Postscript

Ecology's oldest pattern?

In *Species Diversity in Space and Time*[1], Rosenzweig proposed that the species–area relationship was the first diversity pattern noticed by ecologists, placing its discovery between 1835 and 1859. He also wrote 'The species–area curve may be the first diversity pattern described by ecology, but the latitudinal gradient is the most famous'. The second phrase in this sentence is undoubtedly true, because there are few people who are not aware that the Tropics harbor more diverse floras and faunas than do the temperate regions. But the first phrase is debatable. Papers on the latitudinal diversity gradient[2,3] typically cite books written between 1855 and 1878, indicating that naturalists were aware of the pattern then and were attempting to explain it. Such attempts to understand the gradient continue, although the number of 'explanations' is increasing rapidly, with over 30 hypotheses in the literature and new ones appearing almost yearly. But it appears to be forgotten that both the existence of the latitudinal diversity gradient and an explanation for it had been presented long before the species–area relationship was noticed.

In 1799, Baron Alexander von Humboldt convinced King Carlos IV of Spain to allow him to travel in the American colonies of Spain as a mining geologist, ostensibly to discover new mineral deposits, but also to indulge his passion for botany. Between 1799 and 1804, von Humboldt traveled extensively in northwestern South America and Mexico, returning to Europe after a brief trip to the USA. In 1807, while in Berlin, von Humboldt published the first edition of a series of essays initiated while he was in South and Central America under the title '*Ansichten der Natur*', translated variously as '*Aspects of Nature*' or '*Views of Nature*'. One of the four essays that compose the first edition, 'Ideas for a physiognomy of plants' contains the following paragraph (from an 1850 translation[4]):

'But although life is everywhere diffused, and although the organic forces are incessantly at work in combining into new forms those elements which have been liberated by death; yet this fulness of life and its renovation differ according to differences of climate. Nature undergoes a periodic stagnation in the frigid zones; for fluidity is essential to life. Animals and plants, excepting indeed mosses and other Cryptogamia, here remain many months buried in a winter sleep. Over a great portion of the earth, therefore, only those organic forms are capable of full development, which have the property of resisting the considerable abstraction of heat, or those which, destitute of leaf-organs, can sustain a protracted interruption of their vital functions. Thus, the nearer we approach the tropics, the greater the increase in the variety of structure, grace of form, and mixture of colors, as also in perpetual youth and vigour of organic life.'

This paragraph is interesting in several aspects. Although the modern terms 'diversity' or 'species richness' are not used, it is clear from the rest of the essay that the final sentence represents a statement of the latitudinal diversity gradient (as well as some other gradients no longer considered interesting!). But, in addition to recognizing the pattern, von Humboldt also provided a general hypothesis for latitudinal gradients (climate), as well as a specific causal factor (winter temperatures) and a mechanism (loss of fluidity; i.e. freezing). All things considered, as a statement of a hypothesis for the latitudinal diversity gradient, this paragraph offers a degree of clarity not always achieved in modern hypotheses. It should also be noted that, by the 1820s, analysis of the plant diversity gradient had become quite sophisticated. For example, when von Humboldt discussed ferns in Illustration 28, which he added to the physiognomy essay in later editions, he said 'In receding from the tropics (where on the large continents d'Urville [1825] estimates the proportional number at 1/20), the relative frequency of ferns decreases rapidly as we advance into the temperate zone…The relative frequency again increases considerably towards the frigid north. Here, the family of ferns decreases much slower in the number of species than does that of phanerogamic plants'[4]. Clearly, the existence of the gradient was by then taken for granted, and he was more interested in major taxonomic differences in the floras of different latitudinal zones.

Whether von Humboldt was right about why the latitudinal diversity gradient exists is beside the point. The funny thing is that his *ca.* 200 year-old idea represents one of the major hypotheses currently being tested by ecologists and biogeographers to account for geographical variation in species diversity. Although space availability constrains a discussion of the state of the art, von Humboldt's temperature–fluidity hypothesis is alive and well in the form of 'water–energy dynamics'[5]. Finally, it is prudent to note that a more thorough search of the literature might turn up an even older statement of the latitudinal diversity gradient, or an earlier description of some other ecological pattern. Until then, ecologists should consider that the largest-scale pattern in ecology might also be the longest known, and we should never forget that we are still standing on the shoulders of giants.

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 0169–5347/01/$ – see front matter PII: S0169-5347(01)02197-8