

## LETTER

# Assembly history dictates ecosystem functioning: evidence from wood decomposer communities

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### Abstract

Community assembly history is increasingly recognized as a fundamental determinant of community structure. However, little is known as to how assembly history may affect ecosystem functioning via its effect on community structure. Using wood-decaying fungi as a model system, we provide experimental evidence that large differences in ecosystem functioning can be caused by small differences in species immigration history during community assembly. Direct manipulation of early immigration history resulted in three-fold differences in fungal species richness and composition and, as a consequence, differences of the same magnitude in the rate of decomposition and carbon release from wood. These effects – which were attributable to the history-dependent outcome of competitive and facilitative interactions – were significant across a range of nitrogen availabilities observed in natural forests. Our results highlight the importance of considering assembly history in explaining ecosystem functioning.

### Keywords

Assembly rules, biodiversity, carbon sequestration, climate change, community assembly, ecosystem functioning, New Zealand *Nothofagus* (beech) forests, priority effect, saprotrophic fungi, wood decomposition.

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## INTRODUCTION

Community structure is now considered a key determinant of ecosystem functioning (Loreau *et al.* 2001; Hooper *et al.* 2005). For example, recent studies have emphasized the species diversity and composition of producers (e.g., De Deyn *et al.* 2008; Weedon *et al.* 2009) and decomposers (e.g., Deacon *et al.* 2006; Hanson *et al.* 2008) as a driver of ecosystem carbon dynamics. These studies have helped to integrate two research fields that are closely related, yet, until recently, conceptually separated – community ecology and ecosystem ecology. Nevertheless, understanding how community structure affects ecosystem functioning remains challenging because consequences often appear highly idiosyncratic and difficult to predict (e.g., Lawton 1999; Emmerson *et al.* 2001; Wardle 2002; Heimann & Reichstein 2008). Despite this difficulty, a clear understanding of ecosystem functioning is essential both for advancing ecological theory and for solving environmental issues such as mitigating adverse effects of carbon emissions (Heimann & Reichstein 2008).

The apparent idiosyncrasies observed in carbon dynamics and other ecosystem functioning may result from a current lack of historical perspectives (Ostfeld & LoGiudice 2003). Numerous studies have suggested that community assembly history, or the sequence and timing in which species join an ecological community, can profoundly affect species diversity and composition (e.g., MacArthur 1972; Drake 1991; Chase 2003; Shurin *et al.* 2004; Kennedy *et al.* 2009). Furthermore, the strength of these historical effects has been shown to depend on predation (e.g., Morin 1984; Steiner & Leibold 2004; Louette & De Meester 2007), disturbance (e.g., Jiang & Patel 2008), productivity (e.g., Steiner & Leibold 2004), ecosystem size (e.g., Fukami 2004), and other environmental conditions (Chase 2003). However, surprisingly few studies have evaluated the role of assembly history in explaining ecosystem functioning. Notably, one microcosm study examined effects of colonization sequence on ecosystem functioning (algal biomass production), but only two species were introduced to each microcosm (Zhang & Zhang 2007). Although another study used more species, only one measurement of ecosystem

functioning (plant biomass) was examined (Körner *et al.* 2008).

We suggest that filling the conceptual gap between assembly history–community structure relationships on one hand, and community structure–ecosystem function relationships on the other, is crucial to achieving a comprehensive understanding of ecosystem functioning. Potential links between assembly history, community structure and ecosystem functioning are not necessarily straightforward. For example, even a small historical effect on community structure may result in large variation in ecosystem functioning if the small compositional difference is because of one, or a few, functionally important species occupying different communities. In contrast, if variation in assembly history results in taxonomically divergent, but functionally convergent community structure (e.g. Fukami *et al.* 2005), assembly history may be important to community structure, but not to ecosystem functioning. These possibilities have rarely been tested.

In this article, we experimentally test the hypothesis that community assembly history affects ecosystem functioning via its effect on community structure, using wood-decaying fungi as a model system. Our laboratory study involved direct manipulation of species immigration history, an approach necessary for a rigorous test of the role of biotic historical contingency in community assembly and its consequences for ecosystem functioning. The high level of experimental control afforded in the laboratory would have been impossible to achieve under most field conditions, necessitating the laboratory approach (Cadotte *et al.* 2005). We will, however, use our results to discuss why we expect fungal community assembly history to influence carbon dynamics in natural forest ecosystems across a wide range of spatial scales.

### Wood-decaying fungi as a model system

Decomposition by wood-decaying fungi plays a central role in the storage and release of carbon and nutrients in forest ecosystems (Harmon *et al.* 1990; Zimmerman *et al.* 1995; Delaney *et al.* 1998). Furthermore, wood-decaying fungi form an important system for studying immigration history and carbon dynamics, for several reasons. First, fungal species differ markedly in the way they decompose wood (Harmon *et al.* 1994; Worrall *et al.* 1997), making decomposition rates dependent on fungal community structure (Boddy *et al.* 1989). Second, immigration history can be highly variable in these fungi. Although some species tend to colonize wood earlier than others (Coates & Rayner 1985; Jonsson *et al.* 2008), both spore dispersal and mycelial spread through soil – two main colonization strategies – contribute to stochastic variation in the timing of species immigration among wood substrates (Jonsson *et al.* 2008).

In addition, some fungal species may already be present in functional sapwood or bark as latent propagules (Boddy 2000), which may affect colonization success of fungal species that arrive later. Third, once they colonize a substrate, fungal species affect others through strong antagonistic (combative) and facilitative interactions (Coates & Rayner 1985; Holmer & Stenlid 1997; Heilmann-Clausen & Boddy 2005). Strong interactions, coupled with variable immigration history, have the potential to cause multiple trajectories of fungal community development (Coates & Rayner 1985) and, consequently, wood decomposition.

## MATERIALS AND METHODS

### Overview

We inoculated 10 species of fungi onto wood disks in laboratory microcosms, manipulating assembly history by inoculating one species 4 weeks before the remaining nine species, while holding constant the set of species introduced and the spatial position of inoculation. We created 7 different assembly histories (logistical limitations prevented all 10 species from being used as initial species). In addition, in order to test whether assembly history effects vary with environmental conditions, we also manipulated initial nitrogen availability. Our experiment had a fully factorial design, with three levels of nitrogen addition spanning the natural variability in soil nitrogen found in our study system. We monitored wood decomposition and carbon dynamics for a year after we introduced all fungal species.

### Fungal cultures

Pure cultures of 96 fungal species were isolated onto malt extract agar (12.5 g malt extract and 20 g agar in 1000 mL water) from a total of 143 fungal collections made over a 2-day period (11–12 May 2006) in a nearly monospecific *Nothofagus solandri* forest (Allen *et al.* 2000; Clinton *et al.* 2002) at Craigieburn Forest Park, South Island, New Zealand (43°8.556 S, 171°42.825 E, 1000 m elevation). Fungal strains were derived by isolation either directly from fruiting bodies or from supporting substrate immediately adjacent to the fruiting body. All of our strains are therefore presumed to be heterokaryotic. Ten of the 96 species were selected for experimental use (Table S1) based on feasibility of handling in culture, phylogenetic spread across the Ascomycota and the Basidiomycota, and so as to ensure a minimum 9 bp separation of the nuclear ribosomal internal transcribed spacer (ITS) polymerase chain reaction (PCR) product lengths (final range 522–808 bp). Fungal cultures were initially maintained on plates of malt extract agar. The cultures have been archived in liquid nitrogen in the International Collection of Micro-organisms from Plants

(ICMP). Collected sporocarps have been accessioned into the New Zealand Fungal Herbarium (PDD; Table S1). We confirmed that when inoculated alone, all species grew on wood under the experimental conditions.

### Wood disks and experimental jars

Twenty-eight live trunks of *N. solandri* were felled in a regenerating stand of mixed beech in the Maruia Valley, South Island, New Zealand. Wood disks (machined wet to 8 cm diameter, 1 cm thick, across the grain) were obtained from these trunks. Disks were dried at room temperature for approximately 20 days, oven-dried for 48 h at 40 °C, and individually weighed (initial dry diameter  $7.6 \pm 0.1$  cm, thickness  $1.1 \pm 0.03$  cm, weight  $28.8 \pm 0.08$  g; mean  $\pm$  one SEM). Disks were then soaked in tap water for 48 h prior to placing on dry soil in each jar.

Eight-hundred grams of well-mixed dried infertile mineral soil (from the forest where the fungi were collected) and a wet wood disk were placed in each 2-L glass jar, and 400 mL of tap water added. Wood disks were randomly assigned to jars. Prior to adding the water, varying amounts of ammonium-nitrate ( $\text{NH}_4\text{NO}_3$ ) were added to the water (see below). The jars were then autoclaved twice for 45 min at 121 °C with a 24-h gap between each autoclaving before initial fungal species inoculation. Each of 42 treatments in a factorial design (i.e., 7 immigration histories  $\times$  3 levels of nutrient availability  $\times$  2 harvest times; see below) was replicated 5 times. Throughout the experiment, the jars were covered by loose lids and stored in the dark in the laboratory, arranged randomly in a block design, at a mean temperature of 20.6 °C and a mean relative humidity of 55.9%.

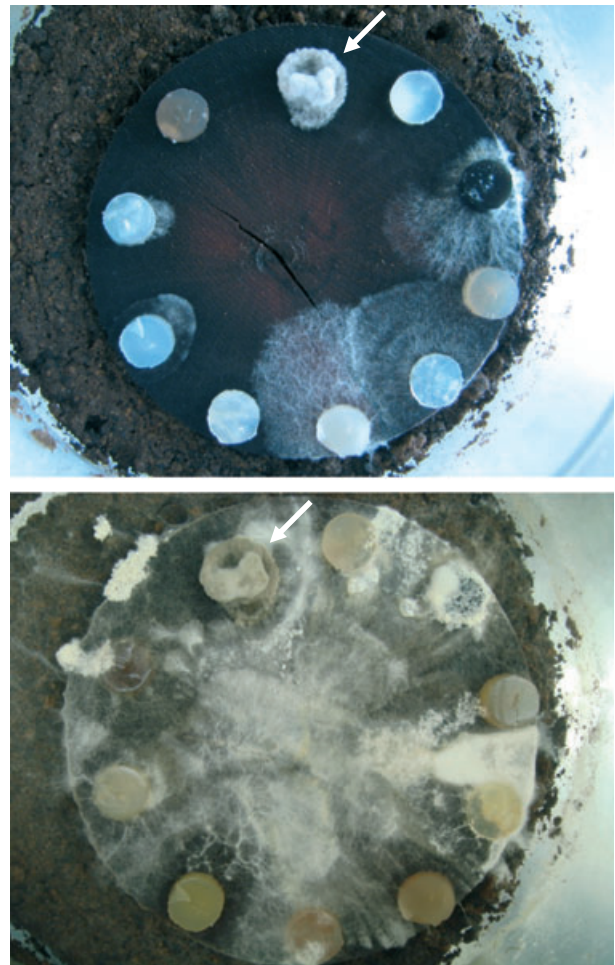
### Nitrogen availability

Initial nitrogen level was manipulated by adding 0, 0.5 or 1.0 g of  $\text{NH}_4\text{NO}_3$ , dissolved in 400 mL water, to 800 g of soil per jar. This range was used so as to capture the spatial variation observed in natural forest soils: the highest amount of  $\text{NH}_4\text{NO}_3$  added matched the level of nitrogen in the soil organic layer and exceeded the level of nitrogen in the most fertile mineral soils in the mountain range where the fungi were collected (Allen *et al.* 2000; Clinton *et al.* 2002). We used  $\text{NH}_4\text{NO}_3$  for nitrogen addition in order to minimize pH changes using a charge balanced source. Although we do not have information on which of the fungi use  $\text{NO}_3$ , it is relevant as a nitrogen source for the following reasons. Both  $\text{NO}_3$  and  $\text{NH}_4$  are present in New Zealand *Nothofagus* forest soils (Clinton *et al.* 1995; Dickie *et al.* 2009). Furthermore, nitrogen from  $\text{NO}_3$  and  $\text{NH}_4$  ends up in similar compounds during organic matter decomposition in these forests (Clinton *et al.* 1995). Finally,  $\text{NO}_3$  levels increased following

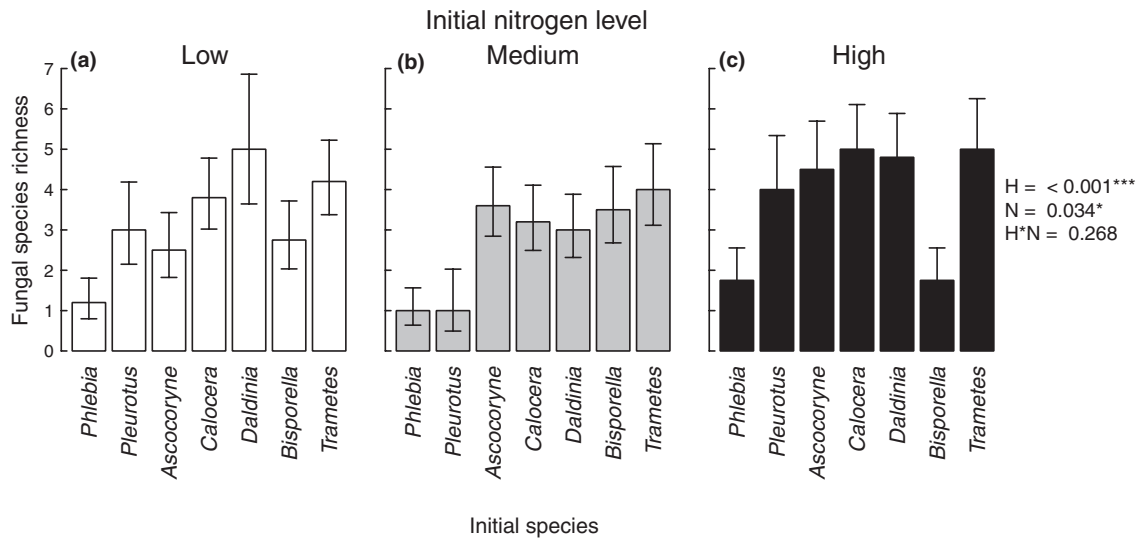
a major disturbance (approximately, from 1/10 to 1/2 of  $\text{NH}_4$  levels), so arguably, a major dead wood input event might occur along with a  $\text{NO}_3$  pulse (Dickie *et al.* 2009).

### Immigration history

From colonies on agar plates of each of the 10 fungal species, 5 mm diameter plugs were aseptically removed, and one plug of each species was placed onto a pre-determined location on each wood disk contained within the experimental jars (Fig. 1). One of the 10 species was inoculated aseptically by itself, and the other 9 inoculated 4 weeks after



**Figure 1** Representative example of the experimental setting, viewed from above the jar, showing the 8 cm diameter disk, the agar plugs placed on the disk for species inoculation, and the mineral soil on which the disk was placed. In each jar, 10 plugs were used to introduce 10 species. This photograph was taken 6 weeks (upper panel) and 18 weeks (lower panel) after the initial species (in this case, *Bisporella citrina*, indicated by arrow) was introduced, and 2 and 14 weeks (respectively) after the nine other species were introduced.



**Figure 2** Effect of fungal immigration history on fungal species richness. Species richness (mean  $\pm$  1 SEM) was measured 12 months after all species were introduced. *P* values from ANOVAs are provided for effect of immigration history (*H*), effect of initial nutrient level (*N*), and their interactive effect (*H\*N*). Asterisks indicate  $*P < 0.05$ ,  $**P < 0.01$  and  $***P < 0.001$ .

the first species inoculation, spaced evenly about the circumference of the disk (Fig. 1). Immigration history was manipulated by varying the species for the first inoculation. Seven of the ten species (Fig. 2) were randomly selected for use as initial species. The relative locations of inoculation points of the species were held constant across history treatments (Figures S1–S3). Our method of giving a single species a head start facilitated interpretation of how each early-arriving species affected late-arriving species.

### Species occurrence

At two harvest dates (4 and 12 months after all species were introduced), fungal community composition was determined at nine pre-determined spatial points on each wood disk. For this purpose, we destructively harvested wood disks (i.e., different wood disks were sampled first at 4 months and then at 12 months). Working inside a laminar flow cabinet, we removed wood disks from the experimental jars and split the disks along eight radial lines, aligned according to the location of the initial fungal inoculation points (see Figure S1 for sawdust sampling locations), using custom manufactured wood-splitting devices to expose internal wood without contamination from the surface of disks. Sterilized (ethanol flamed) 1.5-mm drill bits were used to obtain 5.5 mg (mean;  $n = 20$ , range 2.0–9.0 mg) of sawdust from the split-edge exposed interior of disks, directly collected into sterile 0.2-mL tubes. Although we do not have data to confirm that the amount of sawdust does not affect the frequency of species occurrence, there was no systematic bias between treatments in the amount of

sawdust sampled. A modified length-heterogeneity polymerase chain reaction (LH-PCR) assay was used to identify fungal species. Specifically, DNA was extracted and PCR of the ITS region carried out using the Sigma REDExtract-N-Amp Plant PCR kit, and primers ITS1F-6FAM and ITS4-VIC following standard protocols (Dickie *et al.* 2009). The length of PCR products was determined by 50-cm capillary electrophoresis in a 3130xl Genetic Analyzer (Applied Biosystems, USA). Results were analysed with a modified version of TRAMP software in R (FitzJohn & Dickie 2007). As species had been selected to insure a minimum 9 bp separation in PCR product lengths, this provided a robust method of species identification.

### Carbon and decomposition measurements

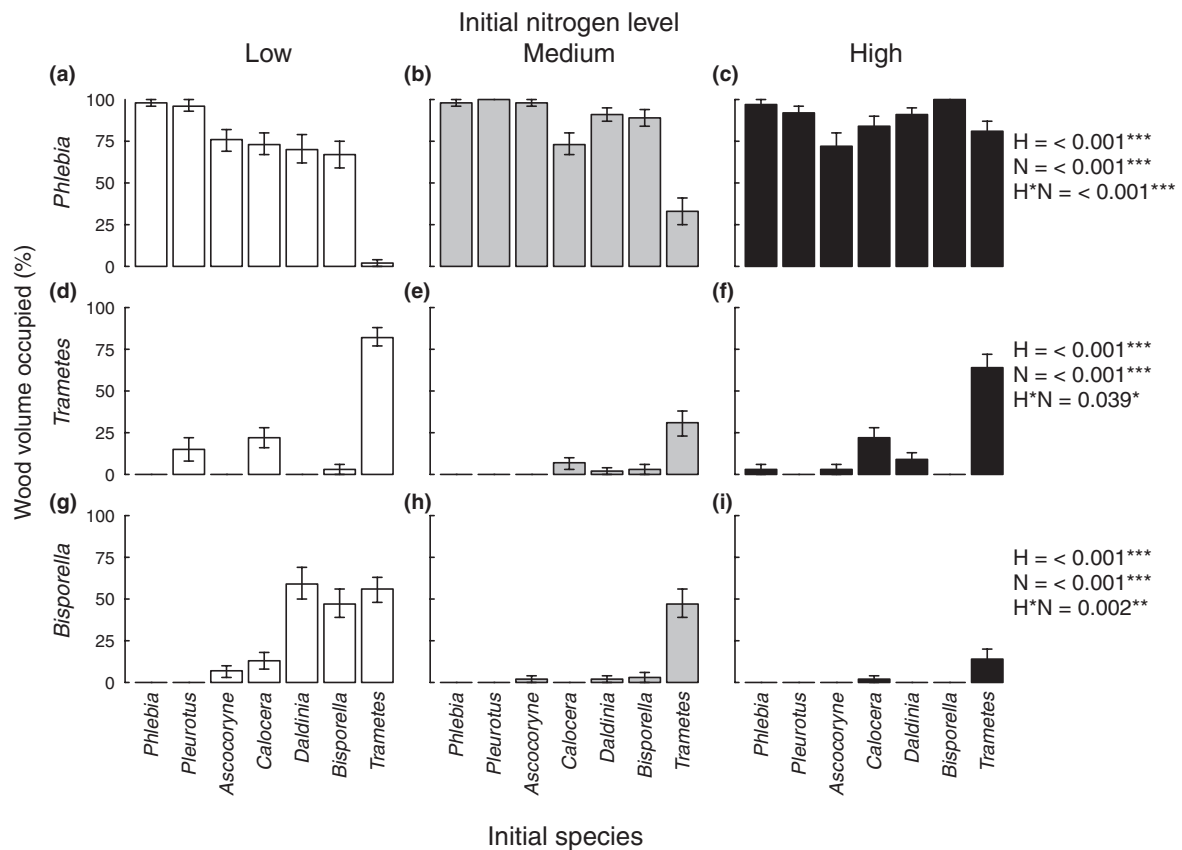
Respiration rate was measured 0, 2, 4, 6, 9 and 11 months after all fungal species were introduced, by temporarily sealing jar lids closed, then sequentially drawing three 5-mL atmospheric samples across a period of 25 min through a gas port inserted into jar lids. The gas headspace volume was approximately 1 L (i.e. jar volume minus soil volume). Atmospheric CO<sub>2</sub> concentrations were determined by injection into a PP Systems EGM-4 Environmental Gas Monitor for CO<sub>2</sub> (PP Systems, USA). The increase in gas concentration over time (median  $R^2 = 0.98$ ) was used to calculate respiration rate. At the 4- and 12-month harvests (4 and 12 months after all species were introduced), nitrogen and carbon concentrations of each wood disk were measured from a combined sawdust sample comprising 8 sub-samples each from a different split-edge interior

disk surface using 2-mm drill bits. In addition, at the 4- and 12-month harvests, percentage wood mass remaining (including fungal biomass in wood) was measured for each disk as the proportion of dry weight at the harvest to initial dry weight (after drying at 40 °C). We also measured nitrogen and carbon concentrations of the soil in each jar at the start of the experiment and at the 4- and 12-month harvests. Soil nitrogen and carbon showed little change over time.

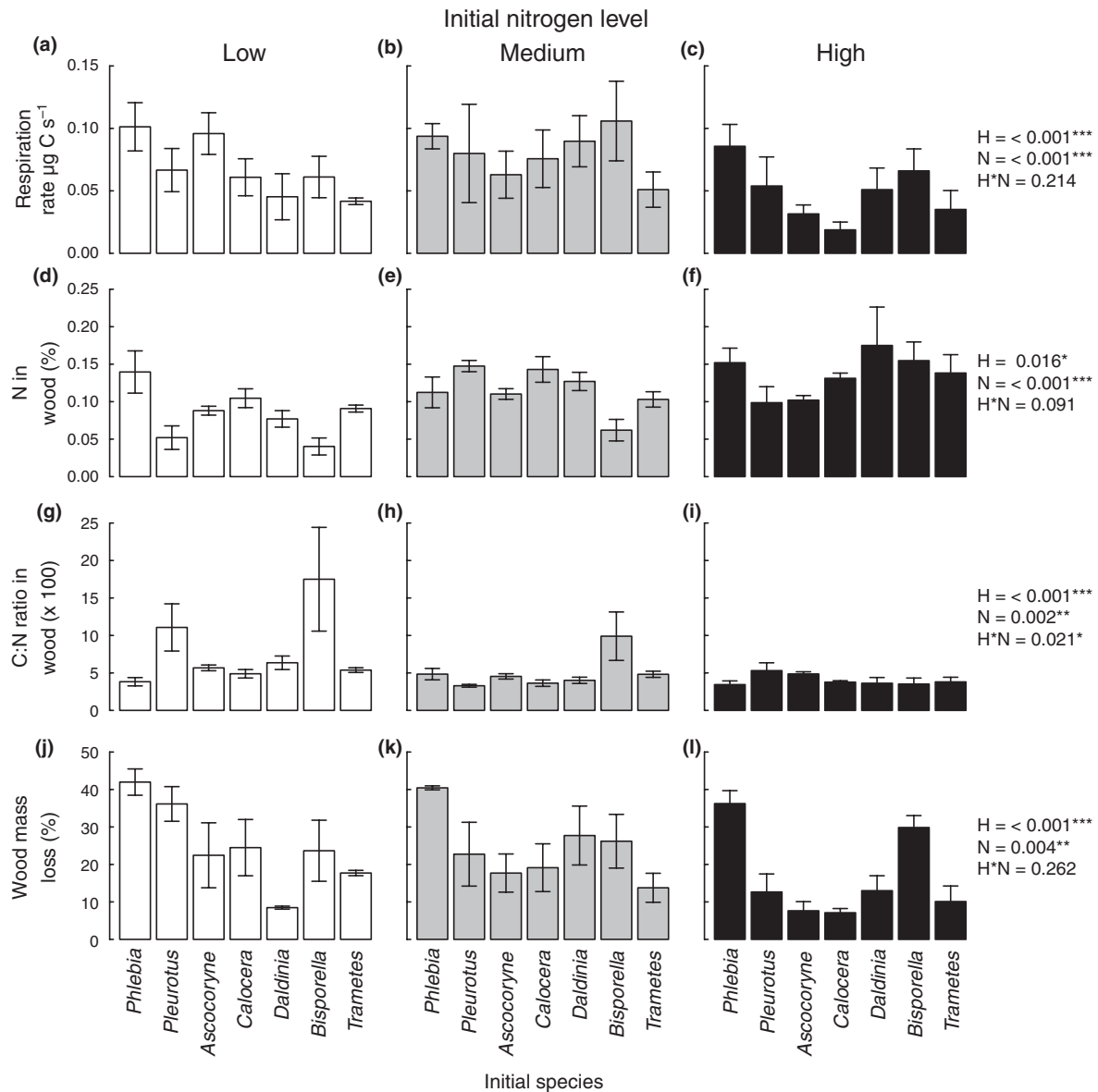
### Statistical analysis

To evaluate effects of initial species and nitrogen level on fungal community structure, a principal component analysis (PCA) was performed, with the frequency (percentage of wood volume occupied) of each of the 10 species as variables. Species frequency was calculated as the percentage of the sawdust samples in which the species was detected out of the nine sawdust samples from each wood disk (more than one species may occupy the same sawdust

sample concurrently). PCA is a statistical tool to reduce many variables (in this case, species) to a small number of newly derived variables that summarize the original information. Non-metric multidimensional scaling (NMDS), which is also commonly used for the same purpose as PCA but with less restrictive assumptions, yielded qualitatively identical results to the PCA results. Multivariate analysis of variance (MANOVA) was also conducted, with initial species, nitrogen level and their interaction as independent variables and the frequency of each of the 10 species as dependent variables. Permutational multivariate analysis of variance using distance matrices (ADONIS) yielded qualitatively the same results as the MANOVA results. To test for effects of initial species and nitrogen level on individual species frequencies and on ecosystem measurements, analyses of variance (ANOVAs) were performed, with initial species, nutrient level and their interaction as independent variables and species frequencies (Figs 2, 3 and Figures S2–S4) or ecosystem measurements (Fig 4 and Figure S5) as dependent variables.



**Figure 3** Effect of fungal immigration history on wood volume occupied (mean  $\pm$  1 SEM) by *Phlebia notbofagi*, *Trametes versicolor* and *Bisporella citrina* 12 months after all 10 fungal species were introduced. Wood volume occupied is the percentage of the sawdust samples in which the species was detected out of the nine sawdust samples from each wood disk (more than one species may occupy the same sawdust sample concurrently). *P* values are as in Fig. 2.



**Figure 4** Effect of fungal immigration history on wood decomposition and carbon dynamics. Respiration rate (a–c) was measured 11 months after introduction of all fungal species (see also Figure S5). Other measures (d–l) were taken 12 months after all species were introduced. *P* values are as in Fig. 2.

## RESULTS

### Effects of assembly history on community structure

Manipulation of early assembly history during the initial 4-week period of the experiment resulted in substantial variation in fungal community structure, which persisted for at least 12 months (Fig. 2, Figures S2 and S3). Across the wide range of nitrogen availabilities observed in natural forests (Allen *et al.* 2000; Clinton *et al.* 2002), fungal species richness showed up to three-fold differences between

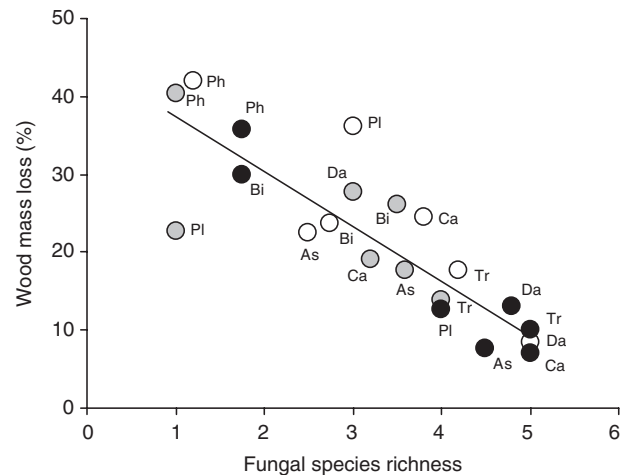
history treatments (Fig. 2), ranging from  $1.3 \pm 0.1$  in treatments where *Phlebia nothofagi* was introduced first to  $4.4 \pm 0.3$  in those where *Trametes versicolor* was introduced first (mean  $\pm 1$  SEM;  $P < 10^{-5}$ , ANOVA). A principal component analysis (PCA) revealed that species composition was also strongly affected by immigration history, showing in some cases more than a three-fold difference in the distance in the PCA multi-dimensional space (Figure S4a–c). For example, within high nitrogen treatments, wood disks to which *Bisporella citrina* or *P. nothofagi*

were introduced first were clearly distinct in final species composition from those to which *Ascocoryne sarcoides*, *Calocera cf. sinensis* or *T. versicolor* were introduced first (Figure S4c). The effects of immigration history were consistently significant at all nitrogen levels (MANOVA,  $P < 10^{-9}$ ), even though the distribution of communities in the PCA space differed between nitrogen treatments (Figure S4a–c).

Our data indicate that these differences in community structure resulted from complex inter-specific interactions whose outcome depended on immigration history and nitrogen availability. We highlight the behavior of three species – *P. nothofagi*, *T. versicolor* and *B. citrina* – as illustrative examples (Fig. 3). *P. nothofagi* was ubiquitous, occupying more than 70% of disk volume in most cases (Fig. 3a–c). However, when *T. versicolor* was introduced first, *P. nothofagi* occupied less than 5 and 40% of disk volume under low (Fig. 3a) and moderate (Fig. 3b) nitrogen levels, respectively. *T. versicolor* itself was uncommon when introduced after any other species. In contrast, it was widespread when introduced first (Fig. 3d–f). Meanwhile, *B. citrina* was also unable to establish in the majority of cases (Fig. 3g–i), but when *T. versicolor* was introduced first, *B. citrina* occupied more wood volume than otherwise in moderate (Fig. 3h) and high (Fig. 3i) nitrogen treatments. These patterns, together with the spatial distribution of the species (Figures S2 and S3), suggest that *T. versicolor* facilitates *B. citrina* by becoming dominant and suppressing the otherwise inhibitive *P. nothofagi*, but that this facilitation is realized only when *T. versicolor* arrives first, and it is more apparent at higher nitrogen levels.

### Effects of assembly history on carbon dynamics

Assembly history also had striking effects on wood decomposition and carbon dynamics. For example, we found as much as three-fold differences between history treatments in the rate of carbon release by fungal activity. Across the nitrogen gradient (Fig. 4a–c), these differences persisted over time, with significant effects at both initial and final stages of the experiment (Figure S5). Consistent with this result, wood mass loss – an indicator of cumulative carbon respiration over the course of the experiment – was strongly affected by immigration history (Fig. 4j–l). Although our measure of wood mass included both the wood itself and any fungal biomass accumulated in the wood, wood mass was in some cases reduced to almost half of the initial value by the end of the experiment (Fig. 4j–l), indicating that experimental duration encompassed a significant proportion of decomposition and carbon respiration. Historical effects were also significant on wood nitrogen content (Fig. 4d–f) and wood carbon-to-nitrogen ratio (Fig. 4g–i) at all initial nitrogen addition levels. Overall, for all but one (wood nitrogen content) of the ecosystem



**Figure 5** Relationship between fungal species richness and wood mass loss 12 months after all fungal species were introduced. Data presented are means for history treatments. Letters indicate the first two letters of the species used as initial species. White, grey and black circles indicate low, medium and high initial nutrient levels, respectively. Linear regression line is shown ( $R^2 = 0.70$ ,  $P < 0.001$ ).

properties measured, immigration history exerted an equally strong or greater effect than did initial nitrogen availability (Fig. 4), indicating that history affected wood decomposition at least as strongly as the nutrient environment.

The relationship between fungal community structure and wood decomposition confirms that the two are indeed tightly linked. Fungal species composition, as measured by the first PCA axis, explains 81% of the variation in decomposition (Figure S4d–f). Similarly, fungal species richness explains 70% of the variation in decomposition rate across the nutrient levels, showing that high fungal diversity is associated with slow decomposition (Fig. 5). The same significant pattern as in Fig. 5 also holds for respiration rate (i.e., if the  $y$ -axis in Fig. 5 is respiration rate shown in Fig. 4a–c instead of decomposition rate).

### DISCUSSION

Taken together, our results show that community assembly history determines the outcome of species interactions (Fig. 3), which in turn influences not just community structure (Fig. 2 and Figure S4a–c), but also ecosystem functioning (Fig. 4), across a broad range of nitrogen conditions. The negative diversity–functioning relationship (Fig. 5) likely resulted from species interactions (Boddy *et al.* 1989; Boddy 2000). One possibility is that in more diverse communities, fungi invested more in antagonistic interactions, such as production of secondary metabolites (Holmer & Stenlid 1997; Heilmann-Clausen & Boddy

2005), than in growth and decomposition. Information on the stage of wood decay at which the species occur in natural forests would facilitate interpretation of our results, but this information is currently not available for our species, except for sporocarps (Allen *et al.* 2000), the occurrence of which is not always correlated with fungal biomass within wood. Regardless of the exact mechanism, however, what is intriguing is that the functionally important gradient of fungal species diversity (Fig. 5) and composition (Figure S4d–f) emerged from simple manipulation of early immigration history, even with the same set of species introduced to all replicate communities. In this respect, our study contrasts with recent studies in which the set of species introduced was not standardized between treatments (e.g., Strickland *et al.* 2009).

Decreased decomposition and respiration rates in response to nitrogen addition (Fig. 4a–c and 4j–l) are consistent with a recent meta-analysis showing that nitrogen additions generally inhibit decomposition of high-lignin material (Knorr *et al.* 2005). Several hypotheses have been proposed to explain this effect (Knorr *et al.* 2005). Our results suggest a new hypothesis by linking nitrogen availability and decomposition rate to assembly history. It has been shown that elevated nitrogen reduces the spatial extent of initial resource exploration by fungi (e.g., Dickie *et al.* 1998). Under elevated nitrogen, late-arriving fungi may therefore have a better chance of survival because resource has been captured to a lesser extent by early-arriving species. Consequently, greater nitrogen may promote fungal diversity, a prediction consistent with our results (Fig. 2). As communities develop, however, greater fungal diversity may cause the co-existing species to invest more in antagonistic interactions than in decomposition, as discussed above, ultimately resulting in slower decomposition (Fig. 5).

The extent to which our laboratory results apply to natural ecosystem dynamics remains to be investigated. In particular, moisture and temperature have large effects on decomposition rates. It has also been indicated that CO<sub>2</sub> levels, which can be higher inside larger pieces of wood, influence the behavior of fungi and the outcome of species interactions. Furthermore, our experiment involved colonization by fungal mycelium from an agar plug, which simulates colonization by mycelium in the field. However, colonization also occurs via infection by a single spore, in which case the resultant colonizing mycelium will be at least initially homokaryotic. As stated in the methods, our strains are presumed to be heterokaryotic. Homokaryotic mycelium might differ in physiological properties (e.g., growth form and enzyme secretion) from the heterokaryon that forms only after mating between two compatible homokaryons. Such physiological differences might influence interspecific interactions. The importance of immigration history relative to these factors remains unknown.

Nevertheless, there are several reasons to expect that fungal assembly history influences carbon dynamics in natural forest ecosystems. First, theory predicts that historical effects become more important as the number of potential colonizers is increased, owing to more complex species interactions (Chase 2003; Fukami 2010). Our experiment, which used 10 species, may therefore underestimate the role of fungal immigration history in natural forests, which are typically inhabited by many more species of wood-decaying fungi (e.g., Allen *et al.* 2000). Second, disturbances affecting forests – such as storms, earthquakes and fires – may cause fungal community structure and wood decomposition to follow variable trajectories at a range of spatial scales. For example, forest carbon dynamics may show idiosyncratic variation at the scale of entire forest stands if the timing of large-scale disturbances varies from stand to stand, relative to the seasonal phenology of fruiting, spore dispersal and mycelial spread by wood-decaying fungi. Third, global climate change appears to affect fungal fruiting phenology, with considerable variation between species in their phenological response (Gange *et al.* 2007; Kauseurud *et al.* 2008). Thus it seems likely that fungal immigration history is being altered around the world, affecting forest carbon dynamics at both local and global scales.

## CONCLUSION

Despite the recent progress in our understanding of carbon dynamics and other ecosystem functioning (Heimann & Reichstein 2008), models that make predictions based on environmental conditions do not fully explain observed ecosystem processes. It is now widely recognized that biotic factors involving decomposers and other organisms limit the usefulness of these models (Bardgett *et al.* 2008; Wall *et al.* 2008; Chapin *et al.* 2009). The novel finding of our study is the possibility that the ecosystem-level effects of biotic factors can be understood only by considering species immigration history. Idiosyncratic historical effects present a major obstacle to predicting ecosystem carbon dynamics and other ecosystem functioning. However, further progress can be made through investigation of the environmental conditions (Chase 2003) and spatial scales (Chase 2003; Shurin *et al.* 2004; Fukami 2010) under which assembly history matters. Moreover, knowledge of historical effects can serve as a useful tool for managing carbon sequestration in restored ecosystems by using specific sequences of species introductions. Given that immigration history affects community structure at multiple scales (Chase 2003; Shurin *et al.* 2004; Fukami 2010) and not only in fungi but also in bacteria, protists, plants and animals as well (Drake 1990; Chase 2003; Shurin *et al.* 2004; Kennedy *et al.* 2009; Fukami 2010), we propose that more reliable prediction and



management of carbon dynamics, in particular, and ecosystem functioning, in general, require greater attention paid to historical influences of community assembly.

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## SUPPORTING INFORMATION

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

**Figure S1** Sawdust sampling locations.

**Figure S2** Spatial species distribution 4 months after all species were introduced.

**Figure S3** Spatial species distribution 12 months after all species were introduced.

**Figure S4** Effect of fungal immigration history on fungal community structure, and relationship between fungal community structure and wood decomposition rate.

**Figure S5** Rates of carbon release from experimental microcosms over time.

**Table S1** Species used.

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