Gayana 63(2): l65 170. 1999 ISSN 0016-531X

Review:

HISTORICAL BIOGEOGRAPHY: STATUS AND GOALS FOR THE 21ST CENTURY

BIOGEOGRAFIA HISTORICA: ESTADO Y OBJETIVOS PARA EL SIGLO XXI

Julián Monge-Nájera*

ABSTRACT

The current state of the debate among dispersalists, panhiogeographers and vicariists is reviewed. Dispersalism has few supporters, possibly because scientific tests of center of origin and dispersal route hypotheses is difficult. Recent panbiogeographic papers basically originate in Latin America, Europe and New Zealand. Vicariance biogeography numerically dominates recent literature. Retrovicariance. non-parametric statistical analysis and reversible parsimony are promising new techniques. Quantitative biogeographic and ecological data should be considered simultaneously and organic evolution should be incorporated to the core of biogeographic analysis. Biogeographic papers are widely scattered and can only be reliably retrieved through indices, particularly Biological Abstracts. Considering population. the European Union, Canada and Chile are the most productive countries.

KEY WORDS: Historical biogeography, Panbiogeography. vicariance biogeography. new techniques. bibliometry.

RESUMEN

Se reseña el estado actual del debate entre dispersionistas. panbiogeógrafos y vicaristas. El dispersionismo tiene pocos seguidores, posiblemente porque es difícil evaluar científicamente hipótesis sobre centros de origen y rutas de dispersión. Los artículos panbiogeográficos recientes se originan principalmente en América Latina. Europa y Nueva Zelandia. El vicarismo predomina numéricamente en la literatura reciente. La “retrovicariancia”. el análisis estadístico no parametrico y la “simplicidad reversible” prometen ser técnicas útiles en el futuro. Se recomienda el análisis simultáneo de datos biogeográficos y ecológicos de tipo cuantitativo, así corno Ia incorporación de la evolución orgánica al análisis biogeográfico. Los artículos biogeográficos se publican en muchas revistas y el lector debe remitirse a Índices como *Biological Abstracts* para estar bien informado. Considerando su población. la Unión Europea, Canada y Chile son los países más productivos.

PALABRAS CLAVES: Biogeografía histórica. Panbiogeografía, biogeografía vicariante, nuevas técnicas, bibliometria.

INTRODUCTION

Modern biogeography is by nature a multidisciplinary branch of science, but it was part of Theology for centuries, when authors such as Augustine and Kircher applied reproductive biology models to explain geographic dispersal “after the Universal Deluge” (Papavero & Pujol-Luz. 1997; Chiquieri *et at.*. 1998). Today. biogeographers test hypotheses about why organisms inhabit some areas of the planet, but not others (ecological biogeography, see Rivas *et a!.*, 1997 for a modern quantitative approach) and about how they colonized - if at all- those areas (historical biogeography, e.g. Crisci & MoiTone. 1992).

In the last decade, a series of important books have dealt with specific regions (e.g. Darwin & Welden. 1992: Lourenço 1996) or have summarized the history and methods of historical biogeography (e.g. Espinosa & Llorente, 1993; Papavero & Pujolluz. 1997), but I am not aware of any paper that summarizes the state of the debate among schools of thought that include dispersalists, panbiogeographers and vicariists. This paper presents that summary and highlights avenues for future work.

*Bioiogia Tropical. Biologia *15*, Uniersidad de Costa Rica, 2060 San José. Costa Rica (Telefax *5062075550:* julianm@cariari.ucr.ac.cr)

THE THREE BASIC SCHOOLS

Dispersalism

Dispersalist biogeography (from the Latin *dispersus,* to disperse) is based on the assumption that taxa originated in relatively small areas (“centers of origin”) and tries to reconstruct the routes that organisms covered to colonize known past or present ranges. The names of Wallace. Darwin, Mathews, Mayr. Darlington and Simpson are often associated with the origins of dispersalism, but they were in fact late representatives of this school whose beginning is at least two millennia old. Even Augustine’s analysis in *De Cii’itate Del* (413 AD) is unlikely to have been the first (considering Asyrian and Babylonian ideas about the origin of life). Augustine was followed but the extensive biogeographic work of two Jesuits, the Spaniard Joseph D’Acosta and the German Athana.sius Kircher (Papavero & Pujol-Luz. 1997).

D’Acosta dealt extensively with dispersal, land bridges and anthropic influence in *Historia natural moral de las Indias* (1590). Kircher *(Arca Noae,* 1675) believed that asexual organisms developed by spontaneous generation everywhere after the Deluge, but that Noah’s Ark was the center of origin for other organisms. He explained that dispersal -including anthrophoresis- was done sometimes over now submerged land and followed by cladogenesis through vicariant adaptation and hybridization (Papavero & Pujol-Luz, 1997).

Panbiogeography

The origin of Panbiogeography is associated with Leon Croizat-Chaley, the son of Italian and French parents who spent much of his life in Venezuela, where he published an extensive book titled *Panbiogeography* in 1957 (but his ideas were presented in limited form in his 1952’s *Manual of Phvtogeographv).*

The name roots are Greek *(pan* all, *bios* life, *Geos* earth, *graphe’* drawing) and refer to his desire of covering all the major biogeographic trends in his work. Basically, he plotted the known distribution of as many taxa as he could, and connected the isolated areas inhabited by each with lines that he called *tracks.* He discovered that tracks were equal for several taxa, including many that were not close relatives, and called this repetition a “statistical” evidence, albeit he applied no statistical tests to them.

His books show an impressive erudition and are difficult to understand, but basically he concluded that the tracks connected areas that had been connected geographically and biologically in the past. J.R. Rojas (1999 pers. comm.) has summarized this school as follows: “Panbiogeography assumes that taxa evolve in two stages. In Stage 1, when climatic and geographic factors are favorable, organisms actively expand their geographic ranges. During Stage 2, when they have colonized all the available geographic or ecological space, their ranges become stable and new barriers cause both geographic separation and speciation of the isolated populations. The five basic concepts of panbiogeography are individual track, generalized track, baseline, center of mass and node”.

Croizat-Chaley stressed that changes in geography caused isolation of populations and that isolation in turn caused speciation. He did not use data from geology as a basis for his work and ardently attacked dispersalist biogeography for presenting “stories” about routes of dispersal as if they were scientific results. When he speaks of *dispersal* in his books he refers to *position in a map,* not to organism migration. To understand his books, this use of “statistical” and “dispersal” must be born in mind. However, a quantitative approach to panbiogeography has emerged on the basis of graph theory and character compatibility (see Espinoza & Llorente, 1993). New Zealand author R. Craw is one of the most prolific panbiogeographers today.

Vicariance biogeography

The term vicariance biogeography was popularized by G. Nelson, N. Platnick, D.E. Rosen and E.O. Wiley in the USA (around 1973); it originates in the Latin *vicarius* (substitute of a religious authority) and refers to administrative *divisions* of the Church. Vicariance biogeography attempts to reconstruct the historical *divisions* of biogeographic areas without using data from geology as a first step. Nevertheless, they accept geology as an additional source of information (Rosen, 1978). A quantitative measure of vicariance-based cladograms consistency was published by Simberloff (1987).

The representatives of this school were inspired by Panbiogeography and use biological systematics (often, cladistic techniques) to reconstruct the phylogenies of several taxa. Their goal is to obtain the phylogenies of many groups and then to build a “phylogeny” of the areas they inhabit. Taxa are considered characters of a cladistic analysis of the areas where they occur. The principle is simple: the areas whose organic inhabitants are closely related taxonomically, were connected in recent geologic times. This procedure starts with the area cladograms for several organisms whose ranges do not overlap. Then, the taxa are replaced by the areas in the cladogram and the result is an area cladogram.

The opposite of this method, Retrovicariance, was proposed half a decade ago to reconstruct the phylogenies of some taxonomically problematic organisms, on the basis of geologic-paleogeographic data (Monge-Nájera. *1995).* This method proved its value when an independent cladogram (produced 90 years earlier) was rediscovered and compared with paleomaps based on external *(i.e.* paleontological) evidence (Monge-Nájera, 1996).

THE CURRENT STATUS OF THE THREE BASIC SCHOOLS

The countries that published most biogeographical papers in 1998 were Japan, France, Spain, the USA, Germany, the United Kingdom, Australia and Italy (Table I), but when population size is considered for countries that published at least two papers (Figure 1), the most productive countries are Finland, Spain, Australia, Israel and France (the Seychelles Islands have the highest range if countries that published only one paper are included) . The middle range of productivity is shared by many countries. The best positioned Latin American countries are Chile, Argentina, Mexico and Brazil, in descending order (Figure 1).

Dispersalism

I found only one clearly dispersalist paper in my review of the most recent literature. This suggests that it has relatively few supporters among active biogeographers, similarly to the related "Expanding Earth Hypothesis" (see Shields 1998). The two basic concepts of dispersalism, the center of origin and the dispersal route, are also its basic weaknesses. To identify the center of origin, dispersalists developed several rules and each author tends to apply his/her favorite one without noticing inconsistency among rules (Croizat-Chaley, 1957).

Some rules state that the center of origin is the area with the oldest fossil, or with the most primitive species, or with the greatest biodiversity for a taxon. I applied several rules to the Chelonia and obtained completely contradictory results (Monge-Nájera, unpublished). Similarly. it is nearly impossible to reconstruct dispersal routes more than 150 years old because earlier cultural records are non existent or unreliable, and the fossil record is very imperfect. Even with the shortest scientifically accepted span, this means that dispersal and center of origin records are lacking for 99.99999 % of the history of life and greatly reduces the potential value of dispersalism biogeography.

The only dispersalist paper that I found (Lessios *et* a!., 1998) applied mitochondrial DNA analysis to the sea urchin *Echinothrix diaderna.* It rejected the hypothesis that populations at both sides of the Pacific were conservative remnants of an ancient wide ranging population. It concluded that both are genetically very close and indicate a massive and recent dispersal event, maybe triggered by the El Niño phenomenon. This approach is far from the traditional dispersalist approach and seems to be scientifically robust.

Panbiogeography

The panbiogeographic papers are from Argentina, France and New Zealand. Lopreto & Mon-one (1998) applied tracks to Syncarid crustaceans and concluded that they have at least two ancestral biotas (Pacific temperate and Atlantic tropical). Track analysis has also been applied to relictual scorpion families (Lourenço, 1998) and to Calanoid copepods (Jamieson, 1998). The second author stated that panbiogeography not only explained copepod ranges better than dispersalism, but also that it was in better agreement with data from other organism groups. A recent paper by Hajdu (1998) analyses marine panbiogeography. Panbiogeography has been applied to conservation biology with interesting results (e.g. Grehan, 1989; Cortés & Franco, 1992; Morrone & Crisci, 1992).

Vicariance biogeography

Recently, the vicariance biogeography method has been applied to Deropristiid trematode parasites (Choudhurg & Dick, 1998), Chironomid dipterans (Oyewo & Saether, 1998), Ceroplastine coccids (Qin *et* a!., 1998), Carabid coleopterans (Liebherr & Zimmerman. 1998) and *Gentiana* plants (Hungerer & Kadereit. 1998). but these authors have not discussed the positive or negative aspects of the method itself.

Even though icariance biogeography is. at least by number of papers. the dominant school today, it is far from being fully satisfactory. For example. after a detailed study of freshwater gastropods (Melanopsidae). Altaba (1998) criticized the value of both vicariant congruent area cladograrns and panbiogeographic tracks. Mitochondrial DNA tests applied to neotropical birds showed that adaptive habitat redistribution can greatly obscure vicariance patterns (Garcia. 1998).

NEW DEVELOPMENTS

Non-parametric statistical analysis of absence- occurrence patterns was applied to Quaternaiy and Present biogeographic quadrates five years ago. That seems to be one of the earliest cases of simultaneous mathematical study of extant and paleo-habitats (Monge-Najera. 1994) and represents a mathematical merge of historical and ecological biogeography. This approach rejects *de fticlo* the incompatibility belief explained by Espinoza and Llorente (1993). Multivariate statistics ordination of echinoderm ecological data did not support a dispersalist hypothesis but were unable to decide between panbiogeographic and vicariant interpretations (O'Hara. 1998). Three-dimensional cost matrix optimization, applied to isolated events that include dispersal episodes (instead of general patterns), is now available to better deal with this sort of problem (Ronquist, 1998).

A new method, reversible parsimony, can distinguish at least some dispersal events from vicanance, and is reportedly superior to the Brooks and the Component methods in biogeographic reconstruction (Hausdorf. 1998).

GOALS FOR THE NEW MILLENTUM

We should make an effort to go beyond the traditional descriptive papers by stating objective hypotheses about geographic and taxonomic distribution and then proceed to test them mathematically (Barrientos *&* Monge-Nájera, 1995; Monge-Nájera. 1996; Hausdorf, 1998). Biogeographic and ecological data should be considered simultaneously with appropriate mathematical tests, which often are non- parametric statistics (Monge-Nájera. 1994b: Monge-Nájera and Alfaro. 1995: Ronquist. 1998). My final advice is to incorporate organic evolution to the core of biogeographic analysis whenever pertinent *(e.g.* Monge-Nájera and Lourenço, 1995).

CONCLUSION

A review of the 1997-1999 papers cited in the references list shows that the great majority (15) belong to the vicariance school, few (Jamieson. 1998: Lopretto. 1998: Lourenço. 1998) are panbiogeographic and only one is dispersalist (Lessios. 1998). The 1970's and 80's biogeographic debate that filled the pages of *Systematic Zoology* is now rare in that journal and even though *Biogeographica, Revista de Biología Tropical* and *Journal of Biogeography* appear repeatedly here under References, it is clear that biogeographic papers are widely scattered and can only be reliably retrieved through indices, particularly *Biological Abstracts.* The availability of on-line paleo-atlases (e.g. Tropiweb's *Continents Evolving* in www.ots.ac.cr) should facilitate biogeographic analysis in the future. The Société de Biogeographic (57 Rue Cuvier F-75005, Paris) is the oldest organization dedicated exclusively to the subject and has produced important contributions since 1924.

ACKNOWLEDGMENTS

My special thanks to José Rodrigo Rojas M. (University of Costa Rica) and J. R. Pujol Luz (Universidade Federal do Rio de Janeiro) for careful suggestions to greatly improve an earlier draft and to Andrés 0. Angulo, Editor of *Gavana,* for his invitation to write this review. I thank D. Brooks, William Eberhard, G.F. Estabrook. K. Fiala, Jorge Llorente-Bousquets, W. Maddison, Wilson Lourenço, N. Papavero, N. I. Platnick and R. Pujol-Luz for taking the time to share my interest in biogeography throughout these years and for providing basic literature. Gabriela Perez and Fred Madrigal kindly prepared the figure.

REFERENCES

ALTABA *C.* R. 1998. Testing vicariance: Melanopsid snails and neogene tectonics in the Western Mediterranean. Institut Mediterrani dEstudis Avancats. Spain. J. Biogeogr. 25: 541-551

BARRIENTOS. *Z. &* J. MONGE-NAJERA. 1995. Geographic homogenity among insect communities in Neotropical paramos: a hypothesis test. Caldasia 18 (86): 49-56.

CHIQUIERI**.** A; N. PAPAVERO *&* D.M. TEIXEIRA**.** 1998. Abraham van der Myl et son "De origine animalium et migratione populomm' (1637). Historia Natumlis 1: 255-310.

CORTÉS. R. & P FRANCO. 1992. Análisis panbiogeográfico de La flora Chiribiquete. Colobia. Caldasia 19: 465-478.

CROIZAT-CHALEY. L. 1976. BiogeografÍa analítica y sintética ("PanbiogeografÍa") de las América. Academia de Ciencias FIsicas, Matemáticas y Naturales. Caracas (two volumes).

CHOUDHUR**.** A. & D. TERRY A. 1998. Systematics of the Deropristiidae Cable and Hunninen. 1942 (Trematoda) and biogeographical associations with sturgeons (Osteichthyes: Acipenseridae). Syst. Parasitol. 41: 21-39.

CRISCI. J. & J. MORRONE. 1992. Panbiogeografía y biogeografía cladística: paradigmas actuales de la biogeografía histórica. Ciencia 6: 87-97.

DARWIN. S.P. & A. L. WE! DEN. 1992. Biogeography of Mesoamerica. Proceedings of a symposium. Tulane University. New Orleans. 342 p.

ESPINOZA O.D. & J. LLORENTE B. 1993. Fundamentos de biogeografías filogenéticas. Universidad Nacional Autónoma de Mexico. Mexico. DR 133 p.

GARGA. MJ.: P ARCTANDER & J. FJEDLSA. 1998. Pre Pleistocene differentiation among chat tyrants. Condor 1(X): 629-640.

GREHAN. J. 1989. Panbiogeography and conservation science in New Zealand. N. Zealand J. Zool. 16:431-478.

HAJDU. F. 1998. Toward a Panbiogeography of the Seas: Sponge Phylogenies and general Traks. P 95-108 Tn: Y. Watanabe & N. Fusetani (Eds.). Sponge Sciences— Multidisciplinaiy Perspectives. Springer. Tokyo.

HAUSDORFB, B. 1998. Weighted ancestral area analysis and a solution of the redundant distribution problem. Syst. Biol. 47 (3): 445-456.

HUNGERER**,** K.; K. BERNHARD *&* W. JOACHIM. 1998. The phylogeny and biogeography of *Gentiana* L. sect. *Ci,ninalis* (Adans.) Dumort.: A historical interpretation of distribution ranges in the European high mountains. Persp. Plant Ecology Evol. Syst. 1: 121-135.

JAMIESON. C. D. 1998. Calanoid copepod biogeography in New Zealand. Jamieson Ecol. New Zealand. Hydrobiologia 367: 189-197.

LESSIOS, HA.; B. D. KESSING & DR. ROBERTSON. 1998. Massive gene flow across the wold's most potent marine biogeographic barrier. Proc. Royal Soc. London Biol. Sci. 265 (1396): 583- 588.

LIEBHERR J.K. & F. Z1MMF.RMAN. 1998. Cladistic analysis, phylogeny and biogeography of the Hawaiian Platynin (Coleoptera: Carabidae). Syst. Entomol. 23 (2): 137-172.

LOPRETTO, E.C. & J. MORRONE**.** 1998. Anaspidacea, Bathynellacea (Cnistacea. Syncarida). generalised tracks. and the biogeographical relationships of South America. Zool. Scripta 27(4): 311-318.

LOURENÇO, W. 1996. Biogeography of Madagascar. Institut Francais de Recherche Scientifique pot Ic Developpement en Cooperation. Paris. 588 p.

LOURENÇO. W. 1998. Panbiogeography. dismpted distributions and the concept of relictual family in scorpions. Biogeographica 74(3): 133-144.

MONGE-NÁJERA. J. & JR. AI.FARO. 1995. Geographic variation of habitats in Costa Rican velvet worms (Onychophora: Peripatidae). Biogeographica 71: 97-108.

MONGE-NÁJERA. J. & W. LOURENÇO. 1995. Biogeographic implications of evolutionary trends in onychophorans and scorpions. Biogeographica 71(4): 179-185.

MONGE-NÁJERA, J. l994a. Ecological Biogeography in the Phylum Onychophora. Biogeographica 70: 111-123.

MONGE-NÁJERA. J. 1994b. Reproductive trends, habitat type and body characteristics in selvet worms (Onychophora). Rev. Biol. Trop. 42: 611-622.

MONGE-NÁJERA. J. 1995. Phylogeny. biogeography and reproductive trends in the Onychophora. Zool. J. Linn. Soc. (London) 114: 21-60.

MONGE-NAJERA. J. 1996. Jurassic-Pliocene biogeography: testing a model with velvet worm (Onychophora) vicariance. Rev. Biol. Trop. 44: 159-175.

MORRONE. J. & J. CRlscI. 1992. Aplicación de métodos filogenéticos y panbiogeogrrificos a Ia conservación de Ia diversidad biológica. Evolución Biológica 6: 53-66.

NELSON. G. & NI. PLATNICK. 1981. Systematics and biogeography, cladistics and vicariance. Columbia University. New York.

O'HARA**.** T. 1998. Origin of Macquarie Island echinoderms. Dep. Zool., Univ. Melbourne. Australia. Polar Biol. 20: 143-151.

OYEWO. E.A. & O.A. SAERHER. 1998. Revision of Afrotropical *Polvpediluin* Kieftèr suhgen. *Uresipediluni* Sasa et Kukuchi. 1995 (Diptera: Chironomidae), with a review of the subgenus. Ann. Limnol. 34: 315- 362.

PAPAVERO**,** N. & JR. PuJot Lui. 1997. Introducao histórica a biologia comparada. corn especial referencia a biogeografia. IV. Dc Descartes a Leibniz (1628-1716). Editora Universidade Federal Rural do Rio de Janeiro. Rio de Janeim, Brazil. 282 p.

QINTING. K.; P.J. GUILAN & W.C. BEATTIE**.** 1998. Biogeography of the wax scales (Insecta: Hemiptera: Coccidae: Ceroplastinae).. J. Biogeogr. 25: 37 45.

RIVAS, R.M.; V. H. MENDEZ & J. MONGE-NAJERA. 1997. Distribution of Costa Rican epiphytic bromeliads and the Holdridge Life Zone System. Rev. Biol. Trop. 45: 1021-1031.

RONQUIST, F 1998. Three dimensional cost matrix optimization and maximum cospeciation. Cladistics 14: 167-172.

ROSEN, D. 1978. Vicariant patterns and historial explanations in biogeography. Syst. Zool. 27: 159-188.

SHIELDS. 0. 1998. Upper Triassic Pacific vicariance as a test of geological theories. J. Biogeogr. 25: 203-2 1 1.

SIMRLOFF, D. 1987. Calculating probabilities that cladograms match: a method of biogeographical inference. Syst. Zool.36: 175-195.

TABLE I. Total number of biogeographical papers published by country in I 998. according to the Biological Abstracts.

TABLA I. Número total de artículos publicados por país en 1998. de acuerdo al Biological Abstracts.

Country	Papers	Country	Papers
Japan	22	Chile	2
France	19	China	2
Spain	19	Israel	2
USA	14	Kenya	2
Germany	10	Sweden	2
United Kingdom	9	Switzerland	2
Australia	7	Colombia	1
Italy	7	Hong Kong	1
Canada	5	Jordan	1
Finland	5	Liban	1
Mexico	4	Mongolia	1
Netherlands	4	Norway	1
Russia	4	Seychelles	1
Brazil	3	Slovakia	1
Czech Republic	3	South Korea	1
South Africa	3	Taiwan	1
Argentina	2	Turkey	1
Belgium	2	Venezuela	1

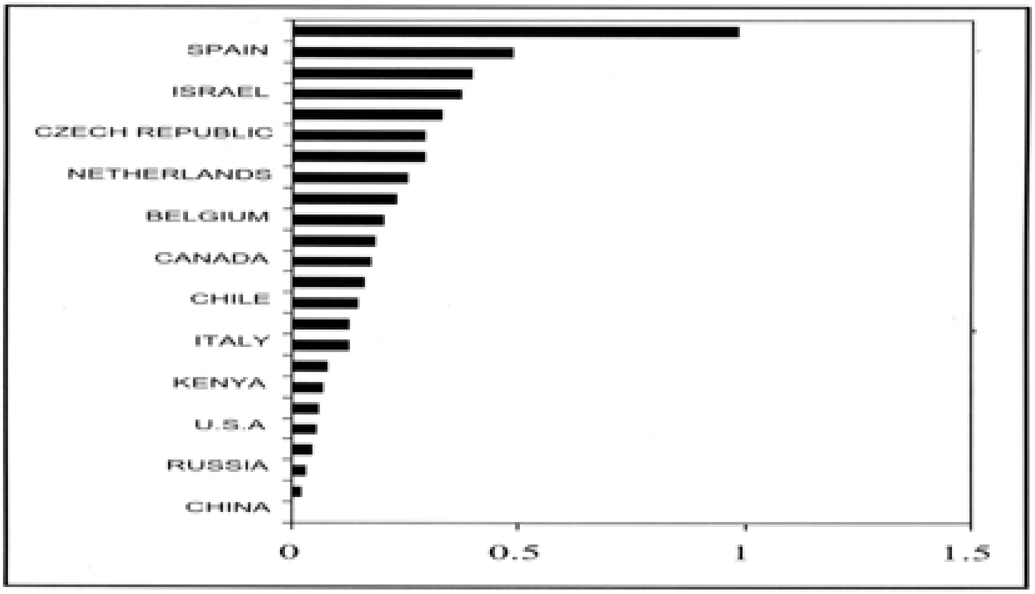

FIGURE 1. National productivy in the field of biogeography when all papers are considered. Number of papers divided x million inhabitants to correct for population size. Vertical axis: country. Horizontal axis: papers/million inhabitants.

FIGURA 1. Productividad nacional en el campo de la biogeografía cuando todas las poblaciones son consideradas. Número de trabajos por millones de habitantes para corregir el tamaño poblacional. Eje vertical: País. Eje horizontal: Trabajos/millones de habitantes.