



Coexistence and invasibility in a two-species competition model with habitat-preference

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ABSTRACT

The outcome of competition among species is influenced by the spatial distribution of species and effects such as demographic stochasticity, immigration fluxes, and the existence of preferred habitats. We introduce an individual-based model describing the competition of two species and incorporating all the above ingredients. We find that the presence of habitat preference—generating spatial niches—strongly stabilizes the coexistence of the two species. Eliminating habitat preference—neutral dynamics—the model generates patterns, such as distribution of population sizes, practically identical to those obtained in the presence of habitat preference, provided a higher immigration rate is considered. Notwithstanding the similarity in the population distribution, we show that invasibility properties depend on habitat preference in a non-trivial way. In particular, the neutral model results more invulnerable or less invulnerable depending on whether the comparison is made at equal immigration rate or at equal distribution of population size, respectively. We discuss the relevance of these results for the interpretation of invasibility experiments and the species occupancy of preferred habitats.

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1. Introduction

A central problem in community ecology is to understand the ecological forces leading to the observed patterns of coexistence or exclusion of competing species (Ricklefs and Schluter, 1993; Brown et al., 1995). This issue is important for understanding both simple communities made up of few species (Chesson, 2000) and “biodiversity hotspots” with a large number of coexisting species (Leigh et al., 2004). Historically, this problem has been approached at two distinct levels. On the one hand, focus has been put on the detailed mechanisms of interaction between species (e.g., intra- and inter-specific competitions) caused by their differentiation in exploiting resources, resulting in the concept of the ecological niche (Chase and Leibold, 2003). For example, it has been shown how habitat heterogeneity (Beckage and Clark, 2003) or a tradeoff in dispersal range strategies (Bolker and Pacala, 1999) may promote coexistence. An alternative explanation for the observed species richness and distribution is in terms of processes intrinsically due to chance, such as colonization, immigration and extinction (MacArthur and Wilson, 1967), disregarding differences among species.

In recent years, the neutral theory of biodiversity (Hubbell, 1979, 2001; Bell, 2001) considerably developed the latter

approach by explicitly assuming equivalence among species at the individual level. The interest in the neutral theory has been triggered by its ability to successfully predict several biodiversity patterns observed in tropical forests, such as species-abundance distributions in different permanent sampling plots (Bell, 2001; Hubbell, 2001; Volkov et al., 2003) and species-area relations (Durrett and Levin, 1996; Bell, 2001; Hubbell, 2001). Its success underlined the importance of stochasticity (ecological drift) and dispersal limitation in the assemblage of natural communities (Chave, 2004; Alonso et al., 2006), which are now recognized as key ingredient also in niche-based models (Tilman, 2004). However, niche-based models yield predictions for the biodiversity patterns which perform similarly to neutral ones when compared with data (Chave et al., 2002; McGill, 2003; Mouquet and Loreau, 2003; Gilbert and Lechowicz, 2004; Tilman, 2004). This suggests that these patterns tend to average out the dependence on the details of the theory (see also the discussion in Pueyo et al., 2007) and thus cannot be used to discriminate the relative importance of niche-based and neutral forces. In this perspective, the study of dynamical properties such as invasibility can be a promising way to disentangle these effects (Daleo et al., 2009).

To understand the key differences between neutral and non-neutral competition, it is useful to consider models that can be continuously tuned from niche-based to neutral settings by varying some parameters (Chave et al., 2002; Gravel et al., 2006; Adler et al., 2007). An obvious difficulty with this program

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comes from the unavoidable complexity of realistic niche-based models (Chase, 2005), where species are not equivalent and the environment is heterogeneous both in space and time. This suggests an approach whereby simplified models with few parameters are studied, for example by making some specific assumptions on how neutrality is violated.

In this paper we study the dynamics of two species A and B that compete for space. The model is devised in such a way that a single parameter controls the overlap between the niches occupied by the two species, from complete—neutral—to no overlap—two independent niches. The model is individual-based and incorporates the basic ingredients of neutral theory: coexistence results from immigration from a metacommunity, balancing demographic stochasticity, which alone would lead to extinction. Niches are introduced in this neutral scenario via preferential habitats: half of the sites in the ecosystem are favorable for the colonization of individuals of one species and the other half are favorable for the other species. The ecological advantage is realized through a biased “lottery” (Chesson and Warner, 1981). We consider a symmetric situation by choosing the same statistical bias, γ , for individuals of species A and B to colonize their respective preferred habitats. When $\gamma=0$ (no habitat diversification) the model reduces to the voter model (Holley and Liggett, 1975; Cox and Griffeath, 1986), which is a prototype of neutral dynamics. Increasing γ , species acquire an advantage in colonizing some sites and a disadvantage in others. A very large γ eventually leads to segregation of the two species to their preferential habitats. Segregation will be complete when the choice of dispersal allows individuals to reach all their preference sites or incomplete in the presence of dispersal limitation.

The aim of this work is to use this simple model to understand the effect of habitat diversification on coexistence and dynamics of ecological communities. In particular, our concern will be on contrasting the effect of habitat diversification with the neutral model where no preferred habitat exists.

2. Model

We consider an individual based, spatially explicit model of a community made of two competing species A and B with population N_A and N_B , respectively. The community lives in a patch made of $N=L^2$ sites on a square lattice of side L , on which we assume periodic boundary conditions. Each lattice site is occupied by a single individual of one of the two species. For the sake of simplicity, we assume that the patch is saturated, i.e. with no empty sites—each dead individual is immediately replaced, so that the total number of individual is constant, $N_A+N_B=N$. The latter hypothesis is commonly assumed for its convenience (Hubbell, 2001; Chave et al., 2002) and, strictly speaking, corresponds to considering infinite fecundity. However, a finite but reasonably high fecundity would lead to almost-saturated ecosystems with qualitatively similar dynamics (Durrett and Levin, 1996; Chave et al., 2002).

Our main interest here is to study the effect of habitat preference on competition. To this aim, we assign to each site a specificity: half of the sites are favorable (as below specified) to individuals of species A and the other half to individuals of species B . We denote such sites by a and b , respectively. The site specificity can have several different (often concomitant) ecological origins such as abundance of resources, predation pressure (see, e.g., the review by Amarasekare, 2003), and/or environmental conditions such as elevation, temperature, soil moisture or other parameters as in Zillio and Condit (2007) and as suggested by observations (Beckage and Clark, 2003). The net effect of these different mechanisms is here assumed to increase by a factor γ the

chance of individuals to colonize a preferred site. This is illustrated in the top panel of Fig. 1, to be compared with the bottom cartoon which shows the neutral model, without site specificity. Similar models have been proposed also in the context of heterogeneous catalysis (Frachebourg et al., 1995) and social dynamics (Masuda et al., 2010).

For the sake of simplicity, site specificity is randomly assigned at the beginning and left unchanged during the dynamics. Of course, in natural ecosystems, spatial arrangement of sites with a certain specificity will usually be characterized by a certain degree of correlations, which will in general tend to enhance niche effects. In this respect, we expect that our choice will tend to underestimate the effect of habitat preference. Clearly, the model can be generalized by introducing asymmetries, i.e. different γ 's for the two species or different fractions of advantageous sites. Here we shall limit our analysis to the simple symmetric case, so that no species has a net advantage and the degree of habitat preference is controlled by a unique parameter.

We also assume a continuous immigration in the patch of individuals A or B at rate v . This inflow is necessary to avoid the drift to extinction of one of the two species.

For any given size L of the patch, which fixes the number of individuals $N=L^2$, the model is controlled by two parameters only: the colonization advantage γ and the immigration rate v . The elementary step of the dynamics is as follows:

- (i) a site is randomly chosen and the individual there residing is killed;
- (ii) with probability $(1-v)$, the individual is replaced by a copy of one of the four neighbors, chosen via a lottery which gives a competitive advantage (modeled as a weight γ) to individuals having that site as preferred habitat (see the sketch in Fig. 1 and Eqs. (1) and (2) below);
- (iii) with probability v , the individual is replaced by an immigrant. For simplicity, we assume the two species being equipopulated at the metacommunity level, so that the probability of being replaced by an individual of one of the two species is $1/2$, apart from the competitive advantage on the specific empty site.

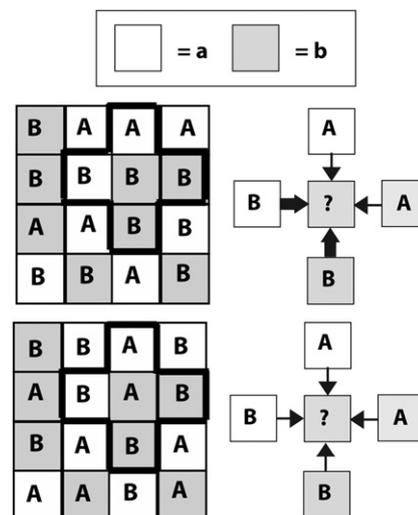


Fig. 1. Sketch illustrating the model with (top) and without (bottom) habitat preference. Two representative configurations of 4×4 systems are shown, white squares are advantageous to A , gray ones to B , and on the right we sketch the lottery dynamics (Eqs. (1) and (2)): the width of arrows represents the habitat preference intensity γ . Notice that in the bottom panel the width of arrows is insensitive to the site specificity.

In formulas, steps (ii) and (iii) can be expressed as follows. If the individuals is killed in a site of type a advantageous for individuals of species A , the probabilities of being replaced by an individual A or B are given by

$$W_A^a(n_A, n_B) = (1-v) \frac{(1+\gamma)n_A}{(1+\gamma)n_A + n_B} + v \frac{1+\gamma}{2+\gamma},$$

$$W_B^a(n_A, n_B) = (1-v) \frac{n_B}{(1+\gamma)n_A + n_B} + v \frac{1}{2+\gamma}, \tag{1}$$

respectively, where n_A and n_B denote the number of individuals of species A and B in the neighborhood of the considered site. Similarly, if the individual is killed in a site of type b , we have

$$W_A^b(n_A, n_B) = (1-v) \frac{n_A}{n_A + (1+\gamma)n_B} + v \frac{1}{2+\gamma},$$

$$W_B^b(n_A, n_B) = (1-v) \frac{(1+\gamma)n_B}{n_A + (1+\gamma)n_B} + v \frac{1+\gamma}{2+\gamma}.$$

The competitive lottery (1) and (2) used in step (ii) represents a biased (non-neutral) generalization of that used in neutral models (Hubbell, 2001). Indeed, for $\gamma=0$, the neutral dynamics of the voter model with only two species is recovered (Holley and Liggett, 1975).

Notice that the model is set up in such a way that the fitness advantage to be on colonization: after having colonized a site, mortality and dispersal do not depend on being on a preference site. In other terms, the fitness advantage belongs to the seeds and not to the individuals themselves. In this interpretation, and at variance with Chesson and Warner (1981), we excluded from the contribution to the (implicit) seed pool of the individual who died. Although the latter may be more realistic in modeling, e.g., perennial plants (Lin et al., 2009), we preferred the first to directly compare the neutral version of the model ($\gamma=0$) originally proposed by Hubbell (1979) with the non-neutral ($\gamma > 0$) variants. We do not expect big differences in the outcome of the two models, a part from a weak discrepancy in the percentage of occupancy of preferential habitats. We also note that this difference becomes less relevant when longer dispersal is introduced. Indeed, the model can be generalized to different form of dispersal mechanisms, e.g., with a given finite range. Previous investigations on similar models (Rosindell and Cornell, 2007; Zillio and Condit, 2007; Pigolotti and Cencini, 2009) have shown that different dispersal mechanisms yield qualitatively similar results, as far as they are finite-ranged and all species adopt the same dispersal strategy. Here, we consider the two limiting situations of nearest-neighbor and global dispersal.

In the global dispersal case, all individuals present in the patch can colonize the site left empty by the dead one. This limiting case strongly simplifies the simulations of the model since it makes the distance and spatial distribution of the sites irrelevant. The global dispersal model may be thought as a two islands model (Wright, 1931), where each of the two islands has room for $N/2$ individuals and contains all the sites favorable to one of the two species. The state of the system is then unequivocally identified by the numbers N_{Aa} and N_{Bb} of individuals of the two species occupying the respective sites of preference. All the other variables can be expressed in terms of N_{Aa} and N_{Bb} , for instance: the number of individuals of species A (resp. B) outside their preference sites is $N_{Ab} = N/2 - N_{Bb}$ (resp. $N_{Ba} = N/2 - N_{Aa}$) and the total number of individuals of species A (resp. B) is $N_A = N/2 + N_{Aa} - N_{Bb}$ (resp. $N_B = N/2 + N_{Bb} - N_{Aa}$). The evolution of the system is thus determined by the probabilities per elementary step that N_{Aa} and N_{Bb}

increase or decrease by one unity:

$$\mathcal{W}_{N_{Aa} \rightarrow N_{Aa}+1} = \left(\frac{1}{2} - \frac{N_{Aa}}{N} \right) W_A^a(N_A, N_B),$$

$$\mathcal{W}_{N_{Bb} \rightarrow N_{Bb}+1} = \left(\frac{1}{2} - \frac{N_{Bb}}{N} \right) W_B^b(N_A, N_B),$$

$$\mathcal{W}_{N_{Aa} \rightarrow N_{Aa}-1} = \frac{N_{Aa}}{N} W_B^a(N_A, N_B),$$

$$\mathcal{W}_{N_{Bb} \rightarrow N_{Bb}-1} = \frac{N_{Bb}}{N} W_A^b(N_A, N_B), \tag{2}$$

where W_Y^X is given by Eqs. (1) and (2) with n_A and n_B replaced by N_A and N_B , respectively.

For $\gamma=0$, the model is neutral and reduces to the ordinary voter model with only two species and immigration (the multi-species version was considered in Durrett and Levin, 1996) in the spatially explicit case, or to the Moran (1958) model with mutation in the global dispersal version. Conversely, when γ becomes very large, the competitive advantage gets so intense that individuals tend to localize in their preferred habitats, with an extremely low chance of colonizing the rest of the ecosystem, so that the two species do not compete anymore.

3. Results

3.1. Extinction times and fixation probabilities

In the absence of immigration ($v=0$) and for any choice of N , γ and dispersal range, persistent coexistence is not possible, since species cannot recover from a local extinction event. Ecological drift will ultimately drive one of the two species to extinction, and the dominance of the other will become stable—reaching fixation as from population genetics terminology, see, e.g., Gillespie (1994). Studying the properties of the dynamics toward extinction is, however, interesting and informative (Chesson and Warner, 1981; Chesson, 1982). In particular, the time needed for the extinction of one of the species is important to understand how crucially biodiversity depends on a steady immigration flux. Moreover, the way the extinction time and the probability of fixation of one of the two species depend on the deviation from neutrality allow to quantify to what extent habitat preference promotes coexistence.

We start describing a set of simulations in which the two species are equipopulated at the initial time, i.e. $N_A = N_B = N/2$, and individuals are randomly placed in the system. The dynamics is then followed until the extinction of one of the species. By averaging over many realizations of the dynamics (from 5×10^3 to 10^4), we can access the extinction time. Here we focus on the average time, T , though also the fluctuations have an ecological relevance (Pigolotti et al., 2005). The average extinction time T as a function of the community size N and for several values of γ is shown in Fig. 2 as obtained with the global dispersal model. As customary in models with overlapping generations, we measure T in generations, where the time unit corresponds to N successive time steps (i)–(iii) described in the model section. For $\gamma=0$, we recover the result expected for the Moran (1958) model, i.e. $T \propto N$. While the presence of habitat preference $\gamma > 0$ leads to a dramatic increase of the average extinction time: for large enough populations, T becomes exponentially large in the community size N , i.e.

$$T \sim C \exp(C(\gamma)N),$$

where C depends on γ (as shown in the inset of Fig. 2a). The exponential dependence implies that the coexistence may be

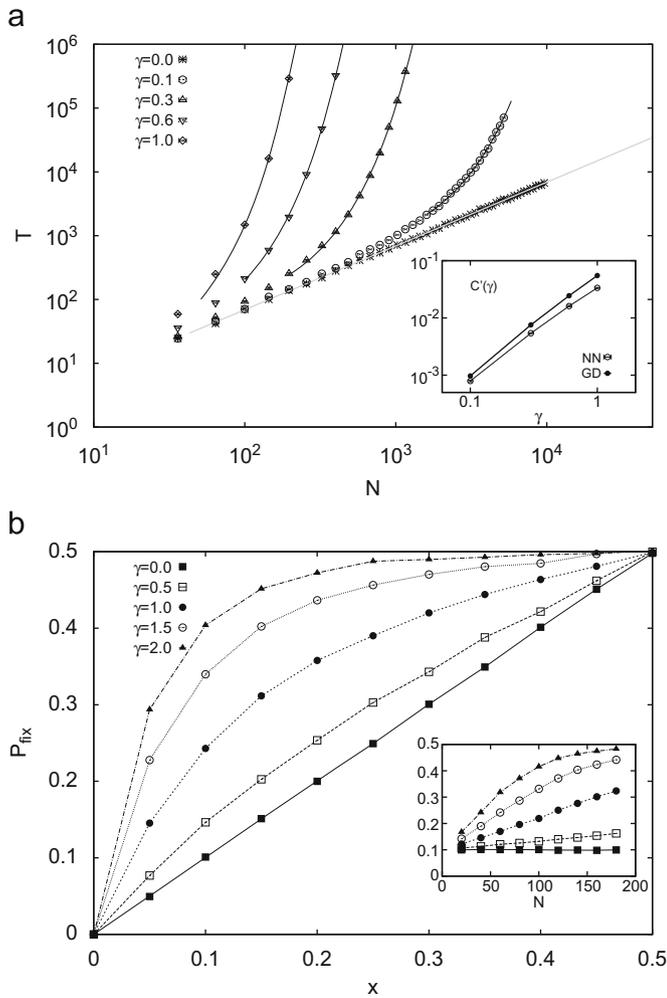


Fig. 2. Results for the model with global dispersal without immigration ($v=0$): (a) mean extinction times T as a function of N for different γ , as in label. The black lines indicate exponential fits of the form $T = C \exp(C(\gamma)N)$ while the gray straight line indicates the neutral expectation $T \propto N$. The inset shows $C(\gamma)$ vs γ for both the global dispersal (GD) and nearest neighbor (NN) models. (b) Probability of fixation P_{fix} of A vs the initial fraction $x = N_A/N$ for $N=40$. Inset: P_{fix} vs N holding fixed $x = N_A/N = 0.1$.

considered stable for large N (Chesson, 1982). The spatially explicit version of the model (not shown here) presents the same qualitative features with small quantitative changes: in the neutral case $\gamma=0$, logarithmic corrections are present $T \propto N \log(N)$ (Krapivsky, 1992) and the exponential rates for $\gamma > 0$ are slightly different from those obtained with global dispersal (inset of Fig. 2a). In large communities, even a tiny habitat preference leads to a dramatic increase in the average extinction time, stabilizing the system on any realistic timescale.

To further confirm the stabilizing effect of habitat preference, we consider a different setting in which species A is present at initial time with a fraction of individuals $x = N_A/N$. By averaging over 10^5 realizations for each x , we computed the probability that species A becomes fixated, $P_{fix}(x)$ (Fig. 2b). In the neutral case, $P_{fix}(x) = x$ (Gillespie, 1994), while $P_{fix}(x)$ is closer to $\frac{1}{2}$ when γ is increased, the effect being stronger the larger is the community size (see inset). Therefore, strong habitat preference tends to compensate any initial disproportion between two large populations, making equally likely the fixation of one of the two species. In particular, if A is the invading species, i.e. the less represented at the beginning ($x \ll \frac{1}{2}$), its chances of invading the systems greatly increase in the presence of habitat preference, in

agreement with other models and observations (Melbourne et al., 2007).

3.2. Regimes of coexistence

The presence of an immigration pressure allows species to recover from local extinction events, ensuring dynamical coexistence, as illustrated in the left panels of Fig. 3, where the evolution of the population N_A is shown over 10^3 generations at varying the rate of immigration v . The figures refer to the global dispersal model with a habitat-preference intensity $\gamma=0.3$. We mention that qualitatively similar features are observed also in the nearest-neighbor dispersal case and also when the model is neutral.

As expected from classical theories (MacArthur and Wilson, 1967), increasing the immigration pressure enhances the degree of coexistence of the two species. At fixed N , if v is small, one of the two species dominates for most of the time. Stochastic fluctuations, whose amplitude decreases at increasing N , lead to an alternation in the dominating species (top panel of Fig. 3). The turnover in the dominating species takes place on timescales rapidly growing with N (roughly of the order of the average extinction time). At intermediate values of v , coexistence is possible, but episodic local extinctions can rule out a species from the system for several generations (middle panel). Finally, increasing v even further, local extinctions cannot persist and coexistence becomes the rule: it is more and more likely to observe states in which the two species are roughly equipopulated (bottom panel). We quantify these three behaviors in terms of the functional shape of the probability $P(N_A)$, averaged over time, of one of the two species to occupy a given fraction of the ecosystem (see, e.g., Loreau and Mouquet, 1999). We recall that there is a complete symmetry between A and B so that $P(N_A) = P(N - N_A) = P(N_B)$. In particular, with reference to the right panels of Fig. 3, from top to bottom we can distinguish the following classes of distributions corresponding to different regimes of coexistence, as determined by the number of maxima of $P(N_A)$:

Monodominance: $P(N_A)$ is U-shaped, achieving its two maxima at $N_A=0$ and $N_A=N$;

Mixed: $P(N_A)$ has three maxima at $N_A=0$ and $N_A=N$ as before plus $N_A=N/2$, meaning alternation between states of monodominance and pure coexistence as defined below;

Pure coexistence: $P(N_A)$ is bell-shaped and has a single maximum at $N_A=N/2$, so that most of the time the populations fluctuate around the equipopulated state.

We quantify the stabilizing effect of habitat preference by studying for which values of the parameters γ , v , and N , the above defined regimes are observed. Fig. 4 shows, for different values of γ , how the monodominance (white), coexistence (gray) and mixed (patterned) regimes organize in the $N-v$ plane for both global (left) and nearest-neighbor (right) dispersal.

As observed for the extinction times, nearest-neighbor and global dispersal models display qualitatively similar features. The only difference is that in the neutral case $\gamma=0$ the global dispersal model never shows a mixed distribution; conversely, with nearest-neighbor dispersal, a tiny region of mixed phase exists also for $\gamma=0$, compare Fig. 4a and d. For $\gamma=0$ and global dispersal, the transition between monodominance and coexistence can be analytically obtained and occurs for $v > v_c(N) = 2/(2+N)$ (see Appendix A).

The most surprising feature is that the critical immigration rate $v_c(N)$ for observing coexistence seems to be independent of γ and of the dispersal. Indeed, we could not determine appreciable

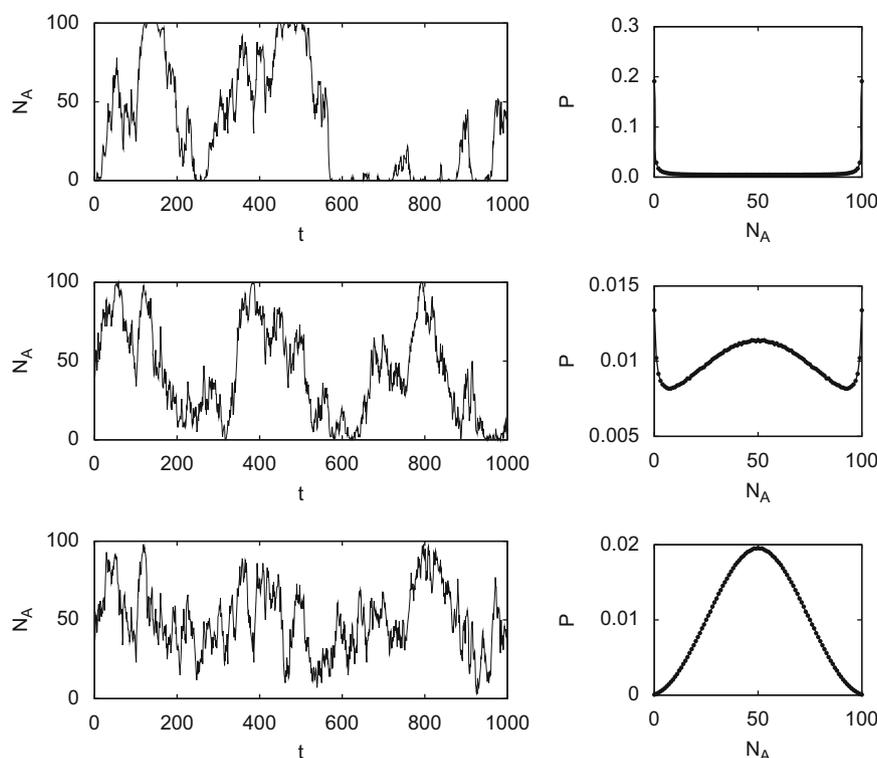


Fig. 3. Different regimes of coexistence in the presence of immigration in the global dispersal model with habitat preference: evolution of the population N_A across 10^3 generation for a system of $N=100$ individuals (left) and the corresponding distributions $P(N_A)$ (right). The three panels are obtained holding the habitat-preference intensity fixed $\gamma=0.3$ and varying the immigration rate v : (top) $v=0.003$ corresponding to monodominance; $v=0.015$ leading to a mixed phase; $v=0.05$ displaying coexistence (see text for details).

quantitative differences between the two extrema of global and nearest-neighbor dispersal. In all cases, the transition to coexistence occurs for values of the immigration rate well described by the neutral prediction, $v_c(N) \approx 2/(2+N)$. Unfortunately, we could not systematically explore larger values of γ or N as it requires huge statistics for distinguishing between the mixed and coexistence regimes. In fact at increasing γ and/or N the distribution becomes strongly peaked on $N/2$ with very low probabilities on the tails, so that the region where the differences between mixed and pure coexistence manifest is inaccessible (see Fig. 5).

Summarizing, the main effect of increasing γ (from top to bottom in Fig. 4) is to stabilize the coexistence by increasing the portion of the $N-v$ plane where the mixed regime is realized. An equivalent analysis could in principle be performed by plotting the transition lines in the $N-\gamma$ and/or in the $v-\gamma$ plane. However, the difficulty in sampling the tails of the distribution strongly limits the range of values of γ and N which can be explored, so that these plots would not add much information to Fig. 4.

3.3. Neutral vs non-neutral: coexistence and invisibility

We now directly compare neutral and non-neutral dynamics by exploring whether the former ($\gamma=0$) can reproduce/mimic the latter, e.g., in terms of generating similar patterns of coexistence such as the distribution $P(N_A)$. As both γ and v promote coexistence, it is natural to expect that the lack of habitat preference in the neutral model could be compensated by a larger immigration rate v to reproduce similar distributions. However, as we will see, the different stabilizing effects of immigration and habitat preference have interesting dynamical consequences.

In particular, we consider two attempts to reproduce non-neutral distributions with neutral ones for two different community sizes

$N=100$ (Fig. 5a) and $N=400$ (Fig. 5b). In both cases, we proceed as follows. We fixed the habitat preference intensity, $\gamma=1$ in this specific example. Then we simulated the neutral version of the model ($\gamma=0$) and varied v until the distribution looked as similar as possible to that obtained with habitat preference. In other words, we searched for the value of the immigration rate v that compensated best the absence of habitat preference. As expected, this compensation is obtained by using a larger value of v .

For $N=100$, the agreement between the curves is very good in the central peak, meaning that the differences between the two models can be appreciated only when one of the two species is dominating. For $N=400$ the distributions are almost indistinguishable. The fact that the non-neutral system of Fig. 5a is in the mixed phase is clear by looking at the distribution tails; however, this feature could be difficult to detect in an experimental time series. In Fig. 5b, the tails have such a low probability that are essentially inaccessible even in long simulations, so that we cannot distinguish between mixed and coexistence phases.

For large N , both in the coexistence and mixed phases, the distributions around the central mode are well fitted by a Gaussian. In the neutral model, the limiting Gaussian distribution can be analytically derived (see Appendix B), showing that the variance in this case is proportional to N . Numerical simulations (not shown) suggest that variance in the non-neutral version of the model scales in the same way with N , with a prefactor rapidly decreasing at increasing γ reflecting the presence of niches.

Even if the difference between the models is essentially undetectable when looking at the distributions, it can play an important role when studying invisibility properties, i.e. by considering a situation in which one of the species is absent at the initial time (which means to directly test the tails of the distribution). As an example, for the same parameters of Fig. 5 we prepared the initial state with only species B present and we computed the average time it takes to reach perfect coexistence

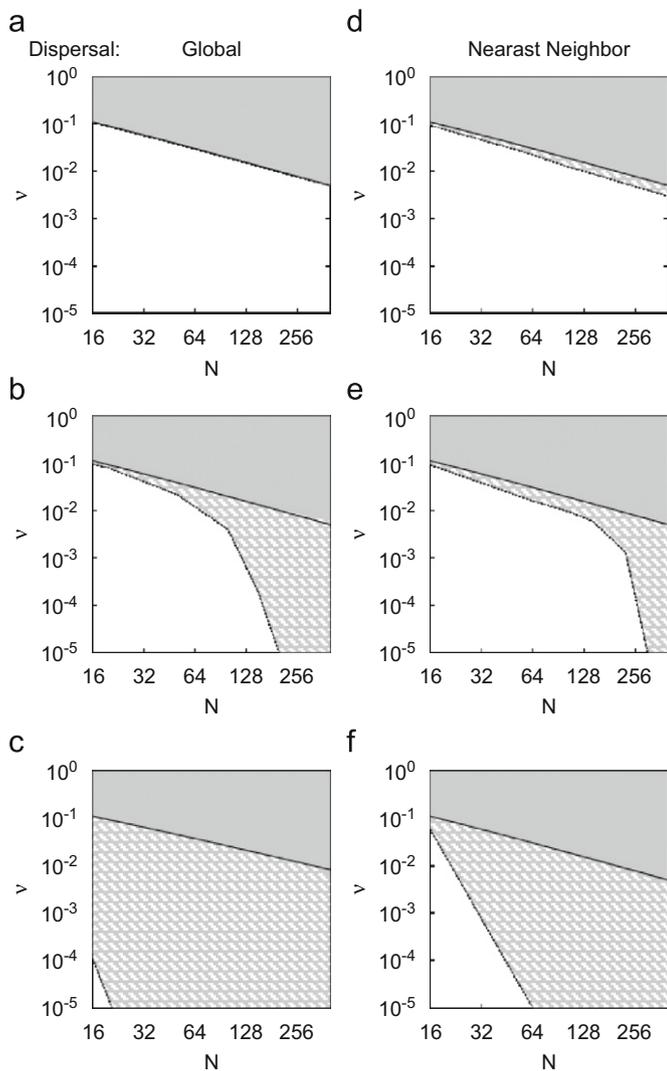


Fig. 4. Phases in the N - v parameter space. White regions denote monodominance, gray-filled regions pure coexistence, and dashed regions mixed phases. On the left (panels a–c) data obtained with the global dispersal model, while on the right (panels d–f) with the nearest-neighbor model. The three rows correspond to different values of $\gamma = 0, 0.3, 1.0$ (from top to bottom). Axes are in log scale. Notice that for $\gamma = 1$ and global dispersal (panel c) we could not show the curves for $N > 240$ due to lack of statistics.

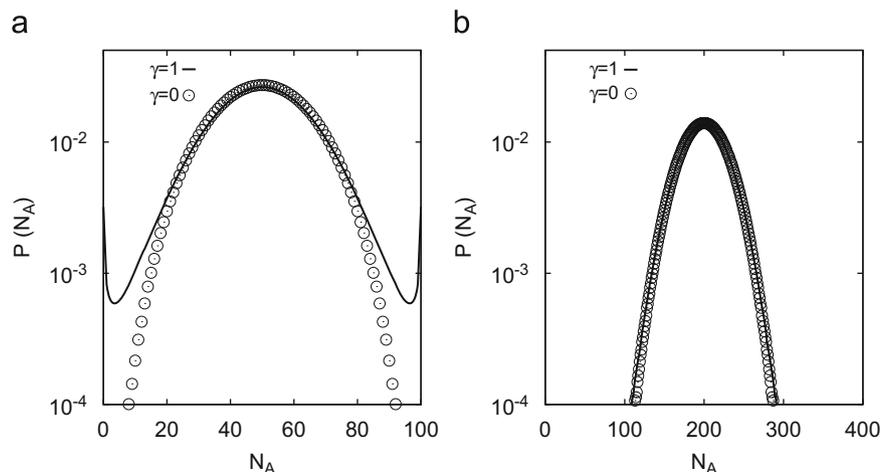


Fig. 5. Non-neutral vs neutral distribution of population $P(N_A)$: (a) for $N=100$ with $\gamma = 1$, $v = 0.005$ (solid) and $\gamma = 0$, $v = 0.12$ (symbols); (b) for $N=400$ with $\gamma = 1$, $v = 0.001$ (solid) and $\gamma = 0$, $v = 0.123$ (symbols). In both cases, the y -axis is in logarithmic scale.

($N_A=N_B=N/2$) for the first time. When $N=100$ (a), this time is roughly equal to 46 generation for the model with habitat preference and 17 generation for the neutral one, while for $N=400$ (b) the difference is even more pronounced (61 vs 21 generations, respectively).

3.4. Habitat preference statistics

We now investigate the role of preference sites in achieving coexistence and determining the spatial distribution of species. The natural quantity to look at is the average fraction of individuals of both species occupying their preference sites, $P_{occ} = (N_{Aa} + N_{Bb})/N$. This quantity is a suitable measure of the non-neutrality of the system: it is equal to $1/2$ in the neutral case, as individuals have no reason to prefer one of the two site types. The average occupation increases with γ eventually reaching 1 when the distribution of sites strongly determines the spatial distribution of the two species.

The average occupation P_{occ} as a function of γ is shown in Fig. 6. For illustrative purposes, here, we fixed $N=100$ and varied v . As one can see the curves are weakly dependent on the choice of v , especially when γ is large. The dependence on N is not shown but it is also rather weak. We remark that in the nearest neighbor case it is crucial to average over different realizations of the dynamics and of the distribution of advantageous sites: different spatial arrangements of the sites may be harder (or easier) to occupy for one of the species.

When the two species are exactly equipopulated and with global dispersal, one can easily derive from (2) that the average occupation must be equal to $(1+\gamma)/(2+\gamma)$. This prediction is shown for comparison in Fig. 6a. Significant deviations are present for small γ and v values, for which pure coexistence is not achieved and species are not equipopulated, i.e. the system is in the monodominance or mixed phase. However, it must be noticed that with nearest-neighbor dispersal (Fig. 6b) even for large γ the prediction $(1+\gamma)/(2+\gamma)$ is never realized due to dispersal limitation, which can prevent species from colonizing advantageous sites. In this case the average occupation does not reach 1 even for very large γ . The presence of patchiness in the distribution of preference sites is expected to enhance this effect: one could encounter situations in which a whole patch is unreachable because it is surrounded by patches being advantageous to the other species. On the other hand, a longer dispersal range could compensate for the presence of patches. In other

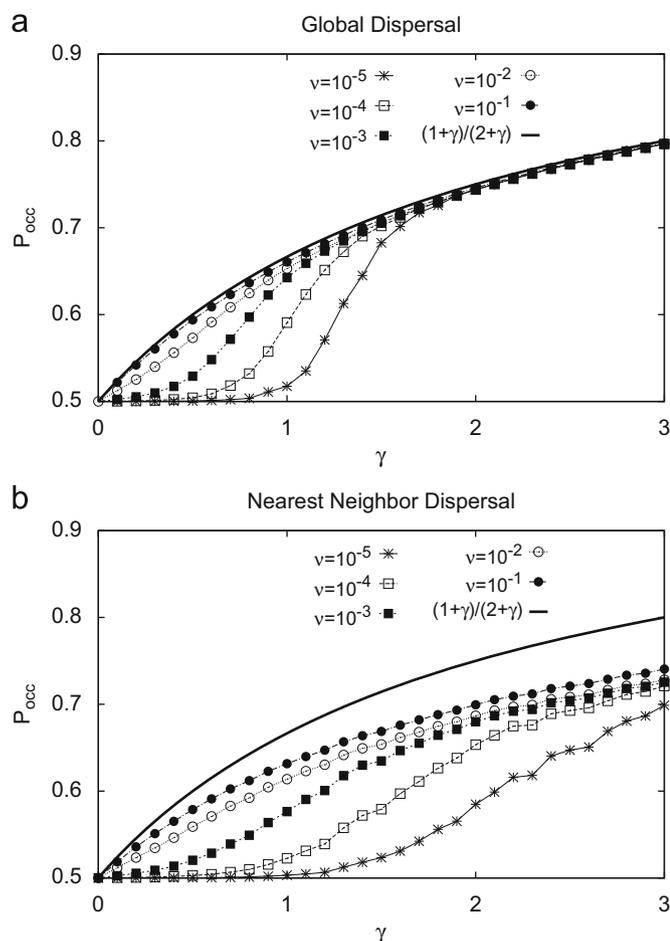


Fig. 6. Average preference occupation P_{occ} as a function of γ for $N=100$ and several values of v as in labels. (a) Results obtained with global dispersal, (b) nearest-neighbor dispersal. Data have been averages over 10^6 generations. Data obtained with nearest-neighbor dispersal are also averaged over 200 independent realization of the initial distribution of preference sites. The continuous curve represents the simple prediction $P_{occ} = (1 + \gamma)/(2 + \gamma)$ (see text).

words, the possibility for the occupation to reach one for large γ will depend on the ability of species to reach all the favorable patches, which is known to be a crucial feature in fragmented landscapes (Keitt et al., 1997).

We conclude this section by discussing whether the results of Fig. 6 are determined by the particular choice of the ecological advantage. To check the robustness of our results, we simulated the variant of the model in which the advantage gives rise to a lower mortality in the preference sites, instead of a larger colonization probability, obtaining very similar curves to those of Fig. 6.

4. Discussion

We have introduced an individual-based model of competition between two species in the presence of habitat preference. As is typical in stochastic models of community assembly, the system drifts towards the extinction of one of the two species when immigration from the metacommunity is not taken into account (MacArthur and Wilson, 1967; Loreau and Mouquet, 1999). Nevertheless, even without immigration, habitat preference has a strong stabilizing effect on the coexistence in large communities, leading to a dramatic increase of the average time for the extinction of a species, consistently with studies of niche models (Tilman, 2004; Adler et al., 2007; Lin et al., 2009). In particular, Lin et al. (2009), extending previous results (Zhang and Lin, 1997; Yu

et al., 1998; Wright, 2002), introduced a model where both mortality and fecundity were varied among the species in such a way that the averaged life-history fitness of several species is the same, so to fulfill the weaker requirement of the equivalence of average fitness of the neutral theory (Hubbell, 2006). The presence of birth/fecundity tradeoffs (globally equalizing the performances of different species) has a stabilizing effect, without affecting the ability of predicting biodiversity patterns.

The main message of the present study is that neutral and non-neutral coexistence may yield almost identical patterns such as the population distribution (see, e.g., Fig. 5b) while dynamic properties may be significantly different, as revealed by invasibility experiments (Daleo et al., 2009). In this perspective, the advantage of the proposed model is to allow for quantitatively comparing niche and neutral competition in a simple setting and thus for providing an insight on the origin of such differences. It is thus worth discussing the predictions of the model for invasibility experiments.

The simplest setting is that of an isolated ecosystem (i.e. without migratory flux), in which a new species with a small population is introduced. This corresponds to Fig. 2b, where the probability of the invading species to take over grows with γ . The ecological interpretation is that niche-based assemblies are easier to invade than neutral ones if the niches are not saturated, simply because the availability of a free niche facilitates the invasion (see Melbourne et al., 2007, for a recent review on the role of heterogeneity on invasibility properties).

Another possibility is to consider the invasion of an ecosystem initially populated by a dominant species in the presence of a regular flux of immigrants species from the metacommunity. In this case, if we compare neutral and non-neutral dynamics at equal immigration rate there is hardly any difference with respect to what is observed in the absence of immigration.

Conversely, the response may be quite different if the comparison is made at equal realized distributions (see Fig. 5). The neutral model realizes patterns of coexistence similar to non-neutral ones by compensating with a larger immigration pressure. Under these circumstances, if some catastrophic event leads to the extinction of one of the species, the non-neutral dynamics takes longer than the neutral one to recover the equipopulated state. Therefore, non-neutral coexistence is more robust, but it is also harder to achieve. The presence of two habitats makes both the two species coexist and one species hard to invade; in other words, niche-based coexistence is history-dependent. An important practical consequence is that inferring immigration rates from the fit of the distributions with neutral models could result in overestimates, even in situations in which the quality of the fit is very good.

The above result agrees with the observation that large scale, species-rich patches are easier to invade (Robinson et al., 1995; Stohlgren et al., 2003), contrarily to the prediction of theories of competitive exclusion via niche partitioning and data from small scale observations (Tilman, 1997). These contrasting evidences constitute the so-called “invasion paradox” (Fridley et al., 2007). Neutral theory predicts that the chances of establishment of an alien species depend on the frequency of introduction of new individuals only (Daleo et al., 2009). On the other hand, in a non-neutral community this chance is strongly influenced by habitat diversity and availability of free niches. Our results suggest that, when comparing the invasibility properties of ecosystems, it is crucial to establish in which measure the diversity is maintained by the intensity of the immigration flux and/or by niche availability. The two-species framework considered here the stationary solutions have not the same complexity as those of multi-species models. However, previous studies (Chave et al., 2002; McGill, 2003; Tilman, 2004) also pointed out that species abundance distributions of neutral and niche-based multi-species models are

very similar, provided suitable parameters are tuned and suggesting that at least the qualitative features of invasibility dynamics here identified should hold also in the multi-species case. We recall that in multi-species models speciation, as well as immigration, contributes to the introduction of new species, especially when large systems are considered. Therefore, the problem of inferring these rates from observed patterns becomes even more dramatic, since it is hard to compare these estimate with reliable measures of speciation rates. This could explain the high speciation rates predicted by neutral theory (see Ricklefs, 2003, and also Hubbell, 2003; Haegeman and Etienne, 2009).

Finally, the occupation probability provides a measure of the departure from the static equilibrium case in which each species is confined to its preference sites. It is known that models correlating species distributions with environmental and climatic features cannot fully determine the observed geographical range of species (Svenning and Skov, 2004). In fact, a complete predictive power of species-distribution models would require the existence of a static equilibrium state (Guisan and Thuiller, 2005), an assumption that is directly challenged by the neutral theory and partially violated by niche-neutral models like the one presented in this paper. The departure from the equilibrium case is enhanced by dispersal limitation, as shown by the comparison between the nearest neighbor case and the global dispersal of Fig. 6. Indeed, this observable is the one showing the most significant dependence on the choice of the dispersal among those considered in this work. This difference will become more dramatic if one adopts the more realistic choice of a correlated environment, i.e. a distribution of preference sites being correlated in space. As it has been studied for the case of fragmented landscapes (Keitt et al., 1997), the comparison of dispersal ranges and characteristic size of patches determines whether species will be able to reach all their preference sites or will be arrested by dispersal limitation.

Summarizing, we studied the effect of habitat preference on the stochastic competition between two species. In the absence of immigration, demographic stochasticity eventually leads to the extinction of one of the two species. However, habitat preference leads to a dramatic increase of the extinction time. The drift to extinction is arrested by introducing an immigration rate. When the latter is large enough, the model generates a coexistence state in which both species occupy a significant fraction of the system. By compensating with a larger immigration rate the loss of specificity, the neutral case ($\gamma=0$) can generate distributions which are essentially indistinguishable from those obtained in the presence of habitat preference ($\gamma>0$). In spite of the pattern similarity, the dynamics of the two cases is very different. When only one species is present at the beginning of the simulation, the neutral variant of the model is much easier to invade than the non-neutral one. This latter result reproduces in a simplified framework what is observed in species-rich community models: neutral and non-neutral models reproduce similar patterns of species abundances, here of population distribution, but can be distinguished by looking at dynamical properties.

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Appendix A. Condition for coexistence in the neutral model with global dispersal

For $\gamma=0$, i.e. in the absence of habitat preference the model with global dispersal reduces to the Moran (1958) model with

mutation. In this case the transition rates can be expressed in terms of a single population N_A . In particular, Eq. (2) reduce to the birth and death rates of population N_A , i.e. $\mathcal{W}_{N_A \rightarrow N_A \pm 1} = W^\pm(N_A)$ which, incorporating the effect of immigration, read (Karlin and McGregor, 1962):

$$\begin{aligned} W^+(N_A) &= \frac{N-N_A}{N} \left[(1-v) \frac{N_A}{N} + \frac{v}{2} \right], \\ W^-(N_A) &= \frac{N_A}{N} \left[(1-v) \frac{N-N_A}{N} + \frac{v}{2} \right]. \end{aligned} \quad (\text{A.1})$$

These rates can be used to calculate the equilibrium distribution $P(N_A)$ through the detailed-balance relation

$$\frac{P(N_A+1)}{P(N_A)} = \frac{W^+(N_A)}{W^-(N_A+1)}, \quad (\text{A.2})$$

which must hold at stationarity since the process is one dimensional (Gardiner, 2004). The above expression can be used to determine the critical value of the immigration rate for the transition from monodominance to coexistence. It is enough to determine the value of v for which $P(N_A)$ passes from being a decreasing function of N_A (we are assuming $N_A < N/2$) to an increasing one. Coexistence is thus obtained when $P(N_A+1) > P(N_A)$, which using (A.1) and after some algebra can be recast as

$$[(2+N)v-2](N-2N_A-1) > 0. \quad (\text{A.3})$$

Therefore, whenever $v > 2/(2+N)$ the distribution is increasing up to $N_A=(N-1)/2$ then decreasing, i.e. there is coexistence. When $v < 2/(2+N)$ the opposite happens and there is monodominance. We conclude noticing that for $v = 2/(2+N)$, i.e. at the transition between the two classes of distributions, the distribution becomes uniform, i.e. $P(N_A)=1/N$. This is true only for the neutral model with global dispersal.

Appendix B. Gaussian limit of the neutral model

In this appendix we show that the stationary solution approaches a Gaussian in the large N limit, at least in the neutral, global dispersal case. We perform the calculation in the diffusion approximation; the procedure is similar to the classic results for the Moran model, see, e.g., Karlin and McGregor (1962), apart from small differences in how the immigration (mutation) mechanism is defined. From the rates (A.1) the diffusion approximation yields the Fokker–Planck equation:

$$\partial_t \rho(x,t) = -\partial_x(a(x)\rho(x,t)) + \frac{1}{2}\partial_x^2(b^2(x)\rho(x,t)), \quad (\text{B.1})$$

where $x=N_A/N$ and

$$a(x) = \frac{v(1-2x)}{2}, \quad b^2(x) = \frac{2x(1-x)(1-v)+v}{N}. \quad (\text{B.2})$$

The stationary distribution is easily found to be

$$\rho_s(x) \propto [2x(1-x)(1-v)+v]^{Nv/2(1-v)-1/2}. \quad (\text{B.3})$$

When N is large, an expansion around the maximum $x_0 = \frac{1}{2}$ leads to the Gaussian distribution:

$$\rho_{st}(x) \sim \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(x-x_0)^2}{2\sigma^2}\right] \quad (\text{B.4})$$

with $\sigma^2 = (1+v)/[4(N+1)v-4]$. This shows that the relative fluctuations around the maximum have the expected characteristic size $1/\sqrt{N}$.

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