# Independent species in independent niches behave neutrally

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A (re)current theme in community ecology is the reconciliation of niche and neutral processes. However, analytical models combining these processes are scarce. Chisholm and Pacala (2010, hereafter referred to as CP10) strived to fill this void by assuming several independent (i.e. non-overlapping) niches each of which behaves neutrally as in Hubbell's neutral community model (Hubbell 2001). They observed that their model predicts species abundance distributions (SADs) that resemble the neutral predictions when community diversity is high. They concluded that neutral processes prevail over niche processes in determining SAD patterns for highly diverse communities. Here we argue that their result is an artefact due to a particular property of their model for high diversity: species independence. To show that species independence explains their results, we present a model consisting of independent (i.e. non-interacting) species. We show that 1) our model is equivalent to the model of CP10 when community diversity is high, and that 2) our model predicts SADs that are identical to neutral predictions for *all* levels of diversity. Hence, species independence is the sole cause of the neutral SADs observed in CP10.

Like CP10, our model considers two scales, the larger metacommunity scale and the smaller local community scale (Hubbell 2001). The metacommunity consists of a large number of species. Each of the species is attributed to one of $K$ niches. Species inside a niche undergo neutral dynamics. This is all identical to CP10's model. Our model differs in two minor aspects. First, we do not impose the zero-sum constraint on the neutral dynamics inside a niche. This constraint, which introduces a special kind of species interdependence, is imposed in the model of CP10. Second, we assume that the local community is a sample from the metacommunity with all niches confounded. This means that individuals from the metacommunity are sampled irrespective of the niche they belong to. This differs from CP10's model, where it is assumed that the sample has *exactly* the same niche composition as the metacommunity. In this case, the niches in the metacommunity are sampled separately. Our model is more in line with the observation that on a local scale some niches may not be occupied due to chance or due to dispersal limitation. These effects are two sides of the same coin, because they can be regarded as dispersal-limited sampling effects (Etienne and Alonso 2005).

The mathematical structure of the two models is summarized in Table 1. The metacommunity composition inside a niche is given by Hubbell's metacommunity distribution. The model of CP10 imposes the zero-sum constraint, whereas our model does not. Hence, the two models differ only in the sizes of the metacommunity niches. The absolute niche sizes (i.e. the number of individuals in a niche) are infinite in both models; the relative niche sizes (i.e. the fraction of individuals in a niche) are fixed in the model of CP10, and are randomly distributed in our model. This distribution tends to the fixed niche sizes of CP10's model for high diversity, so that the two models coincide for highly diverse metacommunities. The local community is a sample from the metacommunity, that can be taken with or without dispersal limitation. For both models, the local community SAD inside a niche is given by the Ewens (without dispersal limitation; Ewens 1972) or the Etienne (with dispersal limitation; Etienne 2005) distribution. The models only differ in the niche sizes: fixed in the model of CP10, and randomly distributed in our model. Again, the latter distribution tends to the fixed niche sizes of CP10's model when the diversity in the local community is high, so that the two models coincide for highly diverse communities.

Our model has an additional property: the community composition for all niches taken together has the same structure as the community composition inside the niches. For example, the metacommunity composition with all niches confounded is given by Hubbell's metacommunity distribution, which also describes the composition inside a metacommunity niche. Similarly, the local community SAD with all niches confounded is the Ewens or Etienne distribution, which is also the SAD inside a local community niche. Hence, the SAD for the community with all niches taken together is identical to the SAD of a community without any niche structure at all. Note that this property holds for *all* levels of diversity in our model. In CP10's model the property does not hold generally, but is only valid for high levels of diversity, for which the two models are equivalent.

We have found that in our model the SAD for the local community with all niches confounded is identical to the SAD of a fully neutral model. This result is easy to understand intuitively. Hubbell's neutral community model without zero-sum constraint is nothing but a group

**Table 1.** Comparison between the model of Chisholm and Pacala (2010) and the model defined in this paper. Both describe a community model consisting of $K$ niches each of which behaves neutrally. The model variables are: $s_j$, the fraction of species in niche $j$ in the metacommunity; $p_j$, the fraction of individuals in niche $j$ in the metacommunity; $N_j$, the number of individuals in niche $j$ in a sample of size $J$. The model parameters are: $K$, the number of niches; $\beta_j$, the fraction of niche $j$; $\theta$, the metacommunity diversity; $I$, the dispersal parameter; $J$, the sample size.

| | Model of Chisholm and Pacala (2010) | Model defined in this paper |
|---|---|---|
| **Metacommunity** | | |
| Distribution of fraction of species $S_j$ in niche $j$ | fixed: $S_j = \beta_j$ | fixed: $S_j = \beta_j$ |
| Distribution of fraction of individuals $p_j$ in niche $j$ | fixed: $p_j = \beta_j$ | Dirichlet distribution: $\dfrac{\Gamma(\theta)}{\Pi_j \Gamma(\beta_j \theta)} \prod_{j=1}^{K} p_j^{\beta_j \theta - 1}$ |
| Abundance distribution of metacommunity for niche $j$ | Hubbell's metacommunity model with zero-sum constraint, and diversity parameter $\beta_j \theta$ | Hubbell's metacommunity model without zero-sum constraint, and diversity parameter $\beta_j \theta$ |
| Abundance distribution of metacommunity (with all niches confounded) | combination of $K$ distributions for Hubbell's metacommunity model with zero-sum constraint | Hubbell's metacommunity model without zero-sum constraint, and diversity parameter $\theta$ |
| **Local community (sample from metacommunity) without dispersal limitation** | | |
| Distribution of number of sampled individuals $N_j$ belonging to niche $j$ | fixed: $N_j = \beta_j J$ | multinomial distribution: $J! \prod_{j=1}^{K} \dfrac{p_j^{N_j}}{N_j!}$ |
| Abundance distribution of sample for niche $j$ | Ewens distribution* with parameters $\beta_j \theta$, $\beta_j J$ | Ewens distribution with parameters $\beta_j \theta$, $N_j$ |
| Abundance distribution of sample (with all niches confounded) | convolution of $K$ Ewens distributions | Ewens distribution with parameters $\theta$, $J$ |
| **Local community (sample from metacommunity) with dispersal limitation** | | |
| Distribution of number of sampled individuals $N_j$ belonging to niche $j$ | fixed: $N_j = \beta_j J$ | $\dfrac{J!}{(I)_J} \prod_{j=1}^{K} \dfrac{(p_j I)_{N_j}}{N_j!}$ ,† |
| Abundance distribution of sample for niche $j$ | Etienne distribution‡ with parameters $\beta_j \theta$, $\beta_j I$, $\beta_j J$ | Etienne distribution with parameters $\beta_j \theta$, $P_j I$, $N_j$ |
| Abundance distribution of sample (with all niches confounded) | convolution of $K$ Etienne distributions | Etienne distribution with parameters $\theta$, $I$, $J$ |

*The Ewens distribution is the stationary abundance distribution for Hubbell's local community model without dispersal limitation, see Ewens (1972).

†The notation $(a)_n$ stands for the Pochhammer symbol, $(a)_n = a(a+1)... (a+n-1) = \Gamma(a+n)/\Gamma(a)$.

‡The Etienne distribution is the stationary abundance distribution for Hubbell's local community model with dispersal limitation, see Etienne (2005).

of non-interacting species with independent abundance dynamics (Etienne et al. 2007). Hence, a niche in our model consists of independent species. Combining $K$ such niches without any interaction between the niches (i.e. without any overlap) results in a model in which all species, irrespective of whether they belong to the same or to different niches, are independent. This is again Hubbell's model without zero-sum constraint, but now for all species in the community, i.e. with all niches confounded. The argument clearly shows that the niche structure of our model is superficial; attributing species to niches does not affect the neutral community dynamics in any way.

The model of CP10 tends to our model for high community diversity. Using the result of our model analysis, we find that also in their model, when community diversity is high, the niche structure does not influence the neutral community. Hence, the result of CP10 is explained as a direct consequence of species independence. The model of CP10 does not describe a mechanism for the emergence of neutrality for complex communities. Rather, the niche structure of their model is so simple that species independence and neutrality are present from the outset. The only species dependence present in the model of CP10 is introduced by the zero-sum constraint, which affects the community when diversity is low. But the zero-sum constraint is a basic ingredient of the standard neutral community model (Hubbell 2001, Etienne et al. 2007), and is not related to niche structure. The model of CP10 does not leave the realm of neutral community models, and seems therefore of limited value in studying how niche and neutral processes interact.

To clarify the interaction of niche and neutral processes, one must consider models in which species are no longer independent but interact differently when they belong to the same niche than when they belong to different niches. However, the analysis of somewhat general models with this property seems to be quite challenging (Haegeman and Loreau 2011). The model we have introduced in this paper certainly does not possess this property, nor do we claim that it is any better than the model of CP10. We introduced our model only to sustain our claim that CP10's model effectively describes independent species. Our model is only a minor modification of theirs, and the two models share the same shortcomings; they are based on overly simple assumptions, as is typical for neutral community models.

General conclusions about the prevalence of neutral or niche processes based on such simple models, like ours or that of CP10, are premature.

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