The unified neutral theory of biodiversity – can an analytical solution be obtained?

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A central problem in ecology is to understand the factors that control biodiversity. Hubbell (2001) developed a *Unified Neutral Theory of Biodiversity and Biogeography*, by starting with some simple assumptions and deriving a so-called zero-sum multinomial distribution of relative species abundance. The term 'neutral' means that, within a trophic level, all individuals are essentially identical and obey the same rules. Caswell (1976) introduced this idea to ecology, in order to investigate predictions of models that specifically *exclude* factors such as environmental responses, predator-prey interactions, competition and niche effects. By excluding such effects, which are commonly held to be important contributors to biodiversity, neutral theories are somewhat controversial. Hubbell's theory has therefore created much discussion among ecologists.

Hubbell (2001) solved his equations using linear algebra techniques, resulting in a so-called zero-sum multinomial distribution for species abundance. But an analytical form for this distribution was not obtained, making it difficult to test the theory. McGill (2003), for instance, explicitly noted that the lack of an analytical form makes it quite complicated to fit the distribution to data.

In light of this, I attempt to produce a more utilizable solution, perhaps even an analytical one. I start with the same assumptions as Hubbell, but proceed to solve the resulting equations using alternative techniques. My approach involves rewriting Hubbell's initial stochastic equations in a slightly different form. If $N(t)$ is the number of individuals of a particular species at time t, then the aforementioned equations specify the

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probabilities that, during a short interval of time, $N(t)$ will increase by 1 individual, decrease by 1 individual, or remain constant. I then derive a probability generating function $G(s,t)$, where s is a variable.

For a closed community with no immigration, Hubbell's first scenario, this approach results in a partial differential equation for $G(s,t)$:

$$\frac{\partial G}{\partial t} = \frac{(s-1)^2\mu}{J(J-1)}\left[(J-1)\frac{\partial G}{\partial s} - s\frac{\partial^2 G}{\partial s^2}\right], \qquad (1)$$

where J is the constant total number of individuals in the community, and μ is essentially a death rate (more strictly, μh is the probability of any individual dying in a short time interval of length h). The boundary and initial conditions are $G(1,t) = 1$ and

$$G(s,0) = \sum_{x=0}^{J} s^x \mathrm{P}\left(N(0) = x\right), \qquad (2)$$

where the initial probabilities are assumed known.

I solve these equations to give $G(s,t)$, which then yields the time-dependent probabilities $\mathrm{P}(N(t) = x)$ for $x = 0, 1, 2, ..., J$, i.e. $G(s,t)$ yields the probability density function for the abundance of the given species. Immigration is then introduced, and a similar approach taken. The aim is to see whether this method can be extended to all of the cases considered in Hubbell's book; if so then the results should prove valuable to ecologists who wish to test the theory against data.

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