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Dispersal stochasticity mediates species richness in source–sink metacommunities

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Although it is well-known that dispersal of organisms within a metacommunity will influence patterns of coexistence and richness, theoretical and experimental studies generally assume that dispersal rates are constant through time. However, dispersal is often a highly variable process that can vary seasonally and/or when stochastic events (e.g. wind storms, droughts, floods) occur. Using a well-known source–sink metacommunity model, we present novel predictions for local and regional species richness when stochasticity in dispersal is expressly considered. We demonstrate that dispersal stochasticity alters some of the predictions obtained with constant dispersal; the peak of the predicted hump-shaped relationship between dispersal and local species richness is diminished and shifted towards higher values of dispersal. Dispersal stochasticity increases extinction probabilities of inferior competitor species particularly in metacommunities subjected to severe isolation events (i.e. decreases of dispersal) or homogenization events (i.e. sudden increases of dispersal). Our results emphasize how incorporating dispersal stochasticity into theoretical predictions will broaden our understanding of metacommunities dynamics and their responses to natural and human-related disturbances.

The structure of local communities (e.g. the numbers and types of species) was historically thought to be primarily influenced by an interaction between local environmental (e.g. productivity, disturbance) and biotic (e.g. competition, predation) factors, whereas more recent advances have emphasized the importance of regional processes such as dispersal and habitat heterogeneity (Leibold et al. 2004, Massol et al. 2011). The formalization of the idea that variation in dispersal can influence local community structure dates at least as far back as the theory of island biogeography (MacArthur and Wilson 1963, 1967), and has been an important consideration for issues of biodiversity conservation in the face of increased habitat isolation (and thus lower dispersal) that occurs with anthropogenic habitat fragmentation (Gonzalez et al. 1998, Fahrig 2003, Damschen et al. 2008).

Understanding the role of dispersal as driver of patterns of species diversity in among and within communities is a main focus of metacommunity theory (Leibold et al. 2004, Chase et al. 2005, Holyoak et al. 2005). The effects of dispersal on patterns of species richness can depend on the underlying model assumptions that influence coexistence (reviewed by Chase et al. 2005). For example, when coexistence is achieved by a regional balance of competitive abilities across heterogeneous sites, dispersal rates can influence patterns of diversity in a source–sink metacommunity whereby sustained fluxes of immigrants can override local competitive hierarchies and promote local coexistence (Mouquet and Loreau 2002, Leibold et al. 2004). At high levels, however, dispersal can be detrimental for local coexistence by creating conditions allowing the dominance of a single best regional competitor (Mouquet and Loreau 2002, Mouquet et al. 2002). While empirical studies have generally found an increase in local species richness (albeit variable) with increased dispersal (reviewed by Myers and Harms 2009), there is some circumstantial meta-analytical evidence for the predicted (Mouquet and Loreau 2003) hump-shaped dispersal–diversity pattern in experiments that carefully controlled dispersal of organisms among localities (Cadotte 2006, Logue et al. 2011).

Dispersal in theoretical models and in controlled experimentation is typically implemented as a constant. In theoretical models, a fixed proportion of individuals disperse from one habitat to another (or immigrate from a mainland) in each unit of time (MacArthur and Wilson 1967, Loreau and Mouquet 1999, Mouquet and Loreau 2003). Experimental investigations have either emulated this relative constancy in dispersal (reviewed by Cadotte 2006), or simply added species from the regional species pool once (or a few times) near the beginning of the experiment (reviewed by Myers and Harms 2009). Natural communities, however, more likely experience dispersal that is variable through time. This variability can either result from seasonality, where organisms typically disperse in one part of the season, but not others (reviewed by Nathan et al. 2000, Levin et al. 2003), or simply due to the stochastic vagaries of weather conditions or other environmental and demographic factors (Engen et al. 2005, Grotan et al. 2005). Furthermore, it is becoming well accepted that climate change is not only altering the average of environmental conditions (Schar et al. 2004), but more likely, is changing the variability in those conditions, leading to more extreme temperatures and precipitation events (Karl and Easterling 1999). This increased climatic variability may also increase the stochasticity in dispersal dynamics among communities (e.g. more frequent/intense droughts, floods, storms).

In this manuscript, we address how dispersal stochasticity can influence patterns of species coexistence and diversity in source–sink metacommunities. We extended a previous modelling framework of a source sink metacommunity (2002, 2003, see also Mouquet et al. 2006) to illustrate how dispersal stochasticity influences the coexistence among species and overall diversity in a metacommunity. That is, we examine how temporally variable dispersal (e.g. very high during some time periods, and very low during others) might alter the interactions among species, and likelihood for coexistence, differently than if dispersal was the average of low and high dispersal events. This modelling framework has been widely discussed and was therefore considered appropriate to conduct a theoretical examination of the effects of temporally variable dispersal on metacommunities (reviewed by Leibold et al. 2004, Logue et al. 2011, Massol et al. 2011). Here, we present theoretical predictions for local and regional species richness when dispersal and dispersal stochasticity are explicitly considered at different spatial scales. We investigate the effects of dispersal stochasticity on species richness at two different spatial scales – the entire metacommunity and the local community – to simulate different sources of stochasticity in natural communities at local (e.g. patch isolation within complex landscapes; Ricketts 2001) and regional (e.g. climatic fluctuations as in Driscoll and Lindenmayer 2009) scales.

Methods

The model

We begin with Mouquet and Loreau's (2002, 2003) source–sink metacommunity model. At the local scale, P_{ik} is the proportion of microsites occupied by species i in community k. The metacommunity is constituted of N communities that differ in their local conditions, where S species compete for a limited proportion of vacant microsites $(1 - \Sigma_{i=1}^{S} P_{ik})$. Each species i is characterized by a set of reproduction parameters, c_{ik}, each of which measures the potential local reproductive rate of species i in community k, and a set of mortality rates, m_{ik}. The distribution of parameters is such that each species exhibits different reproductive rates in the different communities, allowing them to potentially coexist regionally.

When there is no dispersal ($a = 0$) between localities, the species with the highest local basic reproductive rate (c_{ik}) excludes all other species in each locality, since mortality rates (m_{ik}) are the same for all species. In contrast, if localities are linked by dispersal ($a > 0$), local coexistence is possible because each species has a locality in which it is favored, and thus emigration from these 'source' areas allows them to (co-) exist in 'sink' areas where they are competitively inferior. The main equations of the model are:

$$\frac{dP_{ik}}{dt} = (I_{ik} + (1-a)\, c_{ik} P_{ik})\,(1 - \sum_{i=1}^{S} P_{ik}) - m_{ik} P_{ik} \qquad (1)$$

with immigration $$I_{ik} = \frac{a}{N-1} \sum_{l \neq k}^{N} c_{il} P_{il} \qquad (2)$$

We used a recent implementation of this model (Mouquet et al. 2011) that relaxes the strict assumption of regional similarity with a simple parameter that regulates the degree of regional similarity (ω; see Supplementary material Appendix A1 for details), which was set so that the source–sink dynamic was strong ($\omega = 0.8$), resulting in a hump-shaped pattern of local diversity with dispersal. Under these conditions, we tested the effect of temporal variability in dispersal on patterns of species richness in metacommunities. See Supplementary material Appendix A1 for details on the model parameters.

Temporal variation in dispersal

In developing this model, we assume that all emigrants from a local community are combined and equally redistributed at a constant rate to other communities, with no individuals returning to the community from which they emigrated. We introduced temporal variability in dispersal by changing the proportion of dispersers through time to generate predictions about the effect of dispersal stochasticity on local and regional species richness. Variable dispersal dynamics were generated using a sequence of random numbers from a uniform distribution. We calculated realized dispersal (i.e. actual dispersal value used in the model equations) for each dispersal event as: $a = \bar{a} \pm s$; where a is realized dispersal; $\bar{a}$ is mean dispersal ($\bar{a} = 0$: no dispersal; $\bar{a} = 1$: all individuals dispersed); s is a random number from a uniform distribution between 0 and 0.5. We evaluated other distributions of random numbers (e.g. Gaussian) and found that, under these model parameters, there were no qualitative differences on the effects of dispersal stochasticity. The signal of s was randomly assigned for each dispersal event to simulate either increases (homogenization events) or decreases in dispersal (i.e. isolation events). When $s = 0$, there is no stochasticity and all realized dispersal values are equal to mean dispersal ($a = \bar{a}$); as s increases, the deviations from mean dispersal increase leading to an increase in dispersal stochasticity. Because dispersal is bounded between 0 and 1, we constrained the variability to the range of possible dispersal values in order to avoid border effects that would come from high values of s. For example, at mean $a = 0.2$, values of dispersal were only simulated with a maximum s of 0.2 so that no negative dispersal values could be generated.

Spatial scale of variability

Any source of dispersal stochasticity in natural communities is likely to be mediated by the combination of process occurring at local and regional scales (Ricklefs 1987, Zobel 1997). From this, we extended our modelling framework to investigate the effects of dispersal stochasticity at two different scales – metacommunity and community. Dispersal stochasticity at the metacommunity level means that all species in all communities have the same realized dispersal value in every unit of time (Mouquet and Loreau 2002, 2003). This simulates, for example, variability in isolation and connectedness of local communities at regional scales as a response to large-scale fluctuations (e.g. climatic fluctuations as in Driscoll and Lindenmayer 2009). The predictions generated at this scale of stochasticity (i.e. regional), are comparable with previous results found with the previous models that did not considered dispersal stochasticity (Mouquet and Loreau 2002, 2003). Alternatively, stochasticity was implemented at community level, where each community has a different value of realized dispersal in each unit of time; all species within each community have the same dispersal value. This scenario corresponds to a lower scale fluctuation regime, as for instance, through patch isolation within complex landscapes (Ricketts 2001).

Numerical simulations

Each metacommunity consisted of 20 local communities, each initiated with 20 species. At the start of each simulation, we attributed the same proportion of microsites to each species in all local communities ($P_{ik} = 0.01$, for all i and k). In order to investigate the joint effects of dispersal stochasticity and mean dispersal on species richness, we generated predictions for every combination of dispersal parameters (0 to 1 with increments of 0.1) and dispersal stochasticity (0 to 0.5 with increments of 0.1). For each dispersal scenario, we generated 100 independent simulations using an Euler approximation ($\Delta t = 0.01$) of Eq. 1 until equilibrium was reached in all local communities within a metacommunity. Dispersal stochasticity was only implemented after equilibrium was reached (100 000 iterations), after which community dynamics were simulated for an additional 100 000 iterations under variable dispersal. Preliminary work had shown that the final communities were qualitatively similar whether stochasticity was implemented at the initiation of the simulation or at equilibrium, although it was impossible to distinguish between the two sources of extinctions (i.e. deterministic or stochastic) when dispersal stochasticty was implemented at the beginning of simulations. We thus opted to implement dispersal stochasticity after communities reached equilibrium to disentangle extinction events that result from deterministic competitive interactions within each local community under constant dispersal from those resulting from increased dispersal stochasticity.

We kept mortality rates constant across species ($m_{ik} = 0.3$), and based competitive hierarchies on potential local reproductive rate c_{ik} (species i in community k). After the very early stage of community development ($t = 2000$), we assumed that a species went extinct from a local community when its proportion of occupied sites was lower than an extinction threshold (= 0.01). We computed values for local richness (α), regional richness (γ), and species turnover (β) at the end of each run. These measures were calculated assuming additive partitioning of components of species diversity (sensu Lande 1996): $\gamma = \beta + \bar{\alpha}$. Where $\bar{\alpha}$ is the mean α diversity in the metacommunity (i.e. across all communities). Additionally, to account for the influence of dispersal and dispersal stochasticity on the relative abundance of species, we used the Rao quadratic entropy decomposition of diversity in α, γ and β (de Bello et al. 2010). This additional analysis is presented in Supplementary material Appendix A2. For every combination of dispersal and dispersal stochasticity, we analyzed the average values over the 100 simulations. Figure 1 gives an example of the dynamics of the same community with and without dispersal stochasticity. During the time series, we recorded dispersal sequences and the identity of species that went extinct in each community. Additionally, we also calculated the dispersal deviation ($= (a - \bar{a})/\bar{a}$) at each extinction event, which measures the degree to which extinction occurred following a low or high dispersal event.

Results

Species richness and dispersal stochasticity

Without dispersal stochasticity, we found the expected hump-shaped relationship between dispersal and local species richness (Mouquet and Loreau 2002, 2003). With the inclusion of increased dispersal stochasticity, the position of the peak (hump) of species richness shifted from intermediate to higher values of dispersal, and the height of the peak was reduced, allowing for the coexistence of fewer species locally (Fig. 2). This effect was stronger when dispersal was implemented at the community level (i.e. each community had a different dispersal sequence); for instance at intermediate levels of dispersal ($a = 0.5$), local species richness was reduced up to 25% (16 to 12 species) under metacommunity-level stochasticity, while under community-level dispersal stochasticity, the reduction was up to 50% (16 to 8 species).

Increasing dispersal stochasticity shifted the predicted decline of spatial turnover of species (beta diversity) to intermediate levels of dispersal and was consistent at metacommunity- and community-level dispersal stochasticity (Fig. 2a–b). This effect is clearer from low to intermediate levels of dispersal where the spatial turnover of species was enhanced more than tenfold with dispersal stochasticity (e.g. 1 to 14 species at $a = 0.3$; Fig. 2a). Finally, we found that increased dispersal stochasticity at the metacommunity-level did not have a discernable effect on regional richness (Fig. 2a). At the community level, however, there was a reduction in regional species richness at intermediate levels of dispersal (14 to 8 at $a = 0.6$; Fig. 2b). Results from the Rao diversity index of species turnover, local, and regional richness (Fig. 2a–b), which incorporate patterns of relative abundances by down-weighting the importance of

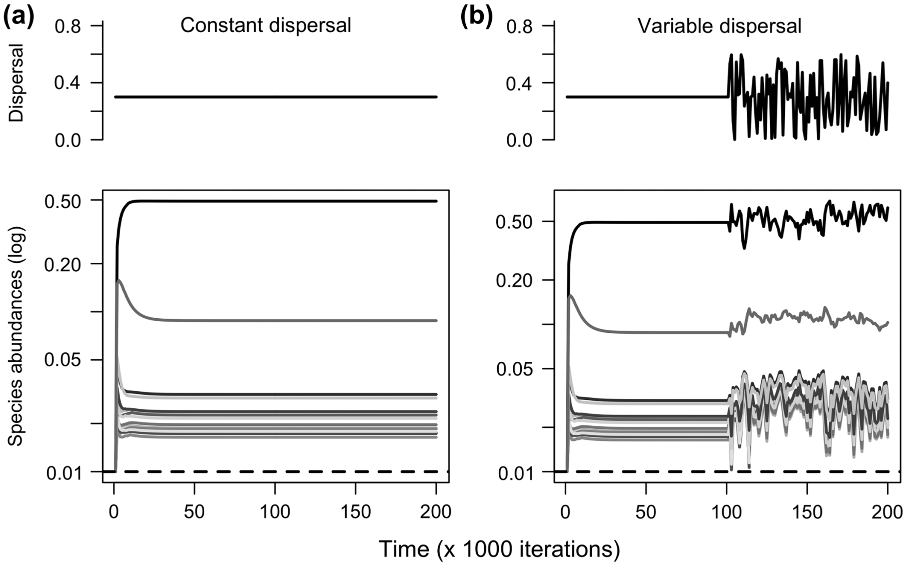

Figure 1. Examples of simulations of community dynamics under (a) constant and (b) variable dispersal dynamics. Metacommunities with variable dispersal (*a* = 0.3; *s* = 0.25) are quite responsive to changes in dispersal, leading to more extinctions than metacommunities with no dispersal stochasticity (*a* = 0.3; *s* = 0). In the bottom graphs, each solid line indicates the abundance of a different species in the community; dashed lines indicate the extinction threshold (= 0.01).

rare species, were generally similar to those produced when only considering patterns of species richness (Supplementary material Appendix A2). However, the magnitude of the effect of dispersal stochasticity on species diversity was reduced as a direct result of the down-weight of rare species, inherent of using Rao's diversity index.

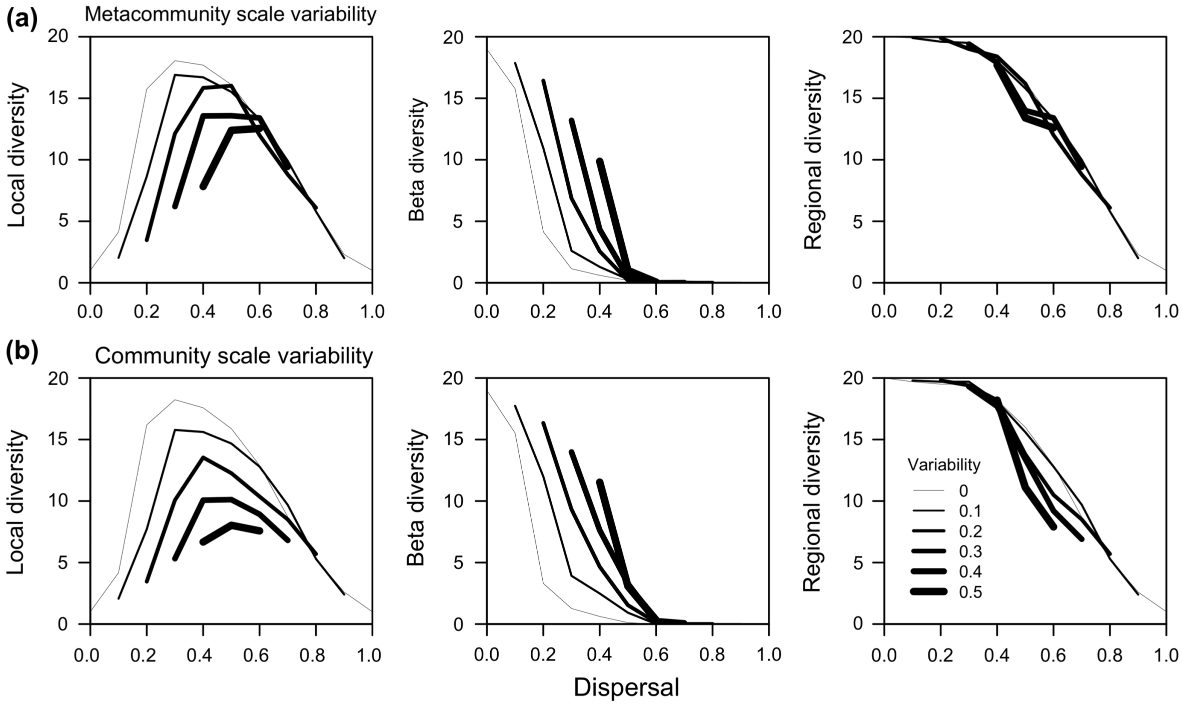

Figure 2. Local richness (alpha), spatial turnover (beta) and regional (gamma) species richness as function of dispersal (x axis) for two spatial scales of dispersal stochasticity – (a) metacommunity and (b) community levels; lines with increasing thickness indicate values of dispersal stochasticity (i.e. 0, 0.1, 0.2, 0.3, 0.4 and 0.5). We present means over 100 simulations (standard deviations are omitted for clarity but are always inferior to 2%). Predictions are only presented for scenarios where deviations from mean dispersal do not exceed realized dispersal of 0 or 1. For example, for *a* = 0.2, values of dispersal stochasticity are only shown for a maximum dispersal stochasticity of 0.2 so that the range of dispersal values were between 0 and 0.4. This procedure avoided any potential border effect (see Methods section for details).

Pattern of species extinctions

Most species that went extinct as a result of increased stochastic dispersal were those with lower local reproductive rates (i.e. the worse local competitors) (Fig. 3a). These results were similar for both dispersal scenarios (Supplementary material Appendix A3). More than 90% of the extinctions occurred after reductions in dispersal at low to intermediate levels that match the peak in local species richness ($a < 0.5$; Fig. 3b) and were caused by isolation events rather than by increasing dispersal events (i.e. reductions in dispersal; Fig 3c). In fact, the great majority of dispersal events leading to extinctions (> 93%) were negative (i.e. isolation events) with respect to mean dispersal at the time of extinction (Fig. 3c). At high mean dispersal, extinctions were caused by both isolation and homogenization events (Fig. 3c).

Discussion

Consequences of dispersal stochasticity on species richness

Overall, our results show that dispersal stochasticity mediates local and regional richness in source–sink metacommunities. We found a strong negative effect of increased dispersal stochasticity on local species richness and a shift in the position of the peak in the dispersal–local species richness relationship to higher levels of dispersal than found in previously published models without dispersal stochasticity (Mouquet and Loreau 2003). This result might help to explain some of the observed disparity between empirical results and theoretical predictions (Logue et al. 2011). For example, most empirical studies that have manipulated dispersal typically find increases in local species richness, while very few have found the predicted declines in local species richness at high levels of dispersal (reviewed by Myers and Harms 2009). This might be expected from our predictions that suggest that the maximum species richness is attained at rates of immigration much higher than are typically implemented in experimental studies (Cadotte 2006).

We have found that regional species diversity was mainly affected by dispersal stochasticity at the community level, but not at the metacommunity level. This lack of a major effect on regional species richness can be attributed to the fact that most species extinctions occurred at the local community scale and did not directly translate to increased regional extinctions. On the other hand, values of species spatial turnover at intermediate levels of dispersal were higher with dispersal stochasticity at both the local and regional scale, reflecting the strong effect on local, but regional, diversity. While dispersal stochasticity does not strongly affect regional species richness, it does add heterogeneity in the distribution of species richness among communities. These responses to unpredictable dispersal events altered metacommunities differently depending on their initial mean levels of dispersal. Reductions in dispersal generally benefit species that are better local competitors and therefore exclude worse competitors from localities.

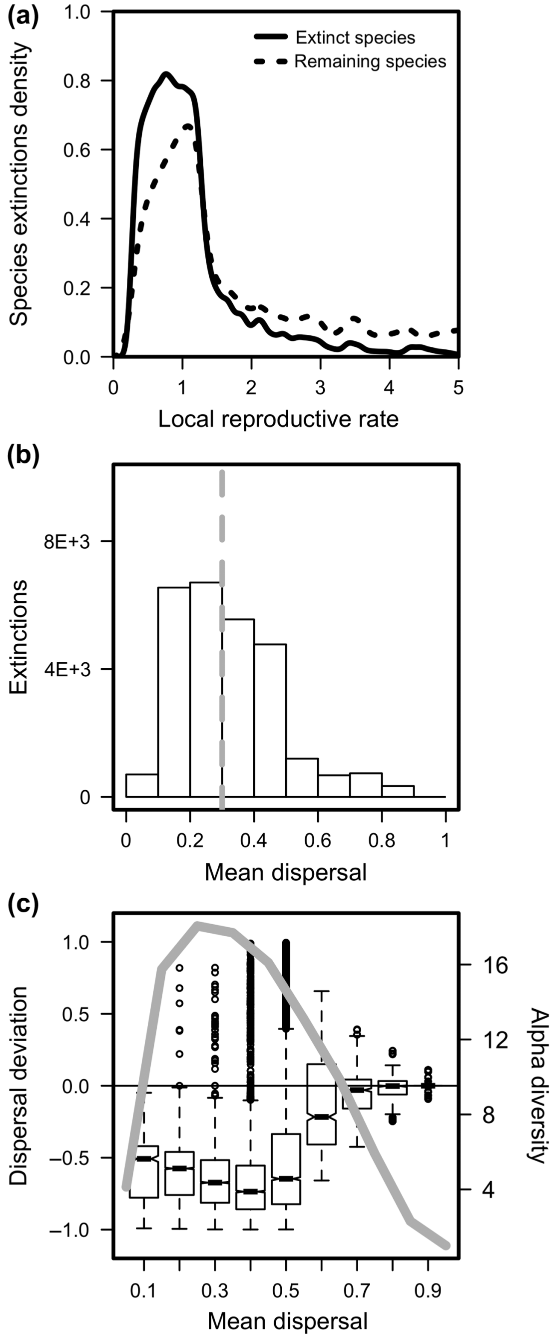

Figure 3. Species extinctions under variable dispersal dynamics: (a) densities of extinct and remaining species in relationship to their local competitive abilities (as indicated by their local reproductive rate). These analyses were done using all recorded extinction events following the implementation of dispersal stochasticity (i.e. pooled across all levels of stochasticty). Densities were calculated using a kernel density estimation procedure (*Density* function; base package; R Development Core Team) (b) Histogram of frequencies of species extinctions at each dispersal level; dashed grey line indicates the median = 0.3. (c) Boxplots showing deviations from mean dispersal at time of extinction; deviations were calculated as $(a - \bar{a})/\bar{a}$ with a as realized dispersal and $\bar{a}$ as mean dispersal at time of extinction; this measure ranges between −1 and 1. Solid grey line indicates the general predictions of local richness for different mean dispersal under no dispersal stochasticity Fig. 2). (Black circles indicate 'outliers' that fall outside the boxplot maximum or minimum range (i.e. < 5% of the data points).

Alternatively, increases in dispersal affect communities in both directions; from low to intermediate levels, increases in dispersal events benefits species that are worse local competitors. At very high mean dispersal, however, further increases in dispersal favour better regional competitors and homogenize of the metacommunity (Mouquet and Loreau 2003; empiral examples in Forbes and Chase 2002, Kneitel and Miller 2003, Matthiessen and Hillebrand 2006, Ostman et al. 2006). As a consequence, the landscape is homogenized by species that have great competitive abilities at the scale of the metacommunity, thus making it less likely to undergo extinction as a result of further stochastic events.

As expected, dispersal stochasticity had a qualitatively similar, but weaker effect on species diversity than on species richness (Supplementary material Appendix A2). This is because Rao's diversity, like other diversity estimates, down-weights the importance of rare species which play a strong role in the observed richness results. Thus, while our results are quite relevant for conservation concerns for rare species vulnerable to extinctions, they are moderated somewhat by the more common species that dominate diversity measurements. Dispersal stochasticity might be less important for diversity than for richness, which may play a stronger role in ecosystem functions dominated by common species. However, rare species may play a particular role in the stability of ecosystems if they possess functional traits that provide insurance to the functioning the ecosystem in response to environmental variation (Loreau et al. 2003, Lyons et al. 2005). Future work should explore the functional consequences of dispersal stochasticity in spatially structured ecosystems (Massol et al. 2011).

As a result of our theoretical study, we suggest that any predictions about the effects of dispersal stochasticity in natural communities should be relative to mean dispersal of those communities (i.e. whether communities are highly or poorly connected) and also include information on the nature of extreme dispersal events (i.e. isolation or homogenization events). For example, changes in dispersal that result predominately in dispersal reductions (e.g. following a drought) may have greater effects on species that can coexist locally in communities that are isolated from neighboring communities (e.g. isolated fragments) by further increasing species extinction risk. Further investigations on the effects of dispersal stochasticity could extend this framework by including different relative proportions of high–low dispersal events to mimic specific stochastic dispersal scenarios or the colour of environmental variability (i.e. whether or not it is temporally autocorrelated; Vasseur and Yodzis 2004). Moreover, these predictions could be tested in a variety of experimental venues (Logue et al. 2011) by implementing variable dispersal in spatially structured metacommunities (Carrara et al. 2012).

Scale of dispersal stochasticity

We found a stronger effect of dispersal stochasticity on local and regional diversity when dispersal varied at the community scale than at the metacommunity scale. As discussed above, dispersal stochasticity at the local scale inflates the effect of stochasticity by spatially 'desynchronizing' the dispersal sequences. It results in a greater number of variable dispersal events when stochasticity is implemented at local scale and thus enhances the probability of extreme dispersal events. With metacommunity-scale stochasticity, there were only 200 realized dispersal values per simulation, whilst with community-scale stochasticity, we simulated 4000 realized dispersal values for each community. Such unevenness across scales reflects the hierarchical nature of metacommunities. For example, regional processes that are likely to affect overall metacommunity dispersal (e.g. changes in wind patterns, ocean currents, etc.) are more likely to occur at different scales than stochasticity at the community level (e.g. disturbance, fire, etc.). We know of no competitive metacommunity experiments that have manipulated the scale of dispersal stochasticity explicitly. In predator-dominated systems where resistance to predation is analogous to competition (Chesson and Kuang 2008), Cadotte and Fukami (2005) showed that dispersal had a positive or neutral effect at local scales but consistently negative effects on the metacommunity scale. These results were explained by an interaction between scale-dependent effects of dispersal and the removal of spatial refuges from predators. Even though this experiment focused on a different community assembly mechanism (predation vs competition), it generally supports our conclusion that the scale of dispersal stochasticity is central to building a more predictive understanding of the ecological consequences of extreme dispersal events on community richness, composition and dynamics. This is particularly important given the increasing numbers of reports suggesting that spatial and temporal patterns of environmental variability are becoming more unpredictable with global change (e.g. more frequent/intense droughts, floods, storms, etc.; Karl and Easterling 1999, Schar et al. 2004).

Species extinctions patterns

We found that dispersal stochasticity had an asymmetrical effect on community species composition by increasing the extinction probability of worse local competitors within each local community. Metacommunities with low to intermediate levels of mean dispersal were also more likely to lose species as a result of increased stochasticity relative to highly connected metacommunities. The inclusion of stochasticity in dispersal revealed that probabilities of extinction in dispersal-limited communities were much higher than anticipated under constant dispersal dynamics. Such underestimation of species extinction probabilities can have implications in terms of forecasting changes in species diversity in isolated communities during the fragmentation processes (e.g. isolated fragments; Gonzalez et al. 1998, Fahrig 2003, Damschen et al. 2008). In contrast, from intermediate to high levels of dispersal, metacommunities are homogenised and dominated by strong competitors (Mouquet and Loreau 2002) that are more abundant and less vulnerable to variability on dispersal. This is consistent with empirical evidence of the potential impacts of increases in dispersal on metacommunities such as those in freshwater ponds (Forbes and Chase 2002) and pitcher plant micro-ecosystems (Kneitel and Miller 2003).

Extending dispersal stochasticity to other metacommunity paradigms

We generated predictions for a particular type of metacommunity source–sinks. However, dispersal stochasticity will likely be important for communities assembled under different coexistence mechanisms, including neutral or competition–colonization metacommunities (Leibold et al. 2004). Unravelling the consequences of dispersal stochasticity in competitive metacommunities with these alternative mechanisms of coexistence will require additional theoretical work, but we here make some general conjectures.

Under neutral dynamics, local diversity is determined by migration rates from the metacommunity and local community size (Hubbell 2001, Etienne 2005). Increasing dispersal generally leads to homogenization among communities by increasing local diversity and decreasing beta diversity (Economo and Keitt 2008). These effects are mediated by rates of speciation (or immigration from outside the metacommunity) and are likely to also be affected by dispersal stochasticity. Extreme dispersal events (i.e. isolation or homogenization) are thus likely to lead to extinctions that will or not will be compensated by new species arrivals depending on the rates of speciation (or immigration). For example, high speciation rates are likely to enhance community differentiation (Richardson et al. 2001, Latimer et al. 2005), which would be further enhanced with reductions in dispersal events (i.e. isolation). In contrast, if speciation rates are low, a series of extreme dispersal events are unlikely to alter the regional diversity (Economo and Keitt 2008).

Competition–colonization tradeoffs occur when there are costs associated with either competitive or dispersal abilities (Hastings 1980, Tilman 1994, Calcagno et al. 2006); coexistence occurs because inferior competitors are able to persist in the landscape due to their higher colonization ability (Tilman 1994). Depending on the strength of the tradeoff, there are colonization rates below which coexistence is not possible, and upper thresholds above which only the superior colonizer survives (Calcagno et al. 2006). In this scenario, we expect that increased stochasticity in colonization rates (as a result of dispersal stochasticity) would reduce the 'window' of coexistence by driving either the strong or the weak competitors extinct (depending on the direction of stochasticity). Since colonization rates in this model framework are species-specific, it is foreseeable that the impacts of stochasticity would depend on whether stochasticity is modelled separately for either colonizer and the competitor (i.e. species-specific stochasticity), or whether both species are subjected to a similar stochasticty regime (metacommunity-level).

Conclusions

In natural systems, dispersal rates are often likely be variable owing to a variety of stochastic factors, be they environmental, demographic and/or otherwise. However, most theoretical and empirical studies treat dispersal rates as a constant. Furthermore, global climate change is expected to increase the frequency and magnitude of environmental extremes (Karl and Easterling 1999), which can also increase stochasticity in dispersal among species within metacommunities (Nathan et al. 2000, Levin et al. 2003). Our results illustrate that temporally variable dispersal patterns can have an important influence on species' coexistence and richness at local and regional spatial scales. In our source–sink metacommunity model, the principal mechanism underlying such an effect is the increased risk of extinction of inferior competitors during episodes of reduced dispersal (isolation). Increased dispersal stochasticity is thus more likely to affect dispersal-limited metacommunities than highly connected metacommunities (Cottenie et al. 2003). To achieve a broader understanding of the consequences of dispersal stochasticity on metacommunities dynamics, it will be useful to extend this framework to other relevant metacommunity paradigms. Incorporating dispersal stochasticity in metacommunity theory is an important step to enhance our understanding of the role of dispersal in community dynamics and should be considered in future empirical and experimental studies on metacommunities in an increasingly variable and heterogeneous world (Myers and Harms 2009, Logue et al. 2011).

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Supplementary material (available online as Appendix O20479 at www.oikosoffice.lu.se/appendix). Appendix A1–A2.