

LETTER

Convergence and divergence in a long-term old-field succession: the importance of spatial scale and species abundance

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Abstract

Whether plant communities in a given region converge towards a particular stable state during succession has long been debated, but rarely tested at a sufficiently long time scale. By analysing a 50-year continuous study of post-agricultural secondary succession in New Jersey, USA, we show that the extent of community convergence varies with the spatial scale and species abundance classes. At the larger field scale, abundance-based dissimilarities among communities decreased over time, indicating convergence of dominant species, whereas incidence-based dissimilarities showed little temporal trend, indicating no sign of convergence. In contrast, plots within each field diverged in both species composition and abundance. Abundance-based successional rates decreased over time, whereas rare species and herbaceous plants showed little change in temporal turnover rates. Initial abandonment conditions only influenced community structure early in succession. Overall, our findings provide strong evidence for scale and abundance dependence of stochastic and deterministic processes over old-field succession.

Keywords

Beta diversity, Buell-Small Succession Study, community assembly, historical contingency, null model, stochasticity, successional pathways, temporal turnover.

Ecology Letters (2016) **19**: 1101–1109

INTRODUCTION

The investigation of plant successional dynamics has been a central theme of community ecology, but elucidating plant successional trajectories and mechanisms remains a major challenge (Meiners *et al.* 2015a). This issue is reflected in the ongoing debate about how stochastic and deterministic processes influence community assembly over succession (Dini-Andreote *et al.* 2015). The traditional view holds that plant succession is largely deterministic, driven by abiotic and biotic filters such as resource availabilities (Drury & Nisbet 1973), facilitation (Connell & Slatyer 1977) and competition (Huston & Smith 1987). However, there is an increasing awareness of the role of stochasticity in succession, including probabilistic dispersal, colonisation and local extinction (e.g. del Moral 1999; Kreyling *et al.* 2011). Notably, although the value of long-term longitudinal data for understanding succession has been recognised (e.g. Pickett 1989; Taverna *et al.* 2005; Norden *et al.* 2015), most successional studies remain focused on chronosequences, a space-for-time substitution approach inferring temporal trends from studies of sites with different successional ages. Chronosequence-based inferences, however, can differ markedly from longitudinal dynamics in natural communities (Feldpausch *et al.* 2007; Johnson & Miyanishi

2008), pointing to the need for longitudinal data in well-studied successional systems (e.g. old-field succession).

With the availability of long-term data, analysis of the directionality, convergence and rate of change in succession would provide complementary insights into community assembly (Facelli & D'Angela 1990). Under the deterministic perspective, successional changes are directional, with both dissimilarities among patches and successional rates decreasing over time, as communities converge towards similar stable states resistant to further colonisation and invasion (Lepš 1987; Anderson 2007). The influences of initial conditions should also decline over time, as competition intensifies with increasing population sizes overriding the effect of historical events (Margalef 1963). In contrast, stochastically structured plant communities should remain divergent and the temporal turnover rates of these communities are not necessarily associated with time. A lack of convergence could be driven by stochastic events acting independently on sites (e.g. stochastic dispersal, colonisation and local extinction), which could maintain or even increase beta diversity among sites over time (Chase 2003; del Moral & Lacher 2005). Historical events, such as different initial states of local communities, could initially select different species early in succession and then either deter or facilitate the colonisation of particular species

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through priority effects (Chase 2003; Fukami 2015). Some ecologists have suggested that the influences of initial conditions may persist through succession, maintain variation among communities and result in the generation of alternative community states (Egler 1954; Prach *et al.* 2007; Kreyling *et al.* 2011). These scenarios have been examined in previous plant succession studies, which have reported both convergence (Prach 1985; Alday *et al.* 2011) and divergence (Fukami *et al.* 2005; Tsuyuzaki 2009; Taylor & Chen 2011), as well as more complex patterns (Christensen & Peet 1984; Inouye & Tilman 1988; del Moral & Lacher 2005), yielding few general conclusions (Meiners *et al.* 2015a).

The consideration of spatial scale and species abundance is likely key for understanding the divergent results across studies. Presumably, the patterns observed at coarser spatial scales are less likely to be influenced by stochastic events such as probabilistic dispersal and priority effects that influence finer scales, but are instead governed more by deterministic environmental filtering of species that are present in the regional pool (Allen & Hoekstra 1990; Bazzaz 1996). Therefore, plant succession could be more convergent at coarser spatial scales, as environmental conditions determine the available niches and select the species that best fit the niches. At finer spatial scales, stochastic dispersal, colonisation and extinction processes are expected to vary from site to site, and local communities may remain divergent over time as local diversity is dominated by spatially patchy events (Kreyling *et al.* 2011). Likewise, dominant species may be strongly affected by deterministic filtering as they occupy core niche positions across communities (Umaña *et al.* 2015), whereas rare species may be more affected by demographic stochasticity due to their small population sizes (Orrock & Watling 2010). Therefore, we hypothesise that the composition of dominant species converges at coarse scales over succession, while that of rare species diverges at fine scales during plant succession. However, previous studies have typically focused on a single spatial scale and have not examined the role of dominant vs. rare species in the context of successional trajectories, hindering our ability to fully understand the potential scale and abundance dependence of community assembly over long-term plant succession.

Here, we report the analysis of a continuous, long-term study of old-field secondary succession, the Buell-Small Succession Study (see Appendix A in Supporting Information). In this study, the species composition and abundance in 480 plots (fine scale) of 10 fields (coarse scale) have been continuously monitored for more than 50 years, making this study the longest continuous study of post-agricultural secondary succession (Pickett *et al.* 2001; Cadenasso *et al.* 2009). By analysing the long-term longitudinal data from this system, we aimed to address three interrelated questions on community assembly of old-field secondary succession:

- (1) Do communities converge towards a similar community state?
- (2) Do successional rates decline over time, with communities becoming more stable?
- (3) Do the influences of initial conditions on communities persist or decline with time?

MATERIALS AND METHODS

Study site and data collection

The Buell-Small Succession Study is a long-term successional experiment located within the William L. Hutcheson Memorial Forest Center of New Jersey, USA (40°30'N, 74°34'W). This study consists of 10 abandoned agricultural fields where farming was experimentally ceased from 1958 to 1966, with pairs of fields abandoned in alternate years (Myster & Pickett 1990; Li *et al.* 2015a; Meiners *et al.* 2015b). The initial conditions of the 10 fields were directly manipulated, where the fields varied in following characteristics of abandonment: season of abandonment (spring, fall), final crop (hay, row crop) and final ploughing regime (ploughed, unploughed) (Table S1). Since abandonment, 48 permanent 1-m² plots were arranged in a regular pattern in each field to effectively represent the entire area of the fields (Fig. S1; Pickett 1982). In each year (alternate years since 1979), all plots were non-destructively sampled in late July for coverage of each species present in the plots. The Buell-Small Succession Study observes a typical successional trajectory of the Eastern Deciduous Forests of North America, and has undergone the transition from open agricultural land, to annual and perennial herbaceous species, to liana and shrub dominance and to the formation of young deciduous forests (Figs S2 and S3).

To assess the effect of spatial scale on community patterns over succession, we performed our analyses at two discrete spatial scales: field scale (community dissimilarity among 10 fields) and plot scale (dissimilarity among the 48 plots within each field). For field scale analyses, we averaged coverage of each species across the plots within each field to obtain an estimated abundance of each species. As the 10 fields were sampled in alternate years later in succession, data from consecutive years were condensed into 2-year intervals to maintain even replication over time (Li *et al.* 2015b). Our field scale analyses were restricted to years 1967–2009, when data are available for all fields. For plot scale analyses, we examined the 48 plots within each field since abandonment, rather than considering all 480 plots with different initial conditions together.

Testing for community convergence

We quantified beta diversity as the dissimilarities among all fields or plots within each field during succession, using both incidence-based (Jaccard's) and abundance-based (Bray–Curtis) metrics. To examine whether different fields and plots moved along similar directions over succession, we performed Nonmetric Multidimensional Scaling (NMDS) analysis in a two-dimensional space based on both matrices to display the trajectories of each field or plot over succession. To examine whether fields/plots converged to a similar community state, we computed the mean pairwise dissimilarity between each pair of fields or plots within each field for each sampling year. Mean pairwise dissimilarities were then modelled as functions of sampling year by ordinary least squares (OLS) regression, to examine whether beta diversity changed with time. Because the 10 fields were abandoned in different years and located in two different blocks, we also computed the mean pairwise

dissimilarity between each pair of fields with the same age (rather than absolute year; Fig. S4), and the beta diversity between the two blocks (rather than 10 fields; Fig. S5). To test if our results are robust to different approaches, we performed community rarefaction to remove potential sampling artefacts (Fig. S6) and compared the temporal patterns across multiple spatial scales (Fig. S7).

To further quantify whether beta diversity deviated from the expectations of a random (stochastic) assembly process, the observed beta diversity values were compared to expected values generated from null models. For incidence-based metrics (Jaccard's), an independent swap algorithm (Gotelli 2000), which maintains the species richness of each community and species occurrence frequency among communities, was used to produce species assemblages in each community by randomly sampling species from the regional species pool. For the abundance-based metrics (Bray–Curtis), we used the null model to produce species assemblages by randomly placing individuals into each community while preserving the relative abundance of each species across all communities and the total cover in each community (Kraft *et al.* 2011). The overall procedure was repeated 999 times to obtain a null distribution of beta diversity for each field/plot. The standardised effect size (beta deviation) was calculated as the difference between the observed and mean expected beta diversity divided by the standard deviation of expected values (Kraft *et al.* 2011; Myers *et al.* 2013). Positive and negative beta deviation indicate higher and lower beta diversity than expected by chance, respectively, whereas a beta deviation of zero indicates that the observed pattern does not differ from random sampling. Following Kraft *et al.* (2011) and Swenson *et al.* (2011), we used $|\text{beta deviation}| < 1.96$ as the criterion for assigning statistical significance. To further test whether the assembly processes varied among species with different abundance distributions, species within each field were categorised as dominant (>5% relative cover), common (5–0.05% relative cover) or rare (<0.05% relative cover) species, following the work of Meiners *et al.* (2015b). Here, we strictly classified the status of species based on their cover in each field on an annual base, rather than defining them into predetermined groups. We then repeated our analysis for the three abundance groups, to investigate the potential difference in the assembly drivers for different groups.

Temporal changes in succession rates

To quantify temporal changes in succession rates, we calculated the pairwise dissimilarity metrics (i.e. Jaccard's and Bray–Curtis) between pairs of consecutive samples of the same fields (i.e. year T and $T + 2$), and the average turnover rates of the 10 fields were considered as the field level turnover rates. Similarly, we calculated the average turnover rates of the 48 plots within each field as measures of plot level succession rates. Temporal turnover rates were then modelled as functions of sampling years to test whether successional rates decreased over time. To discern whether the changes in successional rates mainly represented the transition from shorter lived herbaceous to longer lived woody communities, or herbaceous assemblages followed the same successional

trajectories as found in the overall vegetation, we repeated our analysis for herbaceous species (Fig. S8).

Influence of initial conditions

To assess the influence of initial conditions on community structure over succession, we conducted PERMANOVA (Anderson 2001; McArdle & Anderson 2001) comparing both incidence- and abundance-based dissimilarities between each pair of the 10 fields within every year with 999 permutations, in which year of abandonment, season of abandonment, final crop and ploughing regime were used as explanatory variables. The explained variance (partial R^2) was used as a measure of the contribution of initial conditions on community structure for each year. These statistical analyses were performed with the *vegan* package (Oksanen *et al.* 2013) in R version 3.10 (R Core Team 2014).

RESULTS

Successional dynamics were highly directional in the Buell–Small Succession Study (Fig. 1), transitioning from communities dominated by short-lived herbaceous species in the Poaceae and Asteraceae to communities primarily composed of long-lived perennial herbs and shrubs (e.g. Rosaceae) to trees (e.g. Fagaceae, Sapindaceae and Oleaceae) with a diverse herbaceous understory. During the study period, the sites have undergone changes from an open agricultural land to a young forested system (Figs S2 and S3). These directional changes were robust to spatial scale (i.e. field vs. plot) and the inclusion of species abundance data (i.e. Jaccard's vs. Bray–Curtis metrics) (Fig. 1).

Do communities converge towards a similar community state?

At the field scale, we did not observe any systematic change in beta diversity based on species incidence (i.e. using Jaccard's dissimilarity), with no sign of convergence among fields ($P = 0.912$, Fig. 2a). In contrast, abundance-based analyses (i.e. using Bray–Curtis index) showed that the dissimilarities among fields significantly decreased over time ($P < 0.001$, Fig. 2a). Consistent with this result, the beta diversity of dominant species among the 10 fields significantly decreased over succession ($P < 0.001$, Fig. 3a), indicating that these fields moved towards similar community states with similar dominant species. In contrast, we found evidence for significant divergence among the 48 plots within each field (Figs 2b and S9). Moreover, multiple spatial scale analysis revealed no sign of convergence with species incidence data at any scale, but stronger convergence based on species abundance at larger scales (Fig. S7).

Beta deviation showed qualitatively similar temporal trends with observed beta diversity. At the field scale, incidence-based beta deviation was not associated with time, and did not differ from the null expectation during succession (Fig. 2c). In contrast, abundance-based beta deviation significantly decreased over time (Fig. 2c). Beta deviation of rare and common species showed no significant trends over time and exhibited patterns not different from the null expectations

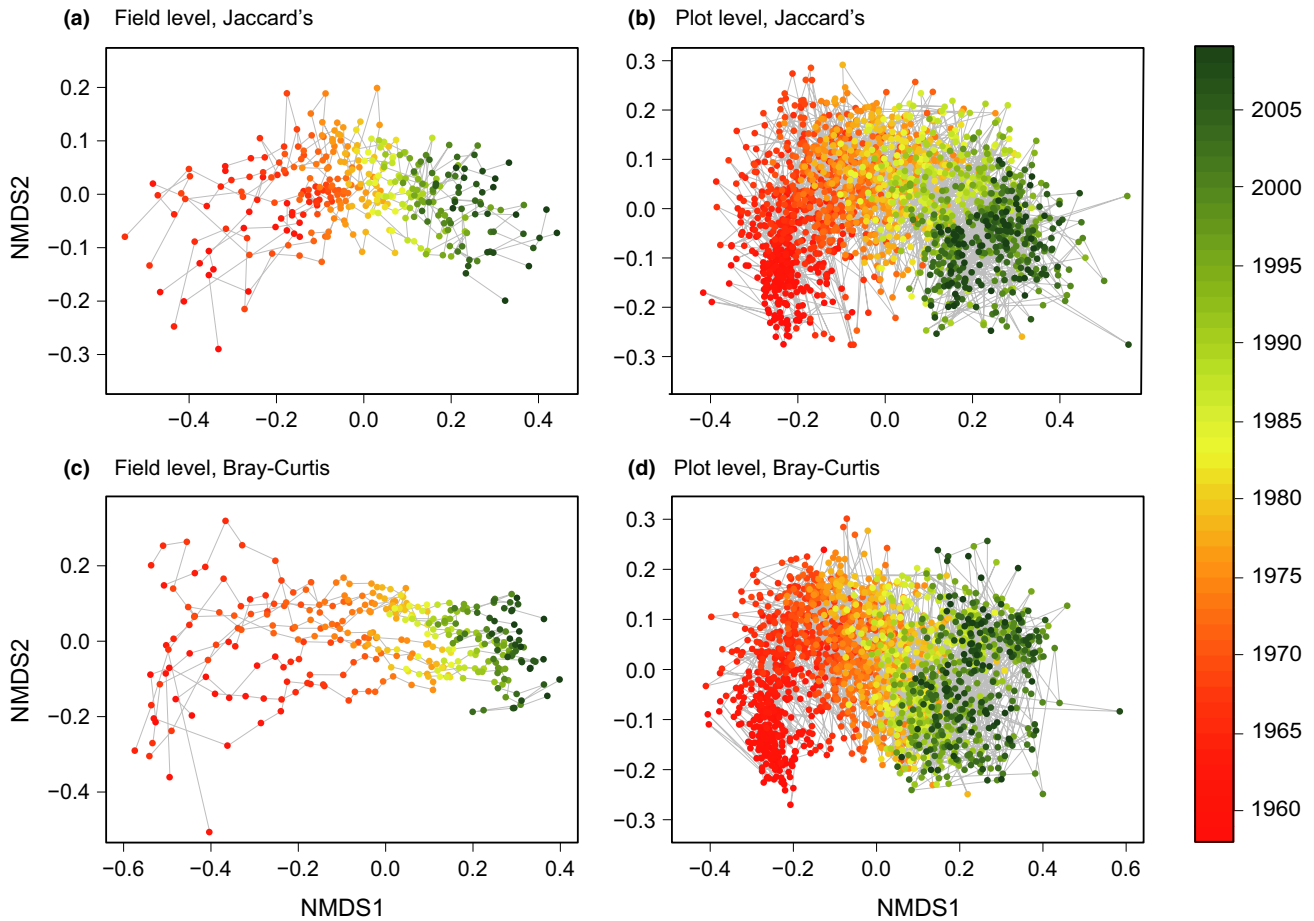


Figure 1 Ordination of community structure over succession by nonmetric multidimensional scaling (NMDS) at both field and plot levels. Distances among communities were measured as incidence-based (Jaccard's) and abundance-based (Bray–Curtis) dissimilarities. The communities are coloured by their sampling year, and the grey lines show the successional trajectories of the 10 fields (a, c) or the 48 plots within one field (b, d). For plot level analysis, only the results of 48 plots within one field are shown, as the plots within other nine fields show qualitatively similar patterns.

(Fig. 3b). However, beta deviation of dominant species was initially indistinguishable from random expectations, but subsequently decreased and became significantly lower than the null expectations (Fig. 3b). At the plot scale, abundance-based analyses showed that beta deviation among plots within each field significantly increased over time, transitioning from early homogenisation to random assembly later in succession (Figs 2d and S9d). Incidence-based beta deviation showed weaker temporal changes and exhibited random patterns (Figs 2d and S9c). These contrasting patterns at field and plot scales are robust to the use of successional age vs. year in the analysis (Fig. S4), the different definitions of fields (i.e. 10 fields vs. two blocks; Fig. S5), the consideration of sampling artefact (i.e. rarefaction vs. raw data; Fig. S6) and the inclusion and exclusion of woody species (Fig. S8).

Do successional rates decline over time, with communities becoming more stable?

Based on species incidence data, we did not observe temporal change in successional rates at either field or plot scales (Figs 2e, f and S9e), which indicates that species composition did not become more stable over time. In contrast,

abundance-based successional rates significantly decreased with time (Fig. 2e, f). Similarly, the temporal turnover of dominant species significantly decreased over time, whereas common, rare and herbaceous species still exhibited high species turnover later in succession (Figs 3c and S8e, f).

Do the influences of initial conditions on communities persist or decline with time?

Not all initial conditions had discernible effects on the trajectories of succession over time. The season of abandonment and ploughing regime did not have significant effects on succession patterns ($P > 0.05$, Fig. 4). The year of abandonment significantly influenced the structure of the fields early in succession, but its contribution decreased over time and became non-significant later in succession. Likewise, the last crop only significantly influenced community structure at the beginning of succession, and its contribution quickly decreased (Fig. 4).

DISCUSSION

The directionality, convergence, temporal turnover and importance of historical events over time are central issues

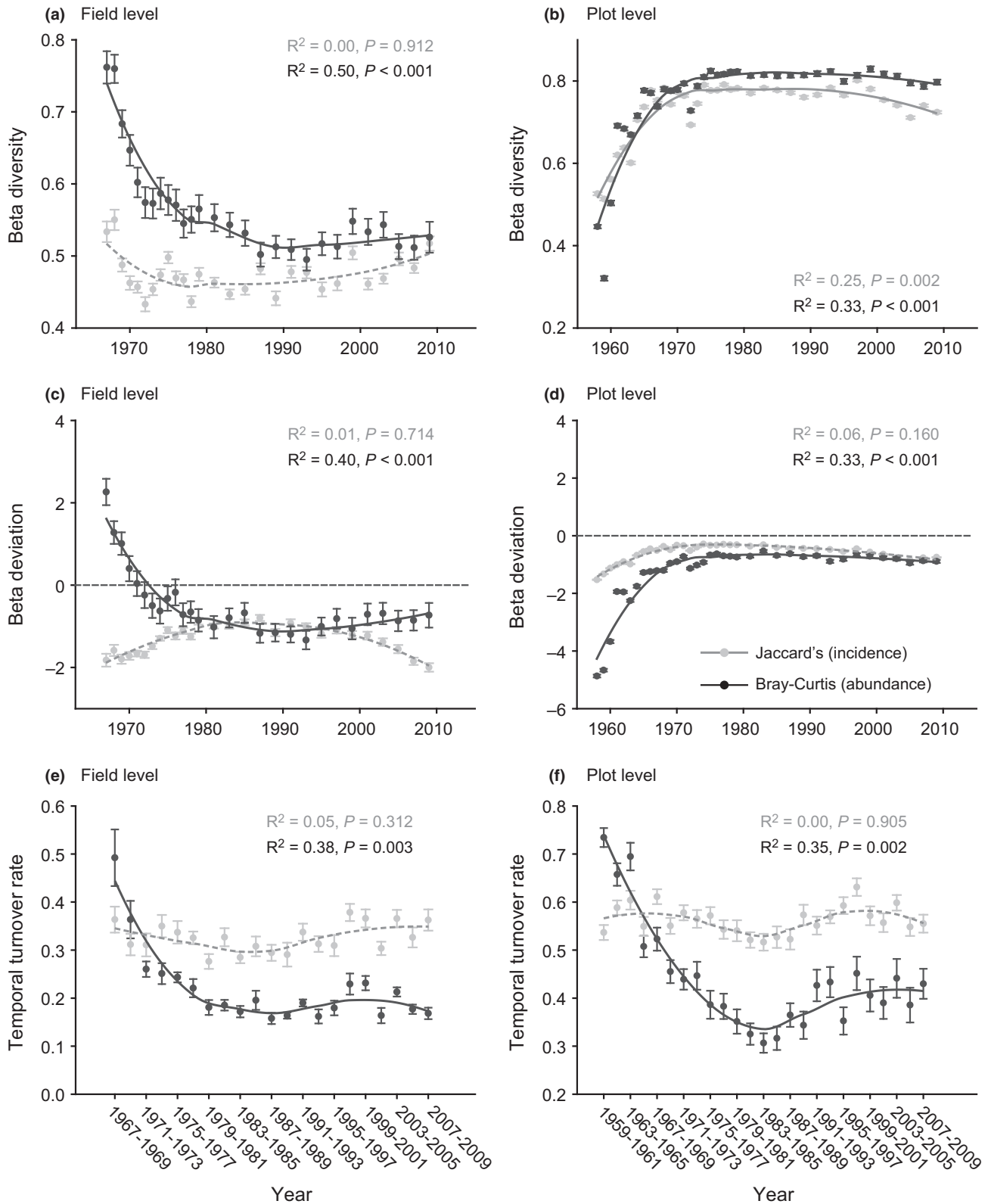


Figure 2 Temporal trends in beta diversity and temporal turnover at both field and plot scales. Beta diversity and turnover rates were measured as incidence-based (Jaccard's, grey) and abundance-based (Bray-Curtis, black) dissimilarities. The standardised effect sizes (beta deviation) shows the magnitude of deviation between observed beta diversity and the values generated from null models. Negative values indicate lower beta diversity than random assemblages, whereas positive values indicate the opposite. Temporal trend lines are coded solid if significant ($P < 0.05$) and dashed if not significant. Error bars represent standard errors. For plot level analysis, only the results of 48 plots within one field are shown, as the plots within other nine fields show similar patterns (see Fig. S9).

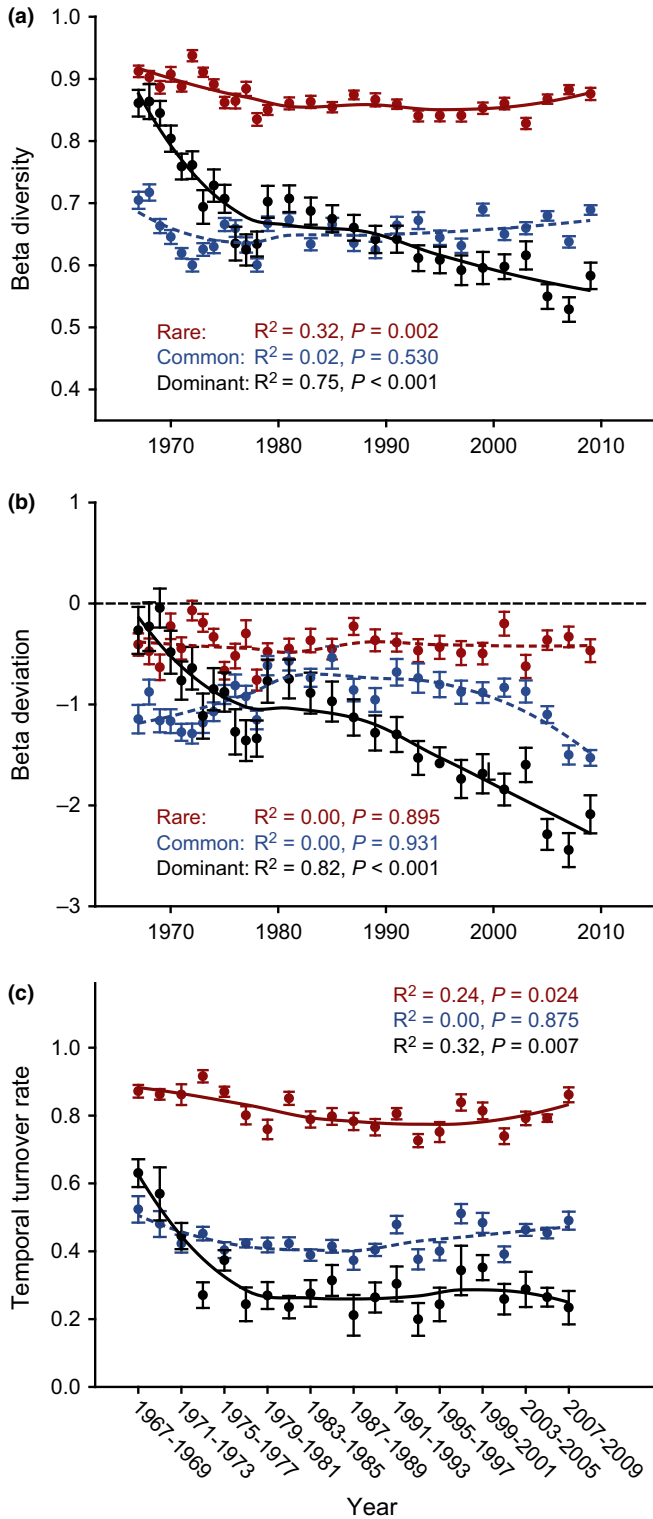


Figure 3 Temporal trends in beta diversity of rare (red), common (blue) and dominant (black) species among the 10 fields over succession. Species within each field were categorised by their relative cover for each sampling year: rare (<0.05% relative cover), common (5–0.05% relative cover) and dominant (>5% relative cover). Beta diversity was measured as Jaccard's dissimilarities for each abundance group. The standardised effect sizes (beta deviation) shows the magnitude of deviation between observed beta diversity and the values generated from null models. Error bars represent standard errors.

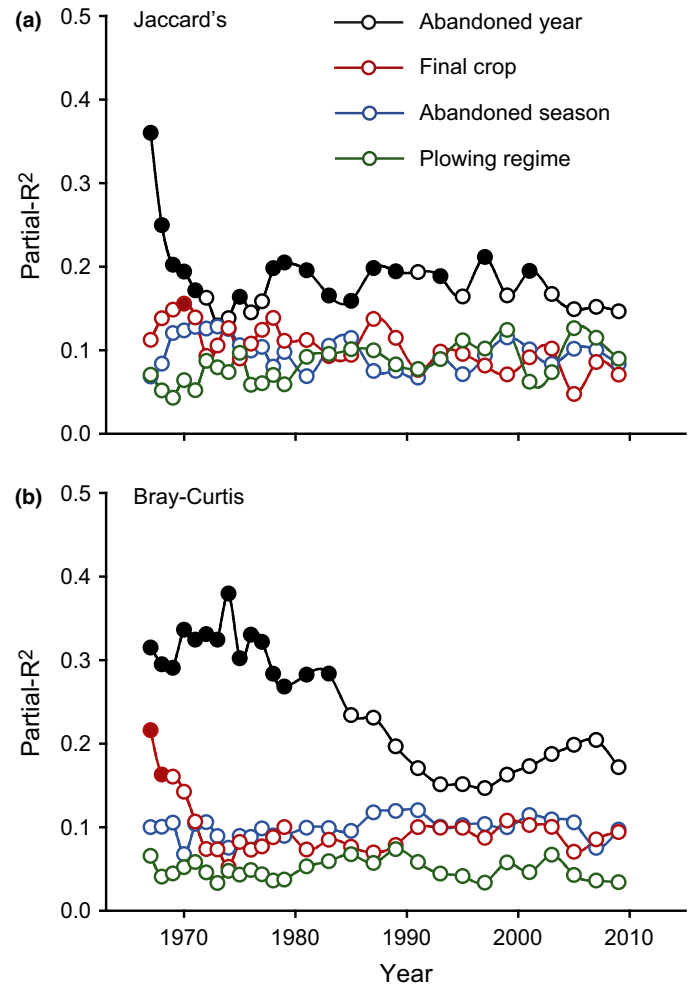


Figure 4 The fraction of variance in beta diversity among the 10 fields explained by year of abandonment (black), final crop (red), season of abandonment (blue) and ploughing regime (green). The explained variance (partial- R^2) was calculated by permutational multivariate analysis of variance (PERMANOVA) based on Jaccard's (a) and Bray-Curtis (b) dissimilarities. PERMANOVA with 9999 permutations were performed separately for every year. The solid circles show those with significant treatment effects ($P < 0.05$).

in succession and community assembly. Although these issues have been studied for over a century, much research has relied on indirect inferences from chronosequences, and rigorous tests with sufficiently long longitudinal data have been rare. By examining a 50-year post-agricultural secondary succession, our study showed that successional trajectories depend on the focal spatial scale and inclusion of species abundance. Although succession at both the coarse (field) and fine (plot) scales was directional, convergence only occurred at the coarse scale for abundance-based data, whereas the fine-scale plots within each field diverged over time. While dominant species became more stable over time, rare species (e.g. herbaceous understory) still exhibited high species turnover later in succession. Initial conditions played important but transient roles in determining community composition over succession. These results suggest that both stochastic and deterministic processes contribute to

community succession, but their relative influences depend on spatial scale and species abundance.

It has been suggested that the structure of early successional communities is largely determined by initial abiotic conditions and stochastic immigration, and that subsequent deterministic processes would generate more predictable community structure as succession proceeds (Margalef 1963; Dini-Andreote *et al.* 2015). The temporal decline in abundance-based beta diversity among fields is consistent with this idea. The 10 fields with different abandonment conditions initially favoured different subsets of pioneer species and as a result showed considerable variation in community structure (indicated by high beta diversity) early in succession (Fig. 2a, c). This result supports the idea that historical events, such as the different abandonment conditions of the fields, may result in alternative transient states (Fukami & Nakajima 2011, 2013). However, in our study, initial abandonment conditions did not have a lasting impact on the assembled communities as suggested by Egler (1954). As the influence of initial conditions declined with time (Fig. 4), the deterministic niche-selective forces became more prominent later in succession. In our study, the 10 fields converged to become increasingly dominated by the later successional species (such as *Juniperus virginiana*, *Acer rubrum* and *Ageratina altissima*) (Fig. S3). These results indicate that woody species with high competitive ability, as well as shade-tolerant herbs, dominated all the fields regardless of initial conditions, as light becomes more limiting during old-field succession.

In contrast, the 48 plots within each field significantly diverged over succession (Fig. 2b, d), which may suggest the increasing importance of stochasticity. The 48 plots within each field shared the same initial conditions and therefore favouring similar pioneer species early in succession, which resulted in more homogeneous community structure than expected from random assembly (Fig. 2d). As succession unfolded, however, stochastic events became progressively more important at the fine scale (Fig. 2d). Sparsely established individuals, such as long-lived woody species, could randomly disperse into plots and became dominant, resulting in a compositionally heterogeneous mosaic of vegetation. Smaller community sizes at the plot level could also effectively make local competition more neutral and the outcome of competition less predictable, leading to more divergent community structures (Orrock & Watling 2010). A third explanation is that the number of individuals in the plots would decrease as woody species became dominated and therefore these small plots tended to be more affected by stochasticity due to the decreased sample sizes over time. Finally, early colonists could modify the environment in such a way that it increases the microhabitat variability and resource heterogeneity within the fields, which could also contribute to the divergence of the 48 plots at the fine scales (Li *et al.* 2015a). Taken together, multiple ecological processes could drive compositional divergence among fine-scale plots, and future studies integrating long-term monitoring of community composition and microhabitat dynamics (e.g. soil conditions) would provide increased sensitivity for unravelling the mechanisms of ecological succession.

It is also important to note that only abundance-based beta diversity and dominant species showed clear temporal trends,

whereas beta diversity of species composition and subordinate species were less associated with time (Figs 2a–d and 3a, b). This pattern is consistent with our hypothesis that stochastic processes play more important roles for subordinate species, as their dissimilarities were statistically indistinguishable from the null expectation across the entire successional sequence. It is possible that these subordinate species (e.g. common and rare species) were undersampled and therefore less predictable than the dominant species. However, we found nearly identical temporal patterns after factoring out sampling effects by null models (Fig. 2c, d) and rarefaction (Fig. S6), suggesting such pattern could not be solely attributed to sampling artefacts. An alternative explanation is that, subordinate species were more strongly influenced by stochastic immigration and extinctions events, random dispersal and year-to-year variation in environment conditions, due to their small population sizes (Orrock & Watling 2010). These stochastic processes could have overridden the influences of deterministic factors on rare species, making their occurrence less predictable than dominant species at both field and plot scales.

Successional rates based on incidence and abundance data also showed contrasting patterns. Abundance-based successional rates and dominant species became more stable over time, whereas species composition and rare species still exhibited high temporal turnover later in succession (Fig. 2e, f). As woody species established and dominated local communities, low turnover rates could be largely driven by the lack of year-to-year variation due to the long life span of these species (Meiners *et al.* 2015b). In contrast, the stochastic immigration and extinction events of rare species, such as the replacement of herbaceous understory, continued during latter successional stages (Figs 2e, f, 3c and S8e, f). This continued high turnover is surprising, because composition is generally thought to become more stable in later successional stages (Drury & Nisbet 1973; Anderson 2007; Prach *et al.* 2007). Note that most of our knowledge on plant succession is based on chronosequences, which are unable to provide robust estimates of the rate of succession since the real temporal turnover cannot be documented. Therefore, our results highlight that the rates of community change over succession should be directly measured using long-term monitoring, rather than chronosequences.

Although these observed patterns of beta diversity and turnover rates are consistent with our framework, several limitations of our study should be noted. First, successional trajectories could vary depending on the organisms and ecosystems considered. Our study only examined old-field secondary succession and cannot inform us whether the patterns we observed are general characteristic of succession, which remains to be tested in other systems. Second, our 1 m² permanent plots were sufficient to characterise the diversity, structure and composition of herbaceous species, but they are not likely to capture the temporal patterns of woody species. Although our conclusions were robust when herbaceous species were considered alone (Fig. S8), a better approach would be to use nested plots to fully characterise species with differing life forms at different spatial scales. Third, even as the longest continuous study of old-field succession, our study still could not capture the full temporal range of recovery to a mature forest. The continual monitoring of the Buell–Small

Succession Study, which is ongoing, provides an opportunity for future generations of ecologists to gain additional insight into successional assembly mechanisms over longer time scales.

In conclusion, we have shown here that there is no simple reconciliation of the convergence–divergence or stochastic–deterministic debate for ecological succession. Even within a single ecosystem, the relative influences of different ecological factors depend on the spatial scale of observation and the focus on community members of different abundance classes. These findings suggest that the common practice evaluating community assembly based on single spatial scale and species occurrence data is unreliable, and results obtained must be viewed with caution.

ACKNOWLEDGEMENTS

We are grateful to the originators of the Buell–Small Successional Study, Drs. Helen Buell (1901–1995), Murray Buell (1905–1975) and John Small (1900–1977), and many field workers who sampled the fields every year for the past half century. We also thank Xingfeng Si, Daijiang Li, Xian Yang and three anonymous reviewers for their insightful and detailed suggestions that have helped to improve the quality of the manuscript. This work was funded by the National Science Foundation of the USA (DEB-1257858 and DEB-1342754) and the National Natural Science Foundation of China (31361123001) to L.J. SJM was supported by the National Science Foundation of the US (DEB-0424605). MWC was supported by the TD Professor of Urban Forest Conservation and Biology chair and Natural Sciences and Engineering Research Council of Canada (386151). TF acknowledges US NSF (DEB 1149600 and 1555786) and Stanford University Terman Fellowship for support.

AUTHORSHIP

SPL, MWC and LJ developed and framed research questions. SJM collected the data used in this analysis. SPL and ZP analysed the data. SPL wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION

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Editor, Marcel Rejmanek
Manuscript received 8 February 2016
First decision made 21 March 2016
Second decision made 27 May 2016
Manuscript accepted 13 June 2016