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 environmental factors may modify the effects of species interactions on species co-occurrence. Here we extend a spatially explicit neutral model by including competitive effects on birth and death probabilities to assess whether competition alone is able to produce non-random patterns of species co-occurrence. We show that transitive and intransitive competitive hierarchies alone (in the absence of environmental heterogeneity) are indeed able to generate non-random patterns with commonly used metrics and null models. Moreover, even weak levels of intransitive competition can increase local species richness. However, there is no simple rule or consistent directional change towards aggregation or segregation caused by competitive interactions. Instead, the spatial pattern depends on both the type of species interaction and the strength of dispersal. We conclude that co-occurrence analysis alone may not able to identify the underlying processes that generate the patterns.

Ecologists have devoted much effort to understanding the role of competitive interactions in shaping ecological communities (reviewed by Weiher and Keddy 1999, Chesson 2000, Chave et al. 2002, HilleRisLambers et al. 2012). Within the framework of competitive exclusion (Gause 1934), a simple dominance hierarchy of competitive strengths (species A > species B > species C…) should eventually lead to a monoculture of the competitively superior species. But this is rarely seen in nature (Soliveres et al. 2015). Instead, most communities are characterized by a small number of common species (which may be competitively dominant), and a large number of rare species (which may be competitively inferior).

How are inferior competitors able to persist in a community? Proposed mechanisms include niche segregation (Chesson 2000), environmental heterogeneity (Amarasekare 2003), abiotic stress (Bowker et al. 2010), disturbance (Watt 1947, Grime 1977), and limited dispersal (Hurtt and Pacala 1995, Kerr et al. 2002, HilleRisLambers et al. 2012). These mechanisms may also explain the observed high diversity and co-existence of ecologically similar species (Fox 2013). In this respect, Grime (1973) highlighted the importance of context-dependent competitive strength, in which the ordering of species in a competitive hierarchy changes in different environments (Chamberlain et al. 2014, Gioria and Osborne 2014).

If competitive strength is context-dependent, species richness and abundance should differentially co-vary with environmental factors that most limit reproduction, leading to segregated occurrences of competing species along the environmental gradient. Diamond (1975) used examples of perfectly segregated species pairs ("checkerboard pairs") as evidence for competitive exclusion (Diamond 1975, p. 387), although he did not explicitly invoke context-dependent competitive interactions. Subsequent null model analyses of species co-occurrence have frequently detected individual species pairs and assemblages in which there is less co-occurrence than expected by chance (Gotelli and McCabe 2002, Ulrich and Gotelli 2010, 2013).

Following Diamond's (1975) approach, many authors have inferred past or present competitive exclusion from spatially segregated co-occurrence patterns (Pitta et al. 2012, Kennedy et al. 2014, but see Connor et al. 2013). Comparing communities at different times, Zaplata et al. (2013) and Ulrich et al. (2016) found that local plant assemblages became increasingly spatially segregated during early succession, and that these changes were associated with spatial variability in soil attributes.

Although empirical and statistical support for segregated and aggregated species pairs is widespread (Lyons et al. 2016), these community patterns are hard to generate from theoretical models. Only a few studies have so far evaluated whether and to what degree competition alone (without additional habitat effects like filtering) is able to produce a spatially segregated pattern of species occurrences (Wootton 2001). With appropriate parameter settings,

simple two-species (Levin 1974) and three-species (Caraco and Whitham 1984) interaction models can predict aggregated or segregated occurrences. However, patterns of species aggregation and segregation are more difficult to generate for models of diffuse competition in multi-species assemblages (Hastings 1987).

A number of theoretical (Allesina and Levine 2011, Ulrich et al. 2014) and empirical (Soliveres et al. 2015, Ulrich et al. 2016) studies suggest that competitive intransitivity is an important mechanism that allows species to coexist within a single community in spite of strong competitive interactions. Intransitive competitive networks (Gilpin 1975) are formed by loops in the hierarchy of competitive strength. For example, in the rock–scissors–paper game, the competitive hierarchy species A> species B> species C> species A forms a loop that can theoretically promote coexistence (Huisman et al. 2001, Kerr et al. 2002, Laird and Schamp 2006, 2009).

Ulrich et al. (2014) demonstrated that transitive and intransitive competitive hierarchies in ecological communities can be unequivocally translated into a stable state distribution of abundances by means of a Markov chain model (Horn 1975). This model predicts constant abundance distributions within a homogeneous environment and no spatial segregation of species occurrences among sites (Ulrich et al. 2016). However, if competitive hierarchies differ among sites because of environmental conditions, species abundance distributions and co-occurrence patterns change. In this scenario, species segregation among sites is solely linked to environmental heterogeneity and not caused by the underlying competitive hierarchy (Ulrich et al. 2016).

Models of context-dependent competition among sites and intransitive competitive hierarchies within sites make different assumptions about equilibrium conditions. Context dependency explicitly includes environmental spatial and temporal variability (Chamberlain et al. 2014) and thus applies to both equilibrium and non-equilibrium conditions. It does not make precise predictions about changes in species abundances and dominance orders in space. In contrast, models of intransitivity are most relevant to equilibrium conditions and have so far been applied only to closed assemblages in which species compete locally and are not affected by migration (Allesina and Levine 2011). But some local communities are organized as an open metacommunity, which is defined by Gilpin and Hanski (1991) and Leibold et al. (2004) as a set of interacting local communities that are linked by the dispersal of multiple, potentially interacting species. For open metacommunities, it is unclear whether models of intransitivity will predict constancy in the richness (and abundances) of local assemblages. For example, Soliveres et al. (2015) reported that local dryland and grassland plant communities often contained intransitive loops, but that these competitive hierarchies explained little of the spatial variation in species richness. Interestingly, the frequency of intransitivity decreased with increasing habitat heterogeneity (Soliveres et al. 2015) suggesting that species richness might be controlled by both intransitive networks and context-dependent competition.

In this study, we ask how competitive transitivity and intransitivity translate into dominance orders in a meta-community that incorporates dispersal and non-equilibrium dynamics at local scales. The neutral model framework (Hubbell 2001) allows us to generate predictions of local abundance and species composition from a set of first principles (birth/death processes, dispersal, and speciation). These predictions can then be compared to patterns in real assemblages (Gotelli and McGill 2006, Rosindell et al. 2012).

In their original formulation, neutral models were based on assumptions of random dispersal and the ecological equivalence of species (Hubbell 2001, Chave 2004, Etienne 2005, Etienne and Alonso 2005). Recent extensions of models of stochastic community dynamics to include asymmetric species interactions (Jabot 2010, Jabot and Chave 2011, Rosindell and Phillimore 2011) have paved the way for a more detailed analysis of context-dependent competitive effects. Such models including competitive interactions link the predictions from equilibrium based competitive theory with those from dispersal dynamics and population growth processes. Because these models do not incorporate environmental variability, empirical deviations from model predictions may implicate environmental factors influencing competitive hierarchies and context dependent competition.

Existing non-neutral community models incorporate species-specific density dependent mortality (Jabot and Chave 2011) or environmentally determined speciation probabilities (Tittensor and Worm 2016), but do not incorporate direct competitive interactions between species. Here, we use a spatially explicit neutral dispersal model and incorporate density dependence and direct asymmetric competitive interactions between individual pairs of species. Our aim is to deduce which patterns of species co-occurrence are expected from competitive interactions alone. With this model, we address four questions:

(1) Does competitive intransitivity increase local species richness?
(2) Does competition change the spatial or temporal variability in local richness?
(3) Does competitive intransitivity alone lead to species segregation across sites within a meta-community?
(4) Do diffuse and direct competitive interactions predict different patterns of species co-existence?

Material and methods

The dispersal-limited competition model

The present study is based on a simulation platform for community modelling that was previously used to show that appropriately parameterized neutral models are able to generate segregated spatial distributions of species co-occurrence (Ulrich 2004) and that ground beetle meta-community structures are indistinguishable from neutral predictions (Ulrich and Zalewski 2007). In our original simulations, we use a square grid of 100 patches initially populated randomly by a total of 10 000 individuals belonging to 30 species. This placement procedure leads to a grid of patches with different maximum numbers of individuals per patch (carrying capacities) and a Poisson distribution of species richness.

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 π_i of an individual of species i in a community of j species is given by:

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

where d_i is the density of species i and δ is the density-dependence parameter. For $\delta = 0$, death probabilities are proportional to the observed abundance distribution and thus equal for all individuals. For $\delta < 0$, the model penalizes abundant species (diffuse A) by higher local death rates, and if $\delta > 0$, the model penalizes rare species (diffuse R). For $\delta = 1$ species mortality rates are identical irrespective of abundance. This modification incorporates effects of diffuse (indirect) competition from the entire assemblage.

Second, we incorporated the effects of direct pairwise competition on birth rates using the Markov chain approach of Ulrich et al. (2014). These authors showed that any $j \times j$ matrix C of pairwise species interaction effects can be translated into a unique column stochastic transition matrix P (cf. Fig. 1). The inner product $PA_0 = A_1$ provides the vector of expected species abundances A_1 after one time step, given initial abundances A_0. Within a neutral model framework, birth probabilities are proportional to current abundances. Therefore, the inner product

$$PA_0 = A_1 \propto Q_1 \tag{2}$$

generates the vector Q, which (after normalization) contains the local birth probabilities of an individual in the community. In this way, our model incorporates effects of direct (pairwise) competition on birth rates and effects of indirect (diffuse) competition on death rates. In the absence of dispersal this model of competition yields three qualitative predictions for isolated local communities:

(1) A fully transitive competitive hierarchy modulates abundances in favour of the stronger competitors by increasing their fecundity while leaving death probabilities unchanged (Fig. 1). Because the respective transition matrix (P) generated from the matrix of competitive strength (C) describes an absorbing state (Fig. 1) (Ulrich et al. 2014), this Markov model predicts that the final result of transitive competition is a monoculture of the strongest competitor, independent of the model settings.

(2) An intransitive competitive hierarchy generates a non-absorbing ergodic transition matrix and therefore predicts coexistence of species (Fig. 1). Intransitivity might either increase or decrease the equilibrium species richness compared to the predictions of the simple neutral model.

(3) Diffuse competition that penalizes death rates of less abundant species has the same effect as strong competitive hierarchy in favouring abundant species and accentuating dominance orders. Therefore it should increase the tendency of the model to generate a monoculture of the strongest competitor.
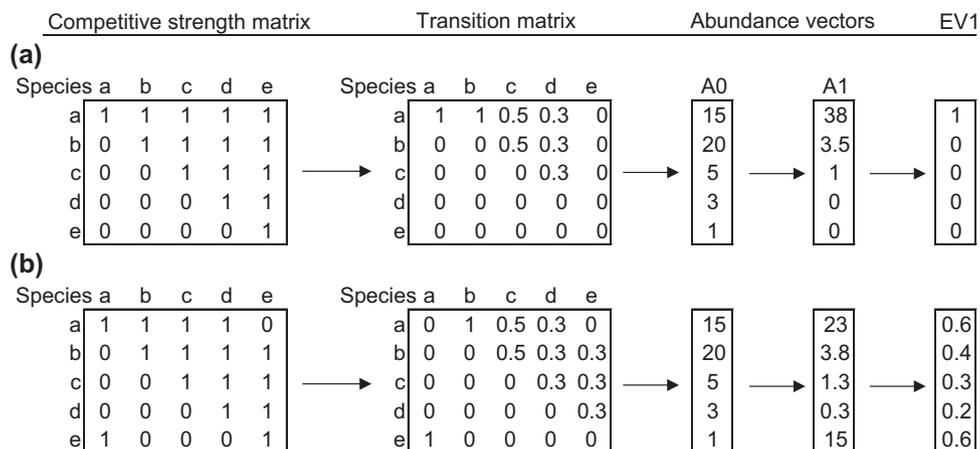

Figure 1. Fully transitive (a) and intransitive (b) competitive strength matrices (as defined by Laird and Schamp 2006 and Ulrich et al. 2014) of five species can be unequivocally transformed into respective column stochastic transition matrices (entries denote probability levels of transition) by the algorithm derived in Ulrich et al. (2014). The latter provide estimates of temporal changes in abundances (A0, A1, …) and equilibrium abundances (the dominant eigenvector EV1 of the transition matrix). 1s in the competitive strength matrix indicate competitive superiority. For example, in panel (b) species a (in rows) is superior to all species except species e. Matrix multiplication of the associated transition matrix with the abundance vectors now returns species abundances in the next generations. The dominant eigenvector of this matrix predicts species abundances at equilibrium. In this model of an isolated local community, intransitivity predicts increased equilibrium species richness.

Using stochastic simulations, we ask whether these predictions still hold in a spatially explicit model of an open metacommunity that incorporates dispersal.

Simulation protocol

To assess the influence of interspecific competition on otherwise neutral communities, we created a factorial design of five binary model parameters. We crossed two levels of dispersal limitation (unconstrained = all cells are equally likely to be the target of dispersal, limited = only the adjacent cells (the 'moore neighbourhood') can reached in a single dispersal step), with two levels of migration rates (low, high), with two levels of diffuse competition penalizing either rare ($\delta = 0.5$) or abundant ($\delta = -0.5$) species, and two levels of competitive interactions (intransitive, transitive; cf Supplementary material Appendix 1 and 2, respectively). Together with the four neutral scenarios of $\delta = 0$ and $\mathbf{P} = \mathbf{I}$ (I being the identity matrix), we considered a total of $2^4 + 4 = 20$ parameter combinations. Because variability in the model output within parameter sets was low, we replicated each parameter combination only 10 times.

Transitive competitive interactions led to monocultures of the best competitors, although the time to complete competitive exclusion was very long for some parameter combinations ($> 90\,000$ time steps). To ensure that the slowest- running model (diffuse competitive interactions and high dispersal rates; Table 1) reached equilibrium, we ran all models for $92\,000$ time steps, which incorporated $1\,010\,000$ birth/death, immigration/emigration, speciation/ extinction events, that is approximately 100 cycles of complete turnover in species composition. Equilibrium conditions were defined by a change of < 1 species per single time step of the moving average of species richness in the grid. We further traced the decrease in average species richness among sites (S_M) from the initial 27 to 30 species per site with the slope z of the semi-logarithmic regression model $S_M = S_0 - z \ln(t)$ where t denotes the time step of the model and S_0 the initial species richness. The semi-logarithmic model provided the best linear fit to the decay of species richness through time.

Analysing community structure and co-occurrences

For each grid, we quantified the degree of species segregation (negative species associations) with the common C-score of species co-occurrences (a normalised count of the number of

Table 1. In the pure neutral model migration probability and the degree of dispersal limitation influenced final mean species richness, the spatial variability in richness, the edge effect of the lattice, and the slope of the logarithmic decrease model. Given are partial η^2 values of a general mixture linear model. Significant parametric $p(F) < 0.001$ in bold.

Factor	DF	Mean species richness	Lloyd	Edge	Slope
Migration probability	1	**0.61**	**0.39**	0.00	**0.89**
Dispersal limitation	2	**0.31**	**0.42**	0.01	**0.88**
Migration × Dispersal	2	**0.46**	**0.30**	0.03	**0.87**
Mean species richness	1	–	**0.34**	0.01	**0.81**
Error	53				
r² (whole model)		**0.74**	**0.51**	0.08	**0.93**

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 (**n**estedness from **o**verlap and **d**ecreasing **f**ill) 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 β_{sor} (a metric of dissimilarity in community composition) into a component representing the difference in species richness among sites (β_{nest}) and a component representing the spatial turnover of species (β_{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 ΔS in richness between the 12 cells at each of the four grid corners and the 12 cells in the centre of the grid. Increases in species richness towards the centre of the spatial grid will yield a negative ΔS. To assess the spatial variability in species richness, we used Lloyd's (1967) variance – mean ratio $I = \dfrac{\sigma^2}{\mu^2} - \dfrac{1}{\mu} + 1$, with μ and σ^2 being the mean species richness and its variance, respectively. $I = 1$ is the expected value in the case of a Poisson random distribution, $I < 1$ indicates equitability in richness across the grid, and $I > 1$ indicates clumping.

For comparison among model settings, we used the normalised effect sizes (NES = (observed – expected scores)/expected scores) and standardized effects sizes [SES = (observed – expected scores)/standard deviation of expectation]. Under the assumption of a normal distribution of errors, $|SES_{score}| > 1.96$ indicates approximate statistical significance at $p < 0.05$ (two-tailed test). These measures of
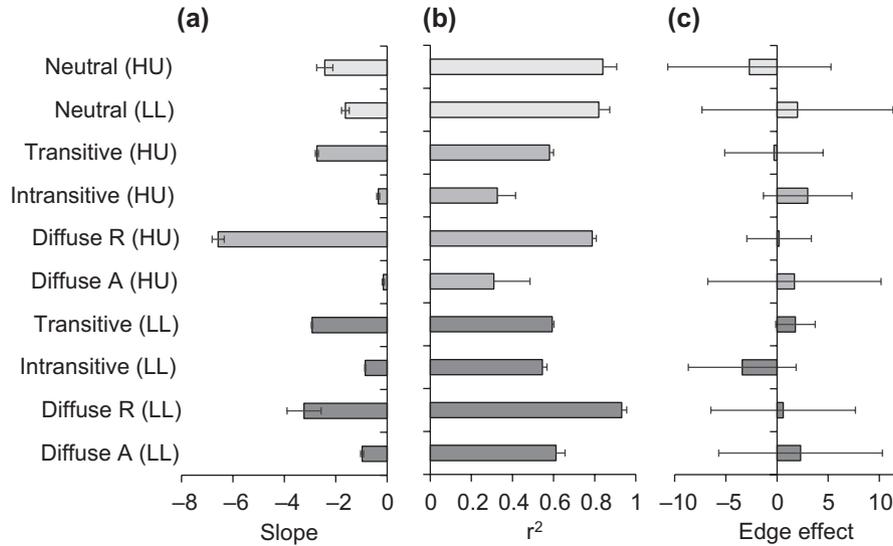
Figure 2. Average slope of the exponential species decay curve (a), and the respective coefficient of determination r² (b), and the effect of grid edges (c) for neutral models with high migration probability and unlimited dispersal (HU, grey) and low migration probability and limited dispersal (LL, dark grey) for neutral communities (light grey) and for neutral communities with additional transitive and intransitive competition hierarchies, and diffuse competition penalizing rare (Diffuse R) and abundant (Diffuse A) species. Error bars are one standard deviation.

effect size allowed for comparisons among different model results, but they did not completely remove the influence of species richness: SES values of simulated assemblages were moderately correlated with species richness of the meta-community for both the proportional null model (all $r^2 > 0.47$, $p < 0.001$) and the equiprobable null model (all $r^2 > 0.20$, $p < 0.001$). NES values performed better except for the clumping score – equiprobable null model ($r^2 = 0.67$, $p < 0.001$) and the C-score – proportional null model ($r^2 = 0.47$, $p < 0.001$) combinations.

In both cases, the low equilibrium average richness of one to two species per cell generated by the transitive and diffuse R competition models were responsible for these correlations. Therefore, we used linear models and covariance analysis with NES as the dependent variable and average species richness and squared average richness per site as covariates to assess the effect of competition and dispersal on patterns of species co-occurrences. We note that the standardized effect sizes (proportional null model) of the C-score and β_{sim} were strongly positively correlated ($r = 0.86$), whereas the standardized effect sizes of the C-score and the clumping score were strongly negatively correlated ($r = -0.76$). The standardized effect size of NODF was negatively correlated with the C-score ($r = -0.53$), β_{sim} ($r = -0.64$), and the clumping score ($r = -0.30$). The complete raw data used in the present study are contained in the Supplementary material Appendix 2.

Results

In the pure neutral model, limited dispersal and low migration probability reduced the time to species equilibrium (Table 1, Fig. 2a–b). The logarithmic decay model explained on average 85% of the variability in richness and the model fit was independent of dispersal strength (Fig. 2b). Competitive

effects reduced the fit of the exponential decay model (Fig. 2b) but edge effects were of minor importance (Fig. 2c) and did not significantly change between model settings (Table 1). Dispersal limitation significantly decreased average species richness in the pure neutral communities (Fig. 3a, Table 1). Spatial patterns of richness within the grid (Fig. 3b) matched a Poisson distribution.

Irrespective of the degree of dispersal limitation, transitive pairwise competition severely decreased average species richness per patch in comparison to the neutral expectation (Fig. 3a). The strongest competitor, as defined by the
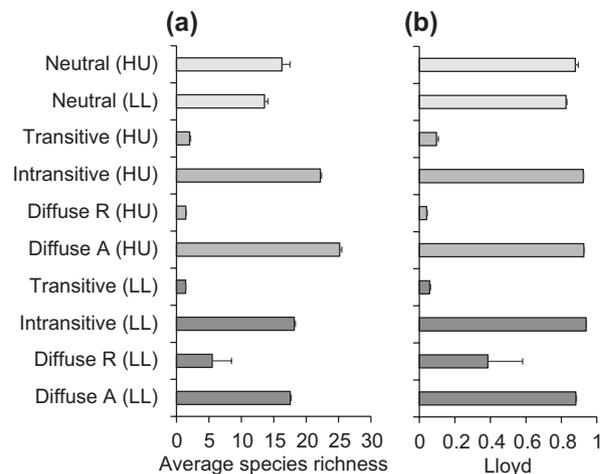

Figure 3. Average species richness (a), and the spatial variability in richness as quantified by the index of Lloyd (b) for neutral models with high migration probability and unlimited dispersal (HU, grey) and low migration probability and limited dispersal (LL, dark grey) for neutral communities (light grey) and for neutral communities with additional transitive and intransitive competition hierarchies, and diffuse competition penalizing rare (Diffuse R) and abundant (Diffuse A) species. Error bars are one standard deviation.

Table 2. Main effects general linear modelling of normalized effect sizes of C-score, clumping β_{sim}, and NODF (partial η^2 scores) identified particularly pairwise competitive interactions to influence average species richness, spatial variability in richness (Lloyd index), and patterns of co-occurrence. Significant parametric p(F) < 0.001 in bold.

Factor	DF	Mean species richness	Lloyd	Equiprobable null model				Proportional null model			
				C-score	Clumping	β_{sim}	NODF	C-score	Clumping	β_{sim}	NODF
Migration probability	1	**0.07**	**0.04**	**0.06**	0.02	0.01	0.01	**0.03**	<0.01	<0.01	<0.01
Dispersal limitation	2	**0.03**	0.02	**0.04**	0.01	<0.01	<0.01	0.02	0.01	0.01	<0.01
Diffuse competition	2	**0.46**	**0.20**	**0.10**	0.01	<0.01	**0.05**	0.01	0.02	<0.01	0.01
Pairwise competition	2	**0.84**	0.01	**0.42**	**0.06**	0.01	0.02	**0.03**	**0.08**	<0.01	**0.04**
Mean species richness	1	–	**0.54**	0.05	**0.11**	0.01	**0.30**	**0.24**	0.04	0.04	0.09
Squared mean species richness	1	–	**0.49**	<0.01	**0.08**	0.01	**0.25**	**0.24**	0.05	0.03	0.13
Error	530										
r² (whole model)		**0.86**	**0.86**	**0.75**	**0.61**	0.06	**0.65**	**0.66**	**0.24**	**0.23**	**0.23**

transition elements of the competition matrix **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 diffuse (Table 2) competition significantly altered species co-occurrences compared to the neutral expectation. The C-score and clumping indices, but not β_{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).
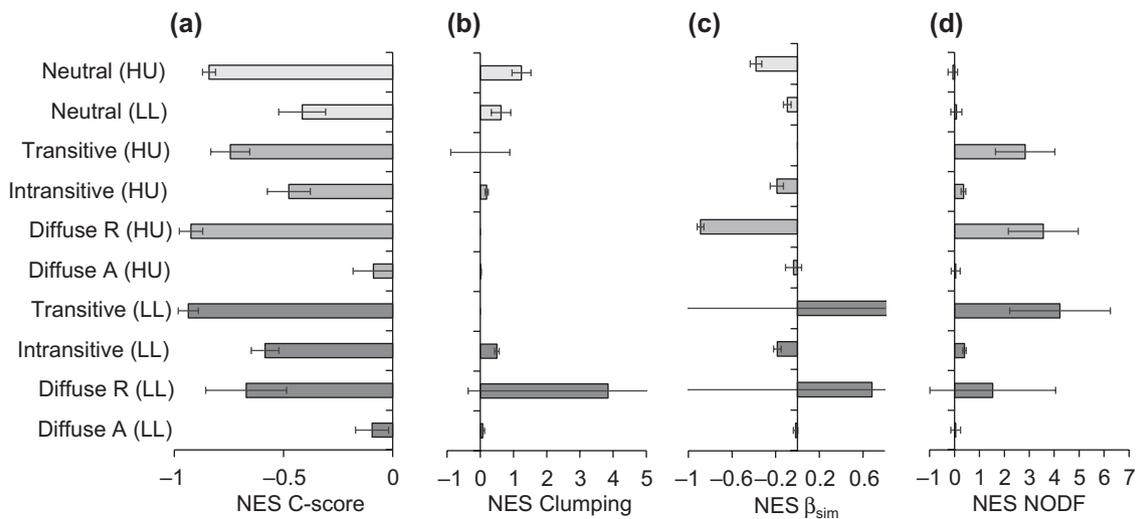

Figure 4. Normalized effects sizes NES (equiprobable null model) the C-core (a), the clumping score (b), β_{sim} (c), and NODF (d) for neutral models with high migration probability and unlimited dispersal (HU, grey bars) and low migration probability and limited dispersal (LL, dark grey) for neutral communities (light grey) for those with additional transitive and intransitive competition hierarchies, and diffuse competition penalizing rare (Diffuse R) and abundant (Diffuse A) species. Error bars are one standard deviation obtained from 10 replicates each.
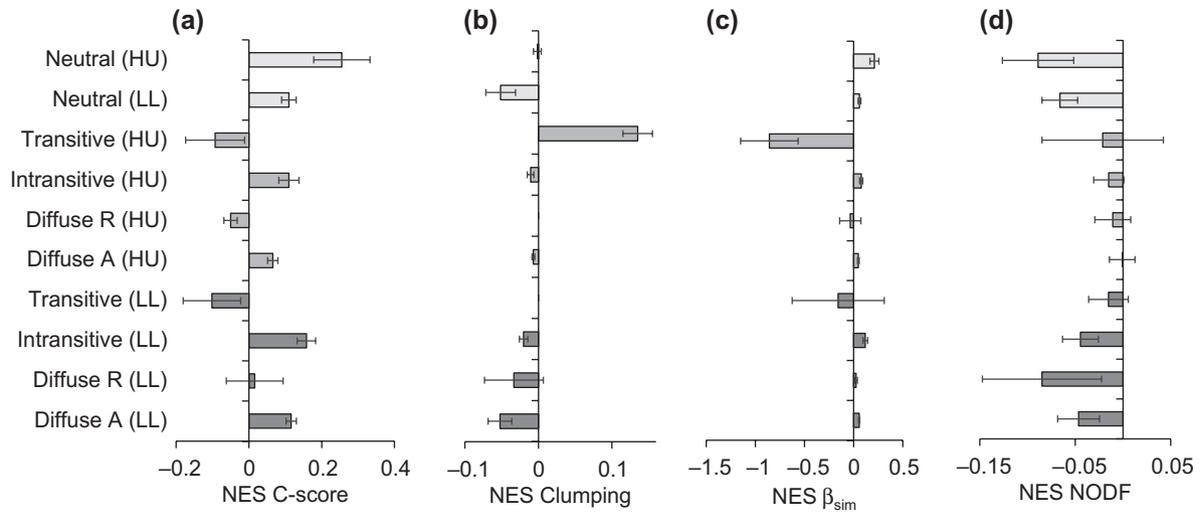
Figure 5. Normalized effects sizes NES (proportional null model) the C-core (a), the clumping score (b), β_{sim} (c), and NODF (d) for neutral models with high migration probability and unlimited dispersal (HU, grey bars) and low migration probability and limited dispersal (LL, dark grey) for neutral communities (light grey) for those with additional transitive and intransitive competition hierarchies, and diffuse competition penalizing rare (Diffuse R) and abundant (Diffuse A) species. Error bars are one standard deviation obtained from 10 replicates each.

At low dispersal both null models detected trends towards aggregation in intransitive communities (Table 3). Irrespective of the null model transitive communities tended to have an aggregated and/or nested structure compared to their pure neutral counterparts (Table 3, Fig. 4, 5). This is in line with a higher species turnover among sites (β_{sim}) at high dispersal rates (Table 3, Fig. 5) compared to the neutral expectation (proportional null model).

Diffuse competition penalizing rare species (diffuse R) had on average similar effects on the spatial distribution of species than transitive competition (Fig. 4, 5), while diffuse A communities equalled intransitive ones qualitatively in behaviour.

Discussion

In the tradition of the competitive exclusion principle (Gause 1934), a large number of co-existing species is often attributed to weak competitive interactions (Gilpin 1975,

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 for species co-existence, although there is little empirical evidence so far (Reichenbach et al. 2007, Kraft et al. 2015, Soliveres et al. 2015). Our simulation corroborates these predictions. Even a weak degree of intransitive competition significantly increased average local richness above the pure neutral expectation (Table 2, Fig. 3). Therefore we argue that competitive intransitivity might be a neglected factor that increases local richness (Kraft et al. 2015, Soliveres et al. 2015). Further, our results suggest that increased species richness can occur purely from intransitive competition, and does not require environmental variability and associated differential habitat filter processes (Keddy 1992).

Neutral community dynamics did not cause a modular pattern of species occurrence with regions of higher and lower richness (Fig. 3). We speculated (question 2) that competitive

Table 3. Tukey post hoc significances p(F) for pairwise competitive model comparisons (unequal slope covariance analysis with average final species richness and squared richness as covariates) for models without diffuse competition ($\delta = 0$) with high migration probability and unlimited dispersal (HU) and low migration probability and limited dispersal (LL). Normalized effects sizes (NES) entered the models as dependent variable. First NES < second NES in white (black letters), first NES > second NES in grey with white letters.

	Equiprobable null model				Proportional null model			
	C-score	Clumping	β_{sim}	NODF	C-score	Clumping	β_{sim}	NODF
Comparison				HH				
Neutral – Transitive	0.02	0.001	<0.001	<0.001	<0.001	0.87	<0.001	0.005
Neutral – Intransitive	<0.001	0.84	<0.001	0.11	<0.001	<0.001	0.21	0.002
Transitive – Intransitive	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.94
				LL				
Neutral – Transitive	<0.001	<0.001	0.007	<0.001	<0.001	<0.001	0.11	<0.001
Neutral – Intransitive	<0.001	0.18	0.95	0.82	0.01	<0.001	0.80	0.07
Transitive – Intransitive	<0.001	<0.001	0.004	<0.001	<0.001	0.28	0.04	0.02

interactions in combination with low dispersal might cause a respective spatial patterning leading to a richness landscape within a homogeneous environment. This was not the case (Fig. 3). Neutral as well as communities governed by intransitive and diffuse A competitive hierarchies (Fig. 3b) retained a Poisson random distribution of species richness among the grid cells. In contrast, transitive and diffuse R competition had a significant tendency of equalizing richness among cells within the overall species poor landscape (Fig. 3b). We note that this results might stem, at least partly, from a statistical bias due to the low number of species per cell. We also note that at equilibrium, spatial and temporal variability in richness are equivalent. Thus our results do also show that competition does not lead to increased temporal fluctuations of species richness in single grid cells.

Since the seminal work of Diamond (1975), replicated patterns of negative species association (segregation) are often seen as evidence for interspecific competition (reviewed by Götzenberger et al. 2012) although many other reasons for species segregation are known (Blois et al. 2014). Starting with Grime (1973), several authors (reviewed by Chamberlain et al. 2014, Gioria and Osborne 2014) argued that context-dependent competitive strength in heterogeneous environments might be the major driver of species segregation among habitats, whereas trait differentiation and small-scale environmental variability allows for local co-existence (Adler et al. 2013).

However, many studies of community assembly rules do not refer to these mechanistic models of species interactions and often treat species spatial segregation as sufficient evidence for competition (Price et al. 2012). Here, we focused on the question of whether competitive effects alone permit species coexistence and generate non-random species associations. A related question is whether habitat heterogeneity and habitat filtering (Zobel 1997) are primarily responsible for non-random species associations.

We found strong evidence that competitive effects alone are indeed able to influence the geometry of species occurrences (Table 3, Fig. 4, 5, Supplementary material Appendix 2 Fig. A1–A2). However, there was no simple rule or consistent directional change caused by species interactions. Instead, the spatial pattern depended on both the type of species interaction and the level of dispersal. Specifically, intransitive competition increased species turnover and decreased clumping when compared to the predictions of a neutral model with unlimited dispersal (Table 3). However, the opposite pattern – decreased species turnover and increased clumping – emerged when compared to the predictions of a neutral model with limited dispersal (Table 3). It seems that dispersal limitation and intransitivity are both able to generate small scale clusters of communities with distinct species composition. That means from co-occurrence analysis alone we cannot draw simple (simplified) conclusions about the effect of competitive interactions on the patterns of species co-occurrences (cf. Kraft et al. 2015 for a similar conclusion).

Soliveres et al. (2015) recently reported a pattern of nested community structure associated with intransitive competitive hierarchies in dryland plant assemblages. However, it remained unclear whether this effect was due to environmental heterogeneity or due to the internal dynamics of species interactions. Our results partly corroborate Soliveres et al. (2015): transitive competition increased the degree of meta-community nestedness relative to a neutral assemblage (Table 3, Fig. 4, 5). This trend is not biased by low species richness because the NES transformation effectively removed the richness effect on the NODF metric. The influence of intransitive competition on the degree of nestedness is less clear. Although we observed the trend Soliveres et al. (2015) reported, statistical corroboration was weak (Table 3). Nevertheless, our results suggest that negative species interactions alone might suffice for a trend towards nested community structure.

Magnitude and direction of effect sizes in null model analyses depend on the choice of the algorithm and therefore on the underlying assumption about the constraints applied to randomization (Ulrich and Gotelli 2012). Different null model approaches frequently lead to contradictory effect sizes making the interpretation of pattern challenging. In the present case the effect sizes of the C-score of the two null models were partly contradictory (Fig. 4, 5), yielding a pattern of aggregation when compared to the equiprobable expectation, but a pattern of segregation when compared to the proportional null model.

In the present case, we used the liberal equiprobable null model, the more conservative (proportional) null model, and the pure neutral model (Rosindell et al. 2012) as standards for comparison. Specifically, we compared patterns generated by three community models with and without competition. The three different null models served to control for differences in species abundances, species richness, and matrix fill. Only this combination allowed for an unequivocal interpretation of the results.

Recently, Rosindell et al. (2012) argued that neutral models provide process based adequate standards for ecological patterns. However, the major drawback of neutral modelling is the sensitivity to parameter settings, and the fact that those parameters cannot be estimated in a non-circular way from the presence–absence matrix. The simplest neutral models are based on at least four free parameters: species pool size, dispersal limitation, birth rate, and speciation rate. Additionally, total spatial extent and associated edge effects might influence the outcome (Babak and He 2009). Thus we argue that process-based neutral models may be just as sensitive to model structure as traditional null model analysis. Whether empirical data are compared to a neutral model or a null model, a thorough sensitivity analysis with different model variation may be necessary to fully understand the results.

One useful distinction that emerged here is the idea that the null model reveals non-random patterns above and beyond those generated by matrix constraints such as row and column totals, matrix size, or matrix fill. To tease apart mechanisms of habitat filtering, species interactions, or dispersal limitation requires additional data and additional tests on the spatial pattern of occupied and unoccupied sites, and on the habitat structure of those sites (Blois et al. 2014). In contrast, the neutral model formulation explicitly models random dispersal and a lack of species interactions, though often with a zero-sum constraint imposed. If the parameters for such a model can be estimated independently of the co-occurrence data, the neutral model can

also be used to generate an expectation for comparison with real data. Alternatively, the neutral model predictions can themselves be compared to the predictions of a null model (Ulrich 2004, Gotelli and McGill 2006). Neither approach by itself is complete, but the combination of null and neutral modelling may be the best way forward.

Our work has influence on the interpretation of observed patterns of species co-occurrences in field studies. Many authors (Gotelli and McCabe 2002, Götzenberger et al. 2012, Connor et al. 2013) have interpreted non-random segregation as evidence for competitive interactions (but see Ulrich and Gotelli 2010, Blois et al. 2014), whereas positive associations (aggregation) have usually been interpreted in terms of habitat filtering and facilitation (Götzenberger et al. 2012, Vaz et al. 2015). Our results identified clear tradeoffs between the type of competitive interactions and the degree of dispersal: competitive interactions can generate species aggregation, and segregation may stem from dispersal limitation alone. Possibly, some reported effects of competition on the geometry of species occurrences might require reassessment. Consequently, future empirical work on the spatial structure of meta-communities needs to include independent information on dispersal ability and resource utilization, as well as information on habitat heterogeneity, for a proper interpretation of co-occurrence patterns.

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