He and Hubbell Reply: In Ref. [1], we developed percolation models to describe two fundamental metrics characterizing the distribution of species on landscapes. One is the total edge length of the distribution of a species over the landscape, denoted as L; the other is the number of clusters, denoted as T. Our Letter presented two main results. The first result demonstrates the existence of two functional links between L, T, and the abundance of the species, N. These links are made through an occupancy probability derived from the negative binomial distribution:

$$p = 1 - \left(1 + \frac{aN}{Ak}\right)^{-k}, \tag{1}$$

where A is the area of the entire landscape under study, a is the size of an individual cell, and k is an aggregation parameter. The second result is the derivation of two percolation thresholds in species abundance N_{cL} and N_{cT}.

Perrier *et al.* [2] raise a concern about an inconsistency in these two thresholds. However, we show here that this concern is unwarranted because L and T represent two fundamentally different types of percolation processes and, therefore, are not comparable.

(1) Perrier *et al.*'s misunderstanding arises from their confusion of *bond* percolation with *site* percolation [3]. The edge length is defined as the number of joins (interconnections) between occupied cells and empty cells. A join is the side shared between two adjacent cells. Edge length defines bond percolation. The bond percolation threshold is exactly 0.5, at which point one can cross the landscape through the interconnection of cells from one side to the other side of the area. Although bond percolation historically came first, it is no longer the focus of most theoretical studies of percolation, and, thus, it is less well known. In contrast to the bond percolation, site percolation deals with the number of clusters and cluster size. In site percolation, one crosses the landscape through occupied sites. T is a site percolation. It is well known that site percolation has a threshold 0.5927. The difference between bond and site percolation explains the difference between N_{cL} and N_{cT}.

(2) There is nothing new in Eqs. (1) and (2) of Ref. [2]. They are just special cases of Eqs. (1) and (3) of Ref. [1], respectively, at $k \longrightarrow \pm\infty$. This is a very well-known result. When $k \longrightarrow \pm\infty$, Eq. (1) is an occupancy probability for the Poisson distribution [4,5], resulting in Eq. (1) of Ref. [2].

(3) The formulation of Eq. (3) of Ref. [2] is incorrect. It uses the site percolation threshold to model bond percolation. That this invalid model fits the empirical data in Fig. 4 of Ref. [1] is artifactual and arises simply because the majority of the species on Barro Colorado Island, Panama are not randomly distributed but aggregated, and the site percolation threshold 0.592 inflates $N_{c\text{Theoretical}}$ of Ref. [2]. If species are not randomly distributed, one should use Eq. (3) in Ref. [1] in order to take their clumped dispersion into account, rather than use Eq. (2) or (3) of Ref. [2].

(4) Perrier *et al.* ignore spatial correlation, which is not acceptable practice in analyzing ecological data, even in a 50 ha plot. The consequences of ignoring spatial aggregation can be significant. For example, consider the case in the upper-left panel in Fig. 4 in Ref. [1], in which $A = 500\,000$ m^2, $a = 25$ m^2, and $k = 2$. The N_{cL}, calculated from Eq. (3) of Ref. [1], is 16 568.54, or $\log(16\,568.54) = 9.72$. Equation (2) of Ref. [2] results in $N_c = -(A/a) \times \log(1 - 0.5) = 13\,862.94$, or $\log(13\,862.94) = 9.54$, while Eq. (3) of Ref. [2] is $N_c = -(A/a)\log(1 - 0.5927) = 17\,964.11$, $\log(17\,964.11) = 9.80$. Although the three log-transformed values are very similar, the actual critical abundances N_c are not. They can differ by as much as 30% ($17\,964/13\,863 \approx 1.30$). Perrier *et al.* may consider 13 863 and 17 964 to be similar, but we do not. Differences of this magnitude are substantial and significant in ecological terms.

(5) If species are not randomly distributed, then Eq. (1) of Ref. [2] does not hold. Regardless of the spatial distribution that species exhibit, the overall bell-shape distribution will still hold. However, the threshold N_{cL} will change with a change in the aggregation parameter k, as described by Eq. (3) of Ref. [1]. In the nonrandom case, this model should always be used.

In summary, Perrier *et al.*'s Comment arises from their misunderstanding of bond and site percolations. Their Eq. (2) is a special case of our Eq. (3) and it is a bond percolation model. Their Eq. (3) is conceptually incorrect and mistakenly uses the site percolation threshold to model bond percolation.

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