When can we distinguish between neutral and non-neutral processes in community dynamics under ecological drift?

Abstract
Determining whether the composition of ecological communities (species presence and abundance), can be predicted from species demographic traits, rather than being a result of neutral drift, is a key ecological question. Here we compare the similarity of community composition, from different community assembly models run under identical environmental conditions, where interspecific competition is assumed to be either neutral or niche-based. In both cases, species colonize a focal patch from a network of neighbouring patches in a metacommunity. We highlight the circumstances (rate and spatial scale of dispersal, and the relative importance of ecological drift) where commonly used community similarity metrics or species rank–abundance relationships are likely to give similar results, regardless of the underlying processes (neutral or non-neutral) driving species’ dynamics. As drift becomes more important in driving species abundances, deterministic niche structure has a smaller influence. Our ability to discriminate between different underlying processes driving community organization depends on the relative importance of different drift processes that operate on different spatial scales.

Keywords
Bray & Curtis, community composition, dispersal, ecological similarity, metacommunity, neutral model, percent similarity.

INTRODUCTION
A long-standing, yet pertinent question in community ecology is whether natural communities obey general and predictable assembly processes (Diamond 1975; Law & Morton 1996), mediated through species sorting along environmental gradients (Chase & Leibold 2003). An alternative hypothesis is that communities are structured by neutral drift in species’ densities (Bell 2001; Hubbell 2001). Species composition (including species-specific abundances) is often sampled at a given time and compared between ‘replicate’ communities found under similar (or different) conditions using various measures of ecological similarity (e.g. Chase 2003; Tuomisto et al. 2003; Morris 2005). A pair of communities that have a high similarity score will have the same set of species present at similar densities at a given time, while those with a low similarity score can either have the same species present but at different densities, or a different set of species present. Niche-based assembly should lead to similar community patterns at a given time (from similar initial conditions), because species differ in their traits and established species are more likely to inhibit the invasion of other ecologically similar species (Diamond 1975; Samuels & Drake 1997; Fargione et al. 2003). Alternatively, neutral models are expected to generate random assembly patterns due to individual and species level equivalencies in competitive ability (Bell 2001; Hubbell 2001), leading to community composition driven by dispersal limitation and demographic stochasticity.

In short, niche theory emphasizes species-specific differences in explaining patterns in community organization and biodiversity, while neutral theory emphasizes stochastic drift. Both views have gained support from empirical studies (Drake 1991; Samuels & Drake 1997; Chase 2003; Clark & McLachlan 2003; Tuomisto et al. 2003; Volkov et al. 2007; Kraft et al. 2008). The rate and scale of dispersal are also potential factors affecting community similarity (Chase
of species in the metacommunity, and the influence of dispersal rate, dispersal distance, habitat size and the number (niche-based) communities. We consider different levels of different assembly conditions and whether there are different community patterns.

Because of the dominant role of drift (for simplicity, we denote all population changes caused by stochastic variation as ‘drift’, as opposed to deterministic changes), changes in the composition of communities governed by neutral dynamics resemble a random walk (Clark & McLachlan 2003; McGill et al. 2005). This can in turn lead to unpredictability in some community patterns, particularly those based on metrics that relate species identity and abundance (e.g. Volkov et al. 2007). However, a recent investigation by Dornelas et al. (2006) has shown that patterns in the similarity of community composition can be more predictable in neutral communities than previously appreciated. The observation that, e.g. species richness and immigration rate can substantially modify patterns in neutral community similarity (Dornelas et al. 2006) is likely to confound attempts to separate community patterns from underlying, deterministic community processes. Our aim is to investigate how patterns in community similarity are affected by ecological drift processes in both neutral and niche-structured communities. Specifically, we try to find conditions under which these contrasting community processes result in distinguishable patterns in community similarity.

The predictability of the composition of natural communities is an important issue touching many fields of applied ecology. In many instances it is desirable that similar (and familiar) assemblages arise after large disturbances, e.g. in population management and conservation. Compositional similarity between communities has been measured using various indices of species similarity across different natural systems (Sale & Douglas 1984; Dornelas et al. 2006; Chase 2007; Volkov et al. 2007). The precision of such measures is sensitive to, e.g. variation in habitat composition (when samples from replicated ‘homogeneous’ entities exist), species demography, and migration. Most of these factors are extremely difficult to control for with empirical data. Therefore, population models are valuable for evaluating the credibility of different proposed hypotheses to generate different community patterns.

Here we ask how community similarity is affected by different assembly conditions and whether there are differences in similarity between neutral and non-neutral (niche-based) communities. We consider different levels of dispersal rate, dispersal distance, habitat size and the number of species in the metacommunity, and the influence of environmental stochasticity. We use a model where species, which differ in their abilities to utilize a focal habitat, migrate between a focal site and a surrounding landscape in a metacommunity. The metacommunity consists of $N$ patches and each species migrates between these patches (within a neighbourhood of $m$ patches). This model is used to generate replicated communities, assembled through dispersal into competitive systems with local renewal and extinction processes. We measure similarity by comparing replicate communities (assembled in identical environments) by a commonly applied index (the Steinhaus coefficient) scoring the similarity in species abundances. The results are contrasted with those generated by a neutral model where species are equivalent in their demographic traits. Thus, the main question here is whether between-species differences in demographic traits affect community similarity, and if so, under which conditions this occurs?

We find that the composition of communities at a given time ranges from being very similar to very different, depending on the strength and relative importance of the following interacting stochastic (drift) processes, at the level of local communities and the entire metacommunity: The scale and rate of dispersal, and local extinctions drive drift in the presence of different species in local communities. Competition and demographic uncertainty (affected by local carrying capacities) influence drift in local population densities, which is important for local species persistence. These aspects influence local dispersal regimes, while landscape (metacommunity) size influences drift in the global species pool (larger landscapes are more ‘stable’). Less drift promotes visibility of deterministic processes while more drift leads to a dominant signature of neutral dynamics, even with species differences. The results presented here indicate that our understanding of factors driving local and global patterns in biodiversity will be enhanced with an improved understanding of the relevant drift processes, operating at different scales and circumstances in natural communities.

**METHODS**

**Model system**

Our aim is to study whether communities that are assembled through either neutral or niche-mediated (non-neutral) competition differ in their replicate similarity. We will consider a landscape of $N$ patches, each containing a local community. These patches are arranged in a ring, where each patch is connected to its $m$ nearest neighbours ($m/2$ on each side). The local communities are connected along the landscape via density-independent dispersal, where a fraction of $p$ individuals of each species is removed from a given
patch at each time step and redistributed among its neighbours. The renewal of population density \( X \) in species \( i \) from time \( t \) to \( t + 1 \) within patch \( k \) follows:

\[
X_{i,k}^{t+1} = (1 - p)f(X_{i,k}^{t}, X_{j,k}^{t}, j \neq i, j \neq k) + \frac{k + m}{2m} \sum_{l=k-m, j \neq k}^{k+m} f(X_{l,k}^{t}, X_{j,k}^{t}, j \neq i, j \neq k),
\]

where \( m \) is the size of the dispersal neighbourhood in either direction from patch \( k \). We consider two extreme scenarios with either nearest-neighbour (local) dispersal (\( m = 1 \)) or global dispersal (\( m = (N - 1)/2 \)) between patches. Further, \( f(X_{i,j}^{t}, X_{j,k}^{t}, j \neq i, j \neq k) \) is modelled by the Ricker function for the local dynamics in patch \( k \) for species \( i \) (\$ in total):

\[
f(X_{i,j}^{t}) = \text{Poisson} \left( X_{i,j}^{t} \exp \left( r_i - \frac{1}{K_i} \sum_{j=1}^{S} a_{ij} x_{j} X_{i,j}^{t} \right) \right)
\]

where \( r_i \) is intrinsic growth rate, \( K_i \) is carrying capacity, and \( \alpha_{ij} \) is the per capita effect of species \( j \) on the renewal of species \( i \). Unless stated otherwise, these parameter values are assumed to be homogeneous across all population patches. At each time step, we take the Poisson expectation for \( f(X_{i,j}) \) to model demographic stochasticity (Ranta et al. 2006). For simplicity, we set \( r_i = r = 1 \) (results are not qualitatively affected by changes in \( r \)).

In the neutral model interspecific interaction coefficients \( \alpha_{ij} \) are set equal to 1 (Loreau & de Mazancourt 2008) and \( K_i = K = 1000 \), which sets all species equivalent in their demographic traits. In such community any reduction in a single species’ density is compensated by an increase in other species’ densities. In case of non-neutral competition, species are assumed to differ in their abilities to compete in given environmental conditions. Here the interacting species have different optima (\( \mu \)) along an environmental gradient, which influences their demographic traits. With the environment peaking at \( \mu \) (with variance \( \sigma^2 = 0.09 \)), species-specific carrying capacities are:

\[
K_i = \frac{K \sigma 10/4}{\sigma \sqrt{2\pi}} e^{-(x_i - \mu)^2/2\sigma^2},
\]

resulting in a closely matching long-term biomass to that of the neutral community where \( K_i = K \). Parameter \( K \) influences the relative strength of demographic stochasticity; small populations (low \( K \)) are more susceptible to local extinctions than larger populations (high \( K \)). This has an influence on results based on measuring species composition (Figure S4 in Supporting Information). The scaling factor in eqn (3), \( \sigma 10/4 \), ensures that long-term biomass in non-neutral communities is similar to that of neutral communities.

Interspecific interaction coefficients are found as (May 1974):

\[
\alpha_{ij} = \exp[-(x_i - x_j)^2/4\sigma^2].
\]

The parameter \( \sigma \), also present in eqn (3), can be interpreted as the breadth of species resource tolerances. By varying \( \sigma \), one can in principle change how ‘neutral’ the community is; low values of \( \sigma \) lead to species differences, while the neutral model is recovered as \( \sigma \rightarrow \infty \). We consider a global community initiated with 20 species, further investigations were carried out with 10 and 100 species communities. With these modifications eqn (2) represents an unfeasible community when all species are present, i.e. at least one species has a deterministic equilibrium density \( N^* \leq 0 \). If all species are initiated at positive density, an unfeasible community will face deterministic species loss in the absence of immigration.

We assume that the metacommunity is represented by, e.g. a forest landscape composed of a mosaic of different forest types, due to variation in local physical conditions. This assumption assures that all species are likely to have at least one locality in the landscape where they can sustain positive growth in the absence of immigration, while other patches may be sinks. Under non-neutral competition, environmental conditions in all patches (parameter \( \mu \) in eqn 3) are drawn from a uniform random distribution between (0, 1). In the focal patch, \( \mu_F = 0.5 \). With neutral competition all patches are equal and the identity of the focal patch is arbitrary. We record the similarity of community composition in the focal patch, while the remaining \( N - 1 \) patches serve as a species pool for the focal patch. Populations in each patch are initiated at a random density [drawn from a uniform distribution between (0, 100)], except the focal patch, where all \( X_{i,1} = 0 \). All results are based on 100 replications of the system described above. We initially look at a community distributed over 30 patches and also investigate the effect of varying landscape size from 10 to 100 patches.

**Analysis**

We record the mean abundance of extant species (in the focal patch) calculated over the final 10 time-steps (from \( t = 991 \) to 1000). This period (prior to sampling) is long enough to avoid the effect of initial transients on community composition. We tested the effect of varying the time of sampling, with no major effect on our results (Figure S5 in Supporting Information). The predictability of the emerging community (similarity between replicated community samples) is measured by scoring the similarity among replicated communities using the Steinhaus Similarity Index:

\[
S_{\text{Steinhaus}} = \frac{2W}{A + B}
\]

Here \( W \) is the minimum abundance of shared species in two replicate communities \( i \) and \( j \), and \( A \) and \( B \) are the total

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abundance of all species in sites $i$ and $j$ respectively (Legendre & Legendre 1998). This measure is often referred to as percent similarity. Using this measure assumes that species abundances reflect those species able to adapt to underlying local environmental conditions. The Steinhaus Index is the complement of the Bray & Curtis Index ($S = 1 - BC$). The particular choice of association measure can have an influence on the results, depending on the amount of information used to score similarity (Supporting Information).

In addition to indirectly comparing the neutral and non-neutral communities by community similarity, we also compared them directly using species rank-abundance curves (abundance ranks averaged over 100 replicates) and community ordination in the focal patch. Non-Metric Multidimensional Scaling (NMDS) was used for community ordination (based on 100 replicates for each community type). NMDS is a method that finds an optimal configuration of sites in a desired number of dimensions (here we require a two-dimensional solution) according to the similarity in species composition between sites. In other words, it reduced the dimensionality of an $n$-dimensional data with $n$-species. NMDS analysis was performed in r v2.6.2 (R Development Core Team 2005) using the metaMDS function in the vegan package (Oksanen et al. 2007).

Environmental stochasticity

We also explored the similarity of community composition under variable environmental conditions. This analysis was motivated by recent speculation around the influence of environmental variation and community similarity (Dornelas et al. 2006). Environmental stochasticity is modelled as either temporally uncorrelated white noise or positively autocorrelated pink noise (Halley 1996), considered to be ecologically the most realistic proxy for environmental variation (Vasseur & Yodzis 2004). Environmental variation is modelled as sinusoidal noise (1 variation ($Vasseur & Yodzis 2004$). Environmental variation is ecologically the most realistic proxy for environmental autocorrelated pink noise (Halley 1996), considered to be either temporally uncorrelated white noise or positively

Components of drift

As such, our model formulation allows for several sources of drift. First, (A) local populations fluctuate randomly due to demographic stochasticity (the Poisson operator in eqn 2), which can be deterministically amplified by the number of interacting species (Purves & Pacala 2005). Second, these random fluctuations combined with potentially limited dispersal between localities (the rate, $p$, and scale of dispersal, $m$, in eqn 1), and local and global species extinctions (again due in part to the Poisson operator in eqn 2) can influence (B) local and (C) global species composition, which affects drift in population densities in local communities. Third, (D) variation in local environmental conditions can further enhance the influence of (A), (B) and (C) in driving stochastic variation (drift) in local species composition. We discuss our results from the perspective of these different components of ecological drift in our model.

RESULTS

Dispersal rate and scale (local vs. global) both have strong, but differing impacts on the similarity of neutral and non-neutral communities. While increasing dispersal rate ($p$) leads to matching similarity patterns in neutral communities connected by either local or global dispersal (where similarity scores tend to be close to 0.5), important differences remain in the distributions of similarity scores when increasing $p$ in non-neutral communities with different dispersal scales (Fig. 1). While comparing community similarity between neutral and non-neutral communities, general patterns arise. The variability in similarity scores is substantially higher in non-neutral communities with local dispersal than in neutral communities, while the median remains similar (Figs 1 and S1). In contrast, variability in similarity scores is relatively similar between the two models under global dispersal, while non-neutral communities tend to have higher median similarity than neutral communities. Direct comparison between neutral and non-neutral communities clearly illustrates a convergence between neutral and non-neutral communities in both the species rank–abundance relationship (Fig. 2a,c) and community composition (Fig. 2b,d) associated with the switch from local to global dispersal.

Both landscape ($N$) and metacommunity size ($S$) influence community similarity, but in opposite directions (Figs 3, S2 and S3). Niche and neutral assembly processes can be distinguished with a large number of patches and
Figure 1 Influence of dispersal limitation [scale (local or global) and rate \( p \) of dispersal] on community similarity (measured as percent similarity between replicate community samples), in neutral and non-neutral communities. Increasing dispersal rate \( p = (a) 0.01, (b) 0.1, (c) 0.5, (d) 0.9 \) initially increases, then decreases the similarity of neutral and non-neutral community samples. Dashed and solid lines indicate local and global dispersal results respectively. Parameter values: \( S = 20, N = 30 \). With local dispersal, the dispersal neighbourhood has a size of \( m = 1 \) (nearest neighbours), while in the case of global dispersal \( m = N \). In all cases, distributions for neutral and non-neutral communities are significantly different at the risk level \( \alpha = 0.001 \) (Kolmogorov-Smirnov test).

Figure 2 Increasing the dispersal range from local \( [m = 1, (a–b)] \) to global \( [m = N = 30, (c–d)] \) leads to more similar rank – abundance \( (a, c) \) and community ordination \( (b, d) \) relationships (Non-Metric Multidimensional Scaling; see Methods). In \( (b, d) \) concentration ellipses, with 95% of all observation fitting within the circles, are plotted, while the ‘+’ represent group centroids. Parameter values \( S = 20, N = 30, p = 0.5 \). © 2009 Blackwell Publishing Ltd/CNRS
localized dispersal, or with small local communities, but is unlikely to be straightforward under other scenarios. Increasing the number of patches in a metacommunity with global dispersal increases community similarity (Fig. 3a,b), as species are less likely to go globally extinct. Smaller communities are more similar with each other than larger ones (Fig. 3c,d), again relating to extinction risk, which is increased under the higher competition, which reduces species’ population densities. It is easier to distinguish between non-neutral and neutral communities when fewer species are present.

Community similarity is also affected by the size of local populations, which influences the relative strength of demographic stochasticity (Fig. S4). While increasing population sizes tend to increase similarity in both neutral and non-neutral communities, non-neutral communities remain more variable in their similarity scores. Again, localized dispersal is associated with clearer differences in community similarity between neutral and non-neutral communities, than global dispersal.

Introducing environmental stochasticity into the system has no impact on the similarity of neutral communities (Fig. 4). Similarly, introducing white (temporally uncorrelated) environmental stochasticity has no marked influence on the similarity of non-neutral communities (Fig. 4a). However, environmental reddening (positively autocorrelated stochasticity) decreases the median (but not variability) in the similarity distributions in non-neutral communities (Fig. 4b). Once again, the strongest effect of reddened environmental variation is associated with local dispersal (Fig. 4c). In general, differentiating between assembly models is harder under global dispersal and easier under local dispersal.

Both the model and the results generated are relatively complex. The expected qualitative influence of several components in our modelling framework on differentiating neutral and non-neutral communities are therefore summarized in Table 1.

**Discussion**

Our results demonstrate how a common underlying process may generate a wide range of possible outcomes in community composition. Stochastic population processes make predictions of community composition more challenging than previously appreciated, even in a stable environment. This can be attributed to priority effects arising from high demographic uncertainty and competitive pressure at low densities, even for dominant competitors, during colonization (Case 1990). One major assumption that underlies much of empirical community ecology is that common patterns in, e.g. community composition, reflect a common driving force, such as niche or neutral processes being dominant in community assembly and structuring. Recent theoretical investigations question this approach (Chave et al. 2002; Purves & Pacala 2005; Walker 2007). Our results highlight the potential for two different assembly methods to generate identical patterns in community composition.
structure under certain ecological conditions. Global dispersal promotes convergence in community metrics such as the similarity of species composition between replicated communities, or rank–abundance relationships, when different methods are used to assemble communities (Figs 1 and 2). Reducing connectivity between habitat patches increases drift in community composition in general, supporting empirical observations (Chase 2003, 2007).

Neutral patterns are known to arise through non-neutral ecological processes (e.g. Alonso et al. 2006). For example, increasing community size increases convergence between neutral and non-neutral communities under global dispersal, due to increased drift (Purves & Pacala 2005). However, this is likely to be restricted to a narrow parameter range (Walker 2007). It has been suggested that competition can also lead to the emergence of suites of nearly neutral species in species rich communities (Scheffer & van Nes 2006). Such near-neutrality might arise when stabilizing forces (promoting species to increase when rare) are relatively weak, and equalizing forces (diminishing differences in species-specific responses to non-regulatory environmental factors) are strong, and is more likely to be more strongly associated with some taxa and environmental conditions, than others (Holt 2006). Chave et al. (2002) showed that non-neutral processes can generate patterns in species’ relative abundance that contrast those produced by a neutral process, independently of the scale of dispersal. Whether dispersal rate (p) and landscape size (N) are useful parameters for discriminating between neutral and non-neutral processes underlying population growth depends on the scale of dispersal (local/global; Figs 1 and 3); i.e. we can discriminate more accurately with local than global dispersal. Adler et al. (2007) recently proposed a collection of empirical tests that can be utilized when testing the neutrality hypothesis. However, these tests can be very difficult to apply to real circumstances due to strong requirements on data. Our results provide useful guidelines for planning effective empirical studies for testing neutrality predictions, if necessary.

Partitioning components of drift

Our findings indicate that the relation between pattern and process can be understood by consideration of relevant ecological drift processes. There are three main drift processes simultaneously operating in our (neutral and non-neutral) metacommunities in the absence of environmental variation: (A) Population densities change (drift) due

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**Table 1** A summary of the qualitative influences of different model aspects on the ability to differentiate between neutral and non-neutral communities, based on distributions of community similarity

<table>
<thead>
<tr>
<th>Model aspect being increased</th>
<th>Dispersal Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dispersal rate, p</td>
<td>Divergence</td>
</tr>
<tr>
<td>Community size, S</td>
<td>Convergence</td>
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<tr>
<td>Landscape size, N</td>
<td>Divergence</td>
</tr>
<tr>
<td>Demographic stochasticity</td>
<td>Convergence</td>
</tr>
<tr>
<td>(decreased K)</td>
<td>No effect</td>
</tr>
<tr>
<td>Environmental reddening</td>
<td>Divergence</td>
</tr>
<tr>
<td>Sampling time</td>
<td>Divergence</td>
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</table>

For example, increasing dispersal rate (p) results in increasingly different community similarity distributions (divergence) between neutral and non-neutral communities under local dispersal, whereas these distributions tend to become increasingly similar (convergence) under global dispersal.

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**Figure 4** Coloured environmental stochasticity can alter community similarity distributions in neutral (grey lines) and non-neutral communities (black lines). Environmental variation is either (a) white, (β = 0) or (b) pink (β = 1) in colour. Parameter values S = 20, N = 30, p = 0.1, w = 0.2. Dashed lines = local dispersal (m = 1), solid lines = global dispersal [m = (N – 1)/2]. In all cases, distributions for neutral and non-neutral communities are significantly different at the risk level a = 0.001 (Kolmogorov-Smirnov test).
to (i) demographic stochasticity and (ii) interspecific competition. (B) Species composition (presence/absence) in local communities drifts due to local extinctions (through demographic stochasticity and/or deterministic local extinctions in non-neutral communities) and dispersal limitation. (C) The global species pool that provides immigrants to each local community also experiences drift as individual species become globally extinct. Drift in population densities (A) is generally stronger in neutral communities, but increasing species richness (or interaction strength, \( p \)) increases its importance in non-neutral communities (Purves & Pacala 2005). Drift in species composition (B) and the global species pool (C) are both affected by dispersal scale (local vs. global), dispersal rate \( (p) \) and landscape size (the number of patches, \( N \)). Our results suggest that non-neutral communities are affected more (i.e. experience stronger drift) by changes in the dispersal regime (scale and landscape size) than neutral communities. This is because the local neighbourhood should not differ much (on average) from the global landscape in a neutral metacommunity, whereas it can differ considerably from the ensemble average in a non-neutral metacommunity. Therefore, the relative importance of different sources of drift determine whether a non-neutral process resembles a neutral process in terms of community similarity metrics. For example, non-neutral communities tend to drift more strongly than deterministically neutral communities under localized dispersal.

Dornelas et al. (2006) recently compared an extensive data set of coral communities with predictions from Hubbell’s (2001) neutral model and concluded that there was higher variance in the similarity between real coral communities than predicted by neutral theory. This discrepancy was suggested to indicate a strong role for environmental variability in determining patterns of community similarity on coral reefs. However, no results were presented to back up this idea. We show here that non-neutral competition results in more variable community similarities than neutral competition (Fig. 1), but this is not due to environmental stochasticity (Fig. 4). Reddened environmental variation has a tendency to decrease the similarity of non-neutral communities, as it creates temporal refugia for different species at different times (Gonzalez & Holt 2002). As a result, the observed community composition is heavily dependent on the time of sampling, a feature that is not shared with the neutral model (since all species should react similarly to changes in the environment). This indicates that while reddened environmental variation can improve the discrimination between neutral and non-neutral processes, increased variability in community similarities in non-neutral communities is unlikely to arise due to environmental forcing. Our investigation of the impact of environmental variation adds a final point to the above list of ecological drift processes: (D) Reddened environmental stochasticity increases drift in local population densities, which is only realized in non-neutral communities.

In addition to comparing community similarity patterns between those in natural coral reefs and a neutral model, Dornelas et al. (2006) also showed that increasing diversity tends to decrease (neutral) community similarity, while increasing immigration rate increases the similarity between replicated neutral communities. The decrease in community similarity with increasing diversity arises ‘because in species-rich communities there are more species whose abundances can vary among communities’ (supporting information in Dornelas et al. 2006), which is in agreement with the findings of Purves & Pacala (2005), as well as our results. The increase in community similarity with increasing immigration relies upon an infinite dispersal pool in the neutral model, which precludes global species loss. Our results indicate that a limited landscape can restrict the maximum similarity that can be reached with increasing dispersal rate, due to global species extinctions. The same pattern is also apparent in niche-structured communities.

**Understanding biodiversity through drift processes**

Stochastic processes in population renewal and dispersal may act to override deterministic features of community assembly, which can make the detection of non-neutral competition challenging. Therefore, one should be cautious when interpreting apparent resemblance between a given model and observed data (e.g. Dornelas et al. 2006; Volkov et al. 2007). Determining the strength and other important characteristics (e.g. autocorrelation) of environmental forcing acting upon focal communities remains a critical challenge in population biology (Inchausti & Halley 2002; Ruokolainen & Fowler 2008; Ruokolainen et al. 2009). In addition, the uncertainty of other parameters estimated (e.g. dispersal rate and distance, and strength of interspecific interactions) influencing ecological drift may also have to be taken into account when testing whether natural data reflects underlying neutral processes or not. Depending on the questions asked, the choice of species association measure may not influence the discrimination between neutral and non-neutral processes (e.g. McGill et al. 2005; Chase 2007). Our investigation indicates that in some conditions (e.g. under localized dispersal) binary indices of similarity (e.g. Jaccard) can lead to considerably stronger differences in community similarity between neutral and non-neutral models than quantitative indices (Supporting Information). This is because binary measures are much more sensitive to stochastic local and global extinctions. In non-neutral communities this can lead to relatively low similarity. While this might appear counterintuitive, it indicates the presence of alternative states in species composition (due to priority effects), which is not observed.
in neutral communities. As different types of similarity metrics highlight different aspects of ecological data, a combination of methods may be useful when empirically testing for neutral predictions.

Given these challenging issues, we attempted to find conditions where neutral and non-neutral processes can be distinguished. Although neutral and non-neutral communities can be separated in terms of their similarity in many circumstances, the results reported here and elsewhere suggest that common tests of neutrality (e.g. a comparison of similarity patterns generated by neutral and non-neutral assembly processes) could result in false identification as a neutral pattern when non-neutral processes actually underlie community dynamics. This can happen as different ‘drift’ processes are able to produce ‘neutral’ community patterns in non-neutral communities. Even when species clearly differ in their demographic traits, communities can appear to be neutral under some conditions, by definition (i.e. the observed dynamics are dominated by drift processes). Non-neutral processes (e.g. niche-based) make clear predictions as to how dynamics will behave as the importance of drift processes is reduced. The outcome of neutral dynamics is less clear, e.g. in our model formulation the neutral dynamics are entirely dictated by initial conditions as species do not otherwise differ in their traits. Because neutral communities do not have specified underlying dynamics (except for ‘neutral’ dynamics), it may not be sensible to place neutral communities on a continuum, unless it is accepted that species-specific differences are important in the absence of drift processes. While the question: what drives deterministic dynamics in natural systems? remains open, our findings suggest that to understand local patterns in biodiversity, it is essential to understand the stochastic drift processes involved, acting upon community assembly and dynamics.

The majority of the literature testing the neutral hypothesis concentrates on patterns in sample data. It is becoming clear that many aspects influence the ‘visibility’ of deterministic processes, e.g. community composition, species dispersal abilities and landscape structure; therefore, manipulative experiments may be required to properly test whether presence and abundance of species in communities is controlled by niche (or neutral) structuring in natural systems.

**Sensitivity to model assumptions**

Patterns in community similarity are somewhat sensitive to the time of sampling (on time scales longer than that considered here), depending on, e.g. dispersal scale (local vs. global) or the similarity metric used (Fig. S5). Both neutral and non-neutral metacommunities tend to loose species over time due to demographic stochasticity. Our choice of sampling time (at \( t = 1000 \)) means that we consider transient, non-equilibrium global dynamics in the metacommunities. While the sensitivity to temporal scale is important to keep in mind, it does not compromise our conclusions, as both neutral and non-neutral communities are sampled at the same point in time. Transient dynamics are prevalent in natural communities (e.g. Hastings 2004) – natural disturbances, such as forest fires, influence the maximum duration of successional trajectories (McCarthy et al. 1999; Pennanen 2002; Wallenius et al. 2005). In this light, it is reasonable to compare similar patterns in different community models under transient dynamics, as such a comparison is more useful for empirical ecologists dealing with transient conditions in natural systems.

Our modelling framework can be used to further examine the continuum between niche and neutral models (e.g. Chesson 2000), by varying the parameter \( \sigma \). Low, positive values of \( \sigma \) will produce communities containing species with very different carrying capacities (\( K_i \)) and less competition between species (\( a_{ij} \)). As \( \sigma \) tends to infinity, species will tend lose differences in their demographic rates, becoming more ‘neutral’. However, varying \( \sigma \) can have rather unintuitive effects on the distribution of similarity scores for neutral and non-neutral communities; increasing \( \sigma \) from very low to intermediate values (0.1–0.5) leads to convergence between similarity scores, while further increases (\( \sigma = 1.5 \)) result in divergence in similarity scores (Fig. S6). These patterns can be understood by considering changes in species composition due to stochastic global species extinctions. In addition, large changes in total biomass are associated with changes in \( \sigma \). We avoided this problem by including a scaling factor (\( K \times 10 \sigma /4 \)) in eqn 3.

The issue of scaling becomes more complex over a wide range of \( \sigma \) values, representing an interesting avenue for further exploration.

The connectedness between local communities is highly important in driving local community dynamics (Table 1). Given the continued interest in the applicability of the neutral theory of biodiversity to natural systems, our simulation results provide guidance that can help differentiate between community patterns generated by underlying neutral or non-neutral processes. Having said that, the amount detailed information and number of replicates required to reliably differentiate between these alternative processes suggests making robust predictions from empirical data remains hugely challenging for community ecologists.

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article.

**Figure S1** Influence of dispersal rate on similarity scores.
**Figure S2** Influence of initial species richness on similarity scores.
**Figure S3** Influence of landscape size on similarity scores.
**Figure S4** Influence of demographic stochasticity on similarity scores.
**Figure S5** Influence of sample time on similarity scores.
**Figure S6** Influence of $\sigma$ on similarity scores.

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