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The fractal nature of the latitudinal biodiversity gradient

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Abstract: For a long time ecologists have questioned on the variations of biodiversity across the latitudinal gradient. Recently, it has emerged that the changes in β-diversity are caused simply by changes in the sizes of species pools. In this study, the species pool size and the fractal nature of ecosystems was combined to clarify some general patterns of this gradient. Considering temperature, humidity and NPP as the main variables of an ecosystem niche and as the axis of the polygon in the Cartesian plane, it is possible to build fractal hypervolumes, whose fractal dimension rises up to three moving towards the equator. It follows that the best figure that graphically synthesizes the evolutionary forces that fit this ecosystem hypervolume is the fractal cauliflower.

Key words: latitudinal gradient; biodiversity; fractals; ecosystem niche; cauliflower

Introduction

One of the most interesting questions in ecology is why tropics are so diverse or, in other words, why there are variations of biodiversity across the latitudinal gradient. Since the extent of tropical diversity compared to temperate areas became evident during the XIX century, a large number of different factors have been suggested as possible explanations (for a summary see Pianka 1966). Recently, it has been evidenced that the changes in β-diversity are caused simply by changes in the sizes of species pool. In fact, after correcting for variation in pooled species richness (γ-diversity) the differences in β-diversity disappear. Thus, differences in local assembly processes are not the causes of latitudinal and altitudinal patterns of biodiversity, where the variation in biogeographic processes that set the size of the species pool is a more plausible explanation (Nathan Kraft et al. 2011). One of the most corroborate ecological and evolutionary hypotheses about the latitudinal gradient is that Climate (C) influences Net Primary Production (NPP) in such a way that, by rising/lowering available biomass (B) and so increasing/decreasing the number of Individuals (I), it "controls" the number of Species (S). So far the Climate→NPP→I→S relation has not been clearly demonstrated, because it seems not being directly mediated by the biomass. I will show that it is not I or B that influence S, but rather the extent of Climate and NPP on niche variables.

Material and methods

To test the best figure that fits the ecosystem hypervolume (a polygon with T, H and NPP as dimensions) I analysed different fractal equations and the relative Hausdorff fractal dimension (D) of their representations (Falconer 1990). Cauliflowers or, better, broccoli and romanesco are examples of natural elements with a typical fractal tree-like structure. Differently from the fractal tree (Fig. 1A), the most typical example of fractals in living nature, the classical fractal cauliflower (Sang-Hoon 2005) (Figs 1B, C), has a higher D ($\sim$ 2.6–2.8) which is closed to the hypervolume ($D = 3$).

The fractal tree has a very simple mathematical formula:

$$z_{n+1} = (z_n + 1)/c \text{ or } z_{n+1} = (z_n - 1)/c$$
$$\text{for resp. } x > 0 \text{ and } x < 0.$$

The number of iterations is related to the number of branches. The fractal image of a tree is constructed with a so called 'if-then-else' formula. Gaston Julia (1918) described a set of complex points derived from successive iterations, where J(f) is the smallest closed set containing at least three points which is completely invariant under f:

$$\text{Julia: if } x > 0 \text{ then } z_{n+1} = (z_n + 1)/c$$
$$\text{else } z_{n+1} = (z_n - 1)/\text{conj}.c,$$

where the branches on the stem originate from the power of two for $(z_n - 1)$ or $(z_n + 1)$.

Anyway its representation is oversimplified and does not reach any high D, even for the 3-branches tree. In fact, each branch carries 3 branches and the fractal dimension of the entire tree is the fractal dimension of the terminal branches, i.e., the 2-branches tree has a fractal dimension of 1. Because of the need to model the addiction/speciation of new species in a self-similar way (Tsang 1986) that allows more and more small ecological niches to be created within the ecosystem niche (3-D niche) and the necessity of an iterative process which can fill it, I improved the basic cauliflower equation:

$$\text{Julia: if } (x \geq 0) \text{ then } z_{n+1} = (z_n - 1)^2/c,$$

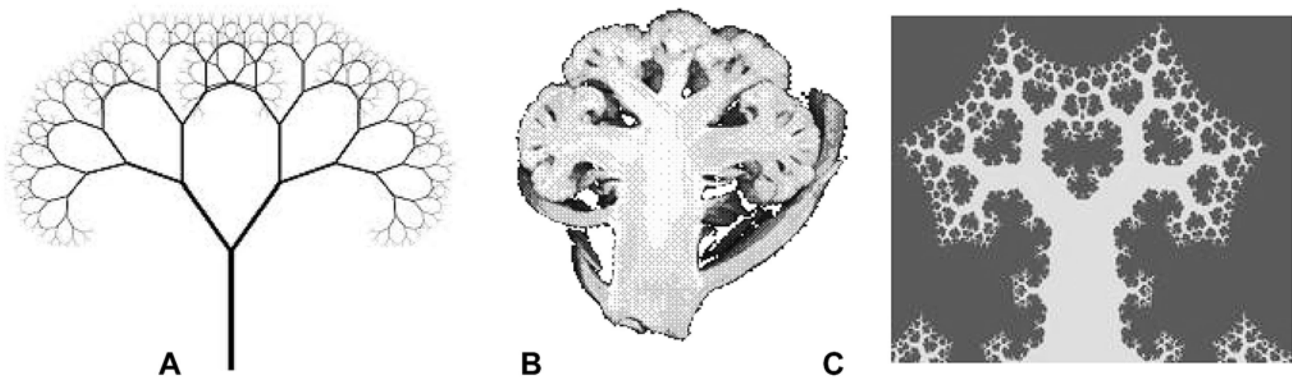

Fig. 1. The simple fractal tree is a good representation of species iteration in filling a fixed niche space (A), but it does not account for the complexity of ecosystems and does not fit with the fractal dimension of the hypervolume. Cauliflowers, broccoli and romanesco (B) are the optimized natural elements with a $D = \sim 3$. The fractal equation system and representation (C) considers iterative processes (such as the addiction/speciation of new species) and, at the same time, the creation of new available niches (branches). The 3-D improved version better fulfills this purpose.

$$\text{else } z_{\mathrm{n}+1} = (z_n + 1)^2/\text{conj}.c$$

I added the third dimension and a more complex power of three building an "efficient broccoli" with a $D = \sim 3$. It better accounts for an optimized natural system where each species begets new niches for other ones, just with its own presence in that ecosystem. The higher the number of species (so that of iterations of the fractal equation), the higher the number of available niches and the quantity of space filled within the ecosystem hypervolume.

The improved fractal cauliflower equation is:

$$\begin{cases} n_s = a + \mathrm{i}b + c \\ n_{s+1} = (n_s - 1)^3 n_{\mathrm{s}} \vee (n_s + 1)^3 /\text{conj}.n_s \end{cases}$$

if $x \geq 0$ V $x \leq 0$ respectively; where n_s is the niche of the first species s; a, b and c are the variables (and the dimensions of axes of the Cartesian hypervolume), that can be considered as T, H and NPP of the 3-D ecosystem.

The fractal dimension D has been calculated as (Mandelbrot 1977):

$$D_n = \lim_{\mathrm{L}\to 0} \frac{\ln(S)}{\ln(L)}$$

where L is the linear scaling and S is the result of size increasing. In the "improved fractal cauliflower" D is about 2.8–2.9.

The ecosystem niche amplitude has been calculated considering climatic (T, H) and ecological variables (NPP) as:

$$V_n = \sqrt{T^2 + H^2 + \mathrm{NPP}^2}$$

where V_n is the niche amplitude, T is temperature, H is humidity (which, in marine ecosystems, cold be substituted with light quantity) and NPP the Net Primary Production.

Results

It is possible to extend the ecological niche concept to an ecosystem dimension to better define the size of species pool invoked by Nathan Kraft et al. (2011). This "ecosystem niche", therefore, can be imagined as the sum of the niches of each species included in the pool. In an Hutchinsonian view, an ecosystem niche is an n-dimensional hypervolume, where the dimensions are environmental conditions ($C = H + T$) and resources (NPP) that define the requirements of all the species in an ecosystem to reproduce themselves.

Furthermore, examples of the fractal nature of nature have been argued continuatively during the last years (Brown et al. 2002). Different elements of the natural world have been associated to or defined as fractals, but only considering them separately and not in a holistic perspective (Vernadsky 2012). That ecosystems are structured in a fractal way (made by relationships that are self-similar over a wide range of spatial or temporal scales as well as the single elements whose they are composed), is becoming an intriguing idea in ecology. I combined these two apparently distinct concepts, the ecosystem niches and the fractal nature of them, in an attempt to clarify some general patterns of biological diversity.

Here I show that latitudinal gradient of biodiversity can be explained as differences in fractal dimension of ecosystem niches (Fig. 2A). Let's reduce the variables that can shape the ecological niche to the fundamental ones. Temperature (T) is surely one of these (McArthur 1972). Different authors suggested that the richness of species which cannot regulate their internal temperature (ectothermic) can be predicted from environmental temperature (Blackburn & Gaston 1996; Janzen & Pond 1975). Then, the second fundamental variable of an ecosystem hypervolume is humidity (H), which shows different values in terrestrial regions, but it is constant in marine environment, where temperature and photic zone depth are the analogous factors. The latitudinal variation of both these variables is shown in Fig. 2B. By merging temperature and humidity from pole to pole it is possible to estimate the curve of Net Primary Production (NPP). This latter shows a triple-humped-shape, with one big hump between about 20° N and 20° S from the Equator and two moderate humps over the temperate areas. The lowest values of NPP are in polar and deserts regions where T and/or H are reduced, respectively. Simple models of spatial dynamics (Kay et al. 1997) accurately predicts the increase

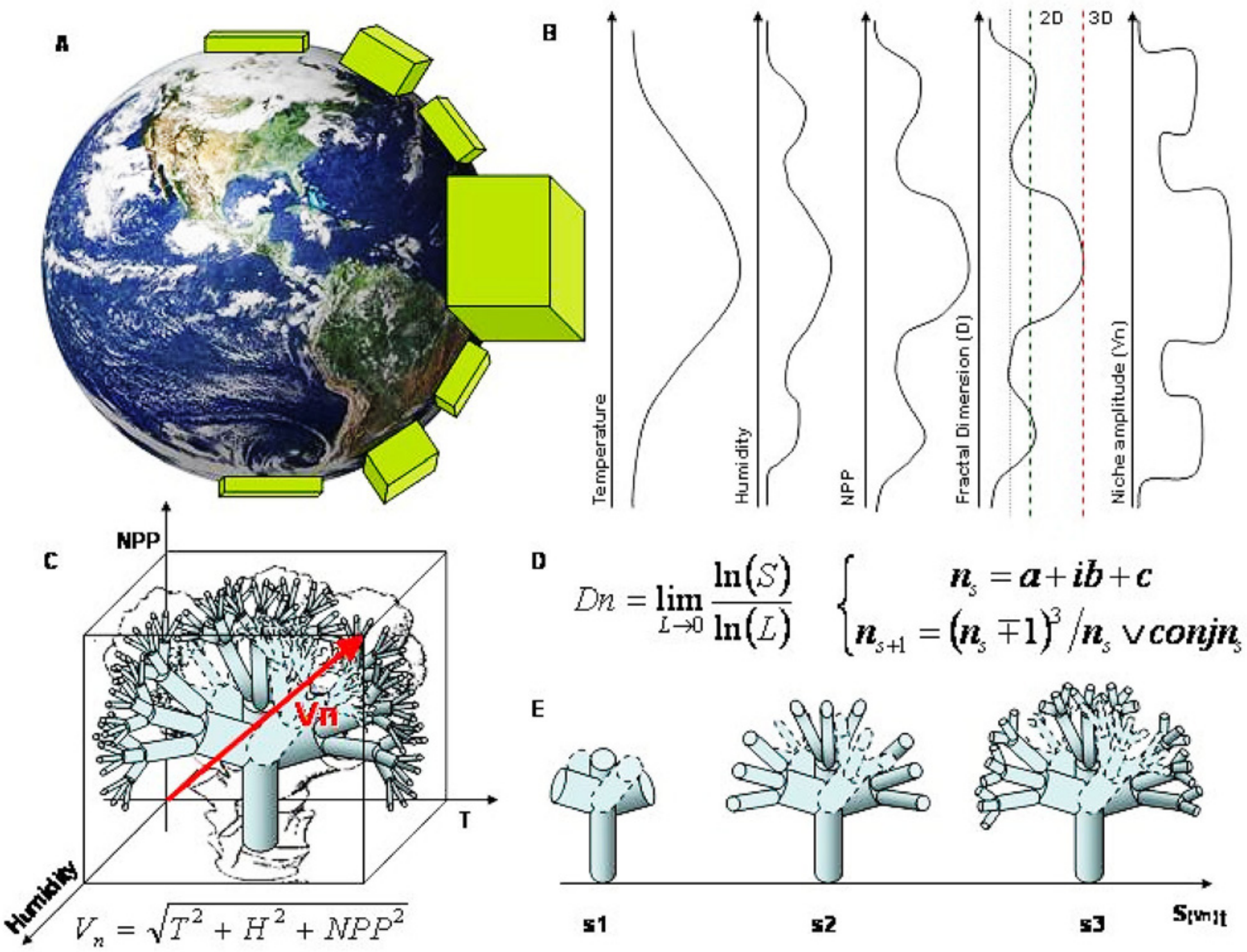

Fig. 2. The latitudinal gradient of biodiversity can be explained as differences in ecosystem niche amplitude (A) and fractal dimension derived by the combination of T, H and PPN (B). These three variables are the axes of the fractal hypervolume (C and green polygons in A). The fractal 3-D cauliflower (D) is the best fitting mathematical object (E) that takes into account the addiction of new species within the fractal ecosystem niche (C). The number of species in each region are, thus, dependent on the number of possible iterations of the fractal function (E) which is constrained by the ecosystem niche amplitude (V_n).

in species richness with increasing environmental productivity (i.e. "energy richness hypothesis"). It seems reasonable that autotrophic organisms diversity may be principally driven by humidity (or light, in marine environment), that of ectotherms by temperature, whereas resource availability (NPP) is the fundamental variable that allows differentiation of endothermic species. Thus, both T and H are constituent and co-variables of NPP in the ecosystem niches. Therefore, considering this niche as a polygon in the Cartesian plane where the x, y and z axis are T, H and NPP (Fig. 2C) I demonstrate that where T, H and NPP, and this latter particularly, are close to zero like in polar or deserts areas, the fractal dimension (D, Fig. 2D where L is the linear scaling and S is the result of size increasing) of this polygon is lower than two (~ 1.5). This means that there is rather a hypersurface available for the species than a hypervolume. Moving along latitude and following the NPP curve, the fractal dimension increases towards 2.5 reaching a value close to 3 (a 3-D shape) at the Equator (Figs 2A, B). Explicitly, here I consider the D value of the ecosystem hypervolume as a proxy of the available space for the species pool. Evidently, the greater T and H, and so the NPP, the higher D and the bigger the ecosystem niche amplitude (V_n, Figs 2B, C). This seems to solve the "niche conservatism" (Wiens & Graham 2005) and the "energy richness" hypothesis' problems (such as the misunderstanding influence of B or the weaker correlation between NPP and I than between NPP and S).

Discussion

Once defined the ecological causes of "biodiversity dimension", it is then fundamental to focus on the evolutionary processes that can fill the available niche space. The best figure that graphically synthesizes the evolutionary forces that fit the ecosystem hypervolume is the fractal cauliflower. In fact, for each iteration that can be assumed as the addiction/speciation of a new species (s), the niche volume can be filled up to reaching a value close to 3 D (such as 2.8–2.9 of the equations in Fig. 2D). The simple system in Fig. 2D accomplishes in the most efficient way the filling of an available functional space, where n_s is the ecosystem niche occupied by species ecological niches and a, b and c the portion of the three fundamental variables (T, H and NPP) used by each species. The branches of the fractal cauliflower are created step by step (Fig. 2E) by the addition/speciation of new species towards the maximum amplitude (V_n) allowed by NPP and consequently by D. Each segment constitutes a new available ecological niche within the ecosystem hypervolume which other species can occupy, as suggested by the hypothesis of the diversity that begets diversity (Currie et al. 2004; Cazzolla Gatti 2011, 2016).

Conclusion

The patterns described above, which can be synthesized as "the fractal hypothesis of biological diversity", although they could appear oversimplified, can be also extended to other biodiversity gradients (such as elevational) and they shed more light on ecological and evolutionary processes that shape biodiversity on Earth.

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