

LETTER

Species divergence and trait convergence in experimental plant community assembly

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Abstract

Despite decades of research, it remains controversial whether ecological communities converge towards a common structure determined by environmental conditions irrespective of assembly history. Here, we show experimentally that the answer depends on the level of community organization considered. In a 9-year grassland experiment, we manipulated initial plant composition on abandoned arable land and subsequently allowed natural colonization. Initial compositional variation caused plant communities to remain divergent in species identities, even though these same communities converged strongly in species traits. This contrast between species divergence and trait convergence could not be explained by dispersal limitation or community neutrality alone. Our results show that the simultaneous operation of trait-based assembly rules and species-level priority effects drives community assembly, making it both deterministic and historically contingent, but at different levels of community organization.

Keywords

Alternative states, assembly history, assembly rules, community convergence, dispersal limitation, ecological restoration, historical contingency, neutral theory, priority effects, succession.

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INTRODUCTION

Whether the structure of ecological communities is deterministic or historically contingent has become increasingly controversial (Samuels & Drake 1997; Belyea & Lancaster 1999; Chase 2003). The deterministic view, rooted in Clements's (1916) climax concept of succession, suggests that communities converge towards a common structure determined by environmental conditions, irrespective of the history of community assembly. The alternative view, originated from Gleason (1927) and

popularized by Diamond (1975), suggests that community structure is historically contingent: stochastic forces producing variation in the sequence and timing of species arrivals can cause divergence in community structure among localities, even under identical environmental conditions and regional species pool (Drake 1990; Law & Morton 1993). Although these views at the heart of basic ecology have also gained applied importance in guiding the practice of biodiversity restoration (Dobson *et al.* 1997; Lockwood 1997; Young *et al.* 2001, 2005; Temperton *et al.* 2004), their validity remains little

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understood because it is difficult to manipulate or reconstruct assembly history in real ecosystems at sufficient scales and in sufficient detail (Samuels & Drake 1997; Belyea & Lancaster 1999; Chase 2003).

One approach to reconcile the two views has been to suggest that whether communities converge or diverge depends on the level of community organization considered. Community assembly is thought to be deterministic in the general composition of trait-based functional groups, but historically contingent in the specific composition of species (Fox 1987; Wilson 1999; Walker & del Moral 2003; Temperton *et al.* 2004). According to this hypothesis, environmental conditions determine the types of available niches and therefore the functional groups that can fill them (Weiher *et al.* 1998; Díaz *et al.* 1999; Watkins & Wilson 2003), while species compositions within functional groups are influenced stochastically by the history of species arrivals [Egler 1954 (but see Wilson *et al.* 1992); Sutherland 1974; Drake 1990; Law & Morton 1993]. This hypothesis has been applied explicitly or implicitly to various systems, including island birds (Diamond 1975), desert mammals (Fox 1987), intertidal invertebrates (Berlow 1997) and grassland plants (Fargione *et al.* 2003; Kahmen & Poschold 2004), and to both ecological and evolutionary community assembly (Gillespie 2004).

However, despite its central role in understanding community assembly, this hypothesis has rarely, if ever, been experimentally tested. Most relevant studies have used observational data to employ null-model approaches, in which observed structures are compared with what would be expected if trait-based assembly rules were absent (e.g. Weiher *et al.* 1998; Wilson 1999). While valuable, these studies have in large part, made the hypothesis controversial because it is difficult to objectively determine what constitutes appropriate null models, in spite of increasingly sophisticated methods (e.g. Stone *et al.* 2000 vs. Brown *et al.* 2002). Several other studies have taken experimental approaches on community convergence (e.g. Myster & Pickett 1994; Rodríguez 1994; Inouye & Tilman 1995), but the primary purposes of these studies were not to test the hypothesis in question. Instead most experiments focused on effects of environmental conditions and did not involve direct manipulation of initial community states or other aspects of assembly history, without which it is not possible to rigorously assess biotic historical contingency in community assembly.

Here, we report the results of a 9-year grassland experiment in which we directly manipulated initial community composition under standardized initial environmental conditions. During community assembly, we monitored temporal changes in community dissimilarity in both species composition and trait-group composition in a directly comparable way in order to test the above

hypothesis. Grassland plants are a suitable model system for our objective because a variety of ecological species traits that can be used to construct trait groups are available from the literature (e.g. Grime *et al.* 1988).

MATERIALS AND METHODS

Study site

We conducted the experiment on former agricultural land surrounded by heath, mixed forest and other former agricultural land in Mossel, Hoge Veluwe, in the Netherlands. Prior to the experiment, maize (*Zea mays*) had been grown in a rotation with sugar beet (*Beta vulgaris*), potatoes (*Solanum tuberosum*), barley (*Hordeum vulgare*) and rye grass (*Lolium perenne*) on this sandy loam soil (Van der Putten *et al.* 2000).

Experimental design

We manipulated initial plant species composition by sowing different seed mixtures on bare ground in 1996. We used a randomized block design with five blocks as replicates, with four 10 × 10-m plots in each block. We assigned four treatments to plots in each block: (i) high diversity sowing; (ii) low diversity sowing; (iii) natural colonization control; and (iv) continued agricultural rotation (the last treatment was not analysed in this study). All high-diversity sowing replicates received the same seed mixture of mid- to late-secondary successional species typical of the local species pool, whereas each low-diversity sowing replicate received a different subset of the high-diversity sowing mixture in order to ensure a wide range of initial composition (Table 1). After sowing, we allowed natural colonization of plants and other organisms in all plots without weeding until the end of 2004. Every September to October, we mowed and removed aboveground biomass from all plots and border rows. The plots were separated by 2-m wide border rows. While these rows are unlikely to completely prevent species dispersal across plots, such dispersal is an integral part of this community assembly experiment; this is in contrast with biodiversity–productivity experiments (e.g. Hector *et al.* 1999), in which it is crucial to remove species contamination to maintain experimental diversity gradients.

Measurements

Every year at peak standing biomass in July, we recorded the per cent cover of each plant species in 12 1 × 1-m permanent subplots established in each plot. Per cent covers were estimated using approximate midpoints of six classes (i.e. < 1% estimated as 1%, < 5% as 2%, < 10% as 5%, < 25% as 15%, < 50% as 25% and > 50% as 50%)

Table 1 Sown densities (seeds per m²)

Treatments	HDS	LDS1	LDS2	LDS3	LDS4	LDS5	NCC
Grasses							
<i>Phleum pratense</i> *(4)	500	1250	0	0	0	1250	0
<i>Festuca rubra</i> (4)	500	1250	1250	0	0	0	0
<i>Poa pratensis</i> n.s. (2)	500	0	1250	1250	0	0	0
<i>Anthoxanthum odoratum</i> n.s. (4)	500	0	0	1250	1250	0	0
<i>Agrostis capillaris</i> * (1)	500	0	0	0	1250	1250	0
Legumes							
<i>Lotus corniculatus</i> (12)	100	500	0	0	0	0	0
<i>Vicia cracca</i> n.s. (12)	20†	0	100†	0	0	0	0
<i>Trifolium pratense</i> n.s. (12)	100	0	0	500	0	0	0
<i>Trifolium dubium</i> n.s. (14)	100	0	0	0	500	0	0
<i>Trifolium arvense</i> n.s. (14)	100	0	0	0	0	500	0
Other forbs							
<i>Plantago lanceolata</i> n.s. (13)	100	500	0	0	0	0	0
<i>Hypochaeris radicata</i> * (13)	100	0	500	0	0	0	0
<i>Tanacetum vulgare</i> (1)	100	0	0	500	0	0	0
<i>Hypericum perforatum</i> n.s. (1)	100	0	0	0	500	0	0
<i>Linaria vulgaris</i> (1)	100	0	0	0	0	500	0

Treatments (HDS, high-diversity sowing; LDS, low-diversity sowing; NCC, natural colonization control) each had five replicates. Replicate numbers are shown for LDS. The numbers in parentheses following species names indicate the trait-groups that species belong to (see Table 2 and Table S1). In 2004, most species were either more abundant in natural colonization control plots than in high-diversity sowing plots (marked with *) or showed no significant difference between natural colonization control plots and high-diversity sowing plots (marked with n.s.) (*t*-tests on log-transformed abundance). A large-seeded species was sown at 20% of standard densities (†).

until 2001, and were measured directly from 2002. We confirmed that these methods were comparable: the direct measurement of per cent covers of all grasses combined corresponded very closely to the total midpoints of classes for all grasses. We averaged per cent covers in the 12 subplots to obtain an estimated per cent cover of each species in each plot. A total of 87 non-sown plant species colonized our plots, and *c.* 20–40 species occurred within plots at a given time, typically with a gradual increase in species richness over time.

Constructing trait groups

We constructed trait groups using the literature information on as many ecologically important species traits as possible (Tutin *et al.* 1964–1980; Grime *et al.* 1988; Thompson *et al.* 1997). These traits were related to life history, growth, dispersal, phenology, mycorrhizal association and other characteristics (see Table S1). Although certain plant traits are plastic, all of the traits we used, possibly except seed weight, are static and do not vary substantially with environmental conditions, making the literature information adequate for our purpose (see also Hérault *et al.* 2005). We ran these trait data through hierarchical clustering using

Ward's method (Lepš & Šmilauer 2003) and used 14 clusters as our trait groups (Table 2). The cut-off for the number of clusters was partly determined by the limited species pool (there would be little point in clustering if too many groups were occupied by a single species), and partly by looking at the results of successive iterations. After 14 clusters, the successive subdivisions were difficult to describe in biological terms.

Complete information on the 17 traits we focused on was available from the literature for 87 of the 102 species recorded in our plots (Tutin *et al.* 1964–1980; Grime *et al.* 1988; Thompson *et al.* 1997). Our analyses on both species and trait-group compositions used these 87 species. The other species were extremely rare (they collectively shared 0.20% of the total cumulative per cent covers, and the most abundant of these species shared 0.07%), showed no significant response to the sowing treatments, and should thus have negligible effects on the results. We acknowledge that species may not always fall into distinct functional groups and that it is often not straightforward to identify the ecologically most relevant way to construct trait groups (e.g. Lavorel & Garnier 2002; Petchey & Gaston 2002). Nonetheless, we found that non-hierarchical clustering using *K*-means (Legendre & Legendre 1998) produced

Table 2 Summary of trait groups constructed

Trait group	Number of species	Group description
1	12	Tall, patch-forming perennials with erect growth form and light seeds
2	8	Perennials of medium height, with erect growth form, limited vegetative spread, light wind-dispersed seeds and persistent seed bank
3	5	Perennial forbs of medium height, with erect, semi-rosette form, very limited vegetative spread and heavy seeds
4	7	Perennial grasses of medium height, with limited lateral spread, transient seed bank and dependence on seasonal regeneration from seed
5	7	Autumn germinating annuals, typically tall with semi-rosette form and wind-dispersed seeds
6	11	Short-lived forbs of medium height with semi-rosette or leafy form, typically with light seeds and persistent seed bank
7	5	Tall, competitive perennials forming large patches, typically with heavy seeds
8	11	Spring germinating annuals, typically large with heavy seeds and persistent seed bank
9	1	Tree with light, wind-dispersed seeds and persistent seed bank
10	3	Autumn germinating annual forbs, typically short with decumbent or procumbent habit with heavy seeds and persistent seed bank
11	3	Autumn germinating annual climbing forbs with leafy growth form and heavy seeds
12	7	Short, patch-forming perennial forbs with leafy growth form, procumbent or sprawling habit and heavy seeds
13	3	Short perennial forbs with rosette form, very limited vegetative spread and heavy seeds
14	3	Autumn germinating annual forbs, typically low growing with leafy growth form and light seeds

See Table S1 for further details.

qualitatively the same pattern as did Ward's method, indicating the robustness of our results to trait construction methods.

Compositional changes

We performed two principal component analyses (PCA) to investigate plant compositional changes during community assembly. PCA is a statistical tool to reduce many variables (e.g. species and trait groups) to a small number of newly derived variables that summarize the original information (Lepš & Šmilauer 2003). In one PCA, we determined how plots changed in species composition from 1997 to 2004, using log-transformed per cent cover estimates (Fig. 1). In another PCA, we determined how plots changed in trait-group composition, using log-transformed per cent cover estimates summed over all species belonging to each trait group (Fig. 2). The first four principal components accounted for > 50% of variation in both analyses. Data indicated that PCA was more suitable than detrended correspondence analyses (DCA) according to Lepš & Šmilauer (2003, p. 50) criteria (i.e. the longest gradient length was shorter than 3.0), but we found that DCA gave qualitatively the same pattern.

Testing for community convergence

We tested for convergence in both species and trait-group compositions by determining whether compositional dissimilarity among plots in blocks decreased over time (Fig. 3).

As an index of compositional dissimilarity among plots, we used Euclidean distance in the first four principal components (Myster & Pickett 1994; Krebs 1999). Because Euclidean distance is for pair-wise comparisons, and each block contained three plots, we calculated all pair-wise dissimilarity values within each block and averaged them to obtain block dissimilarity values. The qualitative results remain the same when Euclidean distance is calculated with the log-transformed percent covers of species or trait groups rather than the principal component values. The results also hold qualitatively when dissimilarity is measured by average Euclidean distance, an index that standardizes Euclidean distance to take account of the possibility that Euclidean distance increases with the number of species in the samples (Krebs 1999).

Randomization test

We conducted a randomization test to ascertain whether the apparent community convergence observed in trait-group composition (as described below in Results and discussion) was significantly different from random chance. This test involved: (i) randomly assigning species to trait groups, while keeping the number of trait groups and the number of species belonging to each trait group the same as for the observed trait groups; and (ii) calculating mean dissimilarity measures based on PCA the same way as described above for the observed trait groups (the results remain qualitatively the same when Euclidean distance is calculated with the

Figure 1 Changes in plant species composition from 1997 (square, diamond or circle) to 2004 (end of arrows). A high-diversity seed mixture (HDS), a low-diversity mixture (LDS), or no species (natural colonization control) (NCC) was sown in 1996 (Table 1). All graphs are based on a single common principal component analysis (see Materials and methods).

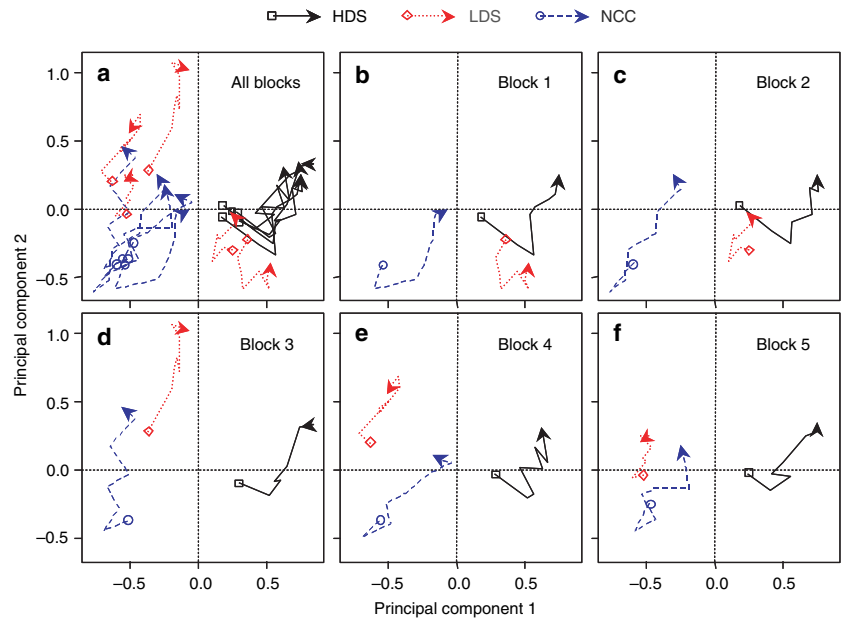
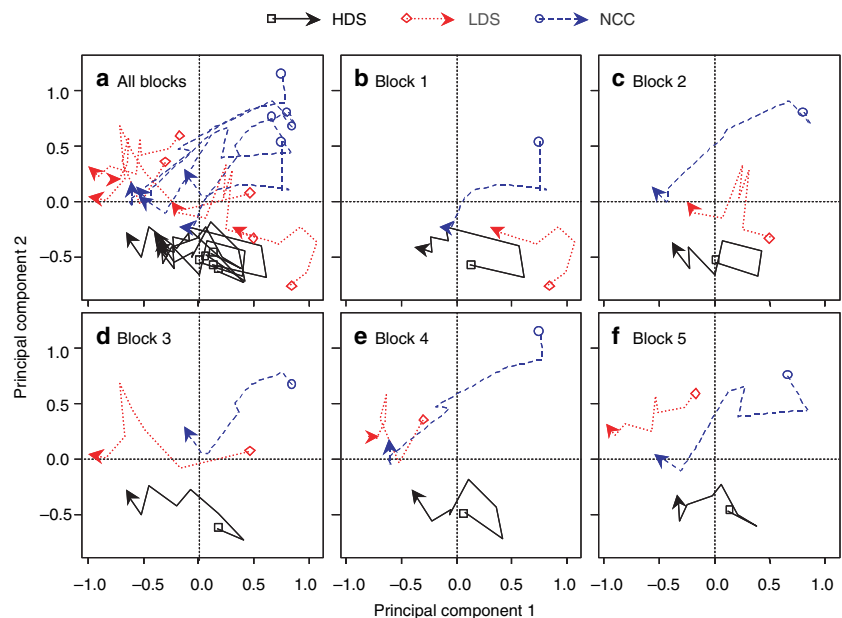


Figure 2 Changes in plant trait-group composition from 1997 to 2004. Symbols are as in Fig. 1. All graphs are based on a single common principal component analysis (see Materials and methods).



log-transformed per cent covers of trait groups rather than the principal component values). Randomization was repeated 100 times.

RESULTS AND DISCUSSION

The sowing treatments caused rapid community divergence in the first year of the experiment (starting from bare ground), successfully establishing experimental variation in initial community composition in both species and trait groups. In 1997, 1 year after we sowed seeds, replicates

within the natural colonization control treatment were very similar to one another both in species composition (circles in Fig. 1a) and trait-group composition (circles in Fig. 2a), and the same was true for the high-diversity sowing treatment (squares in Figs 1a and 2a), while the two treatments were clearly separated from each other (compare circles and squares in Figs 1a and 2a). In the same year, low-diversity sowing replicates showed considerably greater variation both in species composition (diamonds in Fig. 1a) and trait-group composition (diamonds in Fig. 2a) than did natural colonization control or high-diversity sowing

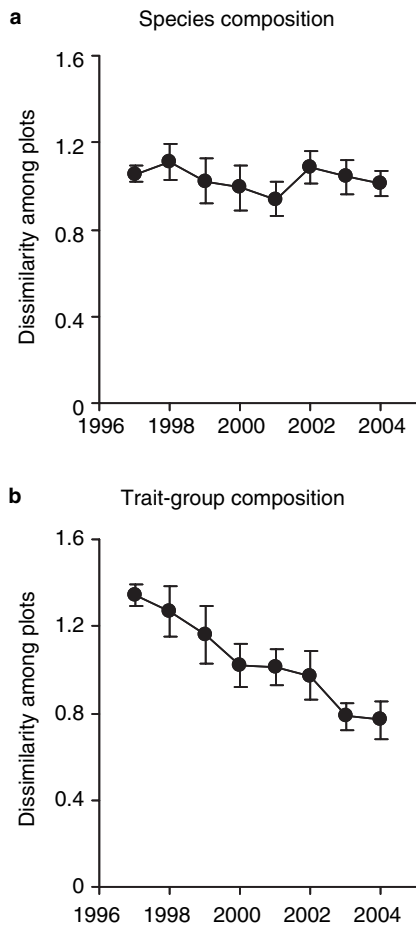


Figure 3 Changes in plant community dissimilarity calculated as the compositional difference among plots within blocks (mean \pm SEM, $n = 5$ blocks). Dissimilarity in species composition (a) showed no significant change ($t = -0.69$, $P < 0.53$), while dissimilarity in trait-group composition (b) declined significantly over time ($t = -4.62$, $P < 0.01$).

replicates. All these patterns are the expected outcome of the sowing treatments, closely reflecting the extent to which plots differed in sown species and trait groups (Table 1). No

clear differences in pattern initially existed between species composition and trait-group composition.

However, subsequent trajectories of community assembly showed a striking contrast between species composition and trait-group composition. Although substantial temporal changes occurred in both species (Fig. 1) and trait groups (Fig. 2), the directions of trajectories differed markedly between the two. In species composition, plots continued to be as different from one another as they were immediately after the rapid divergence in 1997, with no sign of subsequent convergence among blocks (Fig. 1a) or within each block (Fig. 1b–f). In contrast, plots were gradually converging in trait-group composition, both among blocks (Fig. 2a) and within each block (Fig. 2b–f). Community dissimilarity measures confirmed these trends statistically: dissimilarity showed no significant overall change over time in species composition (Fig. 3a), whereas dissimilarity declined significantly in trait-group composition (Fig. 3b). Importantly, this decline (Fig. 3b) was significantly greater than would be expected from random formation of trait groups (Fig. 4). Therefore, consistent with the hypothesis we sought to test, trait-group composition converged while species composition remained divergent during the first 9 years of community assembly in this experiment.

We emphasize that we determined effects of initial community composition by directly manipulating it without changing initial environmental conditions (cf. Myster & Pickett 1994; Rodríguez 1994; Inouye & Tilman 1995). As such, we can attribute species divergence to the experimentally created variation in initial composition. An alternative potential explanation of our results is that species divergence occurred because sowing simply subjected plots to very different pools of colonizers. However, by 2004, 11 of the 15 sown species (73%) became at least as abundant in natural colonization control plots, in which they were not sown, as in high-diversity sowing plots, in which they were sown (Table 1). We can thus eliminate the possibility that dispersal limitation alone caused species divergence. Therefore, the divergence due to initial biotic variation strongly

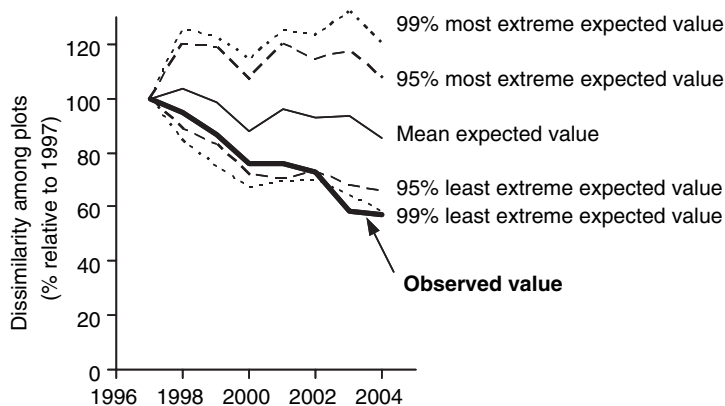


Figure 4 Results of the randomization test, showing that observed dissimilarity became increasingly smaller than mean expected dissimilarity over time, falling below the 95% least extreme expected value by 2002 and below the 99% least extreme expected value by 2003. Dissimilarity is expressed in percentage relative to 1997 so as to make expected and observed values comparable.

indicates the operation of biotic drivers of community assembly such as inhibition and facilitation (Connell & Slatyer 1977). In other words, sown species directly or indirectly affected the potential of later immigrants to establish, and these priority effects collectively caused the initial high degree of species divergence to persist among plots of different sowing treatments.

On the contrary, the fact that trait-group composition converged while species composition remained divergent indicates that deterministic assembly rules governed assembly at the trait-group level of community organization. The non-random community structuring by trait-based assembly rules demonstrated in this (Fig. 4) and other (e.g. Fargione *et al.* 2003) studies argues against neutral assembly driven by random sampling from regional species pools (Hubbell 2001). Specifically, in this study the initially variable communities converged to become increasingly dominated by trait group 1 (moving left along the first axis in Fig. 2; see Fig. S1), which consisted of tall, patch-forming perennials with erect growth form and light seeds (Table 2 and Table S1). This makes intuitive sense from what we know about grassland succession. What is intriguing is that this non-random convergence occurred even though communities were clearly diverging in specific species composition even within this trait group responsible for the convergence (Fig. S2).

CONCLUSION

Despite the widely recognized potential to resolve the controversy over deterministic vs. historically contingent community assembly (e.g. Samuels & Drake 1997; Walker & del Moral 2003; Temperton *et al.* 2004), the hypothesis that assembly is convergent in species traits and divergent in species identities has long lacked definitive empirical support. By manipulating initial community states directly and monitoring changes in species identities and species traits in a comparable way, this 9-year study has provided the first experimental demonstration, to our knowledge, of species divergence and trait convergence within the same community. Future research should apply similar experimental approaches to other systems to assess the generality of our findings. However, circumstantial evidence suggests that our findings are likely to be general across a variety of habitats and taxa (e.g. Diamond 1975; Fox 1987; Berlow 1997; Wilson 1999; Fargione *et al.* 2003; Gillespie 2004; Kahmen & Poschlod 2004). Moreover, although this study has focused on community structure, the contrasting dynamics in species vs. trait-group compositions may also have profound implications for ecosystem functioning (e.g. Thompson *et al.* 1996; Hooper & Vitousek 1997; Tilman *et al.* 1997; Grime 2002; Foster *et al.* 2004). We propose that the simultaneous operation of trait-based assembly rules and species-level priority effects, as revealed in this study, may

drive community assembly in many ecosystems, making them both deterministic and historically contingent at different levels of community organization.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Figure S1 Loadings of trait groups in the PCA shown in Fig. 2.

Figure S2 Changes in species composition within trait group 1 from 1997 to 2004.

Table S1 Species traits used to construct trait groups.

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