perspectives in biogeography

Christen Raunkiær – one of several early island biogeographers

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Islands, especially isolated oceanic islands, have always held a fascination for me, both emotionally and intellectually. Likewise they have fascinated travelers ever since the first oversea transportation means were invented and employed. This fascination and fantasy created early a fertile substrate for tales, epics and accounts on island life, as evidenced by Homer's Odyssey, Sheherazade' tales on Sindbad, and the Atlantis myths. The romantic novel was nourished in the same medium, as evidenced by Gulliver, Robinson Crusoe, and The Treasure Island.

In island literature exaggerations are almost mandatory. The scientific literature on islands, of course, does not allow exaggerations but there is still a marked tendency to focus on island organisms or phenomena that are peculiar in one way or another. No island birds are more commonly known as the monstrous Mauritius dodo and hardly any island plants as admired as the Seychelles giant coco or the silver sword of Hawaii. This trend to concentrate on the odd island organisms (the dodo approach, Adsersen 1995) is of course fascinating but it does not tell the whole truth on island biology. Neither does the focus on peculiar insular processes like evolutionary radiation as shown by Darwin finches or Hawaiian honeycreepers. No matter how seminal this approach (the finch approach) has proven to be for ecology and evolutionary biology it elucidates only part of the island scenario. The good stories on dodos and finches have the mark of anecdotes as long as they are not compared to something else. This "something" could be the rest of the organisms in the island, or the organisms of comparable areas on continents, or a general global pattern. In other words, it is necessary to consider the island biota as entities that may be quantitatively assessed and characterized.

MacArthur and Wilson's classical works constitute a paradigmatic breakthrough of this approach, and by their work island biogeography was established as a discipline (MacArthur and Wilson 1967). Their equilibrium theory of island biogeography (ETIB) has been cyclically admired, criticized, rejected, reformulated, and modified ever since their modest-looking book was published, and this discourse will probably go on. But everyone participating in this debate acknowledges that island biotas may and should be assessed quantitatively and that island biotas are dynamical entities subject to qualitative and quantitative changes in time and space. Maybe this is the kernel of their message, and maybe its simplicity is the reason why it has had such a profound impact on evolutionary science, biogeography, and (macro)ecology. Now when the first forty years of island biogeography has been celebrated by a magnificent symposium at Harvard it seems apposite to ask whether Mac Arthur and Wilson had any predecessors in this quantitative approach. Marc Lomolino in his contribution to the symposium did so, focusing mainly on the American arena. Here I wish to draw attention to some important European contributors to early island biogeography.

Right after the publication of The Theory of Island Biogeography there was a marked tendency to try to support or even prove the theory by demonstrating mathematical relationships between species richness S and area A (species-area relationships, SPAR). Nice SPARs like the Arrhenius equation (log $S = C$

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+ z log$A$) or the Gleason equation ($S = K + p$ log$A$) (Gleason 1922) may be found by the quantitative approach and they may be result of ETIB; but ETIB could be explained by several other mechanisms, so there is no direct link between SPAR and ETIB. SPARs are important ("Ecology's most general pattern", Lomolino 2000) but not limited to island biogeography. Even Arrhenius' pioneering work (Arrhenius 1921) was not an island biogeography work: it was indeed done on islands in the Stockholm archipelago but his S and A assessment were done in nested plots within the islands, so he could only obtain monotonously increasing functions, and there is no reference to total island S or A. Maybe Darlington's rule of thumb (tenfold island area yields double species number, or $S = c\ A^{\log 2} = c\ A^{0.301}$) is the first SPAR employed on true island entities (Darlington 1957). Numerous reviews and textbooks enlighten the history and relations between SPAR and ETIB.

SPARs are based on numbers of species S in limited, defined areas. Islands normally have hard borders and well-defined area, so that S may be assessed rather precisely.

It is therefore not surprising that some of the first quantitative data in biogeography are number of species on islands. J.D.Hooker studied Darwin's plant collections from Galápagos and published in 1847 a remarkable treaty: On the Vegetation of the Galapagos Archipelago, as compared with that of other Tropical Islands and of the Continent of America. He set up three main questions to answer:

– How are the species distributed into major taxonomical groups?

– How many species are "peculiar" (endemic) and where do the species with wider distributions occur elsewhere?

– How are the species distributed within the archipelago?

Hooker not only tried to answer the questions but also managed to compare the patterns to that of other tropical archipelagos and to continental situations. His approach to question 3 is especially interesting. It is a numerical analysis of the number of plant species (the *Florulæ*) of the 4 islands that Darwin visited. In this analysis he repeatedly related the number of "peculiar" species to the total flora, and he even presented the data in a clear tabular form.

Name of island.	Total number of species.	Confined to Galapagos, *i.e.* total excluding those common to America.	Absolutely peculiar to the islet.	Confined to the group, but found likewise on other islets.
Charles Island ….	96*	47	32	13
James Island …..	100	48	38	10
Albermale Island ..	47	27	20	7
Chatham Island ..	40	21	17	4
Whole group ….	253	123		16

* I have excluded seventeen species from the flora of this islet, as being almost certainly introduced with cultivation.

Table I. *Original Hooker's data on the* florulæ *of the Galápagos Islands*.

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His material was not complete, of course, even if he apparently managed to get access to all herbarium material in England and France. His estimate of total species number was 265, of which 17 were considered introduced by man. Today we assume that S ~ 600 and the number of naturalized plant species about the same. In the table beneath the modern figures (based on Lawesson et al 1987) are inserted. None of Hooker's conclusions will hold but considering that only four of the major islands were included some of the relative figures (e.g. percent of plants confined to Galápagos) are quite accurate.

Hooker's approach is quite modern and for his time extraordinarily quantitative, although we today to each question would add "and why?" He maintained his interest in islands throughout his career, maybe best expressed in his lecture to the British Association in 1866 (reprinted and commented in Williamson 1984). In this lecture, which admittedly is much more verbal than numerical, he builds up both anecdotal and quantitative evidence that the pattern we may observe in island biogeography can be explained only if we assume evolution ("derivative origin of species"), and that the derivate origin of species became evident "when Zoology and Botany became the subjects of exact scientific studies"! So certainly Hooker should be regarded as one of the progenitors of quantitative island biogeography.

Half a century after Hooker's lecture a Finnish botanist, Alvar Palmgreen, meticulously censused the flora of islands in the Åland Archipelago of the Gulf of Bothnia, and remarkable papers followed: "The species richness as a plant geographical parameter" – "Chance as a plant geographical parameter" – "Remoteness as a plant geographical parameter". The papers were in German and Swedish – they were read at the time but also forgotten. Haila and Järvinen, however, call to the attention that Palmgreen not only studied species-area relationships; species isolation relationships, and stochasticity in species dispersion but also came very close to formulation of ETIB (Haila and Järvinen 1982). It is, however, difficult to read Palmgren's papers, even if you understand the language. His style is very wordy and even if he compares quantities like species number or isolation he does it verbally. There is hardly one graph or one

Name of island.	Total number of species.		Confined to Galapagos, *i.e.* total excluding those common to America.		Absolutely peculiar to the islet.			Confined to the group, but found likewise on other islets.
Charles Island ….	96*	**255**	47	**97**	**11**	32	**15**	13
James Island …..	100	**298**	48	**103**	**9**	38	**11**	10
Albermale Island ..	47	**417**	27	**128**	**10**	20	**25**	7
Chatham Island ..	40	**298**	21	**92**	**9**	17	**17**	4
Whole group ….	253	**532**	123	**184**				16

* I have excluded seventeen species from the flora of this islet, as being almost certainly introduced with cultivation.

Table II. *Hooker's data on the* florulæ *of the Galápagos Islands. Recent data inserted. In the column "Absolutely peculiar to the islet." the inserted column to the right left refer to the four islands mentioned, the one to the left refer to the entire archipelago.*

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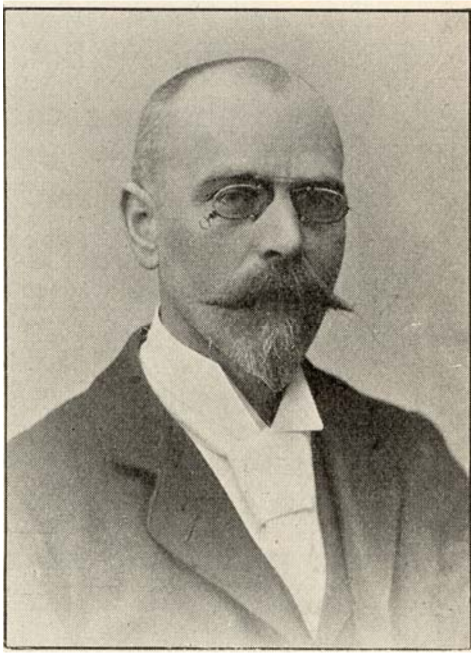
mathematical formulation in his entire opus. Nevertheless, as Haila and Järvinen expressed it, his thoughts antedate MacArthur's and Wilson's by half a century.



Christen Raunkiaer in 1902

Christen Raunkiær from Denmark was contemporary with Palmgreen, but unlike Palmgreen he was not forgotten. His life forms, frequency analyses, and contemplations on species abundance distributions are still cited in most modern text books on ecology and biogeography. His life form system was outlined in Danish in 1904 (Raunkiær 1904). Next step was to introduce the system and its application in biogeography, which he did in French in a preliminary form in 1906. The final version came in 1907 in his most renowned publication Planterigets Livsformer og deres Betydning for Geografien. (The Life-Forms of plants and their bearing on geography) (Raunkiær 1907). The system was immediately seized by Scandinavian and continental botanists and ecologists. It became almost as paradigmatic in ecology as ETIB and it is quite apposite to celebrate its first century together with ETIBs 40 years. His works were after a long delay translated to English with the title: "The Plant Life Forms and Statistical Plant Geography" (Raunkiær 1934) and world wide acknowledged.

There are probably two reasons why Raunkiær's life form system attained its high regard: The one is that the life forms are based on clear logical and biological reasoning and any plant species can without to much difficulty be categorized even by non-experts – and the second is his strict quantitative approach. With his own words: "-then Plant Geography as a botanical science gives place to Plant Geography as a geographical science" His combination of clear-cut concepts and exact biogeographical analyses on large scales made it possible for him to formulate precise definitions of biomes and to compare plant communities across biomes.The same combination is one of the reasons for MacArthur and Wilson's success.

Even though the word "statistical" recurs in several of Raunkiær's titles, he had no great knowledge on statistics as practiced today. Parametric distributions, hypothesis testing and significance were concepts unknown to him, as they where to Hooker, Palmgreen and Arrhenius. First after Fischer's paradigmatic contributions to statistics these concepts became applicable to biogeographers and soon important contributions emerged. Within island biogeography Preston's monumental papers on Commonness and Rarity of Species (Preston 1948, Preston 1962) seem to be best known but the equally monumental monograph Patterns in the Balance of Nature by C.B. Williams (1964) (a coworker of Fischer's) deserve as much recognition. Both Preston and Williams took their approach from abundance distributions (lognormal and logseries, respectively) in communities and ended up by reflecting on SPARs – very much fertilizing the ground for ETIB.

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Abundance distribution was another of Raunkiær´s interests. He invented the frequency analysis in vegetation ecology and observed the recurring pattern known as the Raunkiærian J (Figure 1). He even postulated that mature homogeneous vegetation could be recognized by this pattern. Such a daring postulate would of course raise discussion. McIntosh (1962) reviewed the discussion and concluded that the Raunkiærian J is one of those "ideas that seems to be invulnerable to attack and persist although subjected to multiple executions" (another parallel to ETIB?). Raunkiær's observation was a seminal inspiration for Preston (1948) and he demonstrated that the Raunkiaerian J may be derived from the lognormal abundance distribution, (which on its side will lead to the Arrhenius equation). Later on Williams (1964) showed that it may be derived also from the logseries distribution (which lead to Gleason equation). Even very recently the Raunkiærian J attains attention, now under the more general term "hollow species abundance distributions" (McGill et al 2007).

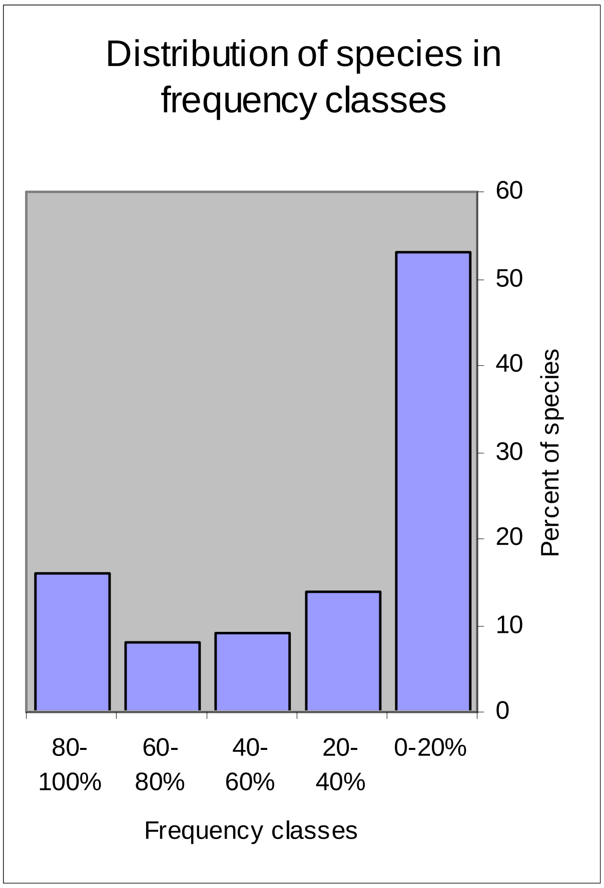

Figure 1. *The Raunkiaerian J*

It is less known that one of Raunkiær's last publications was on island biogeography: The Life-Form Spectrum of Some Atlantic Islands. The reason why it is almost forgotten is that it appeared in the series *Botaniske Studier* (published by himself) that comprises several of his emeritus works. It is an 80 page monograph in which he compares the life-form spectra of most Atlantic archipelagos from Svalbard in the north to South Georgia in the south. His questions were almost the same as Hooker's first two questions above, except that, instead of taxonomical supraspecific groups, he considered ecological ones:

1. How are the species distributed into life-form groups?
2. How many species are "peculiar" (endemic) and does their life-form spectrums differ from that of species with wider distributions occur elsewhere?

He also added a "why" to his question – and found that his climatically derived life form biome types give good explanations. His discussion on this is lengthy because he had not the necessary tools to make up the relevant exact evaluations but he would probably have been pleased to see the ordination diagram in figure 2. It is based on his data, and however incomplete they may have been they give very good support to his ideas.

Raunkiær was not the first to use quantitative data in biogeographical analyses. Early biogeographers like Schouw, De Candolle, Hooker and Warming used quantitative expressions to support their idea. The novelty in his approach was that he demanded and devised exact methods to gather the data and from the emerging patterns he generated his general ideas.Thus, even if his missed the

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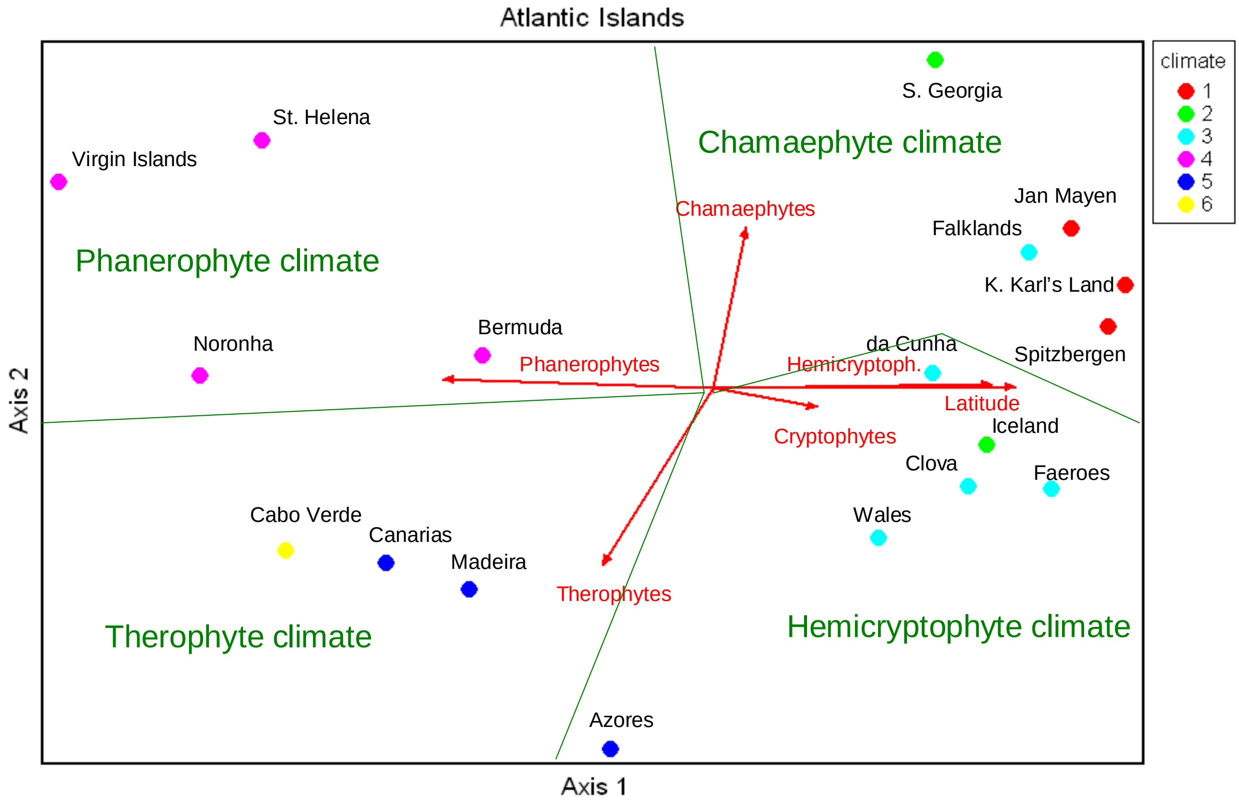

***Figure 2.** Nonmetric multidimensional scaling of Raunkiær's data on life form spectra from Atlantic islands. The ordination was run in PC-ORD 5 with Euclidian Distance as dissimilarity measure. The diagram is highly significant (P<0.01, Monte Carlo test). The correlation between distances in the ordination plane and in the original 5- dimensional life-form space is 0.972. The red vectors express the strength and directions of the variables. The ordination diagram was rotated so that axis 1 became parallel to the latitude vector. The green lines divide the ordination plane in four parts corresponding to Raunkiær's assignments to this life-form based biomes. Legend to meteorological climate: 1 (red) high arctic; 2 (green) subarctic; 3 (light blue) temperate; 4 (pink) wet tropical; 5 (dark blue) subtropical; 6 (yellow) dry tropical.*

mathematical and statistical skill of today he must be regarded as a pioneer of exact quantitative analyses of biogeographical data. He was very keen on this approach. Already in his first paper on frequency analysis (Raunkiær 1909) he expresses his motto: Numbers are the poetic meters of science (Tal er videnskabens versefødder). In this light it is not surprising that he chose 1000 plant species selected at random from the Index Kewensis when he set up his "normal" life form spectrum, and that he based his species abundance distribution J on 1000 vegetation analysis from all over the world.

According to the many anecdotes told about him at the University of Copenhagen his exactitude gave the impression that he was pedantic and, as he also was rather introverted, he was not liked by his students – they rather feared him. In his time as professor ordinarius of botany (1911-1923) he had residence in the Botanical Garden and he insisited that the students use the garden as a living book of botany. Part of his teaching was questioning the students whenever he met them and often rather brusquely so. But at one point he surprised all the students because instead of all his unpleasant questions he just asked them to fold their hands – he then observed them, nodded, thanked and left them puzzled. The

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numbers he gathered was how many of them had the right thumb on top. Many of us know this analysis to be a classic in elementary statistical textbooks. Raunkiær may very well have been the first to make an exact count (on 1000 persons??). So he was actually very broadminded in his pedantry. Anyway, he took up his demanding behavior towards the students again, so much that the students sent a timid delegate to the professor to ask politely for a change. His response was remarkable: he looked coldly at the shivering student and said: "I will not change my methods or my demands, but if the students are not satisfied by my teaching I will resign!" - and so he did, at an age of 63. This secured him a rather long emeritus period where he had peace to pursue his whims.

The allusion to poetry in his motto is another sign of his wider view. He must have been a keen reader of poetry. After his retirement he started "botanizing" in Danish poetry and he applied his "frequency analysis" as a method to characterize poets and epochs. The sample units were not circular area samples but verse lines and the observed objects were plant names. He ploughed through millions of verse lines written by hundreds of poets – so there was a need to define what a true poet is: It is a person who has published at least 1000 verse lines or one volume of poems. He determined the plant species spectrum for each of these poets in terms of total species richness and abundance distribution (abundance measured by number of mentions/1000 verse lines). So if you are interested and dedicated (and able to read Danish) you may learn that the neoclassicistic period had a much lower species richness and density then the romantic period, that Hans Christian Andersen was only the second Danish poet to mention heather, and that it is possible to distinguish between poets from Jutland and Zeeland by their predominant species. The style and stringency in his three publications on such matters are brilliant – and fun to read.

Shortly before he died he took up his old interest in plant geography. In one paper he adresses the relationship between range, species-genus rate, and life forms. He selected the 10 largest plant families with in total 2772 genera and 43594 species (his own count!). He was able to show that genera that comprise more than one life form have considerable higher species to genus ratio, and a wider geographical range. This search on the global scale for relationships between geographical features, taxonomical features and functional traits/types is a focal approach in biogeography even now.

And now we return to his island biogeography paper. It is from the same period, and apart from its undisputed scientific relevance it also contains statements about attitudes and sentiments that are shared by island biogeographers today. For instance its first sentence: "Islands, especially isolated oceanic islands, have always held a fascination for me, both emotionally and intellectually" – which happens to be the first sentence also of this essay. Thus, even if Raunkiær never would have ventured to add exaggerations or fantasies to his scientific publications, he certainly did not refrain from showing his sentiments. He also expresses modesty and self critique. His motto: "Numbers are the poetic meters of science" is the prologue paragraph of his "Investigations and statistics of plant formations" from 1909. The paper has also an epilogue: "Numbers are the poetic meters of science. Verses may halt, and so also may the numbers of science. I hope the numbers given in this work will be found to halt no more than their human origin inevitably entails". This paragraph has never been more apposite than now: Biogeographers must remember that their brilliant theories and sophisticated models build on numbers (field data) that are of human origin, and as such they will sometimes halt so much that the entire theoretical construction becomes highly tottering.

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Additional information about Christen Raunkiær including a complete list of his works and some biografies can be found at http://www.macroecology.ku.dk/resources/default.asp?p=Raunkiaer

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outreach — communicating our research

Communicating biogeography

Robert J. Whittaker, *editor-in-chief of* ***Journal of Biogeography***.

Some months ago, Joaquín Hortal approached me to write a piece for this newsletter, with the remit of providing some pointers as to what we look for in papers submitted to *Journal of Biogeography*. In some respects this is easy to do in that the journal policy is to be inclusive of major traditions within the field and international in scope, within which we give preference to papers posing and answering clearly phrased questions or testing hypotheses of general interest. However, having been given the opportunity, I also wanted to make some comment pertaining to presentation and rigour of papers in the natural sciences generally (i.e. not just submissions to *Journal of Biogeography*), which is a rather more risky thing to do. Not least because I might see my own words thrown back at me by referees of my papers in the future with the admonishment that I cannot follow my own guidelines as to best practice! I say this because I think it is deceptively difficult to write scientific papers well.

Editor's note: *With this first commentary from Robert J. Whittaker we start a new series for the IBS Newsletter. We hope to open a discussion within the biogeographical community, starting with views from the editors of key journals publishing biogeography papers about current trends in publishing biogeography, the kind of manuscripts they would like to receive to be considered for publication in their respective journals, and how to improve the quality of our work. Here, the editors will have the opportunity to write on the topics of their choice, with the general aim of improving how research in biogeography is communicated to the scientific community and the public. However, this section is not intended to be a one-way dialogue set up with some invited editors. Rather, texts and comments from referees, authors, journalists and other editors are welcome. If you are interested in participating, please contact the editor at* ibs@mncn.csic.es.

Robert J. Whittaker was sole editor and then editor-in-chief of Global Ecology and Biogeography *from 1995 to April 2004. He has been editor-in-chief of* Journal of Biogeography *since October 2004.*

The process of writing the paper should not be regarded as just the bit that comes at the end, after all the challenging scientific stuff of laboratory analysis, experimentation and sophisticated statistical analysis has been done; rather it is integral to shaping the interpretation and developing ideas and arguments, which rarely come to the page fully formed. It involves establishing the context of the work through making multiple connections to the existing literature, which continues to grow at a phenomenal rate. All of this presents significant challenges to the scientific author, requiring a systematic and thorough approach to the task of constructing a paper. The end result must be accurate, meaningful and clearly communicated so that it is understandable by the target audience.

So how well are we doing and are there particular problems facing those starting out in biogeography? If this were a school report, I think the answer to the first part of the question would probably be an enigmatic 'could do better.' In illustration of concerns that I share, Todd et al. (2007) provide some quantification of the extent of mis-citations in a sample of 306 ecological papers selected from 51 journals, focusing on specific assertions made in the sampled papers. They report that some 7% of citations did not support the original statement at all, 11% were ambiguous, 6%