SPECIES-AREA RELATIONS AND NON-EQUILIBRIUM MODEL OF PHANEROZOIC DIVERSITY.

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In recent biota. the number of species living in an region has been related to the extension of the habitat area according to an equation ($S = kA^z$). Species number (S) increases as a power z (very constant value around 0.30) of the area A. This positive relation has been empirically found in many recent (usually terrestrial) biota and in marine ancient faunas. Global recent biota however shows a very strongly unbalanced distribution of biodiversity. more than 75% of the species crowding less than 10% of the total area. and only 1% occupying 67% of the space.

Many. but not all. authors found species-area positive relation useful as an evidence for an equilibrium (area becomes saturated regarding the number of species that can coexist) which is described with the logistic equation. A dynamic equilibrium (with high turnover) or a stability during ecological time is envisaged. Applications to the fossil record generally consider dynamic equilibrium only (stability cannot be sustained for evolutionary time).

We test the species-area relation in the fossil record at a regional scale. The extension of land in the Mediterranean region was measured in five paleogeographical (palinspastic) reconstruction from Late Cretaceous to Late Miocene. The number of mammal species was estimated for the same period. after count for sampling. paleoecological and taphonomic biases. Although there is a general co-variation (land area and species numbers tend to increase in time). there are discrepancies with the expected positive relation of equilibrium model. 1) Latitude increased. and number of isolated regions decreased. both factors are supposed to lower the number of species: consequently. the increased number of species is much more important than expected. 2) An important fall of mammalian diversity is significantly noted at the early Oligocene (Stehlins' Great Rupture). which corresponds with an increase in area (Oligocene regression). contrary to the model. 3) A reduction in area in the Lower Miocene (Burdigalian transgression) does not correspond to a fall or a flat as expected. but to a high in mammal species.

A general survey for diversity-area relations during the Phanerozoic supports a far-from-equilibrium model. The case of land biota shows a general increase of both. diversity and area. during the Phanerozoic. but data estimations are less reliable. In the case of shallow sea biota. which has the best fossil and paleogeographic record. the diversity shows a negative correlation ($r = -0.77$) with the extension of the area. Data seem consistent at different taxonomic levels and with different author's estimations.

If a trend for sustained increase is maintained long-time. across many perturbations. or if there is a negative species-area correlation. the equilibrium model falls in their assumptions and seems severely flawed. The evolutionary process shows no inner limits to diversity density. and the exponential equation is necessary to describe it instead of the logistic equation. It has important consequences for ecological theory.

All biological processes are far-from-equilibrium in thermodynamic terms. needing a continuous input of high-level energy and a high cost in entropy export. Equilibrium models in theoretical ecology. damping fluctuations and allowing regulatory feedback. need less energy to be maintained than far-from-equilibrium models. We must consider that the ultimate physical energy feeding ecosystems is the sun energy. which is decreasing with time.

In far-from equilibrium systems. fluctuations may be very frequent and feedback may be positive. evolving in an accelerated pace and consuming an increasing amount of energy. This seems to be the case of the increasing and crowding biodiversity during the Phanerozoic.

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