Migration and niche partitioning simultaneously increase species richness and rarity

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ABSTRACT

To understand species abundance distributions effectively, it is essential to consider the forces which create the overwhelmingly long 'tail' of rare species. Both neutral and niche theory have been invoked to explain the rarity of certain species in ecological assemblages: niche theory stresses the importance of the resource division process, while neutral theory focuses on stochastic drift in densities of competitively identical species. Here, we show how migration and niche partitioning can act simultaneously to increase both the number of rare species and the total species richness. By simulating the dynamics of a metacommunity using an interconnected network of local communities, we incorporate niche partitioning into the otherwise per capita equivalent processes of birth and death. Niche partitioning is defined by the species niche fitness function, which is measured by the species optimal environmental conditions, the fundamental niche breadths of each species, and by the breadth of the environmental gradient of each local community. For a given niche breadth at the local community scale, unimodal relationships appear between the rate of migration, the number of rare species, and the total species richness. At the metacommunity scale, species richness was at first unaffected by increasing migration, but then crashed. At wide niche breadth, both the number of rare species and the total number of species started to decline at a low rate of migration. In contrast, when niche breadth was narrow, neither the number of rare species nor the total number of species started to decline until migration rates were much higher. This is because, for a given migration rate, niche breadth can affect the proportions of individuals coming from adjacent local communities. The integration of niche partitioning and migration therefore provides a rational explanation for the widespread rarity of species in ecological communities.

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1. Introduction

With the continuing development of neutral theory (Hubbell, 2001), stochastic forces such as random birth, death and dispersal limitation are being recognized as critical factors in the structuring of ecological communities (Alonso et al., 2006; Etienne and Alonso, 2007). In contrast, traditional niche theory involves the partitioning of an *n*-dimensional hyperspace in which each species occupies a unique position (Hutchinson, 1957). Under niche theory, species coexistence is determined by specific traits, the result of adaptations to a heterogeneous environment (Chesson, 2000; Tilman, 1982; Tilman and Pacala, 1993). While it is clear that niche partitioning is a genuine feature of ecological communities (Diamond, 1973; Schoener, 1974), classical niche partitioning cannot explain

why large numbers of species coexist on the same or similar resources (Armstrong and McGehee, 1980; Bengtsson et al., 1994; Levin, 1970; MacArthur and Levins, 1964; Tilman and Pacala, 1993).

Neutral theory per se is, however, somewhat controversial. Two of neutral theory's key assumptions have attracted criticism, namely ecological equivalence among species (Hubbell, 2005, 2006; Yu et al., 1998; Zhang and Lin, 1997) and excessive speciation rates (Desjardins-Proulx and Gravel, 2012; Ricklefs, 2003; Rosindell et al., 2010). Zhang and Lin (1997) proposed that even slight variations on the assumption of equality of species could cause a considerable decline in the persistence time of species, concluding that the speciation rates needed to offset extinctions in a model with competitive differences was so high that it would be rarely or never observed in nature.

Another controversial aspect of neutral theory is the nature of the metacommunity. The concept of a metacommunity was originally defined as a set of local communities linked by migration (Leibold et al., 2004; Wilson, 1992). One advantage of this network metacommunity framework is that a sophisticated set of quantitative tools is available for the characterization of its structure

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(Newman, 2003; Urban and Keitt, 2001). Neutral models frequently assume one large—even frozen—metacommunity (Hubbell, 2001; Volkov et al., 2007). Some authors (McGill et al., 2006) consider it biologically unrealistic to assume that the metacommunity is large enough to ameliorate the dynamics of local populations, while being small enough that all individuals can have equal probability of migration into the local community. Yet most original network metacommunity models consider migration to be consistent throughout the landscape, irrespective of spatial scale (Mouquet and Loreau, 2002, 2003).

To understand the mechanisms underlying species abundance distributions in natural communities, the effects of spatial scale on the commonness and rarity of species must be addressed (Cao et al., 1997; Preston, 1948). 'Rare' species are those which occur at low frequencies, or with low abundance in samples of a certain size, which is typically small compared with the size of the whole community (Cao et al., 1998). In natural communities, such as the tropical rainforest of Barro Colorado Island (Hubbell, 1979, 2001), rare species outnumber common species (McGill, 2003; McGill et al., 2007) and constitute the largest component of species richness (Gotelli and Graves, 1996; Krebs, 1985; Putman, 1994; Williams, 1964). But because rare species are seen as functionally unimportant, they are often neglected (Goldwasser and Roughgarden, 1997).

Understanding the nature of rarity is therefore a pressing question (Bell, 2000; Cotgreave and Pagel, 1997; Hughes, 1986), and both neutral and niche theory have been invoked to explain rarity in species assemblages. According to neutral theory, the rarity or commonness of a species is not because of its traits or the traits of its competitors but rather solely because of stochastic drift in densities of competitively identical species. In contrast, niche theory associates rarity with the resource division process (Gaston, 1994; Kunin, 1997). Meanwhile, it has been suggested that niche differences are unlikely to be the sole factors responsible for the rarity of certain species (Kunin and Gaston, 1993; Siqueira et al., 2011). Although neutral theory works surprisingly well in predicting the abundance distributions of certain species, and better than niche theory in some cases (Alonso et al., 2006; Bell, 2000; McGill et al., 2006; Rosindell et al., 2011), neutral theory makes the controversial assumptions of ecological equivalence, a large metacommunity structure, and unrealistically high rates of speciation (Hubbell, 2001).

Here, we use a metacommunity pattern defined by Leibold et al. (2004) to reconcile the stochastic processes of birth, death and dispersal limitation with two processes fundamental to niche partitioning among species: migration rates and niche breadth. In our model, niche partitioning is defined by the species niche fitness function, which is measured by the species optimal environmental conditions, the fundamental niche breadths of each species, and by the breadth of the environmental gradient of each local community. We introduce environmental heterogeneity into the model both within and between local communities. In the absence of ecological equivalence, unrealistically high rates of speciation and a large metacommunity, we set out to investigate whether species rarity can be explained by niche partitioning and migration among local communities.

2. Methods

2.1. General framework

An individual-based, spatially explicit stochastic model of sessile organisms is the basic framework of our model. The metacommunity consists of n local communities connected by migration. The landscape of each local community is defined as a square lattice with length L, and there are $L \times L$ sites in the square lattice. In order to avoid edge effects, the square lattice is a torus. In the initial state, species number is M, the abundance of each species is $L \times L/M$, and species distribute themselves across the landscape randomly, with one individual occupying one site. Communities in our model experience the zero-sum dynamics of the lottery model, which means that the community is saturated with individuals and remains at a constant size; if an individual dies it is replaced by a new individual (Gaston and Chown, 2005; Hubbell, 2001). We assume that all individuals have equal mortality d. When an individual dies, the empty site is filled by recruits either drawn from the local community or an adjacent one.

2.2. Community dynamics

2.2.1. Neutral community dynamics

Recruitment of an individual follows the lottery model used by Gravel et al. (2006), and hence the recruitment probability R_i of species i in a closed neutral community is

$$R_i = \frac{\sum_{r=1}^{\sigma} N_{i,r} K(r)}{\sum_{j=1}^{s} \sum_{r=1}^{\sigma} N_{j,r} K(r)} \quad (1)$$

where $K(r)$ is a Gaussian dispersal kernel (Chave et al., 2002):

$$K(r) = \left(\frac{r}{\sigma^2} \right) \exp\left[-\frac{r^2}{2\sigma^2} \right] \quad (2)$$

σ^2 represents the mean squared dispersal distance, which we assume to be equal among all individuals. $N_{i,r}$ is the total number of individuals of species i at all r distances from the recruited site; $N_{j,r}$ is the total number of individuals of species j at all r distances from the recruited site.

2.2.2. Niche community dynamics

Each local community has a simple monotonic environmental gradient which is unaltered in the simulation process. We use monotonic gradients in the model for the sake of simplicity; such gradients may be observed in nature at small spatial scales, or in particular habitats (e.g. vernal pools and steep elevation gradients). Following Schwilk and Ackerly (2005) the environmental factor $E_{x,c}$ is a linear function of position on the lattice:

$$E_{x,c} = E_{\min,c} + \left(\frac{x}{X} \right) E_{range} \quad (3)$$

We divide the lattice equally into X subsections and each subsection has two dimensions. We label all subsections from 0 to $X - 1$. The value of X thus determines the grain size of the environment. $E_{x,c}$ is the value of the environmental factor of subsection x in local community c, $E_{min, c}$ is the minimal value of E in local community c, and E_{range} is the range of E. We use $E_{min,c}$ and E_{range} to control the environmental heterogeneity of local community c. At a given $E_{min,c}$, the variance in environmental conditions increases with E_{range}.

When there is niche partitioning, the survival probability of species i at site x in local community c, $\lambda_{i,x,c}$, is associated with the environmental factor of site x in local community c, $E_{x,c}$, the species optimal environmental condition μ_i, and the niche breadth of each species w (Gravel et al., 2006), as follows:

$$\lambda_{i,x,c} = \exp \frac{-(E_{x,c} - \mu_i)^2}{2w_i^2} \quad (4)$$

The niche breadth (w) of each species is identical. We label the species from 1 to M and the value of the optimal environmental condition of species i is (Schwilk and Ackerly, 2005):

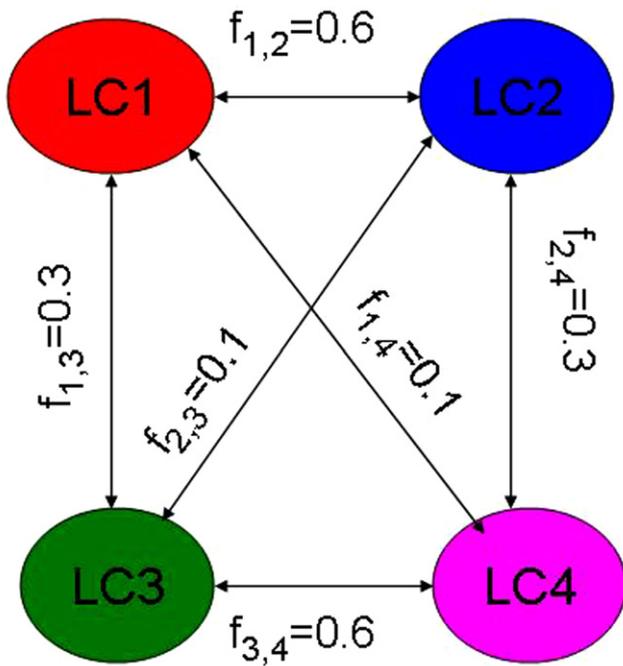$$\mu_i = \left(\frac{i}{M} \right) E_{range} + \frac{1}{2M} \quad (5)$$

Fig. 1. Schematic representation of the network metacommunity, consisting of four interconnected local communities, *LC1*, *LC2*, *LC3* and *LC4*. The lines with double-headed arrows indicate bidirectional movement of species between two local communities. The weight of the edge, given by $f_{c,c'}$, represents the strength of the links between local communities c and c', and m is the migration rate per time step of each local community from other local communities.

Hence, the recruitment probability $R_{i,x,c}$ of species i in section x in a closed niche model community c is

$$R_{i,x,c} = \frac{\lambda_{i,x,c}}{\sum_{j=1}^{s} \lambda_{j,x,c}} \tag{6}$$

2.3. Network metacommunity dynamics

Given the computational costs, which grow substantially with the number of local communities, we constructed a metacommunity with only four local communities interconnected by migration (Fig. 1). These four local communities, described as *LC1*, *LC2*, *LC3* and *LC4*, are fully connected and the network is symmetric. Initial species numbers of each local community are identical, all species have identical abundance and all individuals distribute in each local community randomly. The environment is heterogeneous both within and between local communities. The variance of the environmental conditions between local communities is determined by E_{range} and $E_{min,c}$ which is arbitrarily assigned. The migration rate per time step is denoted as m, and $f_{c,c'}$ is the weight of the edge between local community c and c'; the weight of the edge thus represents the strength of the links between local communities (Proulx et al., 2005). Hence, the migration rate from local community c' to local community c is $mf_{c,c'}$. The migration between two local communities is non-directional.

Taking both the niche and neutral models into account, the recruitment probability $R_{i,x,c}$ of species i at site x in local community c is as follows:

$$R_{i,x,c} = (1-m)\frac{\sum_{r=1}^{\sigma} \lambda_{i,x,c} N_{i,r,c} K(r)}{\sum_{j=1}^{s}\sum_{r=1}^{\sigma} \lambda_{j,x,c} N_{j,r,c} K(r)} + \sum_{c'=1, c' \neq c}^{n-1} mf_{c,c'} P_{i,c'} \tag{7}$$

The first term in this expression denotes that the empty site will be occupied by individuals of species i coming from the same local community c; the second term represents those individuals coming

Table 1
Model parameter values which were held constant for all simulation experiments while varying m and w.

Parameter	Meanings	Value
L	Community size $L \times L$	120
M	Diversity of initial condition	40
D	Mortality of species per time step	0.1
Σ	Mean dispersal distance	6
$F_{c,c'}$	The weight of the edge	$f_{1,2} = f_{3,4} = 0.6$
		$f_{1,3} = f_{2,4} = 0.3$
		$f_{1,4} = f_{2,3} = 0.1$
X	The number of small sections	10
$E_{min,c}$	The minimum of environmental factor	$LC1$:0.0125
	E of local community c	$LC2$:0.0375
		$LC3$:0.0625
		$LC4$:0.0875
E_{range}	Range of environmental factor E	1

from local communities other than community c; $P_{i,c'}$ represents the abundance of species i in local community c' that are connected with c. The dispersal kernel occurs within each local community rather than between local communities.

2.4. Set parameter values

The simulation experiments were performed by varying either migration rate m or niche breadth w. The environmental heterogeneity of local community c was determined by $E_{min,c}$ and E_{range}. E_{range}, was identical for all local communities. We ran simulations for all combinations of the following: migration rate m selected to be 0, 0.001, 0.01, 0.1, 0.5, or 1 and niche breadth $w = 0.01$ or 0.1. Table 1 summarizes the values of other parameters that were held constant during the simulations. To allow time for the community to reach dynamic equilibrium, we ran each simulation experiment for 10^6 time steps and 50 replicates.

3. Results

Fig. 2 illustrates the proportional abundance of species in *LC1* which came from the four local communities under different migration rates and niche breadths. We define those species which exist in closed ($m = 0$) communities as residents; the relative abundance of these species is determined by niche partitioning. The species abundance of a local community under $m = 0$ was the reference for our analysis. Species arriving from neighbouring, open ($m \neq 0$), communities were defined as immigrants. Under $m = 1$ a local community is completely open and a single species would occupy the whole community; the following analysis for Fig. 2 did not therefore include this case.

When $0 < m < 1$, at both $w = 0.1$ and $w = 0.01$, increasing migration led to increases in the local abundance of immigrant species, whereas the abundance of resident species decreased. For a given m, the number of successful immigrants was larger under $w = 0.1$ than $w = 0.01$. For example, at $m = 0.1$ ($w = 0.01$), immigrants account for only 9.59% of the whole local community, whereas at $m = 0.1$ ($w = 0.1$) this proportion increased to 67.06% (Fig. 2). In the same way, for given migration rates, the proportion abundance of individuals coming from neighbouring communities differed between $w = 0.01$ and $w = 0.1$. At $m = 0.5$ ($w = 0.01$), the proportion of resident species was 58.14%: 19.54% belonged to *LC2*; 12.62% belonged to *LC3*; and 9.70% belonged to *LC4*. When $m = 0.5$ ($w = 0.1$), the proportion of resident species was 22.03%: 23.93% came from *LC2*; 27.45% came from *LC3*; and 26.59% came from *LC4*. Hence, the number of individuals from neighbouring communities depends on the strength of the links between local communities at $w = 0.01$, but it disappears at $w = 0.1$.
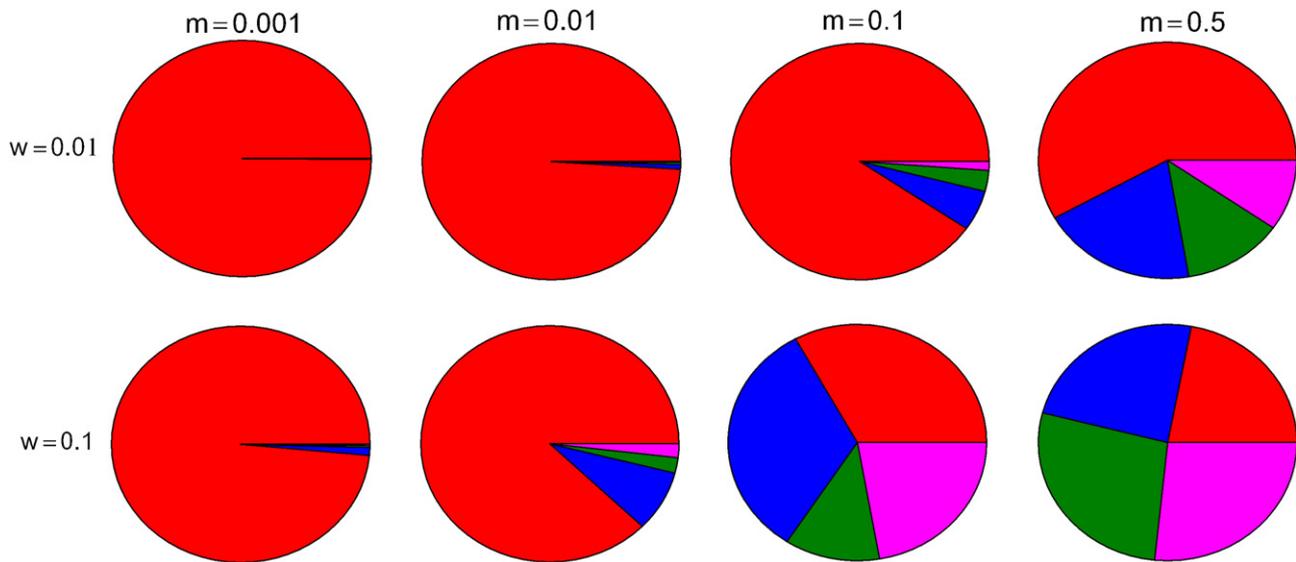
Fig. 2. The proportional abundance at equilibrium of species arriving at *LC1* from the four local communities under different migration rates and niche breadths. The proportional abundance of these species is different at smaller niche breadths (top panel) and larger niche breadths (bottom panel) as migration rate increases (the panels from left to right). Different colours (consistent with Fig. 1) represent the proportional abundance of species coming from *LC1* (red), *LC2* (blue), *LC3* (green) and *LC4* (purple). The specific abundance proportions for each combination of niche breadth and migration are: $w = 0.01$ and $m = 0.001$: *LC1*: 99.86%, *LC2*: 0.08%, *LC3*: 0.04%, *LC4*: 0.02%; $w = 0.01$ and $m = 0.01$: *LC1*: 98.96%, *LC2*: 0.62%, *LC3*: 0.31%, *LC4*: 0.11%; $w = 0.01$ and $m = 0.1$: *LC1*: 90.41%, *LC2*: 5.52%, *LC3*: 2.85%, *LC4*: 1.22%; $w = 0.01$ and $m = 0.5$: *LC1*: 58.14%, *LC2*: 19.54%, *LC3*: 12.62%, *LC4*: 9.70%; $w = 0.1$ and $m = 0.001$: *LC1*: 98.47%, *LC2*: 1.08%, *LC3*: 0.25%, *LC4*: 0.20%; $w = 0.1$ and $m = 0.01$: *LC1*: 87.70%, *LC2*: 8.30%, *LC3*: 2.10%, *LC4*: 1.90%; $w = 0.1$ and $m = 0.1$: *LC1*: 32.94%, *LC2*: 32.93%, *LC3*: 11.90%, *LC4*: 22.23%; $w = 0.1$ and $m = 0.5$: *LC1*: 22.03%, *LC2*: 23.93%, *LC3*: 27.45% and *LC4*: 26.59%. All simulations were averaged over 50 replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

In this study, we define rare species as those species whose proportional abundance accounts for less than one percentage of the overall abundance. When m is low, immigrant species are rare, but when m is high, some immigrant species become common. The relationship between the number of rare species and migration rate under different niche breadths is illustrated in Fig. 3. There is a unimodal relationship between rare species number and migration rate (Fig. 3). The greatest number of rare species appeared at $m = 0.01$ for $w = 0.1$, while it occurred at $m = 0.1$ for $w = 0.01$. When the local community is completely closed ($m = 0$) or open ($m = 1$), the rare species number is 0.
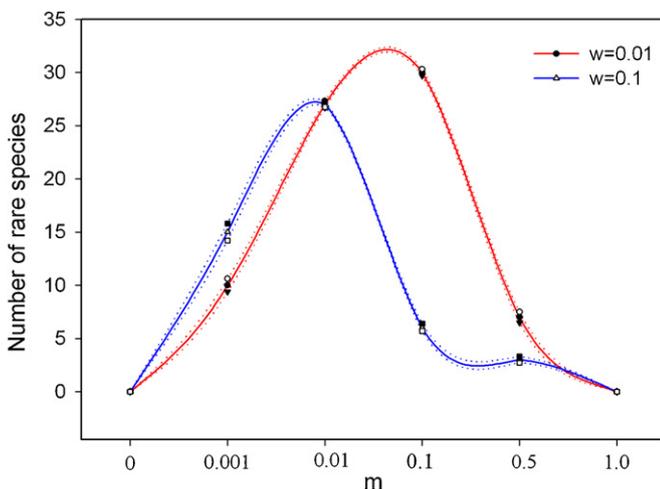

Fig. 3. Relationship at equilibrium between rare species number and migration rate for *LC1* under different niche partitioning. When $m = 0$, 0.01 and 1.0, the points of $w = 0.01$ and $w = 0.1$ overlap. The dotted line represents the 95% confidence interval. When $m = 0$ or $m = 1$, the number of rare species is constant, so the C.I. = 0 at these two points. The relationships between the number of rare species and the migration rates of other local communities (not shown here) are the same as *LC1*. Data points are means of 50 replicates.

We also found the same relationship between local species richness and migration rate; as with the number of local rare species, the highest local species richness appeared at $m = 0.01$ for $w = 0.1$, while it occurred at $m = 0.1$ for $w = 0.01$. When $m = 1$, all local communities eventually collapsed to a single species. When $m = 0$, species sorted themselves across the landscape according to their niche partitioning; the number of coexisting species was 10 in the local community (Fig. 4A), and 40 in the metacommunity (Fig. 4B). The number of coexisting species in the metacommunity first remained constant, and then declined as migration rate increased (Fig. 4B). The critical point at which species richness began to decrease was $m = 0.01$ for $w = 0.1$, and $m = 0.5$ for $w = 0.01$.

Fig. 5 shows the relative species abundance distributions for *LC1* under different values of migration rate and niche breadth. When $m = 0$, the abundance of coexisting species distributed regularly at $w = 0.01$, whereas there was a small disparity between species abundance at $w = 0.1$ (not shown). As migration rate increased from very low values, the number of species in the local communities first increased and then decreased, leading to the SAD curves becoming progressively flatter at $w = 0.01$, but progressively steeper at $w = 0.1$ (Fig. 5).

4. Discussion

Our results highlight the importance to the maintenance of species rarity of niche partitioning and migration among local communities. These results were achieved without including neutrality's unrealistic assumptions of ecological equivalence, high speciation rates and a large metacommunity. Through the combination of niche partitioning in resource hyperspace, random birth and death processes, and migration among local communities, we offer a novel explanation for species rarity in ecological communities.

Rare species are a common feature of natural communities (Magurran and Henderson, 2003), and this feature was confirmed in our model. For example, Figs. 2–4A reveal that in a local community with wide niche width and low migration ($w = 0.1, m = 0.01$), 10
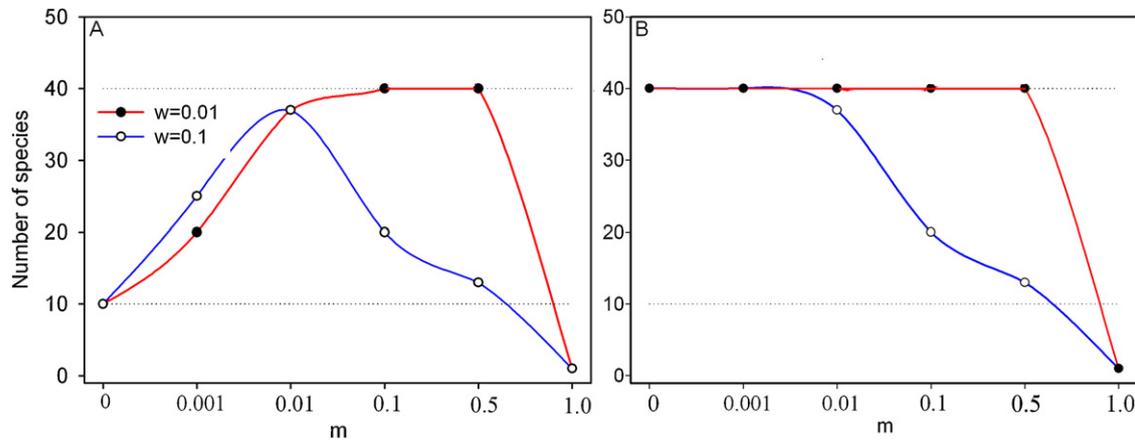
Fig. 4. Relationship at equilibrium between species richness and migration rate for the local communities (A), and for the metacommunity (B) under different levels of niche partitioning. The dotted lines show the maximal environmental heterogeneity for the metacommunity (upper) and for the local communities (lower). This relationship for local communities is shown for *LC1*; other local communities were the same as *LC1* with the metacommunity being the sum of the four local communities. Data points are means of 50 replicates.

resident species accounted for 88% of the overall abundance, with the remaining 12% being accounted for by 27 immigrant species. Conversely, in a local community with narrow niche width and high migration ($w = 0.01$, $m = 0.1$), 10 resident species accounted for 90% of the overall abundance, with the remaining 10% being accounted for by 30 immigrant species. In our model, the diversity of rare species is highly dependent upon the interaction between migration rate and niche partitioning. The greatest number of rare species appeared at intermediate migration rates, i.e. $m = 0.01$ for $w = 0.1$ and $m = 0.1$ for $w = 0.01$ (Fig. 3). Our results therefore differ from other studies which have proposed that the number of rare species would increase with migration rate (Bell, 2000; Gravel et al., 2006; Hubbell, 2001). In our model, there was a unimodal relationship between the number of rare species and migration rate (Fig. 3). Migration allows the transfer of species that can only coexist outside of the local community when the community is closed, but which can also coexist locally when communities are open. Niche partitioning determines how long the migrant can survive. When migration is zero, all species are residents and have high abundances. As the migration rate increased, more migrants appeared and more rare species were maintained. However, when the migration rate was very high, communities became more similar in species composition, rare species richness therefore decreased, and some migrant species became more common. Although migration among local communities is important in maintaining large numbers of rare species, niche partitioning

was the basis for stable species coexistence in all local communities. Hence, it is only by invoking niche partitioning and migration among local communities *simultaneously* that species rarity can be explained.

According to Bell (2000), increasing migration leads to an increase in species richness. However, there is a unimodal correlation between local species richness and migration rate in our model (Fig. 4A). For local communities, our results demonstrate that both niche partitioning and migration working together could maintain more species than either completely closed ($m = 0$) or completely open ($m = 1$) communities. For example, 10 species could coexist in local communities when we only considered niche partitioning, but the number increased to 37 at $w = 0.1$, and 40 at $w = 0.01$ when we simultaneously incorporated migration with niche partitioning (Fig. 4A). When $m = 1$, the community collapsed to a single species and niche partitioning ceased.

When communities were completely open ($m = 1$), both the local community and the metacommunity would be occupied by a single species. In this situation, as an individual dies it is replaced by an immigrant determined by the abundance of this species in an adjacent community. As in neutral theory (Hubbell, 2001), our model allows a migrant individual to successfully occupy a new site in a given local community without competing with other individuals. If $m = 1$, the metacommunity thus functioned as a single large community, in which the best regional competitor excluded all other species. This outcome has been shown before
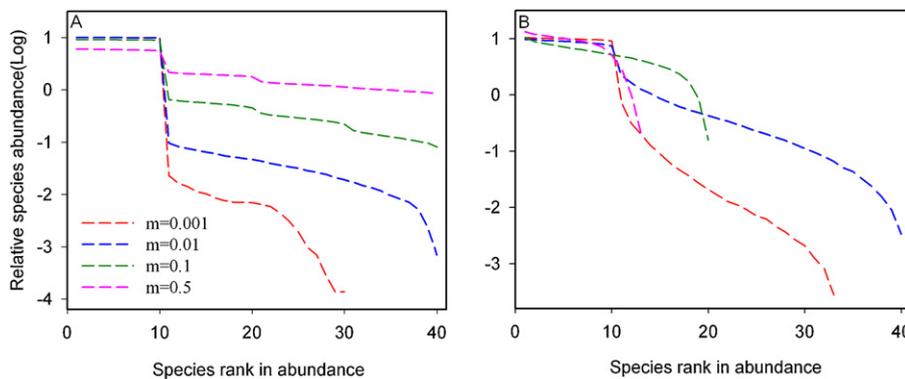

Fig. 5. Species abundance distribution (SAD) curves for local communities at equilibrium, showing the effects of different migration rates under niche partitioning of $w = 0.01$ (A) and $w = 0.1$ (B). Because the local community is occupied by a single species when $m = 1$, SAD curves for this case are not shown, neither are the SAD curves for $m = 0$, because with zero migration species sorted out on the landscape according to niche partitioning only. These SAD curves show only *LC1*; the other local communities are the same as *LC1*. The percentage relative abundance is log transformed on the *y*-axis. All simulations were averaged over 50 replicates.

(Mouquet and Loreau, 2002, 2003), with increasing migration leading to a more homogeneous metacommunity, and an eventual collapse in the number of species (Fig. 4B).

The correlation between species richness and migration rate (Fig. 4) in our model also agrees with other studies (Cadotte, 2006; Kneitel and Miller, 2003; Mouquet and Loreau, 2003). Our results show that when niche breadth was wide, both the number of rare species and the total number of species started to decline when migration rates were low. In contrast, when niche breadth was narrow, neither the number of rare species nor the total number of species started to decline until migration rates were much higher. For example, species richness declined when $m \geq 0.01$ for $w = 0.1$, and $m \geq 0.1$ for $w = 0.01$ at both the local and the metacommunity level (Fig. 4). Broader niche breadth indicates that more resources can be used by a species and results in increasing niche overlap, which in turn determines the intensity of competition (Mutshinda and O'Hara, 2010). High migration rate implies a high probability of species encounters, leading to intense competition between species. May and McLean (May and McLean, 2007) proposed that the limiting similarity $D/w \geq 1$ was the condition necessary for species coexistence where D was the distance between the optima of two adjacent species and w was the niche breadth of each species. This value was approximately equal to 1 when $w = 0.1$ in our model, and the SAD curves with migration were similar to natural communities under $w = 0.1$ (Fig. 5B). Furthermore, in our model, the SAD curves fitted a logarithmic normal distribution best when $w = 0.1$ and $m = 0.01$. When niche breadth was small ($w = 0.01$), the community did not reach the threshold of limiting similarity, and species could invade the local communities more easily (Abrams, 1996; Pacala and Tilman, 1994).

Many models have used either a network metacommunity structure (Economo and Keitt, 2008, 2010) or a heterogeneous environment (Gravel et al., 2006; Mouquet and Loreau, 2002, 2003; Schwilk and Ackerly, 2005) to study species richness. However, our model differs from previous models in two ways. First, the weight of the edges, which represents the strength of the links between local communities (Proulx et al., 2005), is different, whereas in other models the edges were equal (Economo and Keitt, 2008, 2010; Mouquet and Loreau, 2002, 2003). Second, in our model, the environment is heterogeneous not only between local communities but also within local communities, whereas only environmental heterogeneity between local communities was considered in the models of Mouquet and Loreau (2002, 2003). Similarly, only the environmental heterogeneity within local communities is considered in the models of Gravel et al. (2006) and Schwilk and Ackerly (2005). Our model uses stochastic process that are known to play an important role in community structure (Hubbell, 2001; Law and Morton, 1993; Tilman, 2004), while focussing on the spatial arrangement of local communities and the heterogeneity of the environments; both are key factors in spatially explicit studies (Cottenie et al., 2003).

5. Conclusions

We have developed a new model to investigate whether niche partitioning and migration between local communities could explain the existence of large numbers of rare species in local communities. Our results indicate that niche partitioning and migration, working simultaneously, can indeed explain large numbers of rare species. We found a unimodal relationship between rare species number and migration, which led to the appearance of a unimodal correlation between local species richness and migration rate. Species richness and the number of rare species both decline at lower migration rates when niche breadths were wider than when niche breadths were narrower. This is because, for a given migration rate, niche breadth affects the proportions of individuals coming from adjacent local communities.

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