

Time course of plant diversity effects on *Centaurea jacea* establishment and the role of competition and herbivory

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Abstract

Aims

Invasion resistance in experimental plant communities is known to increase with increasing diversity and further to depend on the presence of particular functional groups. To test whether these effects also hold true for the invader establishment phase beyond the seedling stage, we studied survival and performance of *Centaurea jacea* L. (brown knapweed) planted into experimental grassland communities of varying plant biodiversity over three consecutive years. Moreover, we analysed the role of insect herbivory and biomass of the recipient community for mediating diversity effects.

Methods

In 2005, seedlings of *Centaurea* were transplanted into experimental grassland communities (the Jena Experiment) covering a species richness (1–60) and functional group richness (1–4) gradient. Half of these transplants and the community surrounding them in each plot were sprayed with insecticide while the other half served as control. In 2006 and 2007 (during the second and third year after transplantation), we recorded survival, growth-related (e.g. transplant biomass, height) and reproduction-related traits (e.g. number of flower heads). Annual data on community aboveground biomass served as covariate to investigate mediating effects of aboveground competition with the recipient community.

Important Findings

Species richness was the most important factor responsible for *Centaurea* limitation. Higher levels of diversity decreased survival and

all performance traits in both years. These diversity effects were partly driven by community biomass, but not fully explained by that covariate, suggesting the importance also of further processes. The influence of functional group richness was strong in the second year after transplantation and weaker in the third year. Among the particular functional groups, only the presence of legumes showed strong negative effects on *Centaurea* survival and weak negative effects on growth and reproduction, the latter two being mediated by biomass.

Insect herbivore reduction considerably benefited *Centaurea* in sprayed monocultures, where it grew significantly larger than in all other diversity levels and than in the control subplots.

We conclude that effects of plant community properties on invading individuals change in the course of establishment, that plant species richness effects are also important during later stages of establishment, and that biomass (especially at high diversity) and herbivory (especially at low diversity) of the recipient community are important in mediating community effects on invaders.

Keywords: invasion resistance • aboveground competition • biomass • Jena Experiment • experimental grassland • *Centaurea jacea*

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INTRODUCTION

The establishment of new members of an ecological community is governed by interactions between the prospective immigrant and resident species, such as competition for resources and facilitation. One of the oldest ecological hypotheses on the establishment success of immigrants was phrased in the context of invasion biology and predicts that more diverse communities are more resistant against invasion because the available 'niche space' is reduced in more diverse communities (Elton 1958). For grassland ecosystems, a number of studies have shown that the chance of establishment of newly arriving plants decreases with increasing plant diversity (e.g. Burke and Grime 1996; Crawley *et al.* 1999; Fargione and Tilman 2005; Fargione *et al.* 2003; Hector *et al.* 2001; Kennedy *et al.* 2002; Tilman 1997; van Ruijven *et al.* 2003). However, the presence of particular plant species (Crawley *et al.* 1999; Dukes 2002; van Ruijven *et al.* 2003) or plant functional groups (Fargione *et al.* 2003; Mwangi *et al.* 2007) has in some cases been shown to be more important in influencing invader success than diversity. Invading plant individuals are often more limited by species of the same than of other functional groups, as those may show very similar requirements (Fargione *et al.* 2003; Mwangi *et al.* 2007; Turnbull *et al.* 2005; but see Prieur-Richard *et al.* 2002). Independent of the invading species, the fate of invaders may be affected negatively by the presence of grasses, which with their dense rooting system are highly competitive in the exploitation of soil nutrients and water. Legume presence, on the contrary, often has positive effects on neighbouring individuals (Prieur-Richard *et al.* 2002; Temperton *et al.* 2007) due to soil enrichment with nitrogen through atmospheric nitrogen fixation.

In addition to competition and facilitation, biotic interactions with herbivores may also play a role for plant establishment as herbivores can reduce seedling survival and biomass or reproductive output of plants (e.g. Hulme 1996; Louda and Potvin 1995; Ridenour *et al.* 2008) and may also affect the competitive environment of an invader, suppressing particular plants to the advantage of others (Haag *et al.* 2004). While there have been a large number of studies investigating the role of herbivores for plant species invasion (e.g. Levine *et al.* 2004; Maron and Vilà 2001; Ridenour *et al.* 2008), the role of insect herbivores for plant establishment is rarely studied along with the effects of plant biodiversity (but see Scherber *et al.* 2006).

One particular aspect of plant invasion into an existing community is the temporal scale. Plant establishment occurs in several phases and ideally, all of these should be investigated because different factors may be important at different times during the establishment process (Thompson *et al.* 2001). However, most experiments testing invasion resistance of plant communities were undertaken as 'seed addition experiments' or 'weeding analyses' and investigated but a short period of the process—mainly the germination stage, the most critical one during the establishment process of plants. Only little attention

has been paid to phases beyond the seedling stage that may be more crucial to the successful reproduction and hence spreading of the invading population (but see Roscher *et al.* 2009a).

In this study we investigated the effects of plant species richness, functional group richness, particular functional groups and insect herbivore reduction on the establishment success of seedlings of the focal species *Centaurea jacea* L., s. l., transplanted into the experimental communities of a large biodiversity experiment, the Jena Experiment (see below).

By placing *Centaurea* within and outside insecticide subplots and hence communities that are affected by or relieved from insect herbivores, we explore how a possible change in its competitive environment due to herbivore reduction affects establishment of *Centaurea*. We consider comparing identical communities under differing herbivory levels to mimic a natural situation as differences in herbivore load will generally affect the whole community an invader may enter, unless it should be completely unaffected by herbivores encountered in the new community.

We also investigated the role of community biomass, as a proxy for aboveground competition, for establishment success and its importance in mediating diversity and compositional effects. Our study was conducted in the experimental grassland communities of the Jena Experiment, with plant communities varying in numbers of plant species between 1 and 60 and functional groups between 1 and 4 (Roscher *et al.* 2004). The focal plants were transplanted as seedlings in 2005, 3 years after the set-up of the experimental plots. Survival, plant growth-related (e.g. biomass, height) and reproduction-related traits (e.g. number of flower heads and shoots) were followed over two flowering seasons (2006 and 2007) starting 1 year after the transplantation of *Centaurea* into the experimental grassland communities.

The focal species *C. jacea* is widely distributed across Europe and several species of the same genus are highly invasive in North American grasslands (Roché and Roché 1991). It belongs to the experimental pool of the 60 species of the Jena Experiment and has been assigned to the plant functional group 'tall herbs'. Being long-lived with first flower set after 1 year, *C. jacea* is suitable for longer term monitoring and likely to persist over several years.

We addressed the following specific hypotheses. (i) *Centaurea* performs better in communities of low species and functional group richness. (ii) Presence of grasses and tall herbs and presence of legumes will, respectively, negatively and positively affect *Centaurea* performance. (iii) Aboveground competition negatively affects *Centaurea* performance and mediates the diversity and composition effects mentioned in (i) and (ii).

MATERIALS AND METHODS

Study species

The brown knapweed *C. jacea* L. s. l. (Asteraceae) is native to Eurasia and common all over Germany. The long-lived perennial hemicryptophyte reemerges in spring (Press and Gibbons

1993) and from the second year on produces vegetative side rosettes, flowers and fruits between June and October (Jongejans *et al.* 2006a). The species inhabits a wide range of different habitats from dry grassland to marshes (Sommer 1990). Several species of the genus *Centaurea* (e.g. *Centaurea maculosa*, *Centaurea diffusa*) are invasive neophytes in North America (Roché and Roché 1991; Seastedt and Suding 2007).

Experimental design

This study forms part of the Jena Experiment, located near Jena, Germany, on the flood plain of the river Saale (for details see Roscher *et al.* 2004). Briefly, 82 large plots of 20 × 20 m each were established in 2002 at plant species richness levels of 1, 2, 4, 8, 16 and 60 species. Species were drawn randomly out of 60 belonging to the species pool of the Arrhenaterion communities characteristic of the surrounding area. Plant species were divided into four functional groups (grasses, small herbs, tall herbs and legumes) by multivariate cluster analysis and all possible combinations of plant species richness × functional group richness were realized from the 60-species pool. Within each plant species richness × functional group richness combination, the occurrences of each of the four functional groups were balanced, allowing for testing of the effects of the presence or absence of individual functional groups. Except for the 16- and 60-species mixtures, each diversity level was replicated 16 times (=16 plots) with different species allocation. Mixtures of 16 and 60 species were replicated 14 and 4 times, respectively. Plots were arranged in four blocks to account for gradients in abiotic conditions (randomized block design) with the same number of replicates per block for each diversity level. Thus, the design of the Jena Experiment allowed us to disentangle the effects of species richness, functional group richness and the presence of particular plant functional groups. To maintain the sown species diversity levels, all plots were weeded once to twice a year. Plots were mown twice each year in June and September and cut biomass was removed from the site. Two subplots per main plot ('insecticide' and 'control') were chosen for planting individuals of *C. jacea*, which belongs to the species pool of the experiment. These insecticide and control subplots were assigned to random positions within a 20 × 5-m margin of each large plot. The control subplot comprised 10 m² and the insecticide subplot 30 m² and focal plants were transplanted close to the plot centre to avoid edge effects.

The insecticide Perfekthion (active substance: 40% dimethoate (C₅H₁₂NO₃PS₂); BASF, Ludwigshafen, Germany) is a semi-systemic organothio-phosphate and has been applied at monthly intervals from April to September since 2003 as an aqueous solution (0.1%) at ~38 (2006) and 30 (2007) ml/m². Dimethoate was shown to efficiently reduce herbivory within our experimental plots (Scherber *et al.* 2006) while having only little direct effects on the growth of plants (Hector *et al.* 2004; Schädler *et al.* 2004).

Inconsistent results from studies on side effects of dimethoate suggest small effects on parts of the soil community. While nematode and enchytraeid numbers and microbial activity were un-

affected by dimethoate application (Endlweber *et al.* 2006; Martikainen *et al.* 1998; Vig *et al.* 2008), epigeic collembolans were reduced in an arable field (Endlweber *et al.* 2006) and microcosm studies (Martikainen *et al.* 1998). Transient increase in Azotobacter numbers following dimethoate application was reported from a 3-year multi-insecticide study (Vig *et al.* 2008), and Eisenhauer *et al.* (2009a) found decreased soil microbial parameters (basal respiration and microbial biomass) and no interaction with sown diversity in soil samples from the Jena Experiment after 3 years of dimethoate application (May 2006).

Both, potentially reduced collembolan numbers and microbial activity may decrease nutrient availability on subplots sprayed with insecticide. A decrease in nutrient availability would be expected to decrease productivity of sprayed compared to unsprayed subplots. In fact, aboveground biomass data from differing subplots show no difference between sprayed and unsprayed subplots in 2007 and even increased productivity in sprayed subplots in 2009 (W. W. Weisser, N. Nitschke, unpublished data), indicating that this particular insecticide side effect must be small or insignificant.

Epigeic collembolans seem of minor importance for nutrient cycling on our field site as this particular group of litter decomposers accounts for only 5 out of 15 collembolan species determined in soil from the Jena Experiment (Sabais *et al.* 2009, under review, *Acta Oecologica*) and the litter input into the system is low as mown biomass is removed from the field site. Decreased microbial activity may result from an indirect insecticide effect, rather than from a side effect. It has been shown that insect foliar herbivory can increase nutrient content in precipitation passing through the vegetation by frass deposition or leaching from damaged plant tissue (e.g. Schowalter *et al.* 1991, Lovett and Ruesink 1995); hence, reduced herbivory reduces nutrients washed down to the ground possibly resulting in decreased microbial activity. Considering the above, we appraise potential side effects of dimethoate to be of little importance in our study system.

Planting of *Centaurea jacea*

Seeds of *C. jacea* were obtained from Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany). Seeds were germinated in late April 2005 and grown on standard compost : perlite mixture (4 : 1) in an unheated glasshouse. In early June 2005, 800 seedlings were transferred into pots containing soil of the four different blocks. Each type of soil received the same proportion of plants, which were then kept outdoors to harden until transplantation into the subplots. In early July 2005, five plants each were carefully transplanted into the two subplots, insecticide and control, of 80 diversity plots (two monocultures had been abandoned due to very low target species cover). *Centaurea* seedlings were planted at 25-cm distance and labelled. They were mown in late June and early September together with the general mowing of the field site.

Plant community measurement

Community biomass of all plant communities was recorded in the untreated core area (150 m²) of each plot by harvesting

biomass within four randomly distributed 20 × 50-cm frames. All plants were cut 3 cm aboveground and plant material was dried (70°C, 48 hours) and weighed. Harvesting took place in August 2005, 2006 and 2007 before the autumn mowing. Mean total biomass of the four samples per year was used as covariate in the statistical analysis of data from the respective year.

Centaurea jacea performance measurements

We recorded growth-related (biomass, height and number of leaves) and reproduction-related traits (number of shoots and number and width of flower heads) of *Centaurea* and tested the effect of insecticide by estimating herbivory. Harvest of the transplants and measurements took place from 23 August to 1 September in 2006 and from 28 to 31 August in 2007. *Centaurea* biomass was determined by cutting each individual 3 cm aboveground. All stems and leaves were collected and stored cool until measurement within the following days. We measured the height of the largest *Centaurea* individual per subplot to the nearest mm and recorded the number of flower heads of all individuals. Then, plants were decapitated, oven-dried at 70°C for 48 hours and weighed.

In 2006, herbivore damage was visually estimated as percentage leaf area missing, including all visible damage on the largest stem leaf of each plant. Leaf templates from millimetre paper served as reference when judging the missing proportion. In 2007, however, herbivore damage was estimated both on the largest stem and basal leaf using a class system. Damage class midpoints (in parentheses) were used for statistical analysis and classes were defined as follows: no damage (0%), almost no damage (0.1%), damage <1% (0.5%), 1–3% damage (2%), 3–5% damage (4%), 5–10% damage (7.5%), 10–20% damage (15%), 20–30% damage (25%) and 30–40% damage (35%). No damage >40% occurred.

In addition, the following traits were recorded in 2007: number of shoots and basal leaves and the width of the largest flower head using a slide gauge. The measure of flower head width served as proxy for seed numbers.

Statistical analysis

Data were analysed using the statistical software R version 2.10 (R Development Core Team, 2008) and if necessary, transformed to meet the assumptions of homogeneity of variances and normality (types of transformation are indicated in Tables 2–5).

We analysed the effects of community terms (i.e. plant species and functional group richness, presence of particular functional groups) and treatment (insecticide vs. control) on survival and performance of *Centaurea* using analysis of covariance with type I sums of squares (Crawley 2002; Schmid *et al.* 2002). The experiment was laid out as a split plot with subplots (insecticide and control) nested within plots. For each dependent variable, only those plots were included in the analysis that gave values for both subplots. All response variables entered the analysis as mean values per subplot.

The fitted model included factors and interaction terms (interactions are marked by '×') in the order listed in Table 1.

The explanatory variable 'community biomass' of the respective year was included as a covariate to test whether effects of particular variables were likely to be mediated by aboveground competition. Community biomass in our experimental plots was shown to be positively related to plant species richness, functional group richness and the presence of legumes (Marquard *et al.* 2009) and generally closely positively correlated with leaf area index (LAI) and aboveground space use. Hence, we consider community biomass a suitable measure for aboveground competition and will use these terms synonymously.

Averages are given as mean ± 1 SE. Differences between years were tested for significant difference from zero with a paired *t*-test (test statistic: *t*) or a Wilcoxon test for paired samples (test statistic: *V*) if the differences between years deviated from normal distribution.

One potential concern regarding statistical analysis was the reduced number of plots entering the model after incomplete data pairs (values from only one out of two subplots) had been excluded. Therefore, we also performed analyses of variance (ANOVAs) on the plot level on mean values of all data recorded, including values from single subplots. As this slightly biased analysis yielded qualitatively equivalent results as obtained from the split-plot ANOVAs on the reduced data sets, we are confident that our results are robust with respect to incomplete data pairs.

RESULTS

Survival of *Centaurea jacea*

Until August 2006, ~13 months after transplantation, 67.4% of 800 *C.jacea* seedlings initially transplanted had survived and this proportion declined further to 53.7% until August 2007. Thus, mortality was highest in the first year after

Table 1: explanatory variables fitted in the model

Explanatory terms— between-plots ANOVA	Explanatory terms— within-plots ANOVA
Block	Treatment (insecticide/control)
(Community biomass)	Treatment × log (sr)
Log (plant species richness) = Log (sr)	Treatment × nrfg
Number of functional groups = Nrfg	Treatment × leg
Presence of legumes = Leg	Treatment × grass
Presence of grasses = Grass	Treatment × therb
Presence of tall herbs = Therb	
Log (sr) × nrfg	
Log (sr) × leg	
Leg × grass	
Leg × therb	

transplantation. Survival until August 2006 (Table 2) and between 2006 and 2007 (Table 4) was negatively affected by species (Fig. 1A) and functional group richness. Moreover, effects of species and functional group richness on survival interacted with each other for 2006 (Table 2). The presence of legumes also had a strong negative effect on survival until 2006 (Table 2). Of all originally planted individuals, $85.9 \pm 3.9\%$ survived in the absence of legumes while merely $47.9 \pm 2\%$ survived in their presence.

Growth of *Centaurea jacea*

Centaurea grew 41% bigger and 34% taller in 2007 than in 2006 (average individual mass: $V = 271$, $P < 0.001$; 2006: 6.26 ± 1.27 g, 2007: 8.82 ± 1.3 g; maximum height: $t = -8.19$, $P < 0.001$; 2006: 37.4 ± 1.7 cm, 2007: 50.0 ± 1.5 cm). In 2006, both *Centaurea* biomass and height were negatively affected by plant species and functional group richness (Table 2; Fig. 1B). In 2007 all growth traits responded negatively to species richness (Fig. 1B). *Centaurea* height was also negatively affected by functional group richness. In addition, grass and legume presence negatively affected *Centaurea* biomass (Table 4).

Reproduction of *Centaurea jacea*

Average number of flower heads was 26% lower in 2006 than in 2007 ($V = 339$, $P = 0.004$; 2006: 13.7 ± 3.4 , 2007: 18.5 ± 3.1). In 2006 and 2007, species and functional group richness as well as legume presence had negative effects on the mean number of flower heads recorded per transplant (Tables 2 and 4; Fig. 1C). The width of the largest flower head, recorded in 2007 only, was negatively affected by species richness and legume presence and the interaction between these factors was significant. Higher species richness negatively affected flower head width when legumes were absent, but not in their presence. Tall herb presence influenced flower head width negatively when legumes were present, but not when they were absent (Table 4). The number of shoots produced in 2007 was negatively affected by species and functional group richness (Table 4).

Reduced insect herbivore loads in the community

Average estimated loss of stem leaf area on *Centaurea* amounted to $4.5 \pm 0.3\%$ and $4.2 \pm 0.5\%$ in 2006 and 2007, respectively. Herbivore damage of stem leaves differed neither between years ($V = 539.5$, $P = 0.274$) nor between treatments (insecticide vs. control, see split-plot ANOVAs,

Table 2: results of type I ANOVA for data from August 2006, subplot paired data, response variables in columns, explanatory variables in rows in their order of entering the analysis (compare Table 1), degrees of freedom (df), mean squares (MS) and *F*-values are given and significant results are indicated by * $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$

August 2006		Survival first year (%) ^a		Herbivore damage on stem leaves (%)		Biomass (g) ^b		Max. height (cm)		Number of flower heads ^b	
No. of observations/plots		80		62		62		62		62	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Between plots											
Block	3	0.122	0.72	29.883	2.06	1.117	0.55	439.000	2.13	4.034	1.00
Log (sr)	1	4.162	24.53***	36.504	2.52	90.887	45.12***	6579.000	31.93***	153.119	37.90***
Nrfg	1	2.224	13.11***	21.407	1.48	10.749	5.34*	1611.700	7.82**	56.198	13.91***
Leg	1	7.057	41.59***	0.156	0.01	2.164	1.07	222.400	1.08	18.714	4.63*
Grass	1	0.004	0.03	3.063	0.21	0.748	0.37	19.600	0.10	1.701	0.42
Therb	1	0.015	0.09	0.422	0.03	0.279	0.14	69.200	0.34	0.157	0.04
Log (sr) : nrfg	1	0.967	5.70*	37.253	2.57	1.074	0.53	404.500	1.96	5.434	1.35
Log (sr) : leg	1	0.152	0.89	7.618	0.53	2.255	1.12	318.200	1.54	5.354	1.33
Leg : grass	1	0.090	0.53	20.897	1.44	0.094	0.05	0.900	0.00	0.021	0.01
Leg : therb	1	0.039	0.23	6.546	0.45	1.736	0.86	294.800	1.43	4.277	1.06
Residuals		0.170		14.478		2.014		206.000		4.040	
Within plots											
Treatment	1	0.117	0.81	2.578	0.41	0.213	0.22	36.700	0.27	0.944	0.30
Treatment : log (sr)	1	0.222	1.52	7.657	1.22	0.466	0.48	369.300	2.75	1.448	0.47
Treatment : nrfg	1	0.043	0.29	1.756	0.28	0.156	0.16	2.000	0.02	0.075	0.02
Treatment : leg	1	0.185	1.27	12.315	1.96	0.723	0.74	12.700	0.09	0.108	0.03
Treatment : grass	1	0.192	1.32	5.053	0.81	0.123	0.13	55.400	0.41	0.981	0.32
Treatment : therb	1	0.000	0.00	0.024	0.00	0.152	0.16	30.300	0.23	0.472	0.15
Residuals		0.146		6.270		0.980		134.100		3.110	

Abbreviations: a = arcsine square root, b = logarithmic, c = square root transformation.

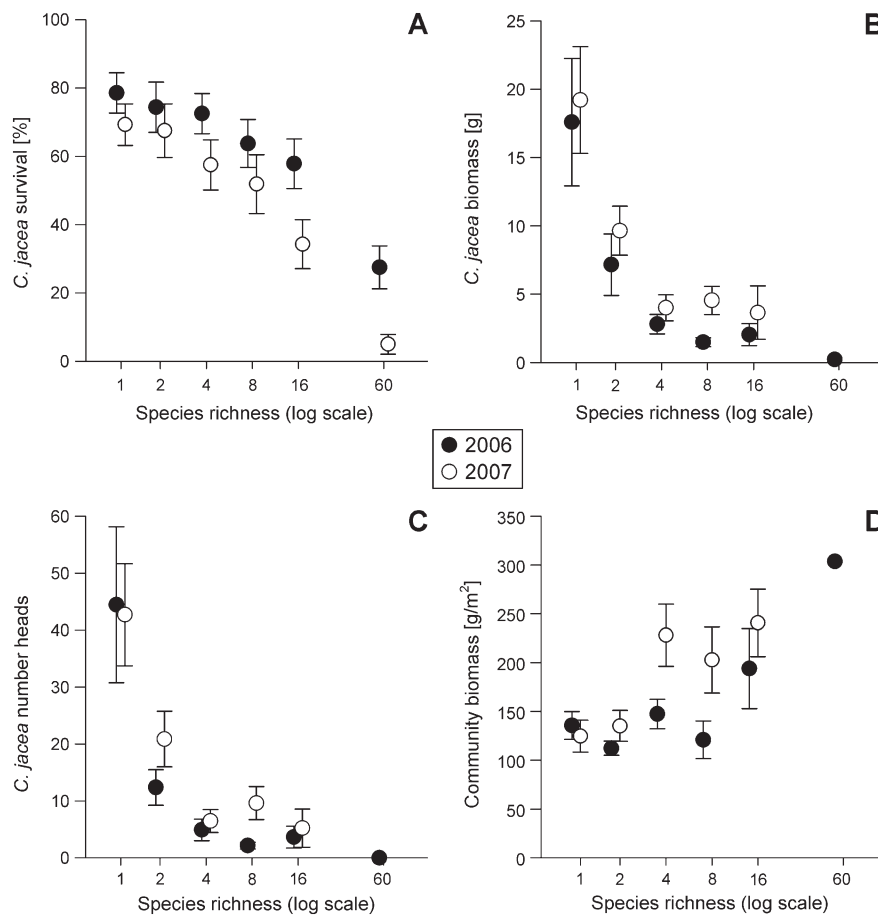


Figure 1: effects of species richness on transplant survival (A), biomass (B) and number of flower heads (C) in 2006 and 2007. (D) Relationship between community biomass and species richness in 2006 and 2007. Graphs show plot mean values \pm 1 SE.

Tables 2 and 4). Basal leaf area loss in 2007 was significantly lower in subplots treated with insecticide ($5.0 \pm 0.1\%$) than in untreated control subplots ($5.8 \pm 0.1\%$, split-plot ANOVA, Table 4), whereas no other response variable was directly affected by insecticide treatment in either year.

In 2007, but not yet in 2006, the responses of *Centaurea* biomass, the numbers of flower heads, shoots and basal leaves to species richness differed between insecticide and control subplots (Tables 2 and 4). This interaction was due to much higher values for all these response variables in the sprayed monocultures compared to all other diversity levels and control subplots. In control subplots, values of these variables were similar for monocultures and two species mixtures, and these were higher than in the more species-rich mixtures (Fig. 2B and C).

The role of plant community biomass in mediating diversity effects

For 2006, the inclusion of community biomass as a covariate resulted in significantly negative effects on survival, transplant biomass and the number of flower heads (Table 3). Although none of the other effects changed, community biomass

explained some variance formerly (i.e. in the analysis without this covariate) explained by species richness; in the case of survival, it also explained variance formerly related to functional group richness and legume presence (Tables 2 and 3). That same year, stem leaf herbivory slightly increased with increasing community biomass and a slightly negative effect of increased species richness became apparent when community biomass entered analysis. Maximum height was independent of community biomass.

For 2007, higher community biomass negatively affected *Centaurea* survival and the number of flower heads, shoots and basal leaves, but all other response variables were independent of that parameter. Where a significant effect became apparent, community biomass explained part of the variance formerly related to species richness without the latter effect disappearing. However, inclusion of community biomass caused several weak effects to disappear. These were mainly legume effects (for *Centaurea* biomass and flower head width) and functional group richness effects (for survival and number of shoots). In two instances, additional weak effects became apparent with inclusion of community biomass (Tables 4 and 5).

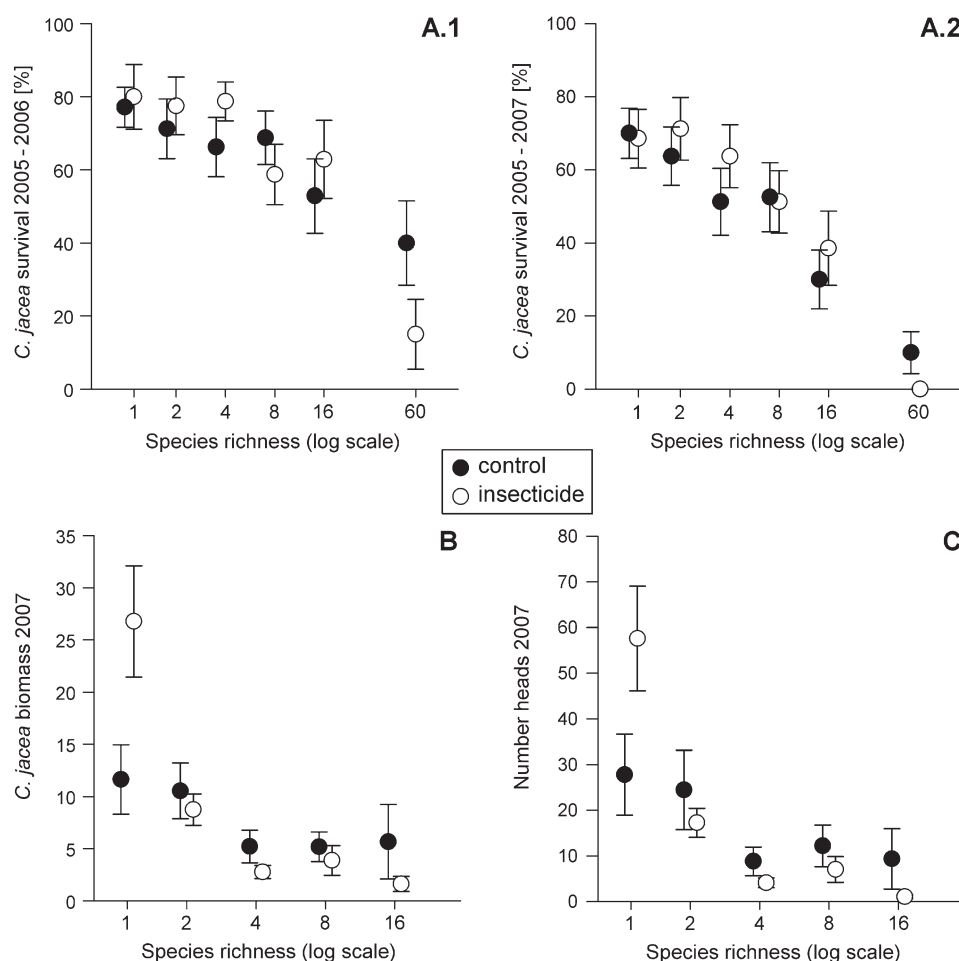


Figure 2: interactions between plant species richness (log-scale) and insecticide treatment in 2007; transplant biomass (**B**) and number of flower heads (**C**). For completeness also the non-significant interaction for survival until 2006 (**A.1**) and 2007 (**A.2**) is shown. Graphs show plot mean values \pm 1 SE.

Overall, comparing the results of models with and without community biomass as covariate indicated that most effects of species diversity were partly mediated by community biomass, whereas several weak legume and functional group richness effects were fully explained by community biomass.

DISCUSSION

Our results showed the importance of species richness effects on later phases of *C. jacea* establishment in grassland communities. Species richness negatively affected survival and all growth- and reproduction-related traits measured in both years of investigation. Among the particular functional groups, only the presence of legumes showed a strong negative influence on survival 1 year after transplantation of seedlings and on plant performance after 2 years. There were no clear trends of responses for either group of traits (growth-related or reproduction-related), but while all traits responded identically in 2006, they differed in their response in 2007. In monocultures, insect herbivore reduction within the commu-

nity considerably affected *C. jacea* establishment. Aboveground community biomass had significant negative effects in both years of investigation.

Statistical issues

A potential concern regarding statistical analysis may be the decreasing number of surviving *Centaurea* transplants from year to year, which raises the question whether effects were driven by the survivors of the preceding years rather than mirroring characteristic responses of a late establishment phase of the focal species. Survivors in plots with high mortality may be larger than those in plots with lower mortality. To test such a potential bias, we exemplarily analysed *Centaurea* biomass on the largest individuals instead of the mean across all individuals per subplot. For 2006, the significant effects turned out identical to our original analysis and for 2007 even a few additional effects of community biomass, functional group richness and grass presence occurred, implying that the original analysis was conservative (Tables S1 and S2 in online Supplementary material).

Table 3: results of type I ANOVA for data from August 2006, subplot paired data—inclusion of community biomass (com. biomass), response variables in columns, explanatory variables in rows in their order of entering the analysis (compare Table 1), degrees of freedom (df), mean squares (MS) and *F*-values are given and significant results are indicated by * $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$

August 2006 (+ comm biomass)		Survival first year (%) ^{aΔ}		Herbivore damage on stem leaves (%)		Biomass (g) ^b		Max. height (cm)		Number of flower heads ^b	
No. of observations/plots		80		62		62		62		62	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Between plots											
Block	3	0.122	0.72	29.883	2.41	1.117	0.55	439.000	2.16	4.034	0.98
Com. biomass '06 ^Δ	1	7.248	42.66***	50.702	4.09*	8.440	4.14*	315.600	1.55	29.895	7.26**
Log (sr)	1	1.269	7.47**	78.793	6.35*	82.506	40.48***	6352.200	31.26***	125.419	30.44***
Nrfg	1	1.628	9.58**	33.880	2.73	11.098	5.45*	1728.100	8.50**	54.351	13.19***
Leg	1	3.617	21.29***	38.263	3.09	4.696	2.30	732.100	3.60	22.778	5.53*
Grass	1	0.001	0.01	0.149	0.01	0.454	0.22	1.900	0.01	1.148	0.28
Therb	1	0.001	0.00	6.731	0.54	0.073	0.04	162.300	0.80	0.007	0.00
Log (sr) : nrfg	1	0.749	4.41*	0.999	0.08	0.164	0.08	79.500	0.39	2.775	0.67
Log (sr) : leg	1	0.213	1.26	2.233	0.18	1.220	0.60	103.700	0.51	4.319	1.05
Leg : grass	1	0.103	0.60	34.903	2.81	0.159	0.08	8.700	0.04	0.027	0.01
Leg : therb	1	0.037	0.22	1.298	0.10	2.038	1.00	377.900	1.86	4.432	1.08
Residuals		0.170		12.403		2.038		203.200		4.120	
Within plots											
Treatment	1	0.117	0.81	2.578	0.41	0.213	0.22	36.700	0.27	0.944	0.30
Treatment : log (sr)	1	0.222	1.52	7.657	1.22	0.466	0.48	369.300	2.75	1.448	0.47
Treatment : nrfg	1	0.043	0.29	1.756	0.28	0.156	0.16	2.000	0.02	0.075	0.02
Treatment : leg	1	0.185	1.27	12.315	1.96	0.723	0.74	12.700	0.09	0.108	0.03
Treatment : grass	1	0.192	1.32	5.053	0.81	0.123	0.13	55.400	0.41	0.981	0.32
Treatment : therb	1	0.000	0.00	0.024	0.00	0.152	0.16	30.300	0.23	0.472	0.15
Residuals		0.146		6.270		0.980		134.100		3.110	

Abbreviations: a = arcsine square root, b = logarithmic, c = square root transformation, Δ = community biomass of 2005 entered analysis of survival from 2005 to 2006.

By 2007, out of originally 42 plots containing legumes, *Centaurea* transplants were present in 19, compared to 35 plots in which legumes were absent by design. A 'balance simulation' was conducted in order to test the reliability of our results. One hundred data sets balanced in legume presence/absence were created from the original data set in 2007 by randomly drawing 19 plots of legume absence from the pool of 35. Split-plot ANOVA on all 100 data sets with *Centaurea* biomass as response variable confirmed our results from the original analysis on the complete data set as the majority of ANOVAs returned the respective effects. The only exception was a grass effect that, contrary to the original analysis, in 70% of the simulation ANOVAs was non-significant (Table S3 in online Supplementary material).

Diversity effects

In both years, increasing species richness decreased *Centaurea* survival and performance, which is in line with our hypothesis (i) and with Dukes (2002), who found decreasing *Centaurea solstitialis* growth with increasing species richness in microcosm experiments. As the effect of species richness was consistently

negative for all traits investigated in both years, it seems a pre-vailing factor also at later stages of *Centaurea* establishment.

A second measure of diversity, functional group richness, had a constant negative influence on *Centaurea* performance and survival in both years. While we found significant effects of functional group richness on all traits measured in 2006, effects in 2007 were limited to only three out of six traits, indicating its decreasing importance for plant establishment with time.

Effects of particular plant functional groups on *Centaurea jacea* performance

The most striking effect of any functional group on *Centaurea* was the strong negative influence of legume presence on survival, which is in accordance with Scherber *et al.* (2006). Legumes are generally associated with positive effects on neighbouring plants (e.g. Fargione *et al.* 2003; Mwangi *et al.* 2007) due to atmospheric nitrogen fixing. However, many biodiversity experiments found that the presence of legumes also increased community biomass (e.g. Mulder *et al.* 2002; Tilman *et al.* 1997), which is equally true in our experimental communities (Marquard *et al.* 2009; Roscher *et al.* 2005). The negative

Table 4: results of type I ANOVA for data from August 2007, subplot paired data, response variables in columns, explanatory variables in rows in their order of entering the analysis (compare Table 1), degrees of freedom (df), mean squares (MS) and *F* values are given and significant results are indicated by **P* ≤ 0.05, ***P* < 0.01, ****P* < 0.001

August 2007		Survival 2006– 2007 (%)		Herbivore damage on stem leaves (%) ^b		Herbivore damage on basal leaves (%) ^b		Biomass (g) ^b		Max. height (cm)		Number of basal leaves ^c		Number of flower heads ^c		Width of largest flower head (cm)		Number of shoots	
No. of observations/ plots		68		44		53		54		45		54		54		43		54	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Between plots																			
Block	3	0.094	0.83	1.963	0.84	3.207	1.44	0.155	0.13	462.800	3.52*	39.223	6.54**	4.986	0.98	0.017	0.75	80.200	1.72
Log (sr)	1	1.463	12.92***	1.932	0.83	0.006	0.00	54.333	45.07***	1496.100	11.37**	72.586	12.10**	231.652	45.56***	0.380	16.92***	1554.050	33.38***
Nrfg	1	0.500	4.42*	0.136	0.06	1.178	0.53	3.020	2.50	897.400	6.82*	6.212	1.04	21.201	4.17*	0.020	0.89	194.180	4.17*
Leg	1	0.216	1.91	1.968	0.84	3.542	1.59	8.266	6.86*	526.500	4.00	0.659	0.11	22.367	4.40*	0.106	4.71*	72.180	1.55
Grass	1	0.013	0.11	1.702	0.73	1.077	0.49	5.047	4.19*	169.700	1.29	0.402	0.07	4.707	0.93	0.058	2.58	26.800	0.58
Therb	1	0.019	0.17	4.469	1.92	1.983	0.89	0.484	0.40	394.600	3.00	9.618	1.60	5.888	1.16	0.025	1.10	37.690	0.81
Log (sr) : nrfg	1	0.210	1.85	0.005	0.00	1.436	0.65	0.463	0.38	20.100	0.15	1.909	0.32	9.727	1.91	0.000	0.01	103.320	2.22
Log (sr) : leg	1	0.007	0.06	3.946	1.69	2.200	0.99	2.820	2.34	84.200	0.64	10.421	1.74	2.354	0.46	0.118	5.27*	66.120	1.42
Leg : grass	1	0.058	0.51	0.357	0.15	1.038	0.47	0.323	0.27	33.700	0.26	12.493	2.08	1.530	0.30	0.047	2.09	2.450	0.05
Leg : therb	1	0.037	0.33	0.002	0.00	3.703	1.67	0.004	0.00	77.200	0.59	0.328	0.05	3.227	0.63	0.169	7.54*	5.740	0.12
Residuals		0.113		2.330		2.221		1.205		131.500		5.999		5.085		0.022		46.550	
Within plots																			
Treatment	1	0.033	0.42	1.624	1.67	8.225	6.75*	0.287	0.39	40.000	0.28	0.043	0.02	0.375	0.09	0.001	0.04	1.810	0.07
Treatment : log (sr)	1	0.048	0.62	1.259	1.29	2.821	2.31	10.229	13.89***	482.700	3.42	14.610	8.35**	36.633	9.02**	0.043	1.68	388.960	14.03***
Treatment : nrfg	1	0.155	1.99	0.860	0.88	0.010	0.01	1.028	1.40	27.000	0.19	0.224	0.13	0.217	0.05	0.001	0.04	13.070	0.47
Treatment : leg	1	0.274	3.51	0.293	0.30	1.984	1.63	0.356	0.48	26.400	0.19	2.181	1.25	3.397	0.84	0.001	0.05	0.900	0.03
Treatment : grass	1	0.002	0.03	3.989	4.09	0.230	0.19	0.641	0.87	35.600	0.25	4.521	2.58	0.586	0.14	0.022	0.86	0.190	0.01
Treatment : therb	1	0.050	0.64	0.022	0.02	0.010	0.01	1.133	1.54	54.200	0.38	0.398	0.23	11.429	2.82	0.027	1.05	48.280	1.74
Residuals		0.078		0.975		1.219		0.736		141.100		1.750		4.060		0.025		27.720	

Abbreviations: a = arcsine square root, b = logarithmic, c = square root transformation.

Table 5: results of type I ANOVA for data from August 2007, subplot paired data—inclusion of community biomass (com. biomass), response variables in columns, explanatory variables in rows in their order of entering the analysis (compare Table 1), degrees of freedom (df), mean squares (MS) and *F* values are given and significant results are indicated by **P* ≤ 0.05, ***P* < 0.01, ****P* < 0.001

August 2007 (+ comm biomass)		Survival 2006–2007 (%) ^Δ		Herbivore damage on stem leaves (%) ^b		Herbivore damage on basal leaves (%) ^b		Biomass (g) ^b		Max. height (cm)		Number of basal leaves ^c		Number of flower heads ^c		Width of largest flower head (cm)		Number of shoots	
No. of observations/ plots		68		44		53		54		45		54		54		43		54	
Source	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Between plots																			
Block	3	0.094	0.83	1.963	0.88	3.207	1.44	0.155	0.13	462.800	3.82*	39.223	7.08***	4.986	0.97	0.017	0.76	80.200	1.68
Com. biomass '07 ^Δ	1	1.398	12.35***	6.008	2.70	3.031	1.36	3.441	2.82	13.300	0.11	66.052	11.92**	26.826	5.20*	0.001	0.06	472.530	9.92**
Log (sr)	1	0.641	5.66*	6.956	3.13	0.555	0.25	52.959	43.37***	1666.700	13.75***	31.120	5.61*	207.004	40.11***	0.446	19.92***	1110.540	23.32***
Nrfg	1	0.386	3.41	2.932	1.32	0.095	0.04	6.720	5.50*	1436.000	11.85**	0.184	0.03	33.360	6.46*	0.067	2.99	165.490	3.48
Leg	1	0.009	0.08	0.000	0.00	2.085	0.94	4.675	3.83	189.300	1.56	0.595	0.11	13.099	2.54	0.052	2.30	78.680	1.65
Grass	1	0.020	0.17	0.203	0.09	0.726	0.33	3.800	3.11	69.900	0.58	0.168	0.03	2.817	0.55	0.034	1.53	21.970	0.46
Therb	1	0.004	0.04	1.132	0.51	3.396	1.52	0.890	0.73	745.900	6.16*	17.653	3.19	8.508	1.65	0.056	2.52	35.700	0.75
Log (sr) : nrfg	1	0.076	0.67	0.359	0.16	1.287	0.58	0.370	0.30	0.008	0.00	2.921	0.53	8.836	1.71	0.005	0.23	103.730	2.18
Log (sr) : leg	1	0.047	0.41	2.143	0.96	1.890	0.85	2.363	1.94	17.100	0.14	16.039	2.89	1.523	0.30	0.077	3.43	68.970	1.45
Leg : grass	1	0.034	0.30	0.000	0.00	1.623	0.73	0.111	0.09	0.500	0.00	4.006	0.72	0.486	0.09	0.077	3.45	4.670	0.10
Leg : therb	1	0.023	0.20	0.291	0.13	3.455	1.55	0.007	0.01	13.200	0.11	0.150	0.03	2.217	0.43	0.134	5.98*	3.930	0.08
Residuals		0.113		2.224		2.228		1.221		121.200		5.542		5.161		0.022		47.620	
Within plots																			
Treatment	1	0.033	0.42	1.624	1.67	8.225	6.75*	0.287	0.39	40.000	0.28	0.043	0.02	0.375	0.09	0.001	0.04	1.810	0.07
Treatment : log (sr)	1	0.048	0.62	1.259	1.29	2.821	2.31	10.229	13.89***	482.700	3.42	14.610	8.35**	36.633	9.02**	0.043	1.68	388.960	14.03***
Treatment : nrfg	1	0.155	1.99	0.860	0.88	0.010	0.01	1.028	1.40	27.000	0.19	0.224	0.13	0.217	0.05	0.001	0.04	13.070	0.47
Treatment : leg	1	0.274	3.51	0.293	0.30	1.984	1.63	0.356	0.48	26.400	0.19	2.181	1.25	3.397	0.84	0.001	0.05	0.900	0.03
Treatment : grass	1	0.002	0.03	3.989	4.09	0.230	0.19	0.641	0.87	35.600	0.25	4.521	2.58	0.586	0.14	0.022	0.86	0.190	0.01
Treatment : therb	1	0.050	0.64	0.022	0.02	0.010	0.01	1.133	1.54	54.200	0.38	0.398	0.23	11.429	2.82	0.027	1.05	48.280	1.74
Residuals		0.078		0.975		1.219		0.736		141.100		1.750		4.060		0.025		27.720	

Abbreviations: a = arcsine square root, b = logarithmic, c = square root transformation; Δ = community biomass of 2006 entered analysis of survival from 2006 to 2007.

influence of legumes could therefore derive from their increasing effect on aboveground competition. Including community biomass into the model explained some variation formerly assigned to the presence of legumes, although it did not fully explain the significant legume effect on survival. Less likely than an effect of aboveground competition, is a strong impact of belowground competition, measured as belowground biomass, in communities with legumes present. Beßler *et al.* (2009) investigated root growth in the Jena Experiment in 2006 and found that legumes invested less into root productivity than non-legumes and more into aboveground plant tissue.

Weak legume effects on *Centaurea* performance traits occurred both in 2006 (in one out of three) and 2007 (in three out of six traits). Contrary to our expectations and other findings on the same field site (Mwangi *et al.* 2007; Scherber *et al.* 2006), legume presence always decreased *Centaurea* performance. The lack of positive legume effects may partly be due to the fact that *Centaurea* has rather modest requirements for nutrients and is capable of inhabiting a wide range of habitats (Sommer 1990). Hence, it may not especially benefit from nitrogen-enriched soils in plant communities containing legumes, whereas other species investigated (*Rumex acetosa* L., *Knautia arvensis* (L.) Coult.) may.

Moreover, previous studies were carried out at an earlier stage of field site establishment. Since the positive effect of legumes on community biomass in the Jena Experiment increased with time (Marquard *et al.* 2009), it is possible that, by the time our study was carried out, the positive effects of nitrogen fixing on neighbouring plants may be cancelled by the legumes' negative effect of aboveground space use (=competition for light) with proceeding maturation of the experimental field site. And indeed, all legume effects in 2007 were mediated by aboveground competition. This pattern is confirmed by other studies on the Jena Experiment. While Roscher *et al.* (2009a) found that legume presence increased biomass, plant individual and species number of spontaneously invading plant species during the first 3 years after the set-up of the field site (2003–2005), species recruitment after seed addition in 2005 (Roscher *et al.* 2009b) showed that legume presence generally affected seedling densities and the number of establishing species negatively. However, these studies also found that the effects of particular functional groups in the biodiversity plots on establishment and growth of species not belonging to originally sown plant communities are largely driven by invader species identity, which is in accordance with the contradictory results of previous and our study in the Jena Experiment.

Contrary to our expectations neither tall herbs nor grasses had pronounced effects on *Centaurea* performance. Single negative effects occurred only once in 2007. While Scherber *et al.* (2006) and Mwangi *et al.* (2007) both found that functional group identity had much stronger effects on performance of *R. acetosa* and *K. arvensis* after 1 year of establishment, our study on *C. jacea* suggests constant prevailing species richness effects after 1 and 2 years of establishment. This pattern also seems to hold for young seedlings, as Eisenhauer *et al.* (2009b) detected

no effects of particular functional groups on biomass or height of 4-month-old *C. jacea* transplants. Hence, the different observations may be attributed to the particular study system.

Influence of insect herbivory on *Centaurea* performance

Insecticide efficiency was demonstrated on herbivore damage of basal leaves in 2007 and was confirmed in records on flower head infestation with tephritid flies that same year (N. Nitschke, unpublished data). Leaf damage levels were similar to those found in *R. acetosa* (Scherber *et al.* 2006) and mean herbivory in some managed montane grasslands in Germany (Unsicker *et al.* 2006; Weisser and Siemann 2004). For plants in monocultures, but not in more diverse communities, insecticide application resulted in increased *Centaurea* performance. Correspondingly, the insecticide \times species richness interaction was significant in several growth- and reproduction-related traits in 2007. Survival of transplanted *Centaurea* was not affected by insect herbivore reduction.

Both herbivory and plant competition are stated to reduce plant growth with competition often reported to be more important (Haag *et al.* 2004). As spraying of the whole community may have changed the competitive environment of our focal plant, increased performance suggests suppression by herbivores and increased competitive ability due to herbivore reduction, not compensated for by other competitive species. The fact that an insecticide effect only occurred in monocultures, not in communities of higher diversity can be explained in two not mutually exclusive ways. First, competition on the plant community level may be very low in monocultures compared to higher diversity levels due to inefficient niche exploitation and lower individual density (N. Nitschke, personal observation). As competition in monocultures may not increase substantially with insecticide reduction, the direct effect of insect herbivory on the focal species becomes visible. In this scenario, insect herbivory was of greater importance than competition. Second, if herbivore loads should be higher in monocultures compared to more species communities, as suggested by the Root (1973) hypothesis, it may well be more important than plant–plant competition in monocultures and lose importance with suggested lower herbivore loads in communities of increasing species richness. This suggests that *Centaurea* establishment is controlled by herbivory in monocultures and by competition at higher diversity levels. However, our 2007 herbivory data on *Centaurea* do not support differing levels of herbivory on different species richness levels, but, as has been pointed out by others, leaf area loss is not always the most reliable parameter to estimate herbivore load (Carson and Root 1999) because it ignores sap sucking insects, which may well have great negative impacts on plant performance via pathogen transmission. The sensitivity of *C. jacea* to insect herbivory is difficult to judge as no studies on the subject could be found. However, investigations of related species of the same genus imply low sensitivity even to high herbivory levels (Callaway *et al.* 2006; Newingham and Callaway 2006).

Aboveground competition effects

Community biomass is generally highly correlated with LAI, a measure of aboveground space use and light penetration (Welles and Norman 1991) and is used as a proxy for aboveground competition. Although, aboveground biomass was higher at higher diversity in the Jena Experiment (Fig. 1D; Marquard *et al.* 2009; Roscher *et al.* 2005) and had negative effects on survival and some performance traits of *Centaurea* in our study, it did not completely explain diversity effects. This suggests that further processes affected by diversity may have played a role. In a separate study in the Jena Experiment, (Scherber *et al.* 2010) detected negative effects of species richness on transplants of *K.arvensis* even when aboveground competition was excluded experimentally (by means of bent down neighbours), proving the importance of belowground competition and other interactions for community resistance to newly arriving individuals. Also using the Jena Experiment, the study of Eisenhauer *et al.* (2009b) on earthworm and belowground competition effects on an early stage of *C.jacea* establishment (4 months after transplantation) also supports these results. Despite reduced aboveground competition by regular cutting of neighbours, their transplants showed decreasing biomass with increasing species richness.

Conclusions

Summarizing, we can state that effects of plant community properties on invading individuals change in the course of establishment as our results indicate decreasing importance of functional richness and identity until the third year of establishment. Increasing plant species richness had the most important negative effect on *Centaurea* survival and performance during both years of investigation and hence is also important during late stages of establishment. Community biomass (especially at high diversity) and insect herbivory in the recipient community (especially at low diversity) are important drivers in mediating community effects on invaders. Plants performed best when relieved from insect herbivores in a community of low competition while increasing community biomass decreased plant performance.

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SUPPLEMENTARY MATERIAL

Supplementary Tables S1, S2 and S3 are available at *Journal of Plant Ecology* online.

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