

Can altitudinal diversity gradients be explained by a reduction in area with altitude?

Species richness at higher altitudes of a region typically decreases with altitude, the usual explanation being that environmental conditions become harsher as altitude increases. On conical or ridge shaped mountains the surface area available within equally spaced altitude bands declines as altitude increases. It has been suggested (Ogden 1995) that this may be responsible for the decrease in species richness. The phenomenon of decreasing species richness with altitude has been further interpreted by Ogden as lending support to the equilibrium theory of island biogeography (MacArthur and Wilson 1967) which predicts that larger areas will contain more species. The hypothesis that a decrease in area is responsible for the decline in diversity with altitude is here considered critically, and the evidence presented in support of it is found to be lacking.

Key words: Altitudinal gradients, Biogeography, Diversity.

OGDEN (1995) notes that woody plant diversity in New Zealand decreases in a fairly consistent way as altitude increases, and he suggests that conservation emphasis in New Zealand should therefore be on lowland forests.

The usual explanation for the decline in diversity with altitude is that altitude is a proxy for environmental variables, and so diversity decreases with altitude because of the way these environmental variables change with altitude. Ogden offers an alternative explanation, this being that the area available at any given altitude also usually decreases as altitude increases — this shall be referred to as the “area hypothesis”.

Ogden relates the area hypothesis to the equilibrium theory of island biogeography (MacArthur and Wilson 1967), which postulates that species number on an island is a function of the size and isolation of the island. Larger islands are predicted to contain more species than smaller islands. Ogden implies, without explicitly stating, that the different sized areas that exist between equally spaced contour lines are analogous to different sized islands, and that the finding that the larger (and lower) altitude bands generally contain more species conforms with the theory of island biogeography. (Elsewhere he describes mountains as high altitude “islands” in a “sea” of lowland, but this concept of whole mountains as islands is not what his area hypothesis relates to).

The “isolation” part of the equilibrium theory of island biogeography appears to have gone unnoticed. Islands, by definition, are isolated from their colonizing species. It is not

valid to arbitrarily divide up the continuous tract of vegetation that covers a mountain and then consider the results of the division as “islands”.

The division of a mountain into different sized areas equates to taking different sized sample areas from the mountain. In the absence of any environmental gradients we would expect that the larger sampling areas may contain more species, because increasing the sample area increases the probability of detecting more species. However, we would not expect species densities to vary across sample areas. At least some of the data presented by Ogden (1995) indicate that species densities do vary across altitude bands.

For example, a portion of these data comes from two ascending transects on the western slopes of Mt. Hauhangatahi, North Island, New Zealand (Druitt *et al.* 1990). It appears that equal areas were sampled within each altitude band, and that fewer species were detected in sample areas in higher altitude bands. This implies that there is some factor (other than a sampling effect) that changes with altitude and influences species richness. To argue that area is the factor in question is analogous to dividing up an actual island into different sized areas and then expecting to find that the smaller areas have lower species densities than the larger areas. Such a result is not predicted by the equilibrium theory of island biogeography, and if it were to happen we would consider that the size gradient must have been confounded with an environmental gradient, which is, of course, exactly what has been done here.

Ogden believes the area hypothesis to be supported by data from Mount Field in Tasmania. On this mountain species richness increases with increasing altitude. Above 1 000 m Mount Field comprises a series of plateaux and so, to quote: “the area available above this altitude (and the range of microhabitats) actually increases with altitude.”

If a plateau is to be regarded as an island it can be compared only with other plateaux, because, as already explained, the other altitude bands cannot be regarded as islands. Also, it is not valid to compare a plateau with a slope and then conclude that the reason they harbour different numbers of species is that they are of different sized areas. It could be, for example, that conditions on the plateau are more benign.

The statement that “the area available above this altitude (and the range of microhabitats) actually increases with altitude” indicates that Ogden considers that the significance of area is to do with habitat diversity, rather than area *per se*. The equilibrium theory of island biogeography, however, connects area to species richness mostly via extinction probability, not via habitat diversity. MacArthur and Wilson (1967) did acknowledge that the increased habitat diversity that may be associated with larger areas could contribute to higher species richness, but this is not what their theory of island biogeography is essentially concerned with. The theory links area with population size, and thus with extinction probability. If area is connected to habitat diversity rather than population size, then it does not

follow that increasing the area of an island will reduce extinction probability for any individual species.

Greater habitat diversity may contribute to greater species richness in larger altitude bands (including the plateaux of Mount Field), but this cannot be inferred from the presented data. Differing levels of habitat diversity would create differences in species totals between altitude bands, but not necessarily differences in species densities. Habitat diversity has not been isolated as a contributing factor. If habitat diversity is the explanation for the greater species richness in larger altitude bands, then invocation of the equilibrium theory of island biogeography is inappropriate. Conversely, an altitudinal species richness gradient can offer no support for the theory if habitat diversity is the explanation for the gradient.

The validity of other evidence presented in support of the area hypothesis is questionable. Figure 3 of Ogden's paper (1995) shows two lines. One is a regression of species richness on altitude. The other, according to Ogden, "is not derived from the data, except that it takes 60 species as the sea-level value. Thereafter the decline in species number with altitude indicated by this line is based on the assumption that the number is proportional to the area available on a perfect cone. The cone was regarded as a superimposed set of concentric

contours. The area between contours (the annulus) was obtained by subtracting the areas of progressively smaller circles. Species number was assumed to be directly proportional to annulus area, with the largest annulus given a value of 60."

The claim that this line is not derived from the data except in that it takes 60 species as the sea-level value (which corresponds to the y intercept), is dubious. The text that accompanies the figure states that the cone in question has an apex at 1 750 m. The apex height specifies the x intercept, making the regression trivial. (Ogden has used an approximation to estimate the cone areas, and so the apex height may not exactly specify the x intercept, but it will be very close).

Ogden states that "The coincidence between the least-squares regression and the conical surface area reduction, suggests that available area could be an important determinant of the local alpha-diversity at different altitudes." No explanation is given of how the apex height of 1 750 m was chosen, and it appears that the similarity of the lines may have been predetermined, rather than arising from coincidence.

Ogden claims that "This appears to be a remarkable vindication of the much discussed 'Theory of Island Biogeography'". The theory has been

misinterpreted, however, and the evidence put forward does not logically support it.

A strategy of conserving areas associated with higher biodiversity may be reasonable, and a focus on the conservation of lowland areas in New Zealand may be reasonable. However, the underlying determinants of diversity may also be important in a consideration of what to conserve, and it is desirable that flawed hypotheses concerning these play no part in discussions about conservation strategy.

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