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The world's biogeographical regions revisited: global patterns of endemism in Tipulidae (Diptera)

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Abstract

This paper explores the distributional data of 4,224 Tipulidae (Insecta: Diptera) species to search for endemism patterns in a worldwide scale and to test the extent to which the global patterns of endemism of the group fit into previously proposed regionalization schemes, particularly Wallace's system and recent revisions of it. Large scale areas of endemism are assessed using the grid-based method implemented in VNDM. VNDM depends on the prior definition of the grid size for analysis, but a criterion for choosing beforehand a particular grid size is not clear. The same holds for the choice of the level of similarity in species composition selected for the calculation of consensus areas. In our study, we developed a methodological approach that helped defining objective criteria for choosing suitable values for these critical variables. Large-scale areas of endemism around the globe are identified and ranked according to endemicity levels: 1—West Palaearctic, 2—Nearctic, 3—East Palaearctic-Oriental, 4—West North America, 5—Australia, 6—Neotropical, 7—Sub-Saharan Africa, 8—Palaearctic, and 9—Middle East. Our main conclusion is that there are still some limitations in applying biogeographical classifications proposed mostly on the basis of vertebrate distribution to other taxonomic groups, such as the Tipulidae. While there is a general congruence of the broad-scale areas of endemism of tipulids with previously proposed regionalization schemes, for some areas, the sharpness of boundaries between traditional regions is not so acute, due to a great level of overlap of part of its biotic elements.

Key words: Areas of endemism, biogeography, VNDM, Tipulidae

Introduction

"*An important problem in Natural History, and one that has hitherto been too little agitated, is that of ascertaining the most natural primary divisions of the earth's surface, taking the amount of similarity or dissimilarity of organized life solely as our guide.*" Philip L. Sclater (1858, p. 130).

More than 150 years had passed since Sclater's early statement. Nowadays, there are numerous studies dealing with biogeographical regionalization, based on zoological and botanical evidences. Even before Sclater's attempt, authors such as Buffon and de Candolle proposed worldwide systems of biogeographical regions (Nelson 1978), but it was only with Wallace's (1876) work that a stable scheme of names for the regions was established and accepted by biogeographers ever since.

The regions recognized by Wallace were Neotropical (South America and Central America as far north as central Mexico), Ethiopian (Africa south of the Tropic of Cancer), Australian (including New Zealand, New Guinea and adjacent islands), Oriental (tropical Asia), Palaearctic (temperate Eurasia), and Nearctic (North America south to central Mexico). He also divided each of the six global regions into four distinct subregions.

In the last two decades, Wallace's scheme has been refined including analytical approaches such as cladistic

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biogeography and panbiogeography (Morrone 2002), clustering procedures and multivariate techniques (e.g., Conran 1995; Proches & Marshall 2001; Proches 2005; Kreft & Jetz 2010; Proches & Ramdhani 2012), and integration of data on global distributions and phylogenetic relationships among taxa (Holt *et al.* 2013).

Following 25 years of cladistic and panbiogeographical studies, Morrone (2002) discussed how some of the traditional phyto- and zoogeographical systems do not actually represent natural unities. In fact, they are often composites of different ages, in the same sense as discussed by Amorim *et al.* (2009). This is the case of South America, recognized by Crisci *et al.* (1991) as a composite area, with its southern portion more closely related to other Austral temperate areas (Australia, Tasmania, New Zealand, New Guinea and New Caledonia), and its northern portion more closely related to Africa. The same is valid for Africa, with a southern temperate element and a northern tropical one. Holt *et al.* (2013) found that the Palaearctic region as traditionally defined lacks support, with the regions of central and eastern Siberia being phylogenetically more similar to the Arctic parts of the Nearctic region.

The biogeographical system proposed by Morrone (2002) divides the world into three kingdoms: (1) Holarctic (Laurasia), constituted by Nearctic and Palaearctic regions; (2) Holotropical (eastern Gondwana, including the northwestern portion of Australia), comprising Neotropical, Afrotropical, Oriental and Australotropical regions; and (3) Austral (western Gondwana), composed by Andean, Antarctic, Afrotemperate, Neoguinean and Australotemperate regions.

Using clustering methods, Proches & Ramdhani (2012) searched for global zoogeographic patterns for the herpetofauna, birds and mammals, and defined 14 zoogeographical regions plus 6 subregions that were largely equivalent to regions or subregions previously recognized by other regionalization studies: Arctic, Nearctic, Caribbean, Neotropical (including Central American and La Plata subregions), Andean, Palearctic (including Sahero-Arabian and Sino-Himalayan subregions), Afrotropical (including Congolian subregion), Madagascan, Indo-Malasyian, Wallacean, New Guinean, Australian, Polynesian (including New Zealand subregion), and Antarctic.

Holt *et al.* (2013) combined data on the distributions and phylogenetic relationships of 21,037 species of amphibians, birds, and mammals, and identify 20 distinct zoogeographical regions which are grouped into 11 realms: Nearctic, Palaearctic, Neotropical, Australian, Oriental, Afrotropical, Panamanian, Saharo-Arabian, Sino-Japanese, Madagascan and Oceanian.

In the present paper, we explore the distributional data of over 4,000 Tipulidae (Insecta: Diptera) species to search for endemism patterns in a worldwide scale. For the first time, the limits of previously established biogeographical regions are tested using the grid-based method implemented in VNDM (Szumik *et al.* 2002; Szumik & Goloboff, 2004). Large-scale areas of endemism around the globe are identified and ranked according to endemicity levels.

Since a single group of organism is being considered, it is beyond the scope of this paper to propose any new classificatory scheme for the major biogeographical areas of the world. Instead, our objectives are twofold: first, to make a preliminary investigation of the global distributional patterns of Tipulidae; and second, to test the extent to which the global patterns of endemism of this group of insects fit into previously proposed regionalization schemes, particularly Wallace's (1876) system and its recent revisions.

Study group. Tipulidae *sensu stricto* is one of the four families within the suborder Tipulomopha (*sensu* Amorim & Yeates 2006). The monophyly of the group has been supported by phylogenetic studies with both morphological and molecular data (Oosterbroek & Theowald 1991; Starý 1992; Ribeiro 2008; Petersen *et al.* 2010). About 4,000 described species are included in the family, which is worldwide distributed (Oosterbroek 2014). Compared with the other crane fly families (Limoniidae, Pediciidae and Cylindrotomidae), the group has been better explored from both phylogenetic and biogeographical perspectives (Oosterbroek 1980; Tangelder 1985, 1988; Theowald 1984; De Jong 1989, 1993, 1994a, 1994b, 1995a, 1995b, 1998; Gelhaus 2005).

Tipulids are an interesting group for testing biogeographical hypotheses. It is worldwide distributed and the relatively large number of described species in every biogeographical region allows assessment of patterns in both local and global scales. Crane fly species display high levels of endemism (De Jong *et al.* 2008). Oosterbroek (1994) estimated the levels of endemism of the group in the Mediterranean region and showed that species of the family Tipulidae have higher levels of endemism than other groups such as lacewings, butterflies, and vertebrates. Based on the distribution of 123 species and subspecies of several Tipulidae genera, De Jong (1998) identified 74 endemic species and subspecies distributed over 13 areas of endemism in the Mediterranean. In a more global scale, Ribeiro & Eterovic (2011) demonstrated high levels of endemism of crane flies species also in the southern hemisphere, and draw attention to the great potential of the group for testing alternative hypothesis with respect to Pacific biogeography.

Methods

Species distribution data. Distributional data for 4,224 Tipulidae species were retrieved from the Catalogue of Craneflies of the World (Oosterbroek 2014; CCW). This is an authoritative and regularly updated online database covering over 17,000 genus-group and species-group taxa of the four families of crane flies (Pediciidae, Limoniidae, Cylindrotomidae and Tipulidae).

In CCW, the information about species distribution is provided, as in most other catalogues and databases, for geo-political areas. The level of geographical detail provided by CCW for each species varies: for some areas, species distributions are given by country only, as is the case of Europe, Africa and South America, but for many others (China, Australia, U.S.A., India, Malaysia, Russia, Japan, among others) the details extend to states, provinces, and other territories such as islands.

The first step of data compilation was the listing of all valid Tipulidae species included in CCW. For each species, we tabulated all distributional records as provided in CCW. Although the data is presented in the form of geo-political units, we used the most refined information available for each country (i.e., states, provinces, islands and territories, depending on the case). To translate the geo-political distributional database into a georeferenced database, the geographical coordinates of the approximate geographic center of each individual geo-political unit were extracted from the USGS Earth Explorer web site (http://earthexplorer.usgs.gov/).

The georeferenced species distribution database is available as a *.xyd file in Appendix S1 (Supporting Information Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.7v8fq). The file contains all the distributional records in geographical coordinates of the over 4,000 included species, and can be directly opened for analysis in VNDM or edited in any text editor.

An objection may be raised regarding the use of the geographic center of artificial geo-political unities such as countries, states and provinces in a study of patterns of endemism. The weight of this objection is highly dependent on the scale and purposes of the study. In the particular case of this study, the following caveats are promptly recognized:

1. Because the geographical details of the database we use vary considerably in different continents, our analysis is biased towards a greater refinement in parts of the Northern Hemisphere, where countries are small (Europe) and data is available at the level of states and provinces (e.g., North America) or islands (e.g., Greece, Philippines). For somsummarized in Table 2e continental areas in the Southern Hemisphere, particularly in Africa and South America, data is available at the level of countries only. This heterogeneity in the database means that more details will be recovered within the areas in the North, but with respect to our major purpose to understand endemicity patterns at a continental scale, this do not invalidate the interpretation of the patterns recovered for the areas in the South. Also, the level of overlap in the fauna of different continents is still possible to evaluate.

2. The "real" distributions records of all species in each geopolitical unit are collapsed into a single coordinate point. This limitation is more or less severe depending on the scale being considered. In our analysis, this effect will be more dramatic for the Southern Hemisphere, particularly in Africa and South America, where data is available at the level of countries only and the countries are large. This problem obviously limits the kinds of comparisons that can be made between the Northern and Southern Hemispheres, but for the specific purposes of this study, which focus on finding large scale areas of endemism, this may have little impact to the outcome of the analysis. The alternative for this would be listing as point coordinate data the known distributional records of all the over 4,000 Tipulidae species. This task would require an enormous amount of time, and considering our purposes, the utility of such effort is clearly questionable. First, the taxonomic literature of most crane fly species does not contain georrefered information on the precise location from where the specimens were collected. Even though the localities are listed in the publications (let's say, Germany: Hamburg), retrieving coordinate points would have to be done *a posteriori* (in this case, the available information would be of the center of the city of Hamburg, which does not necessarily correspond to the precise point of collection of the specimen). Again, it is obviously a matter of scale, and even at its finest resolution, point data are still linked to a geopolitical unit (a city).

Inferring areas of endemism: analysis with VNDM. Szumik *et al.* (2002) and Szumik & Goloboff (2004) proposed a non-hierarchical numerical method for delimitating areas of endemism, referred to simply as VNDM (the meaning of this acronym is not explained by the authors of the method).

VNDM focuses on using an optimality criterion explicitly developed for evaluating candidate areas of endemism, in order to circumvent problems from the application of optimality criteria derived from phylogenetic analyses algorithms (such as in Parcimony Analysis of Endemicity—PAE). For instance, the areas of endemism found by VNDM are unequivocally defined by exclusive species (Nori *et al.* 2011), whereas PAE often gives spurious areas of endemism (i.e., areas not supported by exclusive species), especially for complex or large databases.

When searching for areas of endemism, VNDM attributes score values to the searched areas, which stand for their level of endemicity. Areas with higher endemicity levels receive higher scores than poorly endemic areas. After all, areas of endemism are scientific hypotheses: in practice, the higher the score received by a certain area, the stronger is the evidence for the reality of such area. The program then saves sets of areas with scores equal or above a given threshold, defined by the user. As default, VNDM will save sets of areas of endemism with score above 2. We adopted a higher threshold (8). Thus, using this relatively higher value, we saved sets of areas that are better corroborated by the data in comparison with a lower threshold value. Geographical information of the areas obtained in VNDM was exported as *.acf file to be analyzed in the computer program *Global Mapper version 14*.

Critical Variables: Cartographic and Biogeographic Resolutions. As a grid-based method, VNDM depends on the prior definition of the grid size for analysis. We may refer to the grid size as the Cartographic Resolution of the study. The smaller the grid size, the finest the Cartographic Resolution. Thus, an important decision to be taken concerns the choosing of a particular grid size or grid size interval before analysis. An approach that has been proposed in the context of VNDM analysis is the use of different grid sizes, and to evaluate the areas of endemism provided by the different analyses (e.g. Aagesen *et al.* 2009; Casagranda *et al.* 2009). According to Aagesen *et al.* (2009), areas of endemism recovered under different grids may be considered as robust hypotheses of endemism, whereas those not recovered could be a simple artifact of a particular grid size. Casagranda *et al.* (2009) also noted that smaller grids helped the identification of disjunct areas of endemism, whereas relatively larger grids were convenient for the identification of broad areas that appeared fragmented under smaller grids. The definition of a particular grid size interval to be tested is less critical in regional scale studies (e.g., Casagranda *et al.* 2009; Aagesen *et al.* 2009; Nori *et al.* 2011), where the use of small square grids (e.g., 0.5°, 1°, 2°) are natural choices. In our particular case, defining beforehand a meaningful grid size or grid size interval is more difficult. Some preliminary exploration of different grids has shown that the results can vary significantly and from the perspective of a broad-scale study, some results are more meaningful than others.

As expected for an analysis with a massive amount of geographical records and included areas, hundreds of areas of endemism around the globe were found (details in Results and Discussion, below). Our main interest is to investigate endemism patterns in a broad, global scale. To achieve this, we had to summarize the results using consensus areas.

Two different consensus rules are implemented in VNDM. The first is the "strict" consensus rule (option "*against each of the other areas in the consensus*"). Under this rule, an individual area will make part of the consensus as long as it shares a given percentage of endemic species (we here refer to this percentage as the consensus cut-off value, which must be defined by the user) with all the areas that make up this consensus. The second consensus rule of VNDM is the option "*against any of the other areas in the consensus*". This is the "flexible" or "relaxed" consensus rule. Under this rule, an individual area will make part of the consensus as long as it shares the chosen percentage of endemic species (the consensus cut-off value mentioned above) with any of the other areas in the consensus. The "strict" rule generates more consensus areas from the primary set of areas than the "flexible" rule, because under the first, fewer areas from the primary set will be part of the consensus area.

A detailed explanation of the rationale and applications of each of these two consensus rules is provided by Aagesen *et al.* (2013). In short, the "strict" rule is useful for finding well defined areas of endemism, and is more suitable for regional scale studies. The "flexible" rule may be applied for the identification of diffuse and gradually replacing or overlapping patterns, and may be suitable for broad scale studies.

For the calculation of consensus areas, using more restrictive cut-off values (e.g., more than 80% of species similarity) will generate consensus areas which are almost the same and as numerous as the original set of areas (100% cut-off value will provide the same areas of the original set). For an analysis yielding hundreds of areas of endemism, this situation provides practical difficulties for summarizing the results. On the other hand, lower cut-off values (e.g., less than 10%) will summarize results with much fewer areas, made of the agglomeration of more areas from the primary set. The smaller the cut-off value, the fewer the number of consensus areas obtained. In this case, there will be a trade-off: if too many areas are merged together, a great extent of biogeographical information is simply lost, since our ability to identify areas of endemism is "blurred" by too inclusive consensus areas.

We may refer to the level of inclusiveness of the consensus areas used to summarize the results as the Biogeographic Resolution of the study: the higher the level of inclusiveness, the lower the Biogeographic Resolution. As a general rule, we wanted our results to be expressed with the minimum possible number of consensus areas, and so we choose the "flexible" consensus rule. We also wanted our consensus areas to be biogeographically informative at the global level, i.e., to maintain some degree of Biogeographic Resolution.

To summarize what was explained above in this section, we had to face with the following problems:

1. Finding a meaningful overall Cartographic Resolution (grid size) suitable for a global scale analysis.
2. Finding a meaningful Biogeographic Resolution (level of inclusiveness of consensus areas). Here, there is a trade-off: maximizing Biogeographic Resolution, (which means using a large and more restrictive consensus cut-off value) yields too many areas to be inspected, causing difficulties for summarizing the results. On the other hand, in using a low cut-off value, interesting biogeographical details can be lost.

Given the difficulties concerning choosing beforehand suitable values for grid size (Cartographic Resolution) and the level of inclusiveness of the consensus areas (Biogeographic Resolution, defined by the consensus cut-off value), we have defined an optimization approach considering the results of an extensive exploration of the data (i.e., evaluation of a large number of distinct values for grid sizes and consensus cut-off). Since the number of consensus areas has immediate practical implications for evaluating and summarizing the results, we concentrate our effort on the analysis of the number of areas generated by each combination of these two parameters. The steps we have performed were:

1. We defined square grid sizes from 4° to 20°, with steps of 2°;
2. For each grid size, we estimated the number of consensus areas provided by cut-off values from 10% to 100%, with steps of 5%;
3. To compare the number of consensus areas from different grid sizes for a given cut-off value, we used relative values, obtained for each grid size dividing the number of areas for each cut-off by the maximum number of areas (for 100% of cut-off). For each grid size, the number of consensus areas increases with increasing cut-off values (Fig. 1). This increase follows an exponential growth, thus we fitted the data using an exponential function (Table 1).

TABLE 1. Parameters of the exponential function (y = a*exp(b*x)) and respective measure of fit (r^2) for the relationship among relative number of consensus areas and increasing cut-off (19 levels from 10% to 100%), in each grid size.

Grid size (degrees)	a	b	r^2
4	0.08230	0.02460	0.98612
6	0.06348	0.02736	0.99361
8	0.02515	0.03659	0.98845
10	0.02217	0.03624	0.96263
12	0.01627	0.04133	0.99565
14	0.01887	0.03999	0.98282
16	0.01125	0.04641	0.94923
18	0.01733	0.04076	0.97925
20	0.01455	0.04220	0.99065

4. From the exponential fit we used the exponential growth rate (column "b" on Table 1) to evaluate the relationship between the grid size and the number of consensus areas. Note that, although the relative number of areas seems to be approximately the same for each grid size as shown on Fig. 1, there are differences on the exponential growth rate for each grid, revealing that the grid size do interfere on the number of areas. Plotting these exponential growth rates *versus* the values of grid size (Fig. 2), we can visualize these differences. It is also clear that the differences in the exponential growth rate in the number of areas vanish after a certain value of grid size. In addition, this plot shows that the curve has an S-shaped form, giving us the opportunity to analyze the curve using an optimization approach to find the specific value of grid size after which the differences in the exponential growth rate of the number of areas disappear.

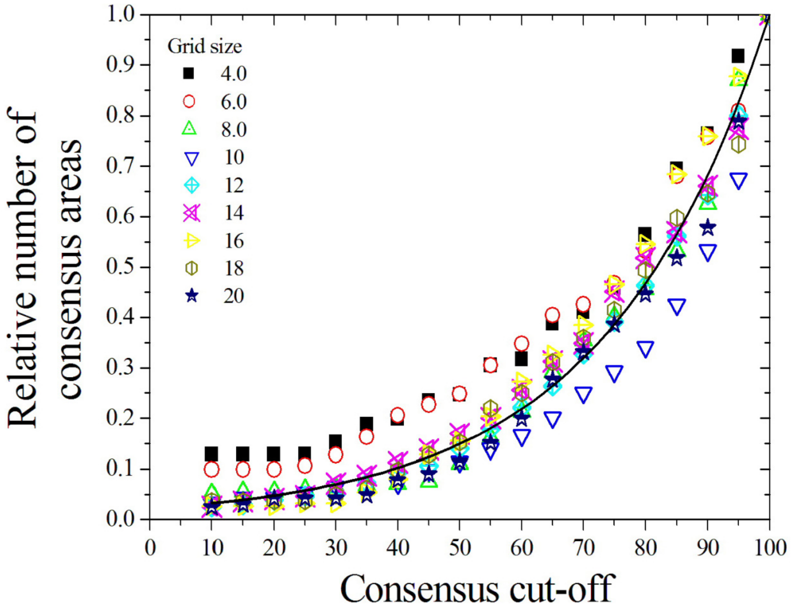

FIGURE 1. Relationship among relative number of consensus areas (based in the number obtained with maximum cut-off) and increasing consensus cut-off values (19 levels from 10% to 100%), in each grid size (4 to 20, in degrees). Also shown is the curve fitted for a grid size of 14° (14) data (see Table 1 for parameters).

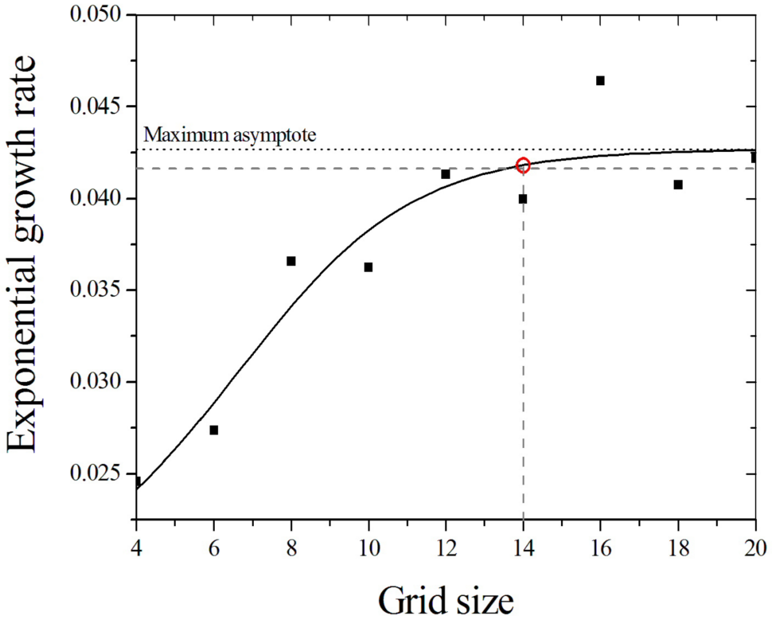

FIGURE 2. Sigmoid function adjusted to the relationship of the slope exponents of curves in Fig. 1 against their respective grid size (y = b+(a-b)/{1+exp[(x-c)/d]}; a = 0.01848, b = 0.0427, c = 6.6460, d = 2.418, r^2 = 0.9101). The saturation point of such logistic curve was defined as an integer grid size whose value corresponds to less than 3% of the upper asymptote for the slope exponent.

5. The optimization approach gives us the maximum value for the grid size where the exponential growth rate is closest to the maximum asymptote (the asymptote tells us that the differences due to grid size vanish after a certain point). This approach is useful, since we can find the smallest value for the grid size (i.e., the maximum Cartographic Resolution) corresponding to the saturation point of the variation of the exponential growth rates in the number of areas. Due to the S-shaped form, we looked for a sigmoid function to fit the curve. The best function should directly give us the maximum asymptote. Therefore, we chose the function given by the equation $\mathbf{y = b+(a-b)/\{1+exp[(x-c)/d]\}}$, with fit parameters: a = 0.01848, b = 0.0427, c = 6.6460, d = 2.418, and measure of the fit $r^2 = 0.9101$, see Fig. 2. Thus, the maximum asymptote is the exponential growth rate equals to 0.0427.

6. To find the optimal grid size (namely, the grid size value corresponding to the saturation point of the variation of the exponential growth rate in the number of areas), we set that the saturation on the exponential growth rate occurs at 97% of the asymptote (or 3% smaller than the asymptote). For this exponential growth rate, we choose the corresponding integer grid size.

Inspection of the areas resulting from the small values of grid size has shown that, for a given consensus cut-off value, the biogeographical information are more variable than the areas yielded by grids above the optimal grid size. In other words, consensus areas provided by small grids are more dissimilar among themselves than those obtained by grids close to the optimal grid size, which are very similar with respect to their biogeographical information. The optimal grid size thus corresponds to the minimum grid size within this area of stability in the area exponential growth rate, and because the Cartographic Resolution will decrease with the increase of the grid size, this is the point of maximum Cartographic Resolution within this area of stability. Also, it corresponds to a grid size that is neither too small nor too large as to preserve some degree of Cartographic Resolution. The optimal grid size we found corresponds to a grid size of 14°. Such a grid size may be seen as rather rough but, as stressed by Proches (2005), when testing for the world's biogeographical regions, large quadrants are appropriate. In his study of the global biogeographical patterns of bats, Proches (2005) defined a grid size of 15°;

7. After the choice of the optimal grid size, we evaluated the relationship between relative number of consensus areas *versus* consensus cut-off value to define the best cut-off value to be used (Fig. 1; Table 1). Figure 1 shows that there is a region below a certain cut-off value where the variation on the number of areas is small. We chose this particular value of cut-off to perform our biogeographic analysis. This value was obtained considering the cut-off value where the relative number of areas increases at most 3% from its minimum value. This corresponds to the cut-off value of 24%. We considered that, from this level on, a little increase in the cut-off results in an undesirable effect of a much larger increasing in the number of consensus areas. This cut-off value may be seen as too relaxed. However, when testing for the world's biogeographical regions, having broad consensus areas that can be compared with the vast land surfaces of the world's biogeographical divisions would be desirable;

8. With both grid size (14º) and cut-off value (24%) defined, we evaluate the geographical pattern of the nine consensus areas that emerged from such adopted parameters.

Results and discussion

Broad-scale areas of endemism for Tipulidae. Analysis of the distribution records of the over 4,000 Tipulidae species in VNDM with the parameters defined above yielded 195 areas of endemism around the globe, which are summarized in 9 consensus areas: six areas in the Northern Hemisphere and three areas in the Southern Hemisphere. We identify these nine areas as follows:

Area 1: West Palaearctic (Fig. 3a).
Area 2: East Palaearctic-Oriental (Fig. 3b).
Area 3: Palaearctic (Fig. 3c).
Area 4: Nearctic (Fig. 4a).
Area 5: West North America (Fig. 4b).
Area 6: Middle East (Fig. 4c).
Area 7: Neotropical (Fig. 4c).
Area 8: Sub-Saharan Africa (Fig. 4c).

Area 9: Australia (Fig. 4c).
The quantitative aspects of these areas are summarized in Table 2.

TABLE 2. Summary of the numerical aspects of VNDM analysis. Areas are ranked according to level of endemicity (score).

Consensus Area	Number of areas included	Score range	Rank position
Area 1 (West Palaeartic)	57	11.84–89.72	1
Area 2 (East Palaeartic-Oriental)	61	9.15–72.55	3
Area 3 (Palaeartic)	5	8.08–12.07	8
Area 4 (Nearctic)	48	8.32–80.59	2
Area 5 (West North America)	4	42.66–65.20	4
Area 6 (Middle East)	1	10.00–10.25	9
Area 7 (Neotropical)	11	8.35–23.82	6
Area 8 (Sub-Saharan Africa)	9	14.32–17.93	7
Area 9 (Australia)	4	24.25–42.16	5

In the Northern Hemisphere, an entire Holarctic element is not recovered, and in both North America and Eurasia, more than one pattern of endemism was found.

In Eurasia, an intricate set of patterns appear in which the recovered areas are largely complementary to each other, with allopatric cores. West Palaearctic (Area 1) and East Palaearctic-Oriental (Area 2) centers of endemism are clearly defined. Even though there is a great overlap between these two areas, the study has shown that endemicity levels reduce progressively eastwards (West Palaearctic) or westwards (East Palaearctic-Oriental) from the core of each of these two main areas. A third pattern within Eurasia is interesting in the sense that endemicity levels are almost constant. This pattern (Area 3), which spans across the entire Palaearctic (and thus is named here as Palaearctic), also demonstrates a bimodal east-west disjunction. Finally, a smaller area centered on the Caspian Sea (Middle East, Area 6) is also recovered as an important center of endemism, even though with lower endemicity levels as compared with the previous mentioned areas. Interesting to note is the complementary relationship between this smaller area and the Palaearctic (Area 3).

In North America, one of the areas (Area 4) includes virtually the entire North American Continent below the Arctic Circle. We named this area Nearctic due to its relative correspondence with the Nearctic Region, even though it extends southwards considerably more than the traditional Nearctic Region, reaching the Caribbean region, where it overlaps with the Neotropical area (Area 7). In this zone of overlap, endemicity levels are reduced in comparison with each of the main North and South centers of endemism. In North America, a second, smaller area is also detected, involving mostly the western part of the continent (West North America, Area 5). Considering that Area 4 has higher levels of endemicity on its eastern margin and that Area 5 also displays high levels of endemicity, our results show a bimodal west-east disjunction pattern within the North American Continent. In the Southern Hemisphere, three major centers of endemism were found, with no overlap between them: Neotropical (Area 7), Sub-Saharan Africa (Area 8) and Australia (Area 9). In the Neotropical area, an interesting pattern is found where endemism levels increase southwards.

According to their endemicity level (score), the recovered areas are ranked as follows: 1—West Palaearctic, 2—Nearctic, 3—East Palaearctic-Oriental, 4—West North America, 5—Australia, 6—Neotropical, 7—Sub-Saharan Africa, 8—Palaearctic, and 9—Middle East.

A comparison with Wallace's biogeographical regions. In this study, we used a non-hierarchical method to search for broad-scale areas of endemism. Information about the phylogenetic relationships among taxa was not included, and the non-hierarchical nature of the method used precludes establishing any kind of hierarchical relationships among the recovered areas. Such aspects of our study must be taken into account in any attempt to compare our results with previously established regionalization schemes, which often use information about phylogenetic relationships of the studied taxa (e.g., Morrone, 2002; Holt et al., 2013) and use hierarchical methods to search for hierarchical relationships among areas (e.g., Kreft & Jetz, 2010; Proches & Ramdhani , 2012).Instead of providing a comprehensive comparison of our results with all previously proposed regionalization schemes, we focus our comparison with Wallace's (1876) system, and the recent revisions of his regions (Kreft & Jetz, 2010; Holt et al., 2013).

Nearctic Region. Wallace's Nearctic region includes the North American Arctic, and extends southwards up to Central Mexico. Proches & Ramdhani (2012) distinguished the Arctic as a distinct region. Holt et al. (2013) found that the North American Arctic is phylogenetically more similar to Siberia, and included these areas in their Palaearctic realm.

Even though several Tipulidae species do occur in the Arctic regions of North America and Greenland (Alexander 1919, 1924), our study did not recovered this part of the North American continent as an area of endemism, and it is not included in any of the consensus areas we recovered for North America (Area 4, Fig. 4a and Area 5, Fig. 4b). Differently from Wallace's original Nearctic region, and from the Nearctic region as defined by Proches & Ramdhani (2012), our Nearctic area (Area 4, Fig. 4a) extends southward considerably beyond Mexico to include the entire Central America.

Palaearctic Region. Our West Palaearctic area (Area 1, Fig. 3a) agrees with Wallace's Palaearctic region, including Northwestern Africa and the north of the Arabian Peninsula. We name this area West Palaearctic mainly because of its Western core with higher endemicity levels, but the area extends eastwards. The Palearctic region of Proches & Ramdhani (2012) includes a Sino-Himalayan subregion that does not make part of our Palaearctic region, but is included in our East Palaearctic-Oriental region. Holt *et al.* (2013) placed north of Africa and the Arabian Peninsula into a separate area, the Saharo-Arabian realm, which is not recovered as an area of endemism for Tipulidae.

Oriental Region. A major discrepancy between the areas of endemism found for Tipulidae with Wallace's regions concerns the Oriental region, which is not recovered as an area of endemism for the group, and appears instead merged with the eastern parts of Eurasia in the East Palaearctic-Oriental area (Area 2, Fig. 3b). Wallace's Oriental region is also not recovered in the study of Proches & Ramdhani (2012). This contrasts with the recent revision of Wallace's regions by Holt *et al.* (2013), which found support for an Oriental realm much similar with Wallace's original scheme.

Ethiopian (*Afrotropical*) *Region.* Wallace's Ethiopian or Afrotropical region includes the African continent south to the Tropic of Cancer, and thus includes a great part of the Sahara desert. Kreft & Jetz (2010) argued that, based on the distribution of mammals, the boundary between the Afrotropical and the Palaearctic region should be positioned much further north. However, our Area 8 (Fig. 4c) is more limited to include mostly the sub-Saharan African continent, which is somehow expected considering the biology of most Tipulidae species, which are found mostly in forested areas and cannot tolerate arid conditions. Our Sub-Saharan Africa area is also more limited southwards compared with the Afrotropical region of Proches & Ramdhani (2012) and the Afrotropical realm of Holt *et al.* (2013).

Neotropical Region. Wallace's Neotropical Region includes South America and Central America as far north as central Mexico. Proches & Ramdhani (2012) also included Central America as a subregion of their Neotropical region. Our Neotropical area of endemism for Tipulidae is more restricted. It does not reach Mexico and its northern limit is placed in the Caribbean. Mexico is mostly included in the Nearctic realm by Holt *et al.* (2013) and the Caribbean is separated from both the Nearctic and the Neotropical realms, forming the Panamanian realm. The Panamanian realm of Holt et al. (2013) is included in our Neotropical area.

Australian Region. Wallace's Australian Region includes Australia, New Zealand, New Guinea and some adjacent islands, and the Pacific Islands. As in Proches & Ramdhani (2012), our Australia area of endemism (Area 9, Fig. 4c) includes only Australia (for reasons explained in the next section of this paper, New Zealand and New Caledonia were not recovered as areas of endemism nor included in any consensus area). Proches & Ramdhani (2012) considered New Zealand as a subregion of the Polynesian Region, and New Guinea is considered as a separated region. Holt *et al.* (2013) included New Guinea and the Pacific islands into their Oceanian realm, with the Australian realm restricted to Australia and New Zealand. In our analysis, the status of New Guinea is unclear as it does not appear in any consensus area (but see next section about missing areas).

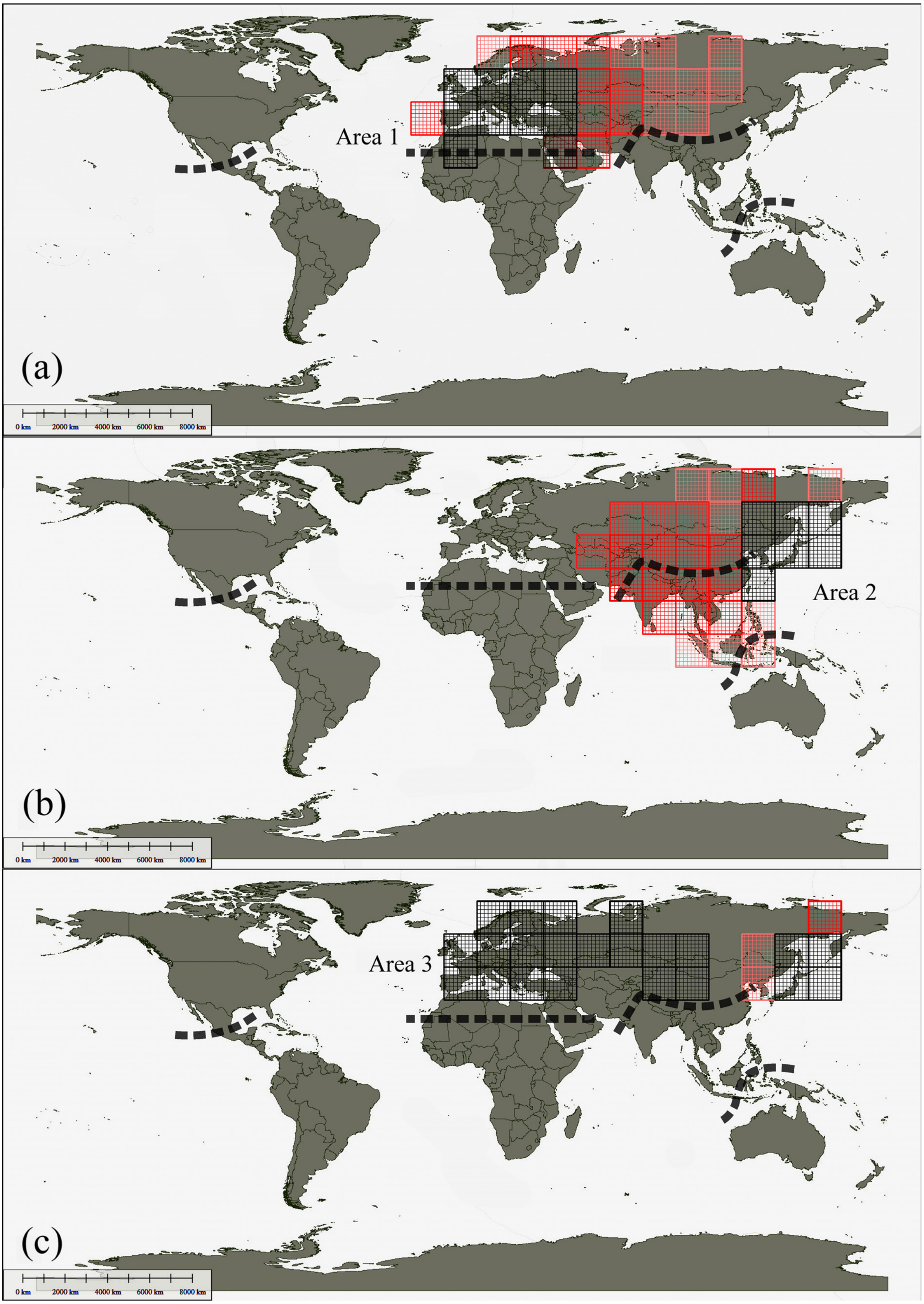

FIGURE 3. Global areas of endemism in Tipulidae. (a) Area 1 (West Palaearctic). (b) Area 2 (East Palaearctic-Oriental). (c) Area 3 (Palaearctic). Increasing endemicity levels (score) are indicated by progressively darker colors. The limits between traditional Wallace's regions are indicated by dashed lines.

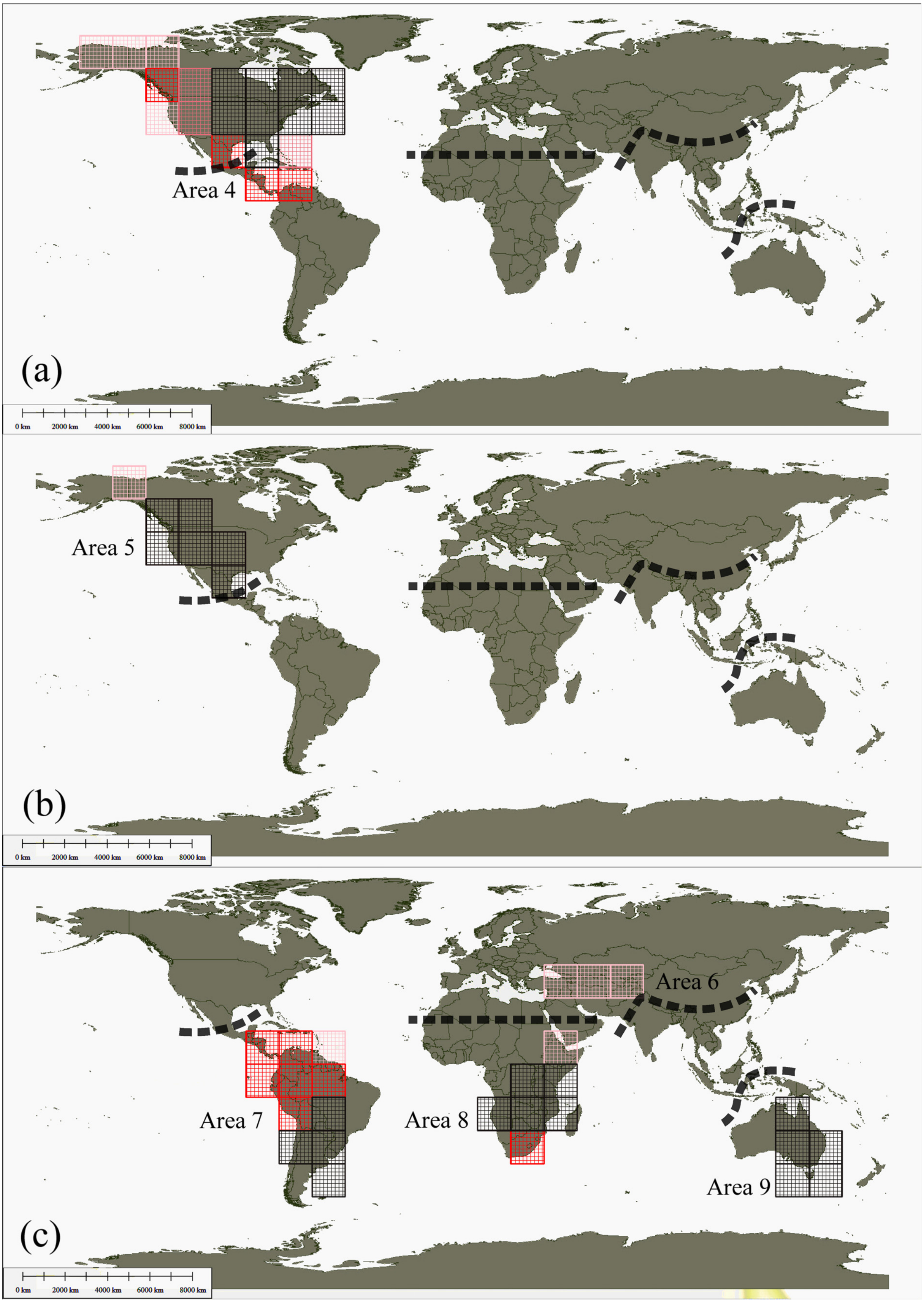

FIGURE 4. Global areas of endemism in Tipulidae. (a) Area 4 (Nearctic). (b) Area 5 (West North America). (c) Area 6 (Middle East), Area 7 (Neotropical), Area 8 (Sub-Saharan Africa), and Area 9 (Australia). Increasing endemicity levels (score) are indicated by progressively darker colors. The limits between traditional Wallace's regions are indicated by dashed lines.

Missing areas. As stated before, VNDM attributes score values to the searched areas, which stand for their level of endemicity. The program then saves sets of areas with scores equal or above a given threshold, defined by the user. We opted for a higher score (8) with the purpose of saving areas with higher endemicity levels, in other words, to keep only those areas which are relatively better corroborated by the data. Hence, the resulting consensus areas contain relatively less areas than they would if we had opted for saving sets of areas with lower score values. Also, some primary areas that could be recovered with lower scores are missing in the analysis with a higher score.

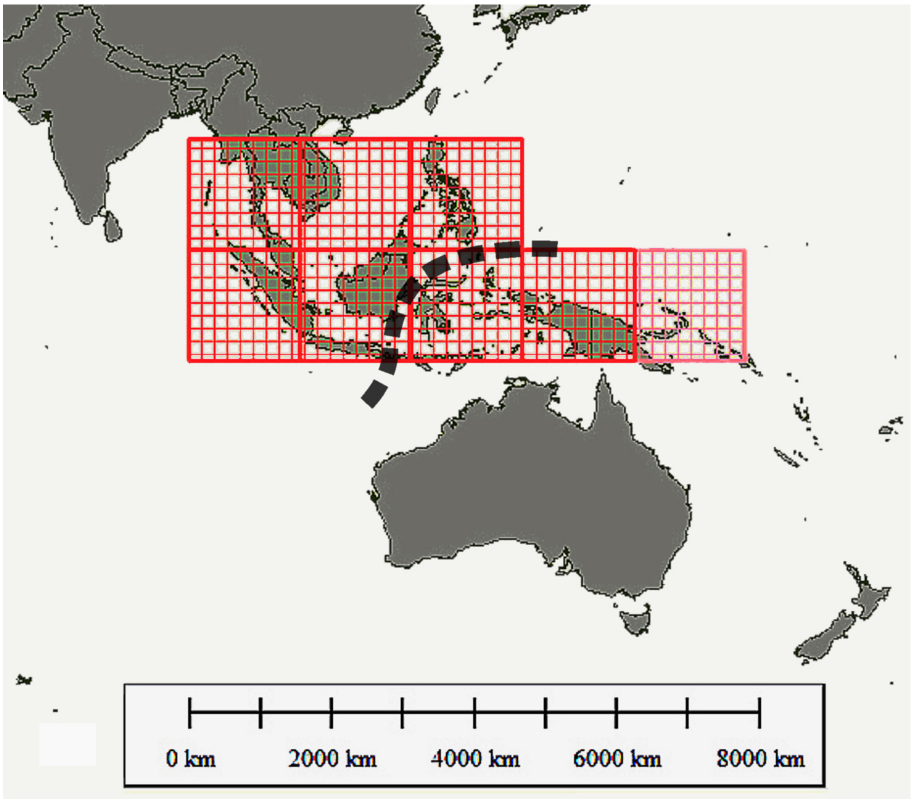

FIGURE 5. Area of endemism including New Guinea, the other islands of the Malay Archipelago and the Indochina Peninsula. This area is only recovered with analysis saving sets of areas with score above 1. The limits between traditional Wallace's regions are indicated by dashed lines.

To explore the effect of a lower score level on the consensus areas that resulted from the analysis with score 8, we performed another analysis with the same parameters, but reducing the score value to 1. A pictorial comparison of the analyses with the two different score values is provided in the comparative chart in Appendix S2. (Available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.7v8fq) . Since the areas recovered with score 1 did not change much in comparison with those found with score 8, we do not expect considerable changes using other intermediary values: if an area of endemism is not recovered with score 1, it will not be recovered under a higher and more restrictive value. The following aspects are noteworthy:

1. Some consensus areas did not change. That is the case of Area 6 (Middle East) and Area 9 (Australia);

2. Some consensus areas are recovered virtually unchanged compared with the original analysis, despite the fact that more primary areas were incorporated into the consensus area. Under this category are Area 4 (Nearctic), Area 2 (East Palaearctic-Oriental), Area 7 (Neotropical), and Area 5 (West North America);

3. Some consensus areas are extended. For instance, Area 1 (West Palaearctic) was extended considerably toward east to reach the eastern margin of Eurasia. However, the same pattern of a western center with levels of endemism progressively decreasing eastwards remains unchanged. Area 8 (Sub-Saharan Africa) was extended northwards to embrace the entire Sub-Saharan African continent, including Madagascar;

4. Area 3 (Palaearctic) is not recovered by the analysis with score 1;

5. With the higher score level, the status of New Guinea is unclear as it does not appear in any consensus area. When we save sets of areas of endemism with score above 1, an area of endemism including New Guinea, the other islands of the Malay Archipelago and the Indochina Peninsula is recovered (Fig. 5). This area overlaps with the

East Palaearctic-Oriental area (Fig. 3b), which also includes the Indochina Peninsula and great part of the Malay Archipelago, but it is a distinct area as it contains a distinct assemblage of exclusive endemic species. The fact that New Guinea does not appear as an area of endemism with a higher score value, but does appear with a lower one only means that this area is not so much corroborated by the data, and to be recovered, it is necessary to relax the endemicity score value used.

6. Some biogeographically important areas of the globe, such as New Zealand, New Caledonia, and other Pacific Islands do not appear in any consensus area, irrespective of the score value we use. Because some of these areas are clearly centers of endemism for Tipulidae, an explanation for their absence is worth mentioning.

New Zealand and New Caledonia are important areas of endemism for Tipulidae. All the 84 Tipulidae species so far described for New Zealand are exclusive of that continent. In New Caledonia, there are 14 Tipulidae species, which are also exclusive of that island. As stated before, VNDM will group cells of the grid according to shared endemic taxa. However, the whole New Zealand area is represented in the study by a single coordinate point that fits within a single grid cell. The same is true for New Caledonia. Due to this scale matter, and the fact that no species is shared between New Zealand, New Caledonia and any other region, these areas are neither recovered as areas of endemism nor appear in conjunction with other areas. However, VNDM does allow inspecting all the single cells with some endemic species, by clicking the command "Ctrl-1". As expected, both New Zealand and New Caledonia demonstrates to be centers of endemism for Tipulidae.

Ribeiro & Eterovic (2011) demonstrated that, at the generic level, crane fly fauna of New Zealand and New Caledonia is more closely related to that of other southern areas of the globe such as southern South America and Australia.

Exploring a smaller grid size: Northern versus Southern hemispheres. In our study, we searched for endemism patterns that could be compared with large scale regionalization schemes such as Wallace's biogeographical regions. With that aim in mind, we tried to define the best overall grid size suitable for analyzing our data and interpreting our results. However, since there is a discrepancy between the North and the Southern hemispheres with respect to the details of the distributional data, we expect a different response, in each of these main areas, to the use of a smaller grid size. To evaluate this, we performed an analysis reducing the grid size by 50% (i.e., using a square grid of 7°), but keeping the other already defined variables unchanged (endemicity score level = 8 and consensus cut-off value = 24%).

The analysis resulted in 184 areas of endemism around the globe, which are summarized in 19 consensus areas. There areas are shown in figures 6–8, where the areas are numbered following the original output numbering of the VNDM analysis (from 0 to 18). A detailed description of these results is beyond of the scope here, because they are not directly comparable with broad scale areas of endemism such as Wallace's regions.

In general, the consensus areas that resulted from the analysis with a grid of 7° are subsets of areas recovered with a grid of 14°. This is especially the case for the Northern Hemisphere, for which the distributional data is more detailed. For the Southern hemisphere, reducing the grid size by 50% yielded different results in different continents, depending on the level of detail of the distributional data. The following aspects are worth mentioning:

1. In North America, two partly overlapping consensus areas are recovered, corresponding to a western and an eastern center of endemism. The two areas combined are relatively smaller than the Nearctic area as recovered with a larger grid, and show no overlap with the Caribbean.

2. In Eurasia, 10 consensus areas were recovered in total. Four of such areas are subsets of the West Palaearctic area as recovered with a larger grid. The remaining six areas are subsets of the East Palaearctic area as recovered with a larger grid. In other words, the results with a smaller grid reinforce the Western-Eastern polarity as suggested by the analysis with a larger grid, as well the great overlap between the traditional Palaearctic and the Oriental regions.

3. In Australia, the distributional data is available at the level of provinces, and the results with a smaller grid correspond with what is found using a larger grid.

4. In the African continent, data is available at the level of countries only. For this continent, two partly overlapping consensus areas are found with a smaller grid. These two areas include countries of the southeastern part of the continent, and this result is not incongruent with the results obtained with a larger grid. The two consensus areas obtained are in fact subsets of the Sub-Saharan Africa as recovered using a grid of 14°.

5. Interestingly, an area of endemism including islands of the Malay Archipelago and the Indochina Peninsula, which is not recovered in isolation in our original analysis, is recovered with the analysis with a smaller grid.

Again, this more restricted area of endemism is in fact a subset of the larger East Palaearctic-Oriental area recovered in the analysis using a larger grid size.

6. For South America, in which the data is also available only at the level of countries, the results using a smaller grid size are more difficult to interpret, and probably does not provide any biogeographically meaningful pattern.

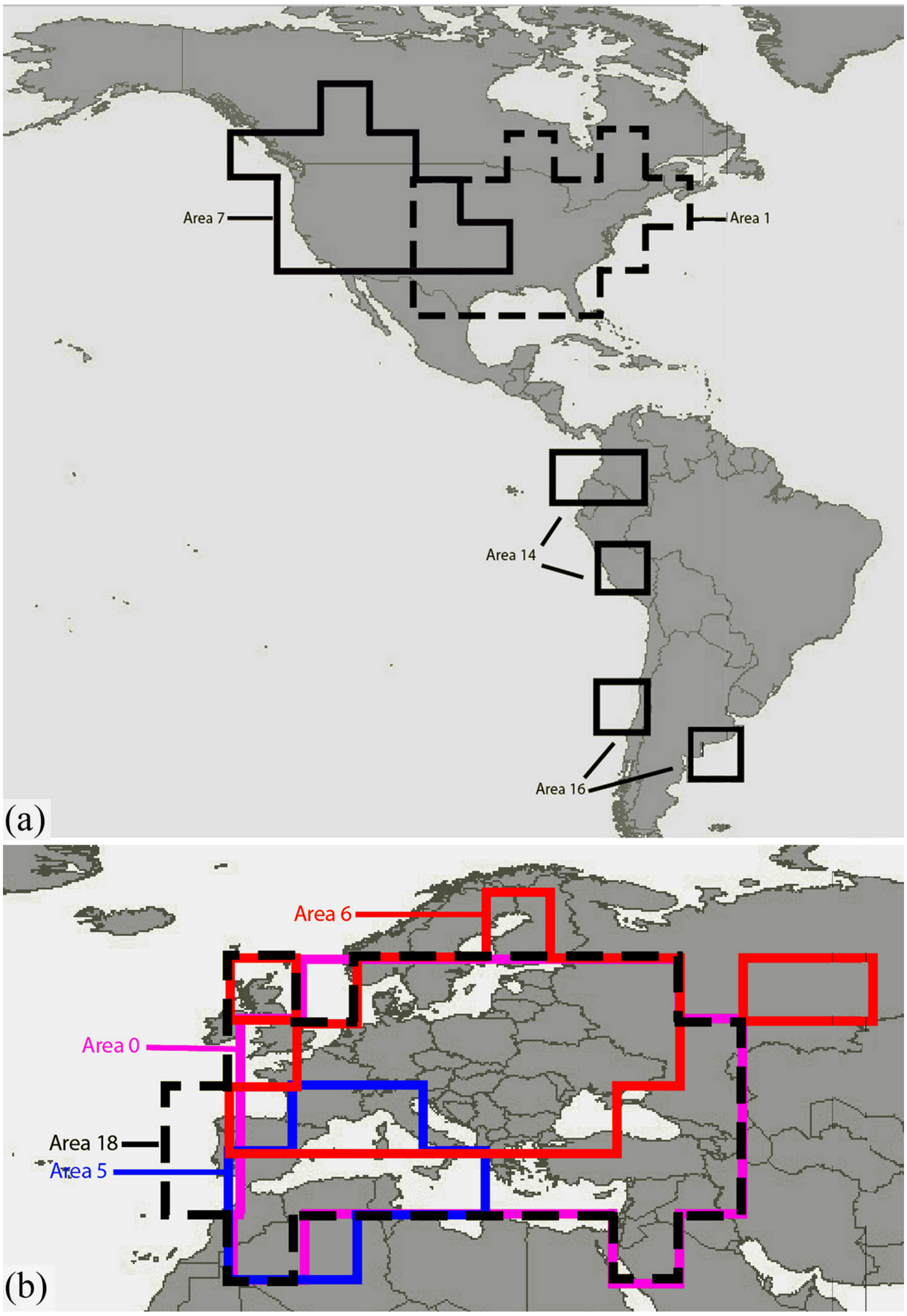

FIGURE 6. Areas of endemism recovered with the analysis with grid size of 7°. (a) North and South America. (b) Europe. (See text for explanations).

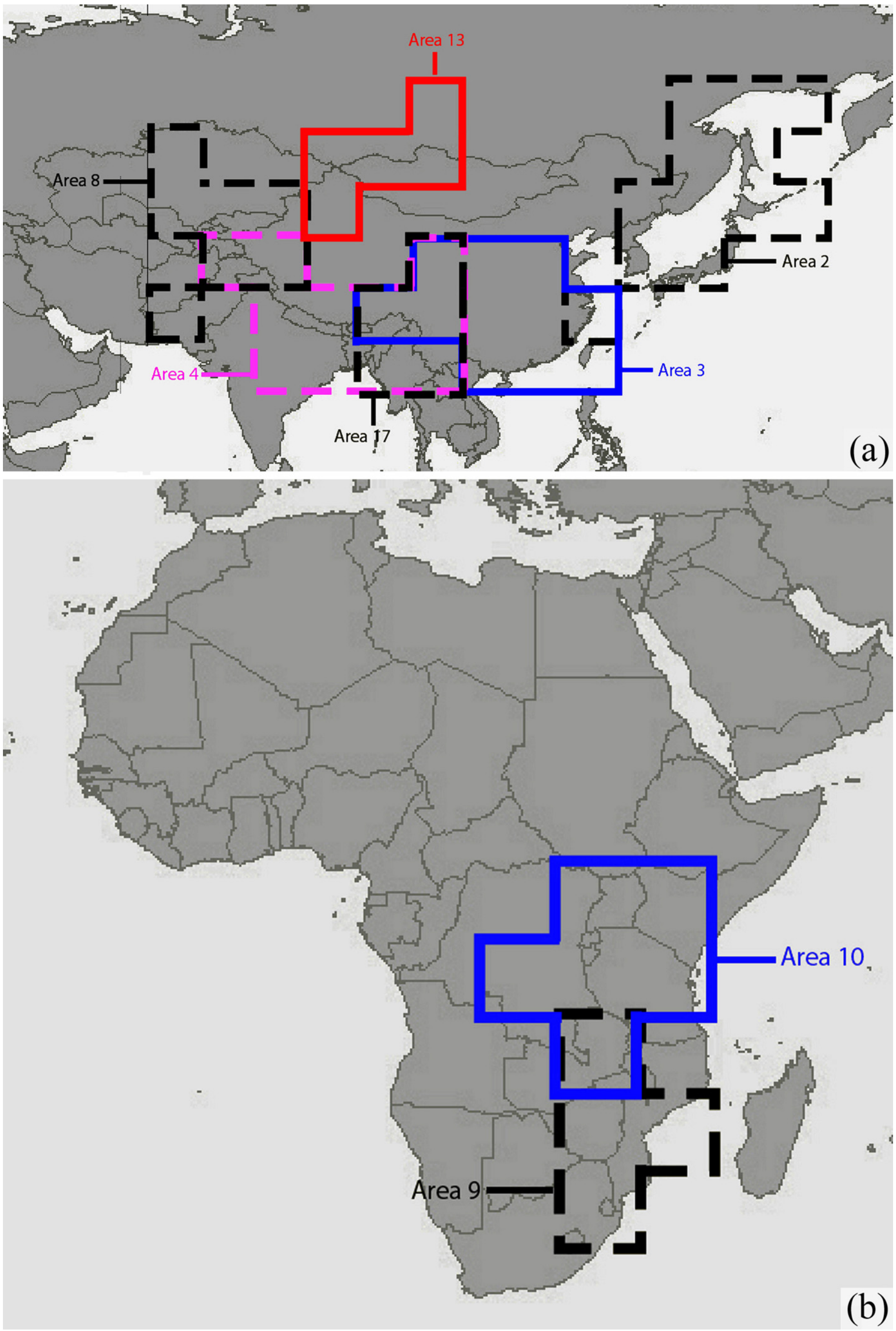

FIGURE 7. Areas of endemism recovered with the analysis with grid size of 7°. (a) Eurasia. (b) Africa. (See text for explanations).

Conclusions

Understanding global patterns of endemism in taxa not yet explored in this context will keep capturing the imagination and the efforts of biogeographers. Such studies are not only interesting for the experts in the taxonomic groups involved, but also represent independent tests of previously established regionalization attempts.

Different taxa will often display different results regarding their broad-scale patterns of endemism, and rigorous analyses of different taxonomic groups with quantitative methods is important for the continuous refinement of global biogeographical classifications. Our case study including all described species of Tipulidae illustrates the limitations of the biogeographical regions proposed mostly based on vertebrate distribution (Wallace, 1876; Proches 2005; Proches & Ramdhani, 2012; Kreft & Jetz, 2010; Holt *et al.*, 2013) when applied to other groups. While there is a general congruence of the broad-scale areas of endemism of tipulids with previously proposed regionalization schemes, for some areas, the sharpness of boundaries between traditional regions seem not to be so acute, due to a great level of overlap of part of its biotic elements.

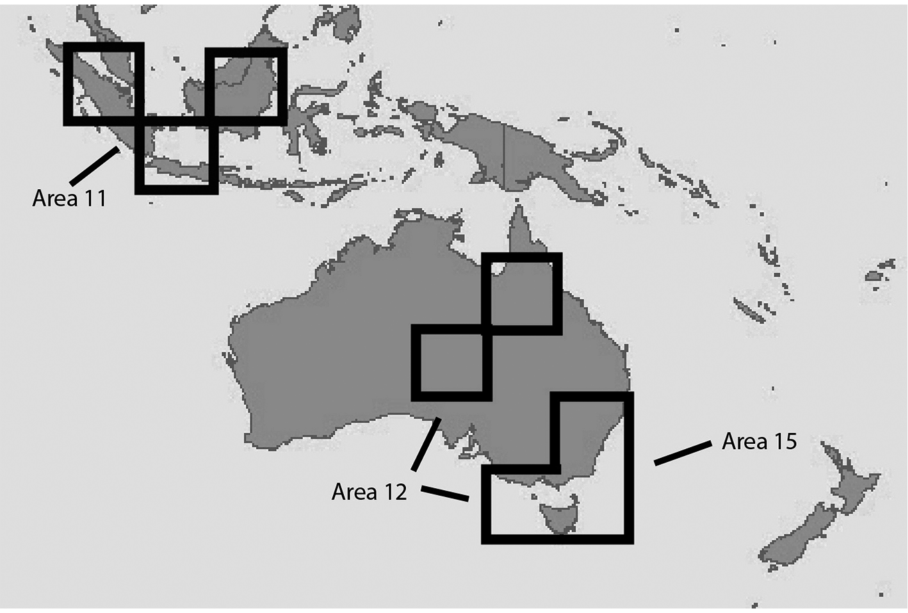

FIGURE 8. Areas of endemism recovered with the analysis with grid size of 7°. Malay Archipelago and Australia (See text for explanations).

VNDM analysis has so far been used in regional scale studies (e.g., Casagranda *et al.*, 2009; Aagesen *et al.*, 2009; Nori *et al.*, 2011,) but has not yet been applied in a global scale. In studies dealing with large scale patterns of endemism, we anticipate the same difficulties we had regarding decisions about grid size (Cartographic Resolution) and level of inclusiveness of consensus areas (Biogeographic Resolution). With respect to grid size, testing the results obtained under different parameters (Casagranda *et al.*, 2009; Aagesen *et al.*, 2009) may be an interesting approach. However, in a global scale study, there may be a large range of possible grids to be tested, which can lead to practical problems. Our analytical approach may serve as a guide for future studies using VNDM. Using this approach, we were able to determine a grid size (14°) very similar with what has been considered appropriate by previous studies (Proches, 2005) for testing large scale patterns such as the world's biogeographical regions.

A final comment must be made regarding to the kind of data we used. Of course, there are several limitations in using the geographic center of artificial geo-political unities such as countries and provinces in a biogeographical analysis. However, we reinforce our opinion that this approximation can be useful depending on the scale of the study. Our results are in several aspects congruent with what has been found using different kinds of data, different taxa, and different kinds of methods. Would congruent results emerge by mere chance? That is unlikely. In our view this demonstrates that, albeit limited, the data we used were able to recover meaningful results. Testing these results against those obtained with more precise data is a necessary second step. However, this will depend on several years of research just to tabulate the detailed distributional records of the over 4,000 Tipulidae species.

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