SAMPLING, DISTRIBUTION, DISPERSAL

Insight into Global Mosquito Biogeography from Country Species Records

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ABSTRACT   To advance our limited knowledge of global mosquito biogeography, we analyzed country occurrence records from the Systematic Catalog of the Culicidae (http://www.mosquitocatalog.org/main.asp), and we present world maps of species richness and endemism. A latitudinal biodiversity gradient was observed, with species richness increasing toward the equator. A linear log-log species (y)–area (x) relationship (SAR) was found that we used to compare observed and expected species densities for each country. Brazil, Indonesia, Malaysia, and Thailand had the highest numbers of species, and Brazil also had the highest taxonomic output and number of type locations. Brazil, Australia, the Philippines, and Indonesia had the highest numbers of endemic species, but excluding small island countries, Panama, French Guiana, Malaysia, and Costa Rica had the highest densities of total species and endemic species. Globally, 50% of mosquito species are endemic. Island countries had higher total number of species and higher number of endemic species than mainland countries of similar size, but the slope of the SAR was similar for island and mainland countries. Islands also had higher numbers of publications and type locations, possibly due to greater sampling effort and/or species endemism on islands. The taxonomic output was lowest for some countries in Africa and the Middle East. A consideration of country estimates of past sampling effort and species richness and endemism is proposed to guide mosquito biodiversity surveys. For species groups, we show that the number of species of *Anopheles* subgenus *Anopheles* varies with those of subgenus *Cellia* in a consistent manner between countries depending on the region. This pattern is discussed in relation to hypotheses about the historical biogeography and ecology of this medically important genus. Spatial analysis of country species records offers new insight into global patterns of mosquito biodiversity and survey history.

KEY WORDS   mosquito, biogeography, country occurrence records, species richness, species–area relationship

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Despite considerable attention given to mosquito vectors of human disease, our knowledge about the biogeography of mosquitoes as a whole is limited. Basic information about species–area relationships (SARs) and global patterns of species richness and endemism is lacking, or not easily accessible. For example, tables of country presence or absence records for species and higher taxa have been produced for some areas (e.g., Edwards 1941, Belkin 1962), but they require the reader to have a good idea of geography to visualize distribution patterns. Maps of malaria epidemiological zones and general location of primary vectors are available (e.g., Russell et al. 1963, WHO 1989), but these seem to depend on simple interpolations between extremes of the species range. A recently published map of the world's most dominant malaria vectors (Kiszewski et al. 2004) is arguably one of the most complete compilations of vector distribution. However, despite the sharp boundaries between mosquito species shown in this map, the true extent of each species is unknown, and despite the solid colors indicating species occurrence, species are not evenly distributed across their range. The lack of detail on the past and present distribution of vectors is a major limiting factor for global modeling of vector-borne diseases (Rogers and Randolph 2003, Tatem et al. 2006).

The number of mosquito species known from an area is a result of the intrinsic species richness, determined largely by environment and history, and sampling effort. A latitudinal biodiversity gradient for mosquitoes, with species richness increasing toward the tropics, has been suggested (e.g., Belkin 1962, Russell et al. 1963), but this idea is untested. Sampling effort may vary according to the preference of the investigators, the safety or ease of access to an area, or the presence of ongoing vector-borne disease control

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programs. For example, U.S. Army facilities in Thailand, the Philippines, Korea and Kenya provided entomologists with logistics to sample local mosquito fauna, thereby increasing the mosquito inventories and taxonomic output for those countries. Separating the effects of sampling effort, taxonomic output and species richness may be difficult, as a species-rich or endemic area will initially result in higher numbers of new species per sampling effort, and may attract the greatest sampling effort.

The number of species in a country is also a function of area. A positive correlation of species numbers with area has long been recognized among organisms (see Rosenzweig 1995 for review) and was promoted by MacArthur and Wilson (1967) through their theory of island biogeography. This theory predicts that species richness increases with area owing to decreasing extinction rate with increasing area. Species-area relationships are fundamental to understanding patterns of biodiversity and for predicting species extinction risk in response to global environmental change (Drakare et al. 2006). An analog of the equilibrium theory of island biogeography, metapopulation dynamics (Hanski and Gyllenberg 1997), also yields predictable SAR, but it is more amenable to biological interpretation (e.g., Matter et al. 2002). Correcting species number for geographic area is necessary to compare countries of different sizes for relative mosquito species density. Species number does not vary linearly with area and the exponential, power and logistic functions have been proposed to describe this mathematical relationship (Scheiner 2003). Consensus favors the power function as the best fit (Scheiner 2003), and this relationship is linear for log-log representations. Mosquito SAR have not been reported to our knowledge.

The online Systematic Catalog of Culicidae (SCC) (http://www.mosquitocatalog.org/main.asp) is the most comprehensive searchable database of the taxonomy and country occurrence of mosquito species. The SCC is a compilation of Knight and Stone (1977) with all its supplements, which built upon Stone et al.(1959) and all of its supplements. A companion to the SCC is the "Reference Database" (http://lrs.afpmb.org/rlgn_app/ar_login/wrbuguest/wrbuguest), which contains the literature cited in the 1977 catalog, and its supplements, and many additional papers from the reprint files of the Walter Reed Biosystematics Unit (WRBU) at the Smithsonian Institution in Washington, DC. The country records of the SCC and reference database provide the most complete, albeit low resolution, data set, available to investigate fundamental questions about SAR, sampling effort, and for global mapping of species richness and endemism. We chose the medically important and well-studied *Anopheles* subgenus *Anopheles* and subgenus *Cellia* to illustrate the potential of a global statistical treatment of country inventory data for particular species groups. To better visualize patterns, we produced global maps of these data, by using geographical information system (GIS) software.

Materials and Methods

The number of valid mosquito species names recorded for a country (Antarctica excluded throughout) was obtained using the search function of the SCC on the WRBU website (http://www.wrbu.org/index.html). We obtained numbers of endemic species for countries by inspecting the underlying SCC database. We considered endemic species to be those that were recorded in the database from only one country.

We used two indices to gauge the species-level taxonomic output for each country. The first index was to obtain the number of nominal taxonomic names (which includes valid species and synonyms, subspecies, and varieties) described from a country (i.e., type locations) via the "Advanced" search function and "like" Boolean operator on the WRBU website. When type locations of one species were listed for more than one country, all these countries were scored as having a type locality. We used current country names, former names and spelling variants of country names in the search. Alternative spellings and former country names, obtained from the Government section of country fact sheets from the Central Intelligence Agency (CIA) World fact book website (https://www.cia.gov/cia/publications/factbook/index.html), were used in the search. Results for Indonesia were the compilation of unique results for East Indies, Netherlands New Guinea, Western New Guinea, Sumatra, Java, Borneo (but not Malaysian Borneo or the small but independent nation of Brunei), Irian Jaya, Hollandia, Timor, Seram, Ceram. Sulawesi, Celebes, Flores, and Bali. Malaysia was the compilation of unique results for Malaya, Malaysia, Sarawak, and north Borneo (which may include Sabah and Brunei). We took care to avoid duplication with countries that have overlapping names, for example Niger and Nigeria.

The second index was the number of publications that have the country name in the publication title obtained by the "Advanced search" option of the Reference Database. We investigated alternative spellings and former country names in the search. For example, a search for "Brazil" revealed 56 publications, whereas "Brasil" revealed a further 53 publications. We allocated results for "Korea" to both North and South Korea. The totals for Papua New Guinea were the result of a search against "New-Guinea" and "Papua" (excluding "New-Guinea"). Results for the United Kingdom were the combined results for "Britain" and "England." We recognize that this search would miss publications that do not mention the country in the title; would fail to find titles that include now-defunct states, such as Yugoslavia; and would miss titles with regions rather than countries (e.g., Europe or Africa).

Countries area was measured as land area, as listed on the CIA World fact book website. We divided countries into island nations (with Australia the largest) and mainland nations. We defined island countries as those that were mostly or entirely surrounded
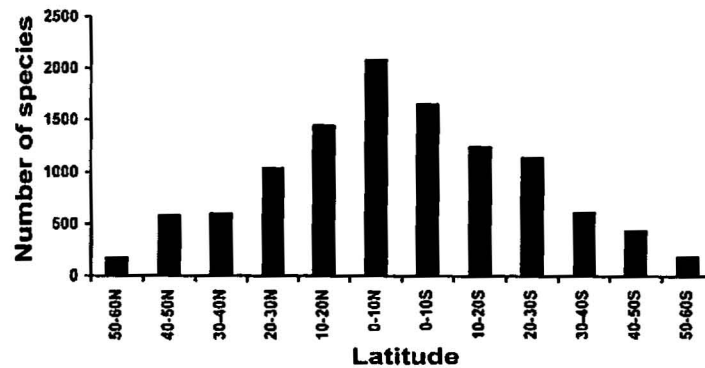
Fig. 1.   Numbers of mosquito species by intervals of 10° latitude calculated from country records in the Systematic Catalog of the Culicidae (http://www.mosquitocatalog.org/main.asp).

by the sea. Species number and country area data were $\log_{10}$ transformed, and simple linear regression was performed using MINITAB version 14.20 (Minitab Inc., State College, PA).

We imported data into ARCVIEW GIS 3.3 (Environmental Systems Research Institute Inc., Redlands, CA) for graphical display. We used a shapefile polygon of the 250 countries (excluding Antarctica) of the world current to 1998 as the template for mapping mosquito data.

We assessed species richness according to latitude in ARCVIEW GIS 3.3 for every 10° of latitude from the equator. A rectangle graphic was drawn for each 10° over a polygon shapefile of countries of the world, and countries intersected by the rectangle were identified. If <10% of the area of a country fell within the rectangle, then this country was not included for that 10° interval. The number of species for the combination of countries in each 10° interval was obtained from the SCC.

Results

Highest numbers of species occur at the equator, with the highest number for the 0–10° N interval (Fig. 1). Most species records (87.7%) occurred between 40° N and S. Figure 1 suggests that there may be a linear relationship between distance from the equator and number of species.

A simple linear regression of the log-log species (y)–area (x) relationship for all countries with at least one mosquito species (Fig. 2) showed a highly significant positive relationship ($y = 0.3019x + 0.0245$, $R^2 = 0.4222$, df = 201, residual mean-square error = 0.205, SE of intercept = 0.1231; SE of slope = 0.02491). The R^2 (multiplied by 100) is the percentage of total variation in (y) explained by (x) and the square-root of R^2 is Pearson's product-moment correlation coefficient whenever a straight-line is fit to the variables (x) and (y). The value of the t-statistic associated with the calculated value of R was 12.12, and the corresponding two-tailed probability was highly significant ($P <$
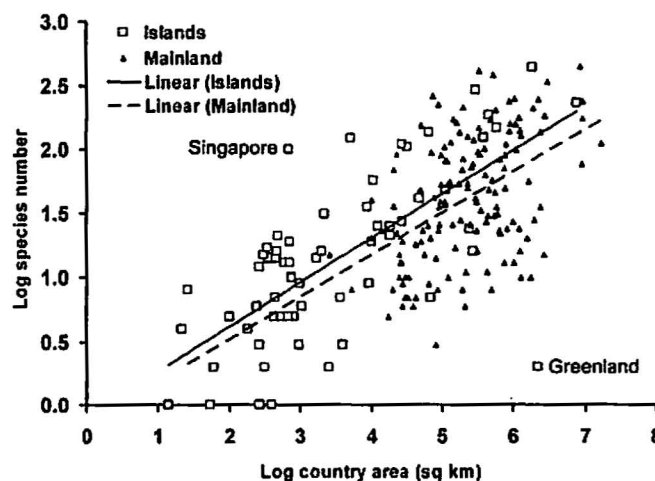

Fig. 2.   Log-log species (y)–area (x) relationship for the number of mosquito species for island and mainland countries recorded in the online Systematic Catalog of the Culicidae (http://www.mosquitocatalog.org/main.asp). Only countries with at least one species are shown and straight lines are linear regressions (see text).
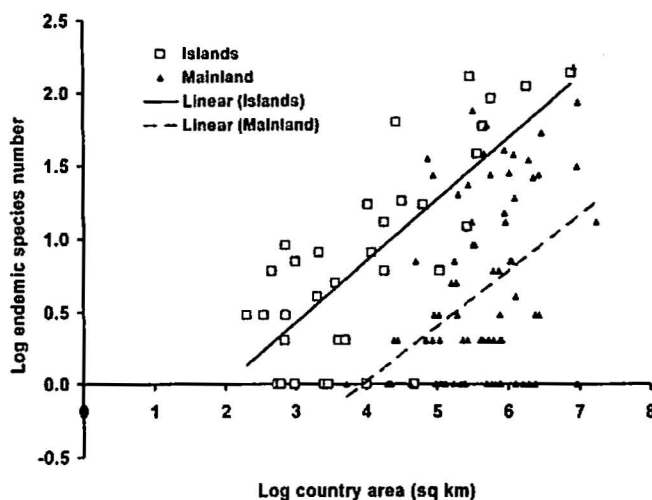
Fig. 3. Log-log species (y)-area (x) relationship for the number of endemic mosquito species for each country recorded in the online Systematic Catalog of the Culicidae (http://www.mosquitocatalog.org/main.asp). Only countries with at least one species are shown and straight lines are linear regressions (see text).

0.0001). The R^2 indicated that 42.22% of the variation in species richness is explained by area, despite outliers such as Greenland and Singapore. The most species-rich countries and their number of species were Brazil (447), Indonesia (439), Malaysia (415), Thailand (379), India (338), Philippines (294), Panama (264), Colombia (251), Democratic Republic of the Congo (248), China (238) and Venezuela (238). Countries with no recorded species included Western Sahara, Bhutan, Kuwait, and Qatar. Island nations are generally smaller (mean = 143,809 km^2 ± 80,171 SE, n = 101) than mainland nations (mean = 791,171 km^2 ± 165,597 SE, n = 149), but there is overlap in area. Island nations had higher numbers of species per area than did mainland nations and the regression lines for island and mainland countries were roughly parallel (Fig. 2). The regression for island nations was y = 0.3439x − 0.0685, R^2 = 0.4664, df = 61, residual mean-square error = 0.240, SE of intercept = 0.1754; SE of slope = 0.04710, t = 7.3, $P <$ 0.0001, and for mainland nations was y = 0.3266x − 0.1317, R^2 = 0.2234, df = 138, residual mean-square error = 0.1889, SE of intercept = 0.2800; SE of slope = 0.05184, t = 6.3, $P <$ 0.0001.

To put this difference into perspective, an island country of 1 million km^2 should contain 99 species compared with 67 species for a mainland country, and an island country of 10,000 km^2 should have 20 species compared with 15 for a similarly sized mainland country. When Greenland and Singapore were excluded the slope for island nations became 0.4041, and intercept −0.2612.

In total, 1816 species names (plus subspecies and varieties) in 117 countries were endemic, i.e., those recorded for only one country. The SCC lists 3,622 names (of which just over 3,400 are valid species names), indicating that global endemicity is ≈50%. The top endemic countries and their number of species were: Brazil (148), Australia (135), Philippines

(128), Indonesia (107), Madagascar (90), China (85), Malaysia (75), Solomon Islands (63), Thailand (59), and Papua New Guinea (58). Total numbers of species (x) and numbers of endemic species (y) for each country were highly correlated (y = 0.2061x − 3.5532, R^2 = 0.628, df = 248, residual mean-square error = 160, SE of intercept = 0.9587; SE of slope = 0.01007, t = 20.46, $P <$ 0.0001). The linear regression for endemic species from island countries (Fig. 3) showed a highly significant positive relationship (y = 0.4191x − 0.827, R^2 = 0.5614, df = 33, residual mean-square error = 0.2018, SE of intercept = 0.2685; SE of slope = 0.06449, t = 6.5, $P <$ 0.0001), the area of island countries explained 56.14% of the variation in numbers of endemic species. The correlation for mainland countries (Fig. 3) was not as strong as for islands (y = 0.3862x − 1.5445, R^2 = 0.1726, df = 80, residual mean-square error = 0.3280, SE of intercept = 0.5329; SE of slope = 0.09455, t = 4.08, $P <$ 0.001).

For a given area, island nations had higher numbers of endemic species than did mainland nations and the regression lines for island and mainland countries were roughly parallel. For example, an island country of 1 million km^2 would have 49 endemic species compared with a mainland country with six endemic species and an island country of 10,000 km^2 would have seven endemic species compared with one endemic species for a similarly sized mainland country. Interestingly, the difference between island and mainland countries in the number of endemic species approximates the difference in total species richness.

Generally, the larger the country, the higher the number of type locations described from that country and the higher the number of publications concerning that country. Brazil had the highest number of types (394) and publications (109). For countries with publications, the regression of log number of publications (y) against log area (x) was y = 0.1797x − 0.1617, R^2 = 0.2077, df = 162, residual mean-square error =
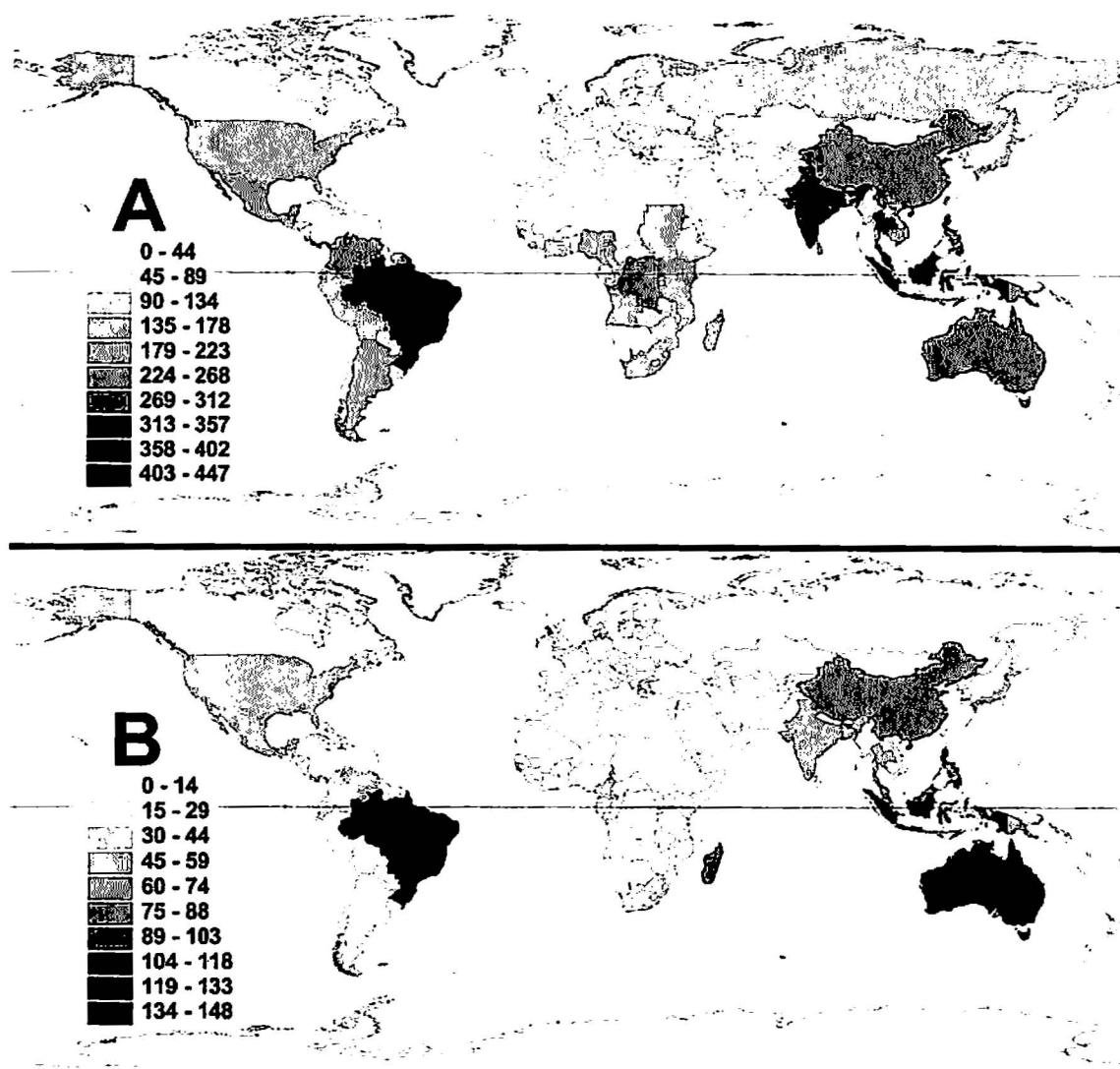
Fig. 4. Global map of total mosquito species number per country (A) and number of endemic mosquito species per country (B) from the online Systematic Catalog of the Culicidae (http://www.mosquitocatalog.org/main.asp).

0.2299, SE of intercept = 0.1377; SE of slope = 0.02757, t = 6.52, P < 0.0001. For countries with type locations, the regression of log number of types (y) against log area (x) was $y = 0.2282x - 0.188$, R^2 = 0.1817, df = 167, residual mean-square error = 0.375, SE of intercept = 0.1881; SE of slope = 0.03747, t = 6.09, P < 0.0001). The regression of number of type locations (x) against publications (y) for all countries explained 64.27% of the variation ($y = 0.2421x + 2.636$, df = 248, residual mean-square error = 81, SE of intercept = 0.6134; SE of slope = 0.01146, t = 21.12, P < 0.0001). For a given area, island nations had a higher number of type locations and publications than did mainland nations. For island countries, area explained 46.76% of the variation in numbers of type locations ($y = 0.3709x - 0.4854$, R^2 = 0.4676, df = 55, residual mean-square error = 0.258, SE of intercept = 0.2062; SE of slope =

0.05337, t = 6.95, P < 0.0001). For mainland countries, area explained less of the variation in the number of type locations ($y = 0.4319x - 1.4174$, R^2 = 0.1911, df = 110, residual mean-square error = 0.3646, SE of intercept = 0.4675; SE of slope = 0.08474, t = 5.1, P < 0.0001). For publications, area explained 59.51% of the variation in numbers of publications from island countries ($y = 0.3031x - 0.4317$, R^2 = 0.595, df = 55, residual mean-square error = 0.1184, SE of intercept = 0.1266; SE of slope = 0.03372, t = 8.99, P < 0.0001). Area explained less of the variation in the number of publications for mainland countries ($y = 0.2933x - 0.8733$, R^2 = 0.1406, df = 105, residual mean-square error = 0.2496, SE of intercept = 0.3923; SE of slope = 0.07076, t = 4.15, P < 0.0001).

Using the regression lines as a guide, we found that for sizeable countries between ≈35° N and S, taxo-
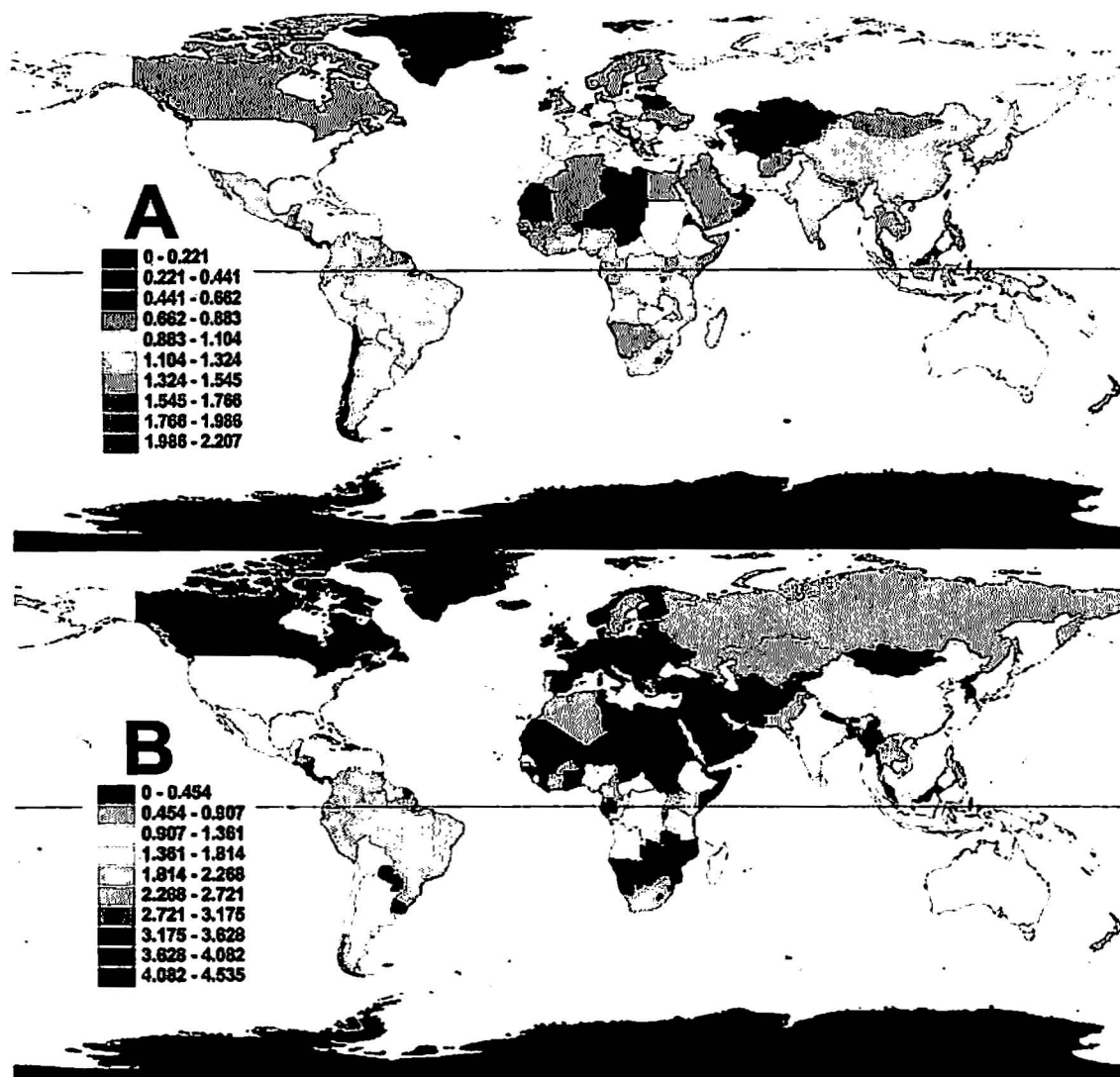
Fig. 5. Numbers of observed versus expected mosquito species per country (A) and number of endemic species per country (B). Observed and expected numbers were obtained from the log-log species-area relationships in Figs. 2 and 3. Warmer colors indicate higher than expected species density and cooler colors lower than expected species density.

nomic output was most below expectation for Mali. This was followed by: Chad, Niger, Guinea, Somalia, Benin, Namibia, Oman, Syria, Qatar, Kuwait, Equatorial Guinea, Guinea-Bissau, United Arab Emirates, Western Sahara, Saudi Arabia, Cyprus, Botswana, Burkina Faso, Tunisia, Bahrain, Malawi, Jordan, Bhutan, Laos, Mauritania, Mongolia, Haiti and Uruguay. The greatest above expected taxonomic output occurred for The Gambia, followed by: Uganda, Israel, India, Thailand, Malaysia, El Salvador, Venezuela, Brazil, Ecuador, Guatemala, Costa Rica, Panama, French Guiana, Belize, and Trinidad-Tobago.

The global country pattern of mosquito species richness (Fig. 4A) shows that countries at lower latitudes had the most species and countries at higher latitudes had the least species, as noted in Fig. 1.

Countries in lower latitude desert areas had fewer species than countries in wetter regions in Asia and the Neotropics. The global pattern of endemic species (Fig. 4B) shows that Australasian and some Asian countries had high numbers of endemic species in keeping with the island nature of many of these countries.

Because the number of species does not vary in a linear fashion with country area, it is not appropriate to correct for country area simply by dividing species number by area or by assuming the log-log slope is equal to 1. A map of log observed species per log expected species number, corrected for area (according to the relationships for island and mainland countries) is shown in Fig. 5A. This measure shows relative species density, with countries laying on the line of
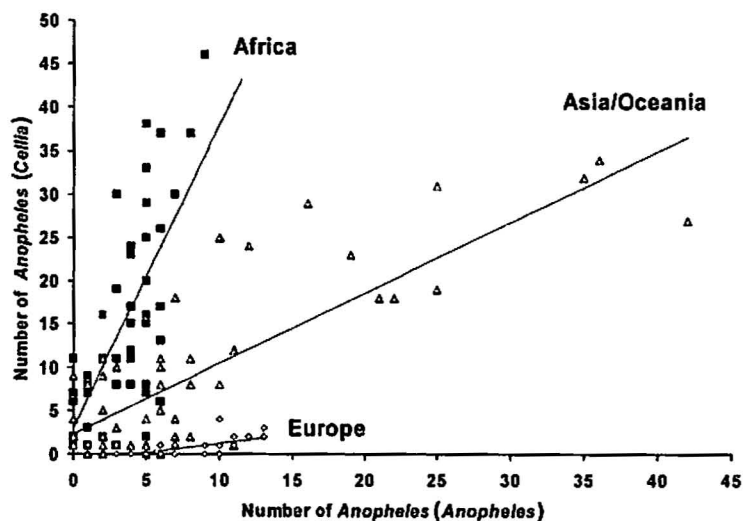
Fig. 6. Numbers of species of *Anopheles* subgenus *Anopheles* against the corresponding number of subgenus *Cellia* for countries in Africa, Asia + Oceania, and Europe. Straight lines are linear regressions (see text). The New World data are not shown but lie along the x-axis, as subgenus *Anopheles* is present in that region but *Cellia* is not.

best fit having a relative density equal to 1. White-colored countries are those that had close to expected relative density for their geographic area, countries with higher than expected numbers have warmer colors and countries with lower than expected numbers have cooler colors. The highest densities of species were for Singapore, followed by Tuvalu, Trinidad & Tobago, Panama, French Guiana, Malaysia, Nauru, Costa Rica, Northern Mariana Islands, and Grenada. The lowest densities for tropical countries occur in Africa. A map of endemic species corrected for area is shown in Fig. 5B. The highest densities of endemic species was for Panama, followed by: French Guiana, American Samoa, Malaysia, Costa Rica, Seychelles, Pacific Islands (Palau), Thailand, Federated States of Micronesia, and Uganda.

As with the total mosquito fauna, a linear log-log SAR was found for countries that had *Anopheles* species ($y = 0.2235x - 0.079$, $R^2 = 0.3783$, df = 172, residual mean-square error = 0.0848, SE of intercept = 0.1133; SE of slope = 0.02185, $t = 10.23$ $P < 0.001$). Highest densities of species in subgenus *Anopheles* occurred in Southeast Asia, whereas greatest densities of *Cellia* occurred in Africa followed by Southeast Asia. Linear regression of the numbers of each of these two subgenera within each country (Fig. 6) revealed that African countries had consistently higher pro- portions of species of subgenus *Cellia* compared with those of subgenus *Anopheles*, whereas countries in Asia + Oceania had roughly equal proportions and European countries had consistently lower propor- tions of *Cellia*. We have not shown New World coun- tries, as *Cellia* are absent there. The regression of subgenus *Anopheles* (x) against *Cellia* (y) for African countries was $y = 3.501x + 2.9865$, $R^2 = 0.4778$, df = 48, residual mean-square error = 69.4, SE of inter- cept = 0.2192; SE of slope = 0.5283, $t = 6.63$, $P < 0.0001$. For Asia + Oceania, $y = 0.8175x + 2.2522$, $R^2 =$

0.6583, df = 46, residual mean-square error = 34.7, SE of intercept = 1.150; SE of slope = 0.08685, $t = 9.41$, $P = <0.0001$. For European countries, $y = 0.2073x - 0.8529$, $R^2 = 0.4066$, df = 37, residual mean-square error = 0.541, SE of intercept = 0.2957; SE of slope = 0.04116, $t = 5.04$, $P < 0.0001$.

Total species number, number of endemic species, number of type locations, number of publications and the land area for each country is given in Table 1.

Discussion

We present global maps of mosquito species rich- ness and endemism based on country species inven- tory data. The richest biogeographic regions for mos- quitoes are the Neotropics and Southeast Asia, which mirrors findings for other groups of organisms (Gaston and Hudson 1994). The suggestion that the majority of mosquito groups occur in the tropics has been made before (e.g., Belkin 1962), but our study is the first to demonstration an increase in species richness toward the equator. We show that mosquitoes are similar to many other organisms in that the total number of species increases with geographic area, according to a linear log-log relationship. We showed that island countries are more species-rich and have a higher number of endemic species than do mainland coun- tries. Island countries also have higher levels of taxo- nomic output (numbers of type locations and publi- cations) than do mainland countries and these numbers increase with land area. Finally, we show that the number of species of *Anopheles* subgenus *Anoph- eles* varies with those of subgenus *Cellia* in a consistent manner between countries depending on the region.

A latitudinal gradient of increasing biodiversity from the poles to the equator has been noted for many organisms (Jablonski et al. 2006). Drakare et al. (2006) found that species turnover as well as species richness

Table 1. Country mosquito data for species richness, number of endemic species, number of type locations, number of publications with the country in the title, country land area, and whether the country is an island nation (I) or occurs as part of the mainland (M)

Country	Island or mainland	Area (km²)	Total species	Endemic species	Types	No. publications
American Samoa	I	199	6	3	4	2
Anguilla	I	102	0	0	0	2
Antigua & Barbuda	I	442.6	7	0	4	2
Aruba	I	193	0	0	0	1
Australia	I	7,617,930	231	135	219	56
Bahamas, The	I	10,070	19	1	11	6
Bahrain	I	665	5	0	1	0
Baker Is.	I	2.1	0	0	0	0
Barbados	I	431	5	0	2	2
Bermuda	I	53.3	1	0	1	0
Bouvet Is.	I	49	0	0	0	0
British Indian Ocean Terr.	I	60	2	0	0	0
British Virgin Is.	I	153	0	0	0	0
Cape Verde	I	4,033	3	2	2	4
Cayman Is.	I	262	12	0	0	1
Christmas Is.	I	135	0	0	2	0
Cocos (Keeling) Is.	I	14	1	0	0	2
Comoros	I	2,170	31	8	8	0
Cook Is.	I	240	6	0	0	1
Cuba	I	110,860	48	6	27	10
Cyprus	I	9,240	9	0	1	0
Dominica	I	754	10	0	3	2
Dominican Republic	I	48,380	41	1	20	1
Falkland Is. (Islas Malvinas)	I	12,173	0	0	0	0
Faroe Is.	I	1,399	0	0	0	0
Fed. States of Micronesia	I	702	19	9	12	2
Fiji	I	18,270	25	13	16	3
French Polynesia	I	3,660	7	5	5	1
French Sth & Antarctic Lands	I	7,829	0	0	0	0
Gibraltar	I	6.5	0	0	0	0
Glorioso Is.	I	5	0	0	0	0
Greenland	I	2,166,086	2	0	2	3
Grenada	I	344	17	3	8	1
Guadeloupe	I	1,706	14	0	5	8
Guam	I	541.3	5	1	4	11
Guernsey	I	78	0	0	0	0
Haiti	I	27,560	27	0	2	3
Heard Is. & McDonald Is.	I	412	0	0	0	0
Howland Is.	I	2.6	0	0	0	0
Iceland	I	100,250	0	0	0	0
Indonesia	I	1,826,440	439	108	201	52
Ireland	I	68,890	7	0	1	0
Jamaica	I	10,831	57	17	45	13
Jan Mayen	I	377	0	0	0	0
Japan	I	374,744	124	38	67	61
Jarvis Is.	I	5	0	0	0	0
Jersey	I	116	0	0	0	0
Johnston Atoll	I	2.6	0	0	0	0
Juan De Nova Is.	I	4.4	0	0	0	0
Kiribati	I	811	5	0	0	0
Macau	I	28.2	0	0	1	2
Madagascar	I	581,540	148	90	112	33
Maldives	I	300	15	0	0	3
Malta	I	316	2	0	1	0
Man, Isle of	I	572	0	0	0	0
Marshall Is.	I	181.3	4	0	1	0
Martinique	I	1,060	6	0	3	3
Mauritius	I	2,030	16	4	11	7
Mayotte	I	374	0	0	6	0
Midway Is.	I	6.2	0	0	0	0
Montserrat	I	102	5	0	1	1
Nauru	I	21	4	0	0	1
Netherlands Antilles	I	960	3	1	1	3
New Caledonia	I	18,575	21	6	7	7
New Zealand	I	268,021	16	12	12	9
Niue	I	260	1	0	1	1
Norfolk Is.	I	34.6	0	0	0	1
Northern Mariana Is.	I	477	21	0	6	0
Pacific Is. (Palau)	I	458	16	6	6	0

Table 1. Continued

Country	Island or mainland	Area (km²)	Total species	Endemic species	Types	No. publications
Papua New Guinea	I	452,860	187	56	192	66
Paracel Is.	I	14.8	0	0	0	0
Philippines	I	298,170	294	128	233	17
Pitcairn Is.	I	47	0	0	0	0
Puerto Rico	I	8,870	35	0	5	10
Reunion	I	2,507	2	1	2	2
San Marino	I	61.2	0	0	0	0
Sao Tome & Principe	I	1,001	9	7	7	4
Seychelles	I	455	14	6	8	4
Singapore	I	682.7	100	2	31	10
Solomon Is.	I	27,510	109	63	68	11
Sth Georgia & Sth Sandwich Is.	I	3,903	0	0	0	0
Spratly Is.	I	5	0	0	0	0
Sri Lanka	I	64,740	137	17	54	27
St. Helena	I	413	0	0	0	0
St. Kitts & Nevis	I	261	3	0	0	1
St. Lucia	I	606	13	1	6	1
St. Pierre & Miquelon	I	242	0	0	0	0
St. Vincent & the Grenadines	I	389	1	0	3	2
Svalbard	I	61,020	0	0	0	0
Taiwan	I	32,260	105	18	56	18
Tokelau	I	10	0	0	0	0
Tonga	I	718	13	3	5	4
Trinidad & Tobago	I	5,128	122	2	56	10
Turks & Caicos Is.	I	430	0	0	0	0
Tuvalu	I	26	8	0	0	0
United Kingdom	I	241,590	24	0	21	24
Vanuatu	I	12,200	25	8	11	11
Virgin Is.	I	346	14	0	0	2
Wake Is.	I	6.5	0	0	0	0
Wallis & Futuna	I	274	1	0	0	1
Western Samoa	I	2,934	7	1	2	8
Afghanistan	M	647,500	22	0	0	2
Albania	M	27,398	13	0	1	0
Algeria	M	2,381,740	35	3	20	2
Andorra	M	468	0	0	0	0
Angola	M	1,246,700	140	19	30	19
Argentina	M	2,736,690	183	27	94	49
Armenia	M	28,400	9	0	0	0
Austria	M	82,444	14	0	4	0
Azerbaijan	M	86,100	8	2	2	1
Bangladesh	M	133,910	113	1	5	6
Belgium	M	30,278	10	0	0	0
Belize	M	22,806	91	1	5	7
Benin	M	110,620	37	1	1	2
Bhutan	M	47,000	0	0	0	0
Bolivia	M	1,084,390	157	7	22	13
Bosnia & Herzegovina	M	51,129	19	0	1	0
Botswana	M	585,370	35	1	2	0
Brazil	M	8,456,510	417	148	394	109
Brunei	M	5,270	8	1	1	1
Bulgaria	M	110,550	39	0	0	0
Burkina Faso	M	273,800	77	2	2	0
Burundi	M	25,650	13	0	4	2
Byelarus	M	207,600	6	0	0	0
Cambodia	M	176,520	137	7	17	5
Cameroon	M	469,440	172	36	36	5
Canada	M	9,093,507	77	1	41	13
Central African Rep.	M	622,984	83	6	7	7
Chad	M	1,259,200	16	0	3	2
Chile	M	748,800	13	6	16	2
China	M	9,326,410	238	85	128	90
Colombia	M	1,038,700	251	28	61	20
Congo, Democratic Republic of the	M	2,267,600	248	26	82	16
Congo, Republic of the	M	341,500	91	9	9	6
Costa Rica	M	50,660	154	7	45	13
Croatia	M	56,414	15	0	0	1
Czech Republic	M	77,276	42	0	0	0
Denmark	M	42,394	18	1	6	4
Djibouti	M	22,980	22	0	1	4

Table 1. Continued

Country	Island or mainland	Area (km²)	Total species	Endemic species	Types	No. publications
Ecuador	M	276,840	118	23	34	23
Egypt	M	995,450	27	0	19	20
El Salvador	M	20,720	69	1	8	3
Equatorial Guinea	M	28,051	19	2	0	0
Eritrea	M	121,320	10	1	3	3
Estonia	M	43,211	7	0	0	0
Ethiopia	M	1,119,683	99	7	14	44
Finland	M	304,473	23	0	3	5
France	M	545,630	46	2	31	8
French Guiana	M	89,150	224	27	54	45
Gabon	M	257,667	72	1	4	3
Gambia, The	M	10,000	40	0	12	2
Gaza Strip	M	360	0	0	0	0
Georgia	M	69,700	20	0	0	0
Germany	M	349,223	33	0	20	2
Ghana	M	230,940	126	1	67	3
Greece	M	130,800	55	0	10	9
Guatemala	M	108,430	105	3	17	11
Guinea	M	245,857	26	1	3	1
Guinea-Bissau	M	28,000	6	0	0	0
Guyana	M	196,850	84	3	22	5
Honduras	M	111,890	82	2	4	6
Hungary	M	92,340	26	0	1	3
India	M	2,973,190	338	53	271	53
Iran	M	1,636,000	56	1	3	14
Iraq	M	432,162	30	0	3	7
Israel	M	20,330	36	1	5	8
Italy	M	294,020	41	0	29	3
Ivory Coast	M	318,000	95	13	19	5
Jordan	M	91,971	26	0	0	1
Kazakhstan	M	2,669,800	15	3	4	1
Kenya	M	569,250	203	27	57	15
Kuwait	M	17,820	0	0	0	0
Kyrgyzstan	M	191,300	8	0	0	0
Laos	M	230,800	50	2	7	3
Latvia	M	63,589	25	0	0	0
Lebanon	M	10,230	20	0	3	1
Lesotho	M	30,355	7	0	0	0
Liberia	M	96,320	89	1	6	7
Libya	M	1,759,540	10	0	0	3
Liechtenstein	M	160	0	0	0	0
Lithuania	M	65,200	9	0	0	1
Luxembourg	M	2,586	15	0	0	0
Macedonia	M	24,856	10	0	1	2
Malawi	M	94,080	39	0	11	0
Malaysia	M	328,550	415	75	306	27
Mali	M	1,220,000	24	0	1	1
Mauritania	M	1,030,400	13	0	0	1
Mexico	M	1,923,040	211	34	91	54
Moldova	M	33,371	7	0	0	0
Monaco	M	1.95	0	0	0	0
Mongolia	M	1,564,116	20	0	0	1
Montenegro	M	13,812	23	0	0	0
Morocco	M	446,300	48	2	5	1
Mozambique	M	784,090	109	1	8	1
Myanmar (Burma)	M	657,740	83	1	13	11
Namibia	M	825,418	24	2	3	1
Nepal	M	143,181	172	0	1	11
Netherlands	M	33,883	10	0	2	1
Nicaragua	M	120,254	81	0	9	3
Niger	M	1,266,700	10	1	1	1
Nigeria	M	910,768	159	13	73	20
North Korea	M	120,410	53	1	5	17
Norway	M	307,442	16	0	2	0
Oman	M	212,460	11	1	2	2
Pakistan	M	778,720	89	3	16	6
Panama	M	75,990	264	35	185	38
Paraguay	M	397,300	63	0	8	6
Peru	M	1,280,000	129	4	18	12
Poland	M	304,465	39	0	0	2

Table 1. Continued

Country	Island or mainland	Area (km²)	Total species	Endemic species	Types	No. publications
Portugal	M	91,951	35	3	6	16
Qatar	M	11,437	0	0	0	0
Romania	M	230,340	54	1	2	3
Russia	M	16,995,800	112	13	13	6
Rwanda	M	24,948	15	2	4	1
Saudi Arabia	M	1,960,582	28	1	1	0
Senegal	M	192,000	69	5	6	6
Serbia	M	88,361	23	0	1	0
Sierra Leone	M	71,620	94	2	34	3
Slovakia	M	48,800	48	0	0	0
Slovenia	M	20,151	8	0	0	0
Somalia	M	627,337	23	2	3	4
South Africa	M	1,219,912	178	37	37	37
South Korea	M	98,190	53	1	5	17
Spain	M	499,542	57	1	6	4
Sudan	M	2,376,000	137	1	47	9
Suriname	M	161,470	161	5	59	12
Swaziland	M	17,203	5	0	0	0
Sweden	M	410,934	27	2	7	3
Switzerland	M	39,770	6	0	0	0
Syria	M	184,050	28	0	1	3
Tajikistan	M	142,700	26	0	1	0
Tanzania	M	886,037	138	15	28	10
Thailand	M	511,770	379	59	86	57
Togo	M	54,385	23	0	4	2
Tunisia	M	155,360	17	0	2	0
Turkey	M	770,760	50	2	5	4
Turkmenistan	M	488,100	8	0	8	0
Uganda	M	199,710	216	20	88	21
Ukraine	M	603,700	31	0	1	0
United Arab Emirates	M	82,880	3	0	0	0
United States	M	9,161,923	175	31	186	54
Uruguay	M	173,620	54	1	1	4
Uzbekistan	M	425,400	11	2	3	1
Venezuela	M	882,050	238	40	91	58
Vietnam	M	325,360	147	9	11	11
West Bank	M	5,640	0	0	0	0
Western Sahara	M	266,000	0	0	0	0
Yemen	M	527,970	30	2	3	6
Zambia	M	740,724	71	1	7	2
Zimbabwe	M	386,670	101	0	31	5

increases toward the equator. Ecological theory has proposed two general classes of mechanisms to account for biodiversity, i.e., dispersal-assembly and niche-assembly mechanisms (Allen and Gillooly 2006). Jablonski et al. (2006) identified origination rate, extinction rate and migration (i.e., dispersal-assembly mechanisms) as the main determinants of spatial patterns of biodiversity. Allen and Gillooly (2006) showed that for fossil ocean plankton, species richness and speciation rates both peak near the equator even after controlling for sampling effort and habitat area. Jablonski et al. (2006) showed that for genera and subgenera of marine bivalves, taxa have preferentially originated in the tropics and expanded toward the poles without losing their tropical presence. An in-depth analysis of the evolutionary dynamics underlying a latitudinal biodiversity gradient in mosquitoes is beyond the scope of the present paper. However, with the development of a robust phylogeny of the Culicidae it may be possible to date genera and subgenera to test whether their average ages increase with latitude, in accordance with an "out of the tropics" scenario.

The number of mosquito species known from a given area is also the result of sampling effort and the intrinsic species richness, which for many organisms can be influenced by climatic or habitat diversity or evolutionary history (Ricklefs and Schluter 1993). We found that the SAR for island countries parallels mainland countries but reveals a higher number of species for a given area. The similar slope of SAR for island and mainland countries that we observed contrasts with the expectations of some authors (Rosenzweig 1995, Hanski and Gyllenberg 1997) but accords with the findings of a recent review of 794 SAR derived from the literature (Drakare et al. 2006). Drakare et al. (2006) concluded that differences in the slope of the SAR between species groups are a strong indicator of the sensitivity of these species groups to habitat and climate-space loss. According to island theory, less dispersed species demonstrate steeper slopes of the SAR and more pronounced spatial patterns. For archipelagos of islands, the slope of the SAR may differ among species at different risks of extinction through habitat and climate-space loss, or those possessing different life history characteristics, such as dispersal

ability and probability of persistence after coloniza-
tion (Ney-Nifle and Mangel 2000, Matter et al. 2002,
Burns 2004, Hovestadt and Poethke 2005). Thus, fur-
ther analysis of SAR may shed light on the colonizing
abilities of potentially invasive species or functional
groups.

It is likely that the mosquito species inventory for
most countries is incomplete, but islands may be more
completely surveyed than mainland countries. We
attempted to gauge sampling effort by measuring the
number of type locations and the number of taxo-
nomic publications for each country. These two mea-
sures were highly correlated among countries, al-
though differences are expected to occur because of
the greater variety of publications in countries that
have long-term infrastructure supporting mosquito
taxonomy. For example, despite roughly six times the
publications with "United States" in the title compared
with "Tanzania" (or "Tanganyika," the former name),
only 5% of U.S. records were new species descriptions
compared with 60% for the latter. Regression analyses
for the number of type locations and publications
indicated higher numbers for island countries com-
pared with mainland countries of similar size. These
observations support the idea of greater sampling ef-
fort and possibly a survey bias toward islands. If the
mosquito inventory of islands were more complete
than for mainland countries, future mosquito taxo-
nomic surveys would more profitably be directed to
mainland countries. However, the higher total num-
bers of species on islands also reflect greater intrinsic
species richness rather than just greater sampling.

If speciation and extinction occur at the same rate
regardless of location then a similarly sized mainland
and island country would have similar total numbers
of species, although the proportion that is endemic
would be higher on islands due to the effect of sea
barriers preventing dispersal to other countries. Thus,
a species arising on the mainland would be more likely
to disperse over land to another country, and thereby
lose its status as an endemic species, than an island
species is likely to successfully disperse over the sea.
However, in addition to this effect, island countries
were more species-rich than mainland countries.
This would further increase the number of endemic
species expected from island countries. The greater
species richness of islands could indicate that specia-
tion rates are higher or species extinction rates are
lower on islands compared with the mainland. Allo-
patric speciation is presumably more common be-
cause of islands, as mosquito populations are more
likely to become morphologically and reproductively
distinct due to geographic isolation. The high percent-
age of endemic species noted here suggests that geo-
graphic isolation and adaptations to localized situa-
tions have played an important role in speciation and
the subsequent distribution of mosquito species. Ac-
cording to the niche-assembly explanation for the
maintenance of biodiversity, natural selection for nar-
rower niches, different modes of interspecific inter-
action, or both allows more species to coexist (Allen
and Gillooly 2006). Evidence for this possibility in

mosquitoes should be easiest to obtain from areas
where potential niches are few or species richness is
high.

Identifying the contribution of sampling effort to a
country's species inventory is difficult, because ento-
mologists may preferentially target a species-rich
country for mosquito taxonomic studies. For a given
area, species accumulation curves at first increase rap-
idly with increasing sampling effort but then plateau
as it becomes harder to find new species (Magurran
2004). A species-rich country would initially result in
higher numbers of new species (and type locations
and publications) per sampling effort. Burkina Faso is
an example of a species-rich country with low relative
numbers of publications and type locations (i.e., hav-
ing a consistent suggestion of low taxonomic output).
If the mosquito inventory in this country is still in the
initial rapidly increasing part of the species accumu-
lation curve, then new species discoveries are more
likely there than for other countries with a more com-
plete inventory.

Areas in need of mosquito surveying have been
identified previously, but not on a global scale. Ed-
wards (1941) and DeMeillon (1947) listed countries of
the Ethiopian zoogeographical region for which the
anopheline fauna is imperfectly known. Similarly, Gil-
lies and DeMeillon (1968) published a map and lists
for sub-Saharan Africa where members of the
Anophelinae have been collected. Large gaps in sam-
pling remained in Angola, Central African Republic,
Chad, Democratic Republic of the Congo, and Zam-
bia. Some of these countries also scored low for our
estimates of taxonomic output. Despite the difficulties
in relating taxonomic output to sampling effort, coun-
trywide estimates of taxonomic effort and densities of
total and endemic species could assist in decisions
about where to conduct mosquito biodiversity sur-
veys.

The regional endemism of mosquitoes suggests that
evolutionary history among regions is more similar
than between regions. We used records for Anopheles
subgenus Anopheles and subgenus Cellia to show the
utility of a global statistical analysis of inventory data
for individual taxa. The absence of Cellia in the New
World is seen as evidence that the evolution of this
subgenus occurred after the breakup of Gondwana
and the separation of Africa and South America ≈95
mya (Krzywinski et al. 2001). Christophers (1933)
noted that the Ethiopian zoogeographical region has
relatively few representatives of subgenus Anopheles,
whereas Series Myzomyia is especially dominant. We
found that the proportion of subgenera Cellia and
Anopheles differed among different geographic re-
gions but that this proportion was relatively constant
for countries within these regions.

Phylogenetic analysis suggests that subgenera
Anopheles and Cellia are sister taxa (e.g., Krzywinski et
al. 2001), and the SCC lists similar numbers of species
for both (subgenus Anopheles, $n = 207$; Cellia, $n = 220$). In addition, species within these two subgenera
are often sympatric, which suggests that they could
experience similar evolutionary forces. If we assume

that these subgenera are the same age and their rates of species evolution are similar, then numbers of species may reflect absolute time of these subgenera in an area. Alternatively, if species within subgenera *Anopheles* and *Cellia* exploit different types of niches, then numbers of species may reflect differences in the number of available niches in a given environment. This would suggest that niches for subgenus *Anopheles* in Africa, for example, are fewer in number than niches for *Cellia*.

The SCC was placed online in January of 2001 and was thought to be current to that time. However, the process of incorporating species records is ongoing, so the results of this study should be viewed with this in mind. Sizeable discrepancies may exist between records in the SSC and the actual number recorded in the published literature. For example, published records indicate that >400 species occur in Thailand (Rattanarithikul et al. 2005, indicate 436 in total), whereas the SSC lists 377 species. Species records reflect collecting activity of a finite number of collectors, and collection locations may be subject to spatial clustering and a bias toward certain habitats (e.g., ground pools). Hijmans et al. (2000) identified four types of bias that we think could apply in the present case. These biases were: species bias (e.g., oversampling species of *Anopheles* due to greater abundance or in connection to malaria studies); species-area bias (e.g., oversampling island endemics compared with mainland species); hotspot bias (e.g., oversampling areas where previous studies indicated a high species richness); and infrastructure bias (e.g., oversampling near roads and towns). It is unknown to what extent human assisted dispersal of mosquito species affects country occurrence records, but this would have increased with the spread of modern modes of transport. Anthropogenic changes in habitats and climate also affect mosquito species distributions, which may distort patterns based on country occurrence records. We did not attempt to distinguish introduced species but at least for the more sizeable countries, these would represent only a small fraction of total species richness. Land area and latitude are interacting, which is why Greenland has a low diversity and Singapore high. In addition, the latitudinal biodiversity gradient, spatial scale and the species-time relationship interact with SAR (Turner and Tjørve 2005, Drakare et al. 2006, White et al. 2006), but it is beyond the scope of this article to investigate these factors in any detail. In this study, we have concentrated on species-level biodiversity, but our approach could be directed to other taxonomic or functional groupings, especially those involved in disease transmission.

Further biogeographical consideration of the data presented here is possible. However, we think that the general trends of the latitudinal biodiversity gradient, the SAR, the location of the major areas of species richness and endemism, and the relationship of subgenus *Anopheles* to *Cellia*, will remain largely unchanged. Knowledge of mosquito biogeography is in its infancy. Analysis and mapping of global species occurrence data are a first step to understanding the causes of global patterns in mosquito species distribution.

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