

# Biology, chance, or history? The predictable reassembly of temperate grassland communities

JANA S. PETERMANN,<sup>1,4</sup> ALEXANDER J. F. FERGUS,<sup>1</sup> CHRISTIANE ROSCHER,<sup>2</sup> LINDSAY A. TURNBULL,<sup>1</sup>  
ALEXANDRA WEIGELT,<sup>3</sup> AND BERNHARD SCHMID<sup>1</sup>

<sup>1</sup>*Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland*

<sup>2</sup>*Max Planck Institute for Biogeochemistry, POB 100164, 07701 Jena, Germany*

<sup>3</sup>*Institute of Ecology, University of Jena, Dornburger Strasse 159, 07743 Jena, Germany*

**Abstract.** Many studies have examined invasion resistance in plant communities, but few have explored the mechanisms of invasion and how subsequent community reassembly affects community functioning. Using natural dispersal and deliberate seed addition into grassland communities with different compositional and richness histories, we show that invaders establish in a nonrandom manner due to negative effects of resident functional groups on invading species from the same functional group. Invaders hence complement communities with originally low richness levels. Consequently, communities converge toward similar levels of species richness, high functional richness, and evenness, but not always maximum productivity. Invasion processes are faster but qualitatively similar when the effect of chance, in the form of dispersal stochasticity, is reduced by seed addition. Thus, dispersal limitation may influence community assembly, but it does not override functionally predictable assembly mechanisms. Some of the most productive communities prior to invasion are unstable in the face of invasion, leading to decreased productivity following invasion. We suggest that invasion into such communities occurs possibly because a pathogen-free niche is available rather than a resource niche. Thus, pathogens in addition to resource niches may be important biological drivers of community assembly.

**Key words:** *biodiversity–productivity relationship; community stability; dispersal limitation; ecosystem functioning; invasion resistance; invasiveness; negative feedback; neutral theory; nonrandom invasion; species richness.*

## INTRODUCTION

Biology, chance, and history must all play some role in community assembly. For example, in order to successfully establish in a new community, a potential invader must first arrive, and dispersal is an inherently stochastic process. However, the relative importance of dispersal limitation and historical contingency vs. deterministic biological interactions is still hotly debated (e.g., Drake 1991, Hubbell 2001, Chase 2003, Fargione et al. 2003, Turnbull et al. 2005a, b).

The first explanations as to why certain species were able to successfully invade new communities were certainly deterministic in nature and focussed mainly on the biology of the invaders (see, e.g., Elton 1958). For instance, some species appeared to be more successful than others at dispersing to new sites, at entering new communities, or at reaching high population sizes and suppressing residents (Crawley 1986, Drake et al. 1989).

This observation led to a focus on the properties of these species and their associated “invasiveness” (Baker 1967, Sutherland 2004, Richardson and Pysek 2006).

Conversely, invasion success might be related to the biology of the invaded or resident community; for example, more diverse communities tend to be more invasion resistant (Crawley 1987, Burke and Grime 1996). This may occur because particular resident species or functional groups provide invasion resistance (Crawley et al. 1999, Levine and D’Antonio 1999, Symstad 2000, Hector et al. 2001, Dukes 2002, van Ruijven et al. 2003, Fargione and Tilman 2005) and these species or functional groups are more likely to be found in higher-diversity communities. The importance of particular species for community invasion resistance is therefore analogous to a sampling effect in biodiversity–productivity relationships (Hector et al. 2001, Wardle 2001).

Finally, interactions between the invader and the invaded community might be key to understanding invasion success, analogous to a complementarity effect in biodiversity–productivity relationships (Hector et al. 2001, Fargione et al. 2003). In this case, not only the identity of the invader or the composition of the resident community, but the match between invaders and communities plus the respective species abundances

Manuscript received 14 December 2008; revised 29 April 2009; accepted 15 May 2009. Corresponding Editor: J. M. Levine.

<sup>4</sup> Present address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4 Canada.  
E-mail: Peterman@uwinst.uzh.ch

would be most important in determining the outcome of invasion (e.g., Fargione et al. 2003, Turnbull et al. 2005b, Strauss et al. 2006). Thus, just like species coexistence in established communities, invasion and community reassembly would be controlled by density-dependent stabilizing mechanisms (Chesson 2000). These stabilizing mechanisms would be expected to facilitate invasion by species or functional groups that are most different from abundant residents (MacArthur and Levins 1967, Abrams 1983, Emery 2007).

The most well-known and studied complementarity mechanism within temperate communities is based on resource-use niches (e.g., Harpole and Tilman 2007), which could lead to preferential invasion by species with complementary resource requirements compared with the residents (Fargione et al. 2003, Questad and Foster 2008). Increased invasion resistance of species-rich communities could, according to this hypothesis, be attributed to the lack of unconsumed resources, as some invasion studies have indicated (e.g., Knops et al. 1999, Hector et al. 2001, Fargione et al. 2003). Another stabilizing mechanism potentially underlying invasion patterns is the presence of pathogens or herbivores—for which the invader is a host or resource—in a community that contains species closely related to the invader. This mechanism is similar to the Janzen-Connell effect, in which the presence of adult trees reduces the recruitment success of conspecific juveniles in tropical forests (Janzen 1970, Connell 1971, Augspurger and Kelly 1984). We have previously found evidence for this mechanism, operating via negative soil feedbacks, in a temperate grassland community where it was a powerful promoter of coexistence between competing functional groups (Petermann et al. 2008). Hence, this pathogen-driven feedback could similarly affect invasion patterns and community reassembly after invasion. Because functional groups are based on species traits, taxonomy, or both (for details regarding the functional-group classification in this paper, see *Methods: Experimental design*, below), we expect species within functional groups to share more pests and pathogens (Gilbert and Webb 2007) and to have more similar resource requirements and resource-use patterns (Fargione et al. 2003). If invasion and community assembly are driven by one of these two stabilizing mechanisms, between-functional-group effects would be expected to be stronger than within-functional-group effects.

In contrast to these deterministic explanations, invasion and community assembly could be independent of the biology of the species and instead be strongly influenced by chance (Hubbell and Foster 1986, Hubbell 2001). If invasion into new communities is viewed in the light of island-biogeographic theory (MacArthur and Wilson 1963, 1967) the probability of colonization by new species inevitably decreases with increasing species richness of the resident community because a larger fraction of the total species pool has already arrived and established. Thus, a negative relationship between

community richness and the number of invading species would be expected. At the same time, the number of species going extinct is predicted to increase with increasing resident species richness, as, for the same area, population sizes are smaller in diverse communities. Equilibrium richness is reached when extinction and colonization rates become equal. Under this neutral scenario, the compositions of the assembling communities would be random, meaning that they are not predictable based on the biology of the species, but instead governed only by demographic and dispersal stochasticity (Hubbell 2001). In the case of established communities of different initial richness and composition, invasion of new species and subsequent community reassembly would then lead to the convergence of species richness but not of composition, even under identical environmental conditions (Fukami et al. 2005). This was indeed found by two recent studies examining spontaneous invasion via natural dispersal into experimental grassland communities of originally different richness levels and compositions (Pfisterer et al. 2004, Rixen et al. 2008). Species have often been shown to be limited by their dispersal abilities (Turnbull et al. 2000, Clark et al. 2007), and propagule pressure has been identified as a major driver of invasion and community assembly (e.g., Kolar and Lodge 2001). Thus, the compositional divergence of different communities observed in spontaneous-invasion studies may well be due to dispersal stochasticity. On the other hand, initial floristic composition (Egler 1954, Collins et al. 1995) or the order of species arrivals (Drake 1990, Chase 2003, Zhang and Zhang 2007) may prevent compositional convergence. In that case, the communities' colonization and establishment history may override all other assembly mechanisms and may have a dominant influence on the final composition of reassembled communities (Drake 1991).

The functioning of plant communities, for example in terms of primary productivity, has been found to be a function of species richness (Tilman et al. 1996, 2001, Hector et al. 1999), phylogenetic diversity (Cadotte et al. 2008), functional richness (Tilman et al. 1997, Hector et al. 1999), evenness (Wilsey and Potvin 2000, Polley et al. 2003, Hillebrand et al. 2008), and composition (Hooper and Vitousek 1997, Tilman et al. 1997, Spehn et al. 2005; for further references see Balvanera et al. [2006]). Therefore, if invasion leads to changes in these properties, it is expected to directly or indirectly influence community functioning (Chase 2003, Hooper et al. 2005). However, the consequences of invasion for the invaded communities, especially with regard to their functioning, are rarely considered (Pfisterer et al. 2004, Rixen et al. 2008).

In the present study, we use an established grassland biodiversity experiment with a species richness and functional-group richness gradient maintained by weeding to study the reassembly of communities by invasion and the resulting effects on ecosystem functioning. After

opening communities with different initial compositions to spontaneous invasion and to invasion assisted by seed addition, we examine whether invasion and reassembly processes are dominated by the biological characteristics of residents or invaders, by the chance effects of dispersal, or by the compositional history of the resident community. Furthermore, we assess the consequence of invasion, not only for richness and composition but also for the functioning of reassembled communities in terms of primary productivity. We show that invasion is biologically predictable on a functional-group basis and only weakly dependent on dispersal effects. Invasion complements species richness and functional composition and thus leads to the decay of positive species richness–productivity relationships. We suggest that the observed community reassembly processes were driven by both resource complementarity and pathogen effects.

## METHODS

### *Experimental design*

The present study was carried out within a large experimental platform at Jena, Germany (50°55' N, 11°35' E). The Jena Experiment is a long-term grassland biodiversity–ecosystem functioning experiment (Roscher et al. 2004). It is situated in the floodplain of the river Saale at an altitude of 130 m above sea level and until 2001 it was used for agricultural crops. The experimental grassland plots were established by sowing in spring 2002. The mean annual air temperature is 9.3°C; the mean annual precipitation is 587 mm.

Seventy-eight experimental plots were sown with randomly assembled species assemblages of 1, 2, 4, 8, or 16 species. The total species pool of the experiment consisted of 60 native central European plant species common in seminatural grasslands. Four plots containing all 60 species were also sown. Prior to assembling experimental communities, the species were grouped into four functional groups according to a cluster analysis using ecological and morphological traits (16 grasses, 12 legumes, 12 small herbs, 20 tall herbs; Roscher et al. 2004). Each functional group was represented at each richness level. In addition, the number of functional groups was varied within species-richness levels as much as possible, including 16 species-richness levels with only one functional group, so that the design was almost completely orthogonal with respect to functional-group composition and species richness (Roscher et al. 2004). There were 16 different species in monoculture; 16 different species compositions at richness levels 2, 4, and 8; and 14 different species compositions at richness level 16 (see Appendix C: Table C1). The plots had a size of 20 × 20 m and were arranged in four blocks. In addition, each plot was assigned *x*- and *y*-coordinates to account for geographical position in later analyses. All plots were mown twice a year and did not receive fertilizer.

Within each plot, we marked four 2 × 2.25 m subplots for our invasion experiment (see Plate 1). One pair of

subplots was used for the invasion treatment “cessation of weeding” (C) and one pair for the treatment “weeding” (W). In each subplot pair, one subplot was randomly assigned to the deliberate seed-addition treatment (+), and the other received only spontaneous-invader seeds (–). The seed-addition treatment included seeds of all species from the original experimental pool of 60 species and we therefore refer to them as “internal invaders” if they are not part of the sown community of a specific plot. Seeds were added at a rate of 1000 viable (according to standard laboratory tests) seeds/m<sup>2</sup> in April 2005 divided equally among the 60 species. Among the spontaneously (= naturally) invading species there were both “internal invaders” and “external invaders,” the latter not belonging to the original pool of 60 species but occurring in the surroundings of the field site. Thus, our experimental design consisted of the following four subplots: subplot “W–” was weeded twice a year like the remainder of the larger 20 × 20 m plot to maintain the original set of species (“residents”) and served as the control (“closed” community). In subplot “W+” internal invader seeds were added and external invader species were removed by weeding, so that only internal invaders could establish. In subplot “C–” weeding was stopped at the end of 2004; hence, internal invaders and external invaders could enter the community spontaneously. In subplot “C+” weeding was also stopped at the end of 2004, so that internal and external species could invade spontaneously; additionally, internal-invader seeds were added. Generally, soil disturbance caused by weeding was kept to a minimum by using small knives to cut weed roots and remove them carefully and by all maintenance being done before the development of a closed canopy (early April at the start of the growing season, and July after the first mowing).

We harvested aboveground plant biomass (above 3 cm) twice a year for three years after the start of the invasion experiment, i.e., from year 4–6 after the initial establishment of the plots. Harvests were timed to coincide with typical grassland harvest times in central Europe (late May and August). In each subplot we randomly selected an area 20 × 50 cm for harvest. We sorted the harvested plant material into species, except in the first of the two harvests in 2005, when we only sorted into residents, internal invaders, and external invaders, and noted the number of species in each category. Harvested biomass was dried and weighed. Comparative data from weeded monocultures of all 60 species and weeded 60-species mixtures were available from another study within the Jena Experiment (Marquand et al. 2009).

### *Data analysis*

We analyzed the biomass and the number of species of residents and internal and external invaders as a function of the design variables and covariates with ordinary mixed-model analyses of variance (Snedecor

and Cochran 1980). Fixed and random terms were fitted sequentially by multiple regression and results summarized in analysis of variance (ANOVA) tables (for more details, see Schmid et al. [2002]). Biomass (in  $\text{g}/\text{m}^2$ ) was analyzed as a yearly total, and species richness (per harvest quadrat) as an average of the two harvests per year. Because sown resident-species richness in the plots was highly correlated with realized resident-species richness in the harvested area at the start of our experiment, we used sown plot richness in all analyses that investigate the influence of preinvasion community properties on invasion. Results did not change when realized richness was used. The number of internal invader species and their biomass was analyzed on a functional-group basis in a “home–away” contrast analysis. This allowed a test of the difference in invasion success between communities where each functional group occurred among the residents (“home”) and where it did not (“away”). In the home–away biomass analysis we included only data from 2006 and 2007, as the biomass of individual functional groups was only available for one of the two harvests in 2005.

The first section of this paper focuses on the influence of community properties and invader-species characteristics on invasion success. Therefore, only data from invaded subplots were used (C–, C+, and W+) in the respective analyses. The second section of the paper deals with community changes in response to invasion. Thus, the development of the non-invaded subplot (W–) was compared with invaded subplots that contained the full invader range (external and internal invaders: C– and C+). All analyses that classify invaders by functional group exclude external invaders because the grouping of internal species into functional groups was based on an a priori cluster analysis (see *Experimental design*, above) and external invaders occurred in very low species numbers and abundance. Data were analyzed using the statistical software R 2.7.2 (R Development Core Team 2008) and GenStat, eleventh edition (VSN International 2008). All error bars and errors accompanying mean values represent  $\pm 1$  standard error of the mean.

## RESULTS

### *Community invasibility*

Following the cessation of the weeding regime, communities of residents accumulated increasing numbers of invader species with time. However, the number and biomass of internal invader species (species that belonged to the species pool of the experiment) and external invader species decreased with increasing resident-species richness, i.e., resistance to invasion increased with resident-species richness (Fig. 1,  $F_{1,63} = 80.23$ ,  $P < 0.001$  for the number of internal invader species;  $F_{1,63} = 32.03$ ,  $P < 0.001$  for internal-invader biomass;  $F_{1,67} = 22.03$ ,  $P < 0.001$  for the number of external invader species;  $F_{1,67} = 13.61$ ,  $P < 0.001$  for external-invader biomass; full ANOVAs can be found in

Appendix C: Tables C2–C4). For internal invaders, this effect may in part be due to the decrease in the number of potential internal invader species in more diverse plots (MacArthur and Wilson 1967, Hector et al. 2001). However, this cannot apply to external invaders because their number is not intrinsically related to the number of resident species. Because the biomass of the resident community increased with sown species richness, we tested its direct effect on invader success by including resident biomass as a covariate in the analysis. Resident biomass had a strong negative effect on the number and biomass of internal and external invader species ( $F_{1,920} = 106.20$ ,  $P < 0.001$  for the number of internal invader species;  $F_{1,920} = 514.27$ ,  $P < 0.001$  for internal-invader biomass;  $F_{1,160} = 79.32$ ,  $P < 0.001$  for the number of external invader species;  $F_{1,160} = 10.36$ ,  $P = 0.002$  for external-invader biomass). Nevertheless, the inclusion of resident biomass as a covariate did not affect the significance of subsequent terms in the ANOVA, indicating that resident biomass effects were additive to the other effects.

### *Invasiveness*

Internal invader species were much more successful than external invaders in invading new communities, even if their seeds were not added deliberately. On average, internal invaders made up 85% of all invader species and 95% of total invader biomass (Fig. 1). Compared with the spontaneous-invasion treatment, the deliberate addition of seeds of internal invaders further increased the number of successfully invading internal species when resident species richness was low (Fig. 1a,  $F_{1,596} = 47.44$ ,  $P < 0.001$  for the interaction “Species richness  $\times$  Seed addition”) and increased internal-invader biomass at all species-richness levels (Fig. 1c,  $F_{1,595} = 8.4$ ,  $P = 0.004$  for the term “Seed addition”). External invaders were neither negatively nor positively affected by the experimental addition of seeds of internal species (Fig. 1b, d,  $F_{1,75} = 2.47$ ,  $P = 0.120$  for the number of external invader species; and  $F_{1,75} = 0.80$ ,  $P = 0.375$  for external-invader biomass). Furthermore, there was no effect of external invaders on invasion success of internal invaders ( $F_{1,155} = 0.25$ ,  $P = 0.620$  for the number of external invader species;  $F_{1,155} = 0.28$ ,  $P = 0.600$  for external-invader biomass).

Because of the small biomass contribution of external invaders further analyses were carried out only for internal invaders. Among internal invaders, functional groups and species still varied widely in their ability to establish in new communities. The most successful invading functional groups in terms of the number of established species were grasses and small herbs ( $1.2 \pm 0.01$  and  $1.1 \pm 0.01$  invader species per harvest quadrat, respectively, vs.  $0.6 \pm 0.01$  legume and  $0.6 \pm 0.01$  tall-herb invader species per quadrat [mean  $\pm$  SE]). Grass and legume invaders produced the highest biomass ( $89 \pm 4 \text{ g}/\text{m}^2$  and  $87 \pm 4 \text{ g}/\text{m}^2$ , vs.  $57 \pm 4 \text{ g}/\text{m}^2$  and  $35 \pm 4 \text{ g}/\text{m}^2$  for small-herb and tall-herb invaders, respectively).

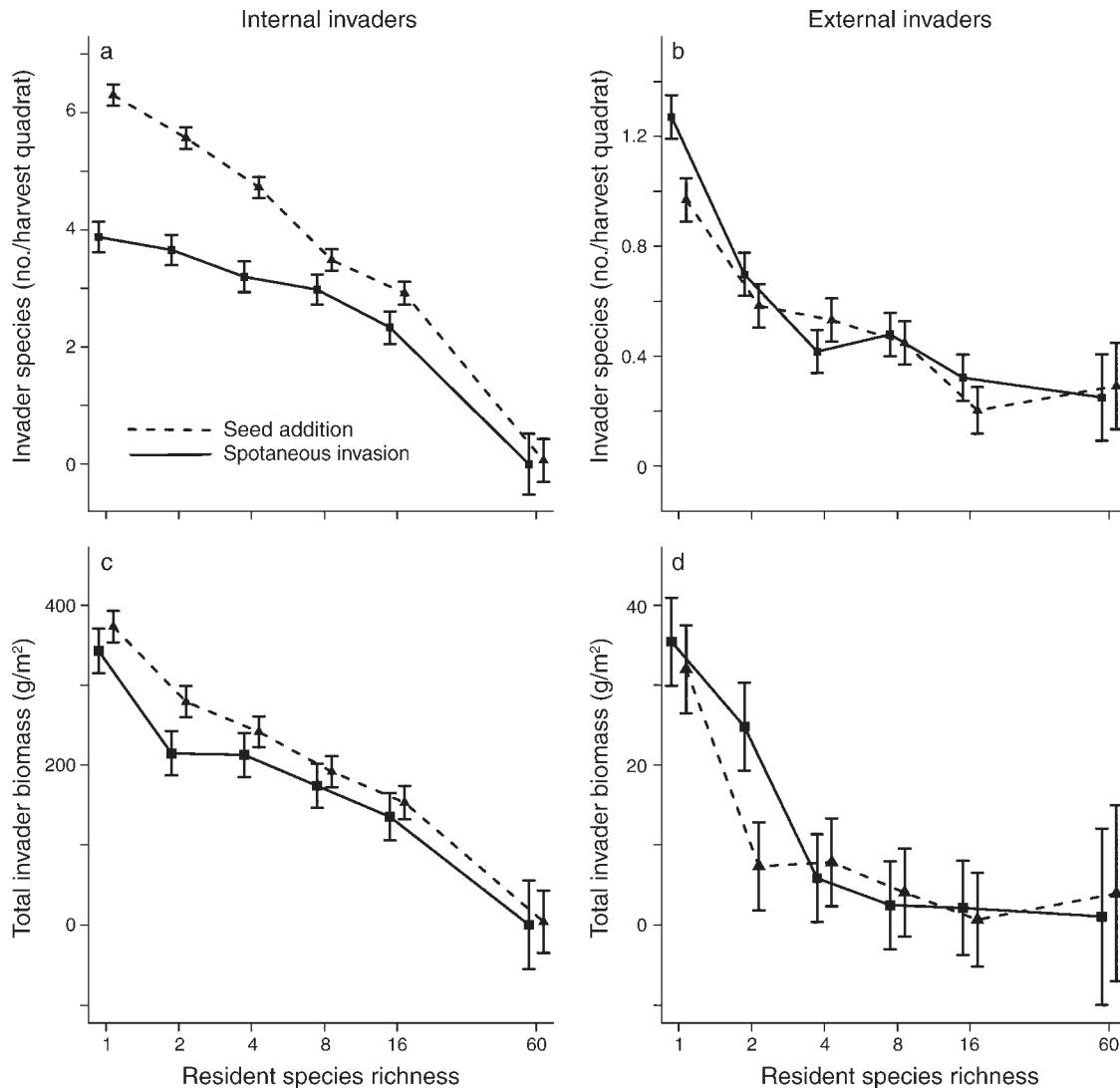


FIG. 1. (a, b) The number of species and (c, d) the biomass of internal and external invaders as a function of resident-species richness (log scale). The solid lines represent subplots without seed addition, and the dashed lines represent subplots with seed addition (see *Methods: Experimental design* for details). The data (mean  $\pm$  SE) were averaged over the six harvests from years 2005–2007. Note the change in the y-axis scale for the internal and external invaders. For statistical analysis, see Appendix C: Table C2.

When all internal invaders were examined separately at the species level, we found that the invasiveness of a species in terms of biomass production in a new community was weakly positively correlated with its aboveground biomass in monoculture ( $R^2 = 0.15$ ,  $F_{1,57} = 10.14$ ,  $P = 0.002$ ) but strongly positively correlated with its aboveground biomass in 60-species mixtures ( $R^2 = 0.51$ ,  $F_{1,55} = 55.29$ ,  $P < 0.001$ ). Thus, the best predictor of invader performance was resident performance of the particular species in highly diverse resident communities.

The success of invader species or functional groups also depended on the interaction between the invader and the resident species in a community. Both the number of internal invader species and their biomass

were reduced when the functional group they belonged to was already present among the residents (“home”), compared to when it was absent (“away,” Fig. 2). We analyzed this negative interaction (negative home-away effect) between the same resident and invading functional groups as a separate contrast within all resident and invading functional-group interactions and found it to be significant ( $F_{1,11} = 37.94$ ,  $P < 0.001$  for species number;  $F_{1,11} = 6.50$ ,  $P = 0.027$  for biomass). Additional interactions between resident and invader functional groups also influenced invader success. However, these other interactions were less important than the negative home-away effect, and the latter was even significant when tested against these other interactions (i.e., the

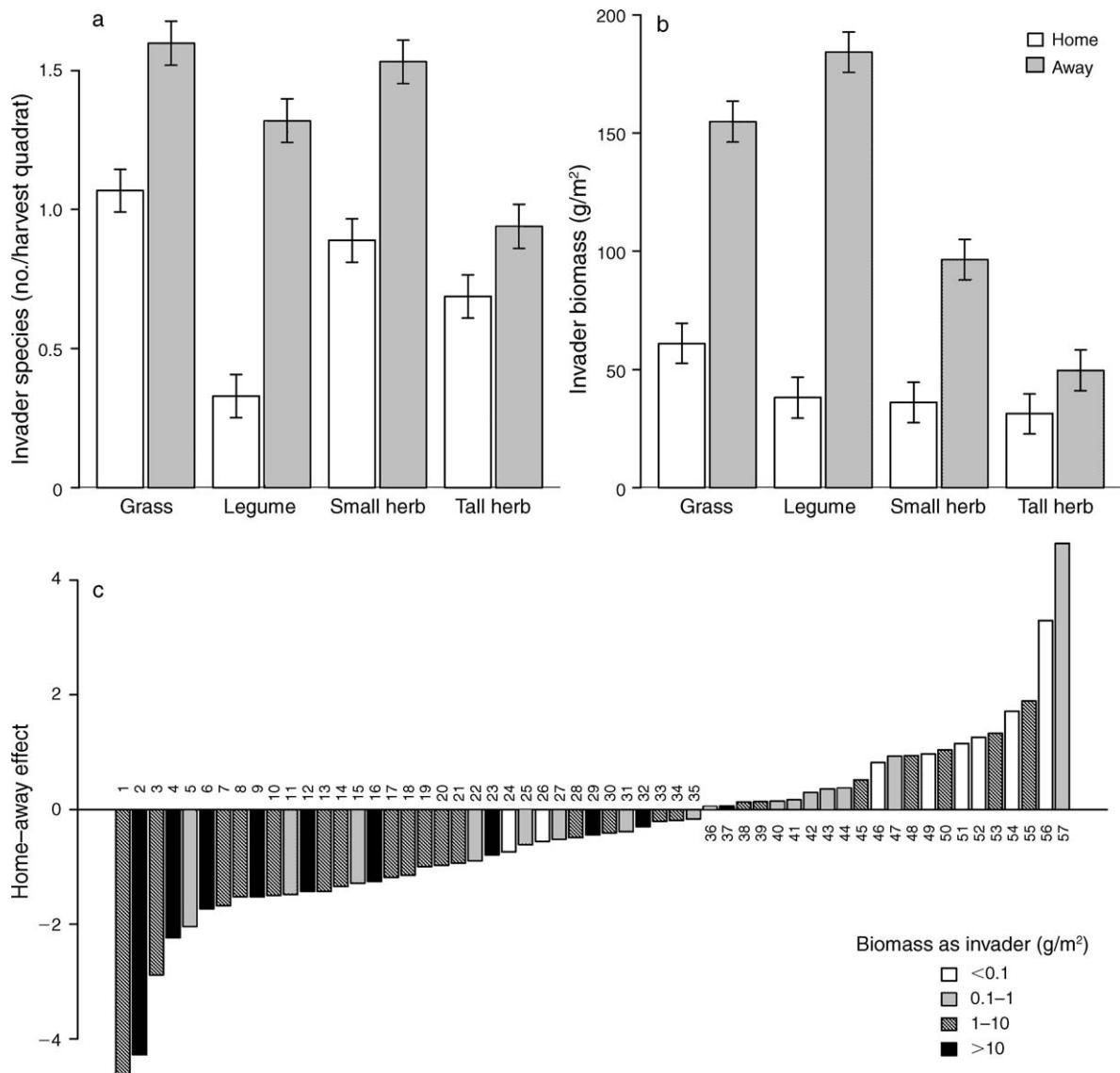


FIG. 2. Negative home–away effect when plants invade communities where their functional group is already present. (a) The number of internal invader species and (b) the internal-invader biomass are shown separated into four functional groups, with paired bars representing plots where the same functional group (FG) is already present with at least one species (white bars, “home”) or where the same FG is not yet present (gray bars, “away”). Data are means  $\pm$  SE. (c) Log-ratio of the home and away biomass of the internal invaders:  $\log(\text{biomass at home}/\text{biomass away})$ . Negative log-ratio values correspond to a disadvantage in a home plot (negative home–away effect); positive log-ratio values indicate a home-plot advantage (positive home–away effect). The effect is based on FG–home and FG–away invasion, but each bar represents a single internal invader species (the number by each bar identifies each of the invader species; for species names see Appendix A). Almost all of the dominant invader species (black bars indicating average biomass in home and away communities  $>10 \text{ g/m}^2$ ) experience negative home–away effects, whereas subordinate species (white bars indicating average biomass in home and away communities  $<0.1 \text{ g/m}^2$ ) show mostly positive home–away effects. The data were averaged across the three subplots (across the spontaneous-invasion [C–] and seed-addition [C+ and W+] treatments), across four harvests from 2006–2007, and across species-richness levels (range: 1–16 species). For statistical analysis, see Appendix C: Table C2.

deviation from main contrast). We found a stronger negative home–away effect with seed addition than with spontaneous invasion ( $F_{1,11} = 20.41, P < 0.001$  for the number of species;  $F_{1,11} = 6.65, P = 0.026$  for biomass).

Because we could not distinguish between invader and resident individuals of the same species, species-level home–away effects on invader biomass could not be

measured. However, when negative home–away effects on invader biomass at the functional-group level were examined separately for all species, it became apparent that about two thirds of the species experienced these negative home–away effects. They were strongest for species that were generally successful invaders (in terms of biomass production), while species with generally low

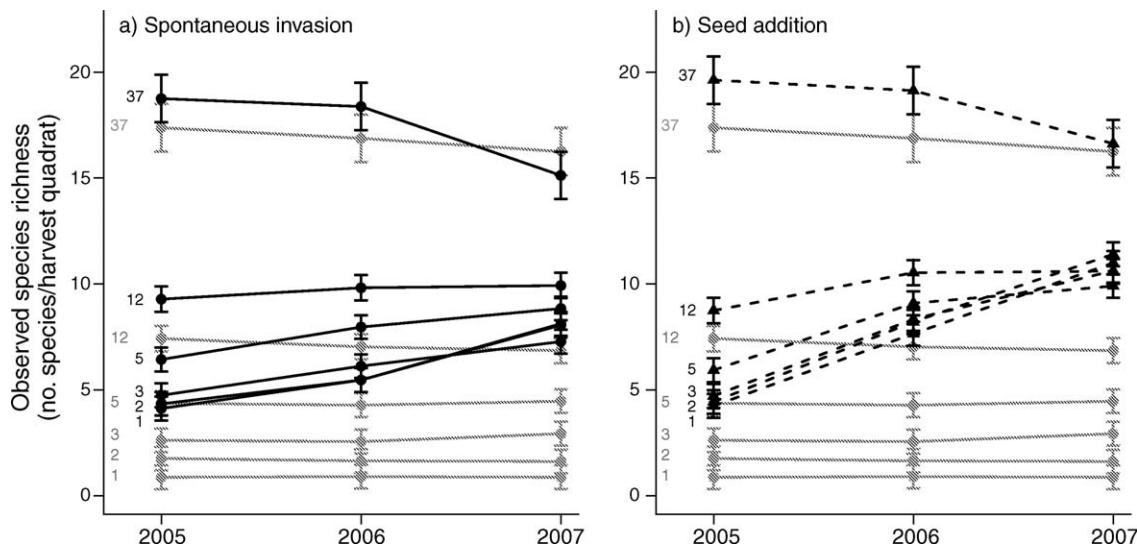


FIG. 3. Convergence of species richness in invaded communities. Note that species richness in weeded controls (gray lines) could only decline because all invaders were weeded out and were therefore not included in harvests. The species richness of invaded communities (black lines) includes residents and invaders: (a) black solid lines show spontaneous invasion (C-); (b) black dashed lines show seed addition (C+). Data are means  $\pm$  SE. The numbers at the beginning of each line depict the average species richness per  $20 \times 50$  cm harvest quadrat of the respective communities in 2003, prior to the start of the invasion experiment. For statistical analysis, see Appendix C: Table C5.

invasiveness experienced neutral to positive home-away effects (Fig. 2c).

#### Community convergence through invasion

*Species richness, functional richness, and productivity.*—Following the cessation of weeding, total species richness of communities with initially low richness experienced a major richness increase while those communities with the highest original species richness showed a slight decrease in species richness, leading to convergence in species richness due to invasion (Fig. 3,  $F_{1,224} = 20.98$ ,  $P < 0.001$  for the interaction “Species richness [ $\log_2$ ]  $\times$  Invasion  $\times$  Year”; the full ANOVA can be found in Appendix C: Table C5). At the same time, the number of resident species in the weeded controls remained relatively constant. Seed addition caused the total species richness of the invaded communities to increase slightly more rapidly than in communities with spontaneous invasion ( $F_{1,224} = 3.02$ ,  $P = 0.084$  for the interaction “Species richness [ $\log_2$ ]  $\times$  Seed addition  $\times$  Year”), especially in communities with originally low resident-species richness, and to reach somewhat higher levels at the end of the observation period ( $F_{1,224} = 27.46$ ,  $P < 0.001$  for the interaction “Seed addition  $\times$  Year”). If the lines in Fig. 3a were extended beyond 2007, monocultures and 60-species mixtures were predicted to cross in 2009 at a richness level of 12 species (per harvest quadrat) with only spontaneous invasion, whereas the lines for communities receiving deliberate seed additions (Fig. 3b) were predicted to cross in 2008 at a level of 15 species. This suggests that with the pressure of seed addition, species richness

converges more rapidly. The number of resident species remained stable during the invasion phase in all plots except the 16- and 60-species mixtures, where slight decreases over time were observed (data for residents not shown separately). All increases in species richness were entirely due to newly establishing invader species and not to a reinvasion of previously extinct residents.

While species richness had not fully converged by the end of the experiment, functional richness increased rapidly in invaded communities and in the last year of observation, 69 and 77 out of 82 communities in the spontaneous-invasion and seed-addition treatments, respectively, contained all four functional groups, even in the rather small area that was harvested. In contrast, only 12 out of 82 control communities contained all four functional groups in an area of the same size. Shannon diversity indices for functional-group (FG) richness remained low in weeded controls until the end of the observation period ( $H = 0.55 \pm 0.02$  if based on the relative number of species in each FG and  $H = 0.41 \pm 0.02$  if based on the relative biomass in each FG) but increased in spontaneous-invasion ( $H = 1.22 \pm 0.02$  if based on the number of species and  $H = 0.94 \pm 0.02$  if based on biomass) and seed-addition treatments ( $H = 1.30 \pm 0.02$  if based on the number of species and  $H = 1.06 \pm 0.02$  if based on biomass). Not only did invasion lead to high FG richness but also to the convergence of FG proportions to similar levels in previously different communities (Fig. 4 and Appendix B: Fig. B1). The average composition of the biomass in invaded subplots at the end of the experiment was 30% grasses, 29%

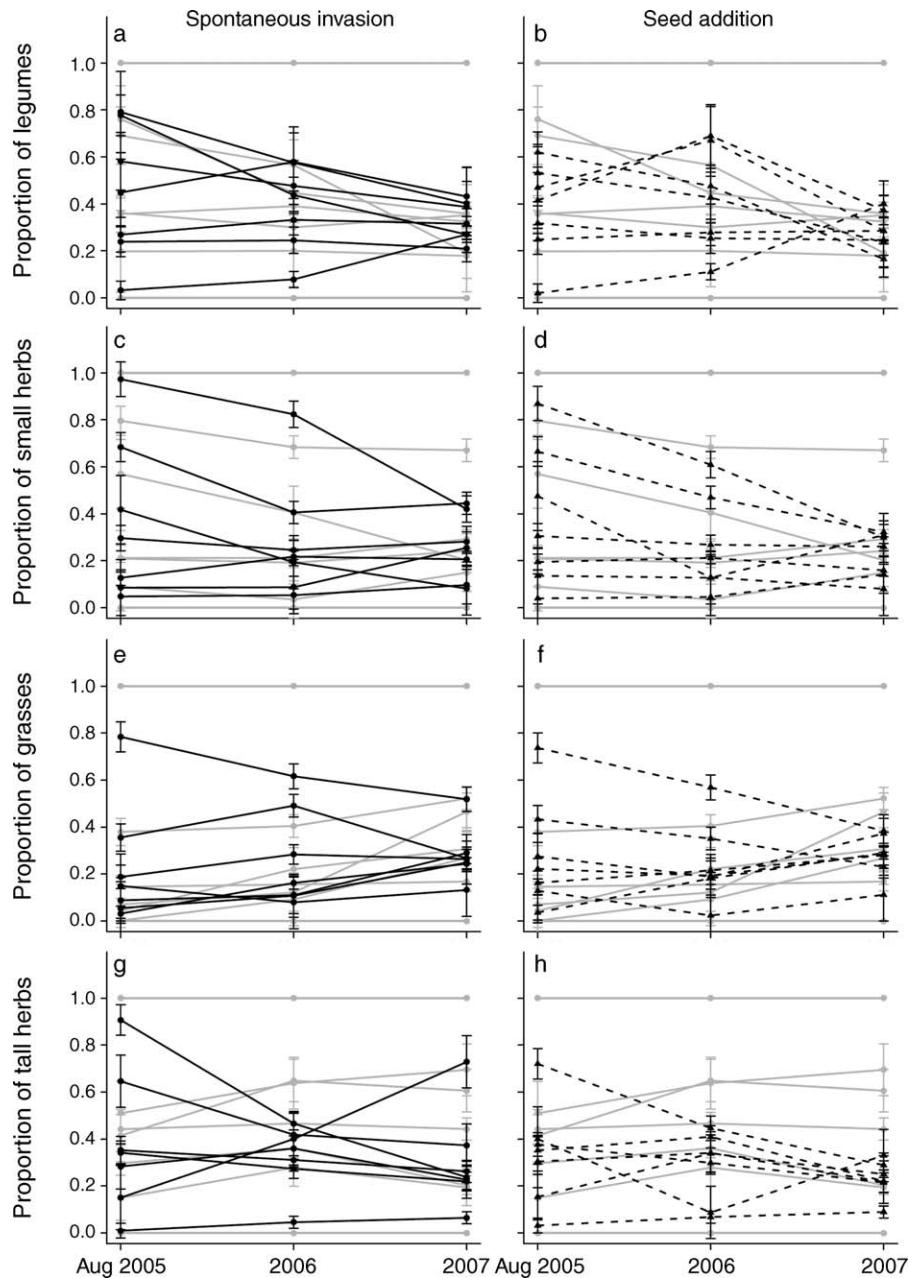


FIG. 4. Convergence of the proportion of biomass accounted for by the four functional groups. Observed (realized) proportions were calculated as observed biomass of the respective functional group per observed total target biomass. Here, external invaders were excluded because they could not be grouped into the same four functional groups, so target species in this case were residents in weeded controls (gray lines, W-), but residents and internal invaders in non-weeded subplots (black lines in the left column show spontaneous invasion, C-; black dashed lines in the right column show seed addition, C+). Data are means  $\pm$  SE. Legumes and small herbs were originally sown (2002) in the following proportions: 0, 0.2, 0.25, 0.3125, 0.375, 0.5, and 1. The proportions of tall herbs originally sown were: 0, 0.25, 0.3125, 0.333, 0.375, 0.5, and 1. The proportions for grasses sown were: 0, 0.25, 0.267, 0.3125, 0.375, 0.5, and 1. In 2005 data were only collected in August; in 2006 and 2007 they were collected in both May and August (the average of the harvests is shown).

legumes, 24% small herbs, and 17% tall herbs, and thus showed very high functional evenness.

Community biomass was much more variable than species richness and functional richness, and this was largely due to the biomass of resident species varying

between years. The biomass of invaders increased over the course of the experiment ( $F_{1,921} = 154.69$ ,  $P < 0.001$ ), except in the 60-species mixtures, where it remained close to 0. In general, total community biomass increased from 2005 to 2007 in invaded

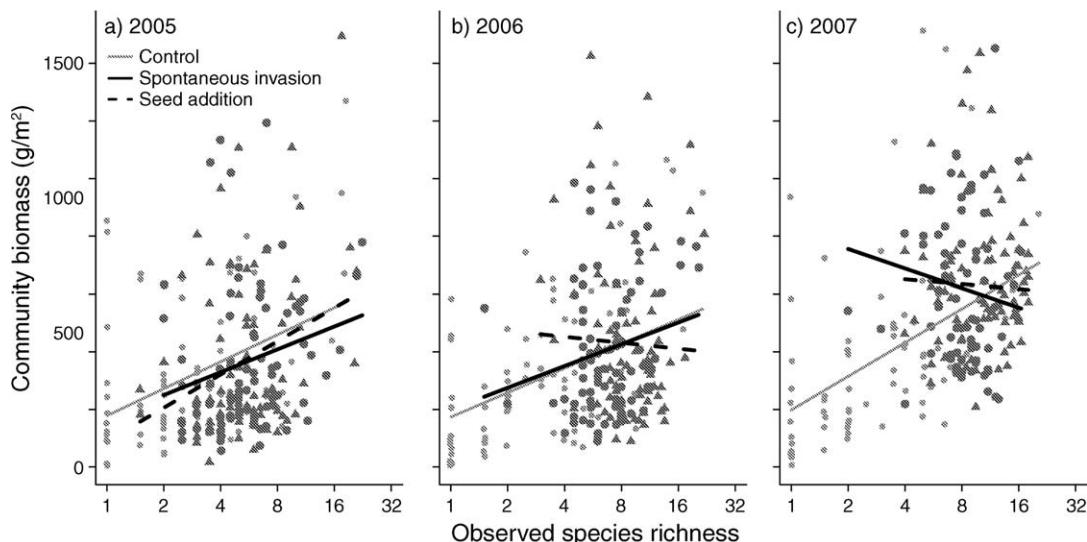


FIG. 5. Observed (realized) species richness–productivity relationships over the course of three years (note y-axis log scale). The light gray line and circles depict the weeded control (no-invaders treatment, W–), the solid black line and dark gray circles depict the spontaneous-invasion treatment (C–), and the dashed line and dark gray triangles depict the seed-addition treatment (C+). Note that regression lines are drawn only across the range of observed species-richness values occurring in that respective treatment (one single outlier in 2006 and two in 2007, all three with very high biomass, are not shown). For statistical analysis, see Appendix C: Table C6.

communities ( $F_{1,224} = 16.54$ ,  $P < 0.001$  for the interaction “Invasion  $\times$  Year”) but increased most strongly in communities with originally low resident-species richness. Therefore, communities of different levels of original species richness and hence different community biomass production became more similar following invasion ( $F_{1,150} = 14.99$ ,  $P < 0.001$  for the interaction Species richness [ $\log_2$ ]  $\times$  Invasion).

**Biodiversity–productivity relationship.**—At the beginning of the experiment in 2005 we found a positive realized species richness–productivity relationship in all subplots (Fig. 5a). This relationship was maintained across the three years in the weeded control subplots (gray lines in Fig. 5). However, in the subplots that were opened to invasion the positive relationship decayed over time (black lines in Fig. 5; Appendix C: Table C6;  $F_{1,239} = 5.80$ ,  $P = 0.017$  for the interaction Realized richness [ $\log_2$ ]  $\times$  Invasion  $\times$  Year). This decay occurred more rapidly in subplots with deliberate seed addition than in subplots with only spontaneous invasion; the positive relationship had disappeared by 2006 in subplots where invasion was assisted by seed addition, and by 2007 in subplots with spontaneous invasion (Fig. 5).

In contrast to the species richness–productivity relationship, the relationships between the proportion of particular functional groups (based on their realized biomass) and community productivity did not decay due to invasion but rather strengthened (Fig. 6; Appendix C: Table C7). Thus, invaded communities with an above-average proportion of legumes had above-average productivity; and invaded communities with an above-

average proportion of small herbs had below-average productivity. The most productive invaded plots (Fig. 6b, c) were originally mainly grass and small-herb monocultures (e.g., *Poa pratensis*, *Festuca pratensis*, *Bellis perennis*, *Plantago lanceolata*) or non-legume mixtures (e.g., a *Plantago media*–*Taraxacum officinale* mixture, and a four-species tall-herb mixture) and had obtained their high, probably unstable, legume proportions via invasion. In contrast, the least productive invaded plots (Fig. 6e, f) were those where small herbs had been present in high proportions from the beginning and had not yet been reduced to the average level of around 24%. Most of these small-herb-dominated communities contained *Prunella vulgaris* and *Ajuga reptans*, two small-herb species that can form dense ground cover and can thus slow down invasion by other functional groups. Among the non-invaded communities, plots with 0% or 100% legumes were less productive than others, and plots with 0% small herbs were slightly less productive than those with a small proportion of small herbs.

## DISCUSSION

### *Invasibility and invasiveness*

Our experiment confirms previous findings, that experimental communities with higher numbers of resident species are more resistant to invasion from both internal and external invaders than species-poor communities (Tilman 1997, Knops et al. 1999, Joshi et al. 2000, Levine 2000, Naeem et al. 2000, Hector et al. 2001, Kennedy et al. 2002, Fargione et al. 2003, van Ruijven et al. 2003, Pfisterer et al. 2004, Maron and

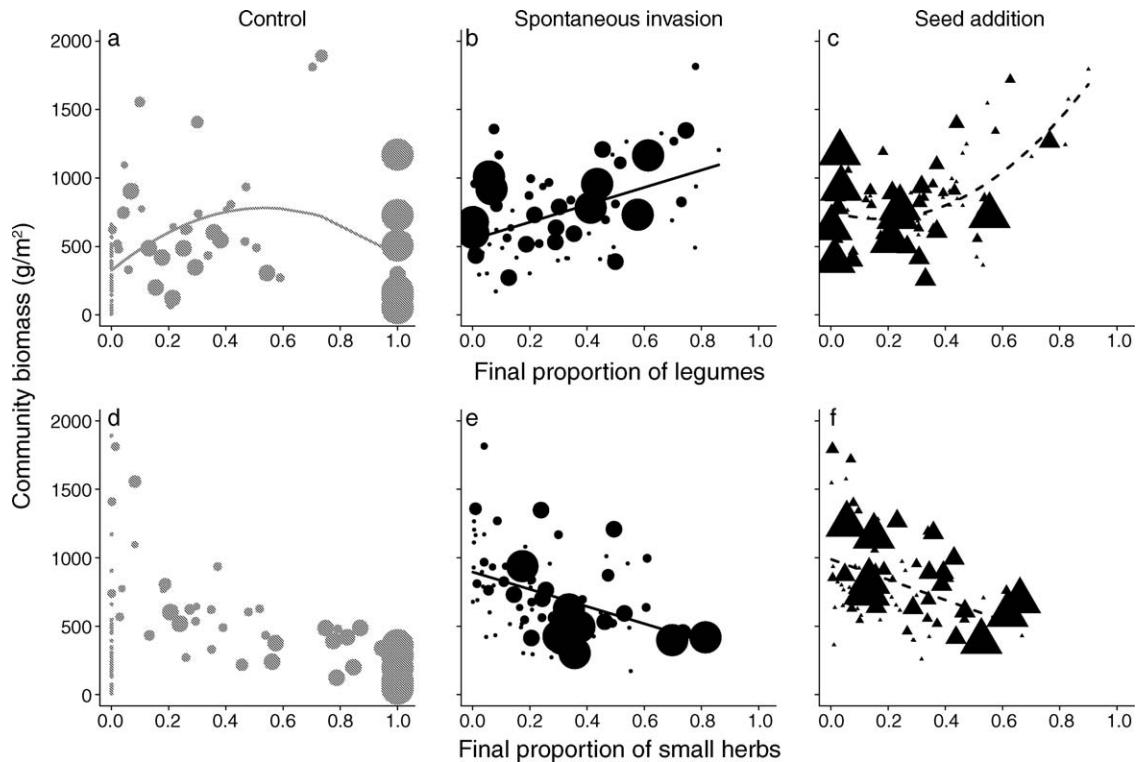


FIG. 6. Legume proportion–productivity relationships and small-herb proportion–productivity relationships in the final year of the experiment: (a, d) control, W–; (b, e) spontaneous-invasion treatment, C–; and (c, f) seed-addition treatment, C+. The plotted symbol size is proportional to the original proportion of the respective functional group in the plot. Note that fitted lines are drawn only when the relationship is significant at  $P < 0.05$  and only across the range of realized proportion values occurring in that respective treatment (three outliers with very high biomass were excluded). For statistical analysis, see Appendix C: Table C7.

Marler 2008, Roscher et al. 2009a). We also found that the invasion process was highly nonrandom on the functional-group level. Invasion success was partly related to the identity of the invader and to the presence of particular functional groups (e.g., legumes) in the resident community. However, invasion success was most strongly dependent on the biological difference between the invader and the invaded community (Strauss et al. 2006, Suter et al. 2007), permitting species that belonged to a functional group absent from a community to invade more easily than species belonging to a functional group already present (Fargione et al. 2003, Turnbull et al. 2005b, Mwangi et al. 2007). This strong negative interaction between residents and invaders of the same functional group could be due to overlapping resource requirements (e.g., Knops et al. 1999, Naem et al. 2000, Fargione et al. 2003, Mwangi et al. 2007) or to the presence of natural enemies (Petermann et al. 2008). We discuss these possibilities in more detail in the next section. However, that the strongest invader species in our study were most strongly inhibited by this negative effect (see Fig. 2c) is supportive of its important role as a stabilizing force in community assembly (Chesson 2000, Chave 2004).

#### *Effects of invasion on community properties and functioning*

After our experimental communities were opened to invasion, initially species-poor communities were supplemented with high numbers of invader species. In contrast, originally species-rich communities tended to lose resident species and our experimental communities converged towards species-richness levels very similar to natural grasslands adjacent to our study plots (15–19 species per harvest quadrat). This suggests a shift of the experimentally assembled communities toward naturally assembled communities, at least in terms of species richness, and supports similar findings from invaded grasslands by Pfisterer et al. (2004) and Rixen et al. (2008). However, their studies lacked a weeded control and a seed-addition treatment, and did not analyze whether invaders entered the community in a random or deterministic way. Both studies observed very little compositional convergence suggesting that stochastic effects strongly influenced the reassembly of their communities (but perhaps the short observation time (Pfisterer et al. 2004) or slow plant growth in an alpine habitat (Rixen et al. 2008) also had an influence). In contrast, in the present study nonrandom invasion led to a rapid convergence of functional-group composition



PLATE 1. Three main plots ( $20 \times 20$  m) of the Jena Experiment in the foreground, with the invasion subplots discernible by the conspicuous white flowers of invading oxeye daisy (*Leucanthemum vulgare*). Photo credit: Forschergruppe—the Jena Experiment.

among plots and resulted in a high functional richness and evenness of most invaded communities by the end of the experiment. Our experimental communities apparently reassembled toward a common community structure determined by site conditions. As a consequence of this reassembly, the communities lost their positive species richness–productivity relationship as indicated by previous experiments (Pfisterer et al. 2004, Rixen et al. 2008, Roscher et al. 2009b). Interestingly, observational biodiversity–ecosystem functioning studies within single sites similarly do not find positive species richness–productivity relationships. Thus, our results from reassembled experimental communities help to reconcile apparently contrasting experimental and observational findings (Schmid and Hector 2004, Hector et al. 2007).

In contrast to the rapid decay of the positive species richness–productivity relationship, relationships between functional-group proportions and productivity were maintained or even strengthened in invaded communities. More specifically, invaded communities with a high proportion of legumes produced more biomass, and even outperformed non-invaded communities containing only legumes (for a detailed analysis of functional-group contributions to productivity in non-invaded communities of the Jena Experiment see Marquard et al. 2009). In contrast, invaded (and non-invaded) communities with a high proportion of small herbs produced less biomass than other communities. Some of these unproductive small herb communities proved to be rather resistant to invasion, potentially due to a dense ground cover, representing a historical effect on community structure (Drake 1991). We know from

another experiment within the same site that the manual removal of these unproductive species leads to a rapid increase in community biomass even with a loss of species richness (Schmitz 2007).

While invasion by legumes was beneficial for community productivity, communities that initially contained only legumes were not those with a high proportion of legumes after invasion, indicating that high legume proportions in these communities are not sustainable in the longer term and are easily invaded in spite of their high productivity. Indeed, the invasion of legume-only communities by other functional groups sometimes led to decreased productivity of the resulting communities. It could be argued that if nonrandom invasion was mainly due to resource complementarity it should lead to increased community productivity because of the use of otherwise-unconsumed resources by the invader. This argument is valid except for the rather unlikely case that invaders enter the community based on available resources but then “waste” resources, decreasing community productivity due to their inefficiency. In the case of legumes, unilateral facilitation, i.e., the enhancement of other functional groups by legumes due to their nitrogen-fixing ability (Temperton et al. 2007), would be another explanation for the invasibility by less productive functional groups. It is more likely, however, that pathogen-driven negative feedbacks promoted the nonrandom invasion of all functional groups into plots where pathogens of that specific functional group had not yet accumulated; in other words where their pathogen-free niche was vacant (Turnbull et al. 2005b, Mwangi et al. 2007, Petermann et al. 2008). For legumes in particular, this mechanism is supported by

reports on the general instability of experimental legume monocultures, which often suffer from extensive pathogen attack (Pfisterer et al. 2004).

#### *The influence of dispersal limitation*

Our seed-addition treatment was intended to reduce the influence of dispersal stochasticity on invasion and community convergence. Indeed, we found that the number of invader species, and, to a smaller extent, invader biomass, was lower in the spontaneous-invasion treatment without experimental seed input. This indicates that even those species that were already present at the site were dispersal limited (Roscher et al. 2009a). Under neutrality, dispersal limitation and the resulting stochasticity in colonization rates are key factors shaping communities (Hubbell 2001, Chase 2003, Chase 2007). With dispersal limitation we would expect a greater stochastic and a smaller deterministic component in the reassembly process (Chase 2007). This was exactly what we found: the deterministic control by functional groups was weaker in plots exposed only to spontaneous seed arrivals and the convergence process slower than when seeds were experimentally added. However, invasion into plots with only spontaneous dispersal was still deterministic on a functional-group basis and led to analogous community convergence in terms of species richness, functional richness, and productivity and to a decay of the species richness–productivity relationship. This supports our conclusion that the deterministic, biological component of community assembly was more important than chance in shaping post-assembly communities, at least in terms of their functional structure. While our experiment was not designed to test species-level determinism, we hypothesize that the nonrandom assembly mechanisms we observed may still operate among species within functional groups, even if in a less stringent way than among species between functional groups.

By following randomly assembled communities of different species and functional composition for three years after opening them to spontaneous and assisted invasion we have shown that invasion success is strongly controlled by the richness of the community and operates in a biologically predictable way, at least on the functional-group level. Specifically, invasion enhances low species richness and rebalances functional-group composition. Consequently, communities with different richness and compositional histories converge at nearly maximum functional richness and evenness, regardless of dispersal limitation, thus rejecting purely neutral concepts of community assembly. Furthermore, we have shown that the invasion process can lead to reduced productivity because communities of high productivity are not necessarily stable. This suggests a role for pathogens as drivers of community assembly, rather than a full control of floristic compositions by different resource requirements of species. We believe that our results and other work on invasion and assembly within

native communities not only contribute to the fundamental understanding of how communities are structured and function, but can also help to direct restoration efforts (Temperton et al. 2004, Funk et al. 2008) and understand, predict, and control nonnative invasions (Shea and Chesson 2002, Funk et al. 2008).

#### ACKNOWLEDGMENTS

We thank U. Wehmeier and A. Oswald for their support with the establishment and maintenance of the invasion experiment, all gardeners and helpers for their assistance in the field, and Jasmin Joshi and two anonymous reviewers for helpful comments on the manuscript. The Jena Experiment is funded by the German Research Foundation (FOR 456) and supported by the Friedrich Schiller University of Jena and the Max Planck Institute for Biogeochemistry, Jena. Additional support was provided by the Swiss National Science Foundation (grant number 31-65224-01 to B. Schmid).

#### LITERATURE CITED

- Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* 14:359–376.
- Augsburger, C. K., and C. K. Kelly. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–217.
- Baker, H. G. 1967. Support for Baker's law—as a rule. *Evolution* 21:853–856.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77:776–790.
- Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences (USA)* 105:17012–17017.
- Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136:489–498.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences (USA)* 104:17430–17434.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7:241–253.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170:128–142.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76:486–492.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer and G. R. Gradwell, editors. *Dynamics of populations*. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Crawley, M. J. 1986. The population biology of invaders. *Philosophical Transactions of the Royal Society of London B* 314:711–731.
- Crawley, M. J. 1987. What makes a community invisable? Pages 429–453 in A. J. Gray, M. J. Crawley, and O. J. Edwards, editors. *Colonization, succession and stability*. Blackwell, Oxford, UK.

- Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2: 140–148.
- Drake, J. A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147:213–233.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1–26.
- Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. *Biological invasions: a global perspective*. John Wiley and Sons, New York, New York, USA.
- Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* 12:602–617.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4:412–417.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Emery, S. M. 2007. Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology* 95:1027–1035.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences (USA)* 100:8916–8920.
- Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* 8:604–611.
- Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8: 1283–1290.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* 23: 695–703.
- Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences (USA)* 104:4979–4983.
- Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446:791–793.
- Hector, A., K. Dobson, A. Minns, E. Bazeley-White, and J. H. Lawton. 2001. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* 16:819–831.
- Hector, A., et al. 2007. Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology* 21:998–1002.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127.
- Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Monographs in Population Biology, Volume 32. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–329 in J. M. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–508.
- Joshi, J., D. Matthies, and B. Schmid. 2000. Root hemiparasites and plant diversity in experimental grassland communities. *Journal of Ecology* 88:634–644.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286–293.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16:199–204.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- MacArthur, R. H., and E. O. Wilson. 1963. *An equilibrium theory of insular zoogeography*. *Evolution* 17:373–387.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Maron, J. L., and M. Marler. 2008. Effects of native species diversity and resource additions on invader impact. *American Naturalist* 172:S18–S33.
- Marquard, E., A. Weigelt, V. M. Temperton, C. Roscher, J. Schumacher, N. Buchmann, M. Fischer, W. Weisser, and B. Schmid. 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology* 90:3290–3302.
- Mwangi, P. N., M. Schmitz, C. Scherber, C. Roscher, J. Schumacher, M. Scherer-Lorenzen, W. W. Weisser, and B. Schmid. 2007. Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology* 95:65–78.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97–108.
- Petermann, J. S., A. J. F. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89:2399–2406.
- Pfisterer, A. B., J. Joshi, B. Schmid, and M. Fischer. 2004. Rapid decay of diversity–productivity relationships after invasion of experimental plant communities. *Basic and Applied Ecology* 5:5–14.
- Polley, H. W., B. J. Wilsey, and J. D. Derner. 2003. Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecology Letters* 6:248–256.
- Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* 11:717–726.
- R Development Core Team. 2008. R 2.7.2. *Foundation for Statistical Computing*, Vienna, Austria. (<http://www.r-project.org>)
- Richardson, D. M., and P. Pysek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30:409–431.

- Rixen, C., C. Huovinen, K. Huovinen, V. Stöckli, and B. Schmid. 2008. A plant diversity  $\times$  water chemistry experiment in subalpine grassland. *Perspectives in Plant Ecology, Evolution and Systematics* 10:51–61.
- Roscher, C., H. Bessler, Y. Oelmann, C. Engels, W. Wilcke, and E. D. Schulze. 2009a. Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *Journal of Ecology* 97:32–47.
- Roscher, C., J. Schumacher, J. Baade, W. Wilcke, G. Gleixner, W. W. Weisser, B. Schmid, and E.-D. Schulze. 2004. The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology* 5:107–121.
- Roscher, C., V. M. Temperton, N. Buchmann, and E. D. Schulze. 2009b. Community assembly and biomass production in regularly and never weeded experimental grasslands. *Acta Oecologica* 35:206–217.
- Schmid, B., and A. Hector. 2004. The value of biodiversity experiments. *Basic and Applied Ecology* 5:535–542.
- Schmid, B., A. Hector, M. A. Huston, P. Inchausti, I. Nijs, P. W. Leadley, and D. Tilman. 2002. The design and analysis of biodiversity experiments. Pages 61–75 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning*. Oxford University Press, Oxford, UK.
- Schmitz, M. 2007. How plant population processes mediate biodiversity effects on ecosystem functioning. Dissertation. University of Zurich, Zurich, Switzerland.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17:170–176.
- Snedecor, G. W., and W. G. Cochran. 1980. *Statistical methods*. Seventh edition. Iowa State University Press, Ames, Iowa, USA.
- Spehn, E. M., et al. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* 75:37–63.
- Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences (USA)* 103:5841–5845.
- Suter, M., D. Ramseier, S. Guesewell, and J. Connolly. 2007. Convergence patterns and multiple species interactions in a designed plant mixture of five species. *Oecologia* 151:499–511.
- Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141: 24–39.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81:99–109.
- Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle. 2004. *Assembly rules and restoration ecology: bridging the gap between theory and practice*. Island Press, Washington, D.C., USA.
- Temperton, V. M., P. N. Mwangi, M. Scherer-Lorenzen, B. Schmid, and N. Buchmann. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia* 151: 190–205.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–238.
- Turnbull, L. A., L. Manley, and M. Rees. 2005a. Niches, rather than neutrality, structure a grassland pioneer guild. *Proceedings of the Royal Society B* 272:1357–1364.
- Turnbull, L. A., S. Rahm, O. Baudois, S. Eichenberger-Glinz, L. Wacker, and B. Schmid. 2005b. Experimental invasion by legumes reveals non-random assembly rules in grassland communities. *Journal of Ecology* 93:1062–1070.
- van Ruijven, J., G. B. De Deyn, and F. Berendse. 2003. Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecology Letters* 6:910–918.
- VSN International. 2008. *GenStat*. Eleventh edition. VSN International, Hemel Hempstead, UK.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95: 161–170.
- Wilsey, B. J., and C. Potvin. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology* 81:887–892.
- Zhang, Q. G., and D. Y. Zhang. 2007. Colonization sequence influences selection and complementarity effects on biomass production in experimental algal microcosms. *Oikos* 116: 1748–1758.

#### APPENDIX A

A list of internal invader species (*Ecological Archives* E091-030-A1).

#### APPENDIX B

A figure depicting convergence of the proportion of the total number of species accounted for by the four functional groups (*Ecological Archives* E091-030-A2).

#### APPENDIX C

One table showing the experimental design and six tables providing the results of statistical analyses (*Ecological Archives* E091-030-A3).