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RESEARCH ARTICLE

The contrasting roles of host species diversity and parasite population genetic diversity in the infection dynamics of a keystone parasitic plant

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Abstract

1. Diversity among species and genetic diversity within species are both important components of ecological communities that can determine the outcome of species interactions, especially between hosts and parasites. We sought to understand the impact of species diversity on host community resistance to infection by a keystone parasitic plant (*Rhinanthus minor* L.) and genetic diversity of the parasite on its successful establishment in a grassland community.

2. We used an experimental approach where large pots were planted with mixtures of mesotrophic grassland species at high and low species diversity. The parasitic plant was sown in a proportion of these with high and low genetic diversity treatments. Establishment of the parasite was monitored over 2 years and the pots harvested at the end of each growing season to determine the impact of infection on plant community biomass.

3. We found a strong effect of host plant species diversity on the establishment of the parasitic plant, with successful establishment considerably lower in the high species diversity treatment. Genetic diversity appeared to promote establishment of the parasite in the high species diversity treatment, and also facilitated longer term fitness in the low species diversity treatment. Host community structure was influenced by *R. minor*, with grass relative biomass decreasing and legume relative biomass increasing when the parasite was present. There was no direct impact of the presence of the parasite on the relative biomass of nonleguminous forbs.

4. *Synthesis*. Our data demonstrate the importance of host community species diversity in deterring the establishment of a generalist parasite. They also highlight the role of genetic diversity in determining the outcome of host–parasite interactions in multispecies communities. These findings, therefore, have important implications for the establishment and management of species-rich grasslands and provide insight into the community dynamics of parasitic plants and their hosts.

KEYWORDS
community resistance, grasslands, hemiparasite, host–parasite interactions, population genetic diversity, species diversity, yellow-rattle

1 | INTRODUCTION

Biodiversity encompasses the total variation among living organisms from all sources, including within-species genetic variation, among-species richness, and among-ecosystems variation (UNEP, 1992). The value of biodiversity can be considered both economically, in terms of the monetary value of the services that the biotic world provides to us "for free" (Constanza et al., 1997), and philosophically, in terms of its inherent value to the world and our responsibility towards maintaining it (Ehrlich & Ehrlich, 1992; Randall, 1991). Biologically, the relative importance of biodiversity for maintaining ecosystem function has been a topic of debate for at least the past 40 years (see Grime, 1997 for overview and Loreau et al., 2001 for a synthesis of findings), and continues to be so (Mori, 2016; Oliver et al., 2015, 2016). Evidence appears to be mounting, however, that there is a broadly positive relationship between species biodiversity and ecosystem services and functions, albeit dependent on experimental system, specific function, and the focal level of organization (i.e., population or community) (Balvanera et al., 2006; Lefcheck et al., 2015; Weisser et al., 2017), and that there is a tendency for these relationships to strengthen over time (Meyer et al., 2016).

One of the main functions that biodiversity is thought to provide for an ecological system is the ability to resist perturbation (Oliver et al., 2015). One form of perturbation is the invasion of new species into an established community (Roscher et al., 2009). Although there is much concern over the invasion of certain alien (i.e., nonnative) species into established plant communities (see Vilà et al., 2011 for overview of effects), not all new colonizing species fall into this category. Rather, the arrival of new species and the loss of established species are also an inherent part of a dynamic ecological community (Simberloff, 1974).

Genetic diversity of organismal traits is an essential component of evolution, enabling populations of species to adapt to change (Futuyma, 2005). It is crucial in the development of host resistance to pathogen or parasite infection (Lambrechts, Chavatte, Snounou, & Koella, 2006), as well as in the determination of pathogen infectivity and virulence (Little, Chadwick, & Watt, 2008; Vale & Little, 2009). Genetic diversity has also been shown to contribute substantially to community resilience postperturbation (Hughes & Stachowicz, 2010; Reusch, Ehlers, Hammerli, & Worm, 2005) and it has become increasingly clear that genetic diversity, particularly in foundation or keystone species, can play an important role in structuring ecological communities (Bangert et al., 2008; Johnson & Agrawal, 2005; Rowntree, Zytynska, et al., 2014). The relative strength of species level and genetic level effects on ecological communities is still under debate and depends on the scale at which it is determined (Bailey et al., 2009), as well as the particular environmental and ecological conditions experienced (Zytynska, Fleming, Tétard-Jones, Kertesz, & Preziosi, 2010). However, there is good evidence that the effects of genetic diversity can at times be comparable to, or exceed the strength of, species level effects (Bailey et al., 2009; Rowntree, Cameron, & Preziosi, 2011).

The generalist hemiparasitic plant *Rhinanthus minor* L. is a natural component of European grasslands (Westbury, 2004), with widespread distribution throughout northern Europe. Although not an invasive species per se, it shows a dynamic habit moving in patches across grasslands over time (Cameron, White, & Antonovics, 2009). It has been promoted as a tool to restore species-rich habitats (Bullock & Pywell, 2005; Hellström, Bullock, & Pywell, 2011; Westbury, Davies, Woodcock, & Dunnett, 2006) and as such is artificially introduced into the environment. The interaction of *R. minor* with its host plants is well studied and has been shown to vary with host species and functional group (Cameron et al., 2005; Cameron, Coats, & Seel, 2006; Rowntree, Fisher Barham, et al., 2014). Success of establishment of *R. minor* in grasslands is variable (Hellström et al., 2011; Mudrák et al., 2014), as is its impact on the host community (Cameron et al., 2005). There is some suggestion that host community diversity may play a role in establishment success, although the relative role of species or functional group diversity remains unresolved (Joshi, Matthies, & Schmid, 2000; Rowntree, Fisher Barham, et al., 2014). As a parasite, it might be expected that populations with broader genetic diversity are better able to establish themselves, particularly in communities with multiple host options (de Vega et al., 2008). Although previous research has demonstrated a role for parasite genetic diversity in determining the outcome of host–parasite interactions in *R. minor* (Rowntree et al., 2011), this area remains underexplored.

Here, we sought to address these knowledge gaps and determine the relative impact of host community species diversity as well as parasite population genetic diversity on the establishment and impact of *R. minor* in a grassland community. For this we used an experimental common garden mesocosm approach where we controlled for initial functional group, and relative abundance of the host community, and planted *R. minor* seed from either single or multiple source populations.

We predicted that the parasite would be less successful in establishing viable populations in the high species diversity communities, but that increased genetic diversity in the parasites (i.e., those from multiple sources) would enable it to establish more successfully. Based on previous studies, we expected the parasite to have a negative effect on grass biomass, but that the effect on legumes and forbs was less certain. We anticipated that the impact of the parasite on host productivity would be less in the high species diversity community.

2 | MATERIALS AND METHODS

The experiment was set up at the Firs Botanical Grounds located on The University of Manchester Campus, United Kingdom (53°26'38.66"N, 2°12'49.88"W).

2.1 | Host species establishment

The plant species used (listed in Table 1) are typical of British mesotrophic MG5 *Cynosurus cristatus–Centaurea nigra* grasslands

TABLE 1 Species names and functional groups of the plants used in the experiment and the number of pots each occurred in according to treatment. "L" indicates low-diversity treatments and "H" indicates high-diversity treatments. Species treatments are listed before *Rhinanthus minor* treatments. "N" indicates the pots where *R. minor* was not planted. Numbers in parentheses are the occurrences in pots where *R. minor* successfully established in year 1 of the experiment

Functional group	Species	Occurrence in pots Host species diversity—*R. minor* genetic diversity					
		L–N	L–L	L–H	H–N	H–L	H–H
Grass	*Agrostis capillaris*	7	6 (5)	10 (8)	25	25 (5)	24 (10)
Grass	*Anthoxanthum odoratum*	2	4 (3)	3 (0)	10	10 (1)	16 (8)
Grass	*Alopecurus pratensis*	6	6 (3)	7 (7)	25	24 (5)	25 (11)
Grass	*Cynosurus cristatus*	7	7 (5)	5 (3)	25	25 (5)	23 (9)
Grass	*Dactylis glomerata*[b]	4	10 (7)	7 (4)	22	22 (5)	21 (9)
Grass	*Festuca rubra* agg.	5	8 (6)	5 (5)	24	24 (5)	23 (11)
Grass	*Holcus lanatus*[b]	7	3 (2)	8 (4)	22	23 (5)	23 (10)
Grass	*Lolium perenne*	8	3 (2)	1 (1)	23	22 (4)	22 (10)
Grass	*Poa trivialis*[b]	4	3 (3)	4 (4)	24	25 (5)	23 (10)
Legume	*Trifolium repens*[b]	11	7 (0)	7(0)	25	25 (5)	25 (11)
Legume	*Lathyrus pratensis*	9	7 (7)	9 (9)	25	25 (5)	25 (11)
Legume	*Lotus corniculatus*	5	11 (11)	9 (9)	25	25 (5)	25 (11)
Forb	*Achillea millefolium*	6	2 (0)	9 (8)	17	20 (3)	21 (9)
Forb	*Cerastium fontanum*[a]	0	0 (0)	0 (0)	19	13 (3)	14 (6)
Forb	*Centaurea nigra* agg.[a]	0	0 (0)	0 (0)	15	14 (1)	10 (4)
Forb	*Hypochaeris radicata*	8	11 (9)	6 (3)	17	20 (5)	21 (9)
Forb	*Leontodon hispidus*[a]	0	0 (0)	0 (0)	18	20 (4)	22 (10)
Forb	*Leucanthemum vulgare*	7	5 (5)	6 (3)	21	21 (4)	19 (8)
Forb	*Plantago lanceolata*	7	12 (9)	10 (8)	20	21 (5)	25 (11)
Forb	*Prunella vulgaris*[a]	0	0 (0)	0 (0)	17	10 (3)	9 (5)
Forb	*Rumex acetosa*	10	10 (7)	9 (7)	23	23 (4)	21 (10)
Forb	*Ranunculus repens*	2	1 (0)	0 (0)	15	17 (5)	21 (8)
Forb	*Taraxacum officinale*	10	9 (6)	10 (7)	18	21 (3)	17 (8)

[a]Species not included in the low-diversity treatment.[b]Grown from amenity seed varieties.

(Rodwell, 1992), and were categorized into three functional groups: legumes; nonleguminous forbs (hereafter referred to as forbs), and grasses.

One hundred and fifty experimental 35-L pots were randomly allocated to low and high species diversity treatments (75 pots per treatment). A layer of grit (approximately 5 cm) was placed in the bottom of each pot and these were then filled with a mixture of John Innes No 1 compost and horticultural sand (mix ratio of 33 L compost to 25 kg sand; Keith Singleton, UK). The sand and compost were mixed together in a cement mixer before being added to the pots and no additional fertilizer was used during the experiment.

Seeds were germinated in John Innes No 1 compost in seed trays in a glasshouse under natural daylight and then transplanted into the experimental pots in early July 2012 at the 2–4 leaf stage. All pots were planted with 38 host seedlings (excluding *R. minor*) and the seedlings were randomly allocated positions within the pots in

a circular grid. The high-diversity species pool consisted of three legume, 11 forb and nine grass species and each high-diversity pot was randomly allocated with eight species each of grasses and forbs and three species of legume (a total of 19 species). Due to availability of seedlings, the species pool for the low-diversity pots only contained seven forbs rather than the 11 in the high species diversity pool (full details are in Table 1). Each low-diversity pot was randomly allocated with two species each of grasses and forbs and one species of legume (a total of five species). In order to separate effects of species diversity from functional diversity, all pots were set up with the same number of plants from each functional group, that is, with fixed legume:grass:forb proportions of 3:8:8. This meant that in the high-diversity pots, there were two individuals of each species and in the low-diversity pots there were eight individuals of each grass and forb species and six individuals of the legume species. This translates to a Shannon–Wiener diversity index of 2.94 for the high-diversity pots and 1.60 for the low-diversity pots.

Host seeds were sourced from commercial seed suppliers (Emorsgate Seeds, Kings Lynn, UK; B&T World Seeds, Aigues-Vives, France). Where possible, seeds originated from wild populations; however, in some cases, only amenity seed sources were available and these are noted in Table 1.

The pots were initially placed in rows in a glasshouse to promote establishment of seedlings until mid-September 2012 when they were all moved outside prior to the first harvest. While in the glasshouse, plants were grown in natural daylight conditions and watered daily. Recorded temperatures in the glasshouse ranged from 8.8 to 35.7°C. Once outside, the pots mainly received water from rainfall, although they were occasionally supplemented with tap water during dry periods, in which case all pots were watered. Pots were monitored throughout the experiment and any new species (i.e., nonplanted) that became established were noted and removed. Wire mesh covers were placed over the pots during the winter months to discourage disturbance from squirrels and other wildlife. In 2015, at the end of the experiment, species richness of the pots was assessed to determine host species change during the experiment.

2.2 | *Rhinanthus minor* establishment

Fifty pots were randomly selected from each species diversity treatment and 60 germinated *R. minor* seeds were planted haphazardly per pot in mid-July 2012. These seeds were originally collected in July 2011 from 10 field sites across England but failed to establish in any of the pots. Therefore, additional *R. minor* seeds from five distinct populations were sourced from four commercial suppliers (Emorsgate Seeds, Kings Lynn, UK; Herbiseed, Twyford, UK; Naturescape, Langar, UK; Goren Farm, Stockland, UK) and sown alongside self-collected seeds from two additional populations directly into the pots in December 2012 (see Table 2 for seed origin details). Seeds were sown at a total density of 11.4 g per pot (where 10 g approximated to 3,000 seeds) in two treatments (high- and low-population genetic diversity) with 25 pots per treatment. High-population genetic diversity treatments contained seeds from three sources (3.8 g each), whereas low-population genetic diversity treatments contained seed from a single source. As different quantities of

seed were available from the different suppliers, seed sources were randomly assigned to treatments and pots according to the amount available (see Table 2 for sowing details). Although seed sources differed from the original sowings in July 2012, treatment assignments to the pots remained the same. Establishment of *R. minor* was monitored with observations of presence throughout the growing season and counts of the number of fruiting stems and seedpods remaining at harvest time in 2013 and then again at the 2014 final harvest.

2.3 | Biomass harvest

Above-ground biomass was measured as an indicator of primary productivity for the mesocosms. Plant biomass was harvested three times during the course of the experiment: in Autumn (October–November) 2012 prior to the sowing of *R. minor* seeds; in September 2013 after the first full growing season and in August 2014. The biomass of each pot was cut with hand shears approximately 7 cm above the surface of the soil, and collected in a bucket. The harvested biomass of each pot was then sorted by hand into functional groups (grasses, legumes, forbs) and placed inside labelled paper bags. *Rhinanthus minor* biomass was collected in separate bags. The biomass was dried in ovens at 80°C for at least 48 hr and weighed. At the same time, the number of flowering *R. minor* stems and seedpods harvested were determined as an indicator of the density of infection. Stems were defined as seedpod-bearing branches. Therefore, a single large plant with many seedpod-bearing stems was equivalent to multiple single-stemmed plants. Stem data were analysed in preference to seed pod data, as many seedpods had disintegrated by harvest time and could not be accurately determined for each stem, while seed pod bearing stems could be easily distinguished from the plant material collected.

2.4 | Statistical analysis

2.4.1 | *Rhinanthus* establishment

Pots where *R. minor* had been planted ($N = 100$) were analysed for successful establishment (i.e., presence) of *R. minor* in 2013 (year 1) using a generalized linear model with a binary distribution and

Seed supplier	Seed origin (County)	Occurrence in pots Host species diversity—*R. minor* genetic diversity			
		L–L	H–L	L–H	H–H
Emorsgate	Somerset	10 (8)	11 (3)	23 (17)	24 (10)
Naturescape	Nottinghamshire	9 (5)	8 (2)	24 (17)	23 (10)
Goren farm	Devon	2 (1)	2 (0)	5 (3)	5 (2)
Herbiseed	Hampshire (Sparsholt)	2 (2)	2 (0)	5 (5)	5 (1)
Herbiseed	Dorset (Ferndown)	2 (1)	2 (0)	6 (3)	6 (2)
Field collected	Gwynedd	0	0	6 (5)	6 (2)
Field collected	Somerset (Skylark meadow)	0	0	6 (4)	6 (6)

TABLE 2 Seed suppliers, origin, and planting plan of the *Rhinanthus minor* used in the experiment. "L" indicates low-diversity treatments and "H" indicates high-diversity treatments. Species treatments are listed before *R. minor* treatments. Numbers in parentheses are the occurrences in pots where *R. minor* successfully established in year 1 of the experiment

"logit" link function where host species diversity, *R. minor* diversity and an interaction between the two were included as factors. Host biomass from the previous year was included as a covariate, as *R. minor* establishment is dependent on host community productivity (Mudrák et al., 2014). Successful establishment was taken to be any pot in which the parasite had been observed throughout the growing season or harvested. There were no pots with *R. minor* that had not been planted with seeds. Pairwise Spearman Rank correlations were performed on the *R. minor* biomass, seedpod, and stem data. The number of fruiting stems (i.e., *R. minor* density) harvested per pot were analysed using a linear model where species diversity, *R. minor* diversity and an interaction between the two were included as factors. Stem data were transformed with the appropriate power value following a Box–Cox procedure. This model provided the best fit to the databased on AIC values compared to a linear model on untransformed data or a generalized linear model with a Poisson distribution.

In 2014 (year 2), only those pots where *R. minor* had originally been planted and where *R. minor* had been observed in 2013 ($N = 52$) were assessed. For these, survival into a second year was analysed using a generalized linear model with a binary distribution and "logit" link function where species diversity, *R. minor* diversity and an interaction between the two were included as factors and total host biomass at the end of 2013 was included as a covariate. As very few high species diversity pots with *R. minor* remained ($N = 2$), analyses on numbers of fruiting stems were only undertaken on the low species diversity pots ($N = 21$). These were transformed following a Box–Cox procedure and analysed using a linear model where *R. minor* diversity was included as a factor. As previously, this model provided the best fit to the databased on AIC values compared to a linear model on untransformed data or a generalized linear model with a Poisson distribution.

2.5 | Host biomass

In 2013 (year 1), pots where *R. minor* had been planted but failed to establish were excluded from the analyses leaving a total of 102 pots. Total host biomass (excluding *R. minor*) was determined and the proportion of the total host biomass calculated for each functional group (grasses, legumes, forbs). Data were analysed using separate linear mixed effect models per functional group, where species diversity, *R. minor* population genetic diversity nested within *R. minor* presence and interactions between these were included as factors and "growing days" was included as a random effect. "Growing days" was included in the model to account for differences due to the timing of the harvests in 2012 and 2013 between the pots and ranged between 318 and 327 days. Data were transformed to improve normality of residuals. Best fit was provided by a power transformation determined by a Box–Cox procedure for the grass biomass data and arcsin square root transformations for the legume and forb data.

In 2014 (year 2), for the *R. minor* treatments, only pots where *R. minor* was originally planted and occurred in both 2013 and 2014, were included. For the control treatments, only pots where *R. minor* was not planted and had not occurred in 2013 or 2014 were included. As only two pots in the high species diversity contained *R. minor*, analyses were conducted on the remaining low species diversity pots ($N = 42$). Total host biomass was determined, proportional biomass for each functional group calculated as previously and data were analysed using linear mixed effect models where *R. minor* population genetic diversity nested within *R. minor* presence was included as a factor and "growing days" as a random effect. "Growing days" accounted for differences in harvest timing in 2013 and 2014 and ranged between 311 and 317 days. Best fit was provided by a power transformation determined by a Box–Cox procedure for the grass biomass data and by using untransformed data for the legumes and forbs.

Species diversity treatments were taken to be those planted in all analyses. Data from the species surveys in 2015 were analysed for the number of species remaining. These were analysed using linear models where species diversity treatment was included as a factor and the number of years *R. minor* infection had occurred in each pot included as a covariate.

Analyses were undertaken using the "lme4" package (Bates, Maechler, Bolker, & Walker, 2015), the "psych" package (Revelle, 2018) and base functions in R (R Core Team, 2015). Box–Cox transformations were determined using the "boxCox" function and significance assigned by Type II likelihood ratio chi-square tests using the "ANOVA" function in the package "car" (Fox & Weisberg, 2011). R scripts are included in the associated digital repository (https://doi.org/10.5061/dryad.5161828; Rowntree & Craig, 2018).

3 | RESULTS

3.1 | *Rhinanthus minor* establishment

Of the 100 pots sown with *R. minor*, the parasite successfully established itself in 52 pots in 2013 (year 1). There was a significant negative effect of the 2012 host biomass ($\chi^2_{1,95} = 31.14$, $p = 2.40 \times 10^{-08}$) with greater establishment in the pots with lower host biomass. There was also a significant effect of species diversity ($\chi^2_{1,95} = 6.98$, $p = 8.25 \times 10^{-03}$) with greater establishment in the low species diversity pots (36/50) compared with the high species diversity pots (16/50). There was no significant effect of *R. minor* population genetic diversity ($\chi^2_{1,95} = 0.29$, $p = 0.59$) but a marginal nonsignificant interaction between species and population genetic diversity ($\chi^2_{1,95} = 3.22$, $p = 0.07$). In the low species diversity treatment, there was successful *R. minor* establishment in 18 of 25 pots for both population genetic diversity treatments. However, in the high species diversity treatment, there was a trend showing greater *R. minor* establishment in the high-population genetic diversity treatment (11/25 pots) compared to the low-population genetic diversity treatment (5/25 pots).

The 2013 stem, seedpod, and *R. minor* biomass data were all highly positively correlated (Figure S1). The number of fruiting stems harvested per pot (i.e., *R. minor* density) in 2013 (year 1) was significantly influenced by species diversity; with a greater number of stems observed in the low-diversity pots ($F_{1,42} = 6.08$, $p = 0.02$; Figure 1a). There

were no significant effects of population genetic diversity ($F_{1,42}$ = 0.20, p = 0.66) and no interaction between the species and population genetic diversity treatments ($F_{1,42}$ = 0.81, p = 0.37; Figure 1a).

In 2014 (year 2), 23 of 52 pots retained *R. minor*. Of these, 2 of 16 were from the high species diversity treatment (one from each *R. minor* treatment) and 21 of 36 from the low species diversity treatment (9 from the high-population genetic diversity treatment and 12 from the low-population genetic diversity treatment). There was a significant effect of species diversity on *R. minor* survival into a further year ($\chi^2_{1,47}$ = 12.36, p = 4.39 × 10^{-04}), but no significant effect of the 2013 host biomass ($\chi^2_{1,47}$ = 2.58, p = 0.11), or the *R. minor* population genetic diversity ($\chi^2_{1,47}$ = 0.27, p = 0.61), and no interaction between species diversity and *R. minor* population genetic diversity ($\chi^2_{1,47}$ = 0.92, p = 0.34). In the low species diversity pots, *R. minor* population genetic diversity had a significant effect on the number of fruiting stems harvested in 2014 with a greater number of stems in the high-population genetic diversity treatment ($F_{1,19}$ = 8.93, p = 0.0076, Figure 1b).
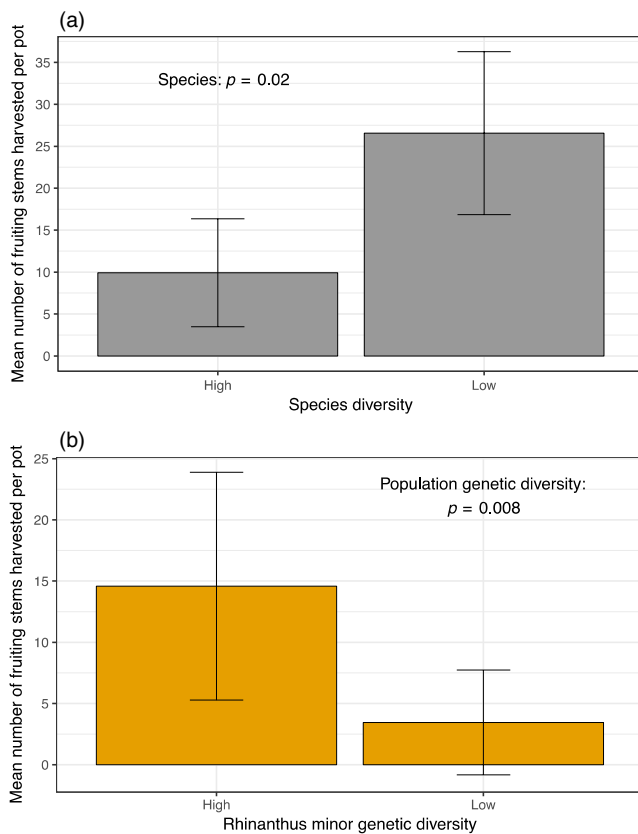
FIGURE 1 (a) Mean number of fruiting stems of *Rhinanthus minor* per pot in the high and low species diversity treatments in 2013 (year 1) with successful parasite establishment. A generalized linear model showed significant effects of species diversity. Error bars are 95% CI. (b) Mean number of fruiting stems of *R. minor* per pot by population genetic diversity in the low species diversity treatment in 2014 (year 2) where *R. minor* was successfully established for two years. Generalized linear models showed significant effects of *R. minor* genetic diversity. Error bars are 95% CI

3.2 | Host community effects

In 2012, prior to planting the *R. minor* treatments, host biomass was higher in the high species diversity pots (Figure S2a), but in 2013, this trend was reversed (Figure S2b). When divided into functional groups in 2013 (year 1), legume biomass was much greater than grass or forb biomass. For grasses, there were significant effects of species diversity ($\chi^2_{1,92}$ = 80.21, p < 2.2 × 10^{-16}) and the presence of *R. minor* ($\chi^2_{1,92}$ = 31.75, p = 1.76 × 10^{-08}) on the relative biomass and a marginally significant interaction between species diversity and the presence of *R. minor* ($\chi^2_{1,92}$ = 4.07, p = 0.04). Grass relative biomass was greater in the high species diversity communities and when *R. minor* was absent, and the impact of *R. minor* was greater in the low species diversity treatments (Figure 2a).

There were marginally significant effects of the presence of *R. minor* ($\chi^2_{1,92}$ = 5.01, p = 0.03) on relative legume biomass. The trend was in the opposite direction from the grass; hence, biomass was greater in the pots where *R. minor* was present (Figure 2b).

There were marginally nonsignificant effects of an interaction between species diversity, *R. minor* presence, and *R. minor* population genetic diversity on relative forb biomass ($\chi^2_{3,92}$ = 7.12, p = 0.07; Figure 2c). Full details of the analyses are included in Table S1.

In 2014 (year 2), in the low species diversity pots, mean host biomass was greater when *R. minor* was present, but variation in the data was large (Figure S2c) Relative biomass of the functional groups was much more evenly balanced than in the previous year. For grasses, there was a significant effect of *R. minor* presence on the relative biomass in the low-diversity pots ($\chi^2_{1,35}$ = 11.82, p = 5.84 × 10^{-04}), where biomass was greater in the pots without *R. minor* (Figure S3a). There was a significant effect of *R. minor* presence on relative legume biomass ($\chi^2_{1,35}$ = 11.40, p = 7.3 × 10^{-04}), where in contrast, biomass was greater when *R. minor* was present (Figure S3b). Relative forb biomass was not influenced by any of the factors in the model (Figure S3c). Full details of the analyses are included in Table S2.

3.3 | Host community change

The number of original species remaining in the pots in 2015 was significantly higher in the high species diversity treatment compared with the low species diversity treatment ($F_{1,147}$ = 954.29, p < 2.0 × 10^{-16}; Figure S4). On average, the high species diversity treatment contained approximately 11 species while the low species diversity treatment contained approximately four species. There was no effect of the number of years of *R. minor* infection ($F_{1,147}$ = 1.68, p = 0.20) (a composite measure of presence over the years) on the number of species remaining.

4 | DISCUSSION

We found there to be a large negative effect of host community species diversity on the establishment of the parasite and some evidence
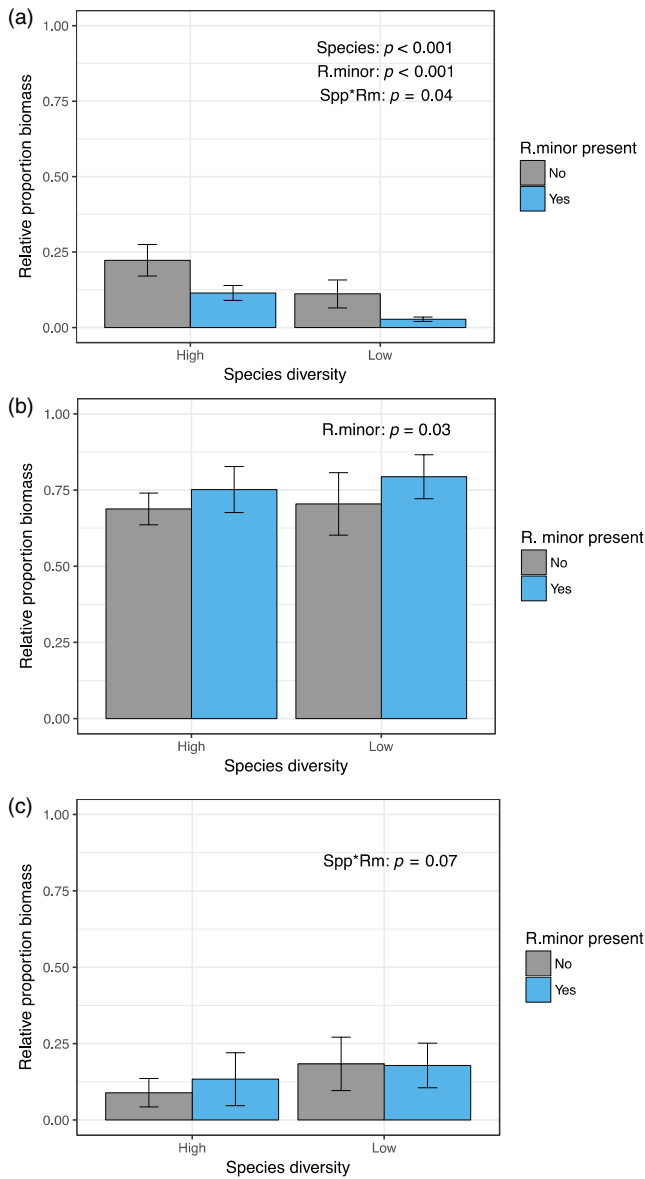
FIGURE 2 Mean relative biomass (excluding *Rhinanthus minor*) of (a) grasses, (b) legume, and (c) nonleguminous forbs in the high and low species diversity treatments, with and without *R. minor* in 2013 (year 1). Linear mixed effect models showed significant effects of species diversity and *R. minor* presence on relative biomass of grass (a), marginally significant effects of *R. minor* presence on relative legume biomass (b) and a marginally nonsignificant interaction between species diversity and *R. minor* presence on relative forb biomass. Error bars are 95% confidence intervals

that population genetic diversity in the parasite enabled establishment in the species-rich communities. As expected, host community structure was influenced by the presence of the parasite. *R. minor* had a negative effect on relative grass biomass, a generally positive effect on relative legume biomass and no effect on relative forb biomass. In the longer term, parasite populations established from multiple seed sources in the low species diversity community displayed higher levels of fitness (in terms of the number of fruiting stems) than

those from single seed sources, suggesting a role for population genetic diversity in the long-term fitness and success of the population.

Our results provide insight into the dynamics of *R. minor* in grassland communities and suggest a new mechanism by which the observed movement of the parasitic plant in space and time through a host community could occur (Cameron et al., 2009). It has been suggested that the impact of *R. minor* on community structure acts via the suppression of grasses, enabling the establishment of less competitive (but more resistant) forbs and that this can lead to changes in community composition (Cameron et al., 2006, 2005). While our data support a negative impact of the parasite on grass biomass, we also show that if the proportion of species per functional group is constant at the time of establishment, there is an additional effect of species diversity, with the initial establishment of *R. minor* more likely to occur in low species diversity patches. This could be due to interspecific variation in susceptibility to the parasite within functional groups (Rowntree, Fisher Barham, et al., 2014), or by the promotion of community level resistance to infection (i.e., an emergent property of a species diverse community).

4.1 | Species diversity effects

Our findings strongly support the idea that species diversity increases community resistance to invasion (Elton, 1958), which is congruous with the results of many previous experiments (Balvanera et al., 2006). However, the causes of this effect are not always clear and while positive relationships between species diversity and invasion resistance are often observed at a local level (as we find here), they can be absent or opposing at a landscape scale (Levine, 2000).

High host community productivity can negatively affect *R. minor* establishment (Mudrák et al., 2014) and correlate with species diversity (Hector et al., 1999; Tilman, Wedin, & Knops, 1996). Therefore, we included the previous year's biomass as a covariate in our establishment analyses. While biomass did significantly influence establishment in year 1, this was not the case in year 2, despite average biomass being much greater prior to the second year of establishment. In both years, species diversity remained a significant factor in establishment success, supporting the hypothesis that host community diversity can protect against *R. minor* infection.

Sampling effects (i.e., where diversity effects are caused by the inclusion of individual species, the probability of which increases with increasing diversity) are frequently cited as the causal mechanism behind positive diversity relationships (Wardle, 2001). By randomly assigning species to the high- and low-diversity treatments from larger species pools, and randomly assigning plant position in each pot, our experiment was designed to minimize a sampling effect and the impact of individual species. However, for practicality, we did not include monoculture treatments and, due to differing germination and survival rates, our species pool for the low-diversity pots was slightly reduced compared to the high-diversity pots. In addition, all of our legume species occurred in all high-diversity pots. Therefore, we cannot rule out the possibility that the presence of specific species promotes resistance to *R. minor* in these assemblages.

Previous studies have suggested that functional group diversity rather than species diversity per se is responsible for increased plant community resistance to infection by *R. minor* (Joshi et al., 2000). We attempted to control for a functional group effect by planting a constant number of individual plants for each of our three main functional groups (grasses, legumes and nonleguminous forbs). This meant that as species diversity increased, the abundance of specific species decreased, but the proportion of plants from each functional group remained the same. With increasing species diversity, the likelihood of *R. minor* encountering a suitable host should, therefore, increase, but the specific influence (i.e., abundance) of any one host in the community, decrease. Our results support the idea that the prevention of *R. minor* establishment in the high species diversity pots is due to an increase in species diversity rather than functional group diversity.

4.2 | Host effects

Over the 2 years of our experiment, we found *R. minor* to have a negative effect on grass relative biomass, a generally positive effect on legume relative biomass and no effect on the relative biomass of nonleguminous forbs. There is a substantial amount of literature documenting the impact of *Rhinanthus* species on these three host functional groups, from both multispecies and single-host experiments (e.g., Ameloot, Verheyen, & Hermy, 2005; Cameron et al., 2005; Davies, Graves, Elias, & Williams, 1997; Fisher et al., 2013; Joshi et al., 2000; Mudrák & Leps, 2010). Although there are species-level effects and the relative impact of the parasite on its hosts varies among experiments, our findings are in general agreement with previous research. Overall, legumes appear to be the most variable hosts, with *Rhinanthus* species sometimes increasing biomass as we found, at other times decreasing biomass or having no effect on legume biomass at all (Ameloot et al., 2005; Cameron et al., 2005; Fisher et al., 2013; Mudrák & Leps, 2010).

4.3 | Population genetic diversity effects

Although species diversity was the most consistent factor influencing experimental outcomes, our results provide evidence that increased population genetic diversity of *R. minor* promotes establishment of the parasite in high species diversity communities and facilitates longer term survival of the populations. Genetic diversity is a well-established component of parasite success more generally, enabling the evolution of virulence and transmission in order to maximize population survival and fitness (Futuyma, 2005). Similarly, invasive species need to be able to adapt to novel environments. While genetic diversity in a founder population of a putative invasive species is often lost during initial establishment, repeated invasions of the same species from multiple sources is associated with more successful establishment in the long term and the evolution of novel genetic diversity (Dlugosch & Parker, 2008; Lavergne & Molofsky, 2007).

Previous work has demonstrated the occurrence of adaptation and coevolution among parasitic plants and their hosts, with different populations or races forming more or less exclusive relationships with particular host species (de Vega et al., 2008; Thorogood, Rumsey, & Hiscock, 2009; Thorogood, Rumsey, Harris, & Hiscock, 2008). In additional work on *Orobanche minor*, Thorogood, Rumsey, Harris, and Hiscock (2009) were able to distinguish groups of specialist and more generalist populations of the parasite using SCAR (sequence characterized amplified regions) molecular markers. Their work provides evidence that host identity and diversity can be a factor explaining genetic differentiation in a parasitic plant, and that the genetic identity of the parasite will influence its survival in a multihost environment. However, unlike in these previous studies, where the parasites were achlorophyllous holoparasites with obligate relationships to their hosts, *R. minor* is a facultative hemiparasite with a broad host range (Gibson & Watkinson, 1989; Rowntree, Fisher Barham, et al., 2014). Where studies have been undertaken, there does not appear to be the same level of host–parasite adaptation in *Rhinanthus* species (Ahonen, Puustinen, & Mutikainen, 2006; Mutikainen, Salonen, Puustinen, & Koskela, 2000), although there is evidence for a genetic basis of the relative effect of particular host species (Ahonen et al., 2006), populations (Mutikainen et al., 2000), and genotypes (Rowntree et al., 2011) on parasite fitness.

In multihost parasitic systems where the parasite is a generalist, it might be expected that levels of parasite genetic diversity correlate with the diversity of potential hosts (Gandon, 2004). As more hosts become available for infection, a wider range of strategies become necessary for the parasite to overcome differential mechanisms of host resistance (Cameron et al., 2006). While the evolutionary complexity of multihost parasite systems is beginning to be explored (Gandon, 2004; Rigaud, Perrot-Minnot, & Brown, 2010), relatively little work exists on parasitic plants. In addition, multihost parasitic plants often show distinct life-history traits making comparison with other parasitic systems more difficult. For example, a single plant of *R. minor* is capable of infecting multiple hosts simultaneously via root haustoria, in a model more akin to mycorrhizal interactions (van der Heijden, Martin, Selosse, & Sanders, 2015) than a traditional multihost parasite such as malaria (Gandon, 2004); that is, they have parallel rather than serial relationships with their hosts. Our work suggests that genetic diversity could be beneficial for facultative hemiparasitic plants in dealing with diverse host species assemblages. However, in order to understand the relative roles of plant parasite genetic diversity and host species diversity more fully in such systems, additional investigations are required.

In our study, we used populations of the parasite as a proxy for genetic variation and were not able to confirm diversity levels through molecular analyses. Previous studies have demonstrated population genetic structure for *R. minor* (Houston & Wolff, 2012), and that there is a population genetic basis for differential responses to hosts (Rowntree et al., 2011). Therefore, pooling seed from different sources should have ensured that the mixed-source seed contained a broader range of individual genotypes than the single-sourced seed. As with the species pools, we sought to reduce

sampling effects by randomly selecting seed sources for each pot and treatment. Due to a poor harvest in the previous year, we were constrained by the availability of *R. minor* seed and our treatments were dominated by two populations, one grown in Somerset and the other in Nottinghamshire. These occurred in all treatment groups, although not always together, and their survival in the low-population genetic diversity pots, where seeds were from a single population, was similar, suggesting that both sources were equally viable. Seeds from three additional sources were included in all treatments, but in fewer pots of each. Of these, all established in at least one low genetic diversity replicate in the first year, again suggesting that all were viable. Two seeds sources were only included in the high-diversity treatments, at the same proportion as the three minor sources. We cannot rule out sampling effects, although the high genetic diversity treatments which contained seeds not included in the low genetic diversity treatments were a minority.

5 | CONCLUSIONS

Both our findings that host species community diversity can prevent, and parasite genetic diversity promote, the establishment of *R. minor*, have implications for the ongoing management of species-rich grasslands. As *R. minor* is often planted in order to promote or maintain grassland species diversity (Hellström et al., 2011), success of establishment can be promoted by taking standing host community species diversity and parasite genetic diversity into account.

AUTHORS' CONTRIBUTIONS

J.K.R. conceived the idea, designed and established the experiment, and analysed the data. All authors collected data and contributed to the writing of the manuscript and gave approval for final publication.

DATA ACCESSIBILITY

Data and R scripts have been deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.5161828 (Rowntree & Craig, 2018).

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SUPPORTING INFORMATION

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