Dispersal and diversity – unifying scale-dependent relationships within the neutral theory

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The response of species diversity to dispersal capability is inherently scale-dependent: increasing dispersal capability is expected to increase diversity at the local scale, while decreasing diversity at the metacommunity scale. However, these expectations are based on model formulations that neglect dispersal limitation and species segregation at the local scale. We developed a unifying framework of dispersal–diversity relationships and tested the generality of these expectations. For this purpose we used a spatially-explicit neutral model with various combinations of survey area (local scale) and landscape size (metacommunity scale). Simulations were conducted using landscapes of finite and of conceptually infinite size. We analyzed the scale-dependence of dispersal–diversity relationships for exponentially-bounded versus fat-tailed dispersal kernels, several levels of speciation rate and contrasting assumptions on recruitment at short dispersal distances.

We found that the ratio of survey area to landscape size is a major determinant of dispersal–diversity relationships. With increasing survey-to-landscape area ratio the dispersal–diversity relationship switches from monotonically increasing through a U-shaped pattern (with a local minimum) to a monotonically decreasing pattern. Therefore, we provide a continuous set of dispersal–diversity relationships, which contains the response shapes reported previously as extreme cases. We suggest the mean dispersal distance with the minimum of species diversity (minimizing dispersal distance) for a certain scenario as a key characteristic of dispersal–diversity relationships. We show that not only increasing mean dispersal distances, but also increasing variances of dispersal can enhance diversity at the local scale, given a diverse species pool at the metacommunity scale. In conclusion, the response of diversity to variations of dispersal capability at spatial scales of interest, e.g. conservation areas, can differ more widely than expected previously. Therefore, land use and conservation activities, which manipulate dispersal capability, need to consider the landscape context and potential species pools carefully.

The positive response of \( \alpha \)-diversity to an increasing dispersal capability can be explained from a metacommunity perspective (Leibold et al. 2004). If local communities within a metacommunity are linked by dispersal, spatial mass effects can establish source-sink relationships between these communities. Sink populations maintained by immigration can substantially increase \( \alpha \)-diversity, for instance by contributing to a higher number of locally rare species (Shmida and Ellner 1984, Pulliam 1988, 2000, Loreau and Mouquet 1999, Esther et al. 2008, Gardner and Engelhardt 2008). This argumentation is supported by many experiments where seed introduction, which mimics dispersal among local communities, leads to an increase of local diversity (Tilman 1997, Hubbell et al. 1999, Turnbull et al. 2000, Ehrlén et al. 2006, Cadotte 2006a, Stein et al. 2008).

The negative response of \( \gamma \)-diversity to increasing dispersal capability can be explained considering spatially limited dispersal and local competitive interactions (Weiner and Conte 1981, Pacala 1997, Bolker and Pacala 1999, Murrell and Law 2003). Low dispersal capability leads to aggregation...
of conspecific individuals and consequently to the spatial segregation of species. If individuals are restricted to interact locally, there will be a relative increase of intraspecific interactions compared to interspecific ones. Therefore, low dispersal capability is expected to slow down competitive exclusion and ecological drift and thus favours high species diversity (Chave et al. 2002, Levine and Murrell 2003). This mechanism of species coexistence was called the 'spatial segregation hypothesis' by Pacala (1997). Empirical evidence for the negative response of $\gamma$-diversity to increasing dispersal in plant communities is scarce, as it is extremely difficult to manipulate dispersal capability and trace the community response at the metacommunity scale (Cadotte 2006a). However, experiments of plant–plant competition confirmed that the spatial aggregation of conspecific individuals, which is consistent with low dispersal capability, can indeed influence species performance and therefore community diversity (Stoll and Prati 2001).

Consequently, in order to understand the scale-dependent response of diversity to dispersal one must consider the spatial scales of dispersal and of local interactions. In that context, it is important to note that the neutral models mentioned above, use a dichotomous, conceptual distinction between local and metacommunity scales and consider dispersal limitation and species segregation only between, but not within local communities (Hubbell 2001, Economu and Keitt 2008, Vanpeteghem and Haegeman 2010). When contrasted with real data, the distinction made by such models between local and metacommunity is usually related to the sampling design, rather than to the scales at which important ecological processes operate. Since in reality, dispersal operates in a continuous space, it remains unclear whether neutral, spatially-implicit models can provide realistic predictions for the relationship between diversity and dispersal capability at the local scale.

Spatially-explicit extensions of the neutral model provide the possibility to overcome this limitation. So far such models have been used to analyze the response of $\beta$-diversity to variations in dispersal capability (Chave and Leigh 2002, Condit et al. 2002) or to study species-area curves (Rosindell and Cornell 2007, 2009, O’Dwyer and Green 2010). However, to the best of our knowledge there has been no study, which relaxes the conceptual distinction between local and metacommunity and addresses the effect of dispersal capability on $\alpha$-diversity in detail.

Here we strive to fill this gap and present a framework that can accommodate several types of response of diversity to dispersal (hereafter called ‘dispersal–diversity relationships’) at several spatial scales. For this purpose, we used a spatially-explicit neutral model with one individual per grid cell and simulated metacommunities within landscapes of different extents. Within these landscapes we analyzed species richness in survey areas of different sizes, avoiding an ad hoc definition of a ‘local community’ of fixed size. With this approach we will answer the following questions: 1) what are the combinations of survey area and landscape size, where increasing or decreasing dispersal–diversity relationships emerge? 2) are there combinations of survey area and landscape size, where both positive and negative effects of dispersal on local diversity emerge and the dispersal–diversity relationship features a local minimum or maximum? 3) if yes, what is the characteristic scale of dispersal where local diversity is minimized or maximized?

### Methods

#### The model

The model used for this study is a spatially-explicit version of the neutral theory (Chave et al. 2002). The landscape is represented as a square lattice, where sessile individuals compete for space. The landscape is saturated with individuals, i.e., each grid cell is occupied by one individual at any given time according to the assumption of zero-sum dynamics (Hubbell 2001, Chave and Leigh 2002, Chave et al. 2002). Each time step, one individual dies at random irrespective of species identity or location and the evacuated microsite is immediately colonized by a new individual. The new individual can be either an offspring of another individual within the landscape, or it may originate from a speciation event, thus introducing a novel species to the community.

In the first case the parent individual is assigned by randomly choosing direction and distance from the vacant cell as follows: a random point within the focal cell is chosen. Then a random draw from a given dispersal kernel determines the distance to the parent cell and the direction is drawn from a circular uniform distribution in the interval $[0, 2\pi]$ assuming isotropic dispersal. The choice of a random point within the focal cell, rather than assuming that an individual is located in the cell centre, was implemented in order to minimize the effect of the discrete cell size.

For each single birth-death event the possibility of speciation is considered. The parameter speciation rate $v$ provides the probability that the newborn individual belongs to a novel species that has not been in the community before, corresponding to the case of speciation by point mutation (Hubbell 2001, Rosindell and Cornell 2007).

For the choice of parent individuals within the landscape, we use two different dispersal kernels 1) the negative exponential kernel (Eq. 1), where the mean and the standard deviation of dispersal distance ($r$) are given by the parameter $\alpha$ (Clark et al. 1998, 1999) or 2) the log-normal kernel (Eq. 2), where the mean and the standard deviation of the log-transformed dispersal distance are given by the parameters $\mu$ and $\sigma$, respectively. The log-normal kernel allows us to study the effect of ‘fat-tailed’ dispersal, i.e. a higher probability of long-distance dispersal events compared to the negative-exponential kernel (Nathan and Muller-Landau 2000, Stoyan and Wagner 2001).

\[ k_{\text{NEG}}(r) = \frac{1}{\alpha} \cdot \exp \left( -\frac{r}{\alpha} \right) \]  
\[ k_{\text{LMN}}(r) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left( -\frac{(\ln r - \mu)^2}{2\sigma^2} \right) \]

Furthermore, we use two different model versions to distinguish the effects of very short dispersal distances. In the first version we allow ‘within-cell recruitment’ whenever the random location of the parent individual lies within the vacant cell. This assumption mimics the in situ replacement of the mother plant by its own offspring (Willson 1993, Clark et al. 1998, Venable et al. 2008). In the second model version we do not allow ‘within-cell recruitment’. In this case we discard draws that positioned the parent within the vacant cell.
and repeat drawing from the dispersal kernel until a parent individual outside of the vacant cell is found.

As an output, the model derives species richness of a square survey area with $N_{\text{Survey}}^2$ grid cells and thus $N_{\text{Survey}}^2$ individuals. This survey area is located in a landscape that is a square grid as well, but with a side length of $N_{\text{Landscape}}$ grid cells.

In order to simulate the equilibrium species richness of the survey area, we make use of the coalescence approach to neutral ecology, which is described in detail in Rosindell et al. (2008). Instead of starting from an arbitrary initial state and simulating forward in time until any criteria for convergence to equilibrium are fulfilled, simulations proceed backwards in time constructing the ancestry (or phylogeny) of all individuals in the survey area. The sequence of ancestors belonging to each microsite is considered as one lineage. A common ancestry of two lineages implies that they belong to the same species. Following all lineages until the most recent speciation event in their ancestry directly leads to a realization of the equilibrium state without additional assumptions about convergence criteria and decay rates of transient system states (Rosindell et al. 2008).

Computational efficiency and the direct derivation of realizations of the equilibrium state constitute two main advantages of the coalescence approach. Furthermore, it enables the analysis of diversity patterns in landscapes of infinite size (Rosindell and Cornell 2007, 2009).

In nature, even the largest metacommunity is essentially located in a landscape of a finite size. In contrast to several previous studies, we conducted model simulations and compared results of both finite and infinite landscapes. In the case of a finite landscape, we used periodic boundary conditions and treated the landscape as a torus.

Simulation scenarios and analysis

We conducted simulations in landscapes of finite sizes with $N_{\text{Landscape}}$ in \{100, 200, 300, ..., 1000\}. We recorded species richness in several survey areas that comprise defined fractions of the landscape. For each landscape size we used 12 different survey areas corresponding to the ratios $N_{\text{Survey}}/N_{\text{Landscape}}$ in \{0.01, 0.05, 0.1, 0.2, ..., 1.0\}. In addition we simulated species richness in infinite landscapes for survey areas with $N_{\text{Survey}}$ in \{10, 20, 50, 100, 200, ..., 1000\}. As speciation rates, we considered the values $v$ in \{1.0 × 10^{-6}, 1.0 × 10^{-3}, 1.0 × 10^{-4}\}, which corresponds to the lower range of speciation rates used in previous simulation studies (Chave et al. 2002, Rosindell and Cornell 2007). In the reference scenario we modelled dispersal using a negative exponential kernel, where mean and variance of dispersal distance are equal. In order to study the effect of a different shape of the kernel, we conducted additional simulations with a log-normal dispersal kernel with mean values (at the linear scale) equal to the reference scenario. For the two parameter log-normal kernel it is possible to define the variance independently of the mean dispersal distance.

For this purpose, we set the coefficient of variation ($\text{cv} = \text{standard deviation/mean dispersal distance}$) to 0.5, 1, 2 (at the linear scale). All simulations were carried out for the case when 'within-cell-recruitment' was allowed and when it was disallowed.

For each combination of survey area, landscape area and dispersal kernel, we evaluated species richness for 20 values of mean dispersal distance, which were equally spaced (at log-scale) and covered the range of 0.1–50 grid cells. From these we constructed the dispersal–diversity relationship by plotting species richness as a function of mean dispersal distance.

The dispersal–diversity relationship can feature four different general shapes: 1) monotonically increasing, 2) monotonically decreasing, 3) hump-shaped with a local maximum, 4) U-shaped with a local minimum of species richness. Therefore, we searched for a local extremum of species richness within the interval of mean dispersal distances used. As we never found a hump-shaped response with a local maximum, we will describe our approach for searching a local minimum only.

The shape of the dispersal–diversity is highly non-linear and species richness is provided as a random variable by the stochastic neutral model. Therefore, we used a generalized additive model (GAM) of log(species richness) vs log(mean dispersal distance) to provide a smooth dispersal–diversity relationship (Wood 2008). The model fit was carried out with mean values for species richness of 30 replicate simulations. We tested if the minimum species richness of the smoothed curve was significantly smaller (based on standard confidence intervals with 30 replicates) than species richness at the minimum and maximum dispersal interval.

If there was significant minimum of species richness within the dispersal interval, the corresponding mean dispersal distance is defined as 'minimizing dispersal distance' (MDD). Otherwise the end of the interval with the lower species richness was defined as MDD. Therefore our results provide three general cases 1) The MDD equals 0.1 grid cells, which indicates a monotonically increasing dispersal–diversity relationship with a positive slope. 2) The minimizing dispersal distance is larger than 0.1 but smaller than 50 grid cells, which characterizes a U-shaped dispersal–diversity relationship with a local minimum and switch from a negative to a positive slope. 3) The minimizing dispersal distance equals 50 grid cells, indicating a monotonically decreasing dispersal–diversity relationship with a negative slope.

Results

As expected, species richness always decreases with increasing dispersal distance, if the entire landscape is sampled (Fig. 1d, h). However, if only parts of the landscape are sampled a continuous spectrum of dispersal–diversity relationships is observed, ranging from positive to negative responses of diversity to an increasing mean dispersal distance. The shape of the dispersal–diversity relationship is determined, to a large degree, by the ratio of survey to landscape area. For small ratios the positive (increasing) branch is dominant (Fig. 1a–b, e–f), while at large ratios the negative (decreasing) branch of the relationship (Fig. 1c–d, h) is dominant. At intermediate survey to landscape area ratios U-shaped dispersal–diversity relationships emerge (Fig. 1b, g).

For infinite landscapes the ratio between survey and landscape area mathematically equals 0, but we still found a negative response of species richness at low dispersal distances, and thus a local minimum in the response curve, at least for relatively large survey areas (Fig. 1a, e).
Figure 1. Dispersal–diversity relationships for different combinations of survey and landscape area. For scenarios with infinite landscapes (a, c) a survey area with $N_{\text{Survey}} = 1000$ was used. Finite landscapes were simulated with $N_{\text{Landscape}} = 1000$ (b–d, f–g). The speciation rate was $1.0 \times 10^{-5}$ in all scenarios shown. The top row of panels (a–d) shows results when within-cell recruitment (WCR) was allowed, while the bottom row (e–g) shows results when within-cell recruitment was excluded. Different symbols correspond to different dispersal kernels (N Exp = negative exponential, LNorm = log-normal) and different variances of dispersal, measured by the coefficient of variation (cv). Points and error bars show mean and standard error of 30 replicates.
Excluding within-cell recruitment does not change these general patterns, but clearly affects dispersal–diversity relationships at low dispersal distances. For any mean dispersal distances below five grid cells, species richness was higher with within-cell recruitment than without. This reduction in species richness implies changes in the shape of the dispersal–diversity relationship. At low ratios of survey to landscape area, the negative branch at low dispersal distances disappears (Fig. 1b, f). At intermediate ratios the negative branch is still present, but features lower species richness (Fig. 1c, g). Species richness at mean dispersal distances larger than five grid cells does not differ between scenarios with and without within-cell recruitment.

The type of the dispersal kernel did not affect the dispersal–diversity relationship, as results for the negative exponential and the log-normal kernel with equal mean and variance do not differ substantially. In contrast, the variance of dispersal did have an effect on species richness and thus on dispersal–diversity relationships. In scenarios with within-cell recruitment and finite landscapes, species richness increased with dispersal variance at intermediate values of mean dispersal distance, but this effect disappears at low and high mean dispersal distances (Fig. 1b–d). In infinite landscapes, the increasing branches of dispersal–diversity relationships for different dispersal variances are parallel (Fig. 1a, e). This indicates that increasing dispersal variance always increased species richness by the same factor (note the logarithmic scaling in Fig. 1). Scenarios excluding within-cell recruitment again showed a different pattern at the negative branch of the dispersal–diversity relationship. There, higher dispersal variance rather reduced species richness (Fig. 1g–h).

In addition to the ratio of survey to landscape area, the absolute value of landscape area, as well as the speciation rate, influence the dispersal–diversity relationship. Speciation rate and landscape area had an analogous effect on local species richness and on dispersal–diversity relationships (compare Fig. 2, left vs right panels). Both, increasing speciation rate and larger landscape sizes result in higher species richness at all sampling scales. This change in species richness feeds back into the dispersal–diversity relationship. At a ratio of \( N_{\text{Survey}} / N_{\text{Landscape}} = 0.2 \), we found a decreasing dispersal–diversity relationship.

![Figure 2](https://example.com/figure2.png)

Figure 2. Dispersal–diversity relationships with equal ratio of survey to landscape area (\( N_{\text{Survey}} / N_{\text{Landscape}} = 0.2 \)). In the panels on the left, landscape area was constant, but speciation rate varied (a, c). In the panels on the right, speciation rate was constant, but landscape area varied (b, d). Speciation rates and landscape sizes (\( N_{\text{Landscape}} \)) are indicated by different symbols and line types, as shown in panel legends.
Much of the variation in the MDD that is not explained by the survey-to-landscape area ratio can be attributed to speciation rate and landscape area. In finite landscapes, the MDD decreases with increasing speciation rate (Fig. 4a). This finding corresponds with the results mentioned above, that a lower speciation rate reduces the positive branch of the dispersal–diversity relationship and more likely leads to a monotonically decreasing relationship (compare Fig. 2). Interestingly, we found the opposite result for infinite landscapes. There, a higher speciation rate, lead to an increase in the MDD (Fig. 4b). According to our findings for single dispersal–diversity relationships, the response to absolute landscape size is analogous to our findings for speciation rate (compare Fig. 2). In finite landscapes, the MDD decreases with an increase in landscape area (results not shown).

The influence of the dispersal variance on the MDD is much weaker than the one of speciation and landscape size. Significant effects of dispersal variance were only found when combined with high speciation ($1.0 \times 10^{-4}$) and relatively large landscape areas ($N_{\text{Landscape}} \geq 500$). In finite landscapes and low ratios of $N_{\text{Survey}}/N_{\text{Landscape}}$, the MDD is lower with high variance of dispersal. However, at $N_{\text{Survey}}/N_{\text{Landscape}} = 0.4$, there is a switch and at higher ratios, higher dispersal variance increases the MDD (Fig. 5a). In infinite landscapes the effect of dispersal variance is relatively weak, but there is a tendency for a lower MDD with high variance of dispersal independently of absolute survey area (Fig. 5b). Excluding within-cell recruitment does not change relationship at low speciation or small landscape size, but a clear U-shaped pattern for high speciation or large landscape size (Fig. 2a–b). In general this means, the lower species richness, either due to low speciation or small landscape area, the weaker are the positive effects of dispersal on species richness.

For scenarios excluding within-cell recruitment these findings hold as well, but as shown earlier at low mean dispersal distances the decreasing branch of the dispersal–diversity relationship disappears. For low speciation rates and/or small landscape areas, this reduction in species richness at short mean dispersal distances, leads to the result, that there is no response of species richness to dispersal at all (Fig. 2c–d).

In order to further explore the effects of various parameter combinations on the dispersal–diversity relationships we used, for any given scenario, the dispersal distance that minimizes species richness as a new response variable. We found that in general the minimizing dispersal distance (MDD) increases with the survey-to-landscape area ratio (Fig. 3a, c). In landscapes of infinite size, the same increase of the MDD is observed with increasing absolute survey area (Fig. 3b, d). For most values of the survey-to-landscape area ratio, MDD was lower when within-cell recruitment was excluded than when it was allowed. This was especially apparent at small survey-to-landscape area ratios when the exclusion of within-cell recruitment resulted in a MDD that equalled the lowest mean dispersal distance simulated (0.1 grid cells), indicating the lack of the negative branch of dispersal–diversity relationships at low mean dispersal distances (Fig. 3, compare top and bottoms rows).

Figure 3. The dispersal distance, where the minimum species richness was found (= minimizing dispersal distance, MDD) as a function of the ratio of survey area and landscape area (finite landscapes, a, b), or survey area only (infinite landscapes, b, d). The boxplots summarize results for all different speciation rates, dispersal kernels and absolute values of survey and landscape area. The panels at the top show results including within-cell recruitment (WCR) and at the bottom excluding WCR.
the results concerning speciation rate, landscape area and dispersal variance qualitatively.

**Discussion**

The scale-dependent effects of dispersal capability on species diversity, reported in previous studies, can be generalized with the following statement: higher dispersal capability increases diversity at the local scale, but reduces diversity at the metacommunity scale (Hubbell 2001, Mouquet and Loreau 2003, Cadotte 2006a, Economo and Keitt 2008). Our study fully agrees with that statement for the metacommunity scale, but it provides a much more detailed analysis, yielding partly contrasting conclusions, for the local scale. We found that at the local scale diversity may increase with dispersal capability due to species immigrations (Loreau and Mouquet 1999), but it may also decrease with dispersal due to increased mixing and reduced species segregation (Pacala 1997). The balance between these contrasting effects leads to various distinct dispersal–diversity relationships at the local scale, ranging from monotonically increasing, via U-shaped to monotonically decreasing response patterns. We suggest that the mean dispersal distance at which species richness for a given community is minimized (MDD), provides a comprehensive aggregated measure of the dispersal–diversity relationship. A low MDD implies dominance of spatial mass effects while a high MDD indicates importance of interspecific interactions.

**Ratio of survey area and landscape area**

In a given local community the response of diversity to dispersal capability strongly depends on the definition of the ‘local’ scale. Our results demonstrate that the ratio of the survey area (i.e. the ‘local’ community) to the total landscape area is an important determinant of dispersal–diversity relationships. When the survey area is much smaller than the landscape, species richness is minimized at smaller distances (short MDD) and our results agree with the results of previous studies regarding local diversity (Loreau and Mouquet 1999, Esther et al. 2008). When the survey area approaches the...
landscape area, species richness is maximized at high dispersal distances (long MDD) and our results agree with dispersal–diversity relationships as predicted for the metacommunity scale (Chave et al. 2002, Levine and Murrell 2003).

**Speciation rate and absolute landscape area**

Recognizing that both speciation rate and the absolute size of the landscape influence diversity in a similar manner, Hubbell (2001) lumped these factors into the ‘fundamental biodiversity number’. Following that insight, we suggest an analogous explanation for the effects of both factors. Both, speciation rate and landscape area determine species richness at the landscape scale and thus the size of the species pool, which provides potential immigrants to any ‘local’ scale. Therefore, the higher speciation rate and/or landscape area, the more important is the increasing branch of the dispersal–diversity relationship and the lower the MDD in any survey area.

When the species pool is small, due to low speciation rate and/or small landscape area, diversity monotonically decreased with dispersal capability, even at small ratios of survey to landscape. This result contradicts the general finding of increasing local diversity with increasing dispersal capability (Hubbell 2001, Econom and Keitt 2008).

In species-poor metacommunities, the limited potential of the species pool to contribute to local diversity is insufficient to balance the negative effect of dispersal due to reduced segregation. Rosindell et al. (2010) suggest that protracted speciation provides a much better fit to species abundance distributions and species life times than specification by point mutation. Protracted speciation leads to less rare species and thus to a lower species richness at the metacommunity scale compared to point mutation (Rosindell et al. 2010). Therefore, we expect that protracted speciation will show similar effects on dispersion–diversity relationships as those of a lower speciation rate in the case of point mutation. In principal, protracted speciation could easily be included into our approach, but a comparison between different modes of speciation is beyond the scope of this study.

**Dispersal variance and kernel type**

Higher moments of the dispersal kernel as variance and kurtosis determine the frequency of both short and long dispersal events (Nathan and Muller-Landau 2000). In our simulations increasing dispersal variance did not significantly affect the negative branch, but it increased species richness at the positive branch. In finite landscapes, this positive effect of high dispersal variance disappears at higher dispersal distances, as the community approaches complete mixing (Fig. 1b). In contrast, the positive effect remains visible in infinite landscapes (Fig. 1a), where increasing dispersal variance always causes a higher frequency of species immigrations over long-distances and thus from regions, which likely provide new species to the survey area (Rosindell and Cornell 2009).

Comparing negative-exponential and log-normal dispersal kernels with equal mean and standard deviation, we found no significant differences of the dispersal–diversity relationship between both kernels. This is surprising, as these kernels differ in their higher moments. For instance the kurtosis, which is often used to quantify the ‘fatness’ of the tail of dispersal kernels equals 6.0 and 34.0 for negative-exponential and log-normal kernel (both with mean = standard deviation), respectively (Clark et al. 1999). Rosindell and Cornell (2009) found that the ‘fatness’ parameter of the dispersal kernel they used, clearly influences species richness and species-area-relationships. However, they did not provide a link of their dispersal parameters to the moments of the distribution and thus did likely not vary variance and kurtosis independently.

In general our results provide some evidence that interspecific segregation is mainly governed by the mean of dispersal distance, while mass effects are influenced by the variance of dispersal as well (Clark 1998, Rosindell and Cornell 2009). Still, this finding is only based on a few scenarios and the comparison of two kernel types only. Therefore, we suggest that the link between the higher moments of dispersal kernels and species diversity requires further and more detailed investigations.

**Within-cell-recruitment**

Excluding the possibility of within-cell recruitment (WCR) did not influence our findings qualitatively. Nevertheless, species richness at low dispersal distances differs clearly between model versions with and without WCR. Allowing WCR means, that recruitment events follow exactly the same distance kernel as dispersal events. The probability that a seedling establishes at the microsite of its parent equals the probability of being dispersed to this site. We argue that this assumption is reasonable for most plant species, where seedlings can emerge below the canopy or fill the gap that was opened by the death of their mother plant (Clark et al. 1999, Venable et al. 2008).

Without WCR, recruitment is impossible within the microsite of the parent and therefore short distance dispersal (within microsite) cannot be realized as recruitment. As the distribution of recruitment probabilities (recruitment kernel) has to sum to one across space, the probability of recruitment events at distances of about half a cell size is drastically reduced, while at the same time the probability of recruitment at distances of about one cell size is increased, relative to the dispersal kernel. This corresponds to the case, where mother plants have strong inhibiting effects on their direct offspring (Nathan and Casagrandi 2004).

Comparing scenarios with and without WCR, but with equal mean dispersal distances reveals that the average distance of recruitment events is higher without WCR. This implies lower species segregation and therefore leads to reduced species richness. However, this difference vanishes for higher mean dispersal distances as recruitment kernel and dispersal kernel get more and more similar for both assumptions.

**Comparison with other neutral modelling approaches**

Previous neutral- as well as non-neutral metacommunity models usually used a dichotomous distinction between local and regional scales and at the same time they did
ignore dispersal limitations at the local scale (Hubbell 2001, Kadmon and Allouche 2007, Economo and Keitt 2008). These models by definition exclude the possibility of species segregation at the scale defined as ‘local’ and therefore ignore the mechanism which generates the negative branch and the local minimum of the dispersal–diversity relationship at the local scale.

Rosindell and Cornell (2007) were the first who analyzed species-area relationships (SARs) for finite survey areas within an infinite landscape. They reported a monotonic increase of species richness with increasing dispersal capability at irrespective of survey area (compare Fig. 2a in Rosindell and Cornell 2007). They missed the local minimum of species richness, as they only used mean dispersal-distances larger than five grid cells, while we found a minimizing dispersal distance of about two grid cells for a survey area of 1000 × 1000 grid cells in an infinite landscape.

Recently, O’Dwyer and Green (2010) provided an approximate analytical solution for SARs based on a spatially explicit neutral model. In contrast to our findings their approach predicts monotonously increasing dispersal–diversity relationships irrespective of sampling area (compare Eq. 10 in O’Dwyer and Green 2010). This qualitative mismatch arises because their model ignores species competitive interactions, which are responsible for the decreasing branch of the dispersal–diversity relationship. Our simulation model explicitly includes competition for space by considering the assumption of zero-sum dynamics. We expect that solving a spatially explicit neutral model including species competition is mathematically very challenging, but this analytical solution would provide an interesting test of our simulation results.

Conclusion

To our knowledge this is the first study which presents U-shaped dispersal–diversity relationships. This pattern fills a gap between the dispersal–diversity relationships reported previously for the local and the metacommunity scale. Our study does not contradict the general findings of increasing local, and decreasing metacommunity diversity, but unifies both patterns, by incorporating them as extremes of a continuous spectrum of dispersal–diversity relationships. Manipulating dispersal and recording the communities’ response is challenging at the metacommunity scale, but experimental validation of results could be done using microbial communities (Cadotte 2006b). Empirical test of our theoretical findings will shed new light on the scale-dependent dispersal–diversity relationships. Increasing species richness by manipulating dispersal capability or landscape connectivity is the aim of many conservation programs. Our findings of complex dispersal–diversity relationships at the local scale ask for careful consideration of such measures and highlight the need to define the scale(s) at which an increase of species richness is desired.

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References


