Species but not genotype diversity strongly impacts the establishment of rare colonisers

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Summary

1. Understanding species coexistence and regulation of biodiversity are major research challenges, yet there is no consensus on the effects of diversity on diversity, including their mediation through plant–plant interactions.

2. We examined how the diversity of recipient communities impacted on the establishment of colonising species. We ran a greenhouse-based community experiment, creating artificial arable crop communities with varying levels of barley genotype and weed species diversity, analysed with structural equation modelling of responses across trophic levels.

3. Colonising arable weed species establishment was significantly reduced when the recipient communities' weed species richness, but not barley genotype richness, increased. Recipient plant communities with higher species richness occupied more total niche space and showed stronger competition with colonising species. In contrast, recipient plant communities with higher genotype richness, even though they had slightly greater niche space occupancy, had no significant effects on the colonisation of additional species.

4. Responses were species specific: colonising common weed species establishment was less affected by the recipient plant communities than that of colonising rare weed species. Strong responses of colonising rare species were related to the abiotic rather than the biotic environment created by the recipient communities. The stronger response of colonising rare species suggests greater niche overlap with and competitive inferiority to the recipient plant community, whereas the relative independence of colonising common species indicates less niche overlap and/or competitive equality or superiority.

5. We observed a negative species diversity effect on colonising species, with the effect size increasing with increasing rarity of the colonising species. This differential responsiveness of colonising rare and common arable weed species to the presence of and diversity in the recipient arable plant communities may be crucial in understanding rarity and may result from differential evolutionary pathways in response to interactions.

Key-words: barley cultivars, biodiversity, common and rare species, community assembly, competition, facilitation, niche construction, plant–plant interactions, soil microbes, structural equation modelling

Introduction

Despite accelerating global biodiversity loss (Cardinale *et al.* 2012), we have poor knowledge about cascading

effects of diversity loss on diversity. If diversity has positive feedbacks on diversity – in other words, if diversity of a recipient community promotes diversity of colonisers – we would expect that diversity loss would have cascading negative impacts on diversity and ecosystem functioning (Isbell *et al.* 2011). In contrast, negative diversity

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feedbacks, where the recipient plant community's diversity limits that of colonising species, could indicate high niche overlap promoting potential species redundancy and resilience of ecosystems to species loss. We therefore need to better understand diversity feedback effects because of their direct relevance for management challenges such as the conservation of species and genetic diversity, management of invasive species or the sustainable management of agroecosystems through promoting biodiversity.

Theoretical concepts give contradictory predictions concerning diversity feedback effects (Vellend 2008). Classic niche theory suggests negative diversity effects on colonising species through niche filling: more species occupy more niche space, increasing competition and leaving less niche space available for others (Chase & Leibold 2003; Tilman 2004). In contrast, the related concepts of biotic sources of environmental heterogeneity (e.g. keystone species) and ecosystem engineering (Harper 1977; Jones, Lawton & Shachak 1994), both of which can be considered part of niche construction (Kylafis & Loreau 2011; Matthews *et al.* 2014), suggest that increasing biotic diversity creates more environmental heterogeneity, increasing facilitation and supporting higher diversity of colonising species.

Empirical evidence of diversity effects of recipient plant communities on colonising species appears inconsistent (Levine & D'Antonio 1999). For example, at local scales exotic plant species richness generally declines under high native species richness (Elton 1958; Levine 2000; Levine, Adler & Yelenik 2004; Fridley *et al.* 2007), consistent with more complete use of the available niche space and stronger competition (Chase & Leibold 2003; Tilman 2004). Nevertheless, positive diversity effects of recipient plant communities on plant colonisation have been indicated by both theoretical models (Vellend & Gerber 2005) and empirical studies (Turkington 1989; Palmer & Maurer 1997; Simberloff & Von Holle 1999).

Importantly, most tests of diversity effects of recipient communities on colonising species arise from studies examining how species richness, or interspecific functional diversity (e.g. Symstad 2000), regulate community resistance to invasive species and are, therefore, examining *species diversity* effects (Hooper *et al.* 2005). However, there is growing evidence that intraspecific *genotype diversity* influences community assembly processes (Booth & Grime 2003; Crutsinger *et al.* 2006; Vellend 2006; Lankau & Strauss 2007; Hughes *et al.* 2008; Fridley & Grime 2010; Gibson *et al.* 2012). Effects of genotype diversity generally concur with species diversity effects in that higher genotype diversity reduces invasibility (Weltzin *et al.* 2003), for example through a more complete use of the available niche space and stronger competition between the resident community and potential invaders (Crutsinger, Souza & Sanders 2008). Alternatively, higher genotype diversity could also increase facilitation if it creates more heterogeneous viable niche space compared to genotype monocultures. However, the relative effect sizes of species and genotype diversity of recipient communities on colonising species, and

biological mechanisms involved in such interactions, remain largely unexplored.

Critically, diversity feedback effects depend on the effects of the recipient communities *and* on the responses of the colonising species to these effects. There is high between-species variability in responses to competition and facilitation (Gross *et al.* 2009). Strong positive or negative responses of colonising species is very often due to high niche overlap with the recipient community, and may also indicate a narrow niche, thus reducing the chance of the incoming species to find some unoccupied niche space. In contrast, species showing high independence likely benefit from niche segregation and the ability to occupy the recipient communities' unaffected, free niche space. Recent work in alpine plant communities demonstrated that different components of local species pools vary in their response to the niche space occupied and created by cushion plants (Schöb, Butterfield & Pugnaire 2012). Beyond keystone species, in multi-species systems there may be species-specific variation in the feedback effects of entire communities on potential colonising species. Although critical in helping understanding the processes structuring plant communities, such species-specific variation in feedback effects among different levels of diversity have rarely been explored, and consequently the associated mechanisms are poorly understood.

To address these considerable knowledge gaps, we explored the relative scale, direction and mechanisms underlying interspecific and intraspecific diversity effects of recipient communities on colonising species. We focused on testing for differential responses of colonising species known to be common or rare in their native communities. Knowing that the resident community effects can be species specific, we explored the possibility that the commonness of species may be related to their response behaviour to established communities. We hypothesised that species are common because of their high independence from other plant species in their host community, whereas rare species show high dependence, requiring the absence (with respect to competition) or presence (with respect to facilitation) of specific neighbours for establishment and survival. This hypothesis of differential responses and underlying mechanisms is predicated by the observation that common and rare species differ in habitat requirements (Magurran & Henderson 2003), with rare species potentially requiring particular abiotic or biotic conditions that may either be eliminated or created by the recipient community.

As a recipient community, our experiment imitated a typical plant community of arable crop fields, including the crop and associated arable weeds, which allowed to easily manipulate and compare the effects of plant genotype and species diversity on colonising arable weed species establishment in a controlled setting. Our study is therefore unusual in not using invasive species, focusing instead on a typical and common UK plant community, going beyond the particular case of the effects of native communities on non-native invasives.

We manipulated intraspecific and interspecific plant diversity in greenhouse mesocosms and assessed the impact of the recipient communities on 10 colonising arable weed species of varying abundance (from very common to very rare) in the UK. As such, this colonisation experiment was used to assess the diversity effects of the recipient communities, consisting of different levels of crop genotype and weed species diversity, on the establishment of the added common and rare weed species. We also assessed recipient plant community effects on potential drivers of colonising species' success: We anticipated that increasing genotype and species richness would increase the occupied niche space (represented through the range of plant traits) of the recipient communities (Kraft, Valencia & Ackerly 2008), which in turn would have stronger effects on the abiotic (light, soil water and nitrogen) and the biotic (arbuscular mycorrhizal fungal and bacterial communities) environment compared to the effects of monocultures on these factors (e.g. Hooper & Vitousek 1997; Wardle *et al.* 2004; Scherber *et al.* 2010). We further predicted stronger effects from species diversity compared to intraspecific genotype diversity. Finally, we expected species-specific positive and negative responses of colonising species, in particular, that the rarest weed species would respond most negatively to the recipient communities.

Materials and methods

EXPERIMENTAL DESIGN

Mesocosm communities imitating typical UK arable crop communities with a single crop species and several common weed species were constructed in an unheated greenhouse at the James Hutton Institute, Aberdeen (UK, 57°8′6″N, 2°9′24″W; see Appendix S1 in the Supporting Information for extended methods). The use of mesocosms allowed us to minimise small- (i.e. plot-) scale environmental heterogeneity, reducing to a manageable scale the level of replication needed. Communities were established in boxes measuring $0.7 \times 0.7 \times 0.3$ m and filled with homogenised loam topsoil from nearby farmland. Into each mesocosm, 60 pre-germinated seedlings of barley and arable weeds were planted. Equal proportions of each cultivar or species in mixtures were randomly allocated to grid cells within each mesocosm box. After planting, mesocosms were regularly watered and monitored. Communities were assembled using combinations of five barley genotypes (i.e. cultivars: Optic, Oxbridge, Sebastian, Tipple and Westminster) and five common weed species in arable fields (Hawes *et al.* 2005): *Capsella bursa-pastoris, Euphorbia helioscopia, Poa annua, Senecio vulgaris* and *Stellaria media*. Weed species had an unknown genetic diversity and were selected to represent substantial phylogenetic diversity (i.e. monocots, core eudicots, eurosids I, eurosids II and euasterids II) in order to maximise the contrast between genotype and species diversity. The five common weed species were a stratified random subsample of initially 10 selected common weed species (two species per phylogenetic group). All genotypes and species were grown in monoculture and in mixtures of either all five barley genotypes with no weeds, all five weed species with no barley, one barley genotype with five weed species or five barley genotypes with five weed species (Fig. S1). There were four replicates of each community composition treatment (=recipient communities) and four control mesocosms without plants, giving 18 weed species × barley genotype combinations plus the control, all randomly allocated to 76 mesocosms in the greenhouse.

PLANT TRAITS, ABIOTIC ENVIRONMENTAL CONDITIONS AND SOIL MICROBIAL COMMUNITY COMPOSITION

Two months after planting of the recipient communities, traits were determined on living plants for five randomly selected individuals of each species or genotype in all recipient communities. For trait measurements [specific leaf area (SLA), leaf dry matter content (LDMC)], we followed standard protocols (Cornelissen *et al.* 2003). SLA is broadly related to relative growth rate, carbon investment and overall resource conditions of the environment, with positive relationships to photosynthetic rate and nitrogen uptake (Pérez-Harguindeguy *et al.* 2013), therefore indicating niche requirements for and impacts on light and nutrients. LDMC is often inversely related to SLA, but is also influenced by soil–water relations (Pérez-Harguindeguy *et al.* 2013). LDMC therefore indicates niche requirements and impact on resource conditions, including water. Consequently, by using these two traits to represent occupied niche space of the recipient communities, we covered a considerable number of the key niche-defining factors above-ground and below-ground. Then, we calculated the range of each trait for each recipient community mesocosm (Jung *et al.* 2010). Two months after planting, photosynthetically active radiation (PAR) at ground level and volumetric soil moisture were measured at three randomly selected points within each mesocosm and averaged; soil nitrogen (N) was determined for a composite of three randomly placed samples per mesocosm. From these composite soil samples we also determined soil microbial community composition. We extracted DNA from 0.2 g soil using the Power-Soil-htp™ 96-Well Soil DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA) following manufacturer's instructions. For characterisation of the community of arbuscular mycorrhizal fungi (AMF), the LSU rDNA region was amplified, and the products digested using TaqI endonuclease and fragments separated by capillary electrophoresis (see Appendix S1 for further information). To characterise the bacterial communities, a 16S rDNA gene fragment corresponding to V3 and V4 regions was amplified (see Appendix S1 for further information) and pyrosequenced on a Roche Junior Genome Sequencer System (Roche) using 454 Titanium chemistry at the NGS facility, Western Sydney University (Richmond, Australia). For all treatments with barley four replicates were analysed, while for other treatments one replicate was randomly discarded (to leave three) in order to reduce the total sample number. Two additional samples were discarded after sample processing due to PCR amplification issues. The 16S rDNA sequences underwent trimming and quality control, and were aligned using the SILVA database. Aligned sequences were clustered into operational taxonomic units (OTUs) defined at 97% similarity cut-off using the average neighbour method.

For further analyses, soil microbial community composition was represented by the first axis of principal component analysis (PCA) applied to either terminal restriction fragments of AMF or the OTUs of bacteria. Fragments of different length and OTUs were considered as 'species' and their relativised peak heights or counts as abundance estimates. The first axis of the PCAs explained 25·8% of the variance in AMF community composition and 7·9% of the variance in soil bacterial community composition.

SEED ADDITION AND QUANTIFICATION OF PLANT–PLANT INTERACTIONS

Two months after planting the recipient communities, we added to each recipient community and the four control mesocosms 30

untreated seeds of each of 10 additional arable weed species, comprising five common arable weed species, four arable weed species rather rare in the UK and one non-native (but naturalised) rare arable weed. UK species rarity was assessed using data from the National Biodiversity Network's Gateway (https://data.nbn.org.uk; see Table S1). In subsequent analyses, species rarity was treated as quantitative variable to account for differences in rarity within the groups of common and rare species respectively. The 10 added weeds (hereafter 'colonising species') are characteristic of arable crop communities in the UK (Hawes *et al.* 2005), and were selected from the same broad taxonomic groups as the weed community used for the recipient communities: (i) common colonising weed species (i.e. the second stratified random subsample of the initially selected 10 common weed species): *Avena fatua*, *Geranium dissectum*, *Matricaria chamomilla*, *Spergula arvensis* and *Urtica urens*; (ii) rare native colonising weed species: *Apera spica-venti*, *Euphorbia platyphyllos*, *Papaver argemone* and *Valerianella rimosa*, (iii) rare non-native colonising weed species: *Alyssum alyssoides*. Forty days after sowing, the number of individuals of each colonising species was determined for each mesocosm. *Apera spica-venti* seedlings could not be unambiguously distinguished from other, unsown grasses, and we excluded this species from analyses. For the nine remaining species, we calculated the species abundance.

Abundance data were used to quantify recipient community effects on colonising species. Given the small stature of the colonising species at the time of harvest (0.0027 ± 0.0014 g per individual), we assumed no significant interactions among them that may interfere with the effects of the recipient community on the colonising species. Lower abundance in recipient communities compared to control mesocosms was attributed to net competition from the recipient community; higher abundance in recipient communities compared to controls was attributed to net facilitation, assuming that environmental conditions among plots were initially homogeneous and then influenced only by the recipient plant communities. The strength of facilitation or competition was quantified as relative change in abundance in recipient communities compared to control mesocosms using a standardised effect size metric [(abundance in the recipient community−mean abundance in the control mesocosm)/mean abundance in the control mesocosm]. This plant–plant interaction measure thus has negative values for competition and positive values for facilitation and allows direct comparison of effect sizes. Quantification of plant–plant interaction intensity was done separately for each colonising species in each recipient community mesocosm.

STATISTICAL ANALYSES

To assess effects of genotype and species richness of the recipient communities on net plant–plant interactions per mesocosm, we applied a linear mixed effects model with the standardised effect size metric for plant–plant interactions as the response variable. As fixed effects we used a number of contrasts that reflect our experimental design of recipient communities, while 'mesocosm' and 'colonising species identity' were included as random effects. The fixed effect contrasts were barley presence (P/A), weed presence (P/A), barley genotype mixture (1 vs. 5 genotypes), weed species mixture (1 vs. 5 species), barley genotype identity, weed species identity and the interaction between barley genotype identity and weed presence. We applied a Gaussian distribution of error terms and a separate error component for each colonising species using the ASREML (Butler 2009) and PASCAL (Niklaus 2005) packages in R (R Core Team 2013).

The relationship between the rarity of colonising weed species and their standardised effect size metric for plant–plant interactions was tested with a linear model, with the plant–plant interaction measure as the response variable and rarity as the fixed effect.

For a mechanistic understanding of how the genetic or species diversity of the recipient communities influenced the sign and intensity of plant–plant interactions with colonising species, we quantified the direct effects of the recipient communities on the occupied niche space and their indirect effects on the biotic and abiotic environment, as well as competition and facilitation, using structural equation modelling (SEM). For the calculation of indirect effects, we considered both significant and non-significant path coefficients. SEM tests measured data against an *a priori*-developed model of the relationships driving observed diversity effects on colonising species (see Fig. S2). The *a priori* SEM was constructed with four different levels and assessed using LAVAAN (Rosseel 2012) in R (R Core Team 2013): Level 1 – the recipient communities consisting of barley and/or weed monocultures or mixtures; Level 2 – the occupied niche space of the recipient communities quantified through the range of two plant functional traits (Jung *et al.* 2010), assuming that these traits describe at least part of the realised niche of the plants (Violle & Jiang 2009); Level 3 – the environmental engineering of the recipient communities through effects on the abiotic and biotic environmental conditions. Abiotic environmental variables were N, soil moisture and PAR expressed for each recipient community mesocosm as % of the control mesocosm. Biotic environmental variables were the compositions of AMF and bacteria communities expressed as the absolute difference in the PCA scores on the first principal component for each recipient community mesocosm compared to the average PCA scores for the control mesocosms; Level 4 – plant–plant interactions experienced by the colonising species from the recipient communities quantified through the effect size metric as described above.

Results

Both the presence of barley and the presence of weeds reduced the abundance of colonising weed species. In addition, we found increasing net competition with increasing species (weed) richness but not with increasing genotype (barley cultivar) richness of the recipient communities (Table 1).

For all colonising weed species, competition from recipient communities prevailed over facilitation (Fig. 1). Prevailing competition reduced abundance of colonising species by 64 (27–86)% (mean and range); in only two out of the 54 community–coloniser interactions examined was there evidence of facilitation (Fig. 1). Nevertheless, responses of colonising weed species to the effect of the recipient communities were highly species specific: six out of nine colonising species (Fig 1c–e and g–i) experienced strong competition (69–86%); two species (Fig. 1a,b) showed weak responses to recipient communities with relatively low competition (27–35%); and one species, *P. argemone* (Fig. 1f), showed an intermediate level of competition (47%) and a diversified response to the different recipient communities, with strong competition in the presence of barley and weaker competition when weeds predominated (i.e. 1S, 5S and 1G5S communities).

The relationship between plant–plant interaction effects of the recipient arable crop–weed communities on the colonising weed species and their UK rarity revealed that colonising rare species experienced more competition than colonising common species (Fig. 2).

Table 1. Results of mixed effects ANOVA testing barley and weed presence, richness and identity effects on plant–plant interactions

Factor	numDF	denDF	F	P
(Intercept)	1	8·4	71·65	**<0·001*****
Barley	1	53·6	4·43	**0·040***
Weed mixture	1	53·6	7·59	**0·008****
Weed	1	53·6	25·36	**<0·001*****
Barley mixture	1	53·6	1·39	0·244
Weed × Barley mixture	1	53·6	0·38	0·543
Weed species	4	53·6	33·60	**<0·001*****
Barley genotype	4	53·6	0·10	0·982
Weed × Barley genotype	4	53·6	0·11	0·978

Random terms	n	VC	SE
Plot	72	0·004	0·007
Added species	9	0·048	0·025
Avena fatua	72	0·113	0·020
Spergula arvensis	72	0·142	0·025
Papaver argemone	72	1·345	0·227
Euphorbia platyphyllos	72	0·135	0·024
Urtica urens	72	0·525	0·089
Alyssum alyssoides	72	0·049	0·010
Geranium dissectum	72	0·086	0·016
Matricaria chamomilla	72	0·045	0·009
Valerianella rimosa	72	0·089	0·016

denDF, degrees of freedom of error term; numDF, degrees of freedom of term; F, variance ratio; P, error probability; SE, standard error of variance component; VC, variance component. *P*-values in bold are significant at α = 0·05. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

The SEM showed an acceptable fit to the data ($\chi^2 = 95$, d.f. = 50, $P = 0.148$; CFI = 0·933) and linked experimental communities to their occupied niche space, their effects on the biotic and abiotic environment, and finally on their effects on colonising weeds. Genotype and species richness of the recipient communities explained the range ($R^2 = 0.76$ and 0·84 for LDMC and SLA respectively) of traits, their effects on the community composition of AMF ($R^2 = 0.12$) and bacteria ($R^2 = 0.10$) in the soil, on PAR ($R^2 = 0.41$), but not the recipient communities' effects on soil moisture ($R^2 = 0.01$) and soil nitrogen (N; $R^2 = 0.03$) and finally their effects on the abundance of colonising weed species ($0.13 \leq R^2 \leq 0.52$).

Increasing richness of the recipient communities expanded the occupied niche space (Fig. 3). Based on standardised effect sizes, species richness effects of recipient communities were on average 7·8-fold stronger than genotype richness effects for trait range (see Table S2), with the stronger effects of species richness on occupied niche space translating into on average 5·0-fold stronger effects on the measured environmental conditions (see Table S2). Species richness of the resident communities impacted particularly on light availability (indirect effect = −0·43), AMF community composition (0·15) and soil bacterial community composition (−0·13), whereas barley genotype richness influenced soil bacterial community composition (−0·09), light availability (0·08) and AMF composition (−0·07). There was no significant directional link between barley genotype or weed species richness of the recipient communities and soil N or soil moisture. Therefore, indirect effects of species richness of recipient communities were substantially stronger than the effects of genotype richness for light (5·1-fold), but less so for AMF and soil bacteria (2·2-fold and 1·5-fold respectively), and similarly weak for soil N and soil moisture. Finally, indirect effects of species richness of recipient communities on the abundance of colonising species were on average 4·4-fold stronger than genotype richness effects, ranging between 1·9-fold (for *P. argemone*) and 10·7-fold (for *U. urens*). Total effects of species richness of the recipient communities on abiotic environmental factors (light, water, N) made up on average 96% of the communities competitive effect, compared to only 4% species richness effects on the biotic environment (AMF, bacteria; see Table S2). The prevalence of species richness effects of recipient communities on colonising species through changes in the abiotic, compared to the biotic, environment was consistent among all colonising species (Table S2).

Discussion

We observed a clear negative effect of increasing species richness of the recipient community on the establishment of colonising arable weed species in our study system, supporting classic niche theory. It suggests greater competition due to enhanced niche filling when species richness increases. Although we also found facilitation for some colonising species in some recipient communities (see Fig. S3), increased competition with increased species richness of the recipient plant communities prevailed. In contrast to species diversity effects, genotype diversity had no feedback effects on colonising weed species. Notably, effects on net interactions of increasing species richness in the recipient communities were highly species specific, being stronger for colonising rare weed species, whereas the two most common colonising weed species appeared to avoid interactions with the recipient plant communities. Furthermore, influences of the recipient communities on abiotic resources, rather than their effects on soil microbes, were the driving force behind their strong – and predominantly negative – influence on colonising rare weeds. For our study system, we can therefore identify mechanisms underlying the observed diversity effects of recipient communities on colonising species: negative species diversity effects on colonising species are predominantly due to competitive interactions for soil resources and light. Although conducted under greenhouse conditions, which may not precisely reproduce field conditions, the use of a barley–arable weed study system allows us to closely replicate the type of plant communities found in temperate arable fields; consequently, our results are likely to be directly transferable to field-based (i.e. 'natural') crop systems.
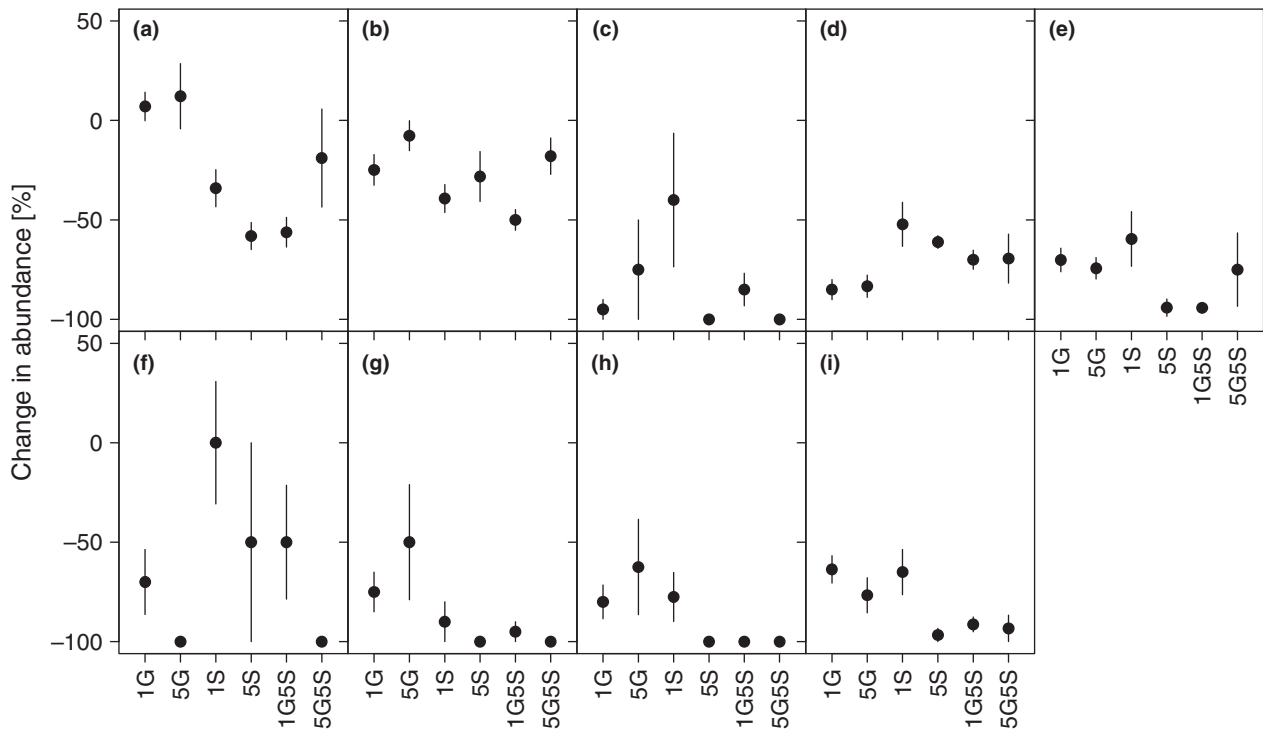
Fig. 1. Net effects of the recipient communities on the abundance of common (a–e) and rare (f–i) colonising species. (a) *Spergula arvensis*: −27% abundance in recipient community mesocosms compared to control mesocosms; (b) *Geranium dissectum*: −35%; (c) *Urtica urens*: −76%; (d) *Avena fatua*: −69%; (e) *Matricaria chamomilla*: −76%; (f) *Papaver argemone*: −47%; (g) *Euphorbia platyphyllos*: −86%; (h) *Valerianella rimosa*: −86%; (i) *Alyssum alyssoides*: −76%. Displayed are means and 1 SE for each recipient community treatment: 1G = genotype monoculture, 5G = genotype mixture, 1S = species monoculture, 5S = species mixture, 1G5S = mixture of one barley genotype with five weed species, 5G5S = mixture of five barley genotypes with five weed species. See Fig. S3 for each barley genotype × weed species combination.

GENOTYPE VS. SPECIES DIVERSITY EFFECTS

Stronger species diversity than genotype diversity effects of recipient communities on invasibility are not surprising (Crutsinger, Souza & Sanders 2008). Diversity effect size often relates to trait variability, as indicated by studies of ecosystem functioning (Schöb *et al.* 2015) or invasibility (Symstad 2000; Díaz & Cabido 2001). In our study, increasing recipient community species richness increased occupied trait space to a much greater extent than increasing genotype richness. The SEM showed that greater occupation of trait space with increasing species richness compared to increasing genotype richness caused stronger effects on the environmental conditions encountered by the colonising species. Indeed, effects of recipient communities on the environment were predominantly detrimental for all studied colonising species.

Stronger effects of species compared to genotype richness in our study may also partly be due to manipulation of genotype diversity using elite barley cultivars. These have likely been selected for similar traits (e.g. yield, grain quality, competitive ability), reducing functional trait variance; natural species may commonly lack such directed selection and therefore show higher intraspecific functional diversity. Notably, however, variation among the traits

measured in our study system was similar between barley and most of the studied weed species (Schöb *et al.* 2015). Therefore, our barley genotype mixtures might not contain an unrealistically low level of trait variance for a species monoculture.

Aside from effects of species and genotype richness, recipient community species composition also had significant effects on the establishment of colonising weed species. Particularly competitive or facilitative species or genotypes can have strong individual effects, leading to sampling effects with increasing diversity (Wardle 2001; Crutsinger, Souza & Sanders 2008). Our analyses suggested particularly strong effects of *S. media* and *E. helioscopia* (see Fig. S3).

SPECIES-SPECIFIC RESPONSES OF THE COLONISING SPECIES TO RECIPIENT COMMUNITIES

While we saw species specificity in colonising species responses, there was also an over-arching pattern, specifically a significant relationship between UK rarity of colonising weed species and their response to recipient communities. Of the three rarest colonising native weeds assessed, *E. platyphyllos* and *V. rimosa* showed the highest level of competitive exclusion (−86%), whereas *P. argemone* showed a high level of competition from barley and

remarkably weak competition from weeds (Fig. 1). Consequently, colonising rare weeds responded more strongly to diversity changes in the recipient communities than more common weeds. This suggests that for rare arable weeds
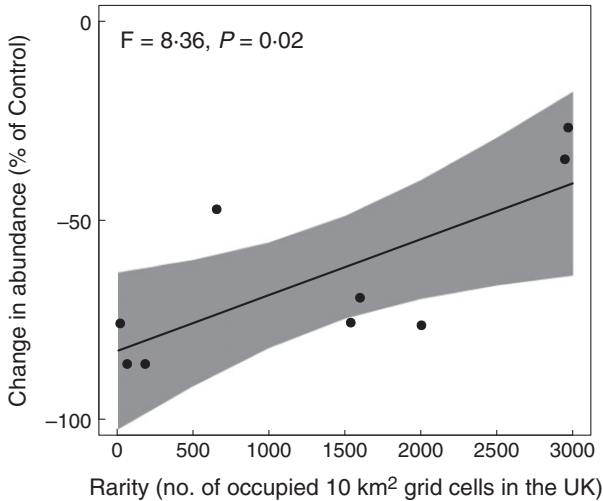

Fig. 2. The relationship between the effect size of the recipient communities on the abundance of colonising species and their rarity in the UK. Lines are mean ± 95% CI of model-predicted estimates showing the relative change in abundance of colonising species in recipient community mesocosms (in %) compared to control mesocosms, dots are the measured values for each colonising species averaged over all recipient community mesocosms. The rarity of colonising species in the UK was quantified as a count of the number of 10×10 km grid cells with a record of presence of the species between 1990 and 2014 according to the National Biodiversity Network's Gateway (https://data.nbn.org.uk) (see Table S1).

the neighbourhood context where they usually grow is very important. Indeed, the fact that the presence of rare weeds was particularly reduced by both the presence of arable crop plants and weed species diversity may have important implications for the conservation of agricultural biodiversity. Weed diversity can help reduce pests and diseases (Marshall *et al.* 2003). Advice for arable weed conservation acknowledges the need to create space for weeds away from the crop, for example, in field margins. However, if these margins are dominated by common weeds the conservation of rare weeds will be inhibited.

In contrast, the two commonest colonising weeds of our study (*G. dissectum* and *S. arvensis*) showed minimal responses to recipient communities, experiencing weak competition and, in the case of *S. arvensis*, even some facilitation by barley monocultures (Optic and Oxbridge; Fig. S3). These two species seem to have different (or at least very broad) niches compared to the species of the recipient communities, thereby avoiding the recipient community's impacts on the environment or even benefiting from them. This indicates that generalist species with a broad niche are more successful weeds (Fried, Petit & Reboud 2010), and that there is potential for crops to facilitate specialised weed species if other components of land-use management, for example, herbicide use, allow (Brooker *et al.* 2016).

The results also indicate that – in this system – impacts on the biotic environment are very limited for regulating the establishment of colonising weed species. This is in contrast to other, more stressful environments, where soil microbes play an important role for plant–plant interactions (Hortal *et al.* 2015). We speculate that the lack of
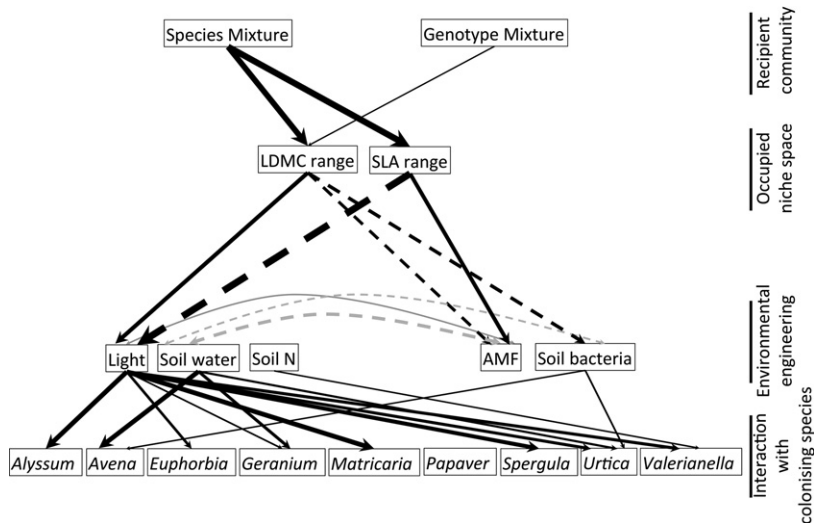

Fig. 3. Mechanistic model of species and genotype mixture effects of plant communities on plant–plant interactions: The effects of species and intraspecific genotype richness of the recipient communities, their occupied niche space [represented through the range of plant traits (specific leaf area – SLA; leaf dry matter content – LDMC)], their effects on the abiotic (light, soil water and nitrogen) and biotic [arbuscular mycorrhizal fungal (AMF) and bacterial communities] environment, on the establishment of colonising species. Displayed arrows show significant positive (solid) or negative (dashed) relationships ($\alpha = 0.05$). Line thickness represents the relative strength of the relationships quantified through standardized path coefficients. Double-headed grey arrows indicate significant correlations, whereas single-headed black arrows indicate causal relationships. Not shown are non-significant tested relationships (see Table S2).

soil nutrient limitations may limit impact of soil microbes here (van der Heijden, Bardgett & van Straalen 2008), in agreement with previous findings emphasising the importance of light competition, but not competition for soil resources, for biodiversity in productive systems (Hautier, Niklaus & Hector 2009).

Intriguingly, the variety of responses of the colonising weed species, ranging from strong competitive exclusion to weak competition and even some facilitation, concurs with recent developments in understanding the evolutionary consequences of plant–plant interactions (Tracey & Aarssen 2014). In communities dominated by strongly competitive species, selection of either highly competitive tall growth forms or small ruderal plants investing resources rapidly in reproduction have been suggested as alternative evolutionary pathways (Schamp, Aarssen & Wight 2013). Applied to our system, the use of unaffected, free niche space by the most common colonising weed species may be explained through selection for niche segregation from the dominant plant forms and enhanced competitive traits (Connell 1980). In contrast, high niche overlap with the recipient communities, probably combined with narrow niche requirements, of the rare weeds may have lead to the alternative development of small-statured reproductive growth forms that avoid strong competition (Tracey & Aarssen 2014). Such species may even adapt to newly constructed niche space, for example, to shading (Givnish 1988), which can then be seen as facilitation (Brooker *et al.* 2016). Although our results provide support for such differential evolutionary pathways for weeds in arable systems, also because this interpretation matches with the – albeit incomplete – description of habitat requirements and competitive abilities of the selected common and rare weed species (Hawes *et al.* 2005), the exact role of differential evolution in explaining current species commonness and rarity in arable systems remains unclear. However, what is clear is that colonising common and rare weed species vary in their sensitivity to the diversity effects of the resident crop–weed community. We therefore suggest that the approach adopted here, linking effects of recipient communities on colonising species via mechanistic processes using SEMs, provides a powerful tool for exploring the generality of biodiversity effects on diversity and ecosystem functioning.

Authors' contributions

Acknowledgements

Data accessibility

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Extended methods.
Fig. S1. Recipient community setup.
Fig. S2. *A priori* structural equation model explaining the diversity effects of recipient communities on plant–plant interactions.
Fig. S3. Net competition and facilitation effects of the recipient communities on the abundance of added species.
Table S1. Frequency of occurrence of the nine colonising species in the UK.
Table S2. Direct effects in the structural equation model.
Data S1. Data.