# Altitudinal diversity gradients and the theory of island biogeography — an explanation

As part of a wider discussion of forest diversity in New Zealand, Ogden (1995) pointed out that the area available between any pair of contours on a conical mountain decreased with altitude in parallel with the decrease in species richness. This correlation is confounded with other environmental variables, such as temperature, which have been widely considered to be causal in the diversity decline. However, generalization has been elusive, and the supposed causal mechanisms are often couched in vague terms such as "harshness". Ogden chose to emphasize area, and invoked the theory of island biogeography of MacArthur and Wilson (1967) by drawing parallels between islands and successively superimposed areas on mountains. Kingston (this issue) objected, mainly on the grounds that the theory of island biogeography refers to "isolated" areas and deals with the equilibrium between immigration and extinction, on which Ogden presented no evidence. In the light of these criticisms the data presented in Ogden (1995) is re-assessed here. I conclude that the "area hypothesis" is at least as good as any other for "explaining" (correlating with) elevational diversity trends. Area is itself correlated with environmental heterogeneity, which is presumably more important as a causal agent. However, Kingston's insistence on the need for evidence on immigration and extinction to support the application of island biogeography theory is acknowledged.

Key words: Altitudinal gradients, Biogeography, Plant diversity, New Zealand.

THE important contribution made by the equilibrium theory of island biogeography of MacArthur and Wilson (1967), irrespective of its validity in part or in toto, lies in the impetus it has given to biogeographers and ecologists to refocus on the general and quantitative, rather than the specific and descriptive, aspects of biodiversity (Schoener 1988). The theory has frequently been applied to terrestrial "habitat islands", especially in the context of conservation biology (e.g., Simberloff and Abele 1982). Mountains, especially isolated summits, have long been recognized as having these insular properties (e.g., Brown 1971; van Steenis 1972). Depending on the altitude chosen for the "shore line", such islands will be bigger or smaller and less or more isolated from other similarly defined montane islands. In this sense an isolated mountain can be viewed as a superimposed set of islands, each smaller island unit at a higher altitude and thus more isolated from similar neighbours. These concepts are derived in a straightforward way from the original theory.

A further step might be to examine the differences in species richness (in equal sized samples) between these different superimposed units by focusing on the annulus of land surface between the contours defining two such units. This step is considered "invalid" by Kingston on the grounds that the "isolation" of the units is zero. MacArthur and Wilson (1967) stress that isolation is a universal feature of biogeography, and that

particular habitats represent isolated mosaics for some species, but not for others. Their model does not explicitly require any particular degree of isolation. Rather, as emphasized by Kingston, the theory of island biogeography deals with the equilibrium between immigration and extinction of species, and simply predicts that a change in this equilibrium will occur as isolation changes on different islands.

In my 1995 paper I examined the idea that a mountain could be treated as a superimposed set of islands. I presented data on woody plant distributions from twelve data sets from nine different mountains, derived from various authors and my own unpublished data (Fig. 2 in Ogden 1995). My aim was to summarize and seek simplifying generalities from the data. I made no attempt to formalize these into the "area hypothesis" referred to by Kingston, although I did speculate that area might be an important (and generally disregarded) variable.

The data from different mountains showed a variety of trajectories against altitude, some of which might be accounted for by chance variability in sample locations. For example, plots at the same altitude might fall on a rocky or a boggy part of the overall sequence, and this would influence their species composition. To overcome this "non-altitudinal" variability, I counted a species as present ("potentially present" Druitt et al. 1990) if it occurred in plots both

above and below the one in question. Considerable variation still remained in the slopes of individual trajectories, but overall a clear monotonic decline in diversity with altitude was apparent. Although this was expected, it should be noted that this pattern is by no means universal (e.g., Whittaker and Niering 1975; Ogden and Powell 1979). A regression line fitted to all the data explained 65.5% of the variance, and the slope of the line implied an average loss of 3.4 woody species for every 100 m of altitude gained.

On a perfect cone the surface area of the annuli between equally spaced contours, and the total area above any particular contour, declines in a regular manner. Consequently, if species richness is related to the area avilable at any altitude on a cone, it should decline monotonically. This is not simply saying that the sample size declines, because species richness refers to equivalent samples from each annulus. I assume that using smoothed data (number potentially present) reflects the number that might have been obtained with larger (but equal) samples at any altitude. If this assumption is false, the results might be interpreted as simply reflecting decreasing sample size with altitude.

The New Zealand data presented come from mountains which can be reasonably represented as cones or steep sided ridges (which are geometrically similar in this context). An "average mountain" can be modelled by (1) assuming it is a cone,

and (2) giving it a height equal to the upper limit of woody growth (not the timber-line). Heights above this are irrelevant in this sense, as they contain zero species (as defined). Of course, the upper limit of woody growth decreases with increasing latitude. As my mountain samples were taken from a wide range of latitudes in New Zealand, some overall average was required. The maximum altitude of the "penalpine zone", the upper limit of woody plants, ranges from c. 1 850 m in the cental North Island (Ruapehu) to c. 1 200 m on Stewart Island (Wardle 1991). Both these sites are represented in the data set analysed. The altitude of the "penalpine zone" in "Central New Zealand" is given as c. 1 750 m by Wardle (1991, Fig. 5.2) and this was taken as the cone height. Given this height, and the estimated woody species richness close to sea-level, and assuming that species richness declines in proportion to the area available on each annulus of the cone, it is possible to plot a straight line connecting the sea-level value to the zero point at 1 750 m.

This line was superimposed on the New Zealand data (Fig. 3 in Ogden 1995). While individual mountains deviate from it, the overall trend defined by the linear regression fits this "area line" almost exactly. So do the data from the almost perfect volcanic cone of Mt Egmont (Taranaki). I conclude that "area available" at any altitude is closely correlated with species richness. This statement does not imply that I have failed to recognize *that area is confounded with many other environmental variables.* Gaston and Williams (1996) emphasize that detailed studies of the confounding effects of area, altitude and species diversity would be valuable.

Two aspects of this confounding were examined, though only one of them was alluded to in the paper in question (which dealt primarily with other matters). First, I compared the New Zealand sequences with one from Mt Field in Tasmania the summit of which rises from a basalt plateau at mid altitude (Ogden and Powell 1979). Consequently, on this mountain, the available space between different elevations varies drastically. Altitudinal diversity trends were the opposite to those on the New Zealand "cones", with species richness increasing with increasing altitude to reach a max-

imum on the plateau between 1 000 and 1 150 m. The higher substrate diversity associated with poor drainage on the plateau may well account for the higher diversity there, although there may also be historical reasons (discussed in Ogden and Powell 1979). Beals (1969) presents evidence that slope (a crude proxy for area) effects plant community composition by changing competitive dominance, vegetation structure and community boundaries, but does not present diversity data.

Area and habitat heterogeneity are almost universally confounded (Williamson 1988). MacArthur and Wilson (1967) stress that "area itself is correlated with environmental diversity, *which exerts a more direct effect on species numbers*" (page 65, my italics). However, as Kingston rightly points out, this is not the main point of the equilibrium theory. Whatever the causation, on Mt Field the positive correlation (r = .882; n. 18; p < .001) between species richness and the distance between the 100 m contour intervals within which the plots fall, stands in stark contrast to a significant *negative* correlation between richness and temperature.

Secondly, I examined the correlations between temperature and species richness as an alternative explanation — the "climate hypothesis". If temperature alone were to determine species richness, a moist air lapse rate of 0.6°C and an average decline of 3.4 species per 100 m would imply that the species were capable of responding to average temperature differences of c. 0.2°C. However, "temperature" is simply a single measure representing a suite of correlated climatic and soil parameters, which together dictate the decline in species richness with altitude (e.g., Wardle 1991). Kingston sidesteps this complexity with the term "harshness". Clearly temperature plays a role for most plant species in most situations, and may frequently determine the upper limits of species' distributions. However, where the decline with altitude is not monotonic other factors and interactions have to be invoked, for example aridity at lower levels. Consequently, it seems unlikely that temperature, or any other single environmental factor, will be found to account for the richness gradient. As demonstrated on Mt Field, opposite temperature correlations can occur. I tentatively propose that, if a number of mountains are

examined, "area available" will be found to correlate with richness at least as well as any single climatic variable.

A prediction arising from the idea that climate controls richness with altitude is that plots at the same altitude on different mountains should have more or less the same richness irrespective of the size of the mountain. When this was found not to be the case, the Massenerhebung (mass-elevation) effect (van Steenis 1972; Huggett and Cheesman 2002) was invoked: bigger mountains have their own climates, causing elevation of the vegetation zones. If, for the data presented in Figure 2 (Ogden 1995), the number of species at 1 000 m is plotted against the total heights of the mountains on which they occur, weak but significant correlations are found. (r = 0.8035; n, 6; p < .10 for N Island mountains; r = 0.7170; n, 9; p < .05 for N and S Island combined. The Rangataua lava flow was excluded, because as explained in Ogden (1995) it is exceptional in terms of substrate and history). These results are not strong, and partially confounded with latitude. They could be taken as confirmation of the Massenerhebung effect, but they also conform to the expectations of the "area hypothesis". Unfortunately, at any altitude big mountains also have bigger areas, and greater environmental heterogeneity, than do smaller ones.

I consider the correlations between area, elevation and species richness to be a "vindication" of the theory of island biogeography in the sense that they demonstrate that consideration of area has been "worthwhile or justified" (Chambers Encyclopedic English Dictionary 1994). They conform to theory in-so-far-as regression analyses show that area alone accounts for most of the variation in species number with elevation (cf. MacArthur and Wilson 1967, page 65). They clearly do not "prove" that area is causal in the sense that area *per se* determines an equilibrium between species immigration and extinction rates. However, perhaps they do indicate that we should consider this possibility, which was the point I made in 1995. I think this approach might be at least as rewarding as resorting to vague and unmeasurable terms such as "harsh" and "benign".

"The proliferation of competing articulations, the willingness to try anything (Ogden), the expression of explicit discontent (Kingston), the recourse to philosophy and debate over fundamentals (both), all these are symptoms of a transition from normal to extraordinary research" (Kuhn 1970; page 91). However, more field-work, new data and hypothesis testing seem to me most likely to advance understanding.

## REFERENCES

Beals, E. W., 1969. Vegetational change along altitudinal gradients. *Science* **165**: 981–85.

Brown, J. H., 1971. Mammals on mountain tops: nonequilibrium insular biogeography. *Amer. Nat.* **105**: 467–78.

Druitt, D. G., Enright, N. J. and Ogden, J., 1990. Altitudinal zonation in the mountain forests of Mt Hauhungatahi, North Island, New Zealand. *J. Biogeogr.* **17**: 205–20.

Gaston, K. J. and Williams, P. H., 1996. Spatial patterns in taxonomic diversity. Pp. 202–29 *in* Biodiversity: A Biology of Numbers and Difference ed by K. J. Gaston. Blackwell Science Ltd. Oxford.

Huggett, R. and Cheesman, J., 2002. Topography and the Environment. Pearson Education Ltd and Prentice Hall, Harlow, Essex, England.

Kuhn, T. S., 1970. The Structure of Scientific Education, 2nd Edition. Chicago University Press, Chicago.

MacArthur, R. H. and Wilson, E. O., 1967. The Theory of Island Biogeography. Princeton University Press. Princeton, New Jersey.

Ogden, J., 1995. The long-term conservation of forest diversity in New Zealand. *Pac. Cons. Biol.* **2**: 77–90.

Ogden, J. and Powell, J. A., 1979. A quantitative description of the forest vegetation on an altitudinal gradient in the Mount Field National Park, Tasmania, and a discussion of its history and dynamics. *Aust. J. Ecol.* **4**: 293–325.

Schoener, A., 1988. Experimental Island Biogeography. Pp. 483–512 *in* Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distributions ed by A. A. Myers and P. S. Giller. Chapman & Hall, London.

Simberloff, D. and Abele, L. G., 1982. Refuge design and island biogeography theory: effects of fragmentation. *Amer. Nat.* **120**: 41–50.

Van Steenis, C. G. G. J., 1972. The Mountain Flora of Java. E. J. Brill. Leiden.

Wardle, P., 1991. The Vegetation of New Zealand. Cambridge University Press, Cambridge.

Whittaker, R. H. and Niering, W. A., 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology* **56**: 771–90.

Williamson, M., 1988. Relationship of species number to area, distance and other variables. Pp. 91–116 *in* Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distributions ed by A. A. Myers and P. S. Giller. Chapman & Hall, London.

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