

explained by a combination of elevated soil nutrients and invasive competitive species (Hockendorff et al., 2021). In the present paper, with a focus on New Zealand grasslands, we report the findings of a study of the ability of plants to procure limiting plant nutrients from soil constrained by nutrient deficiencies. Using a pot experiment, we investigate the apparently contrasting roles of competition and facilitation.

Competition between plants for resources is known to be an important driver of species diversity and processes of vegetation change in terms of complimentary resource use (Burrows, 1990; Yao et al., 2022), shaping both the structure and dynamics of plant communities (Klinerova and Dostal, 2020). Exotic plants become invasive through adaptations that are better suited to local or modified environmental conditions, in New Zealand's grasslands as elsewhere (Buddenhagen et al., 2022). However, in broader terms, competition also allows coexistence when each species can dominate in at least one combination of abiotic and biotic variables at any particular location (Rebele, 2000). In low fertility grasslands, species abundance is regulated by competition for soil nutrients (Mamolos et al., 1995); it appears to be the case that differing competitive abilities between species should be viewed as being compatible in terms of allowing diversity to be maintained (Schippers et al., 1999). An example is seen in root system structures that vary according to both dispersion patterns of soil nutrients and the presence of competitive plants (Craine, 2006) which suggests some degree of complementarity between species.

The role of complementarity or facilitation between species in grassland plant communities is best known in the context of legume-grass mixtures (Annicchiarico et al., 2015). Atmospheric nitrogen (N) fixed by rhizobial symbionts in the root nodules of legumes spills over in soil to facilitate improved growth of neighboring grasses (Lüscher et al., 2014). This beneficial effect may also result in transgressive overyielding in which the combined herbage yield exceeds that of the most productive of these species growing in monocultures (Sturludóttir et al., 2014). In intercropping systems, nutritional benefits within the rhizospheres of combinations of plant species extend beyond N to provide better access to phosphorus and improved uptake of a range of trace elements from the soil leading to increased productivity (Li et al., 2014). Our own earlier studies on low-fertility grassland pasture found that grasses provide reciprocal nutritional benefits to legumes by supplying key nutrients that are required for N fixation (Zhang et al., 2022a). Thus, when grasses and clovers grow together in unfertilized grassland, more nitrogen is procured by both species, and other limiting plant nutrients in the soil are better utilized (Zhang et al., 2022b). This type of complementarity between species effectively shares the differing abilities of each species to procure limiting nutrients from the soil (Zhang et al., 2022c).

The aim of the present study was to quantify nutrient acquisition by plants from soil, using three species with differing functional traits that are commonly found growing together in low fertility grasslands. We compared combinations of a pasture grass, an invasive weed and a clover grown in different combinations in a soil with defined elemental deficiencies. Our hypothesis was that appropriation of nutrients by the more competitive invasive weed might curtail the development of a beneficial relationship between the grass and clover.

The three species of plants used in this experimental work were all exotic species that have become naturalised in New Zealand. Species of *Pilosella* (hawkweeds) are prevalent invasive weeds, widely naturalised over more than 500 000 ha of the South Island, particularly in hill country tussock grasslands (Scott et al., 2001). Once established, *Pilosella* spreads rapidly and outcompetes other species (Rinella and Sheley, 2002; Williams and Holland, 2007). It is quite easy to see the repellent effect that *Pilosella* has on other species, sometimes with a visual halo of bare ground surrounding its dense mats. *Dactylis glomerata* (cocksfoot) is a common and widespread perennial species of pasture grass that was naturalised in New Zealand in the mid-19th century. In our earlier experimental studies, *D. glomerata* consistently provided evidence of the facilitation of nutrient procurement as a companion species to other plants. *Trifolium repens* (white clover) is the most common legume planted or oversown into grassland in New Zealand and worldwide (Annicchiarico et al., 2015). It has stolon and petiole traits that enhance its capacity to spread and forage (Annicchiarico et al., 2019), although a decline in the abundance and diversity of clovers has been associated with increasing N supplies (Tognetti et al., 2021).

2 Materials and methods

Pilosella officinarum (syn. *Hieracium pilosella*, mouse-ear hawkweed) was collected from a non-agricultural site at McLeans Island near Christchurch. This species is a small perennial rosette-forming herbaceous plant that often uses stolons and rhizomes to form interconnecting plants in dense clumps, growing particularly in grasslands, including tussock grasslands, with low to moderate fertility (see the website: New Zealand Plant Conservation Network). Both *D. glomerata* and *T. repens* were collected from paddocks on the Lincoln University campus.

Individual plants of *P. officinarum*, tillers of *D. glomerata* and plantlets of *T. repens* were transplanted into low nutritional potting mix in 3.5 L plastic pots (diameter 15 cm, height 20 cm), either alone or in combination with individuals of one or both of the other species. The basic potting medium contained no peat or other sources of organic

matter. One plant of each species was used. The nutrient content of the soil was routinely analyzed at a commercial laboratory. Each of the seven treatments (*Pilosella* alone; *Trifolium* alone; *Dactylis* alone; *Pilosella* and *Trifolium*; *Pilosella* and *Dactylis*; *Trifolium* and *Dactylis*; *Pilosella* and *Dactylis* and *Trifolium*) had five replicates. Pots were randomly arranged in a single-block design on a bench in unheated glasshouse with ambient sunlight and were watered sparingly to maintain adequate soil moisture for growth. Soil moisture kept approximately the same in the different treatments. The experiment was set up in December 2021 (early summer) and plants were harvested after two months. Aboveground biomass was harvested, sorted into separate species, oven-dried (65°C, 48 h) then weighed. Roots were carefully separated from the soil, washed, and dried in the same way. All plant samples were then finely ground and microwave-digested in 5 M HNO₃ before nutrient analysis. Nitrogen was analyzed using an Elementar Rapid Max N Elemental Analyzer and other nutrients were analyzed by ICP-OES following the standard method. Data not normally distributed were log-transformed before analysis. Differences between means were determined using one-way ANOVA, with a post-hoc Fisher LSD test. All analyses were conducted using Minitab 19.

3 Results

The growth medium was low to deficient in several key elements (Table 1) including available concentrations of N, P and key trace elements. Species growing alone produced more biomass, as would be expected (Fig. 1), which was a particularly large difference for the grass. The presence of *Pilosella* was detrimental to growth of *Dactylis* and *Trifolium*

in both 2- and 3-species combinations. *Pilosella* and *Trifolium* produced the same total yield per pot whether they had grown singly or together (Fig. 2), although the total biomass produced in pots was higher when *Pilosella* had grown in mixtures with *Dactylis* rather than when it had

Table 1 Significant determinants of fertility in the soil used in the pot experiment, with typical ranges in agricultural soils in New Zealand.

Analysis	Units	Concentration	Typical range*
pH [1]	pH Units	6	5.2–6.5
Electrical Conductivity (EC) [2]	mS cm ⁻¹	0.3	0.5–1.8
Nitrate-N [3]	mg L ⁻¹	5	20–80
Ammonium-N [4]	mg L ⁻¹	2	1–20
Phosphorus [5]	mg L ⁻¹	6	5–20
Sulphur [5]	mg L ⁻¹	10	10–20
Potassium [5]	mg L ⁻¹	35	20–80
Calcium [5]	mg L ⁻¹	13	30–70
Magnesium [5]	mg L ⁻¹	12	7–25
Sodium [5]	mg L ⁻¹	14	5–40
Iron [6]	mg L ⁻¹	27.6	20–50
Manganese [6]	mg L ⁻¹	15.6	1–15
Zinc [6]	mg L ⁻¹	1.88	0.3–10.0
Copper [6]	mg L ⁻¹	0.48	0.4–10.0
Boron [6]	mg L ⁻¹	0.11	0.1–0.65

*Typical range for agricultural soils in New Zealand. Method: [1] 1:1.5 (v/v) Water extraction followed by potentiometric pH determination. In-house. [2] 1:1.5 (v/v) Water extraction followed by potentiometric conductivity determination (25°C). In-house. [3] 1:1.5 (v/v) Water extraction followed by Salicylate colorimetry. In house. [4] 1:1.5 (v/v) Water extraction followed by Berthelot colorimetry. In house. [5] 1:1.5 (v/v) Water extraction followed by ICP-OES. In-house. [6] 2 mM DTPA extraction (Australian Standard 3743-1989) followed by ICP-OES. In-house.

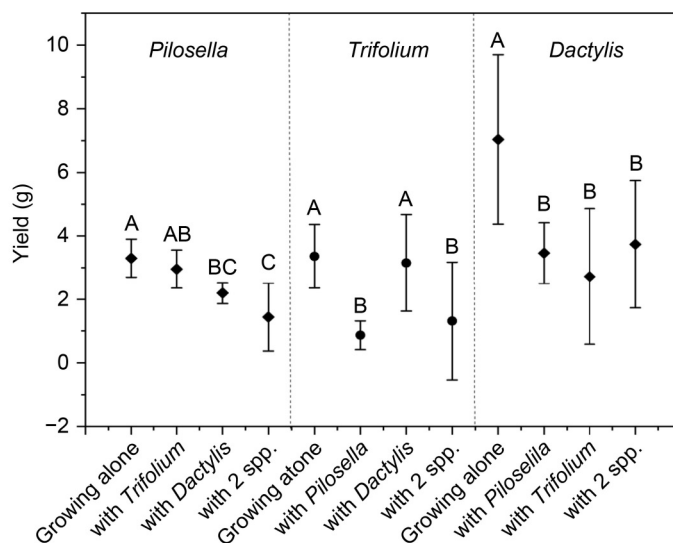


Fig. 1 Individual plant species yields when each species was growing alone or in a mixture with other species. Symbols are means \pm s.d. Letters indicate significant differences ($p < 0.05$) within each block.

grown alone. There were no significant differences in above-ground pot yields in the presence of *Dactylis*, whether it was growing alone or in any combination with other species, although root biomass was lower when this species grew with *Trifolium*.

In each of the three species there were some significant differences in foliar nutrient concentrations when they had grown together with other species (Table 2). *Pilosella* had higher concentrations of Ca and Mg when it had grown with *Trifolium* but lower foliar concentrations of N, P and B when

it had grown with *Dactylis*. *Trifolium* had higher Zn but lower Ca when growing with *Dactylis* than when growing alone, and higher K but less Ca when growing with *Pilosella*. *Dactylis* had more N, and Cu when growing with *Trifolium*.

In terms of mass balance (yield \times nutrient concentration), *Dactylis* and *Trifolium* mixtures procured a larger amount of eight soil nutrients from the soil than when either species was growing alone or with *Pilosella* (Table 3), but this was not significantly different when all three species had grown together.

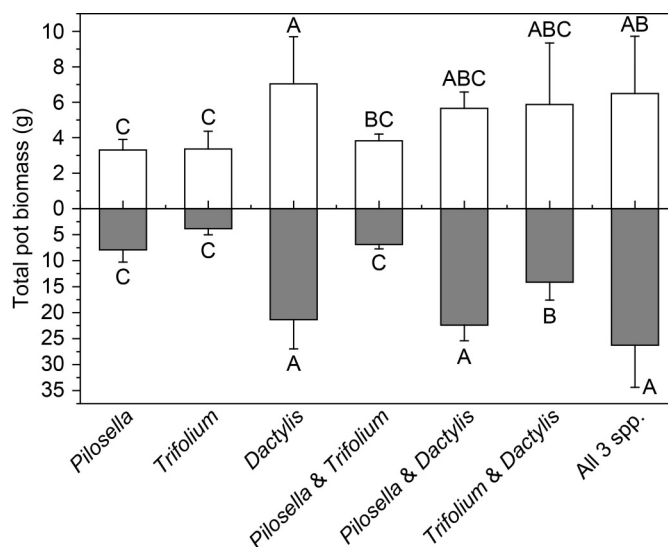


Fig. 2 Total pot biomass (aboveground and underground, $n = 5$). Histogram bars are means + standard deviations. Values are means \pm s.d. Letters showing significant differences ($p < 0.05$) refer to shoots and roots separately.

Table 2 Foliar nutrient concentrations (mg kg^{-1}) in *Pilosella* (A), *Trifolium* (B) and *Dactylis* (C) when each of these species had grown as single species or together with the other species ($n = 5$).

Species/combinations	N (%)	P	K	Ca	Mg	S	Fe	Mn	Zn	Cu	B	Mo	Ni
(A)													
<i>Pilosella</i>	2.06 ^{ab}	4 040 ^a	32 800 ^{ab}	7 300 ^b	2 840 ^b	3 560 ^{ab}	307 ^a	80.8 ^a	46.7 ^a	5.29 ^a	71.1 ^a	0.90 ^{ab}	0.95 ^a
With <i>Trifolium</i>	2.40 ^a	4 150 ^a	37 200 ^a	8 650^a	3 340^a	4 170 ^a	290 ^a	102 ^a	52.8 ^a	4.62 ^a	70.5 ^a	1.22 ^a	0.78 ^a
With <i>Dactylis</i>	1.60^c	3 150^b	29 700 ^b	7 230 ^b	2 790 ^b	3 020 ^b	349 ^a	74.1 ^a	51.5 ^a	5.47 ^a	54.6 ^{ab}	0.64 ^b	0.81 ^a
With 2 spp.	1.84 ^{bc}	2 950^b	34 900 ^{ab}	7 070 ^b	2 800 ^b	3 450 ^{ab}	304 ^a	90.2 ^a	48.3 ^a	4.92 ^a	48.5^b	0.76 ^b	0.79 ^a
(B)													
<i>Trifolium</i>	3.38 ^{ab}	2 770 ^a	28 600 ^b	12 800 ^a	3 720 ^a	3 490 ^b	415 ^a	60.3 ^a	25.5 ^b	4.84 ^{ab}	27.7 ^a	2.66 ^a	0.85 ^a
With <i>Dactylis</i>	3.88 ^a	4 280 ^a	37 700 ^b	13 100 ^a	3 670 ^a	4 650^a	150 ^a	43.6 ^a	32.9^a	4.96 ^a	28.2 ^a	3.58 ^a	0.43^b
With <i>Pilosella</i>	3.05 ^{ab}	3 910 ^a	48 300^a	9 450^b	3 660 ^a	5 020^a	142 ^a	43.8 ^a	30.1 ^{ab}	3.61 ^b	28.1 ^a	4.84 ^a	0.49 ^{ab}
With 2 spp.	2.59 ^b	4 000 ^a	38 400 ^{ab}	12 100 ^a	3 350 ^a	5 170^a	191 ^a	62.3 ^a	29.3 ^{ab}	4.58 ^{ab}	28.7 ^a	2.98 ^a	0.66 ^{ab}
(C)													
<i>Dactylis</i>	0.88 ^b	1 660 ^{ab}	25 700 ^{ab}	2 380 ^a	1 530 ^{ab}	3 260 ^{ab}	95.3 ^a	78.5 ^a	22.9 ^{ab}	3.13 ^b	4.17 ^a	0.89 ^b	0.81 ^a
With <i>Trifolium</i>	1.30^a	2 010 ^a	31 300 ^a	2 350 ^a	1 850 ^{ab}	4 760 ^a	99.9 ^a	90.1 ^a	30.9 ^a	4.68^a	4.41 ^a	2.40^a	0.87 ^a
With <i>Pilosella</i>	1.01 ^{ab}	1 910 ^{ab}	28 800 ^{ab}	2 630 ^a	1 910 ^a	4 430 ^{ab}	83.9 ^a	77.5 ^a	27.5 ^{ab}	4.04 ^{ab}	4.96 ^a	1.77 ^{ab}	1.14 ^a
With 2 spp.	0.97 ^{ab}	1 390 ^b	21 100 ^b	2 050 ^a	1 360 ^b	3 010 ^b	77.8 ^a	65.5 ^a	19.7 ^b	2.83 ^b	10.0 ^a	1.20 ^b	1.17 ^a

Different letters and bold font alphanumeric indicate significant differences ($p < 0.05$).

Table 3 Total pot nutrient uptake (units shown below) into foliage of *Trifolium*, *Dactylis* and *Pilosella* when they were growing either alone or in mixtures with other species ($n = 5$).

Species/combinations	N (g)	P (mg)	K (mg)	Ca (mg)	Mg (mg)	S (mg)	Fe (μ g)	Mn (μ g)	Zn (μ g)	Cu (μ g)	B (μ g)	Mo (μ g)	Ni (μ g)
<i>Pilosella</i>	0.07 ^b	13.0 ^{ab}	108 ^{abc}	24.2 ^{bc}	9.38 ^a	11.8 ^{bc}	1000 ^a	266 ^{bc}	152 ^{ab}	17.3 ^a	242 ^a	3.02 ^b	3.15 ^{bc}
<i>Trifolium</i>	0.11 ^{ab}	8.41 ^b	90.0 ^c	43.7 ^{ab}	12.8 ^a	11.1 ^c	1790 ^a	203 ^c	83.2 ^b	16.1 ^a	90.1 ^{bc}	9.33 ^{ab}	3.19 ^{bc}
<i>Dactylis</i>	0.06 ^b	11.7 ^{ab}	180 ^{ab}	16.1 ^c	10.7 ^a	23.3 ^{abc}	601 ^a	529 ^a	156 ^{ab}	22.1 ^a	28.7 ^c	6.53 ^b	5.55 ^{ab}
<i>Pilosella</i> & <i>Trifolium</i>	0.06 ^b	10.1 ^{ab}	106 ^{bc}	24.2 ^{bc}	9.33 ^a	11.0 ^c	892 ^a	195 ^c	137 ^{ab}	15.0 ^a	144 ^b	5.49 ^b	2.20 ^c
<i>Pilosella</i> & <i>Dactylis</i>	0.07 ^b	13.6 ^{ab}	165 ^{abc}	25.1 ^{bc}	12.8 ^a	22.0 ^{abc}	1080 ^a	443 ^{ab}	207 ^a	25.9 ^a	136 ^b	7.49 ^{ab}	5.92 ^a
<i>Trifolium</i> & <i>Dactylis</i>	0.15^a	16.3^a	195^a	49.1^a	16.4 ^a	25.0^a	684 ^a	371 ^{abc}	182^a	27.3 ^a	102^b	15.6^a	3.20 ^{bc}
All 3 spp.	0.10 ^{ab}	15.0 ^{ab}	181 ^{ab}	36.3 ^{abc}	14.4 ^a	24.0 ^{ab}	1010 ^a	473 ^{ab}	196 ^a	25.9 ^a	138 ^b	9.31 ^{ab}	5.85 ^a

Different letters and bold font alphanumeric indicate significant differences ($p < 0.05$).

4 Discussion

Previous field-based studies in nutrient-poor grasslands have shown that biomass production is enhanced in species-rich swards (Lüscher et al., 2014). Coexistence of grasses and legumes has generally been explained in terms of differing functional traits that provided for better exploitation of light, nutrients and other resources, leading to higher yields than can be achieved by monocultures (Gaëtan et al., 2018). This was not the case in the present study in which interspecific competition was evident; all three species produced higher above ground biomass when growing alone within the confines of the pots. The highest biomass yield was achieved by the grass and in combinations of species that included the grass. However, the results demonstrate the competition for nutrients and the complementary benefits of growing clover and grass together (Fig. 3). Foliar concentrations of various elements were elevated in each of the species when they were growing in combination. It is presumed that the grass acquired N from fixation by the legume (clover root nodulation was observed), but the grass also competed well against *Pilosella* for N, P and B. *Pilosella* clearly had the upper hand in acquiring Ca. The presence of the grass supplied Zn to the legume, as we have demonstrated previously (Zhang et al., 2022b). In terms of mass balance, a larger amount of N and nine other elements were transferred from soil to foliage, and this was often achieved through a smaller root biomass than when clover or grass grew alone.

Mutual facilitation of nutrient procurement between the same species of grass and clover occurs through increased uptake and sharing of trace elements by the grass allows increased nitrogen fixation by the clover (Zhang et al., 2022c). Nyfeler et al. (2011) similarly found stimulatory effects from an accompanying grass on the symbiotic N fixation activity of clover, with acquisition of symbiotic N by the mixture stimulated by the grasses. This is likely to be valuable to legumes which have higher demands than grasses for P and S and other trace elements essential for N fixation, thus

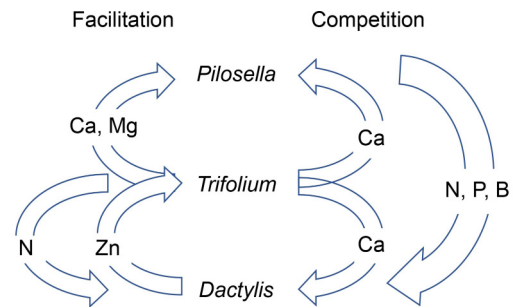


Fig. 3 Facilitation and competition in acquisition of soil nutrients by the three species, based on changes in foliar nutrient concentration when the species grown either alone or combination with the other species (see Table 2).

already creating considerable metabolic demand (Zhang et al., 2022b). Variable herbage concentrations of Ca, Mg and Na associated with graminoid and forb ground cover and different species composition has been recorded in other recent studies reported in this journal (Kajzrová et al., 2022; Kang et al., 2022). Likely mechanistic explanations in grass and clover are discussed in an earlier paper (Zhang et al., 2022a). It is possible that increased Ca (and Mg) recorded in *Pilosella* foliage when it had grown with clover may be due to small changes of pH in the rhizosphere altering mobility of these elements.

There was increased total foliar uptake from the fixed mass of soil of eight nutrients when *Trifolium* and *Dactylis* had grown together (Table 3). This is likely to be a substantial practical significance. Since the 1960s in New Zealand, the role of legumes in agricultural pastures has been displaced by fertilizers, and there has been a continuing decline in the abundance and diversity of forage legumes (Laidlaw, 2014), with an 8-fold increase in N use on dairy farms from 1988 to 1994 (Harris et al., 1996) and a further 3.65-fold increase in N fertiliser sold from 1994 to 2019 (StatsNZ, 2021). In a likely reversal of this trend, it is now widely recognized that a return to increased incorporation of clovers and other legumes into grassland species mixtures will be a critical component of future sustainable agricultural pasture

Table 4 The proportion accounted for by each nutrient of total foliar uptake from the soil that was captured by *Pilosella* in pots containing all three species. *Pilosella* accounted for 22% of biomass yield.

N	P	K	Ca	Mg	S	Fe	Mn	Zn	Cu	B	Mo	Ni
25%	28%	26%	29%	29%	20%	45%	27%	41%	29%	51%	12%	18%

management, with less reliance on urea and ammonia fertilizer (Rubiales et al., 2021). However, the process of nitrogen fixation requires a supply of other key elements, as described above, and mobilising these elements in the rhizosphere appears to be the role of companion grasses through facilitation.

The effects of plants on abiotic (and also biotic) soil components that in turn influence plant performance, is referred to as plant–soil feedback (PSF). Klinerova and Dostal (2020) found PSF reduced differences in competitive ability among 46 plant species. Dostál (2021) showed that nutrient addition attenuated negative PSF. If invasive weeds disrupt the acquisition of nutrients by legumes, as in the present study, there is little possibility of increasing pastoral productivity without the use of fertilisers. The additional presence of *Pilosella* did not alter total uptake (Fig. 3) but this invasive perennial weed is likely to have captured nutrients that otherwise would circulate within the grazing system; prostrate rosettes of *Pilosella* multiply through stolons and can rapidly produce extensive and dense ground cover. This equated to capture of 12% to 51% of the nutrients by *Pilosella* (Table 4). In the case of Zn and B, this is substantially above the 22% accounted for by biomass; these are key elements limiting N fixation and productivity in low fertility grasslands (Zhang et al., 2022b).

In a review of 39 studies of pairs of coexisting plant species, Adler et al. (2018) found that 96% of the studies featured both intraspecific competition and interspecific facilitation. They concluded these are processes that promote stable coexistence. This is likely to be applicable to low-fertility grasslands that are managed for conservation in New Zealand, particularly in the high country. However, the impact of interspecific competition from a recently introduced invasive weed, such as *Pilosella* in the present study, requires further consideration, particularly if its successful establishment is a consequence of environmental change. Grazing mammals were absent from New Zealand until two centuries ago, and their introduction and management has undoubtedly altered soil fertility. It is known that nutrient accumulation in soil due to grazing management can reduce the interspecific competitive ability of native plants and favor the invasion of exotic species (Ba and Facelli, 2022). This has consequences for protection of native species; increasing soil nutrients in combination with invasive competitive species has explained the declining occurrence of plants species in grasslands (Hockendorff et al., 2021).

5 Conclusions

An improved understanding of the impact of coexisting plant species on procurement and management of soil nutrients is clearly required. This represents an opportunity to refine pasture management and also to protect biodiversity in conservation grasslands. Exploiting combinations of plant species that facilitate nitrogen fixation and optimal exploitation of nutrients could reduce fertiliser requirements and enhance and protect biodiversity in pastoral grasslands. In the present study, increased foliar uptake of nutrients when *Trifolium* and *Dactylis* grew together was disrupted in the presence of *Pilosella*. Invasive competitive weeds may disrupt this procurement of key nutrients achieved by facilitation through complementary plant species assemblages. The impact of other biotic and abiotic environmental variables in these processes and of increased soil fertility in nutrient-poor grasslands remains poorly understood.

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Conflicts of interest

The authors declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

Data availability statement

Raw data supporting the findings of this study are available through the website Data@Lincoln. Source data are provided with this paper.

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