

## LETTER

# Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession

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### Abstract

Ecological communities often transition from phylogenetic and functional clustering to overdispersion over succession as judged by space-for-time substitution studies. Such a pattern has been generally attributed to the increase in competitive exclusion of closely related species with similar traits through time, although colonisation and extinction have rarely been examined. Using 44 years of uninterrupted old-field succession in New Jersey, USA, we confirmed that phylogenetic and functional clustering decreased as succession unfolded, but the transition was largely driven by colonisation. Early colonists were closely related and functionally similar to residents, while later colonists became less similar to the species present. Extirpated species were generally more distantly related to residents than by chance, or exhibited random phylogenetic/functional patterns, and their relatedness to residents was not associated with time. These results provide direct evidence that the colonisation of distant relatives, rather than extinction of close relatives, drives phylogenetic and functional overdispersion over succession.

### Keywords

Buell–Small Successional Study, colonisation, community assembly, extinction, phylogenetic community ecology.

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## INTRODUCTION

The assembly and maintenance of ecological communities reflect the net sum of many ecological processes that often act on species similarities and differences. One of the most accepted ideas in community ecology is that communities are the results of species sorting processes through environmental filtering and competitive exclusion (Silvertown 2004). With the advent of phylogenetic and trait-based community ecology, the co-occurrence of phylogenetically and functionally similar species (phylogenetic or functional clustering) is often interpreted as evidence for environmental filtering, while the coexistence of dissimilar organisms (overdispersion) has been generally attributed to competitive exclusion (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). Recently, this phylogenetic-patterns-as-proxy approach has been criticised as simplistic in the way it links mechanisms to observed patterns. In fact, there are a number of fundamental assumptions that are either unrealistic or not adequately assessed (see Goberna *et al.* 2014; Gerhold *et al.* 2015). Importantly, competitive exclusion could also drive phylogenetic and functional clustering, by excluding groups of ecologically similar species with low competitive abilities (Mayfield & Levine 2010), and the competition-overdispersion linkage in natural systems currently lacks evidence (see Bennett *et al.* 2013), though more tests are required.

However, phylogenetic and functional overdispersion are widespread patterns in natural communities across numerous taxa and ecosystems (reviewed in Swenson 2013), and the causes of such patterns remain elusive.

Succession has been a central theme in ecology for nearly a century, and has served as a lens to understand how ecological communities are assembled (Clements 1916; Meiners *et al.* 2015). With few exceptions, ecophylogenetic studies using space-for-time substitutions, which compared communities that differ in time since disturbance, often found that older, late-successional communities consist of more distantly related species (Letcher 2010; Letcher *et al.* 2012; Whitfield *et al.* 2012; Purschke *et al.* 2013; see Table S1 in Supporting Information for a summary). Such an overdispersion pattern has been generally attributed to the extinction of closely related and functionally similar species caused by the competitive exclusion (Purschke *et al.* 2013), but the actual effects of colonisation and local extinction on functional and phylogenetic patterns have never been actually observed. While ecophylogenetic analyses of static communities offer little insight to the dynamic mechanisms generating successional patterns, these mechanisms could be better understood with the availability of long-term data on successional dynamics.

Temporal phylogenetic and functional patterns could reflect several different ecological processes acting on colonisation and

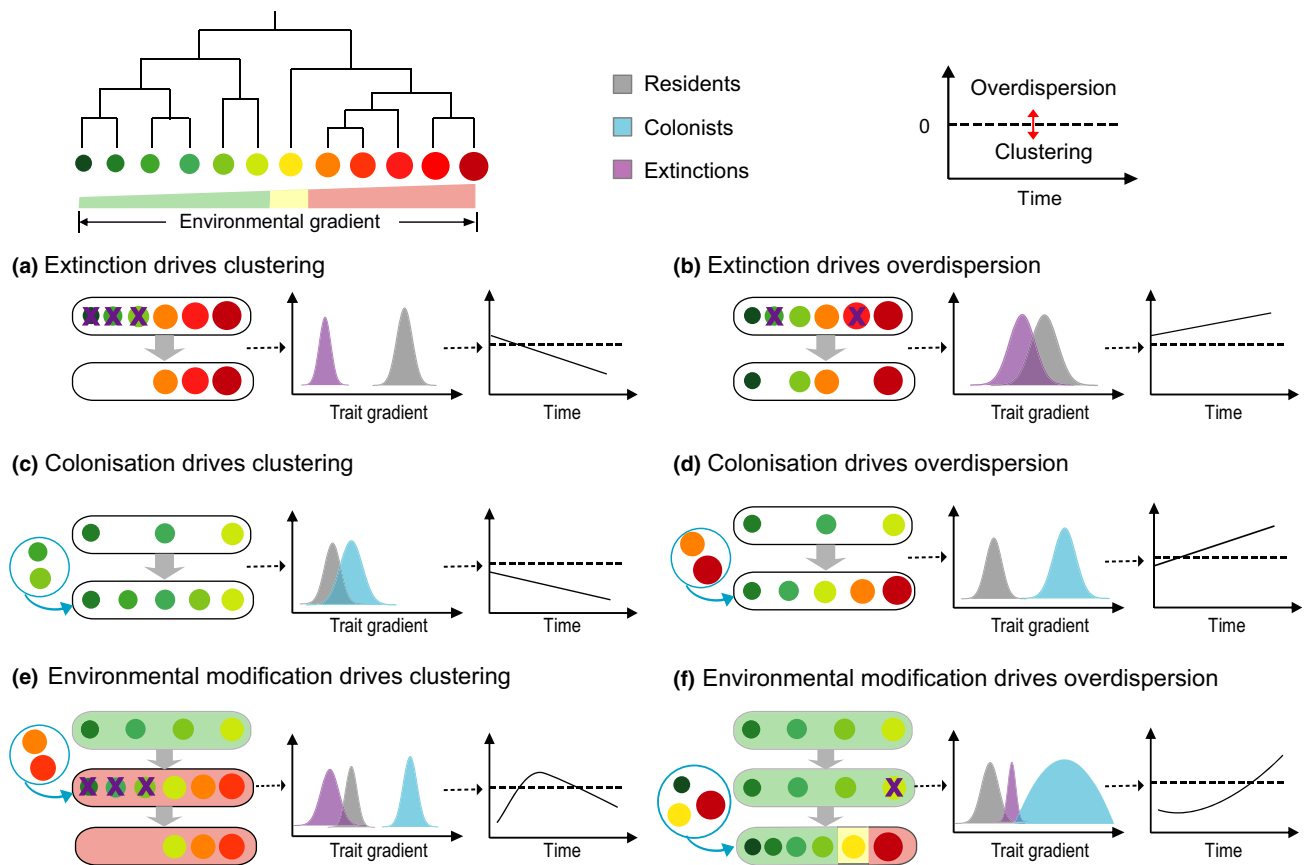
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**Figure 1** Potential effects of species colonisation and local extinction on community phylogenetic and functional patterns over succession. (a) Local species extinction eliminates species that are phylogenetically and functionally dissimilar to the residents, leading to clustering. (b) Extinction eliminates species that are phylogenetically and functionally similar to the residents, leading to overdispersion. (c) Species similar to the residents have higher chance to colonise, leading to clustering. (d) Species dissimilar to the residents have higher chance to colonise, leading to overdispersion. (e) Succession modifies the environment to facilitate the colonisation of the later successional species that are dissimilar to the residents, but eliminates early successional species that are similar to the residents. Dissimilarity among species first increases and then decreases over succession. (f) Environmental modification decreases the strength of abiotic filtering, allows diverse species that dissimilar to the residents to colonise, and community structure moves towards overdispersion.

local extinction, which could not be identified by space-for-time substitutions. Phylogenetic and functional clustering might be driven by the local extinction of species that are phylogenetically and functionally dissimilar to the species present in the community (Fig. 1a), or the colonisation of species that are phylogenetically and functionally similar to the residents (Fig. 1c). Likewise, overdispersion could be driven by the extinction of closely related species with similar traits (Fig. 1b), or the colonisation of species that are phylogenetically and functionally dissimilar to the species present in the community (Fig. 1d). Note that only the extinction patterns reflect competitive exclusion, colonisation is subjected to the influence of biotic resistance, including priority effects among closely related species (Peay *et al.* 2012), or other ecological processes, such as interspecific facilitation (Valiente-Banuet & Verdú 2013) and changes in abiotic conditions. Therefore, understanding the underlying mechanisms of community assembly requires separating the sequential processes of colonisation and local extinction, which are the real drivers of the community structure.

Past phylogenetic and functional analysis of succession have also ignored the dynamic properties of the local environment, and assembly processes were treated as a single event operating

in a single environment. However, it is well accepted that environmental conditions do not remain constant over succession, altering the strength and selectivity of abiotic and biotic filtering processes over time (Connell & Slatyer 1977). At early successional processes, the strong environmental filters may initially select good dispersers or disturbance-tolerant species from several clades of closely related species (Connell & Slatyer 1977; Walker & Chapin 1987; Helmus *et al.* 2010), and communities should show significant clustering. However, these early colonists could modify the environment that facilitates the colonisation of other species (Connell & Slatyer 1977). On the one hand, if environmental modification completely alters the local habitats, succession could be characterised by the wholesale replacement of one group of functionally similar species (e.g., shade-intolerant, fast growing annuals) with another group of functionally similar species (e.g., long-lived, tall perennials). Therefore, late-colonisers would be similar to one another but dissimilar to early colonisers, and early colonisers with similar traits would disappear from the modified habitats (Fig. 1e). Under this scenario, phylogenetic and functional dissimilarities among species might increase at intermediate stages of succession that contain both early and

late successional species, but would move towards clustering again at later stages due to the loss of large clades of early successional species. On the other hand, the strength of environmental filtering might decrease as succession unfolds (Connell & Slatyer 1977; Walker & Chapin 1987). As the strength of abiotic filtering diminishes, resource heterogeneity and the carrying capacity of the local habitat would increase. Thus, not only late successional species with similar traits, but also diverse species with dissimilar traits to the residents might colonise because they are more likely to occupy different microhabitats with minimal resource overlap with the residents (Fig. 1f). Under this scenario, phylogenetic and functional community structures would move from clustering towards overdispersion because of the temporal changes in environmental conditions, challenging the space-for-time inferences that overdispersion implies competitive exclusion.

To explore the applicability of the aforementioned hypotheses to natural communities, we conducted a community functional and phylogenetic analysis on 44 years of uninterrupted succession across 480 permanent plots in 10 replicate fields in the Buell–Small Succession Study located in New Jersey, USA. This study represents the longest continuous study of post-agricultural secondary succession (Pickett *et al.* 2001; Cadenasso *et al.* 2009). We compared the temporal phylogenetic and functional trends for both colonisation and extinction, and specifically examined whether the commonly found overdispersion in later successional stages was caused by the extinction of closely related species with similar traits due to competitive exclusion (Fig. 1b), or the colonisation of distant relatives with dissimilar traits due to environmental modification and other ecological processes (Fig. 1d, f).

## MATERIALS AND METHODS

### Study site and data collection

We used data collected from the Buell–Small Succession Study, a long-term experimental study of successional dynamics within abandoned agricultural land at the Hutcheson Memorial Forest Center (HMFC) in the Piedmont of New Jersey, USA (40°30' N, 74°34' W). The Buell–Small Succession Study comprises ten abandoned agricultural fields that have been continuously monitored to investigate vegetation dynamics following row-crop agriculture. Initiated in 1958, these fields were abandoned in pairs over an 8-year span and varied in the pre-abandonment agricultural treatments. Forty-eight permanently marked 0.5 × 2.0 m plots were arranged in a grid in each field at abandonment. The permanent plots were sampled every year from 1958 to 1979, with the percent cover of species recorded. Since 1979, sampling was switched to alternate years, with half of the fields sampled each year; sample size was, therefore, reduced from 480 to 240 plots for each year. Successional transitions within the Buell–Small Succession Study represent a typical successional trajectory in the Eastern North America, having nearly completed the transition from an open agricultural land to the young deciduous forests (Cadenasso *et al.* 2009). Year of abandonment and abandonment conditions have been found less important than field age in their effect on species composition (Myster &

Pickett 1990). Therefore, our analyses involving time were conducted on field age rather than calendar year following the most recent research on the Buell–Small Succession Study (Meiners *et al.* 2004; Cadenasso *et al.* 2009). Our analyses were also restricted to ages 0–44, as all fields cover this age span. Patterns of community composition over succession were visualised with detrended correspondence analysis, a multivariate technique that ordines plots in all age stands based on similarities in species composition.

### Community phylogeny and functional traits

To construct an appropriate species pool for phylogenetic analyses, we excluded 10 non-seed plants, which collectively comprised 0.05% of the total cumulative cover over succession. The final list for the entire community species pool included 325 seed plants, with 3 gymnosperms and 322 angiosperms. For each species, three sequences were obtained from GenBank: two plastid DNA genes (*rbcL* and *matK*) and one nuclear DNA gene (*ITS*, containing *ITS1*, 5.8s and *ITS2*). Of the 325 species, 259 had at least one gene represented in GenBank. Fifteen species could only be identified to the genus level, and the sequence data of the remaining 51 species were not available in the GenBank. For these 66 species, we used the sequences from congeneric relatives known to occur in North America as a proxy. We also used a species diverged early in seed plant evolution – *Cycas revoluta* – to serve as the outgroup. Sequences were aligned with MUSCLE (Edgar 2004) and the best-fit model of nucleotide substitution for each region was selected by jModeltest (Posada 2008).

We performed Bayesian reconstructions using BEAST version 1.7.5 (Drummond *et al.* 2012), which estimates the phylogenetic relationships and divergence times simultaneously. We used six fossil records (i.e., Angiosperm, Monocots, Eudicots, Rosids, Asterids and Poaceae) as node age priors according to the Angiosperm Phylogeny Group tree (Angiosperm Phylogeny Group 2009). Parameters were estimated by using a Markov chain Monte Carlo (MCMC) simulation for 30 million generations. The selected GTR + G + I substitution model, an uncorrelated lognormal relaxed molecular clock model and a Yule speciation tree prior were used for the three gene regions. We sampled the runs every 1000 generations and the first 3000 trees were discarded as burn-in. Convergence was checked using Tracer version 1.5 (<http://beast.bio.ed.ac.uk/Tracer>). Among the posterior distribution trees, the maximum clade credibility tree was used to quantify community phylogenetic patterns by TreeAnnotator version 1.7.5 (Drummond *et al.* 2012). We also generated a maximum likelihood phylogeny using PHYML with a BIONJ starting tree (Guindon & Gascuel 2003), and a seed plant supertree by using the database Phylomatic (R20120829). As the three phylogenies had similar topological structure, we only report results based on the Bayesian molecular phylogeny in the main text.

The functional trait measurements were performed generally following the protocols of Cornelissen *et al.* (2003). In this study, we collected four continuous traits (potential plant height, seed mass, specific leaf area and leaf dry matter

content) and five categorical traits (growth form, life span, pollination, seed dispersal and clonal reproduction) for our analysis. Growth form was coded with five levels (graminoid = 1, forb = 2, vine = 3, shrub = 4, tree = 5), life span with three levels (annual = 1, biennial = 2, perennial = 3), pollination and seed dispersal with two levels (abiotic and biotic) and clonality with two levels (true and false). These traits were chosen to represent multidimensional functions of plants associated with resource use, dispersal ability, competitive ability, species tolerance and successional strategy. For example, plant height, specific leaf area and leaf dry matter content were used to represent light capture, resource acquisition and allocation strategies of species, which are directly associated with competitive ability (Swenson *et al.* 2012; Lasky *et al.* 2014). Seed mass, pollination, seed dispersal and clonal reproduction are commonly associated with the dispersal ability and colonisation strategies of species (Cornelissen *et al.* 2003). Data on potential plant height, seed mass and all five categorical traits were determined from open database and primary literature (e.g., USDA Plants Database, Seed Information Database). Species leaf area and leaf dry matter content of each species were obtained from 10 or more individuals from the study region whenever possible following standard protocols. To assess the relationship between phylogenetic relatedness and trait similarity, we used Blomberg's  $K$  statistic (Blomberg *et al.* 2003) and Pagel's  $\lambda$  statistic (Pagel 1999) to quantify the phylogenetic signal of the four continuous traits. The significance of the phylogenetic signals was determined by comparing the observed  $K$  and  $\lambda$  values with a null distribution that simulates random trait datasets on the phylogeny for 999 times. The phylogenetic signals of categorical traits were determined by the 'Fixed Tree, Character Randomly Reshuffled' model proposed in Maddison & Slatkin (1991). A Gower distance (Gower 1971), which allows for missing data and categorical data, was used to generate a functional distance matrix that represented the similarity of species in a multivariate trait space. In order to apply identical analytical methods to the trait and phylogenetic data, a functional trait dendrogram was constructed by using the Gower distance matrix and UPGMA clustering (Petchey & Gaston 2002).

### Community phylogenetic and functional structure measures

Mean pairwise phylogenetic distance (MPD) and mean nearest taxon phylogenetic distance (MNTD) among species in each plot were calculated to evaluate the temporal changes in the phylogenetic structure (Webb *et al.* 2002). We performed this analysis by using both abundance and incidence-based data. For abundance-weighted indices, we weighted the pairwise distances among species by their relative coverage. An identical framework was used to calculate the mean pairwise functional distance (MFD) and mean nearest taxon functional distance (MNFD) using the trait dendrogram. Further, these indices were compared to null models to test whether the phylogenetic and functional structures differed from random expectations. Specifically, random communities were generated by maintaining the species richness of each plot, but making the identities of those species random drawn draws from the whole species pool. The standardised

effect sizes (SES) of MPD, MNTD, MFD, and MNFD were calculated as:

$$\text{Standardised effect size} = (\chi_{obs} - \chi_{null}) / SD_{null}$$

where  $\chi_{obs}$  is the observed MPD, MNTD, MFD or MNFD value,  $\chi_{null}$  is the mean of the simulated values and  $SD_{null}$  is the standard deviation of the simulated values. The SES.MPD and SES.MNTD are equivalent to  $-1$  times the net relatedness index (NRI) and the nearest taxon index (NTI) respectively (Webb *et al.* 2002). Positive SES values indicate phylogenetic or functional overdispersion, whereas negative values indicate clustering (Webb *et al.* 2002). We calculated the SES.MPD, SES.MNTD, SES.MFD and SES.MNFD for each plot in every age, and these analyses were performed by Phylocom 4.2 (Webb *et al.* 2008) and R package *picante* (Kembel *et al.* 2010) in R version 3.10 (R Development Core Team 2014). For these and all the subsequent analyses, we removed all plots with a single species at each sampling time.

Recent studies highlight that statistical power of analyses on phylogenetic and functional structures can be sensitive to different phylogenetic and trait approaches (Kress *et al.* 2009), null models (Hardy 2008) and species pools (Cavender-Bares *et al.* 2006). Therefore, we compared the SES values using three different phylogenies (Bayesian phylogeny, maximum likelihood phylogeny and Phylomatic tree), two different functional dissimilarity metrics (dendrogram-based and Gower distance-based), four different null models in Phylocom (null model 0: shuffle species labels across distance matrix; null model 1: randomise community matrix by drawing species from species pool; null model 2: randomise community matrix by drawing species from phylogeny or trait dendrogram pool; null model 3: randomise community matrix with the independent swap algorithm) and four different species pools (entire community species pool including all 325 species, all 322 angiosperm species excluding gymnosperms, a subset of species that were present in each field, a subset of species that were present in each plot) (see Supporting Information for details). We also repeated our analysis at the field scale by summing the coverage of each species in 48 plots within each field to test whether the phylogenetic and functional patterns are robust at a larger spatial scale (see Supporting Information).

### Phylogenetic and functional patterns of species colonisation and local extinction

To assess the relative contribution of colonisation and local extinction to the phylogenetic and functional structures over succession, we first combined time steps into successional stages. Our successional stages were defined as each 4-year period after abandonment. Since data were collected in alternate years after 1979, if the data of age  $T_i + 4$  were not available, we used the data from age  $T_i + 5$  as a proxy. We subdivided the data by classifying the species into three groups at each time frame: colonists (species that did not exist in the plot at  $T_i$  but were present at  $T_i + 4$ ), local extinctions (species that were present at  $T_i$  but were absent from the plot at  $T_i + 4$ ) and residents (species that were present at  $T_i$  and remained in the plot at  $T_i + 4$ ).



The phylogenetic and functional similarities between colonists and residents of each plot at each time frame were quantified using four dissimilarity metrics:  $\beta$ MPD,  $\beta$ MNTD,  $\beta$ MFD,  $\beta$ MNFD. The  $\beta$ MPD and  $\beta$ MFD calculate the mean pairwise phylogenetic and functional distance between colonists and residents in each plot, while  $\beta$ MNTD and  $\beta$ MNFD calculate the mean nearest taxon phylogenetic and functional distance between the colonists and residents respectively. These metrics were standardised by comparing to those expected under null models, using the same formulae as mentioned above. Specifically, we used a null model that kept the residents in each plot unchanged, and maintained the number of colonists, but made the identities of colonists randomly drawn from the species pool by excluding the species already present in the plot. This null model implies that each species has an equal chance to colonise the plot. Negative SES values suggest that colonists are more closely related or similar to the residents than by chance, while the positive values suggest the opposite. Similarly, we calculated the  $\beta$ MPD,  $\beta$ MNTD,  $\beta$ MFD and  $\beta$ MNFD between local extinctions and residents for each plot, which were also standardised by comparing to the values expected under random assembly. For this purpose, we kept the number of species going locally extinct in each plot unchanged, but made the identity of the extirpated species random drawn from the present species in that plot, assuming that each species in the plot has an equal chance to go locally extinct. Negative values suggest the species more closely related to the residents, or more functionally similar to the residents, have a greater chance to go locally extinct. We performed these analyses for each plot at each time frame, by using *comdist* and *comdistnt* function in Phylocom.

Phylogenetic and functional structures shift over succession not only depend on the relatedness of the colonists and local extinctions to the residents, but also on the phylogenetic and functional structures of themselves. Thus, we calculated the SES.MPD, SES.MNTD, SES.MFD and SES.MNFD for the subset of colonists and local extinctions in each plot, using the identical null models for SES. $\beta$ MPD, SES. $\beta$ MNTD, SES. $\beta$ MFD and SES. $\beta$ MNFD as mentioned above (see Supporting Information for details).

#### Phylogenetic and functional patterns in abundance distribution

Besides the gain and/or loss of species, species might also shift their relative abundances during community assembly, which could also contribute to the observed changes in phylogenetic and functional structures over succession. To investigate changes in phylogenetic and functional patterns in abundance distribution during succession, we calculated phylogenetic and functional abundance deviation indexes (APD) for all plots. The APD was calculated by comparing the incidence and abundance measures of MPD (or MFD if calculating functional abundance dispersion indexes) (Hardy 2008; Allan *et al.* 2013):

$$ADI = (MPD - \frac{\sum_i \sum_{j \neq i} f_i f_j PD_{ij}}{\sum_i \sum_{j \neq i} f_i f_j}) / MPD$$

where MPD is the incidence-based mean pairwise distance as we mentioned before,  $f_i$  is the relative abundance of the  $i$ -th

species in the plot,  $f_j$  is the relative abundance of the  $j$ -th species and  $PD_{ij}$  is the phylogenetic or functional distance between species  $i$  and  $j$ . This tends to create confusion as positive values indicate clustered abundance distributions. In our study, we transformed ADI by multiplying it by  $-1$ . As such, we presented  $-1 \times ADI$  for every plot in each year, so that positive values indicate overdispersed abundance distributions, whereas negative values indicate clustered abundance distributions.

#### Statistical analysis

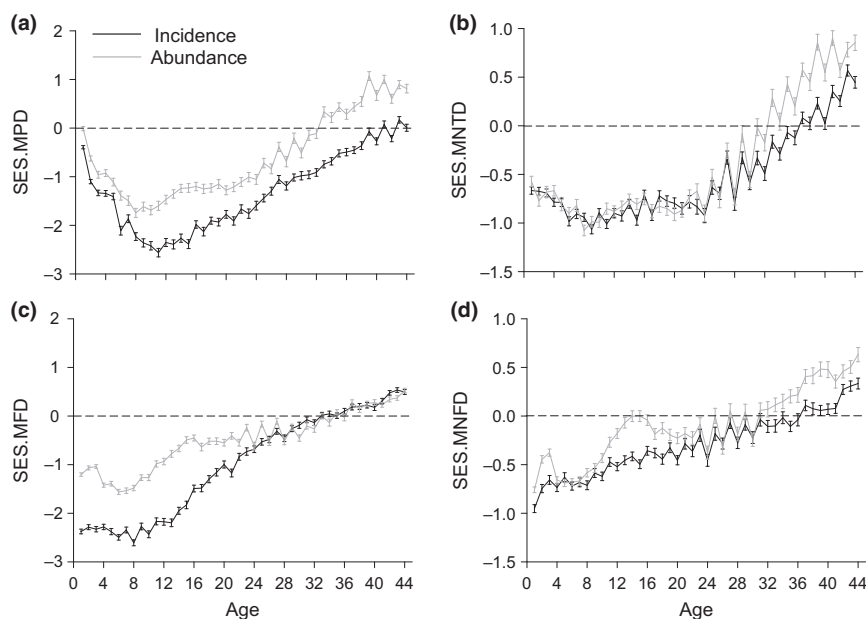
To examine the dynamic changes in phylogenetic and functional community structures over succession, we used mixed effects models to fit SES.MPD, SES.MNTD, SES.MFD and SES.MNFD as a function of successional age, by using the lme4 package in R (Bates *et al.* 2014). Age was treated as a single continuous fixed factor, and the 10 fields and 48 plots nested within each field were considered as random effects. We fitted varying slope and varying intercept models to allow the slope of age to vary by field and plot. Age was entered as a linear or quadratic term, or was not included at all (a model with intercept only). The statistical significance of the fixed effects was estimated by Satterthwaite's approximations, and the model with the best fit was identified based on Akaike's Information Criterion. Identical mixed effect models were used to examine the temporal trends of SES. $\beta$ MPD, SES. $\beta$ MNTD, SES. $\beta$ MFD and SES. $\beta$ MNFD of the colonists and local extinctions to residents, SES.MPD, SES.MNTD, SES.MFD and SES.MNFD of the subset colonists and local extinctions, and phylogenetic and functional abundance distributions.

## RESULTS

### Phylogenetic and functional structures over succession

Overall, the Buell–Small Succession Study represents a typical secondary successional trajectory over time. There were shifts in dominant phylogenetic and functional groups through succession, transitioning from short-lived herbaceous species (Poaceae and Asteraceae), to long-lived perennial herbs and shrubs (e.g., Rosaceae) to trees (e.g., Fagaceae, Sapindaceae and Oleaceae) with a diverse herbaceous understory (Fig. S1a). Accordingly, detrended correspondence analysis revealed that the plots were gradually converging in species composition over succession (Fig. S1b).

All nine measured traits exhibited significant phylogenetic signals ( $P < 0.05$ , Table S2), and both phylogenetic and functional structures of plots in Buell–Small Succession Study showed clear temporal trends over succession (Fig. 2). The best-fit models of phylogenetic community structure included both linear and quadratic terms of age (Table S3). Specifically, the SES.MPD and the SES.MNTD decreased towards significant clustering for the first dozen years of succession, but then consistently increased with time, indicating that the community phylogenetic structure shifted towards overdispersion in later successional stages (Fig. 2a, b). The SES.MFD and SES.MNFD increased monotonically with time since



**Figure 2** Community phylogenetic and functional structures over succession. The temporal changes of phylogenetic and functional structures were measured as standardised effect sizes for mean pairwise phylogenetic distance (SES.MPD, a), mean nearest taxon phylogenetic distance (SES.MNTD, b), mean pairwise functional distance (SES.MFD, c), and mean nearest taxon functional distance (SES.MNFD, d) of the 480 plots over 44 years of succession, on the basis of Bayesian phylogeny and functional dendrogram separately. We performed the analysis using both incidence (black) and abundance-based (grey) data. Positive values indicate overdispersion whereas negative values indicate clustering. Each point shows the mean SES values among all plots within each successional age. Error bars represent standard errors.

abandonment, and communities transitioned from functional clustering at the early stages to overdispersion at the final stages (Fig. 2c, d; Table S3). Temporal patterns based on incidence and abundance measures were congruent with each other (Fig. 2). The increasing trends towards overdispersion were also robust to different phylogenetic and functional approaches (Fig. S2–S3), different null models (Fig. S4) and different species pools (Fig. S5). The temporal changes at field scales were weaker with larger variations, but remained significant (Fig. S6, Table S4).

#### Phylogenetic and functional patterns of species colonisation and local extinction

Colonisation showed qualitatively the same temporal trends with community structure.  $SES.\beta MPD$ ,  $SES.\beta MNTD$  and  $SES.\beta MNFD$  of colonists to residents showed a unimodal relationship with age, slightly decreasing in the early successional stages, but then significantly increasing at later stages of succession (Fig. 3, Table S5). In contrast,  $SES.\beta MFD$  increased monotonically over succession. In general, colonists were more similar to the residents early in succession than expected by chance, but gradually showed decreasing relatedness and similarities to the pool of residents. Further, colonists were initially phylogenetically and functionally clustered, coming from several clades of closely related species with similar traits, but their relatedness and similarities significantly decreased as succession proceeded (Fig. S7, Table S5).

In contrast, phylogenetic and functional relatedness of local extinctions to the residents showed weak relationships with successional stages. Although  $SES.\beta MNTD$  decreased linearly

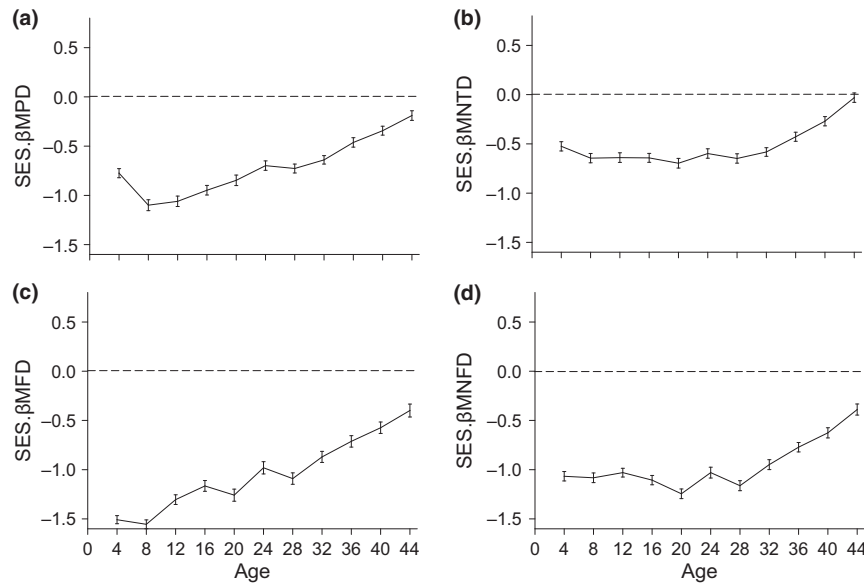
over succession, the intercept-only model had the most support for  $SES.\beta MPD$ ,  $SES.\beta MFD$  and  $SES.\beta MNFD$ , indicating that the phylogenetic and functional patterns of species exclusion were not associated with time (Fig. 4, Table S5). Further, the locally extinct species were generally more distantly related to the residents than by chance, or exhibited random patterns (Fig. 4). We found no evidence that the species more closely related to the residents, or more functionally similar to the residents, had a greater chance to go locally extinct.

#### Phylogenetic and functional abundance distributions over time

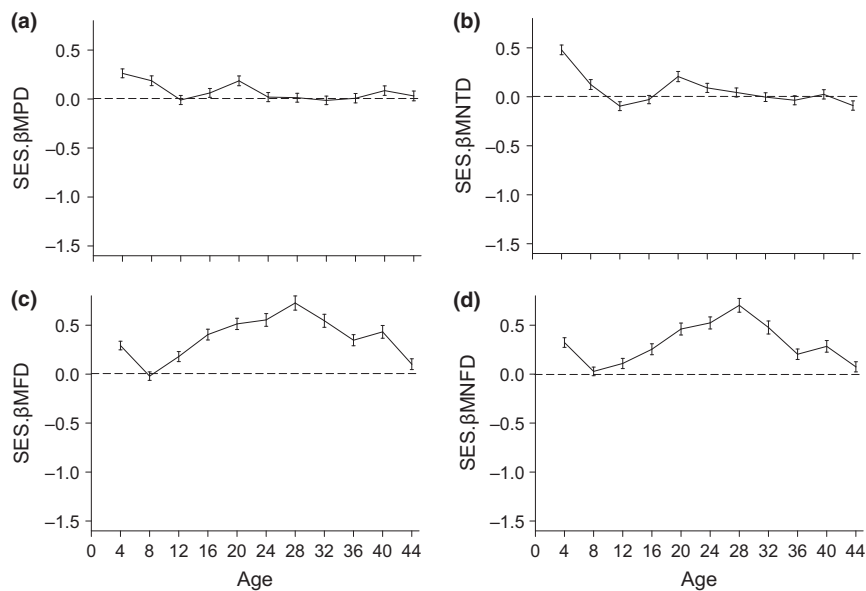
Phylogenetic abundance distributions showed nearly identical temporal trends with phylogenetic community structure. The best-fit model included both linear and quadratic terms of age, indicating that communities gained clustered abundance distribution in early stages, but abundant species tended to be more distantly related with each other later in succession (Fig. 5, Table S5). Communities also developed functionally overdispersed abundance distributions in later successional stages, but such distributions showed larger variability, and was less associated with time, with the intercept-only model receiving the best support (Table S5).

#### DISCUSSION

Phylogenetic and trait overdispersion have been commonly observed in natural communities, especially for the stable and late-successional communities with low disturbance (Letcher 2010; Norden *et al.* 2012; Whitfield *et al.* 2012; Purschke *et al.*



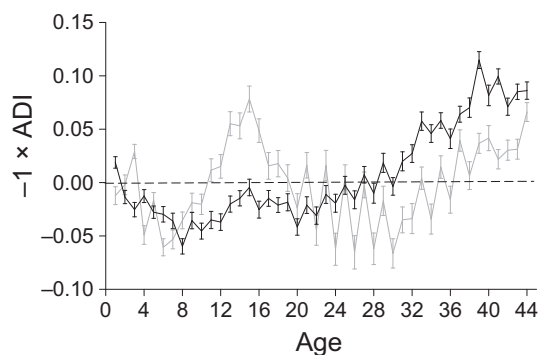
**Figure 3** Phylogenetic distances and functional dissimilarities of colonists to residents over succession. The phylogenetic distances and functional dissimilarities between colonists and residents were calculated as the SES.βMPD (a), SES.βMNTD (b), SES.βMFD (c) and SES.βMNFD (d) in each time frame during succession, by comparing the observed values to the null models that randomly draw colonists from the entire species pool. Negative values indicate colonists are more similar to the residents than random draw from the species pool, while the positive values suggest the opposite. Error bars represent standard errors.



**Figure 4** Phylogenetic distances and functional dissimilarities of locally extinct species to residents over succession. The phylogenetic distances and functional dissimilarities between local extinctions and residents were calculated as the SES.βMPD (a), SES.βMNTD (b), SES.βMFD (c) and SES.βMNFD (d) in each time frame during succession, by comparing the observed values to the null models that randomly draw local extinctions from the species present in the plot. Negative values indicate local extinctions are more similar to the residents than random draw from the species present in the plot, while the positive values suggest the opposite. Error bars represent standard errors.

2013). Competitive exclusion of closely related species is often inferred as the underlying mechanism (Cavender-Bares *et al.* 2009; Swenson 2013). However, recent studies suggest that competitive exclusion might not necessarily lead to overdispersion, but would also trigger phylogenetic clustering (Fig. 1a, also see Mayfield & Levine 2010; Goberna *et al.* 2014), or be

unrelated to phylogenetic structure (Bennett *et al.* 2013). Therefore, understanding the causes of overdispersion in natural communities remains as a major challenge for phylogenetic and functional community ecology. Here, combining well-resolved molecular phylogeny and functional trait data, our results confirmed that both phylogenetic and functional com-



**Figure 5** Temporal changes in phylogenetic (black) and functional (grey) abundance dispersion indexes (ADI) over succession. Positive values of  $-1 \times \text{ADI}$  indicate overdispersed abundance distributions, and negative values indicate clustered abundance distributions. Each point shows the mean values among all plots within each successional age. Error bars represent standard errors.

munity structures could transition from early clustering to overdispersion at later stages. More importantly, by using the long-term data, we demonstrated that such a transition was primarily driven by the colonisation of distantly related species, rather than the loss of closely related species, consistent with our hypotheses that environmental modification drives overdispersion (Fig. 1f). These results urge us to reconsider the traditional theory that overdispersion implies competitive exclusion, which may lead to a new interpretation of phylogenetic and functional community structures.

The core theoretical justification behind recent chronosequence approaches, which suggested the transition from clustering to overdispersion was driven by competitive exclusion (e.g., Table S1), is that: (1) competitive exclusion should be more likely to occur among closely related species with similar traits because of the large niche overlap and (2) such patterns will become more prominent at later successional stages because the strength of the species competition would increase as communities mature (Huston & Smith 1987). Our results challenge these two assumptions. First, if competition excludes closely related species, we would expect the extirpated species to be more closely related to the resident species than by chance (as shown in Fig. 1b). However, we found no evidence that species more closely related to the residents had a greater chance to go locally extinct. In contrast, the extirpated species were either more distantly related to the residents, or not different from a random sampling from the plots (Fig. 4). Extirpated species also became more closely related to each other than by chance at later successional stages (Fig. S8), which suggests that local species extinction could exclude clades of closely related species with similar traits (Fig. 1a). Second, the phylogenetic and functional distances between local extinctions and the residents were not associated with time, in contrast to the assumption that the competitive exclusion of closely related species would become increasingly important as succession unfolds. Together, considering local species extinction alone, the loss of species distantly related to the residents would drive the communities to become even more clustered, rather than towards overdispersion.

The extinction pattern cannot explain why communities went from clustering to overdispersion. Rather, the explanation lies with species colonisation. In our study, early successional communities were dominated by closely related short-lived herbaceous species (Poaceae and Asteraceae), which share similar acquisitive traits to enable rapid growth and resource capture. As succession proceeded, species functionally dissimilar to the residents (e.g., long-lived tall perennials) began to colonise the community (Fig. 3). These results are consistent with our hypothesis that environmental modification facilitated the colonisation of the species that were distantly related and functionally dissimilar to the residents (Valiente-Banuet & Verdú 2013), decreasing the phylogenetic and functional clustering over succession (Fig. 1f). In contrast, our results do not support the idea that succession can simply be characterised as the replacement of one group of functionally similar early successional species with another group of functionally similar later successional species (Fig. 1e). In our study, late-stage colonists included not only closely related species with specialised traits (e.g., Fagaceae, Sapindaceae and Oleaceae), but also species from wider diversity of lineages with diverse traits (e.g., Brassicaceae and Vitaceae). The phylogenetic and functional dissimilarities among colonists significantly increased over time (Fig. S7), which is consistent with the idea that environmental modification could decrease the strength of environmental filtering, increase the carrying capacity of the local habitat and facilitate the colonisation of the species with different functional traits.

An alternative, but not mutually exclusive, explanation of the increasing dissimilarities between colonists and residents is that the presence of close relatives would inhibit the likelihood of a species' colonisation through biotic resistance. For example, the strength of priority effects may be much stronger among close relatives with similar functional traits, because they often occupy similar niches (Peay *et al.* 2012; Tan *et al.* 2012). Therefore, such competition effects could potentially prevent the establishment of species that are phylogenetically and functionally similar to the residents. To distinguish the effects of competition and environmental modification on species colonisation, we repeated our analysis at the field scale, where the role of biotic interactions would be presumably reduced compared to the smaller plot scale (Swenson 2013). We found weaker but still significant patterns at the larger field scale, suggesting that both environmental modification and competition may have played important roles for regulating the phylogenetic and functional patterns of the colonists. Further, communities developed phylogenetically and functionally overdispersed abundance distributions in the later succession stages, which is consistent with a recent study suggesting that competitive interactions, such as limiting similarity processes, may limit maximum abundances for closely related species (Allan *et al.* 2013). These results highlight that competition among closely related species may suppress the immigration of closely related species with similar traits through biotic resistance (e.g., Peay *et al.* 2012), or prevent them from attaining high abundances (Norden *et al.* 2012; Allan *et al.* 2013), but competition does not necessarily lead to the exclusion of phylogenetically and functionally similar species (Gerhold *et al.* 2015).



Using both phylogenetic and trait approaches, we provide the first evidence that the colonisation of more distantly related species drives communities towards overdispersion, overriding the influences of local extinction that lead to clustering. Our study complements recent trait-based approaches that mainly focus on species growth (e.g., Kunstler *et al.* 2012) and extinctions (e.g., Lasky *et al.* 2014), and shows that species colonisation could shape the temporal change in the community structure of successional assemblages. Our results also present challenges to community assembly and species coexistence theories focused solely on extinction and competitive exclusion, which often implicitly assume that species colonisation is a purely neutral process without trait or phylogenetic bias. Although phylogenetic relatedness and our measures of trait dissimilarity may not fully explain the ecological differences between species (Swenson 2013), and that the relative importances of competition and environmental modification for species colonisation need to be further distinguished, our study highlights the importance of long-term, high-resolution data, especially those that document the gain or loss of species over time, in providing mechanistic insights into community assembly and species coexistence.

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#### AUTHORSHIP

SPL, MWC and WSS developed and framed research questions. SJM collected the data used in this analysis. SPL, MWC, ZSH, SJM and LJ analysed the data. SPL and MWC wrote the first draft of the manuscript and all authors contributed to discussing the results and editing the manuscript.

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