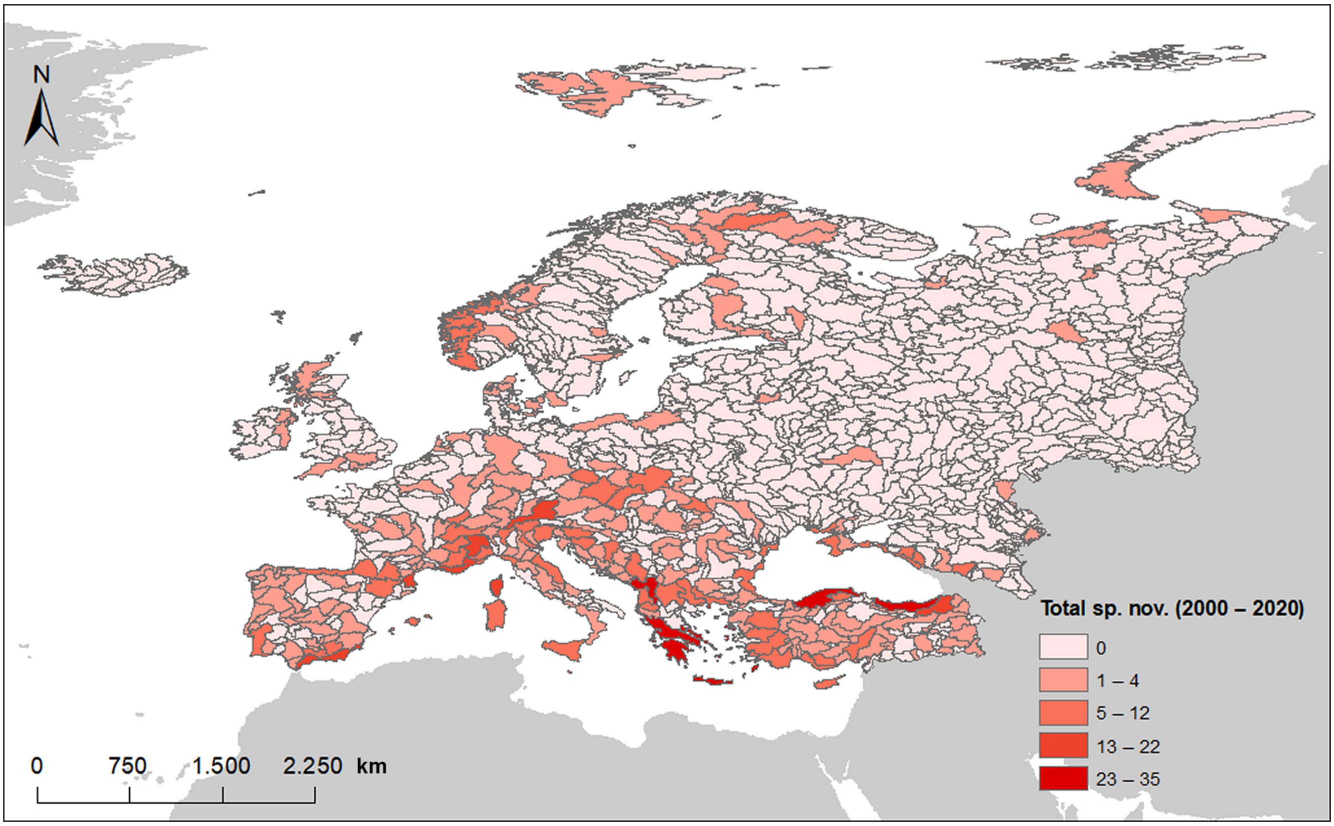

FIGURE 2 Total number of aquatic insect species described between 2000 and 2020 per spatial unit.

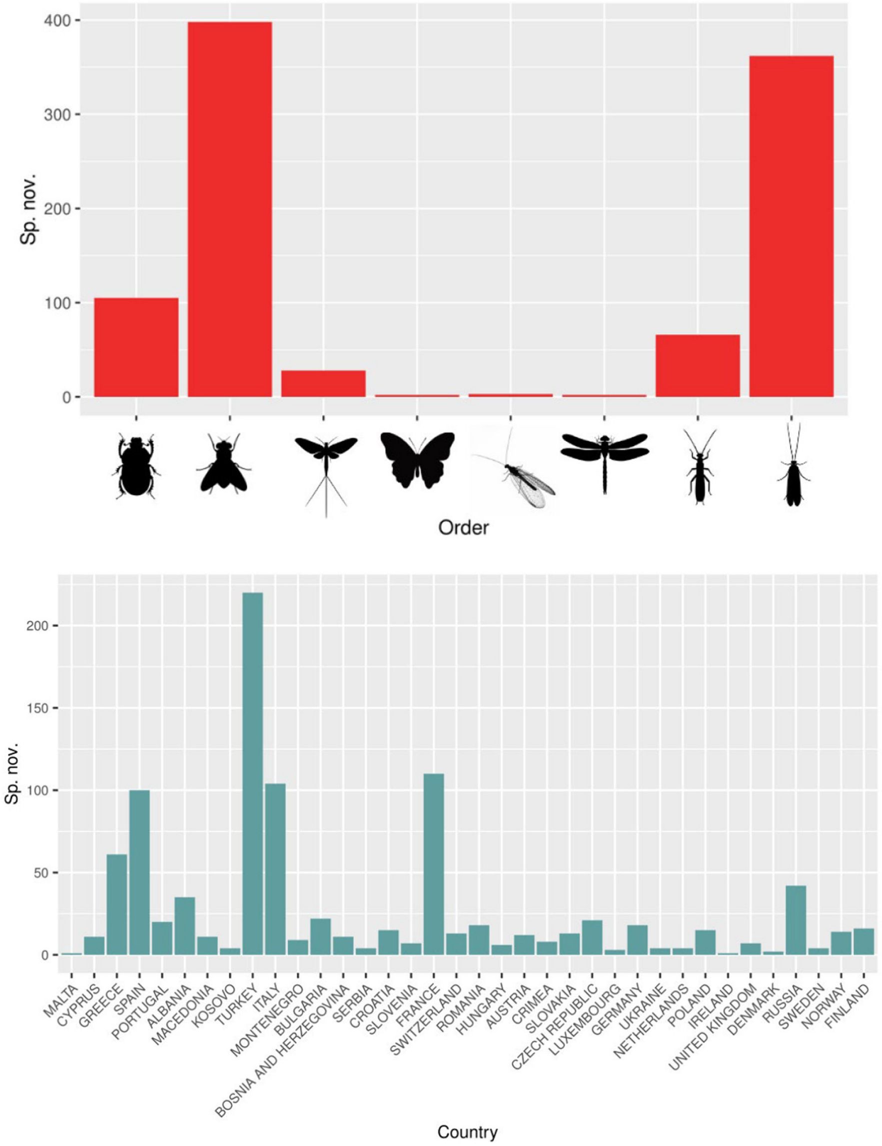

FIGURE 3 Number of recently described species (sp. nov.) in Europe per taxonomic order (2000–2020) (arranged alphabetically: Coleoptera, Diptera, Ephemeroptera, Lepidoptera, Neuroptera, Odonata, Plecoptera and Trichoptera) (top) and per country (2000–2020) (arranged from lowest to highest latitude) (bottom).

was determined by elevation and the number of GBIF records: spatial units at higher elevation and larger number of records in GBIF had a lower probability of finding new species (Table S5). In the case of Trichoptera, elevation and number of universities were the predictive variables with the largest importance at explaining the distribution of the richness of new descriptions of this order: more descriptions were found in spatial units with higher elevation and/or number of universities. Elevation was also a significant variable at explaining the probability of finding new species. Lastly, for Coleoptera, number of universities was the most important predictive variable explaining the description of new species for this order: more descriptions were made in spatial units with more universities. The probability of finding at least one new species was explained by the latitude.

4 | DISCUSSION

Europe is one of the most well-known regions in terms of biodiversity (Fontaine et al., 2012). Yet, the results show that a high number of new aquatic insects have been recently described (around 1000 new species in the span of 20 years). In agreement with the first hypothesis, the results revealed that the unknown biodiversity hotspots in Europe corresponded mainly to the southern areas around the Mediterranean Basin (Figure 2): Turkey, Iberian Peninsula, Pyrenees, Italy, Corsica and Malta, Alps, Dinaric western Balkan, Hellenic western Balkan and Eastern Balkan ecoregions (Illies, 1967). Despite the fact that the Mediterranean Basin is a well-known biodiversity hotspot (Ivković & Plant, 2015; Moubayed-Breil, 2020; Myers, 1990), including aquatic insects (Bonada & Resh, 2013; Tierno de Figueroa et al., 2013), a high number of new species might yet be undescribed in this area according to our results.

The Pleistocene southern refugia during glacial periods and the high topographic barriers limiting species movement from south to north during glaciations (i.e. Pyrenees, Alps, Dinaric Alps) likely explain why the Mediterranean region has the highest number of recently described aquatic insect species in Europe (Blondel et al., 2010; Grigoropoulou et al., 2022; Ivković & Plant, 2015; Tierno de Figueroa et al., 2013). Other reasons are related to the particular

TABLE 3 Results for the model with statistical support.

Count model (Poisson with log link)				
Predictor variable	**Estimate**	**Std. error**	***z* value**	**Pr (>|z|) ≤ 0.05**
Universities	5.156	1.030	5.004	5.62e-07
poly(Elevation, 2)1	6.409	1.608	3.986	6.73e-05
poly(Elevation, 2)2	−6.514	1.318	−4.943	7.79e-07
Population density	−0.170	0.071	−2.403	0.016
Percentage protected	0.087	0.050	1.748	0.081
GBIF occurrences[a]	0.688	0.068	10.178	<2e-16
Latitude	−0.951	0.091	−10.498	<2e-16
Longitude	0.653	0.075	8.721	<2e-16
Precipitation	0.170	0.040	4.292	1.77e-05
Researchers	−0.039	0.041	−0.968	0.333
Zero-inflated model (Binomial with logit link)				
Predictor variable	**Estimate**	**Std. Error**	***z* value**	**Pr (>|z|) ≤ 0.05**
Universities	0.218	0.335	0.651	0.515
poly(Elevation, 2)1	−19.432	3.894	−4.990	6.03e-07
poly(Elevation, 2)2	8.678	2.984	2.909	0.004
Population density	−0.197	0.165	−1.188	0.235
Percentage protected	−0.094	0.125	−0.753	0.451
GBIF occurrences[a]	−0.671	0.163	−4.119	3.80e-05
Latitude	0.626	0.190	3.293	0.001
Longitude	0.238	0.189	1.257	0.209
Precipitation	−0.116	0.112	−1.038	0.299
Researchers	0.250	0.099	2.524	0.012

[a] Transformed using $\log(x+1)$.

environmental conditions (strong seasonal and predictable hydrological fluctuations, including dry/wet phases) and the high landscape heterogeneity in this region, which has led to a higher spatial and temporal taxonomic and functional diversity (Bonada & Resh, 2013; Múrria et al., 2020; Tonkin et al., 2017). Although the largest accumulation of new descriptions was found in the Mediterranean Basin, new species of Diptera were described all-over the studied area. This finding shows that the discovery of new Diptera species follows a unique pattern, most likely because of their complex taxonomy, and suggest that a number future Diptera descriptions could be expected across Europe.

In agreement with the second hypothesis, socioeconomic, environmental, sampling effort and spatial variables explained the distribution of recently described species. First, the majority of the new species descriptions were found in spatial units with low population density (see Figure 4), meaning that (i) human impacts associated with highly populated areas, such as habitat degradation and fragmentation, could have reduced diversity and, therefore, led to impoverished communities (Newbold et al., 2015) and lower the number of new descriptions; and (ii) the few species living close to high population densities have already been described [although centred in Brazilian worm lizards, Colli et al., 2016 provide a good example of this phenomenon].

Second, a high number of new descriptions were found at mid-elevations, ranging between 400 and 1000 m. Low-elevation areas (below 400 m) tend to be heavily impacted by human activities, and, therefore, as explained above could host either an impoverished or well-studied biodiversity. On the other hand, high-elevation areas have been recurrently surveyed in the past (Sánchez-Fernández et al., 2022; Sánchez-Fernández, Lobo, et al., 2008), which could explain the low number of new descriptions at high altitudes. Finally, the habitat of mid-elevation ranges provides an ideal set of conditions to harbour a large number of species, since they have the potential to be colonized by species from both lower and higher elevations (Bertuzzo et al., 2016). This is reinforced by the refugia effect of mountain areas, because their intricate topography increases isolation with elevation (Elsen et al., 2018; Finn et al., 2011; Perrigo et al., 2020). Furthermore, the presence of aquatic insects at mid-elevations, which very often corresponds to mid-order sections, could also be supported by the River Continuum Concept (RCC). The RCC postulates high alfa diversity in mid-order sections [but see Finn et al., 2011 for beta diversity] because of the increasing width,

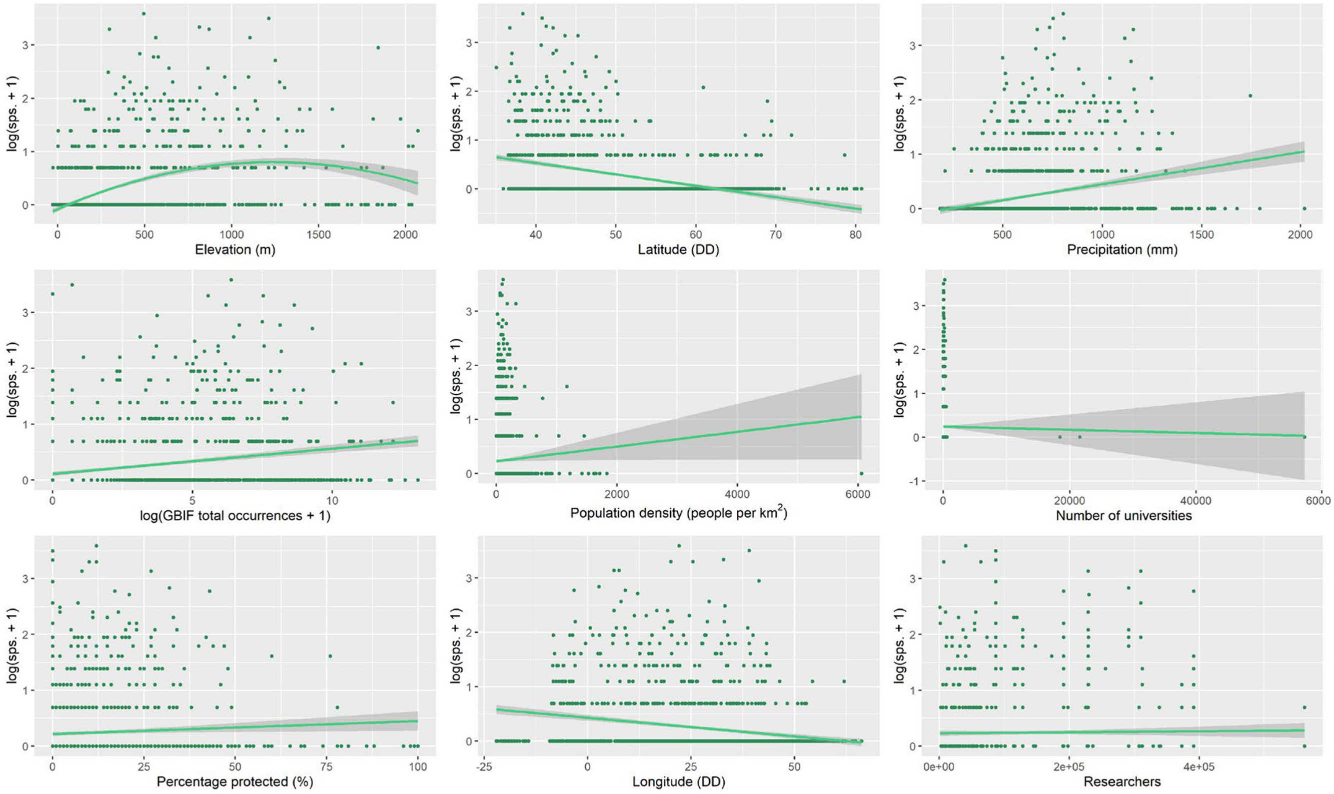

FIGURE 4 Relationship between the log-transformed number of recently described species (sp. nov.) per spatial unit and the non-correlated variables used in the models. The points indicate the number of sp. nov. in each basin, lines represent the regression line, and shaded areas are the confidence intervals of the regression lines.

depth, flow characteristics, temperature and the complexity of the water from headwater to mid-order sections (Vannote et al., 1980).

Third, the northern, western and central European territories had a higher survey density, meaning that these areas are traditionally highly sampled regions and the probability of finding new species is low. Specifically, the areas corresponding to Belgium, the Netherlands and the southern regions of Norway and Sweden present the highest sampling effort levels based on the data provided by GBIF. Although important, high survey intensity is not the only decisive factor in the description of new species. Survey effort has to be accompanied by a sufficient task force of taxonomists that have the knowledge and expertise to determine whether or not we have a new species. The current support for taxonomy is not enough to face the present biodiversity crisis (Guerra-García et al., 2008). According to the European Red List of Taxonomists report (Hochkirch et al., 2022), the taxonomic capacity in Europe is threatened or eroded a 41.4%, meaning that despite recent efforts, we still do not have enough task force to continue with the description of new species. Funding is strongly related to the impact factor of publications, and taxonomic publications have lower impact factors, so the lower the impact factor involves less funding (Hochkirch et al., 2022). Other factors not considered here, such as the number of researchers, research centres and funding specifically dedicated to molecular approaches, could be also relevant considering the recent advantages in the field to detect new species, and should be considered in future analyses.

When looking at the number of different taxonomists that have described the freshwater insect species in the time period considered per order, it resulted that orders with fewer new descriptions had more taxonomic experts (i.e. authors of the species description). For example, Odonata only had two descriptions in the time period considered, but there were four experts behind those descriptions. Meanwhile, Trichoptera and Diptera, two orders with the highest number of new descriptions (362 and 398 respectively) had fewer experts (39 and 164 respectively) (Table S7). As Hochkirch et al. (2022) indicate, the use of Plecoptera and Ephemeroptera for freshwater monitoring programs and the promotion of European pollination programs (that involve Diptera and Lepidoptera), has augmented the number of taxonomists dedicated to those groups, although it is still inadequate.

In the face of the present biodiversity crisis, combined with incomplete species distribution maps and a decline in taxonomic experts, the distribution patterns observed in our models could be used as a starting point for guiding conservation and further research efforts for aquatic insects across Europe. For instance, the results could be used to establish future sampling areas, and to determine where the conservation efforts and resources should be allocated. In this study, it was assumed that unknown biodiversity hotspots are likely located in areas where more species have been described during the last years. Despite this assumption could have the reverse interpretation (i.e. no more species will be described because we have discovered all), it is unlikely that the species discovery has reached a saturation because a large proportion of them were discovered during the last 5 years of the time series (see Figures S1 and S2 in the supplementary materials). Moreover, the high level of endemism found in the eastern and western areas of the Mediterranean Basin (Sánchez-Fernández et al., 2004), suggest that new species will be described in the future. Out of 966 described species in the time period considered, 74.43% of them have been described in areas corresponding to the Mediterranean Basin, compared to the 25.57% found in the rest of the study area, thus emphasizing the importance of its conservation and further research efforts. For instance, the Mediterranean northern Africa (e.g. Morocco, Algeria, Libya) is often overlooked despite evidence showing its high biodiversity of particular freshwater, which is threatened and unprotected (Slimani et al., 2022). Order wise, in the Mediterranean Basin, the highest number of new descriptions corresponds to Diptera and Trichoptera (Figure S3). These orders, together with Coleoptera, are the richest in aquatic ecosystems (Dijkstra et al., 2014). These results show the importance the Mediterranean Basin has in the overall biodiversity of Europe. Additionally, it is known that the European Mediterranean area contains the greatest known diversity for most of the aquatic insect orders of the continent [see Schmidt-Kloiber et al., 2017 for Trichoptera and Boudot & Kalkman, 2015 for Odonata]. One of the most surprising results of the study was the weak significance of the protected areas in explaining the unknown aquatic insect biodiversity. Around 70% of the described species between 2000 and 2020 were found outside the limits of protected areas. There are several potential explanations for this pattern. One the one hand, the acquisition of sampling permits which is usually administratively complex, therefore discouraging researchers to conduct sampling campaigns. Also, most new species in protected areas could have been already discovered because protected areas usually report better species inventories (promoted by local projects) than the surrounding areas, for example, an extensive inventory is necessary condition to those countries that have signed the Ramsar convention (Dudley, 2008). Another reason to explain the observed pattern could be that freshwater ecosystems and aquatic insects are seldom considered when conceiving the conservation plans (Ivković & Plant, 2015), and current protected areas fail to cover the distribution of freshwater biodiversity (Guareschi et al., 2015; Hermoso, Filipe, et al., 2015; Sánchez-Fernández et al., 2021). As a result, protected areas are not designed considering aquatic insects and, therefore, it is not surprising that an important part of the recently discovered species was recorded in unprotected areas (Ivković & Plant, 2015; Payo-Payo & Lobo, 2016). The design of protected areas tends to be biased towards less economically profitable regions, such as high mountainous areas, because the economical profits of farming in those areas are non-existent (Pressey, 1994; Pressey et al., 2002). Therefore, by establishing protected areas in regions with these characteristics, managers are leaving areas that could harbour more biodiversity without protection.

Despite the conservation effort implemented in the las decades, we still need more initiatives to study and protect freshwater ecosystems. Sadly, the Iberian Peninsula is one example of the poor protection of the freshwater habitats and the diversity that they harbour (Hermoso, Filipe, et al., 2015; Sánchez-Fernández, Bilton, et al., 2008). The lack of specific legislation to protect invertebrates (including aquatic insects) and their poor representation under current policy such as the Habitats Directive (Hermoso et al., 2019) is also critical for ensuring the conservation of freshwater biodiversity (Schuldt & Assmann, 2010). Therefore, the results suggest that future biodiversity conservation plans should extend the current network of protected areas towards those that hold a high diversity of taxa currently underrepresented, and also to areas that could still hold unknown and highly vulnerable species. The designation of entomologic (micro)reserves in such areas where insect hotspots have been found could be a promising approach to conserve also unknown freshwater biodiversity. For example, this figure was used in Portugal to create (micro)reserves to protect *Eurypha contentei* (Insecta, Hemiptera, Cicadoidea) and through the Spanish Entomological Association (AEE: Asociación Española de Entomología) five entomologic (micro)reserves have been recently created in Spain (Galante et al., 2015).

5 | CONCLUSIONS

The database generated in this study will be a useful resource of information to complete freshwater biodiversity inventories in Europe, and to know where the unknown biodiversity hotspots of aquatic insects in Europe are located. Based on and assuming that new species of aquatic insects will be described in the coming years (in particular with the boost of molecular approaches), taxonomic efforts to find new species must be directed towards south and eastern European areas at mid-elevations. Future protected areas should also prioritize these areas, where freshwater biodiversity inventories are still incomplete and ecosystems suffer from heavy human impacts.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article. In addition, the database (Table S1 in the Supplementary materials) is also freely available online on Zenodo at 10.5281/zenodo.7554277.

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REFERENCES

Alin, A. (2010). Multicollinearity. *Wiley Interdisciplinary Reviews: Computational Statistics*, *2*(3), 370–374. https://doi.org/10.1002/wics.84

Bertuzzo, E., Carrara, F., Mari, L., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A. (2016). Geomorphic controls on elevational gradients of species richness. *Proceedings of the National Academy of Sciences*, *113*(7), 1737–1742. https://doi.org/10.1073/pnas.1518922113

Bini, L. M., Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., Bastos, R. P., & Pinto, M. P. (2006). Challenging Wallacean and Linnean shortfalls: Knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions*, *12*(5), 475–482. https://doi.org/10.1111/j.1366-9516.2006.00286.x

Blondel, J., Aronson, J., Bodiou, J.-Y., & Boeuf, G. (2010). *The Mediterranean region: Biological diversity in space and time* (2nd ed.). Oxford University Press.

Bonada, N., & Resh, V. H. (2013). Mediterranean-climate streams and rivers: Geographically separated but ecologically comparable freshwater systems. *Hydrobiologia*, *719*(1), 1–29. https://doi.org/10.1007/s10750-013-1634-2

Boudot, J. P., & Kalkman, V. J. (Eds.). (2015). *Atlas of the European dragonflies and damselflies*. KNNV Publishing.

Brown, J. H., & Lomolino, M. V. (1998). *Biogeography* (2nd ed.). Sinauer Press.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag.

Cardinale, B., Duffy, J., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67. https://doi.org/10.1038/nature11148

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Ari Noriega, J., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., … Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. https://doi.org/10.1016/j.biocon.2020.108426

Colli, G. R., Fenker, J., Tedeschi, L. G., Barreto-Lima, A. F., Mott, T., & Ribeiro, S. L. (2016). In the depths of obscurity: Knowledge gaps and extinction risk of Brazilian worm lizards (Squamata, Amphisbaenidae). *Biological Conservation*, *204*, 51–62.

Conti, L., Schmidt-Kloiber, A., Grenouillet, G., & Graf, W. (2014). A trait-based approach to assess the vulnerability of European aquatic insects to climate change. *Hydrobiologia*, *721*(1), 297–315. https://doi.org/10.1007/s10750-013-1690-7

Costello, M. J. (2015). Biodiversity: The known, unknown, and rates of extinction. *Current Biology*, *25*(9), R368–R371. https://doi.org/10.1016/j.cub.2015.03.051

Dijkstra, K. D. B., Monaghan, M. T., & Pauls, S. U. (2014). Freshwater biodiversity and insect diversification. *Annual Review of Entomology*, *59*, 143–163. https://doi.org/10.1146/annurev-ento-011613-161958

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Dudley, N. (2008). *Guidelines for applying protected area management categories* (p. 86). IUCN.

Elsen, P. R., Monahan, W. B., & Merenlender, A. M. (2018). Global patterns of protection of elevational gradients in mountain ranges. *Proceedings of the National Academy of Sciences*, *115*(23), 6004–6009. https://doi.org/10.1073/pnas.1720141115

Environmental Systems Research Institute (ESRI). (2017). *ArcGIS Desktop Release 10.6. Redlands, California, USA*. https://www.arcgis.com/index.html

Fenoglio, S., Merritt, R. W., & Cummins, K. W. (2014). Why do no specialized necrophagous species exist among aquatic insects? *Freshwater Science*, *33*(3), 711–715. https://doi.org/10.1086/677038

Finn, D. S., Bonada, N., Múrria, C., & Hughes, J. M. (2011). Small but mighty: Headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, *30*(4), 963–980. https://doi.org/10.1899/11-012.1

Fontaine, B., van Achterberg, K., Alonso-Zarazaga, M. A., Araujo, R., Asche, M., Aspöck, H., Aspöck, U., Audisio, P., Aukema, B., Bailly, N., Balsamo, M., Bank, R. A., Belfiore, C., Bogdanowicz, W., Boxshall, G., Burckhardt, D., Chylarecki, P., Deharveng, L., Dubois, A., … Bouchet, P. (2012). New species in the Old World: Europe as a frontier in biodiversity exploration, a test bed for 21st century taxonomy. *PLoS One*, *7*(5), e36881. https://doi.org/10.1371/journal.pone.0036881

Galante, E., Numa Valdez, C., & Verdú, J. R. (2015). La conservación de los insectos en España, una cuestión no resuelta. *Revista IDE@ - SEA*, *7*, 1–13.

Grigoropoulou, A., Schmidt-Kloiber, A., & Múrria, C. (2022). Incongruent latitudinal patterns of taxonomic, phylogenetic and functional diversity reveal different drivers of caddisfly community assembly across spatial scales. *Global Ecology and Biogeography*, *31*, 1006–1020. https://doi.org/10.1111/geb.13479

Guareschi, S., Bilton, D. T., Velasco, J., Millán, A., & Abellán, P. (2015). How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters. *Biological Conservation*, *187*, 134–144. https://doi.org/10.1016/j.biocon.2015.04.018

Guerra-García, J. M., Espinosa, F., & García-Gómez, J. C. (2008). Trends in taxonomy today: An overview about the main topics in taxonomy. *Zoologica Baetica*, *19*, 15–49.

Harrell, F. E., Jr. (2021). *Hmisc: Harrell miscellaneous. R package version 4.6-0*. https://CRAN.R-project.org/package=Hmisc

Hermoso, V., Clavero, M., Blanco-Garrido, F., & Prenda, J. (2011). Invasive species and habitat degradation in Iberian streams: An analysis of their role in freshwater fish diversity loss. *Ecological Applications*, *21*, 175–188. https://doi.org/10.1890/09-2011.1

Hermoso, V., Filipe, A. F., Segurado, P., & Beja, P. (2015). Effectiveness of a large reserve network in protecting freshwater biodiversity: A test for the Iberian Peninsula. *Freshwater Biology*, *60*(4), 698–710. https://doi.org/10.1111/fwb.12519

Hermoso, V., Kennard, M. J., & Linke, S. (2012). Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. *Diversity and Distributions*, *18*(5), 448–458. https://doi.org/10.1111/j.1472-4642.2011.00879.x

Hermoso, V., Kennard, M. J., & Linke, S. (2015). Evaluating the costs and benefits of systematic data acquisition for conservation assessments. *Ecography*, *38*, 283–292. https://doi.org/10.1111/ecog.00792

Hermoso, V., Morán-Ordóñez, A., Canessa, S., & Brotons, L. (2019). Four ideas to boost EU conservation policy as 2020 nears. *Environmental Research Letters*, *14*, 101001. https://doi.org/10.1088/1748-9326/ab48cc

Hochkirch, A., Casino, A., Penev, L., Allen, D., Tilley, L., Georgiev, T., Gospodinov, K., & Barov, B. (2022). *European red list of insect taxonomists*. Publication Office of the European Union.

Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Illies, J. H. (1967). *Limnofauna europaea; Eine Zusammenstellung aller die europaischen Binnengewasser bewohnenden mehrzelligen Tierarten mit Angaben über ihre Verbreitung und Ökologie*. Gustav Fischer Verlag (in German).

Ivković, M., & Plant, A. (2015). Aquatic insects in the Dinarides: Identifying hotspots of endemism and species richness shaped by geological and hydrological history using Empididae (Diptera). *Insect Conservation and Diversity*, *8*(4), 302–312. https://doi.org/10.1111/icad.12113

Jackman, S. (2020). *pscl: Classes and methods for R developed in the political science computational laboratory. United States studies Centre, University of Sydney. Sydney, New South Wales, Australia. R package version 1.5.5*. https://github.com/atahk/pscl/

Leandro, C., Jay-Robert, P., & Vergnes, A. (2017). Bias and perspectives in insect conservation: A European scale analysis. *Biological Conservation*, *215*, 213–224. https://doi.org/10.1016/j.biocon.2017.07.033

Lehner, B., & Grill, G. (2013). Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. *Hydrological Processes*, *27*(15), 2171–2186. https://doi.org/10.1002/hyp.9740

Lomolino, M. V. (2004). Conservation biogeography. In M. V. Lomolino & L. R. Heaney (Eds.), *Frontiers of biogeography: New directions in the geography of nature* (pp. 293–296). Sinauer Associates.

Long, J. S. (1997). *Regression models for categorical and limited dependent variables*. Sage Publications.

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, *56*(4), 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Meyer, C., Kreft, H., Guralnick, R., & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nature Communications*, *6*(1), 1–8. https://doi.org/10.1038/ncomms9221

Millán, A., Sánchez-Fernández, D., Abellán, P., Picazo, F., Carbonell, J. A., Lobo, J. M., & Ribera, I. (2014). *Atlas de los coleópteros acuáticos de España Peninsular* (p. 820). Ministerio de Agricultura, Alimentación y Medio Ambiente.

Moubayed-Breil, J. (2020). Chironomidae de l'écosystème méditerranéen de France continentale sensu lato. Données faunistiques et biogéographiques sur les quatre dernières décennies [Diptera]. *Ephemera*, *21*(1), 31–69.

Múrria, C., Dolédec, S., Papadopoulou, A., Vogler, A. P., & Bonada, N. (2018). Ecological constraints from incumbent clades drive trait evolution across the tree-of-life of freshwater macroinvertebrates. *Ecography*, *41*(7), 1049–1063. https://doi.org/10.1111/ecog.02886

Múrria, C., Iturrarte, G., & Gutiérrez-Cánovas, G. (2020). A trait space at an overarching-scale yields more conclusive macroecological patterns of functional diversity. *Global Ecology and Biogeography*, *29*, 1716–2729. https://doi.org/10.1111/geb.13146

Myers, N. (1990). The biodiversity challenge: Expanded hot-spots analysis. *Environmentalist*, *10*(4), 243–256. https://doi.org/10.1007/BF02239720

Newbold, T., Hudson, L., Hill, S., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45–50. https://doi.org/10.1038/nature14324

Nichols, W. F., Killingbeck, K. T., & August, P. V. (1998). The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conservation Biology*, *12*(2), 371–379. https://doi.org/10.1111/j.1523-1739.1998.96237.x

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., Wackers, F. L., Woodcock, B. A., & Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, *26*, 8–23. https://doi.org/10.1016/j.baae.2017.09.006

Payo-Payo, A., & Lobo, J. M. (2016). The unpredictable characteristics of the localities where new Iberian species will be discovered. *Diversity and Distributions*, *22*(1), 73–82. https://doi.org/10.1111/ddi.12386

Perrigo, A., Hoorn, C., & Antonelli, A. (2020). Why mountains matter for biodiversity. *Journal of Biogeography*, *47*(2), 315–325. https://doi.org/10.1111/jbi.13731

Pressey, R. (1994). *Ad Hoc* reservations: Forward or backward steps in developing representative reserve systems? *Conservation Biology*, *8*, 662–668. https://doi.org/10.1046/j.1523-1739.1994.08030662.x

Pressey, R. L., Whish, G. L., Barrett, T. W., & Watts, M. E. (2002). Effectiveness of protected areas in North-Eastern New South Wales: Recent trends in six measures. *Biological Conservation*, *106*(1), 57–69. https://doi.org/10.1016/S0006-3207(01)00229-4

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Resh, V. H., & Cardé, R. T. (Eds.). (2009). *Encyclopedia of insects* (2nd ed.). Elsevier. https://doi.org/10.1016/B978-0-12-374144-8.X0001-X

Ribera, I. (2000). Biogeography and conservation of Iberian water beetles. *Biological Conservation*, *92*(2), 131–150. https://doi.org/10.1016/S0006-3207(99)00048-8

Sánchez-Fernández, D., Abellán, P., Velasco, J., & Millán, A. (2004). Selecting areas to protect the biodiversity of aquatic ecosystems in a semiarid Mediterranean region using water beetles. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *14*, 465–479. https://doi.org/10.1002/aqc.633

Sánchez-Fernández, D., Baquero, R. A., Velasco, L., Aranda, A., & Nicola, G. G. (2021). Assessing the role of the aquatic Natura 2000 network to protect both freshwater European species of community interest and threatened species in a Mediterranean region. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(7), 1901–1911. https://doi.org/10.1002/aqc.3540

Sánchez-Fernández, D., Bilton, D. T., Abellán, P., Ribera, I., Velasco, J., & Millán, A. (2008). Are the endemic water beetles of the Iberian Peninsula and the Balearic Islands effectively protected? *Biological Conservation*, *141*(6), 1612–1627. https://doi.org/10.1016/j.biocon.2008.04.005

Sánchez-Fernández, D., Lobo, J. M., Abellán, P., Ribera, I., & Millán, A. (2008). Bias in freshwater biodiversity sampling: The case of Iberian water beetles. *Diversity and Distributions*, *14*(5), 754–762. https://doi.org/10.1111/j.1472-4642.2008.00474.x

Sánchez-Fernández, D., Yela, J. L., Acosta, R., Bonada, N., García-Barros, E., Guisande, C., Heine, J., Millán, A., Munguira, M. L., Romo, H., Zamora-Muñoz, C., & Lobo, J. M. (2022). Are patterns of sampling effort and completeness of inventories congruent? A test using databases for five insect taxa in the Iberian Peninsula. *Insect Conservation and Diversity*, *15*(4), 406–415. https://doi.org/10.1111/icad.12566

Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, *35*(1), 1–3. https://doi.org/10.1111/j.1600-0587.2011.07338.x

Sastre, P., & Lobo, J. M. (2009). Taxonomist survey biases and the unveiling of biodiversity patterns. *Biological Conservation*, *142*(2), 462–467. https://doi.org/10.1016/j.biocon.2008.11.002

Schmidt-Kloiber, A., Neu, P. J., Malicky, M., Pletterbauer, F., Malicky, H., & Graf, W. (2017). Aquatic biodiversity in Europe: A unique dataset on the distribution of Trichoptera species with important implications for conservation. *Hydrobiologia*, *797*(1), 11–27.

Schuldt, A., & Assmann, T. (2010). Invertebrate diversity and national responsibility for species conservation across Europe – A multi-taxon approach. *Biological Conservation*, *143*(11), 2747–2756. https://doi.org/10.1016/j.biocon.2010.07.022

Slimani, N., Wood, P. J., Guilbert, E., Boumaiza, M., & Sánchez-Fernández, D. (2022). Using biodiversity indicators to identify priority areas for freshwater conservation in the African "Mediterranean Basin" biodiversity hotspot. *Biological Conservation*, *276*, 109783. https://doi.org/10.1016/j.biocon.2022.109783

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, *63*, 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Tachet, H., Richoux, P. H., Bournaud, M., & Usseglio-Polatera, P. (2002). *Invertébrés d'Eau Douce (2nd corrected impression)* (p. 588). CNRS éditions.

Tierno de Figueroa, J. M., López-Rodríguez, M. J., Fenoglio, S., Sánchez-Castillo, P., & Fochetti, R. (2013). Freshwater biodiversity in the rivers of the Mediterranean Basin. *Hydrobiologia*, *719*(1), 137–186. https://doi.org/10.1007/s10750-012-1281-z

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, *98*(5), 1201–1216. https://doi.org/10.1002/ecy.1761

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, *7*(1), 9132. https://doi.org/10.1038/s41598-017-09084-6

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, *65*, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E., & Willis, K. J. (2005). Conservation biogeography: Assessment and prospect. *Diversity and Distributions*, *11*(1), 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. https://CRAN.R-project.org/package=ggplot2

WWF. (2020). *Living planet report 2020. Bending the curve of biodiversity loss: A deep dive into the living planet index*. Marconi, V., McRae, L., Deinet, S., Ledger, S. & Freeman, F. in Almond, R.E.A, Grooten M. & Petersen, T. (Eds). WWF.

BIOSKETCH

The authors have a wide-ranging interest in freshwater ecosystems, macroecology and biogeography.

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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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