

# Competitive interactions change the pattern of species co-occurrences under neutral dispersal

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Non-random patterns of species segregation and aggregation within ecological communities are often interpreted as evidence for interspecific interactions. However, it is unclear whether theoretical models can predict such patterns and how

simple two-species (Levin 1974) and three-species (Caraco

the grid of occupied patches represents the metacommunity, whereas each occupied patch represents a local community. In the following, we will interchangeably use the terms grid/metacommunity and patch/local community.

The subsequent dynamics in each patch follows a zero-sum rule (Hubbell 2001), meaning that each local birth, death, immigration, or emigration (all probabilities set to 0.01) is immediately counterbalanced by a corresponding death, birth, emigration, or immigration. Any grid-wide species extinction is counterbalanced by a single point mutation speciation in a randomly selected patch. In contrast to Hubbell's (2001) original formulation, this point mutation speciation ensures that the total number of species within the meta-community remains constant.

In this study, we added two features to this neutral model. First, we followed Jabot and Chave (2011) and introduced death rates that are species-specific and incorporate interspecific density-dependence. The local death probability  $\pi_i$  of an individual of species  $i$  in a community of  $j$  species is given by:

$$\pi_i = \frac{d_i^{1-\delta}}{\sum_j d_j^{1-\delta}}$$

pairwise mutual exclusions among sites; Stone and Roberts 1990). Species spatial aggregation was quantified by the clumping score, which is a normalised count of the number of pairwise co-occurrences among sites (Ulrich and Gotelli 2013). Nestedness measures the ordered loss of species along a focal environmental or ecological gradient (Patterson and Atmar 1986, Ulrich et al. 2009) and is therefore distinct (although not mutually exclusive) from species turnover (Ulrich and Gotelli 2013). We quantified the degree of nestedness using the standard NODF (nestedness from overlap and decreasing fill) metric, which is a normalized count of the degree of species overlap among the sequence of plots ordered according to decreasing species richness (Almeida-Neto et al. 2008). NODF ranges from zero (perfect species turnover) to 1 (perfect nestedness). Following the method of Baselga (2010), we assessed the degree of spatial species turnover among cells by the additive partitioning of the Sørensen metric  $b_{sor}$  (a metric of dissimilarity in community composition) into a component representing the difference in species richness among sites ( $b_{nest}$ ) and a component representing the spatial turnover of species ( $b_{sim}$ ). Below we focus on this turnover component because it represents the compositional variation of communities after controlling for differences in richness.

Metrics of species co-occurrences depend on matrix row (species) and column (sites) totals and cannot be compared directly. Therefore, we used a null model approach and compared observed scores with those obtained from 200 matrices randomly resampled by two different null algorithms. First, we resampled species incidences where placement probabilities were uniform for all grid cells (the equiprobable null model algorithm). In the second null model, placement probabilities were proportional to observed marginal occurrence totals (the proportional – proportional null model, Ulrich and Gotelli 2012). We did not use the popular fixed-fixed algorithm (Gotelli 2000) because it preserves the marginal totals of the matrix, which would lead to low variation in the NODF and lack of variation in the beta metrics.

Neutral models of limited dispersal (Babak and He 2009) and biogeographic models of the mid-domain effect (Colwell and Lees 2000) predict that random processes can lead to a reduction of species richness near the boundaries of spatial domains. To estimate the size of this effect, we calculated the difference  $S$  in richness between the 12 cells at each of the four grid corners and the

effects reduced the fit of the exponential decay model (Fig. 2b) but edge effects were of minor importance

transition elements of the competition matrix  $\mathbf{P}$ , often excluded all other species, resulting in a monoculture. Slopes of the species loss function were comparably steep (Fig. 2b), and edge effects of minor importance (Fig. 2c).

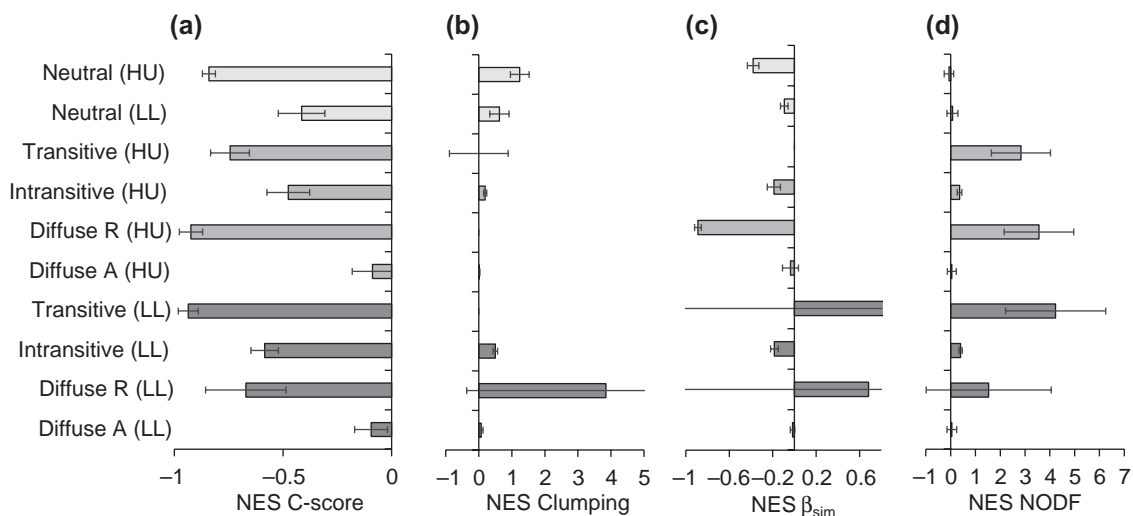
In contrast, intransitive competitive interactions significantly increased species richness in comparison to the neutral expectation (Fig. 3a) and decreased the species richness decay slopes (Fig. 2a). Consequently, a generalized linear model (Table 2) identified the type of competition as being the most important driver of species richness. Transitive competition decreased the variability in species richness among grids, leading to a segregated pattern of richness (Fig. 3b). Neither transitive nor intransitive competition altered edge effects on species richness (Fig. 2c).

Pure neutral communities were more spatially aggregated, with lower spatial turnover in species richness than predicted by the equiprobable null model (Fig. 4a–c, Supplementary material Appendix 2 Fig. A1a), but less spatially aggregated with more species turnover than predicted by the proportional null model (Fig. 5a–c, Supplementary material Appendix 1 Fig. A2a). Neutral community dynamics did

not generate significant patterns of nestedness (Fig. 4d, 5d, Supplementary material Appendix 2 Fig. A1d, A2d).

Pairwise (Table 2, 3) and di use (Table 2) competition significantly altered species co-occurrences compared to the neutral expectation. The C-score and clumping indices, but not  $b_{sim}$ , were most sensitive to competition. Dispersal and competition explained between 5% and 75% of variance in co-occurrences depending on the two types of null expectation (Table 2). Standardized effect sizes of the co-occurrence metrics (Supplementary material Appendix 2 Fig. A1–A2) were highly significant for the majority of competition-dispersal combinations with respect to the equiprobable null model, while only 33 of the 2160 comparisons with the proportional null model were significant at the 5% error level (1.5%).

Type of competition and dispersal limitation interacted and caused specific patterns of co-occurrences (Table 3, Fig. 4, 5). High dispersal caused intransitive competitive communities to be significantly ( $p < 0.001$ ) more segregated (C-score) than neutral ones when compared to an equiprobable null model and less segregated when compared to the proportional null model expectation (Table 3, Fig. 4, 5).



Wootton 2001, Liao et al. 2015). However, recent theoretical models (Huisman et al. 2001, Rojas-Echenique and Allesina 2011), pointed to the possibility that intransitive competitive hierarchies (Vandermeer 2011, HilleRisLambers et al. 2012) might be an important mechanism allowing





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