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Parasite dilution improves lamb growth more than does the complementarity of forage niches in a mesic pasture grazed by sheep and cattle

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Agroecological practices can improve the functioning of livestock farming systems by optimizing their underlying biological processes. Sheep/cattle mixed-grazing is an example of such a practice in which sheep grazing with cattle can achieve a higher liveweight gain (LWG), than sheep grazing alone. We conducted an experiment to assess the relative roles of parasite dilution and forage niche complementarity in improving sheep LWGs. We used continuous grazing and compared the LWGs of 5- to 9-month ewe lambs, grazing alone or with heifers, at two contrasting sheep/cattle ratios (~50/50% and 20/80% in livestock units). The animals were not treated for strongyles (gastrointestinal parasites) before or during the experiment. We assessed parasitism by counting the number of strongyle eggs excreted per gram of feces (EPG) and evaluated the forage niche complementarity through observations of feeding behavior, combined with measurements of fecal nitrogen content (N). We observed that i) the diet was moderately improved by mixed-grazing (+4% of dicots and +11% of young vegetative grass at most, but these improvement were not statistically significant (resp. P=0.28 and P=0.35); ii) N levels were not significantly different across treatments (~2%; P=0.75); iii) EPGs were ~50% lower for mixed-grazing than for monospecific grazing (545 and 716 vs. 1278, P<0.01), iv) LWGs were much higher for mixed-grazing than for monospecific grazing (~40 g per day higher, P<0.001); and v) LWGs and EPGs did not significantly differ between the two sheep/cattle ratios studied (resp. P=0.91 and P=0.56). We thus attributed most of the improved ewe lamb LWGs in our experiment to parasite dilution rather than to forage niche complementarity. In addition, the similar EPGs and LWGs observed in mixed-grazing suggest that the benefits of this practice can be obtained easily, i.e. over a wide range of sheep/cattle ratios. Based on the definition of the adjective operable ('capable of being put into use, operation or practice'), we also conclude that mixed-grazing seems an operable practice from a biological viewpoint.

KEYWORDS

grassland, health management, strongyle (nematodes), diet selection, diet quality

Introduction

Agroecology offers a promising pathway for producing food in a sustainable manner by optimizing biological processes to reduce chemical inputs (Altieri, 1989). When applied to herbivore production, it promotes grass as the main feed source and assumes that incorporating diversity into livestock systems can improve pasture use (Dumont et al., 2013). Mixed-grazing by sheep and cattle is an example of diversification that has received significant attention over nearly half a century (Arundel and Hamilton, 1975; Nolan and Connolly, 1989; Marley et al., 2006; Jerrentrup et al., 2020). A literature review by d'Alexis et al. (2014) concluded that mixed-grazing by sheep and cattle improved sheep liveweight gains (LWG), compared to sheep monospecific grazing (the advantages for cattle were not significant).

Parasite dilution and the complementary use of forage feeding niches by cattle and sheep are assumed to be the drivers of improved sheep LWGs (d'Alexis et al., 2014). Parasite dilution is the reduction of disease transmission that occurs when several species sensitive to distinct pathogens share the same environment (Keesing et al., 2006; Strauss et al., 2015). The complementary use of forage niches can also contribute to improved sheep performance, as the dietary overlap between sheep and cattle is incomplete. Sheep have a strong preference for legumes and most forb species, while cattle consume higher proportions of grasses (Walker, 1994; Dumont et al., 2011). In mixed-grazing systems, by sharing niches with cattle, sheep can thus focus on legumes and forbs that can be more nutritive than grass. In addition, another form of complementarity comes from the facilitation of sheep grazing by cattle. At moderate stocking densities, cattle can create and maintain short patches of vegetation that are at a young and highly nutritive stage (du Toit and Olff, 2014). Sheep can graze these patches after cattle, which provides them with forage of good quality.

The relative roles of parasite dilution and forage niche complementarity, and the conditions under which improvements occur remain poorly understood (Marley et al., 2006; Fraser et al., 2007). The first reason is that experiments studying mixed-grazing have not systematically quantified the two mechanisms at the same time. A second reason is that the proxies used to study the relative roles of the mechanisms have not always been direct. Parasite dilution has been mostly assessed directly by counting strongyle eggs per gram of feces, which is a direct proxy, but the complementarity of forage niches was frequently assessed through indirect proxies, such as variations in sward height and/or composition (Mahieu and Aumont, 2009; Meisser, 2013; Jerrentrup et al., 2020). These sward parameters describe material that can be potentially grazed by animals rather than the actual sward components that are ingested. In addition, the ways in which the sheep/cattle ratio can modulate the benefits of mixed-grazing are largely unknown, as most field studies have investigated only one ratio. We therefore conducted an experiment built on the overarching hypothesis that LWG can be improved in mixed-grazing through parasite dilution and/or forage niche complementarity. To validate this hypothesis we designed our experiment in order to i) assess the relative effects of parasite dilution and forage niche complementarity on sheep LWGs in sheep/cattle grazing and ii) understand how the sheep/cattle ratio modulates these two mechanisms.

Materials and methods

Experimental design

We conducted our experiment at the INRAE/Herbipôle experimental facility of Laqueuille, located in the uplands of central France (*Massif Central*) (doi:10.15454/1.5572318050 9348E12). The experiment took place during the grazing seasons of 2019 and 2020 from mid-May to late October. We used paddocks located at an altitude of approximately 1200 m, in permanent mesic pastures dominated by grasses such as *Festuca rubra*, *Festuca ovina* and *Anthoxanthum odoratum*. The pastures were fertilized with an average of 27 kg of N (mineral), 22 kg of P_2O_5 and 35 kg of K_2O per hectare in the five years preceding the experiment. The mean annual temperature from 1996–2020 was 8°C, with 1094 mm of precipitation. During summer (July-September), the average temperature from 1996–2020 was 15°C, and the precipitation totaled 298 mm. The summers of 2019 and 2020 were drier and warmer than the 25-year average (1996-2020), with 191 and 202 mm of precipitation in 2019 and 2020 (July-September), respectively, and the mean temperature was 16°C in both years (July-September).

The experimental paddocks were grazed by ewe lambs of the *Romane* breed aged 5–9 months (previously weaned at 68 days in average) and Holstein heifers aged 17–20 months, at the beginning of the grazing season (new animals were used each year). We used continuous grazing even though rotational grazing is best suited to control parasitism (Marley et al., 2007). However, we wanted to assess the efficiency of parasite dilution without other confounding factors. In addition, continuous grazing requires less work than rotational grazing, and it was interesting to test agroecological practices that require a moderate amount of work.

We compared three treatments for which the animals were grazed at the same stocking rate: a monospecific sheep flock and two mixed-grazing treatments, with two replicates each year. The mixed treatments consisted of a balanced sheep/cattle group and a group that was significantly skewed toward cattle (sheep accounting for ~50% and ~20% of livestock units, respectively, see Table 1). The monospecific treatment is referred to as 'Monospecific', the balanced mixed treatment is referred to as 'Mixed-', and the mixed treatment skewed towards cattle is referred to as 'Mixed+'. We did not add a monospecific cattle treatment, as cattle do not significantly benefit from mixed-grazing (d'Alexis et al., 2014). A map of the paddocks used is presented in Figure 1.

TABLE 1 Experimental settings and results.

Item	Treatment[1]			RMSE	*P*-value[2]
	Mono-specific	Mixed-	Mixed+		
Experimental setting					
% sheep in group in livestock units (LU)[3]	100%	45%	22%		
Ewe lambs 5-9 months (heads)	20	10	5		
Adult ewes >12 months (heads)	5	2	1		
Heifers 17-20 months (heads)	0	2	3		
Total livestock number (LU)	2.15	2.2	2.3		
Paddock area (ha)	2.63	2.69	2.81		
Stocking rate (LU/ha)	0.82	0.82	0.82		
Initial liveweight (sheep + cattle) (kg/ha)	437	517	554		
Sheep (kg/ha)	*437*	*203*	*97*		
Cattle (kg/ha)	*0*	*314*	*457*		
Experiment results					
Measurements on animal weight					
Final liveweight[4] (sheep + cattle) (kg/ha)	458[a]	617[b]	650[b]	17.32	<0.001
Sheep (kg/ha)	*458[a]*	*242[b]*	*115[c]*	*11.66*	<0.001
Cattle (kg/ha)[5]	*0*	*375[a]*	*535[b]*	*12.45*	<0.01
Overall liveweight gain per ha (sheep + cattle) (g/day/ha)	124[a]	604[b]	582[b]	108	<0.001
Ewe lamb liveweight gain (g/day)	2.36[a]	41.79[b]	44.40[b]	5.74	<0.001
Cattle liveweight gain (g/day)		498	440	115	0.51
Measurements on strongyle infection					
Ewe lamb strongyle infection (eggs per gram of feces)	1278[a]	716[b]	545[b]	196	<0.01
Cattle strongyle infection (eggs per gram of feces)		24	40	14.84	0.19
Measurements on grazing behavior and diet quality					
Ewe lamb fecal N content (% feces mass)	1.98	1.94	2.01	0.10	0.75
Cattle fecal N content (% feces mass)		1.92	1.85	0.08	0.25
Sward bites mostly containing dicots in observed ewe lamb diets (%)	3.82	7.23	8.49	3.95	0.28
Sward bites indicating patch grazing in observed ewe lamb (%)	24.86	25.02	35.77	11.45	0.35

[1]Monospecific: sheep grazing only, Mixed-: mixed-grazing with balanced sheep/cattle groups, Mixed+: mixed-grazing with cattle main species.
[2]ANOVA P-value of the 'treatment' effect in the linear model using 'treatment' and 'year' as predictors.
[3]Ewe lamb: 0.07 LU, Adult ewe: 0.15 LU, and Heifer: 0.6 LU (Vilain et al., 2008).
[4]Includes a virtual ewe lamb to compensate for the sudden death of an individual in a monospecific replicate in 2019.
[5]Differences evaluated with a Kruskal-Wallis test as condition of variance homogeneity between animal groups was not met. No pairwise post hoc test made as there were only two treatments.
[a-c]Values within a row with different superscripts differ significantly at $P<0.05$.

FIGURE 1
Paddocks and treatments (experiment carried out in 2019 and 2020). Monospecific: sheep grazing only, Mixed-: sheep/cattle grazing with balanced groups, and Mixed+: sheep/cattle grazing with groups skewed toward cattle (detailed compositions in Table 1).

We chose the number of animals to comply with our research questions and protocol, and to balance the stocking rates among treatments (Table 1). We used 5- to 9-month-old ewe lambs even though younger animals may have produced clearer results regarding parasitism, as young animals have less efficient immune systems than older animals (Schallig, 2000). We used these animals as a compromise, as their immune system is not fully developed and they were not too shy to allow observations of foraging behavior. As explained below, we used this type of method and during these observations, the animals must be approached to allow the observer to visually determine which component of the sward is consumed, which cannot be done with animals that are easily scared. The ewe lambs in our experiment were also mixed with some adult ewes to 'train' them to graze, as the adult-offspring relationship is known to improve dietary choices (Orr et al., 1995; Glasser et al., 2009). Regarding cattle, the choice of animal type was driven by convenience, since our experiment focused on sheep. We used Holstein heifers as they did not need milking and represented a low LU per individual, which made it easier to balance the stocking rates among treatments (Table 1).

Animals of both species were not treated against strongyle infections before or during the experiment. We tested their infection levels through counts of strongyle eggs per gram of faeces (EPG), prior to their arrival in the paddocks in May. Prior to the experiment, animals of both species were also weighed to create homogeneous groups relative to weight and EPG, across replicates and treatments. All animals were then weighed monthly to calculate their LWG. Because we wanted to study animal performances over the period of a grazing season, we expressed the LWG values (g/day) as the difference in weight between the end and the beginning of the experiment, divided by the experiment duration in days. All animals were continuously checked, and animals presenting rapid health degradation, strong body condition decreases or difficulties in following the group were removed and replaced in the experiment (two removals took place during the experiment). Besides that, during the whole experiment, animals had water at disposal in paddocks, as well as salt licks without cooper to avoid sheep poisoning.

Assessment of the forage niche complementarity

To assess the effects of forage niche complementarity in mixed-grazing, we conducted observations on grazing behavior. These observations were carried out three times during the grazing season in four-hour sessions (one morning and one evening session). We recorded bites made on the sward by animals, and the bites were classified according to criteria of height, botanical composition (grass, forbs, and legumes) and amount of dry material. Bites containing mostly dicot species, i.e. forbs or legumes, and bites made on short and young vegetative patches, were considered the most interesting from a nutritional viewpoint (Dumont et al., 2011). Observations were made on five 'core' ewe lambs per treatment, which were chosen as representative in terms of weights and EPG at the beginning of the experiment. A total of 60 ewes were studied in this way, which included five ewe lambs per treatment over the three treatments, two replicates and two years (5 X 3 X 2 X 2 = 60). The precise methodology of the behavior observations and the bite typology used are given in the Supplementary Materials.

To further assess whether the diet was improved by mixed-grazing through forage niche complementary, we also used a proxy of forage quality, which is fecal nitrogen content in % of dry mass (N) (Leslie et al., 2008). We measured N for the five 'core' ewe lambs and all heifers, which were less numerous. Measurements began in June and were conducted monthly on ewe lambs, but we only conducted three measurements on heifers because of material constraints, and because our experiment focused on sheep. The measurements on heifers were conducted close to the feeding observation sessions. The methodology of the N assessment is provided in Supplementary Materials.

We assessed the possible confounding effects of herbage allowances on animal grazing through monthly biomass measurements, since allowance differences could have affected feeding behaviors and diet quality. We collected vegetation from six 70x70 cm plots per paddock (one paddock per treatment), which was dried at 60°C for 72 h and then weighed.

Assessment of parasite dilution

To assess parasite dilution, we estimated the levels of gastrointestinal strongyle infections based on EPG, on a monthly basis (in the five 'core' ewes and all heifers which were less numerous). We used the McMaster technique to make these EPG counts, which gave us direct estimations of the infestation levels in each animal.

Statistical analysis

We tested the between-treatment differences through a statistical linear model aiming at explaining the variance of LWG, EPG and N values. These parameters were the response variables to explain according to the treatment and the year as predictors (we integrated the year because of the slight rainfall differences between 2019 and 2020). We tested the mean values of response variables and predictors over our studied months, as we wanted to assess the effect of mixed-grazing at the grazing season scale. We also used the mean values of LWG, EPG and N values according to the group of animals in paddocks, so that our independent statistical unit is the group in the paddock, and not the animal. The model is expressed according to Eq 1.

$$R_{i,j,k} = \mu + T_j + Y_k + \epsilon_i \qquad \text{Eq. 1}$$

Where $R_{i,j,k}$ represents the response variable to study (e.g. LWG, EPG and N) in animal group *i*, submitted to treatment *j* on year *k*. μ represents the mean value of the response variable, T_j and Y_k represent, respectively, the effect of treatment *j* and the effect of year *k*, and ϵ_i is the residual error. We tested the residuals normality through Shapiro–Wilk test and checked the variance homogeneity between treatments with a Bartlett test. We conducted in addition a pairwise *post hoc* Tukey tests according to treatments.

To assess the relative roles of strongyle infection and forage niche complementarity on animal growth, we used also a second linear model in which the LWG was the response variable to explain. The predictors were EPG and faecal N (means over the grazing season and within the group of animals in paddocks). The model is expressed according to Eq 2.

$$LWG_i = \mu_{lwg} + N_i + EPG_i + \epsilon_i \qquad \text{Eq. 2}$$

Where LWG_i represents the mean LWG in animal group *i*, and μ_{lwg} represents the mean LWG over the experiment. N_i, EPG_i and ϵ_i represent, in animal group i, the mean N value, the mean EPG value, and the residual error, respectively. Before running this model, we ensured that EPG and N were not significantly correlated in animals (P=0.17). In this way, we ensured that parasitism had not significantly altered the N-related digestive processes, which could have prevented N from being a reliable proxy of diet quality. This absence of alterations in the digestive processes is further supported by the rare occurrences of diarrhea observed during the experiment.

The analyses were performed with RStudio 1.1.463.

Results

Liveweight gain, parasitism and grazing

The liveweight of ewe lambs in all treatments increased from May until August or September, and then slightly decreased (Figure 2). The maximum and final weights differed according to treatments, with ewe lambs in the mixed-grazing treatments having higher final weights (P<0.001) (Figure 2). As a result, the LWGs over the grazing season are significantly higher for mixed than for monospecific treatments (P<0.001) (Table 1). *Post hoc* Tukey tests indicated that there were no significant differences between the Mixed- and Mixed + treatments (P=0.91). The mean LWG of ewe lambs was close to 0 in the monospecific treatment, as their final weights were only slightly higher than their initial weights, whereas the LWGs for the two mixed-grazing treatments averaged ~43 g/day. At the paddock scale

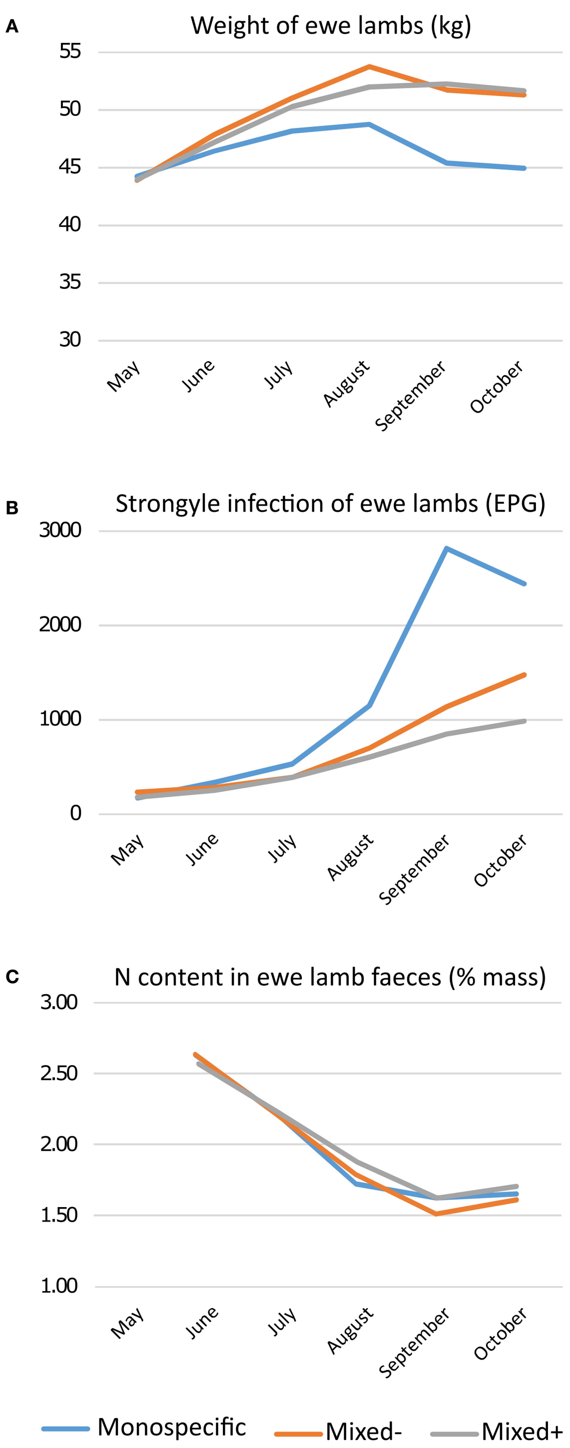

FIGURE 2
Mean values of the parameters measured during our experiment. Weights **(A)** of all animals were measured. EPG (eggs per gram of faeces) **(B)** and N (Nitrogen content) **(C)** were measured on the core animals (except in May for EPG that were measured on all animals to constitute homogeneous groups in each treatment). See the text and Table 1 for the number of animals involved.

(i.e., accounting for the sum of sheep and cattle), the LWGs per ha were significantly higher in the mixed than in the monospecific treatments (P<0.001), without significant differences between the mixed treatments (P=0.95).

Regarding parasitism of ewe lambs, in the mixed treatments the EPG increased steadily from May until October and the monospecific treatment, the EPG increased steadily until September, and then slightly decreased (Figure 2). The average EPG levels over the season were significantly higher in the monospecific than in the mixed treatments (P<0.01), and *post hoc* Tukey tests indicated that there were no significant differences between the mixed treatments (P=0.56).

Fecal N levels of ewe lambs decreased from the beginning to the end of the grazing season, indicating a decrease in quality of the selected diet, with all treatments following the same trend (Figure 2). At the grazing season scale, there were no significant differences among treatments (P=0.75). During the observation sessions of grazing behavior, we recorded 4995 sheep bites and over the whole grazing season, bites made on short vegetative patches accounted for 25% of the total bites in the Monospecific and Mixed- treatments, and 36% of the total number of bites in the Mixed+ treatment. However, these differences were not statistically significant (P=0.35) (Table 1 - seasonal differences are provided in Supplementary Table S3). The bites made on dicots accounted for 4, 7 and 8% of the total bites in Monospecific, Mixed- and Mixed+ treatments, respectively (seasonal differences in Supplementary Materials), but these differences were not statistically significant (P=0.28). Despite these differences, as mentioned above, fecal N was stable across treatments (Table 1). We also found that the mean standing vegetation biomass was 1.39 tons DM/ha over the grazing season, with no differences among treatments (P=0.78). We thus considered that our observations of sheep grazing behaviors and fecal N levels were unaffected by any confounding effects of differences in herbage allowance.

No significant differences in cattle LWG or EPG and N content of feces were observed between the Mixed- and Mixed+ treatments (in which cattle were present) (Table 1). The mean values of cattle LWG (440 and 498 g/day) were close to those observed for this type of animal fed on pasture (500 g/day (Fidloc Conseil Elevage, 2004)). This indicates that no forage allowance limitations took place for the animals during the experiment in the treatments, which were all grazed at the same stocking rate. We thus considered that our LWG results were unaffected by any confounding effects of lack of forage.

Relative contributions of parasite dilution and foraging mechanisms to liveweight gain

Our statistical model for LWG indicates that EPG as a predictor is significant (P<0.01) whereas N is not (P=0.89).

The value of the estimate of EPG as a predictor is -0.046 indicating that EPG is negatively correlated to LWG.

Discussion

Relative contributions of forage and parasitism mechanisms

The first objective of our experiment was to assess the relative contributions of forage niche complementarity and parasite dilution to the improved LWGs of ewe lambs under mixed-grazing. As reviewed by d'Alexis et al. (2014), mixed-grazing by sheep and cattle led to higher sheep LWGs and improved system performance (i.e. sum of the LWGs of sheep and cattle per hectare). Our results for feeding behaviors indicate moderate and non-statistically significant improvements in diet quality, as assessed by the modest increase in dicot and young vegetative grass contents, in mixed compared to monospecific grazing (at most +4% and +11%, respectively). Our results thus indicate that mixed-grazing may have benefited sheep through an easier selection of favorable forage niches, but this improvement was not reflected in fecal N, our proxy of diet quality. This can be explained by the limited size of our dataset and the constraints of the feeding behavior observations that could not be conducted all day. This is a limitation of the method, as sheep are able to modulate their grazing time according to sward quality (Garcia et al., 2003). Observations should thus be conducted at all times sheep eat, which is very difficult to implement. Therefore, by combining our results of fecal N and grazing observations and considering their limits, we consider that there may have been a moderate facilitation of grazing in the mixed treatments, which was anyhow not sufficient to significantly, and importantly, improve the diet of ewe lambs. In contrast, our results indicate a significant and strong effect of the treatments on the levels of strongyle infection, which were ~50% lower under mixed-grazing than under monospecific grazing. This clear and important effect is reflected in the ewe lamb LWGs, which were much higher in the mixed treatments than in the monospecific treatment (~+40 g/day). Based on these comparisons and the results of the LWG statistical model, we thus attribute more importance to parasite dilution than to forage niche complementarity, in the improvement of ewe lamb LWGs in our experiment.

The differences of contribution of parasite dilution and forage niche complementarity to improve LWG in mixed-grazing can be explained by the more or less important metabolic gains obtained from these mechanisms. The parasitic load of strongyle has a cost in terms of metabolizable energy and protein (Méndez-Ortíz et al., 2019), and reduction of this load through parasite dilution can provide a metabolic gain. This gain can in turn benefit LWG. Similarly, an effective forage niche complementarity can improve the quality of ingested vegetation which can produce gains in metabolizable energy and protein (INRA, 2018). These gains can benefit LWG as well. As our results attributed most of the variance in LWG to parasite dilution, we think that the improved liveweight gains in mixed-grazing we observed mostly result from the reduced metabolic burden of parasitism.

The second objective of our experiment was to assess the difficulty in implementing sheep/cattle mixed-grazing. We focused on the difficulty in defining an appropriate species composition and compared two distinct sheep/cattle ratios. We thus did not address the technical difficulties regarding fences and housing to manage two species under mixed-grazing, compared to one species under monospecific grazing. From a group composition perspective, we observed that the benefits of mixed-grazing were not significantly different when sheep and cattle equally contributed to the total livestock units or when the group was skewed towards cattle (no significant differences between Mixed- and Mixed+). These benefits were substantial, as we obtained an LWG of ~43 g/day, which is close to the usual LWG for this breed and weight class (50 g/day for 50 kg animals (OS Romane, 2021)). We thus obtained a usual performance for this breed without using anti-parasite treatments under continuous grazing. These benefits of continuous mixed-grazing with cattle as an alternative for controlling nematode infections in grazing sheep are of particular interest since i) decreasing the use of chemical drugs reduces environmental side effects, ii) chemical solutions are becoming increasingly less efficient due to emerging resistance (Traversa and von Samson-Himmelstjerna, 2016) and iii) the agricultural workforce is becoming increasingly scarce (Conway et al., 2019). These benefits of mixed-grazing were obtained in a herd consisting of ~80% cattle or a herd with ~50% cattle, i.e., over a wide range of sheep/cattle ratios. This result indicates that no fine-tuning of the sheep/cattle ratio was required to obtain the benefits from mixed-grazing. This result suggests that obtaining satisfactory animal performance through mixed-grazing without drug treatments does not seem to be an overly difficult problem in terms of decision-making, regarding group composition.

Comparisons with other studies

Our results attribute more weight to parasite dilution than to forage niche complementarity for improving sheep performance, and these results are consistent with the few previous studies that integrated both aspects. Some experiments did not attribute a higher weight to one of the two mechanisms (Mahieu et al., 1997; Moss et al., 1998; Marley et al., 2006; Fraser et al., 2007), but these studies used anthelmintic treatments, which must have prevented the effects of parasitism from being fully expressed. Mahieu and Aumont (2009) and Meisser (2013) rather attributed improved sheep performance to parasitism dilution and not to foraging mechanisms. None of the above studies thus demonstrated a clear effect of forage processes and rather attributed the gains in sheep performance to reduced parasitism. This lack of a clear foraging effect is also consistent with a recent experiment conducted in Germany, in which the LWGs of mixed sheep/cattle groups were not higher on diverse swards than on grass-dominated swards (Jerrentrup et al., 2020). This suggests that the complementary use of forage niches by sheep and cattle is not automatically obtained in mixed-grazing. Overall, the studies that assessed the contributions of both mechanisms thus seem to attribute more weight to parasite dilution than to forage niche complementarity, and our results are consistent with these findings. Again, the ability of sheep to adjust its foraging behavior could explain these results because this species can adjust to sward quality through selective grazing (Garcia et al., 2003), but it may not be able to adjust to strongyle infection with the same efficiency (especially young animals with immature immune systems).

Our results also suggest that fine-tuning the sheep/cattle ratio is not needed to obtain the benefits of mixed-grazing, as sheep LWGs were not significantly different among the two contrasting sheep/cattle ratios that we used. It would be interesting to confirm this result with more replicates and larger flocks than those we used in our experiment (especially in the Mixed+ treatment where we had only 5 lamb ewes). However, this observation is consistent with two previous works that studied several group compositions. Nolan and Connolly (1989) experimentally compared several sheep/cattle ratios, ranging from 2 to 6.9 ewes per steer, and built regression models showing that the LWG per ha of mixed groups can be maximal, or close to maximal, over a wide range of sheep/cattle ratios. The literature review of d'Alexis et al. (2014) confirmed these results, and both studies indicate that herds that are roughly balanced in terms of LU between species deliver optimal or quasi-optimal LWG per ha. These studies together with ours thus indicate that mixed-grazing does not seem to require fine-tuning of the sheep/cattle ratio, which eases its implementation. This result illustrates that parasite dilution, which was the biological backbone of mixed-grazing in our study, is compatible with a practical implementation of this type of agroecological grazing. In other words, based on the definition of the adjective operable ('capable of being put into use, operation or practice'), mixed-grazing seems a 'biologically operable' practice (*sensu* Joly et al. (2021)).

Conclusion

The improvements in sheep growth under sheep/cattle mixed grazing compared to sheep monospecific grazing have been extensively studied over the last decades. However, the relative contributions of parasite dilution and forage complementarity or facilitation to these improvements remain poorly understood. Under our conditions of continuous grazing of a mesic pasture dominated by grasses, most sheep liveweight gains were attributed to parasite dilution, which is the first outcome of this research. This outcome was obtained through the use of methodologies that directly studied sheep grazing, based on both direct observations and fecal nitrogen, which is an originality of our study.

We also compared two contrasting sheep/cattle ratios to determine whether, and to which extent, these ratios could modulate the benefits of parasite dilution. We observed that fine-tuning the ratio was not obligatorily needed, and we consider that this characteristics contributes to the biological operability of sheep/cattle mixed-grazing. Our study thus suggests that agroecological practices are not necessarily complex to implement from a biological viewpoint, which is the second outcome of this research.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: INRAE repository https://doi.org/10.15454/S7P0HG.

Ethics statement

Ethical review and approval was not required because our study concerned grazing animals that were not exposed to invasive treatments. According to the French law, this absence of invasive treatment makes ethic approval unneeded.

Author contributions

FJ: Conceptualization, Project administration, Writing - Original Draft, Formal analysis, Visualization; PN: Project administration; Writing - Review and Editing; MBa: Project administration; PJ: Methodology, Writing - Review and Editing; SF: Methodology; MBe: Conceptualization, Writing - Review and Editing; BD: Project administration, Conceptualization, Writing - Review and Editing, Methodology. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fanim.2022.997815/full#supplementary-material

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