

# Individual-based models of community assembly: Neighbourhood competition drives phylogenetic community structure

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## Abstract

1. It is now commonplace for community ecologists to infer assembly processes from the evolutionary relatedness of co-occurring species. Such inferences, however, have typically depended on assembly theories that assume competitive equilibrium and that are species based. In reality, all natural communities are dynamic, particularly during the course of succession, and the ecological interactions which drive phylogenetic community structure actually occur among neighbouring individuals rather than species.
2. To bridge this gap between theory and reality, we examine how colonisation, competition, and consequent replacement of individuals translate into phylogenetic community structure by using an individual-based model. The model we use assumes a trade-off between competition and colonisation abilities and that the points where species fall on the trade-off curve are phylogenetically conserved.
3. We find that the phylogenetic alpha diversity of a given community will be equal to or greater than the null expectation generated by randomly drawing individuals from communities at the same time step (i.e. phylogenetic overdispersion). This pattern results from the combination of interspecific differences in colonisation ability and neighbourhood competition that lead to individuals being regularly distributed in two-dimensional space.
4. We also show that phylogenetic beta diversity increases with increasing temporal differences between two communities. However, when this positive relationship is analysed only among the communities at close time steps, it becomes insignificant as they approach competitive equilibrium. We find similar patterns for functional alpha and beta diversity when phylogeny is replaced with functional traits.
5. *Synthesis.* Though questions concerning community assembly have often been spatially framed, our model shows that the span of the time frame can also affect, or even reverse, inferences about assembly processes. Our model also implies that a shift in the frame of reference from species to individuals brings a new perspective to community assembly. Careful consideration of non-equilibrium and individual-level aspects provides better insights into the consequences of the evolutionary and functional similarities of individuals on community assembly.

## KEY WORDS

beta diversity, community phylogenetics, competition, evolutionary history, functional traits, neighbourhood models, phylogenetic diversity, succession

## 1 | INTRODUCTION

The sequence of colonisation, competition, and consequent replacement of individuals of different species (i.e. succession) has been a central theme in ecology, but its consequences for community assembly remain a hotly debated issue (Li, Cadotte, Meiners, Hua, Jiang, et al., 2015; Muscarella et al., 2016; Norden, Letcher, Boukili, Swenson, & Chazdon, 2012). Ecologists often infer the ways in which communities have assembled based on field observations of communities through time or across space. Such an inductive approach often rests on theories of community assembly that link patterns with processes (e.g. Diamond, 1975; Webb, Ackerly, McPeek, & Donoghue, 2002; Mayfield & Levine, 2010). However, commonly articulated theories about the relative roles of competition and environment on community patterns have been based on the assumption that local colonisation and competitive exclusion have been completed and the communities are in equilibrium (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015). However, in reality, essentially all natural communities are subject to dynamic processes that keep communities from reaching equilibrium, with the ongoing turnover of species (Li, Cadotte, Meiners, Hua, Shu, et al., 2015; Meiners, Cadotte, Fridley, Pickett, & Walker, 2015; Mori, 2011). Furthermore, although commonly employed theories have often used species as the unit of observation and assessment, the ecological interactions by which community patterns emerge actually occur among individuals. Here, in an attempt to bridge this gap between theory and reality, we offer a predictive model examining how individual-level dynamic processes of colonisation and competition translate into community patterns during succession.

Phylogenetic approaches are increasingly being used to understand how the evolutionary history of organisms affects community assembly processes (Cadotte & Davies, 2016; Cadotte, Davies, & Peres-Neto, 2017; Cavender-Bares, Kozak, Fine, & Kembel, 2009). For phylogenetic alpha diversity, there are two main competing theories that predict opposite consequences of competitive exclusion on community patterns. On the one hand, coexisting organisms at competitive equilibrium should be more distantly related than expected by chance alone (i.e. phylogenetic overdispersion) (Webb et al., 2002), given that organisms with similar niches compete intensively (MacArthur & Levins, 1967) and that niches are phylogenetically conserved. On the other hand, when differences in the ability to compete for a particular resource are configured in a hierarchy, then the species with a high rank should eventually outcompete the others, leaving a phylogenetically clustered pattern (Mayfield & Levine, 2010). Importantly, these inferences also hold true for functional alpha diversity, given that species' niches and competitive abilities are reflected in their traits. It is also important to note that

environmental filtering, which selects for species based on trait similarities, can also lead to clustering (Webb et al., 2002). However, the mechanisms by which environmental filtering and the competitive hierarchy drive clustering differ in that the former process filters organisms purely based on abiotic factors to determine which species become community members (i.e. a process related to fundamental niches), whereas the latter further narrows the list of members based on biotic interactions such as competition (i.e. realised niches) (Cadotte & Tucker, 2017; Kraft et al., 2015).

Another important facet of phylogenetic diversity that is often used to understand biodiversity patterns across space and time is phylogenetic beta diversity. In community assembly studies, phylogenetic beta diversity has been mostly used to measure the *spatial* turnover in the phylogenetic structure and is often interpreted as the outcome of among-site variations in the type and strength of the environmental filtering and dispersal limitation (Larkin et al., 2015; Swenson, Enquist, Thompson, & Zimmerman, 2007; Wang et al., 2015). It is also possible, however, for community development over *time* to affect phylogenetic beta diversity. Importantly, if the successional niches are phylogenetically conserved (Kunstler et al., 2012; Letcher et al., 2015; Li et al., 2016; Norden et al., 2012), succession could drive temporal decay of the phylogenetic similarity among communities. This could further translate into spatial variation in community structure if a given region consists of communities with different disturbance histories or on different successional trajectories. Succession is a complex sequence of species turnover events that progresses through the colonisation of individuals to vacant spaces created by individual deaths resulting from neighbourhood competition or disturbance (Pacala, 1986; Tilman, 1994). To our knowledge, however, few theoretical predictions have been made about how such individual-level colonisation and competition processes drive spatial and temporal turnover in phylogenetic community structure.

In this study, we develop a theoretical model that simulates community assembly based on competition between individuals and their neighbours. We focus exclusively on two essential mechanisms that drive succession: the competition–colonisation trade-off (Tilman, 1990) and individual-level competition among neighbours (Pacala, 1986). Our model is based on the competition hierarchy hypothesis (Mayfield & Levine, 2010), yet differs in that we assume a trade-off between competitive ability and colonisation ability and in that competition is defined not at the species level but rather at the individual level. In view of recent discussion that the assumption of competitive equilibrium is rarely met (Gerhold et al., 2015), we ask, then, what phylogenetic and functional diversity patterns may arise in non-equilibrium states? Our model first confirms that a competitive hierarchy eventually drives community clustering at competitive equilibrium, as suggested by Mayfield and Levine (2010). We

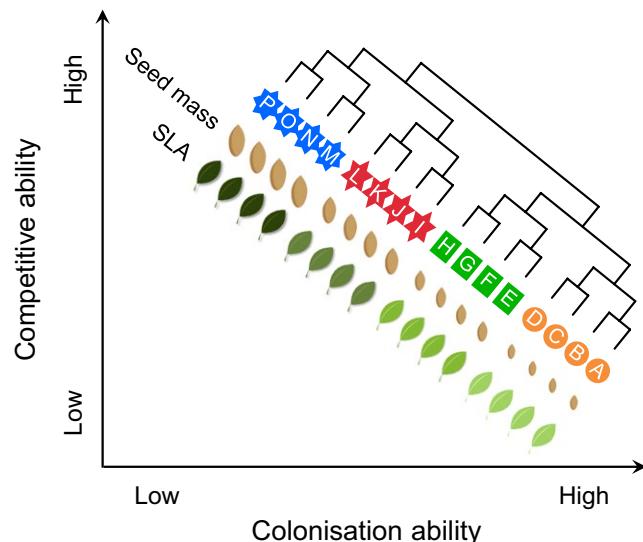
also find that both overdispersed and clustered patterns as well as different levels of phylogenetic and functional beta diversity could arise before the community reaches equilibrium, depending on the selected time frame of the successional stages. An important aim of ours is to highlight how a dynamic and individual-level context might expand our ability to draw inferences about ecological processes from community structure.

## 2 | MATERIALS AND METHODS

### 2.1 | Model overview

In this study, we explore how individuals of different species assemble into communities during succession using a lattice model. We follow Tilman's (1990) concept of competitive and colonisation abilities. Namely, we define competitive ability (denoted  $R^*$ ) as the minimum requirement of a species for a limiting resource to survive (i.e. species with a low minimum are highly competitive) and the concentration to which they reduce the resource. Our only modification from the original definition (Tilman, 1990) is that we refer to resource concentration at the end of each time step, rather than at equilibrium (as we will describe in detail below). We define colonisation ability  $C$  as the time required for a species to reach a given site. Our model assumes that there is a trade-off between the two abilities (Tilman, 1990) and that the points that species occupy on this trade-off curve is phylogenetically conserved (Figure 1). Individuals then compete with their neighbours for a limiting resource within a virtual two-dimensional plot (Figure 2). We keep the basic model as simple as possible by excluding factors other than the competition-colonisation trade-off and neighbourhood competition. In addition, we assume homogeneous site properties so that it is not necessary to account for intra-site variation in abiotic properties.

A key point of our model is that neighbourhood competition causes individuals to be more regularly spaced than would be expected by chance alone (Pielou, 1960). Empirical support for this phenomenon comes from many spatial-pattern analyses (e.g. Kenkel, 1988; He & Duncan, 2000; Stubbs & Wilson, 2004). At the start of our simulation, individuals belonging to the clade with the lowest competitive ability (i.e. those with the highest  $R^*$  value) but the highest colonisation ability (with the lowest  $C$  value) (clade ABCD in Figure 1) colonise an unoccupied plot (Figure 2a). Our basic model simply assumes stochastic colonisation from outside the plot and no reproduction of individuals within the plot (although we also analyse the latter case to provide a comparison; see 2.3 Comparative models for details). The spatial distribution of species transitions from random to an increasingly regular distribution as a result of local density-dependent deaths of some individuals (Figure 2b,c). At the next time step, individuals of the clade EFGH, which have higher competitive ability (i.e. require less of a limited resource) but lower colonisation ability than clade ABCD, begin to colonise the plot (Figure 2d). Some of them will again die due to spatially non-random mortality driven by neighbourhood competition (Figure 2e,f). Such colonisation and mortality processes repeat for clades IJKL and

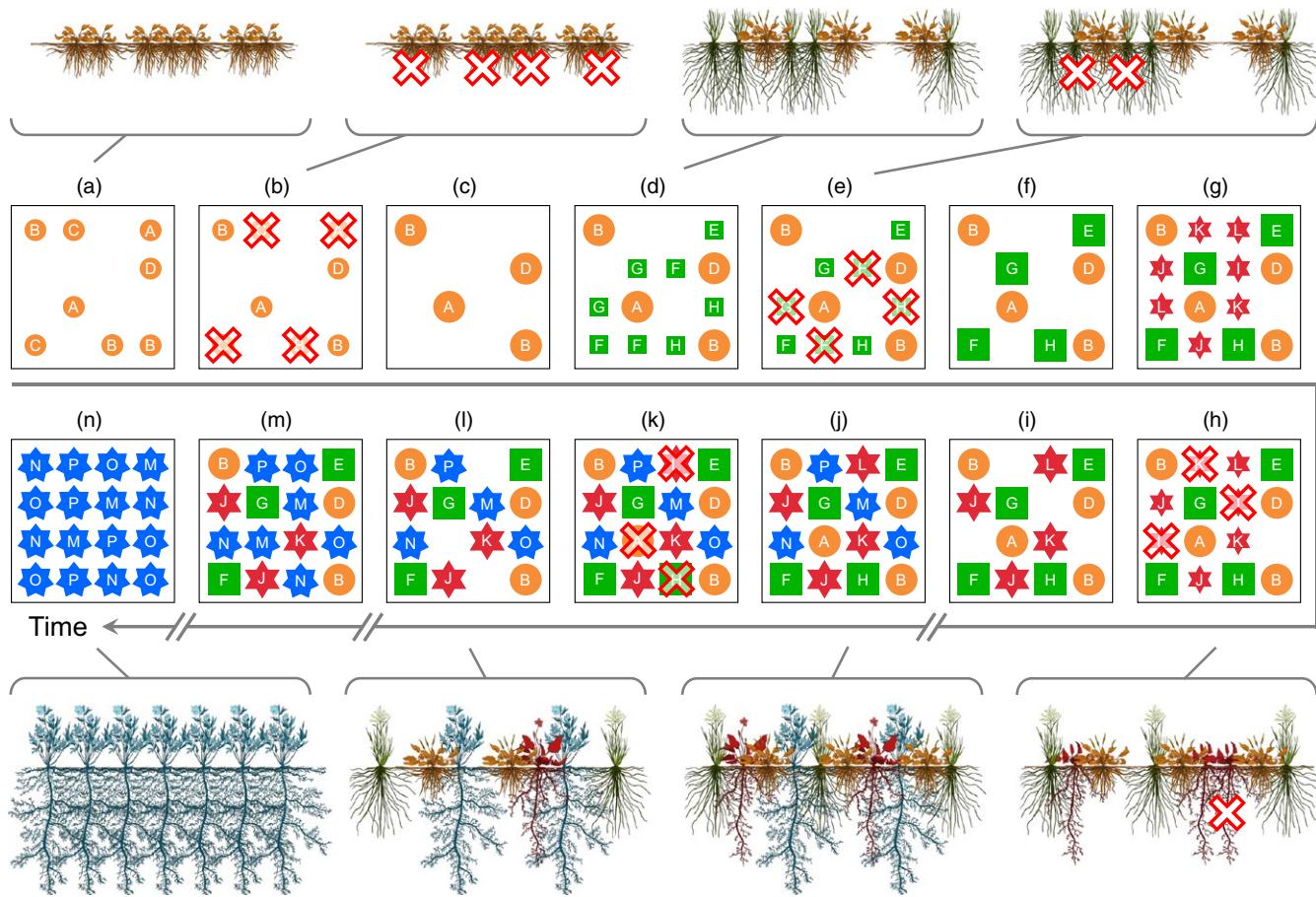


**FIGURE 1** Schematic representation of the assumed trade-off between colonisation ability and competitive ability and the case in which the points where species fall on the trade-off curve are phylogenetically conserved. Seed mass and specific leaf area (SLA) are shown as examples of potential traits responsible for the successional niche of a species. An example of a species pool composed of 16 species (A to P) in four clades is shown. Species with the same successional niches (i.e. clades) are presented using the same colours and symbols

MNOP as well (Figure 2g,h,i). As a consequence, the assemblage of individuals will become composed of species that belong to a larger variety of clades than would be expected by chance alone (Figure 2j). Individuals also die with a fixed probability (i.e. background mortality) (Figure 2k) and the vacant space they leave will be filled with species that can tolerate low resource availability (Figure 2l, m). After successive iterations of the mortality and replacement processes, the plot becomes dominated by the clade with the highest competitive ability (Figure 2n). We define this state, in which species turnover becomes minimal, as competitive equilibrium.

### 2.2 | Community assembly simulations

In our lattice model, each cell of the grid can be occupied by up to one individual. The entire simulated plot consists of 3,600 cells (i.e. a  $60 \times 60$  grid). The plot conceptually represents the surface of a torus; that is, even though it is two-dimensional, individuals compete with neighbours at the opposite edges of the grid as well. The use of a torus plot is a common option when simulating neighbourhood community dynamics with lattice models to avoid spurious edge effects (e.g. Chave, Muller-Landau, & Levin, 2002). The species pool is composed of 256 species. Each species belongs to one of the 16 clades, each of which is composed of 16 species. Species in the same clade are assumed to have the same competitive ability,  $R^*$ , and the same colonisation ability,  $C$  (i.e. their dynamics would be neutral). Specifically, species in clades 1 to 16



**FIGURE 2** Schematic representation of how colonisation, competition, and replacement of individuals progress in the simulation model. Squares in the middle row show the spatial distribution of individuals in two-dimensional plots. The colours and symbols of species A to P correspond to those in Figure 1. Pictures above and below the squares are a side view of the individuals. The competitive ability ( $R^*$ ) of each species is represented by its root depth to provide a visual representation of competition for a limited resource; species with higher competitive ability are illustrated with deeper roots. The red X represents death of an individual due to competition or other factors such as stochastic mortality. (a–j) Spatial distribution of individuals with the same successional niche (presented using the same colours and symbols) transition from a random distribution to a regular distribution as a result of competition among neighbours. (k–n) The plot becomes dominated by species with the highest competitive ability (i.e. the deepest roots). See 2.1. Model overview in the main text for a detailed explanation

have  $R^* = 16, 15, \dots, 1$  and  $C = 1, 2, \dots, 16$  respectively; that is, as  $R^*$  decreases by 1,  $C$  increases by 1 to represent the trade-off. All branch lengths of the phylogenetic tree are defined to be equal (=1). At the start of our simulation, all the cells have resource concentration  $RC = 16$ .

Each step in the simulation is divided into three phases: immigration, competition, and mortality. Individuals immigrate into the plot during the immigration phase of each time step  $t$ . The rate at which each species immigrates ( $I$ ) into each cell is contingent upon species' colonisation ability  $C$ . Namely, we define  $I = 0.1$  if  $C \leq t$  and equals 0 otherwise (e.g. at time step  $t = 10$ , species with  $C$  from 1 to 10 immigrate each cell at the rate of 0.1 but species with  $C$  from 11 to 16 cannot immigrate). In the competition phase, each individual reduces the resource concentration  $RC$  of all cells in a  $3 \times 3$  grid centred on the individual to the level according to their competitive ability  $R^*$ , thereby making the resource unavailable to individuals with a lower competitive ability. We define these nine cells as the "competition

zone." Individuals die when the  $RC$  of any cell in the competition zone decreases below their own  $R^*$ . When the competition zones of multiple individuals with the same  $R^*$  overlap spatially (i.e. when individuals with same  $R^*$  compete for the resource in one or more cells), each of them may die with a probability of  $D = 0.1$ . The competition phase is repeated until there is no overlap of competition zones among any individuals with the same  $R^*$ . Individuals who have become established after surviving this competition phase will not die unless this occurs as a result of background mortality. In the mortality phase, every individual may die based on the stochastic background mortality rate  $M = 0.05$ . The simulation runs for 120 time steps, given that our preliminary test of the model showed no obvious changes in the number of individuals and species from the 100th to the 120th time step (Supporting Information Figure S1). In each simulation, one quadrat (the size of which ranging up to  $20 \times 20$  cells; described in detail below) is established in the middle of the plot. We define the assemblage of individuals within the quadrat as a local community.

### 2.3 | Comparative models

We also construct additional models that account for other relevant factors. The first of these models considers how the form and density of colonisation affect the simulation results. While our original model defined immigration into each cell independent of resident individuals (at a rate of  $I = 0.1$  if  $C \leq t$ ), the revised model allows new individuals to disperse into the cells around the individuals pre-existing from the previous time step to represent their reproduction. At the beginning of each time step, the model disperses new individuals of the same species as existing individuals into the  $5 \times 5$  grid of cells surrounding a focal cell (i.e. 24 individuals in total, because the cell in the middle is already occupied). In addition to this within-plot reproduction, immigrations from outside the plot are retained to allow initial colonisation of species. We vary the immigration rate  $I$  from 0.0001 to 1.0 to examine its influence on colonisation density.

In the next model, we define the background mortality (i.e. individual deaths irrespective of competition) as age-dependent to represent senescence, rather than assuming constant stochastic mortality throughout an individual's life. Individuals older than a threshold age value  $A$  (=the number of time steps after colonisation) die. We simulate cases in which  $A = 10, 30$ , or  $50$ . In these simulations, we eliminate the stochastic mortality unrelated to age to simplify the analysis.

The final model assumes limiting similarity, in which species pairs with similar niches compete intensively (MacArthur & Levins, 1967). In this model, competition strengths are not defined by  $R^*$  but rather by the phylogenetic relatedness of each species pair, which we assume corresponds to the extent of niche overlap (Webb et al., 2002). We define the survival probability  $S$  of each individual at each time step as  $\text{logit}(S) = P_{ij} - 10$ , where  $P_{ij}$  is the phylogenetic distance between individuals  $i$  and  $j$ , which ranges from 0 to 32 (i.e.  $P_{ij} = 0$  for pairs of individuals from the same species and 2 for the most closely related pairs of different species, given that branch length = 1). The function produces a sigmoid (S-shaped) curve with the inflection point at  $P_{ij} = 10$  and  $S = 0.5$ . We use this function to take into account the nonlinear relationships between competitive strengths and the extent of niche overlap among species (May, 1973). The neighbours of a given individual  $i$  are defined as the individuals whose competition zone (a  $3 \times 3$  grid of cells centred on the focal cell) overlaps spatially with that of individual  $i$ , and the phylogenetic distance between individual  $i$  and the most closely related neighbour (i.e. individual  $j$ ) is used to represent  $P_{ij}$ . The colonisation abilities and immigration rates are set equal for all species ( $C = 1$  and  $I = 0.001$ ). All other parameters are the same as in the model that assumes a competitive hierarchy.

### 2.4 | Community patterns

We test the phylogenetic patterns using the mean pairwise phylogenetic distance (MPD) and the mean nearest-taxon distance (MNTD) (Webb et al., 2002). For phylogenetic alpha diversity, we calculate

the mean pairwise phylogenetic distance between all species in each community ( $\alpha\text{MPD}$ ) and the mean phylogenetic distance separating each species in the community from its closest relative ( $\alpha\text{MNTD}$ ). Similarly, we define the phylogenetic beta diversity as the mean phylogenetic distance and mean nearest-taxon distance between pairs of species drawn from two distinct communities ( $\beta\text{MPD}$  and  $\beta\text{MNTD}$  respectively). We compare these indices with null models to calculate the standardised effect size (SES) and to test whether the phylogenetic structure differs from random expectations. The SES is defined as  $(x - \mu_{\text{null}})/\sigma_{\text{null}}$ , where  $x$  is the original value of the index,  $\mu_{\text{null}}$  is the mean value of the null distribution, and  $\sigma_{\text{null}}$  is the standard deviation of the null distribution. The  $\text{SES.}\alpha\text{MPD}$  and  $\text{SES.}\alpha\text{MNTD}$  are equivalent to  $-1$  times the net relatedness index and the nearest-taxon index respectively (Webb et al., 2002). We generate 999 null communities using an individual-based randomisation method (Kraft et al., 2011). This method randomises individuals among the local communities while preserving the number of individuals in each local community and the relative abundance of each species in the metacommunity. We use this randomisation method because we assume that it could best discern the pattern created from our simulation model, which is also individual-based.

We analyse the phylogenetic structure of the simulated communities by mimicking three approaches to constructing species pools for null distributions, and that are widely used in the field: the snapshot, chronosequence, and intermediate approaches. In studies using the snapshot approach, multiple quadrats are often established randomly across a region (e.g. Diamond, 1975; Webb et al., 2002; Mayfield & Levine, 2010) or a large-scale research plot is divided into quadrats (Kembel & Hubbell, 2006; Swenson et al., 2007; Yang et al., 2014). Studies based on the chronosequence approach often establish multiple quadrats across a successional gradient to obtain the set of local communities (Chai et al., 2016; Pastore & Scherer, 2016; Shooher, Chisholm, & Davies, 2015). In our analyses of the snapshot approach, we use a set of 100 local communities, generated by 100 simulations, at each of the distinct time steps ( $t = 5, 10, 15, \dots, 120$ ) to create the null distribution. That is, we calculate the SES by comparing the phylogenetic diversity of a given community with the null distribution generated by using communities at the same time step. For the chronosequence approach, we use the set of local communities at different time steps (i.e.,  $t = 5, 10, 15, \dots, 120$ ) to generate the null distribution. That is, the null model for the community at each time step includes species from all time steps. The intermediate approach generates null distribution for each time step by combining communities of nearby ages (i.e. communities that are the same amount younger and older than the focal community), as done by Letcher (2010). Specifically, we analyse the cases in which the original community at a given time step  $t$  is compared with a null distribution generated by communities at times steps  $t - 5$  to  $t + 5$ ,  $t - 10$  to  $t + 10$ , and  $t - 20$  to  $t + 20$ . The number of replications for each time step  $t$  is 100 for analysing  $\alpha\text{MPD}$  and  $\alpha\text{MNTD}$  and 5 for  $\beta\text{MPD}$  and  $\beta\text{MNTD}$ . We also check how phylogenetic alpha diversity changes in response to changes in quadrat size from 9 cells ( $3 \times 3$ ) to 400 cells ( $20 \times 20$ ) under the snapshot approach. We perform this

analysis because it is possible that the detectability of the phylogenetic patterns depend on the spatial scale (Cavender-Bares, Keen, & Miles, 2006; Kraft & Ackerly, 2010; Swenson et al., 2007; Yang et al., 2014).

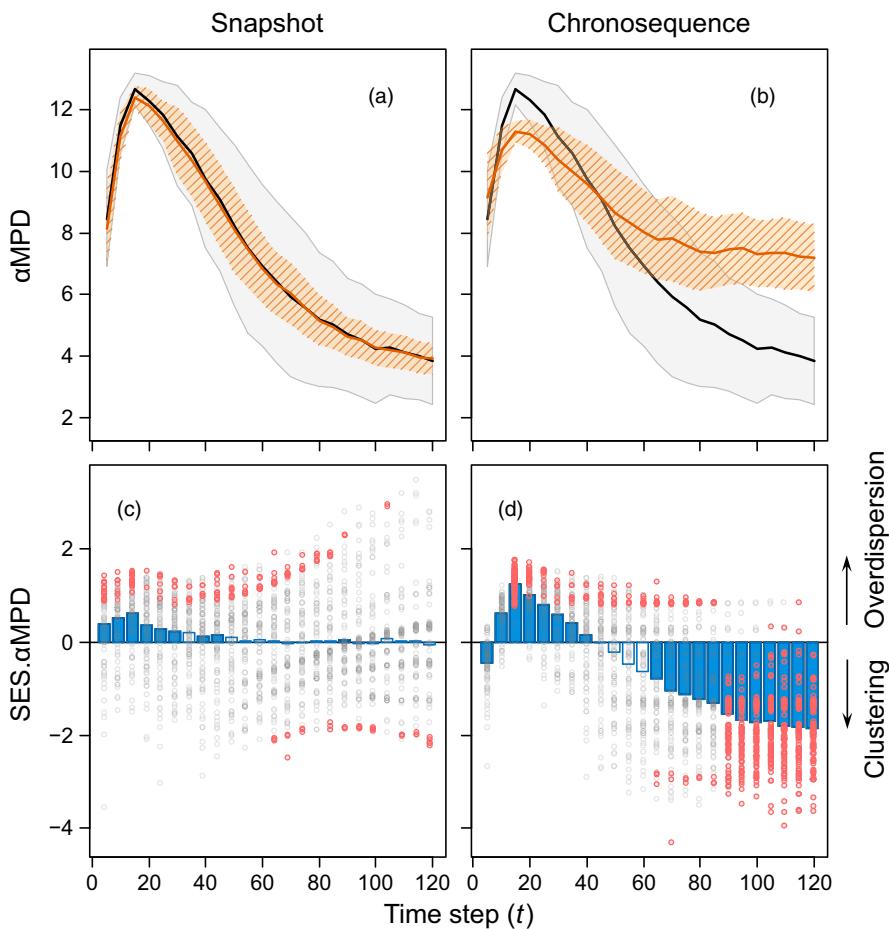
We use the ranks of the original  $\alpha$ MPD and  $\alpha$ MNTD values in the null distributions (from 1st to 1,000th) to test whether each community has higher (overdispersion) or lower (clustering) phylogenetic alpha diversity than would be expected by chance (Swenson, 2014). We further transform these ranks into Q-values (Storey, 2003) to correct for familywise error rates that result from multiple testing. The Q-values are calculated using the set of ranks for 100 communities at each time step ( $t = 5, 10, 15, \dots, 120$ ). To test for overall phylogenetic patterns, we apply the one-sample sign-test to the 100 values of SES. $\alpha$ MPD and SES. $\alpha$ MNTD at each time step. Again, we transform the obtained  $p$ -values into Q-values to correct for the familywise error rates. The Q-values are calculated using the set of 24  $p$ -values across the time steps ( $t = 5, 10, 15, \dots, 120$ ). We test the effects of differences in community ages (i.e. the number of time steps since the onset of succession) on phylogenetic beta diversity between community pairs ( $\beta$ MPD and  $\beta$ MNTD) using multiple-regression-on-distance matrices (MRMs; Lichstein, 2007). We use MRMs because both the community-age differences and beta diversity take the form of distance matrices with a combination number  $C(n, 2)$ , where  $n$  is the number of samples (communities).

We also analyse the functional diversity of communities to examine the cases in which the competitive and colonisation abilities of a species ( $R^*$  and  $C$ ) are reflected in their traits but are not phylogenetically conserved. Here, we define a species with competitive ability  $R^*$  to have a trait value  $T$  that equals  $(R^*)^2$  (e.g.  $T = 100$  when  $R^* = 10$ ). All other simulation settings are set similar to those in the phylogenetic diversity analyses; we divide 256 species into 16 functional groups, each of which with  $R^* = 16, 15, \dots, 1$  and  $C = 1, 2, \dots, 16$ . We measure the functional alpha and beta diversity using the mean pairwise trait distances among species within each community and between pairs of species in different communities respectively, which we considered analogous to  $\alpha$ MPD and  $\beta$ MPD (Cadotte, Albert, & Walker, 2013).

The simulation and statistical analyses were conducted using the R 3.4.2 software (R Core Team, 2017).

### 3 | RESULTS

Both the original and the expected phylogenetic alpha diversity changed over time (Figure 3a,b). Since the analyses using MPD and MNTD yielded qualitatively similar results, we present MPD here and the MNTD results can be found in the Supporting Information (Supporting Information Figure S2). The SES under the snapshot



**FIGURE 3** Temporal change in the phylogenetic alpha diversity measured by the mean pairwise distance ( $\alpha$ MPD) in both the snapshot approach (left) and the chronosequence approach (right). (a, b) Black lines and grey shaded areas represent the mean and the 95th percentile of the original  $\alpha$ MPD values yielded from 100 simulations respectively. The orange lines and orange shaded areas represent the mean and the 95th percentile of the  $\alpha$ MPD values expected from a null model. (c, d) Grey points indicate the standardised effect size for  $\alpha$ MPD (SES. $\alpha$ MPD). The points are filled with red when the  $p$ -values corrected for the familywise error rates (the Q-values) were less than 0.025. Blue bars represent the mean SES. $\alpha$ MPD at time steps  $t = 5, 10, \dots, 120$ . The bars are filled with blue when the mean value differed significantly from 0 (one-sample sign-test,  $Q < 0.05$ ). Results are shown for a quadrat size of 25 cells (i.e. a  $5 \times 5$  grid)

approach was significantly larger than 0 during the early stages of succession (until about  $t = 50$ ) (Figure 3c). The SES under the chronosequence approach was significantly larger than 0 during the early stages of succession (until about  $t = 40$ ) but decreased below 0 thereafter (Figure 3d). Under the intermediate approach, the SES showed a temporal change similar to that under the snapshot approach, but the signature of overdispersion was less clear (Supporting Information Figure S3). The functional diversity showed qualitatively similar results as phylogenetic diversity; the SES was positive during the early succession under the snapshot approach (Supporting Information Figure S4c) and showed a downward convex curve under the chronosequence approach (Supporting Information Figure S4d).

The original and expected phylogenetic alpha diversity both increased continuously with increasing spatial scale (i.e. quadrat size) under the snapshot approach (Figure 4a). The SES peaked at a quadrat size of 64 cells ( $8 \times 8$ ). The SES had positive values irrespective of the quadrat size (Figure 4b), even though we defined the competition zone (i.e. the spatial extent within which individuals reduced the resource) as the cells in a  $3 \times 3$  grid centred on each individual.

The model that assumed dispersal from individuals present from the previous time step (i.e. reproduction) in addition to external immigration yielded results similar to those of the model that assumed only external immigration (Supporting Information Figure S5). The signature of overdispersion became less clear as the density of the external immigration decreased (Supporting Information Figure S6). The model that assumed age-dependent mortality showed a prolonged pattern of overdispersion, and the duration of this pattern depended on the age of senescence (Supporting Information Figure S7). The communities showed almost a constant

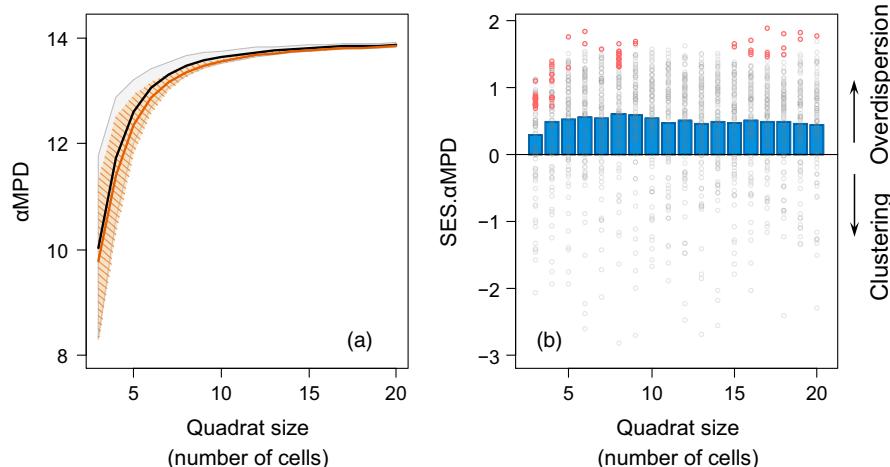
pattern of overdispersion under the assumption of limiting similarity (Supporting Information Figure S8).

The SES of phylogenetic and functional beta diversity increased significantly in response to the temporal difference between the two communities (Figure 5; Supporting Information Figures S9 and S10). When analysed separately for community pairs at early (time step 5–40), mid (45–80), and late (85–120) successional stages, beta diversity was larger than expected by chance for the early stage and smaller than expected for the mid and late stages. The phylogenetic and functional beta diversity increased significantly with increasing temporal differences during the early successional stages, but not during mid and late successional stages (Figure 5; Supporting Information Figures S9 and S10).

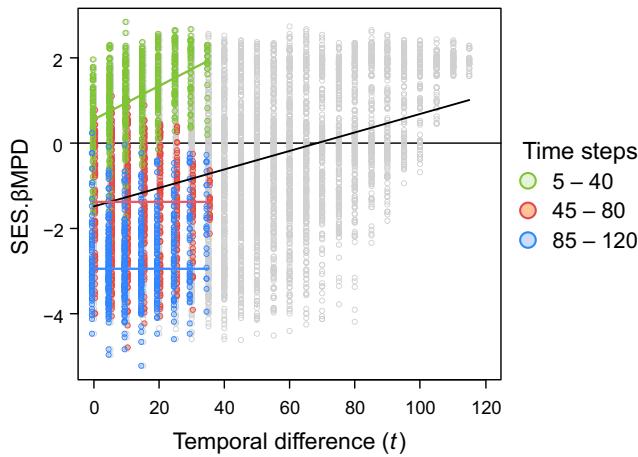
## 4 | DISCUSSION

Although many observational studies have reported the appearance of significant community patterns during succession (Letcher, 2010; Letten, Keith, & Tozer, 2014; Pastore & Scherer, 2016), theories of community assembly have typically assumed competitive equilibrium (as suggested by Gerhold et al., 2015), leaving a gap between theory and reality. In this study, we re-examined community assembly theory with a focus on individual-level competition and colonisation, as well as the trade-off between them. We found that a competitive hierarchy can lead to both overdispersed and clustered patterns before a community potentially reaches competitive equilibrium (Figure 3).

Our study is unique in that we defined the competition at the individual level and assumed that there was a trade-off between competition ability  $R^*$  and colonisation ability  $C$ . It has been widely



**FIGURE 4** Influence of spatial scale (quadrat size) on the phylogenetic  $\alpha$  diversity measured by the mean pairwise distance ( $\alpha$ MPD) under the snapshot approach. The x-axis shows the length of the side of a square quadrat centred on the focal cell. (a) Black lines and grey shaded areas represent the mean and the 95th percentile of the original  $\alpha$ MPD values yielded from 100 simulations respectively. Orange lines and orange shaded areas represent the mean and the 95th percentile of the  $\alpha$ MPD values expected from a null model. (b) Grey points indicate the standardised effect size for  $\alpha$ MPD (SES. $\alpha$ MPD). The points are filled with red when the  $p$ -values corrected for the familywise error rates ( $Q$ -values) were less than 0.025. Blue bars represent the mean SES. $\alpha$ MPD. The bars are filled with blue when the mean value differed significantly from 0 (one-sample sign-test,  $Q < 0.05$ ). The case at time step  $t = 15$  is shown



**FIGURE 5** Temporal turnover of the phylogenetic community structure for the standardised effect size based on the mean pairwise distance separating the different species in two communities ( $\text{SES.}\beta\text{MPD}$ ). The x-axis shows the difference in community ages (i.e. the number of time steps since the onset of succession) between two communities. The lines indicate the results of regressions on the distance matrices. The slopes of the regression lines for community ages 45 to 80 and 85 to 120 were set to 0, given that the influence of temporal differences was not significant. The case when the quadrat size was set to a grid of 25 cells ( $5 \times 5$ ) is shown

assumed in community ecology and evolutionary biology that closely related species will compete more severely than more distantly related species for common resources (Darwin, 1859; Elton, 1946), and that this will drive overdispersion (Webb et al., 2002). In fact, our model which assumed that closely related species with similar niches are less likely to locally coexist predicted that the communities will become overdispersed (Supporting Information Figure S8). Recent experimental studies, however, have suggested that this assumption is rarely supported for terrestrial plants, green algae, bacteria, and amphipods (Bennett, Lamb, Hall, Cardinal-McTeague, & Cahill, 2013; Cahill, Kembel, Lamb, & Keddy, 2008; Fritschie, Cardinale, Alexandrou, & Oakley, 2014; Godoy, Kraft, & Levine, 2014; Venail et al., 2015). Studies using functional traits have also shown that the difference in competitive strength between a given pair of species can rarely be explained by their trait similarity, but is more likely to be explained by a trait hierarchy (Kunstler et al., 2012; Kraft, Crutsinger, Forrestel, & Emery, 2014; but see Lasky, Uriarte, Boukili, & Chazdon, 2014). Our model provided two alternative processes by which overdispersion can arise (Figures 1 and 2). First, under the snapshot approach (in which the phylogenetic diversity of a focal community was compared with a null distribution generated by communities at the same time step), overdispersion can arise by the combination of a time lag in colonisation among clades and of the neighbourhood competition that drives the community towards a regular spatial distribution (Figure 3a,c). Second, under the chronosequence approach (in which the null distribution was generated by communities across different time steps), overdispersion can arise from the local temporal coexistence of distantly related species

due to delayed turnover among clades (Figure 3b,d). Although the latter idea had been inferred previously (Li, Cadotte, Meiners, Hua, Jiang, et al., 2015; Muscarella et al., 2016; Norden et al., 2012), to our knowledge, the present study is the first that quantitatively demonstrated this idea. The above findings also held true when we replaced phylogeny with traits and analysed using functional diversity (Supporting Information Figure S4).

We found that the time frame of the target community and of the reference communities used to generate the null distributions (i.e. snapshot, chronosequence, and intermediate) can have large consequences for the community patterns detected. Under the snapshot approach, the signature of overdispersion was clearer during early stages than later stages of community development (Figure 3a,c). This was because, early on, the vacant spaces that individuals can colonise were created mainly by competition-induced, deterministic death  $D$  of previous colonisers. The community pattern then became random towards the late successional stage, due to the fact that the deaths of individuals were mostly driven by a stochastic background mortality  $M$ . When the background mortality was age-dependent, the duration of overdispersion increased with increasing age at which individuals die (Supporting Information Figure S7). Under the chronosequence approach, the phylogenetic alpha diversity peaked in the early successional stage and decreased thereafter (Figure 3b,d). This result reflects the local temporal coexistence of species with different successional niches (Li, Cadotte, Meiners, Hua, Jiang, et al., 2015; Muscarella et al., 2016; Norden et al., 2012) and their subsequent displacement by clades with high competitive ability (Mayfield & Levine, 2010). Under the intermediate approach, the phylogenetic alpha diversity showed a similar temporal trend with that under the snapshot approach, but the signature of overdispersion was less clear (Supporting Information Figure S3). This was likely because the null model of a given successional stage included clades that would only be found in latter stages, resulting in the focal community to be composed of a relatively limited set of lineages. For phylogenetic beta diversity, there was a positive correlation between temporal differences between communities and beta diversity (i.e. temporal decay of the phylogenetic similarity among communities) (Figure 5). However, when analysed only for communities at close successional stages, this relationship became insignificant as they approached the competitive equilibrium (Figure 5). This result indicates that variation in disturbance histories can drive dissimilarity in phylogenetic structure within a given region, especially when the region consists of communities at early successional stages. Although questions concerning community assembly have often been spatially framed (e.g. Mori et al., 2013; as suggested by Hobbs, Walker, & Walker, 2007), our model shows that the time frame can also affect, or even reverse, the inferences about community assembly processes.

Our model showed that the phylogenetic overdispersion driven by neighbourhood competition can arise regardless of the spatial scale (Figure 4b). In natural systems, overdispersion is mostly detected at a neighbourhood scale, and this phenomenon has been explained by the fact that biotic interactions mainly take place at this scale (Cadotte & Davies, 2016; Cavender-Bares et al., 2006;

Münkemüller et al., 2014; Swenson et al., 2007; Wang et al., 2015). In our model, overdispersion was detected even when the quadrat size was increased to 400 cells (a  $20 \times 20$  grid), despite the fact that we defined the competition zone (i.e. the spatial extent to which individuals reduce a resource) as the cells in a  $3 \times 3$  grid centred on each individual. This somewhat counterintuitive finding derives from the fact that a regular spatial distribution of individuals from each clade was maintained across the entire simulation plot, and therefore the abundances of different clades within a quadrat were more equal to each other than expected by chance irrespective of the quadrat size. In nature, the relative importance of competition among community assembly mechanisms can decrease with increasing spatial scale because of the increased importance of local environmental filtering (since environmental differences often correlate with spatial distances) or dispersal limitation. Nonetheless, our model indicates that the absolute importance of competition can be maintained at any spatial scale. Furthermore, overdispersion was observed even when new individuals were assumed to be dispersed around the pre-existing individuals (i.e. reproduction) in addition to immigration from outside the plot (Supporting Information Figure S5). This was likely because most of the reproduced individuals were outcompeted by individuals of later-arriving species with lower colonisation ability  $C$  but higher competitive ability  $R^*$ .

Successional niches have often been reported to be phylogenetically conserved (e.g. Norden et al., 2012; Letcher et al., 2015; Li, Cadotte, Meiners, Hua, Jiang, et al., 2015) and/or reflected in species' traits (e.g. seed mass, specific leaf area, and wood density; Kunstler et al., 2012; Lasky et al., 2014). Under such conditions (Figure 1), our model predicted that phylogenetic and functional clustering will arise as communities near competitive equilibrium (Figure 3b,d; Supporting Information Figure S4b,d). This prediction was consistent with that of Mayfield and Levine (2010). Actual field studies, however, have often found shifts from more closely related (functionally similar) to less closely related (dissimilar) species assemblages during succession (Letcher, 2010; Li, Cadotte, Meiners, Hua, Jiang, et al., 2015; Shoocher et al., 2015; Pastore & Scherer, 2016; reviewed in Meiners et al., 2015). There are several potential explanations for this discrepancy between the prediction and observations. One possibility is that the systems had not reached a competitive equilibrium at the time of the aforementioned studies (Letcher, 2010; Li, Cadotte, Meiners, Hua, Jiang, et al., 2015; Pastore & Scherer, 2016; Shoocher et al., 2015). For example, despite their analysis of 50 years of successional data, Li, Cadotte, Meiners, Hua, Jiang, et al. (2015) found that their plots transitioned from meadows to early secondary forests, and this ecosystem would likely require many more decades to truly reach equilibrium (however, note that this limitation was reasonable because their main focus was on understanding the change in community patterns during succession, not the equilibrium pattern per se). Another explanation would be the possible influence of environmental gradients other than the successional gradient. If species with similar successional niches result from convergent evolution (i.e. when distantly related taxa evolve to have similar environmental requirements), the assemblage

of those species should show overdispersion. Moreover, the evolution of successional niche specialisation can itself be contingent on other environmental gradients (Letcher, et al., 2015). Succession per se can also alter environmental conditions, as in the case of plant-soil feedbacks (Mori, Osono, Cornelissen, Craine, & Uchida, 2017), and this can drive communities to go through alternative transient states (Fukami & Nakajima, 2011) and perhaps even create greater local heterogeneity (Meiners et al., 2015; Mori, 2011). Therefore, even though we assumed a single axis of niche differences in this study (Figure 1), a natural extension of our model would be to account for the consequences of multiple axes, especially those that vary with the successional age of the communities.

Natural landscapes are almost always a patchwork of local communities that are at different successional stages (White & Pickett, 1985). Our individual-based model indicated that the community patterns could change temporally as a result of the sequential replacement of individuals of different species (Figures 3 and 5). We also showed that the patterns would depend on the structure of the metacommunity in addition to the focal community (Figure 3). These results suggest that careful consideration of the dynamic and individual-level aspects of succession is necessary when inferring community assembly processes in the field, where communities at different successional stages often exist in mixture. This issue might become increasingly important in the future given the increase in human-induced disturbances that initiate succession (Mori, 2011; Seidl, Schelhaas, Rammer, & Verkerk, 2014). Notably, in addition to pattern-based analyses, it would be informative to investigate the demographic parameters as a function of the intensity of neighbourhood competition (Kunstler et al., 2012; Lasky et al., 2014; Tatsumi, Owari, & Mori, 2016; Tatsumi, Owari, Yin, & Ning, 2014) and how this relationship translates into the displacement of individuals. Furthermore, incorporating intraspecific variation in such demographic parameters into individual-based models could allow us to predict the consequences of community assembly for evolutionary processes, including speciation and extinction (Davies, Allen, Bordade-Águia, Regetz, & Melián, 2011; Rosindell, Harmon, & Etienne, 2015). Based on the present results, we believe that theories based on a non-equilibrium, individual-level concept could be combined with long-term, high-resolution data to provide new insights into the consequences of the relatedness among individuals for community assembly.

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## AUTHORS' CONTRIBUTIONS

S.T. conceived the idea for this study and conducted the simulations and statistical analyses. S.T. wrote the manuscript with inputs from M.W.C. and A.S.M.

## DATA ACCESSIBILITY

This study does not include any data.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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