Complex plant–soil interactions enhance plant species diversity by delaying community convergence

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Summary

1. A plant that causes specific changes to soil biota may either positively or negatively affect the performance of the plant that subsequently grows in that location. These effects, known as plant–soil feedback, can affect plant species diversity at multiple spatial scales.

2. It has been hypothesized that positive plant–soil feedback reduces alpha (local) diversity by allowing dominance by early-arriving species, but increases gamma (regional) diversity by promoting community divergence (increased beta diversity) through the emergence of alternative stable states. In contrast, negative plant–soil feedback has been thought to increase alpha diversity by allowing local species coexistence, but to reduce gamma diversity by promoting community convergence (reduced beta diversity). Although widely accepted, these hypotheses do not consider the possibility that plant species differ in their effect on, and their response to, a given other species via soil biota. In reality, plant–soil interactions can be complex, with the strength of the interactions variable between plant species. Using a basic simulation model of plant community assembly, we investigated how complex plant–soil interactions might affect plant diversity during succession.

3. When we included only positive or negative intraspecific plant–soil feedback in the model, with no variation in the strength of interspecific plant–soil interactions, results were consistent with the conventional hypotheses. When we allowed the strength of plant–soil interactions to differ between species, plant–soil interactions enhanced alpha diversity initially and beta and gamma diversity subsequently. Diversity enhancement occurred not necessarily because alternative stable states emerged, but primarily because complex plant–soil interactions lengthened the time during which local species composition changed. Due to the longer time for changes in species composition, the high level of beta and gamma diversity at the early stage of succession was maintained for a long time despite eventual community convergence. Thus, diversity enhancement was often transient, though long-lasting, making the conventional concept of alternative stable states inadequate for explaining diversity.

4. *Synthesis*. Based on these findings, we propose the new hypothesis that complex plant–soil interactions enhance plant species diversity by delaying community convergence. This hypothesis highlights the role of plant–soil interactions as a driver of long-lasting transient dynamics of community assembly.

Key-words: alternative stable states, alternative transient states, beta diversity, delayed convergence hypothesis, dispersal, historical contingency, Janzen-Connell effects, plant succession, plant-soil (below-ground) interactions, priority effects

Introduction

Many processes influence plant species diversity, but one process that is receiving considerable interest is the interaction between plants and soil biota (Klironomos 2002; Porazinska *et al.* 2003; Reynolds *et al.* 2003; Mangan *et al.* 2010;

Kulmatiski, Beard & Heavilin 2012). It has long been recognized that a plant that causes specific changes to soil biota may affect the performance of the plant that subsequently grows in that location (e.g. Müller 1884). These effects, known as plant–soil feedbacks (Bever 2003; Ehrenfeld, Ravit & Elgersma 2005; Kulmatiski *et al.* 2008), can be positive or negative, depending on the net influence of mutualistic organisms such as mycorrhizal fungi and nitrogen-fixing bacteria and antago-

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nistic organisms such as pathogenic microbes and root-feeding invertebrates. One hypothesis commonly encountered in the recent literature (reviewed by Bever, Platt & Morton 2012) is that positive plant–soil feedback reduces alpha (local) diversity by allowing dominance by early-arriving species, but increases gamma (regional) diversity by promoting community divergence (increased beta diversity) through the emergence of alternative stable states, each dominated by the few species that happen to arrive earlier during succession. This is an example of priority effects causing historical contingency in community assembly (Kardol *et al.* 2007). In contrast, negative plant–soil feedback is thought to increase alpha diversity by allowing local species coexistence, but to potentially reduce gamma diversity by promoting community convergence (reduced beta diversity). This is a case of Janzen-Connell effects influencing the maintenance of species diversity (Bonanomi, Giannino & Mazzoleni 2005; Petermann *et al.* 2008).

One limitation of these widely accepted hypotheses is that they do not take into account the possibility that plant species differ in their effect on, or their response to, a given other species via soil biota. Plant–soil feedback is typically quantified in terms of how well plants perform in soil conditioned by conspecific plants, relative to how well they do in soil conditioned by heterospecifics. In most cases, only two types of soil are considered, often referred to as 'own' and 'foreign' soil (Brinkman *et al.* 2010). This categorization assumes that the effect of soil conditioning by heterospecific plants is essentially the same in strength regardless of which species conditions the soil. Recent data indicate, however, that species can differ considerably in the extent to which they affect, and are affected by, a given other species via soil conditioning (e.g. van de Voorde, van der Putten & Bezemer 2011), making plant–soil interactions more complex than generally thought. Currently, little is known about how such complex plant–soil interactions may influence plant species diversity.

Here, we address this question using a basic simulation model of plant community assembly. Our primary goal is to propose a new hypothesis, namely that complex plant–soil interactions enhance plant species diversity by delaying community convergence during plant succession. To develop this hypothesis, we focus on analysing the transient dynamics of plant succession when realistically complex plant–soil interactions are incorporated in the simulation model. We contrast these dynamics with those that occur with no plant–soil interactions, simple positive interactions or simple negative interactions, so that the conventional hypotheses and our new hypothesis can be directly compared. We also study how immigration rate determines the degree to which complex plant–soil interactions affect plant diversity.

Materials and Methods

OVERVIEW

Our model was a modification of the generalized competition model for sessile organisms such as plants (Chesson 1985; Pacala & Tilman 1994; Mouquet, Moore & Loreau 2002; Fukami & Nakajima 2011).

In our model, species of plants were randomly chosen each year from a regional species pool. The chosen species immigrated as a small number of seeds to a local habitat patch consisting of numerous cells that differed in quality. Initially, all cells were empty. Subsequently, only one plant could establish and produce seeds in each cell even when multiple seeds arrived from the regional pool or from within the patch. Of the seeds that arrived at a cell, the one that belonged to the species that best fitted the environmental condition of the cell was able to establish and produce seeds. Plant–soil feedback affected the level of relative fit, as detailed later. Plants produced seeds once a year until they died. Plants died with a fixed probability, and when they did, cells became empty and available for a new plant to establish. This process of immigration, arrival, establishment, reproduction and death was repeated for multiple years. All simulations were carried out using Mathematica 8.0 (Wolfram Research, IL, USA).

REGIONAL SPECIES POOLS AND LOCAL PATCHES

Regional species pools each contained 30 plant species, with species i assigned a trait value, R_i, chosen randomly from a uniform distribution [0, 1]. Species were also characterized by a set of values, S_{ij}, which defined how the presence of a plant belonging to species j during a given year changed the competitive ability of a plant belonging to species i during the following year, as described in more detail later (see '*Plant-soil interactions*'). Local patches consisted of 1000 cells. The condition of cell k was defined by a value, H_k, chosen randomly between 0 and 1 from a beta distribution, where the probability density for value x was proportional to: $x^{a-1} (1-x)^{b-1}$ (Mouquet, Moore & Loreau 2002). In our model, we set $a = b = 50$, which yielded many cells having H_k close to 0.5 and few with a value near either 1 or 0.

COMMUNITY ASSEMBLY

Each year, each species in the regional species pool immigrated to the local patch with a probability I, equal for all species. We used $I = 0.05$, except in the additional simulation conducted to examine the effect of I (see '*Beta diversity as a function of immigration rate*'). At each cell in the local patch, species i arrived with the probability, $1 - \exp[-(P_i + F N_i)/(\text{total number of cells, i.e. 1000})]$. Here, P_i is the number of seeds of species i that immigrate from the regional pool (20 seeds for species chosen that year for immigration from the regional pool, and 0 seed for all other species), F is fecundity (50 for all species), and N_i is the number of plants belonging to species i in the local patch (0 for all species in the first year, i.e. at $t = 1$). When the number of cells that were assigned to receive a seed of species i exceeded $P_i + F N_i$ (which rarely happens), $P_i + F N_i$ cells were randomly selected from these cells and a seed of the species assigned only to the selected cells.

Given this probability, there were three possibilities regarding plant establishment and seed production in each cell. First, if the cell was already occupied by a plant, that plant remained there. Second, if the cell was empty and no species arrived at that cell, it remained empty. Third, if the cell was empty and one or more species arrived at that cell, of those species that arrived, the one with the greatest value of C_{ijk} established to produce seeds. Thus, plants competed for limiting resources such as light and nutrients within cells. The value of C_{ijk}, which defined the competitive ability of species i at cell k when the cell was occupied by species j in the previous year, was given as $(1 - |H_k - R_i|)S_{ij}$. The value of S_{ij} defined the direction and strength of plant–soil interactions. Specifically, it defined the effect of species

j occupying a given cell during a given year on the competitive ability of species i in that cell during the following year. If the value of S_{ij} for all possible pairs of i and j was 1, there was no plant–soil interaction. If $S_{ij} > 1$, this was a positive plant–soil interaction. If $S_{ij} < 1$, this was a negative plant–soil interaction. After plant establishment was completed for all cells, plants occupying a cell died with the probability, m. We set $m = 0.4$ for all species.

We assembled communities by following these rules of immigration, arrival, establishment, reproduction and death for 1500 generations (for $t = 1500$ years). Two observations confirmed that local communities always reached a stable state by the 1500th generation in our model (Fukami & Nakajima 2011). First, there was no obvious long-term change in immigration and extinction rates from the 1200th to 1500th generations, indicating that communities had entered an equilibrium state by, conservatively, the 1500th generation. Second, between the 1200th and 1500th generations, there was virtually no immigration (indicating that communities were resistant to invasion by any additional species from the regional pool) or extinction (indicating that communities had stable species composition with no species lost over time) if immigration and extinction were measured for species having more than 20 plants in the patches, indicating that communities had reached a stable state.

We simulated 20 replicated runs of community assembly (i.e. using 20 independently created sets of a regional species pool, 10 identical local patches and a plant–soil interaction matrix) to examine alpha, beta and gamma diversity (see 'Species diversity') under each of four types of plant–soil interaction (see 'Plant–soil interactions').

SPECIES DIVERSITY

We measured alpha diversity as the mean number of species present in a local patch, averaged over the 10 replicate communities; gamma diversity as the number of species present in 1 or more of the 10 patches; and beta diversity as gamma diversity divided by alpha diversity. This measure of beta diversity is the original multiplicative form proposed by Whittaker (1960). Although other measures of beta diversity have been proposed (Tuomisto 2010; Anderson *et al.* 2011), we used Whittaker's measure for two reasons. First, it can be interpreted as indicating the number of alternative community states observed in different patches in the region, or more precisely, the effective number of distinct local communities in the region (Jost 2007; Wilsey 2010). Thus, multiplicative beta diversity can be used as a surrogate for the effective number of alternative community states. Second, unlike some other measures of beta diversity, the multiplicative measure is comparable between regions even when alpha diversity is variable between regions (Jost 2007; Wilsey 2010).

PLANT–SOIL INTERACTIONS

To examine the effect of different types of plant–soil interactions, we ran the simulation using the following four ways of assigning values of S_{ij} to each pair of i and j: (i) No plant–soil interaction: all values of S_{ij} were 1. (ii) Positive intraspecific plant–soil interactions: each S_{ij} value was 1 when i was not the same as j (i.e. no interspecific plant–soil interaction) and chosen randomly from a uniform distribution [1.0, 1.5] when i was the same as j (i.e. positive intraspecific plant–soil interaction). (iii) Negative intraspecific plant–soil interactions: each S_{ij} value was 1 when i was not the same as j (i.e. no interspecific plant–soil interaction) and chosen randomly from a uniform distribution [0.5, 1.0] when i was the same as j (i.e. negative intraspecific plant–soil interactions). (iv) Complex plant–soil interactions:

each S_{ij} value was chosen randomly from a uniform distribution [0.5, 1.5] when i was not the same as j (i.e. negative and positive interspecific plant–soil interactions) and chosen randomly from a uniform distribution [0.5, 1.0] when i was the same as j (i.e. negative intraspecific plant–soil interactions). This fourth option seemed the best approximation of empirical measurements of inter- and intraspecific plant–soil interactions currently available (e.g. van de Voorde, van der Putten & Bezemer 2011). We also used the same setting as (iv) previously, except that each S_{ij} value was chosen randomly from a uniform distribution [0.5, 1.0], instead of [0.5, 1.5], for all combinations of i and j (i.e. negative intra- and interspecific plant–soil interactions). Results were qualitatively the same between the two settings (Fig. S1).

In addition, we implemented three further extensions of the model to investigate the robustness of the patterns that we observed in plant diversity. First, we modified the model to allow plant–soil interactions to take place not only within cells, but also between adjacent cells. Specifically, of the species that arrived at a given cell k via seed dispersal each year, the one with the highest C_{ijklm} established in the cell. The values of C_{ijklm} were calculated as $(1 - |H_k - R_j|)$ $\sqrt[3]{S_{ij}S_{il}S_{im}}$, where S_{ij} is the effect of species j's occupying cell k in the previous year, S_{il} is the effect of species l's occupying cell k-1 in the focal year and S_{im} is the effect of species m's occupying cell $k + 1$ in the focal year. We assumed that the habitat patch consisted of a linear, circular array of 1000 cells, which were distributed randomly with respect to H_k values. The same matrix of S_{ij} values was used for S_{ij}, S_{il} and S_{im}. If no plant occupied cell k in the previous year, S_{ij} was assumed to be 1. Similarly, if no plant occupied cell k-1 (or $k + 1$) in the focal year, S_{il} (or S_{im}) was assumed to be 1. Second, we modified the model to allow plant establishment to take place not only by seed dispersal, but also by clonal spread to adjacent cells. To simulate clonal spread, we assumed that each plant that occupied cell k in a given year had a 20% chance (e.g. Herben & Wildová 2012) each of spreading to cells $k - 1$ and $k + 1$ before seed dispersal. As mentioned earlier, we assumed that the habitat patch was one-dimensional, with cells distributed randomly. If two species, one present in cell $k - 1$ and one present in cell $k + 1$, attempted to spread to cell k, the one with the higher C_{ij} (measured in the cells that the respective parent plants occupied, i.e. cells $k - 1$ and $k + 1$) was established. Third, we incorporated both of the above-mentioned two modifications in the model. All simulations were otherwise run the same way as specified previously.

ANALYSIS OF TRANSIENT DYNAMICS

Results indicated that transient dynamics, rather than alternative stable states, were the key to explaining the effect of complex plant–soil interactions on species diversity. For this reason, we analysed community assembly further by measuring the following indices of transient dynamics: the total number of colonization or extinction events (S_{cmax} and S_{emax}) and the time it took for half the total number of colonization or extinction events to happen (K_c and K_e). We estimated these indices by approximating the temporal change in the cumulative number of colonization and extinction events with a Michaelis–Menten model (Fig. S2). Thus, the duration and extent of species turnover were quantified by K_c and K_e and by S_{cmax} and S_{emax}, respectively.

To gain further insight into transient dynamics, we also examined whether species would always persist or always disappear after an immigration event during community assembly. For this purpose, we did additional simulations in which we determined whether a given species would persist in a local habitat patch if it was introduced with

10 other species randomly selected from the regional pool of 30 species. For each of the 30 species from the regional species pool, we used 100 sets of 10 other randomly selected species to repeat this simulation 100 times. Each of the 100 simulation runs was initiated by introducing 20 seeds each of the 11 species to a local patch. Each simulation was run with no additional immigration for 100 years, at which time we recorded whether the focal species was still present in the patch or had gone extinct.

Results

SPECIES DIVERSITY UNDER DIFFERENT TYPES OF PLANT–SOIL INTERACTIONS

With no plant–soil interaction (Figs 1a,b and 2a–d), a common deterministic set of species appeared in all local communities regardless of immigration history, often by $t = 50$ years (Fig. 1a,b). This is community convergence by species sorting, as previously shown by Fukami & Nakajima (2011), reflected in a decline in beta diversity over time, eventually reaching a value very close to 1 (Fig. 2b). With positive intraspecific plant–soil interactions (Figs 1c,d and 2e–h), alpha diversity was reduced (Fig. 2e) and beta diversity was enhanced and maintained at around five (Fig. 2f), indicating that there were on average approximately five alternative stable states. With negative intraspecific plant–soil interactions (Figs 1e,f and 2i–l), alpha diversity was slightly enhanced (Fig. 2i), while beta diversity approached 1 over time (Fig. 2j), indicating community convergence. All of these results are consistent with the conventional hypotheses.

With complex plant–soil interactions (Figs 1g,h and 2m–p), communities typically exhibited a great deal of turnover of species (Fig. 1g,h), but temporal patterns in alpha and beta diversity were broadly similar to those under no plant–soil interaction (Fig. 2m,n), with beta diversity eventually

reaching a value close to 1, indicating eventual community convergence (Fig. 2n). However, temporal changes proceeded more slowly (Fig. 2n,o). In other words, complex plant–soil interactions promoted historical contingency in community assembly only during transient dynamics and not for stable-state communities (as seen at $t = 1500$ years), but transient divergence lasted for a long time (more than a century). The delayed decline in beta and gamma diversity (Fig. 2n,o) was also observed when clonal spread and plant–soil interactions between adjacent cells were incorporated in the model (Figs S3–S5).

TRANSIENT COMMUNITY DYNAMICS UNDER DIFFERENT TYPES OF PLANT–SOIL INTERACTIONS

With positive intraspecific plant–soil interactions, the indices of transient dynamics indicated shorter and less extensive species turnover, relative to the dynamics under no plant–soil interaction (Fig. 3). This is expected: with positive intraspecific plant–soil interactions, the few species that arrive early should dominate the community and resist colonization by others, with little subsequent turnover of species (e.g. Fig. 1c, d). With negative intraspecific plant–soil interactions, species turnover was slightly more extensive (Fig. 3c,d), but the duration of turnover was not different from that under no plant–soil interaction (Fig. 3a,b). This is also expected: negative plant–soil interactions should allow colonization by slightly more species than under conditions with no plant–soil interactions. Otherwise, the dynamics were not much different from those under no plant–soil interaction.

With complex plant–soil interactions, the total number and duration of extinction events were both about three times as great as with no plant–soil interaction (Fig. 3b,d). The total number of colonization events was also greater (Fig. 3c). In
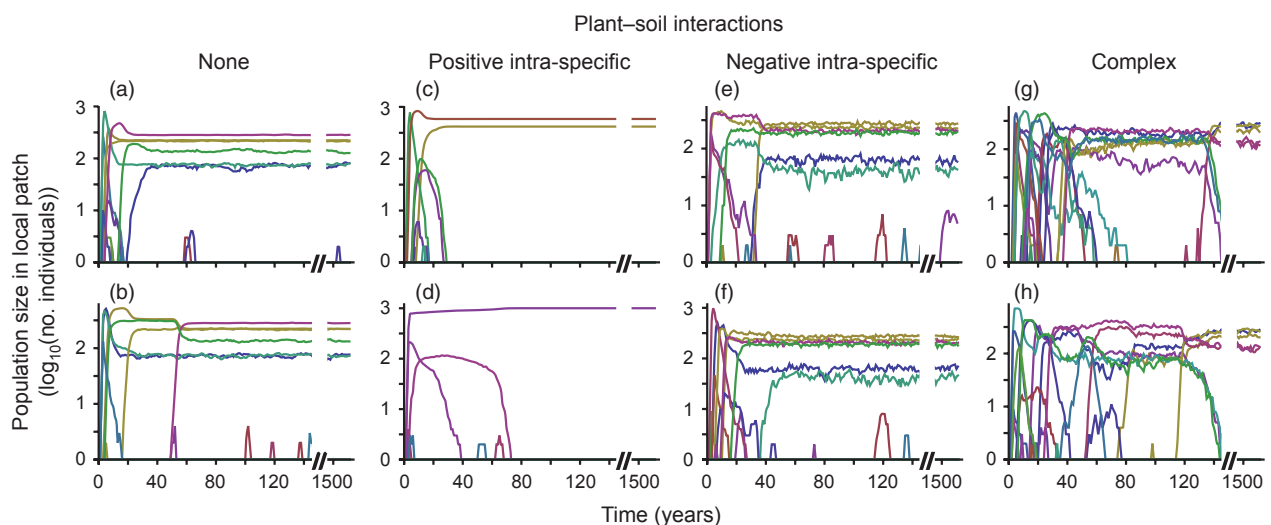

Fig. 1. Representative examples of population dynamics under different types of plant–soil interactions. Shown here for each type of plant–soil interactions are population dynamics in a select 2 of the 10 local patches under the same species pool (i.e. same set of 30 R_i values) and the same patch condition (i.e. same set of 1000 H_k values). In each graph, each line represents a species. Immigration rate is 0.05 (or 5% probability of immigration per species every year) for all cases.
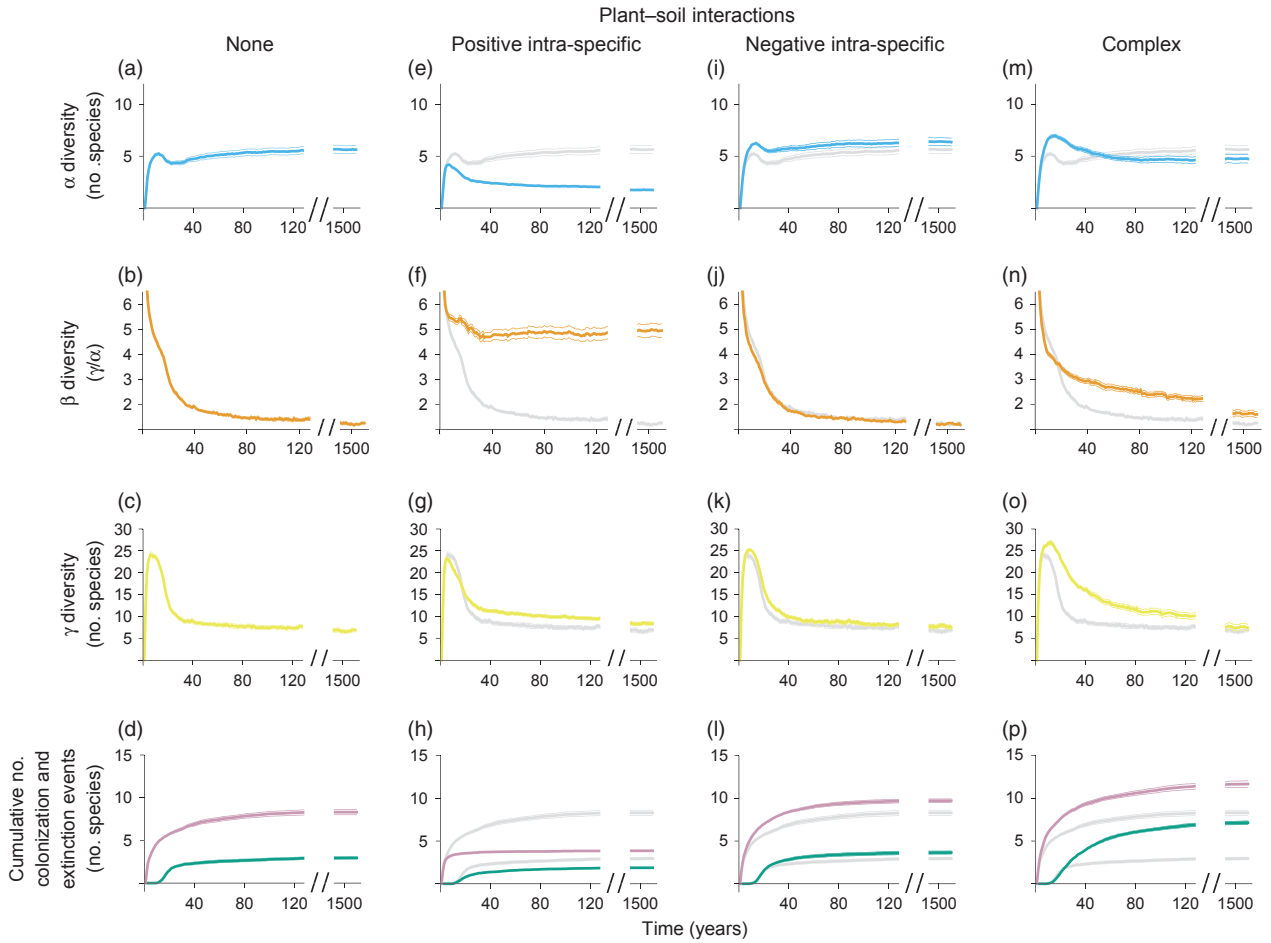
Fig. 2. Temporal change (mean ± SE, $n = 20$) in alpha, beta, gamma diversity and the cumulative number of colonization, S_{ct} (purple), and extinction, S_{et} (green), under different types of plant–soil interactions. Immigration rate is 0.05 (or 5% probability of immigration per species every year) for all cases. In panels (e–p), results for no plant–soil interactions (panels a–d) are shown in gray to facilitate comparison.
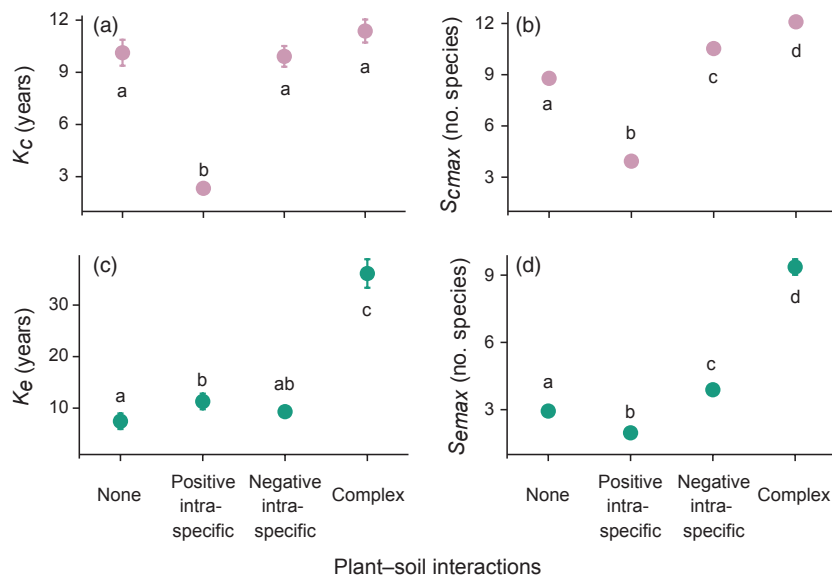

Fig. 3. Effect of plant–soil interaction types on the indices of transient community dynamics (see Fig. S2), including the total number of colonization events (S_{cmax}) and extinction events (S_{emax}) and the time it takes for half the total number of colonization events (K_c) and extinction events (K_e) to happen (mean ± SE, $n = 20$). Letters indicate results of Tukey's HSD tests ($P < 0.05$).

other words, many more species colonized communities, even though many more of them eventually disappeared from the community, under complex plant–soil interactions than under no plant–soil interaction. Further, once species entered a community, those that would eventually disappear often persisted for a long time. Consequently, initial variation in local community composition produced by variable immigration history was sustained for a longer time under complex plant–soil interactions than with no plant–soil interactions. Additional simulation trials, in which the same immigration history was used across all 10 replicate local communities, confirmed that initial variation created by random history was needed for this effect to be realized.

With no plant–soil interaction, most species either always persisted or always failed to persist (i.e. either 0 or 100% chance of persistence), depending on their trait value, as expected (Fig. 4a). There were only a handful of species whose persistence depended on which 10 species they competed against (those with an intermediate level of persistence likelihood). In contrast, with complex plant–soil interactions, even though species showed differences according to their trait values, none of them always persisted, and few always disappeared (Fig. 4b).
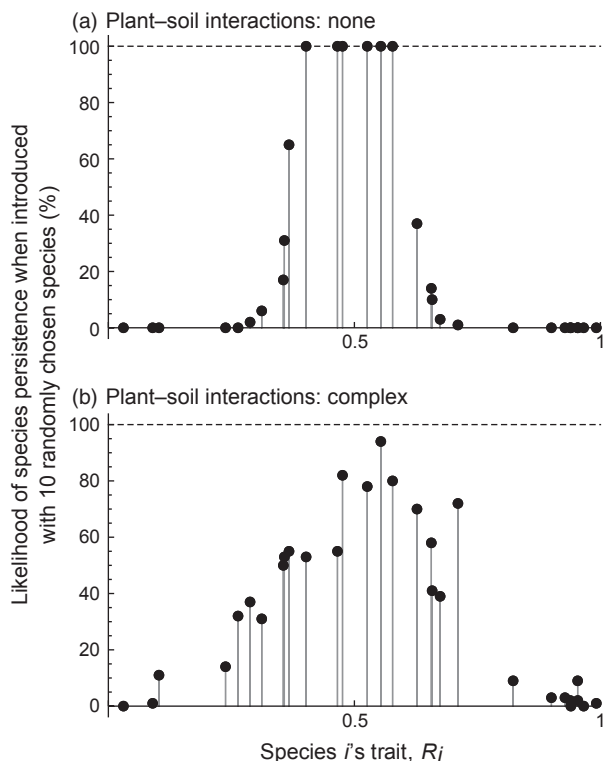

Fig. 4. Likelihood of persistence of species when introduced to an empty patch with 10 other, randomly selected species from the regional pool of 30 species. Persistence was measured after 100 years of population dynamics with no plant–soil interactions (a) or with complex plant–soil interactions (b). Graphs show results for one of the 20 replicate species pools used in Fig. 2. Each dot represents a species; all of the 30 species from the species pool was tested for likelihood of persistence.

BETA DIVERSITY AS A FUNCTION OF IMMIGRATION RATE

By delaying community convergence, complex plant–soil interactions can influence patterns of plant diversity. We illustrate this using immigration rate as an example of factors affecting diversity (Figs 5 and S6). With no plant–soil interaction, beta diversity was higher at lower immigration rate at the early stage of succession (until t = about 20 years) simply because species had not had many chances to immigrate (Fig. 5a). But this pattern soon disappeared, by t = about 60 years (Fig. 5b–d), which is an expected outcome of species sorting. With complex plant–soil interactions, the negative relationship between immigration rate and beta diversity was initially similar to that with no plant–soil interaction (Fig. 5a). However, because convergence proceeded slowly with complex plant–soil interactions, the negative relationship was maintained for a long time (more than a century) (Fig. 5b,c), even though the effect of immigration rate disappeared over long periods (Fig. 5d). Also notable is little effect of immigration rate on beta diversity at equilibrium (t = 1500 years, Fig. 5d).

Discussion

Taken together, our results show that complex plant–soil interactions can cause local plant communities to enter into a prolonged period of species turnover, resulting in transient, yet long-lasting maintenance of the high regional diversity that reflects variable species immigration history early in plant succession. Even though communities may eventually converge given enough time, the period of prolonged species turnover can be so long (e.g. over a century), relative to probable disturbance frequency, that delayed convergence may be a major mechanism for the maintenance of species diversity. To our knowledge, this effect of complex plant–soil interactions has not been suggested before. Much of previous theoretical work on plant–soil feedback and plant species coexistence used mathematical models of two plant species interacting with soil biota (e.g. Bever 2003; Umbanhowar & McCann 2005). Although two-species models have provided significant insight into species coexistence, our results indicate that directly modelling plant community assembly with a realistic number of plant species is needed to understand how plant diversity is maintained (see also Lankau *et al.* 2011).

More generally, the hypothesis of delayed convergence that we propose here highlights the importance of considering long-term transient dynamics in understanding the role of historical contingency in community structuring. The field of community ecology has long relied on the concept of alternative stable states as the theoretical framework for explaining historical contingency (Lewontin 1969; Law & Morton 1993; Schroder, Persson & De Roos 2005). In a foundational paper on this subject, May (1977) argued that 'if there is a unique stable state, historical accidents are unimportant; if there are many alternative locally stable states, historical accidents can be of overriding significance'. In this framework, transient
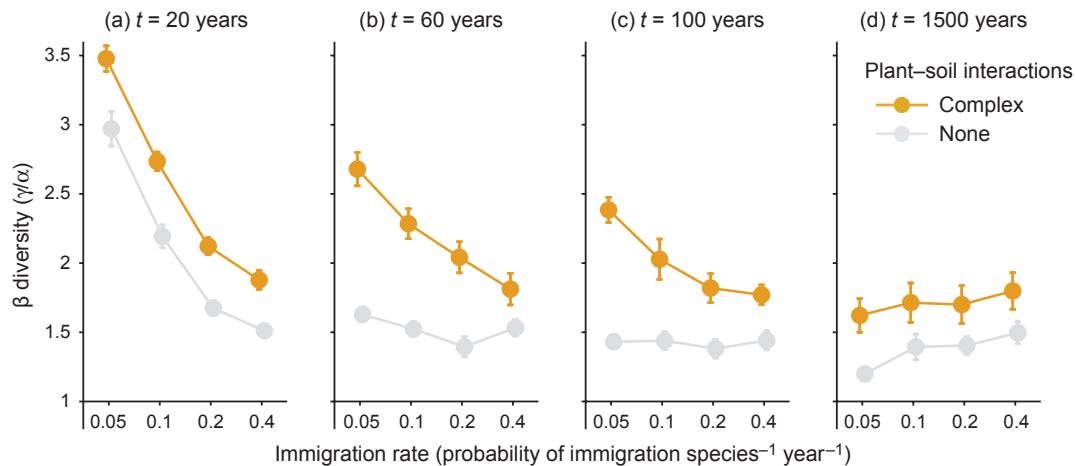
Fig. 5. Beta diversity (mean ± SE, *n* = 20) as a function of immigration rate at different stages of community assembly, for communities with no plant–soil interaction and for communities with complex plant–soil interactions.

dynamics are not explicitly considered. As we have argued recently (Fukami & Nakajima 2011), however, too much reliance on the concept of alternative stable states can be detrimental to advancing our understanding of historical contingency. This is because even when there is only one stable state to which all communities would eventually converge if given enough time, historical accidents, in the form of stochastic immigration history, can play a major role in affecting community structure and diversity before communities reach the stable state. For example, communities may always show a negative relationship between immigration rate and beta diversity—as long as the communities experience disturbance at least once a century—even when no such relationship is expected for stable communities (Fig. 5). Arguably, most ecological communities rarely reach a stable state because disturbance events take communities back to an earlier stage of community assembly too frequently, particularly when transient community dynamics last for a long time relative to immigration rate and generation time, as may be the case in the presence of complex plant–soil interactions.

Our work is only a first step towards understanding plant–soil interactions and transient community dynamics. There are a number of factors that we did not consider. For example, we assumed that the spatial extent of the disturbance that initiated a new round of community assembly was large enough that all local communities in the region were of the same age. It remains unclear how the extent of disturbance affects community convergence and divergence, although it the basic idea of delayed convergence contributing to regional diversity likely applies even when disturbance happens at smaller scales. We also assumed that the species pool that provided immigrants existed externally such that local community dynamics did not affect the species pool. In other words, we allowed only external dispersal and not internal dispersal (*sensu* Fukami 2005). Internal dispersal, where species disperse between communities within the region, is expected to homogenize communities, which may in some cases diminish the role of plant–soil interactions in delaying community convergence. Furthermore, we did not consider

interspecific and interannual variation in mortality, fecundity, immigration rate or seed bank. Although preliminary analysis suggests that the delayed convergence hypothesis holds true in the presence of such variation, more systematic analysis is needed. Finally, another unexplored issue is how ontogenetic and evolutionary changes in the strength of plant–soil interactions (Diez *et al.* 2010; Smith *et al.* 2012) may influence community convergence and divergence.

We interpreted simulation results in terms of biotic feedback between plants and soil biota, but given the simplicity of our model, results should be equally applicable to abiotic feedback between plants and the physical and chemical properties of soil (e.g., Van Wesenbeeck *et al.* 2008). On the other hand, model simplicity also means that the role of soil biota in driving community assembly may not have been fully captured by our model. In particular, immigration of different soil organisms may be a major factor influencing both plant and soil biodiversity, as evidence suggests that dispersal limitation can be more substantial in soil micro-organisms than generally thought (Peay, Garbelotto & Bruns 2010; Eisenlord, Zak & Upchurch 2012). By assuming no dispersal limitation for soil biota, our results probably underestimate the possible duration of delayed community convergence. Future research should make the model more explicit about soil biota, so that predictions regarding both plant and soil biodiversity can be developed (Van Der Heijden, Bardgett & Van Straalen 2008; Miki 2012).

Besides improving theoretical predictions, another important direction of future research is to empirically test our basic hypothesis. One approach may be to first make predictions about temporal changes in plant diversity using computer simulation that incorporates the values of S_{ij} estimated by standard pot experiments (Brinkman *et al.* 2010) and then evaluate how accurately the predictions explain observed patterns of diversity along a chronosequence of plant succession (e.g. van de Voorde, van der Putten & Bezemer 2011). In this exercise, S_{ij} values can be estimated in two ways. One is the conventional approach, where, for each species *i*, two values are estimated: S_{ii}, that is, the effect of 'own' soil, and the S_{ij}

value averaged across all species *j*, that is, the effect of 'foreign' soil (e.g. Reinhart 2012). The alternative is the new approach, where, for each species *i*, the value of S_{ij} is estimated for each species *j* separately (e.g. van de Voorde, van der Putten & Bezemer 2011). The model is expected to predict slower community convergence with the latter approach than with the former approach, and if the delayed convergence hypothesis is true, patterns of diversity predicted by the simulation with the new approach should more accurately describe observed patterns along the chronosequence. This and other approaches combining experiments and simulations (Meyer *et al.* 2009; Van der Putten *et al.* 2009) should allow the delayed convergence hypothesis to be tested and refined most effectively.

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Supporting Information

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

Figure S1. Comparison of results when each S_{ij} is chosen randomly from either a uniform distribution [0.5, 1.5] (panels a–d) or [0.5, 1.0] (panels e–h) when i is not the same as j.

Figure S2. Representative example illustrating how Sc_{max} (maximum cumulative number of colonisation events), Se_{max} (maximum cumulative number of extinction events), K_c (the value of t at which Sc_t is $1/2$ Sc_{max}), and K_e (the value of t at which Se_t is $1/2$ Se_{max}) are determined.

Figure S3. Results of the simulations conducted the same way as in Fig. 2, except that plant-soil interactions took place not only within cells (as in Fig. 2), but also between adjacent cells.

Figure S4. Results of the simulations conducted the same way as in Fig. 2, except that plant establishment in cells took place not only by seed dispersal (as in Fig. 2), but also by clonal growth.

Figure S5. Results of the simulations conducted the same way as in Fig. 2, except that plant-soil interactions took place not only within cells (as in Fig. 2), but also between adjacent cells, and that plant establishment in cells took place not only by seed dispersal (as in Fig. 2), but also by clonal growth.

Figure S6. Effect of immigration rate on temporal change (mean, $n = 20$) in alpha (blue), beta (orange), gamma (yellow) diversity and the cumulative number of colonisation, Sc_t (purple), and extinction, Se_t (green), under no or complex plant-soil interactions.