

INVITED REVIEW

Twenty years of phylogeography: the state of the field and the challenges for the Southern Hemisphere

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Abstract

Phylogeography is a young, vigorous and integrative field of study that uses genetic data to understand the history of populations. This field has recently expanded into many areas of biology and also into several historical disciplines of Earth sciences. In this review, I present a numerical synthesis of the phylogeography literature based on an examination of over 3000 articles published during the first 20 years of the field (i.e. from 1987 to 2006). Information from several topics needed to evaluate the progress, tendencies and deficiencies of the field is summarized for 10 major groups of organisms and at a global scale. The topics include the geography of phylogeographic surveys, comparative nature of studies, temporal scales and major environments investigated, and genetic markers used. I also identify disparities in research productivity between the developing and the developed world, and propose ways to reduce some of the challenges faced by phylogeographers from less affluent countries. Phylogeography has experienced explosive growth in recent years fuelled by developments in DNA technology, theory and statistical analysis. I argue that the intellectual maturation of the field will eventually depend not only on these recent developments, but also on syntheses of comparative information across different regions of the globe. For this to become a reality, many empirical phylogeographic surveys in regions of the Southern Hemisphere (and in developing countries of the Northern Hemisphere) are needed. I expect the information and views presented here will assist in promoting international collaborative work in phylogeography and in guiding research efforts at both regional and global levels.

Keywords: biogeography, conservation biology, evolutionary biology, global biodiversity, population genetics, Quaternary science

Received 10 March 2008; revision accepted 30 May 2008

Introduction

Most species display some degree of population structure that can be interpreted in geographic and chronological contexts. Deciphering spatial and temporal components of population structure and interpreting the evolutionary and ecological processes responsible are major goals of phylogeography. Phylogeography is an integrative field of science that uses genetic information to study the geographic distribution of genealogical lineages, especially those found within species (Avice 2000). Based on appropriate sampling of individuals and genes, phylogeographers can be in a

position to test biogeographic hypotheses, describe the evolution of reproductive isolation of population units, and infer processes underlying the origin, distribution and maintenance of biodiversity. Given that the structure of population genealogies is influenced by demographic history, phylogeographers can also make inferences about temporal changes in the physical and biotic environment of a population using present-day genetic data. For these reasons phylogeography has provided valuable contributions to several areas of study in biology and Earth sciences, such as speciation (Avice *et al.* 1998; Moritz *et al.* 2000; Hewitt 2001; Kohn 2005), historical biogeography (Avice 2000; Riddle & Hafner 2006), human evolution (Beaumont 2004; Templeton 2005; Torroni *et al.* 2006), conservation biology (O'Brien 1994; Avice & Hamrick 1996; Smith & Wayne 1996;

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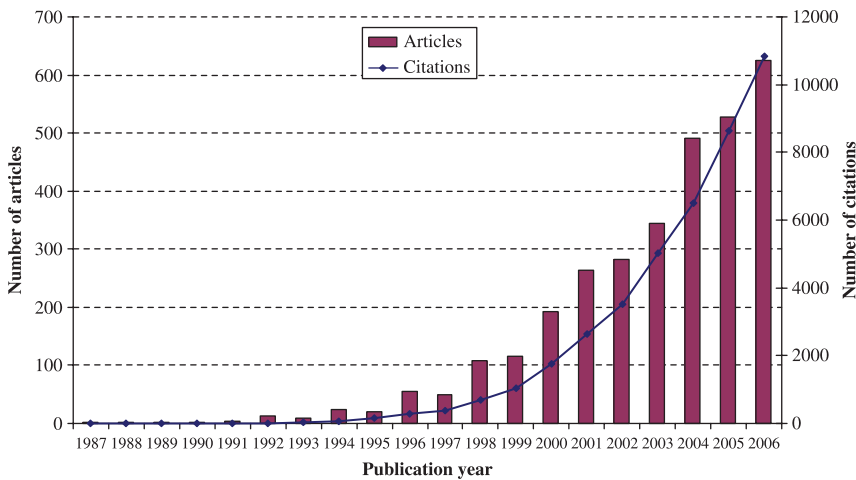


Fig. 1 Number of phylogeography articles published between 1987 and 2006 and corresponding number of citations.

Moritz & Faith 1998; Fraser & Bernatchez 2001; Frankham *et al.* 2002), biodiversity research and taxonomy (Avice & Ball 1990; Taberlet 1998; Beheregaray & Caccone 2007), palaeoecology (Cruzan & Templeton 2000), palaeoclimatology (Hewitt 2000) and volcanology (Emerson 2002).

Last year marked the 20th anniversary of the formal birth of phylogeography. The term was coined by John Avice *et al.* in 1987 to describe a discipline with conceptual and technical roots linked to the incipient field of molecular genetics of the 1970s. Several reviews have described findings in phylogeography and evaluated its contribution to ecology and evolutionary biology (e.g. Riddle 1996; Roderick 1996; Avice 1998, 2000; Taberlet 1998; Walker & Avice 1998; Newton *et al.* 1999; Hewitt 2000; Beheregaray & Caccone 2007). Other articles have assessed how recent advances in DNA technology, coalescent theory and statistical analyses have prompted methodological and conceptual shifts in the field (e.g. Edwards & Beerli 2000; Sunnucks 2000; Hare 2001; Templeton 2001, 2004; Hey & Machado 2003; Knowles 2004; Emerson & Hewitt 2005). Despite the variety of topics reviewed, the literature contains only a few reviews reporting data needed to evaluate the progress, tendencies and deficiencies of the field at a global scale. The last publication to present such information was the book of Avice (2000), the benchmark contribution to the field published before the extraordinary growth of phylogeography observed in recent years (see Fig. 1).

Here I provide a description about the state of phylogeography based on a detailed examination of articles published during the first 20 years of the field (i.e. from 1987 to 2006). I have two broad objectives with this review. The first one is to present a numerical synthesis of the phylogeography literature with information on several topics, including the geographic distribution of surveys, biological groups studied, genetic markers employed, number of taxa used and temporal scales investigated. My second objective is to draw attention to disparities in research productivity in

phylogeography between different regions of the world and comment on the difficult task posed by researchers from less affluent institutions (such as those generally found in many Southern Hemisphere countries) to conduct studies and publish their findings. I expect the information and views presented here will assist in promoting international collaborative work in phylogeography and in guiding research efforts at both regional and global levels aimed at reducing gaps in our knowledge about spatial and temporal components of population history.

Methods

Review database and general statistics

The database used for this review was compiled by conducting searches in Web of Science®. Titles, abstracts and keywords of all articles published between 1987 and 2006 were searched for two terms: ‘phylogeography’ and ‘phylogeographic’. Web of Science is an online academic database from ISI Web of Knowledge® that provides access to information from over 8700 research journals. The following general statistics were obtained through the ‘Analyse Results’ option in Web of Science: subject categories, source titles (i.e. journal titles), document types, publication years, affiliations and countries. The mean number of publications per year of each country was compared with its per capita gross domestic product (GDP) estimated based on the purchasing power parity calculation. For this I used the most recent GDP statistics from *The World Factbook* published on the website of the Central Intelligence Agency.

Review categories and specific statistics

Data from 40 selected categories and other specific statistics were obtained by reading the abstract of each article retrieved. If the required information was not available in

the abstract, then the text of the manuscript was consulted. This strategy, although time consuming and subject to human error, is preferred to using the 'Analyse Results' option. It can provide information about phylogeography that is otherwise unavailable from automated searches and overcomes problems about the way records are stored in the database (see examples below). For this section I excluded the following document types: review articles ($n = 136$), meeting abstracts ($n = 48$), editorial material ($n = 38$) and correction or additions ($n = 16$). Technical notes (e.g. primer and software notes) and articles with a purely taxonomic or systematic focus were also excluded ($n = 377$). This pruning was conducted after reading each abstract (as opposed to conducting a priori sorting by document type in Web of Science). The exclusion of such articles ensured that the statistics presented in this review are a reflection of the work conducted only by empirical phylogeographic studies, and not of other scholarly outputs.

After reading the abstract, information from each article was classified in seven major clusters containing the 40 categories (listed below) and entered into an electronic data sheet for subsequent analysis. Importantly, these classifications were based on the locations where the organisms were sampled – as opposed to automatically sorting studies using the affiliation of authors as implemented by Web of Science. The latter creates biases in data analysis given that in some regions (e.g. the Neotropics), several studies are conducted in collaboration or sometimes exclusively by international institutions, and the location of the study organism is often not recorded in the database. In the first two clusters, studies were sorted by their global scope, hemisphere (Northern, Southern or transequatorial) and continent (and associated oceans). In another cluster, study organisms were assigned to 10 groups: mammals, herps (i.e. reptiles and amphibians), birds, fishes, terrestrial plants, aquatic plants, terrestrial invertebrates, aquatic invertebrates, fungi and micro-organisms. Study organisms were also arranged by type of environment (terrestrial, marine or freshwater) and grouped on the basis of the nature of a particular phylogeographic study. The latter included three mutually exclusive categories: comparative phylogeography, taxon-specific studies, and surveys that used more than one taxon but did not present the study in a comparative manner. A perspective about the timescale of interest of phylogeographic studies was obtained by classifying articles that studied biogeographic scenarios of the Quaternary Period (approximately the last 2 million years), Tertiary Period (c. 2 to 65 million years ago), both Quaternary and Tertiary, or undetermined (i.e. studies in which timescales were not explored). Finally, in the seventh cluster articles were sorted on the basis of four major classes of genetic marker employed: Class I, mitochondrial DNA (mtDNA) or chloroplast DNA (cpDNA); Class II, nuclear DNA sequences, amplified fragment length polymorphisms

(AFLPs), single nucleotide polymorphisms (SNPs), or randomly amplified polymorphic DNA (RAPD); Class III, microsatellites; and Class IV, allozymes. Studies that used more than one class of marker were also classified in five categories of marker combinations: combination of classes 'I & II', 'I & III', 'I & IV', 'three or four markers combined' or 'other combinations'.

Results

Section I: Global Scale

The spectacular growth of a new field of science

A total of 3049 articles published between 1987 and 2006 were identified in the database searches. Phylogeography has experienced exponential growth as measured by the number of articles published each year (Fig. 1). The large number of papers retrieved probably barely reflects the popularity of the field since it was not possible to identify a considerable proportion of phylogeographic studies. These were surveys that might fall within the umbrella of phylogeography but did not use the terms 'phylogeography' or 'phylogeographic' in abstracts, keywords or titles. I verified this discrepancy by comparing the results of my searches with the track record of four phylogeographers for whom I had access to complete publication lists. On average, the review's searches detected 65% of the number of journal articles published in phylogeography by these four researchers (individual 'success rate' ranged from 40% to 92%). This apparent disparity is probably not influencing negatively the results of this review because most comparisons and conclusions were made relative to the total number of articles identified.

Citations numbers

The number of citations of phylogeographic studies has also grown exponentially (Fig. 1). Citations climbed from 368 in 1997 to 10 835 in 2006, with an average annual number of citations of 3172 for the 20-year period. Below I provide a brief account of the main topics covered by the 20 or so most cited journal articles in phylogeography. The paper that named the field and introduced its conceptual ideas (Avise *et al.* 1987) appears as the second most cited publication. Three articles by Godfrey Hewitt about the influence of Pleistocene ice ages on population genetic structure (Hewitt 1996, 1999, 2000) are among the top seven papers with a combined total of over 2000 citations. This highlights well the impact of the interdisciplinary field of Quaternary science in phylogeographic research. Another popular topic is comparative phylogeography: empirical studies and reviews that used genealogical information from multiple codistributed species to identify commonalities

in biogeographic history are the subject of five highly cited papers (Avise 1992; Dumolin-Lapegue *et al.* 1997; Avise & Walker 1998; Bernatchez & Wilson 1998; Taberlet *et al.* 1998). From all articles retrieved, a note published by Clement *et al.* (2000) describing TCS (a computer program to estimate gene genealogies) is the one that tops the list with over 1000 citations. This and other articles related to the method of Nested-Clade Phylogeographic Analysis (e.g. Templeton 1998; Posada *et al.* 2000) are among the top 10 cited studies in phylogeography. The continuous popularity of these three studies since their publication exemplifies well the central position of tree-based frameworks for reconstructing genealogies and population histories. As a comparison, recent years have seen the popularization of studies using methodological developments related to statistical phylogeography and coalescent theory. Accordingly, two publications that advocate the use of statistical models for parameter estimation in phylogeography – the papers of Edwards & Beerli (2000) and Knowles & Maddison (2002) are among the top 25 most cited studies in the field.

Subject categories and journals

The position of phylogeography as a far-reaching scientific discipline is evident in Table 1, which lists the top 50 subject categories in the field. Around 72% of phylogeographic studies can be primarily classified in the fields of ecology and evolution (41% of the total) and molecular biology and genetics (31% of the total). Nonetheless, phylogeographic studies have also addressed a multitude of additional topics in life sciences (e.g. from biodiversity conservation to legal medicine), as well as in earth sciences (e.g. from physical geography to archaeology). Also listed in Table 1 are journal names, representing a great variety of scientific disciplines. Although a large proportion of articles have been published in journals of broad scope (e.g. *Molecular Ecology*, *Molecular Phylogenetics and Evolution*, and *Evolution*), phylogeography has also been very popular with topic-oriented journals (e.g. *Conservation Genetics*, *Biological Conservation* and *Conservation Biology*). The same is true for journals that focus on specific taxonomic groups, such as plants, insects or mammals. In this category, vertebrates and in particular mammals (e.g. *Journal of Mammalogy*, *American Journal of Human Genetics* and *American Journal of Physical Anthropology*) are amongst the most popular.

The geography of publications

Unless otherwise stated, the results of all subsequent sections are based on data collected from reading the abstracts of 2434 articles. This number was obtained by pruning the initial database of 3049 articles published between 1987 and 2006 using criteria described above.

The globe and the continents. Study systems from the Northern Hemisphere were the subject of 77% of all the articles, whereas only 15% of publications focused on systems from the Southern Hemisphere (Fig. 2a). A much smaller proportion (2%) used samples collected across both sides of the equator. On the other hand, a good proportion of studies (6% or 146 papers) were considered of global scale since they included samples from multiple continents or oceans. The research done at the global scale almost invariably included several authors and institutions. I also identified studies that could not be classified as being of global scope, but which nevertheless used samples collected over vast continental regions. This class was represented in 6.2% of all of the Northern and in 2.2% of all of the Southern Hemisphere studies.

When publications are classified based on the continental origin of the organisms (Fig. 3), Europe was the most intensively studied continent with 31% of all articles (779 papers) followed closely by North America with 30%. Within the North American continent, the species-rich region of Central America accounted for only 9.7% of studies. Asia, the world's largest and most populous continent ranked third in this list with 16.4%. Similarly to North America, the species-rich region of Southeast Asia was represented by a relatively small proportion (20%) of the Asian studies. Africa ranked fourth and Australia fifth, with 8% and 7.4%, respectively. Within the Australian continent, c. 5% of papers focused on the islands of Melanesia and nearby archipelagos (i.e. most studies focused on Australia or New Zealand). Ironically, South America, the continental region generally recognized as harbouring the greatest biodiversity on Earth, ranked last among all the human populated continents with only 6.3% of the articles. Finally and predictably, a very small proportion of studies (0.6%) focused primarily on the Antarctic continent.

Countries and the GDP. The top 100 most productive countries in phylogeography are listed in the Appendix. A total of 124 countries had researchers involved with publications in phylogeography. The USA appeared as the most productive nation in terms of absolute number of publications: US-based researchers participated in 1250 articles, or 41% of the total. The other top 10 ranked countries were the UK (422 articles), France (289), Germany (279), Australia (237), Canada and Spain (each with 218 articles), Italy (163), Japan (137) and Sweden (113). Out of the top 20 ranked countries, only three are from the Southern Hemisphere: Australia, Brazil and New Zealand. Unsurprisingly, affluent nations are responsible for the vast majority of articles in phylogeography (Fig. 4), a pattern consistent with the geographic distribution of publications in biomedical research (e.g. Benzer *et al.* 1993). Mean annual productivity appears to be broadly divided based on a threshold of around US\$20 000. All countries with more than three

Table 1 Number of publications in phylogeography for the top 50 subject categories and scientific journals

Subject category	No.	Journal	No.
Evolutionary Biology	1419	<i>Molecular Ecology</i>	648
Ecology	1131	<i>Molecular Phylogenetics and Evolution</i>	229
Biochemistry and Molecular Biology	1008	<i>Evolution</i>	167
Genetics & Heredity	865	<i>Biological Journal of the Linnean Society</i>	96
Zoology	315	<i>Heredity</i>	84
Plant Sciences	248	<i>Journal of Biogeography</i>	78
Marine and Freshwater Biology	222	<i>Conservation Genetics</i>	58
Biodiversity Conservation	123	<i>Proceedings of the Royal Society B</i>	58
Biology	107	<i>Journal of Mammalogy</i>	46
Fisheries	95	<i>Marine Biology</i>	46
Geography, Physical	90	<i>Journal of Evolutionary Biology</i>	40
Multidisciplinary Sciences	67	<i>Molecular Biology and Evolution</i>	40
Entomology	55	<i>Proceedings of the National Academy of Sciences, USA</i>	38
Environmental Sciences	53	<i>American Journal of Botany</i>	37
Ornithology	52	<i>Journal of Heredity</i>	30
Biotechnology and Microbiology	31	<i>Journal of Fish Biology</i>	29
Forestry	28	<i>Plant Systematics and Evolution</i>	29
Oceanography	28	<i>Molecular Ecology Notes</i>	27
Agronomy	23	<i>Zoological Science</i>	26
Anthropology	23	<i>Genetics</i>	22
Parasitology	21	<i>Taxon</i>	22
Horticulture	20	<i>Canadian Journal Fisheries and Aquatic Sciences</i>	19
Microbiology	20	<i>Integrative and Comparative Biology</i>	19
Limnology	18	<i>Journal of Zoological Systematics and Evolutionary Research</i>	19
Mycology	13	<i>Systematic Biology</i>	19
Virology	12	<i>Theoretical and Applied Genetics</i>	19
Agriculture, Dairy and Animal Science	10	<i>American Journal of Human Genetics</i>	18
Veterinary Sciences	8	<i>Annals Entomological Society of America</i>	18
Cell Biology	7	<i>Biological Conservation</i>	18
Tropical Medicine	7	<i>Forest Ecology and Management</i>	17
Geosciences, Multidisciplinary	6	<i>Auk</i>	16
Paleontology	6	<i>Genetica</i>	15
Medicine, Legal	5	<i>Journal of Plant Research</i>	15
Biochemical Research Methods	4	<i>Condor</i>	14
Engineering, Environmental	4	<i>Conservation Biology</i>	14
Public and Occupational Health	4	<i>Journal of Zoology</i>	13
Environmental Studies	3	<i>American Journal of Physical Anthropology</i>	12
Medicine, General and Internal	3	<i>Australian Journal of Zoology</i>	12
Toxicology	3	<i>Botanical Journal of the Linnean Society</i>	12
Archaeology	2	<i>Canadian Journal of Zoology</i>	12
Geography	2	<i>Copeia</i>	12
Immunology	2	<i>Hydrobiologia</i>	12
Infectious Diseases	2	<i>Marine Ecology-Progress Series</i>	12
Urban Studies	2	<i>Trends in Ecology & Evolution</i>	12
Anatomy and Morphology	1	<i>Annals of Human Genetics</i>	11
Astronomy and Astrophysics	1	<i>Genome</i>	11
Industrial Relations and Labour	1	<i>Journal of Phycology</i>	11
Mathematical and Computational Biology	1	<i>American Naturalist</i>	10
Sociology	1	<i>Animal Conservation</i>	10
Urology and Nephrology	1	<i>Herpetologica</i>	10

publications per year have a GDP per capita higher than US\$20 000. The exception is the productivity of Russia, Brazil, China and South Africa. These nations have GDP per capita below this threshold but had an annual publication rate of 4.6, 4.3, 4.1 and 3.4 articles, respectively (Fig. 4).

Taxonomic coverage

The global publication effort in phylogeography is noticeably biased towards vertebrates, which accounted for 57% of all publications. Out of the 10 groups of organisms (Fig. 5),

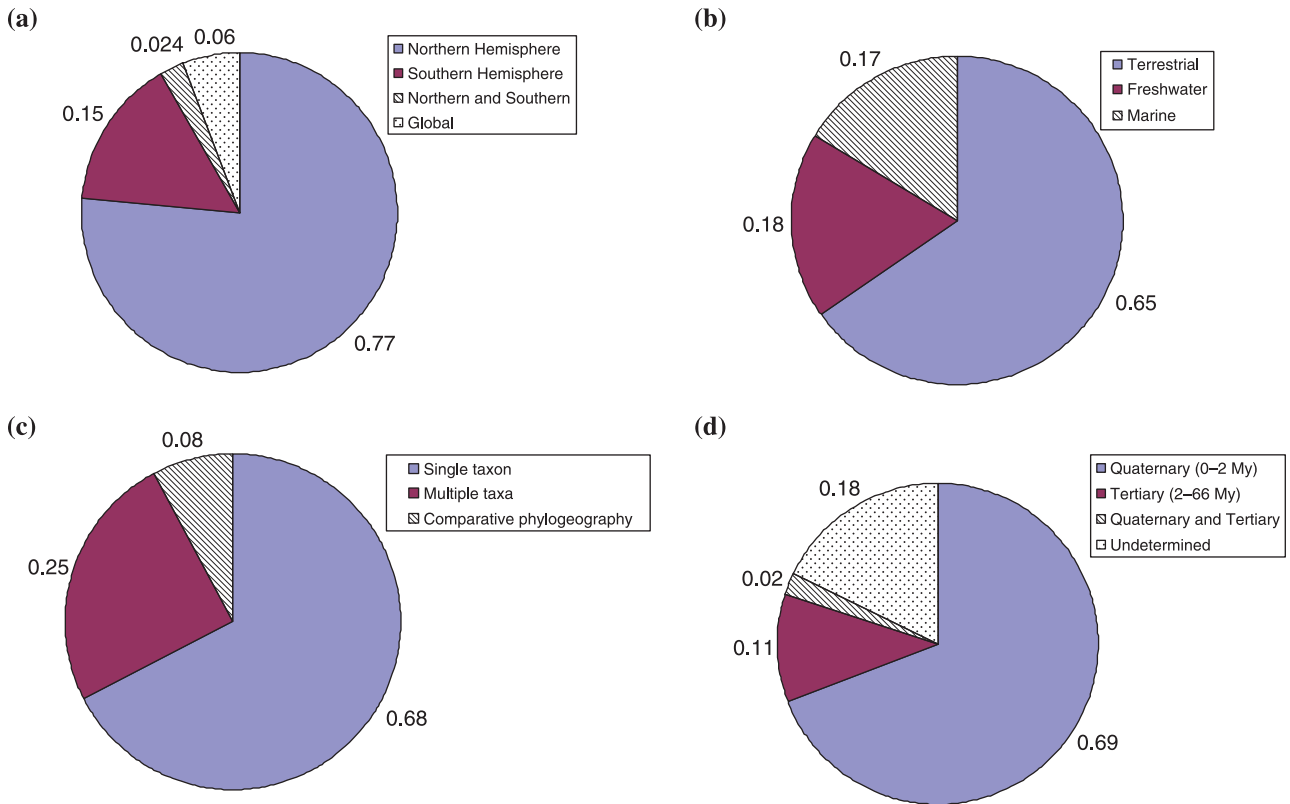


Fig. 2 Proportion of articles in phylogeography published between 1987 and 2006 according to (a) hemisphere or global scale, (b) type of environment, (c) nature of study and (d) timescale (see text for details).

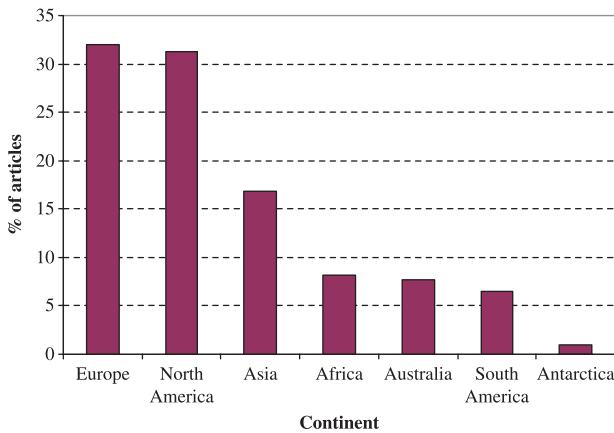


Fig. 3 Continental origin of articles in phylogeography published between 1987 and 2006 based on the location of organisms studied.

mammals were the most popular taxon in phylogeographic research (508 papers or 21% of all articles). Fishes and terrestrial plants ranked second with an equal number of 392 articles each. The next most popular category was the group of terrestrial invertebrates, followed by herps (reptiles and amphibians), aquatic invertebrates and birds (the latter with 182 articles). The remaining categories in this list

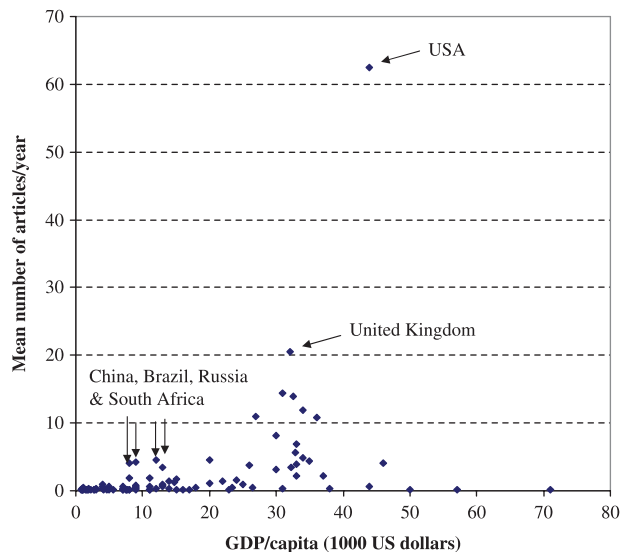


Fig. 4 Research productivity and country's wealth for the 100 most productive nations in phylogeography (see text for details about highlighted countries). Productivity is measured by the mean number of publications per year and wealth by the nation's per capita gross domestic product (GDP).

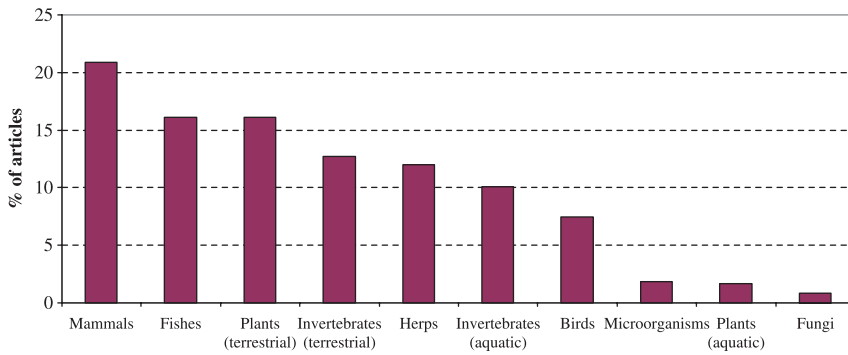


Fig. 5 Taxonomic coverage of articles in phylogeography published between 1987 and 2006.

were micro-organisms and aquatic plants, both accounting for less than 2% of the total number of publications (c. 40 articles each) and lastly the fungi with only 1.8% of the total.

Type of environment, nature of the study and timescale

Most studies in phylogeography focused on the terrestrial environment (65% of the total; Fig. 2b). Despite enormous differences in surface area of habitats, a smaller proportion of studies was conducted on marine organisms (17%) than on freshwater organisms (18%).

The sorting of papers by nature of the study (Fig. 2c) showed that 68% of the articles examined genealogical relationships within one taxon. A large proportion of studies (25% or 674 papers) described phylogeographic patterns in more than one taxon but surprisingly did not explore outcomes using a comparative framework. Although this appeared to be related to sampling design in some studies, others could probably have benefited from testing for congruence in the evolutionary and demographic history of taxa (*sensu* Bermingham & Moritz 1998). Only 8% (188 papers) explicitly compared patterns of multiple codistributed taxa and as such were classified in the category of comparative phylogeography. Nevertheless, the popularization of phylogeography in recent years resulted in an increase in absolute numbers of comparative studies, from 12 articles in 2000 to 54 in 2006. Comparative phylogeographic studies were more common in the Northern than in the Southern Hemisphere (75% and 23%, respectively) and were rarely conducted at global scales (2%).

The analysis according to timescale strongly supports the position of phylogeography as a popular discipline in Quaternary science (Fig. 2d). Around 69% of the output of the field (1679 papers) reported diversifications of biological units temporally associated with the Quaternary Period. A reasonable proportion (11% or 267 papers) reported deeper divergences probably related to geological events of the Tertiary, whereas 2% suggested that the evolution of their study groups spanned both geological periods. Unfortunately, a considerable proportion of articles (18% or 438

papers) did not explore temporal aspects of inferred biogeographic divergences, or lack thereof, and were therefore classified as 'undetermined'.

Genetic markers

Below I summarize results and trends observed at a global level — patterns and idiosyncrasies about marker use in taxonomic groups are presented in Section II. Genealogical information derived from mtDNA was used in 1750 papers (72% of all articles), whereas data from cpDNA appeared in 217 papers (9%, Fig. 6). Together these two markers comprise what I named Class I, a class represented in 81% of all studies. Data from nuclear DNA sequence, SNPs, AFLP or RAPD (Class II) were represented in 536 publications. Microsatellites (Class III) were used in 214 papers and allozymes (Class IV) in 179.

Several interesting trends can be identified when a class of marker is sorted according to the proportion of articles published in a given year (Fig. 7). The proportion of studies based exclusively on uniparentally inherited markers (Class I) decreased from around 90% to 62% during the last 10 years. On the other hand, surveys based solely on Class II markers increased in popularity during the 1990s and apparently stabilized around 13% during the last 5 years (the 50% value for Class II in 1989 is biased since only two empirical surveys were published that year). Microsatellites only started being used as the sole source of information in 1997, but in the last years they already accounted for around 8% of publications. Allozymes on the other hand were quite popular in the 1990s (c. 10% of surveys) but in recent years they were used in only c. 4% of studies. These general trends are consistent with the way the information from different genetic markers was combined. During the 20-year period, the great majority of studies, or 89% of the total, used only one type of marker. This value dropped to around 80% in the last 5 years, a reduction driven in part by the rapid increase of studies combining markers from Classes I and II. This was by far the most popular combination in the last 5 years, accounting for around 10% of all studies. For the same period, combinations of Classes I and

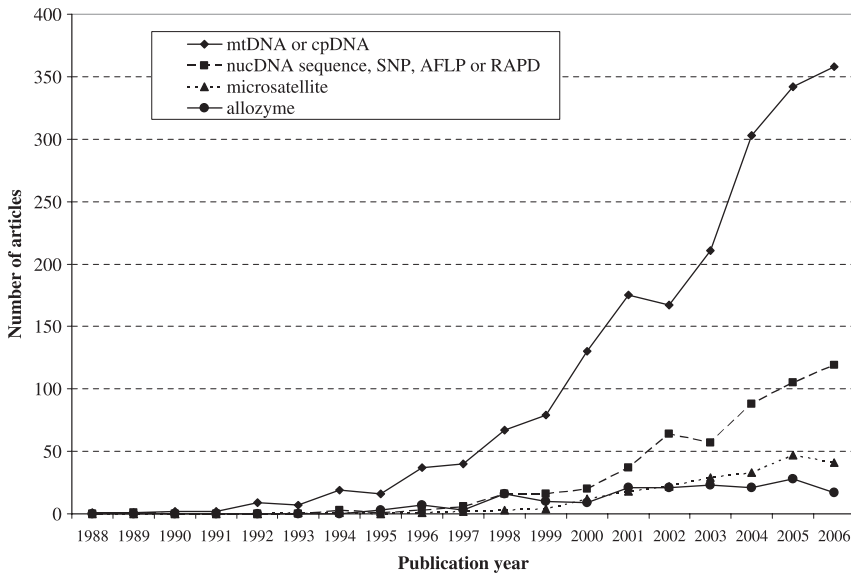


Fig. 6 Number of phylogeography articles published per year sorted according to genetic marker(s) used for data collection (categories are not exclusive, see text for details).

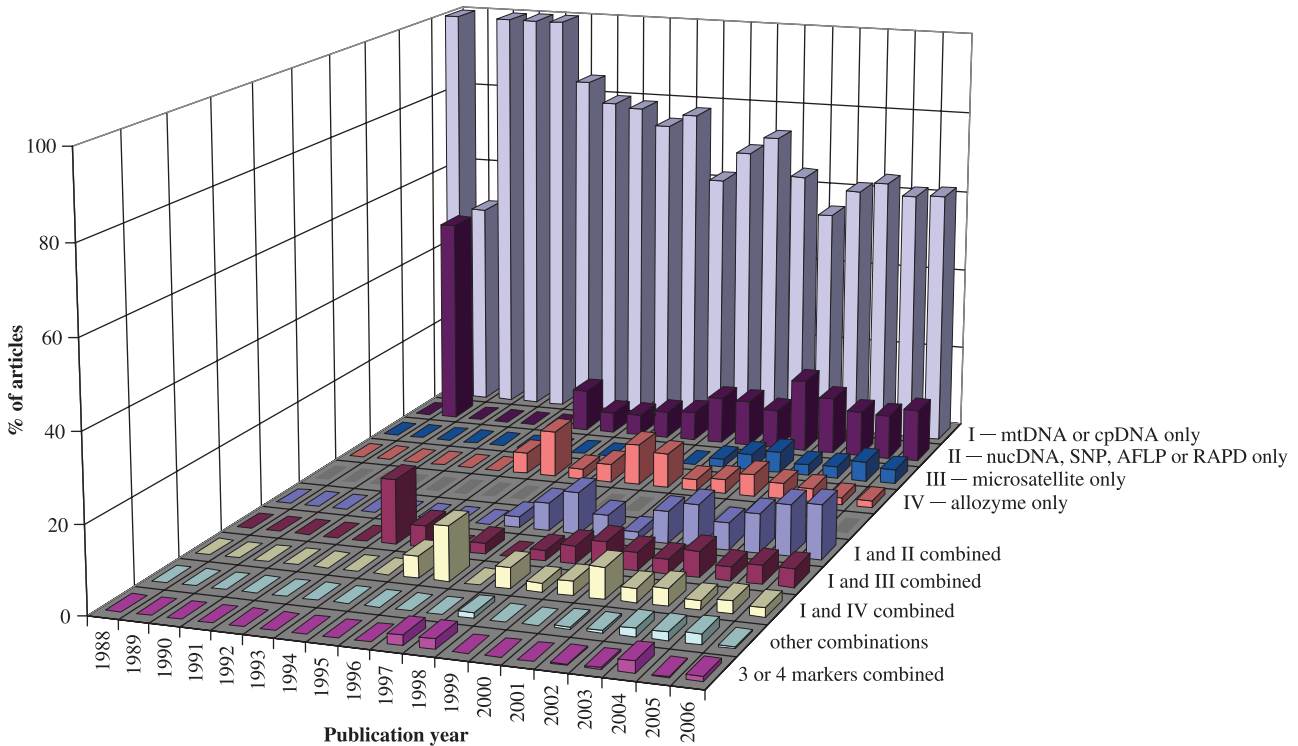


Fig. 7 Proportion of articles published per year in phylogeography sorted by classes of genetic marker or marker combinations (categories are mutually exclusive, see text for details).

III appeared in *c.* 4% and of Classes I and IV in *c.* 2% of the studies. Other types of double marker combinations (i.e. those not involving uniparentally inherited markers) accounted for a very small proportion of articles (1.4%). Finally, only 26 out of the 2424 articles analysed used three or more marker types.

Section II: Taxonomic Groups

Here I summarize results for taxonomic groups listed in decreasing order of popularity. The data presented are based on the geographic origin of the organisms studied (i.e. they are not based on the origin of researchers who conducted the work). I draw attention to group-specific

Table 2 Distribution of phylogeographic studies published between 1987 and 2006 for 10 groups of organisms. Values are the proportion of studies by continent and by hemisphere or global region based on the geographic origin of organisms (see text for details)

Organisms	Continent					Hemisphere				
	Europe	North America	Asia	Africa	Australia	South America	Northern	Southern	Across Northern and Southern	Global
Mammals	0.27	0.24	0.23	0.15	0.04	0.07	0.74	0.16	0.05	0.05
Fishes	0.32	0.36	0.14	0.06	0.07	0.06	0.77	0.16	0.02	0.06
Herps	0.22	0.42	0.09	0.10	0.12	0.10	0.70	0.26	0.01	0.03
Birds	0.25	0.37	0.15	0.06	0.08	0.09	0.76	0.17	0.01	0.05
Plants: terrestrial	0.43	0.23	0.21	0.04	0.05	0.04	0.88	0.08	0.01	0.03
Plants: aquatic	0.32	0.35	0.21	0.03	0	0.09	0.63	0.02	0.05	0.29
Invertebrates: terrestrial	0.34	0.32	0.12	0.06	0.08	0.08	0.79	0.15	0.02	0.04
Invertebrates: aquatic	0.35	0.29	0.14	0.04	0.16	0.02	0.71	0.16	0.04	0.10
Micro-organisms	0.09	0.43	0.23	0.11	0	0.14	0.40	0.16	0.04	0.40
Fungi	0.29	0.36	0.21	0.07	0.07	0	0.57	0	0.05	0.38

results that contrast with outcomes for all taxonomic groups described in Section I. I also use a few selected examples from the literature to illustrate general findings and topics of interest. Descriptions of empirical phylogeographic findings are not within the scope of this review. These have been presented and discussed in detail elsewhere (e.g. Avise 2000) using case studies spanning the diversity of life and a vast variety of phylogeographic scenarios.

Mammals

Mammals have been pivotal in the development of the theory and practice of phylogeography. This has been in part due to the extensive research investment in deciphering the history of human populations at both global and regional levels (e.g. Cann *et al.* 1987; Bonatto & Salzano 1997; Richards *et al.* 1998; Underhill *et al.* 2001; Templeton 2005). Genealogical surveys of our own species have greatly benefited our understanding of patterns in other species, especially those influenced by recent biogeographic scenarios. Considerable achievements in the field have also been made in several other groups of mammals at intraspecific and interspecific levels (e.g. Morin *et al.* 1994; Eizirik *et al.* 2001), as well as in analyses of comparative phylogeography (Da Silva & Patton 1998; Lessa *et al.* 2003).

The number of publications by continent of origin in mammals is not as skewed towards Europe and North America as in other taxonomic groups (Table 2). This is because Asia and Africa account for a relatively high percentage of mammal studies (23% and 15%, respectively). Studies on South American and Australian mammals, on the other hand, accounted for comparatively few publications (7% and 4%, respectively). Globally, the effort concentrated on terrestrial mammals (93%) as opposed to marine (6%) or freshwater mammals (1% of all articles) (Table 3). Mammals were the group with the highest percentage of taxon-specific

studies (77% compared to an average of 68% for all taxonomic groups combined). Yet, most studies that did use more than one taxon explicitly compared patterns across taxa, resulting in an average of comparative phylogeographic studies of 8%. A total of 86% of articles on mammals used data from mtDNA (68% used mtDNA alone and 18% combined it with other markers) (Table 4). Studies based exclusively on nuclear DNA sequence data were much more popular in mammals (8%) than in other vertebrate groups (2% to 3%), a difference attributable to the availability of a large number of target loci in humans and other intensively studied mammals (e.g. Templeton 2005). The reverse is true regarding allozyme markers, which were rarely used in mammals (*c.* 1% of the total).

Fishes

Fishes, the most abundant and species-rich vertebrate group comprised, together with terrestrial plants, the second most frequently studied taxon in phylogeography. Fishes have for a long time fascinated natural historians and evolutionary biologists (Wallace 1876; Nelson 2006). Freshwater fishes often display marked phylogeographic structure strongly connected to historical and ecological changes of the aquatic environment and landscapes (Bermingham & Avise 1986; Bernatchez & Wilson 1998; Rundle *et al.* 2000; Waters *et al.* 2007). In contrast, notwithstanding examples of remarkable philopatry (e.g. Taylor & Hellberg 2003), marine fishes usually show shallow phylogeographic structure associated with the general absence of dispersal barriers and high levels of spatial connectivity (Bowen & Grant 1997). Fish phylogeography has also expanded considerably our understanding of the role of ecology in the speciation process, especially in scenarios where adaptive divergence and reproductive isolation are associated (Orr & Smith 1998; Lu & Bernatchez 1999; Beheregaray & Sunnucks 2001; Schluter 2001).

Table 3 Association with types of environment, and whether studies focused on single or multiple taxa or were of comparative nature for 10 groups of organisms. Values represent the proportion of phylogeographic studies published across the globe between 1987 and 2006 for each category (see text for details)

Organisms	Environment			Nature of the study		
	Terrestrial	Marine	Freshwater	Single taxon	More than one taxon but not comparative	Comparative phylogeography
Mammals	0.93	0.06	0.01	0.77	0.15	0.08
Fishes	—	0.45	0.55	0.64	0.26	0.10
Herps	0.61	0.07	0.32	0.67	0.26	0.07
Birds	0.94	0.06	—	0.64	0.23	0.13
Plants: terrestrial	1.0	—	—	0.67	0.26	0.07
Plants: aquatic	—	0.73	0.27	0.61	0.34	0.05
Invertebrates: terrestrial	1.0	—	—	0.60	0.32	0.08
Invertebrates: aquatic	—	0.60	0.40	0.62	0.28	0.11
Micro-organisms	0.73	0.09	0.18	0.60	0.31	0.09
Fungi	1.0	—	—	0.71	0.24	0.05

Table 4 Application of different classes of genetic marker for 10 groups of organisms. Values represent the proportion of phylogeographic studies published across the globe between 1987 and 2006 that used only one class of genetic marker or combinations of genetic markers (categories are mutually exclusive, see text for details)

Organisms	Class of genetic marker (only one class used)				Combination of genetic markers				
	I mtDNA or cpDNA	II nuclear DNA sequence, SNP, AFLP or RAPD	III Microsatellite	IV Allozyme	I and II	I and III	I and IV	Other double combinations	Three or four markers combined
Mammals	0.68	0.08	0.04	0.01	0.08	0.08	0.02	0.01	0.01
Fishes	0.69	0.03	0.05	0.04	0.09	0.05	0.05	0	0.01
Herps	0.77	0.02	0.03	0.02	0.07	0.04	0.04	0.01	0
Birds	0.81	0.02	0.04	0.01	0.07	0.04	0.01	0	0.01
Plants: terrestrial	0.46	0.28	0.03	0.07	0.09	0.02	0.02	0.03	0.01
Plants: aquatic	0.22	0.39	0.07	0	0.27	0	0	0.05	0.03
Invertebrates: terrestrial	0.66	0.07	0.02	0.06	0.10	0.03	0.05	0	0.05
Invertebrates: aquatic	0.64	0.07	0.01	0.03	0.13	0.02	0.07	0	0.02
Micro-organisms	0.11	0.78	0	0	0.11	0	0	0	0
Fungi	0	0.85	0.05	0	0.05	0	0	0.05	0

The wealth of existing phylogeographic information about fishes is essentially restricted to teleosts, which accounted for 98.5% of all articles. Elasmobranchs, on the other hand, were represented by only six articles, a very imbalanced number given that sharks and rays comprise over 1100 known species (Compagno *et al.* 2005). Over two-thirds of all fish studies (68%) came from North America and Europe, two regions with relatively impoverished ichthyofaunas. On the other hand, South America, the continental region with the highest diversity of freshwater fish on Earth (Reis *et al.* 2004) accounted for only 6% of the studies. Overall, despite the higher diversity of marine fishes, freshwater fishes were more intensively studied accounting for 55% of all articles. Many fish surveys were based on more than one species and included a good proportion of

noncomparative (26% of the total) as well as comparative phylogeographic studies (10%). In terms of genetic markers, 88% of fish articles (344 studies) included data from mtDNA. Around 20% of this value was represented by surveys that combined mtDNA with other markers. The proportion of fish studies based on allozymes (either alone or in combination with other markers) was the highest among vertebrates since obtaining fresh or frozen tissue is possible for many species targeted by commercial fisheries.

Plants

Phylogeographic surveys have been notoriously difficult to conduct in plants because of the difficulties involved in finding genetic markers with resolving power comparable

to animal mtDNA (Schaal *et al.* 1998; Newton *et al.* 1999). Nonetheless, plant phylogeography has come a long way in the last few years with the popularization of nuclear markers for analyses of gene flow, especially microsatellites and AFLPs, and with the collection of data from larger sections of cpDNA. This has resulted in a rapid increase in publications reporting genetic variation in plants related to historical events of fragmentation, range expansion, bottlenecks and speciation (Byrne *et al.* 2002; Petit *et al.* 2002, 2005; Abbot & Brochmann 2003; Miller & Schaal 2005). For example, around 92% of all articles in terrestrial plants were published since 2000. In comparison, the proportion of recently published articles is much lower in other popular groups such as mammals and fishes (84% and 82%, respectively). Research in phylogeography has also advanced considerably our knowledge about the conservation of tree species (Newton *et al.* 1999) and the consequences of species invasion (Saltonstall 2002; Koehler-Santos *et al.* 2006) and Quaternary dynamics (Demesure *et al.* 1996; Dumolin-Lapegue *et al.* 1997; Magri *et al.* 2006) on ecology and evolution of plant populations.

Terrestrial plants from the Southern Hemisphere have been largely left behind in phylogeographic research, with a massive proportion of 88% of studies coming from the Northern Hemisphere. This represents the largest disparity across taxonomic groups analysed in this review (Table 2). Europe dominates the stage with 43% of all publications; North America and Asia are also well represented with 23% and 21% of the articles, respectively. South America, the continent with the highest diversity of plant species (Myers *et al.* 2000), was represented by only 15 surveys, around 4% of the total. Only 11 studies of terrestrial plants have analysed patterns at a global scale, the lowest fraction among all taxonomic groups. For aquatic plants, 30 of the 41 studies identified were in the marine environment and the proportion of articles of global scale was relatively large (29%). The continents of North America, Europe and Asia accounted for 88% of all publications. Only a few studies on aquatic plants (5%) compared phylogeographic patterns across species. The research in terrestrial and aquatic plants showed similar trends in the use of genetic markers. Plant studies relied much less on uniparentally inherited DNA information and used more information from nuclear markers of Class II (28% for terrestrial and 39% for aquatic plants) than most of the other taxonomic groups.

Invertebrates

For practical reasons the extraordinary diversity found in invertebrates was divided into two groups: terrestrial (includes aerial taxa) and aquatic species. The myriad of life histories and evolutionary ecologies found in terrestrial and aquatic invertebrates was represented in the phylogeography literature by only 313 and 253 articles, respectively.

Nonetheless, many studies have provided consequential information about the role of historical and contemporary factors influencing the evolutionary history of invertebrate populations (Roderick 1996; Avise 2000). Phylogeographic studies have informed on the chronologies of adaptive radiations of island arthropods (Fleischer *et al.* 1998; Roderick & Gillespie 1998), the delineation of biogeographic breaks in copepods (Burton & Lee 1994), in estuarine crustaceans (Teske *et al.* 2006), and in springtails (Garrick *et al.* 2007), and the development of extrinsic hypotheses to understand the effects of climatic changes in land snails (Hugall *et al.* 2002) and flatworms (Sunnucks *et al.* 2006). Historical considerations about the distribution of genetic diversity have also contributed to our understanding of invasion biology (Hall & Muralidharan 1989), epidemiology (Rich *et al.* 1995), and to address issues about cryptic biodiversity (Knowlton 1993).

Studies of terrestrial and aquatic invertebrates showed similar trends with regard to the geography of phylogeographic surveys, nature of study and genetic markers used. Europe and North America accounted for the majority of publications but Australian freshwater invertebrates were relatively well represented (Table 2). This remarkable result (Australia is the driest inhabited continent on the planet) can be partially explained because of the work of one productive group at Griffith University. On the other hand, Africa and South America were poorly represented in the invertebrate literature. The prospect that the relative ease with which multiple codistributed terrestrial invertebrates can be collected would result in a good number of comparative studies was not met – only 8% of phylogeographic surveys were classified as comparative, a value lower than those found for fishes and birds. The proportion of global studies followed expectations based on general differences in patterns of organism distribution, being greater for aquatic than for terrestrial invertebrates (10% and 4%, respectively). Despite the supremacy of mtDNA for invertebrates (in particular the popular mitochondrial COI gene), the number of studies using Classes II and IV was greater than in other animal taxa. Conversely, research on invertebrates based on microsatellites (Class III) is still in its infancy compared to any other animal group: only 1.5% and 2.5% of articles used these markers alone or in combination, respectively. This could be in part explained by the propensity of phylogeographers to work on more than one invertebrate taxon for which cross-species amplification of microsatellites is often not feasible, coupled with complications concerning the isolation of microsatellite loci for several invertebrate groups (e.g. Piggott *et al.* 2006).

Herpetofauna

Reptiles and amphibians have been the focus of increasing phylogeographic research in recent years: from the 292

articles identified in this review, over 50% were published between 2004 and 2006. Many of these species are specialists found in patchy habitat or rely on disconnected water bodies and as a result have shown strong phylogeographic structure (Avice 2000). Some groups, such as the speciose frogs, have been the subject of a relatively small number of surveys, whereas others, such as marine turtles, have been intensively studied (e.g. Bowen *et al.* 1991; Laurent *et al.* 1998). Research on herpetofauna have investigated speciation processes using environmental niche models (Graham *et al.* 2004), clarified Pleistocene population histories (Phillips 1994; Alexandrino *et al.* 2000), and assessed recent anthropogenic fragmentation (Cunningham & Moritz 1998) and competing scenarios of evolutionary diversification (Walker & Avice 1998; Loughheed *et al.* 1999; Garcia-Paris *et al.* 2000). Other studies have investigated the roles of volcano emergence, activity, and island ecology in driving evolutionary diversification (Malhotra & Thorpe 2000; Caccone *et al.* 2002; Beheregaray *et al.* 2003, 2004; Keogh *et al.* 2005) and provided essential information for taxonomy and systematics (Zamudio *et al.* 1997; Ashton & de Queiroz 2001).

North America accounted for an amazingly high proportion of the global productivity on reptiles and amphibians (42%) whereas Asia was represented by only 9% of the studies (the lowest value across all taxa for this continent, Table 2). Research in the Southern Hemisphere was proportionally more prolific for the herpetofauna (26% of all articles) than for any other taxonomic group, a result attributable to numerous papers from Australia and the Galápagos Islands. Very small proportions of global and comparative phylogeographic studies were identified for reptiles and amphibians (3% and 7%, respectively), the lowest values among all animals. Compared to the general pattern detected across animal groups, there was less effort in terms of obtaining multilocus data for reptiles and amphibians and a much greater dependence on mtDNA (77% of the studies used mtDNA alone and 16% combined it with other markers). These values are only lower than those found for birds.

Birds

The wealth of information about distribution and diversity on birds is unrivalled among most biological groups. Yet, birds represented the less studied animal group in this review with only 187 publications. Studies on birds have revealed a great variety of phylogeographic patterns, both in space and time, revolutionizing the knowledge about avian population structure and providing insight into the temporal durations of behavioural and morphological specializations (Avice & Ball 1991; Zink 1994, 1996; Avice 2000). Studies have characterized breeding–overwintering connectivity on broad geographic scales (Kimura *et al.* 2002), detected extreme population subdivision and cryptic

species (Baker *et al.* 1995), and reported on deviation from linearity of molecular evolution (Saetre *et al.* 2001) and on prehistoric decline of diversity in endangered species (Paxinos *et al.* 2002). Phylogeographic studies, including comparative analyses, have also generated fruitful debates about the effects of the Pleistocene on bird speciation (Zink 1996; Avice & Walker 1998; Klicka & Zink 1999; Weir & Schluter 2004) and about the significance of subspecies designations in ornithology for the fields of conservation and evolutionary biology (Ball & Avice 1992; Zink 2004).

A large proportion of bird publications (37%) came from North America, whereas the species-rich region of South America accounted for a minor fraction (9%). Marine birds represented 6% of all articles and most of these studies were conducted in Polar Regions. Interestingly, considerable effort was allocated to compare phylogeographic patterns in codistributed birds – this was the group with the highest proportion of comparative studies (13%). Given the great potential for birds to disperse and their propensity to migrate, this was also the group with more work conducted at hemispheric (but not global) scale, with 11% of studies falling into this category. In terms of genetic markers, no other group relied so much on information based on matrilineal diversity: 81% of the studies used only data from the mtDNA genome and another 13% used these data in combination with other markers. Very little work has been published based solely on allozymes and nuclear DNA data from Class II or based on combinations of these markers with mtDNA (2% and 7% of the total, respectively). In contrast, recent years have seen an escalation in the number of bird articles using microsatellites, with 12 out of the 17 papers that used these markers published between 2004 and 2006.

Micro-organisms

Ecological studies about spatial scaling of microbial diversity have demonstrated that, like macro-organisms, both bacteria and microbial eukaryotes exhibit spatially predictable distributions from local to regional scales (Green *et al.* 2004; Horner-Devine *et al.* 2004). However, the application of tools and concepts to study the spatial distribution of genetic variation in the highly heterogeneous and diverse group of micro-organisms is a fairly novel endeavour: 31 out of the 45 identified articles were published between 2004 and 2006. Despite the very low number of publications, the topics addressed were wide-ranging and included phylogeographic analyses of human viruses (Holmes 2004) and sulfate-reducing bacteria in contaminated sediments (Perez-Jimenez & Kerkhof 2005), a study of how interactions between symbiotic organisms can shape population genetic structure (Jones *et al.* 2006), phylogeographic insights into the process of host-race formation (Simon *et al.* 2003), and the proposal of a model of evolutionary history of human and simian

T-cell leukaemia/lymphotropic viruses (Slattery *et al.* 1999). In addition, advances in the field of Environmental Microbiology have created potentially rich sources of phylogeographic data about bacterial diversity in soil and aquatic samples (e.g. Voytek & Ward 1995).

The majority of the studies on micro-organisms were conducted in terrestrial environments (73%). The continents of North America and Asia accounted for a large fraction of the articles (43% and 23%, respectively) and the proportion of surveys of global scope was the highest among taxonomic groups (40%). As observed for the fungi, the most popular marker in micro-organism phylogeography was nuclear DNA from Class II, which was used in 89% of the publications.

Fungi

Lastly we have the fungi, which were represented in the phylogeographic arena by an exceptionally small number of 21 articles. As stated by Kohn (2005), the variety of life-history factors and species of fungi eagerly deserve more attention from the evolutionary biological community. Phylogeographic studies in fungi have the potential to inform on consequential issues about disease control, quarantine, free-trade and conservation (Kohn 2005). From the limited number of surveys conducted I highlight the contributions to taxonomy and biogeography of a multilocus analysis of a phytopathogenic species complex (O'Donnell *et al.* 1998), a study of cryptic speciation and long-distance dispersal in a nonpathogenic fungus (Kausserud *et al.* 2006), inferences on population history and cryptic speciation in the fly agaric (Geml *et al.* 2006), and the role of local landscape to understand dispersal and gene flow in lichens (Walser *et al.* 2005).

Most of the work on phylogeography of fungi comes from the Northern Hemisphere, with North America, Europe and Asia accounting for 86% of the studies. Not a single study carried out exclusively in the Southern Hemisphere was retrieved in the database searches (Table 2). Most fungi surveys concentrated on one taxon or on species complexes and only one study was classified as comparative phylogeography. Nuclear DNA markers from Class I were the preferred source of genetic information for phylogeographic analyses in fungi, being used in 95% of the articles.

Concluding remarks, challenges, and prospects

The state of phylogeography

Phylogeography is an established, integrative and vigorous discipline. The field has experienced dramatic expansion over two decades, with the most noticeable growth spurt observed between 1997 and 2006 – a period when annual

publication rates jumped from around 50 to 540 articles (Fig. 1). The number of published articles is still increasing considerably every year; 2007 experienced a growth rate of around 12% compared to 2006. Pinpointing specific reasons for this growth is probably an ineffective exercise since phylogeography has benefited in diverse ways from the constellation of technological, analytical and theoretical developments experienced in the last two decades by the field of molecular ecology (Hewitt 1996; Avise 1998, 2000, 2006; Templeton 1998; Sunnucks 2000; Rieseberg & Smith 2007). It is interesting to mention though that some noticeable annual increases (e.g. that of the year 2000) followed the publication of seminal work, such as the special issue of *Molecular Ecology* (1998) about Comparative Phylogeography.

The integrative nature of the field can be illustrated by the far-reaching topics addressed and by the great variety of scientific journals that have featured phylogeographic studies in their pages (Table 1). Although most studies can be primarily classified in the subject categories of ecology and evolution, empirical findings have also had valuable ramifications to conservation biology, plant sciences, zoology, aquatic biology, parasitology, microbiology, genetics, animal behaviour and biotechnology. In other words, there seems to be growing awareness among biologists about the importance of adding historical perspectives derived from the distribution of genetic diversity in populations to understand organismal biology, conservation biology, ecology, and evolution.

Phylogeography has also expanded into several historical disciplines of Earth sciences, especially palaeoclimatology, palaeontology and geomorphology, with the majority of the field's output (69% of all papers) reporting scenarios of diversification temporally associated with the Quaternary Period. Here, however, I perceive ample room for more collaboration and a better integration between phylogeographers and Earth scientists (*sensu* Beheregaray & Caccone 2007). On one hand, phylogeographers have often inefficiently (and sometimes incorrectly) explored and interpreted data about Earth's history. These researchers generally lack formal training in Earth sciences and are not updated with recent advances in Late Quaternary dynamics (but several neat exceptions exist, e.g. Magri *et al.* 2006). On the other hand, Earth scientists seem to be generally unaware of the usefulness of genealogical reconstructions to address questions concerning the interaction between physical and biological systems (but a few elegant exceptions also exist in geology, e.g. Craw *et al.* 2008). Clearly, more communication is needed between these scientists. Earth scientists and phylogeographers can mutually benefit by integrating information to fill in temporal and spatial gaps when reconstructing the history of a particular region and its biota, a strategy that can guide and rationalize further genetic and geological sampling over the geographic and temporal landscapes (Beheregaray & Caccone 2007). Another

possible corollary of such integration is a decrease of the overly large proportion of articles in phylogeography (18% of the total, or 438 papers) that did not explore or propose any temporal perspective when making inferences about population history. Adding a temporal component when interpreting biogeographic patterns should be a priority in the research agenda of phylogeographers.

In terms of taxonomic coverage, vertebrates were relatively well represented in the phylogeography literature, accounting for more than half of all publications (1387 papers). This was about twice the number of articles of terrestrial and aquatic invertebrates combined and over three times that of terrestrial and aquatic plants. When comparing across taxonomic groups, a taxonomic bias becomes evident for mammals, which accounted for 21% of all articles. This bias is in part due to the popular status that our own species and the charismatic mammalian megafauna have in phylogeography. In contrast, smaller and hard to notice nonvertebrates have been largely unstudied. Relative to their diversity, more phylogeographic surveys are needed for invertebrates, micro-organisms and fungi than for other biological groups. An increase in research effort in these groups would have wide-reaching ramifications. These would include an improved understating of population histories in poor-disperser species, which can be indicators of localized evolutionary and ecological processes and, therefore, represent conservative benchmarks for biological conservation. The recent ecological findings suggesting that both bacteria and microbial fungi exhibit predictable taxa-area relationships from centimetres up to whole continents (Green *et al.* 2004; Horner-Devine *et al.* 2004) open up an exciting avenue to study the relative roles of environmental heterogeneity and geography in shaping the demographic history and evolution of microbes. Further phylogeographic work with small life forms would also contribute to our understanding of the relationship between demography and species cohesiveness within predominantly asexual taxa (Avice 2000). Plants are another key group that was not well covered in the literature, especially during the 1990s. Fortunately, AFLPs (Bensch & Akesson 2005; Meudt & Clarke 2007) and microsatellites (Squirrell *et al.* 2003) have offered some solutions to initial problems of obtaining genealogical information in plants. This promoted a recent upsurge of phylogeographic surveys, with 92% of all plant articles published since 2000.

The establishment and the vigorous growth of phylogeography have been closely associated with analyses based on information from the mitochondrial genome (Avice 1998). Despite recent developments in gene marker technology and lower genotyping costs, it can be concluded that organellar DNA (particularly mtDNA) still stands as the powerhouse of phylogeography. This was by far the most popular class of marker in the 20-year period, used both in combination with other markers (81% of all articles) or

alone (75% of the total, this stabilized in around 62% since 2002). Related to this, recent years have seen a rapid increase in the amount of animal mtDNA data generated as result of DNA barcoding, which offers a single mtDNA gene approach for large-scale biodiversity survey and discovery (Hebert *et al.* 2003). Although the primary impetus of DNA barcoding is global bio-identification, and its merit is justifiably controversial (e.g. Will *et al.* 2005; Hickerson *et al.* 2006), the barcode data can be considered phylogeographic in its nature since it places specimens in one or another reciprocally monophyletic groups. As such, it represents a large and growing mtDNA database that is amenable to phylogeographic analysis.

Notwithstanding the supremacy of mtDNA, results of this review also illustrate important changes in the way researchers have used genetic markers. Perhaps the most relevant is the escalation of surveys using multilocus DNA data (particularly from introns and microsatellites) that occurred during the late 1990s. The initial boom was short-lived though (Fig. 7) and since 2002 the percentage of studies using nuclear DNA has stabilized in around 31%. Only *c.* 16% of these studies combined nuclear with organellar DNA data. It was also surprising to note that some combinations are not as popular as one would expect. This is the case for the combo 'organelle and microsatellites', which can offer insights about phylogeographic patterns and processes acting at different scales of the evolutionary landscape. For instance, despite the shorter coalescence time of mtDNA, the higher mutation rates of microsatellites create more twigs on the ends of genealogical branches that can be useful to disclose fine-scale structure, cryptic species, and rapid speciation events (e.g. Takezaki & Nei 1996; Petren *et al.* 1999; Beheregaray *et al.* 2002). Most importantly, it is well documented that the analysis of multiple unlinked loci is critical for accommodating coalescent stochasticity and improving the accuracy of inferences about demographic history and estimates of divergence times (Edwards & Beerli 2000; Hare 2001; Templeton 2002; Knowles 2004; Garrick *et al.* 2008). Putting it simply, if the question concerns processes (as opposed to patterns only), the study should be a multilocus endeavour. The unfortunate reality is that many present-day phylogeographers do not have the means to generate multilocus data sets that can be used to statistically assess uncertainty in genealogical estimates. Although it is unlikely that mtDNA will lose its special status as the marker of choice in phylogeography, the number of studies combining multiple loci looks set to increase as new generations of phylogeographers start to experience the benefits of the genomic era and become more familiar with advances in multilocus coalescent theory and analysis. However, I argue below that these benefits and advances might, unfortunately, not be fully available to the phylogeographers who actually have the most difficult job at hand.

The challenges for developing countries of the Southern Hemisphere (and other regions)

A wealth of phylogeographic data is available for many terrestrial and aquatic organisms of the Northern Hemisphere. In fact, a disproportionately 77% of all empirical surveys of the field (or 1874 papers) have focused exclusively on Northern Hemisphere study systems. Postglacially colonized regions of Europe and North America have been particularly well covered, resulting in increasingly coherent explanations (e.g. Hewitt 2000) about the influence of global climate fluctuations on range shifts, extinctions, and speciation of Northern Hemisphere biotas. This contrasts dramatically with the poorly studied Southern Hemisphere, which was represented in only 15% of the publications (or 365 papers) (Fig. 2a). Considerable differences in geomorphologic and climatic history exist between the two hemispheres and much more data are needed before generalizations proposed to Europe and North America can be extended to other parts of the world. Phylogeographic information is currently either inadequate or simply nonexistent for biotas inhabiting many regions of the Southern Hemisphere, such as Patagonia, Amazonia, Brazil's Atlantic Forest, Brazil's Cerrado, Wallacea, Sundaland, New Guinea, Polynesia-Micronesia, Northern and Central Australia, Madagascar, East Africa, and the bulk of marine bioregions. Most of these are found in developing countries, which is consistent with the positive correlation found in this review between research productivity and country's wealth. Several regions from developing countries of the Northern Hemisphere are also data deficient in phylogeography, including Sri Lanka, mountains of Central Asia, Irano-Anatolian region, Himalayas, mountains of Southwest China, and the Philippines.

Importantly, many of the regions named above have been classified as hotspots of biodiversity. These are areas where exceptional concentrations of endemics (e.g. 44% of the world's plant species and 35% of its vertebrate species) are undergoing exceptional loss of habitat (Myers *et al.* 2000). Most of the 25 identified hotspots are located in tropical regions of developing countries where threats to biodiversity are greatest and conservation resources are scarcest (Myers *et al.* 2000). One of such countries is Brazil. Despite being generally considered the world's most biodiverse nation, Brazil ranked only 15th in terms of productivity in phylogeography. Indonesia and Colombia also top the list of Earth's biologically wealthiest countries (Mittermeier *et al.* 2000) but ranked, respectively, a mere 38th and 62nd in the phylogeography ranking (Appendix). Phylogeographic studies, particularly those using large data sets from codistributed species, provide a valuable framework for developing conservation strategies aimed at protecting historical dimensions of biodiversity and the evolutionary processes that sustain it (Moritz & Faith 1998;

Riddle *et al.* 2000; Moritz 2002). These comparative studies, such as the California Hotspots Project, can explore the performance of environmental drivers of diversification to identify regions that maintain rapid adaptive evolution, concentrations of historically isolated populations, or both (Davis *et al.* 2008). However, the limited phylogeographic data available for species-rich regions from most developing countries is essentially precluding the use of comparative phylogeography to inform on biodiversity conservation and management.

In addition to these problems, I also perceive technological challenges for phylogeographers in the developing world. This relates to the arrival of the new era of functional genomics, which has the exciting opportunity of changing the way we make inferences about population history. Mechanistic insights about the geographic distribution of adaptive genetic variation are expected to expand the intellectual horizons of phylogeography and establish a more integrated field (Emerson & Hewitt 2005; Avise 2006). The potential impact of functional genomics in the field can be seen in recent editorials of key journals such as *Molecular Ecology* and *Proceedings of the Royal Society of London B*, which actively encourage submissions of articles describing patterns of genetic diversity in populations related to ecological adaptations and the functioning of organisms. Despite the fruitful consequences of integrating functional genomics with more traditional fields of organismal biology, I anticipate an intensification of some disparities identified here between researchers from the developed and the developing world. My point is that whereas some researchers will benefit from an understanding of the adaptive value of historically partitioned genetic variation (especially that found in well-characterized postglacial populations), others will still face the difficult task of describing (and publishing) patterns of population history in understudied biotas. The latter is especially true for researchers working in species-rich areas with inadequate sampling and taxonomy, such as tropical marine regions and tropical rainforests of the developing world.

What can the phylogeographic community do to ameliorate these problems? One possibility is to establish international collaborations and research networks that will make available resources to rapidly document and compare species phylogeographies in poorly studied regions. Incipient collaborative efforts in developing countries will no doubt face numerous barriers, especially in terms of financial support, infrastructure, linguistics, and licensing for exporting tissue samples and specimens. One way to circumvent some of these barriers is to advocate the development of *in situ* capacity. Research institutions and scientific societies from the developed world could offer more workshops and training opportunities in regional areas of developing countries. They could also foster communication between individuals by increasing travel support for postgraduate

students and young scientists from developing countries to attend international conferences. By creating strategies for developing *in situ* capacity our community will help building intellectual and practical expertise necessary to improve the quantity and quality of research in phylogeography and biodiversity. In addition, this will eventually lead to formal agreements between research institutions that should not fail to generate synergies and rationalize resources. Although several pre-eminent phylogeographers are based in the developing world, they usually do not attract enough funding for conducting large-scale screening of populations using multigene approaches. The contrary is probably true in several developed countries, where funding agencies tend to support scientists that use the latest (and often more expensive) molecular tools. One potential avenue for reducing the technological gap between these two types of scientists is to assess the role of less expensive approaches (e.g. genomic scans using AFLPs; Meudt & Clarke 2007) for disclosing information about the geographic distribution of both neutral and adaptive genetic variation. These approaches can potentially offer insights into the genotype–phenotype interface (e.g. Luikart *et al.* 2003; Bonin *et al.* 2006) in groups of organisms for which it is still unthinkable to use more canonical genomic methods.

Although collaborative efforts similar to those proposed above already exist in a few places, many species and biotas of our natural world still await to be surveyed and compared. The building up of regional comparative phylogeographic syntheses in the Southern Hemisphere (and in developing countries of the Northern Hemisphere) is crucial for the expansion of the field. This would enable testing for differences and generalities in the histories of biotas of the two hemispheres, contribute with regional conservation efforts, and facilitate the integration between phylogeographers and Earth scientists. Phylogeography is a young and integrative field within biological and historical sciences that has experienced fast growth in recent years. Although the growing popularity of the field is set to continue, the intellectual maturation of phylogeography will eventually depend not only on developments in DNA technology, theory, and statistical analysis, but also on syntheses of comparative information across different regions of the globe. For this to become a reality many empirical phylogeographic surveys in developing countries are needed.

Acknowledgements

This paper benefited from comments of A. Caccone, P. Sunnucks, P. Teske, J. Waters and five anonymous referees, and from discussions at the 'Phylogeography and Coalescence Workshop' (Melbourne, 2007) and the Macquarie University Genes-to-Geosciences Research Center. I also thank G. Cooke for her assistance with data collection and F. Valdez for data entry. Acknowledgement is also given to the Australian Research Council (ARC) for funding the

work conducted at the Molecular Ecology Laboratory at Macquarie University (MELMU).

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Appendix

The top 100 most productive countries in phylogeography (period 1987–2006)

Ranking/Country	No. of articles	Ranking/Country	No. of articles	
1	USA	51	Costa Rica	7
2	United Kingdom*	52	Madagascar	7
3	France	53	Peru	7
4	Germany	54	Singapore	7
5	Australia	55	Tunisia	7
6	Canada	56	Ecuador	6
7	Spain	57	Uganda	6
8	Italy	58	Iceland	5
9	Japan	59	Saudi Arabia	5
10	Sweden	60	Bolivia	4
11	Switzerland	61	Bulgaria	4
12	Russia	62	Colombia	4
13	Austria	63	Iran	4
14	Portugal	64	Latvia	4
15	Brazil	65	Luxembourg	4
16	People's Republic of China	66	Mali	4
17	Norway	67	Mongolia	4
18	Belgium	68	Senegal	4
19	New Zealand	69	Ukraine	4
20	Netherlands	70	Albania	3
21	South Africa	71	Bosnia and Herzegovina	3
22	Taiwan	72	Burkina Faso	3
23	Finland	73	Côte d'Ivoire	3
24	Denmark	74	Cuba	3
25	Mexico	75	French Polynesia	3
26	Panama	76	Ghana	3
27	Argentina	77	Kuwait	3
28	Greece	78	Lithuania	3
29	Czech Republic	79	Niger	3
30	Poland	80	Nigeria	3
31	Estonia	81	Palau	3
32	Hungary	82	Papua New Guinea	3
33	India	83	Serbia and Montenegro	3
34	South Korea	84	Sri Lanka	3
35	Croatia	85	Tanzania	3
36	Chile	86	United Arab Emirates	3
37	Turkey	87	Zambia	3
38	Indonesia	88	Bangladesh	2
39	Malaysia	89	Botswana	2
40	Ireland	90	Cambodia	2
41	Thailand	91	Cyprus	2
42	Uruguay	92	French Guiana	2
43	Morocco	93	Gabon	2
44	Venezuela	94	Guatemala	2
45	Israel	95	Namibia	2
46	Kenya	96	Réunion	2
47	Romania	97	Yemen	2
48	Slovakia	98	Armenia	1
49	Slovenia	99	Benin	1
50	Vietnam	100	Bermuda	1

*Includes 293 articles by English, 79 by Scottish, 43 by Welsh and 7 by northern Irish researchers.