



Original article

Can sowing density facilitate a higher level of forb abundance, biomass, and richness in urban, perennial “wildflower” meadows?

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ABSTRACT

Forb species abundance and richness determine both ecological and social values in naturalistic meadows in urban landscapes. However, species loss and dominance through competition are naturally part of meadow ecological processes often leading on productive soils to large grass biomass in the absence of appropriate management. Sowing density is a design tool to manipulate the initial number of emergents of each component species however high sowing densities may not benefit community performance in terms of species richness and diversity in the longer term. This study investigated the effect of sowing density on forb species abundance, biomass and richness. Two sowing densities approximating to 500 and 1,000 emerged seedlings/m² were employed with 29 forb and one grass species. The higher sowing density did not lead to a larger grass biomass that dominated the community, as the grass species used was ultimately less competitive than the forb dominants. Increasing sowing density increased the number of forb seedlings initially but this declined, as did species richness in the longer term. In terms of subordinate forb survival, ability to access light resources to survive intense competition from dominants was key. Tall, and native species were more likely to maintain higher seedling numbers in the longer term. The research suggest that lower sowing rates are likely to be most useful on soils which are either unproductive, do not contain a significant weed seed banks, where weed free sowing mulches are employed or in rural situations where there is less immediate political pressure for rapid development of forb rich meadows.

1. Introduction

Naturalistic meadows, inspired by the complexity of more natural meadow communities, have become fashionable as an alternative to conventional mown grasslands for landscape designers in both Western and Eastern countries (Hitchmough and Dunnett, 2004; Jiang and Yuan, 2017). This approach has potential to improve ecological as well as social value, which is of equal importance for sustainable urban landscapes (Özgüner et al., 2007; Hicks et al., 2016; Southon et al., 2018). Within this context, forb species richness (the number of species per unit area) becomes extremely critical not only to support a diversity of pollinators (Potts et al., 2009; Hicks et al., 2016) but also to deliver aesthetic benefits to the public (Hoyle et al., 2018). Highly flowery, meadow communities rich in forb species have been shown to be one of the greenspace types most appreciated by the public (Southon et al., 2017; Hoyle et al., 2018).

Despite the evidence that urban publics are becoming increasingly

biocentric, social acceptance and social sustainability may largely depend on the clarity of the cues for ecological value (Linde-mann-Matthies et al., 2010; Garbuzov et al., 2015; Hoyle et al., 2017a, 2017b). To adequately deliver these essential cues (Nassauer, 1995; Hoyle et al., 2017a), a good level of forb species coexistence in the longer term is required in meadow communities. It also requires individuals of forb species to have sufficient biomass to have significant floral visual impact, rather than be present as subordinates. The key challenge is that species loss and dominance through intra and inter specific competition is however naturally part of meadow ecological processes (Grime, 2002) and in the absence of appropriate management leads to vegetation (on productive soils) dominated by relatively few species, often mostly grasses. On this basis Bjørn et al. (2016) have proposed that species diverse forb dominated designed vegetation is an illusion in the longer term. This raises the question that can the starting point of meadow creation have any impact on longer term drift to dominance by a few species?

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Sowing as a technique plays a critical role in meadow creation, as it is the tool by which plant initial density in a designed community can be manipulated, potentially assisting with managing competition from invading weeds and achieving desired visual effects from an early stage (Hitchmough and de la Fleur, 2006; Hitchmough, 2017b). It also enables designed meadow communities to be established at large scales with relatively low initial resource input (Dunnnett and Hitchmough, 2004). The sowing process does however require understanding of how effectively the decisions made in this process, and specifically the number of seeds of each species placed into the germination environment, affect the outcome in the short and intermediate term. Sowing density usually refers to the quantity of seeds sown into a unit of area.

Sowing density directly affects the number of initial emergents of each species and the dynamics of intra and inter species competition from the outset. A high density of seedlings increases the competition between leaves and shoots of individual plants for light especially where water and nutrient are abundant (Grime, 2002; Köppler and Hitchmough, 2015). Increasing sowing rate has been used in agriculture as a non-herbicidal means to reduce weed establishment via rapid closure of plant canopies in annual monocultures (Andrew and Storkey, 2017). A higher sowing density can effectively compensate for the problem of low viability seeds (James et al., 2011); and it can also create the desired meadow effect more quickly (Stevenson et al., 1995; Hulvey and Aigner, 2014; Barr et al., 2017). In the longer term (i.e., after four years), Lubin et al. (2019) found that doubling sowing density was still effective in increasing the cover ratio of sown species to spontaneous species and decreasing species diversity of the latter.

However, Nemec et al. (2013) found that the effects of sowing density were diminished after three years with no significant effect on both desired species and weed cover values. This was probably because that this experimental site was highly productive. There will always be a productivity threshold beyond which increasing sowing density ceases to improve desired species establishment in the longer term (Stevenson et al., 1995; Burton et al., 2006). Where conditions naturally support species richness, i.e., where the soil is relatively unproductive or weed seedling density low, increasing sowing density will also become less effective (Stevenson et al., 1995; Scotton, 2019).

Del-Val and Crawley (2005) and Dickson and Busby (2009) suggested grass competition from either spontaneous or sown grass seedlings is likely to override the original design mix, and suppresses the performance of the forb community. Climates such as the UK favour grass dominance especially on productive soil conditions (Pywell et al., 2003; Walker et al., 2004). Grass species usually have advantages over forbs in terms of abundant seedling recruited from soil seed banks (Edwards and Crawley, 1999), high seedling survival (Hitchmough et al., 2001; Jurado and Westoby, 2006; Ben-Hur and Kadmon, 2015), rapid seedling growth rate (Campbell et al., 1991; Hitchmough et al., 2001), tolerance of grazing or cutting (Pywell et al., 2003) and reduced palatability to molluscs (Edwards and Crawley, 1999; Wilby and Brown, 2001; Del-Val and Crawley, 2005).

When grasses are left out of sowing mixes to try to slow down the process of forb elimination, weed invasion tends to be problematic, leading to a parallel decline in desired forb species richness and biomass irrespective to forb sowing density (Dickson and Busby, 2009; Nemec et al., 2013). Thus, there is a dilemma as to whether it is better to include grasses in order to manage spontaneous weeds from the soil seed bank or to leave grasses out and increase forb sowing density to try to better compete with weeds. Most findings from ecological studies, which mostly work with existing vegetation in rural environments, reflect a condition in which scale and resources restrict the capacity to manage site and sowing operations to maximise success from the beginning. Aesthetic outcomes are also a low priority in these studies.

In urban landscape architecture works, which mostly aim to create communities in a relatively smaller scale, there are more resources available than ecological restorations in rural environments for site preparation, design and management, increasing the likelihood of forb

dominated communities persisting in the longer term (Hitchmough, 2017a). The starting point can be more controlled through, for example, stripping off topsoil or sowing into a low productivity mineral mulch layer to greatly reduce the establishment of spontaneous weeds and grass competition (Hitchmough et al., 2004; Hitchmough, 2017a). Plant communities can be designed to utilise different canopy layers and species composition to maximise cover and competitiveness with invading grasses (Hitchmough, 2009; Hitchmough et al., 2017). Weed management can be utilised at critical phases to reduce the development of dominance by undesired species. Within the category of urban landscape design, sowing density, as a gradient, from very high to very low, can be used as a tool to try to achieve the most desirable outcomes for meadow communities given other environmental and management factors. Greater levels of control may allow a relatively low density sowing mix to be sustainable and yet also reduce competitive dominance within the sown vegetation. However, this may delay the delivery of visual benefits which may potentially undermine social support for the meadow.

Previous urban meadow studies based in Sheffield, north England, show that higher sowing densities can deliver aesthetic benefit sooner given sufficient longer-term management (Hitchmough and de la Fleur, 2006). Without this management, high sowing density often leads to a dominance by a few competitive sown or spontaneous species (Hitchmough and Wagner, 2013; Hitchmough et al., 2017). Many studies in urban landscape contexts have mostly involved tall productive forb-only communities or those with minimal grass within the sowing mix. Much less is known about the dynamics of forbs and grasses within urban meadows.

This study explored how two sowing densities of both grasses and forbs under urban conditions affected longer term retention (i.e., over a three-year experiment period) of forbs within sown communities of Western Europe and Inner Mongolian species, many species of which are naturally co-distributed in both of these geographical regions. The theoretic position underpinning the research is the widely observed ecological paradox that as seedling density increases post a disturbance event, finite resource availability inevitably leads (particularly on productive soils) to self-thinning, i.e. increased mortality (Morris and Myerscough, 1991; Burton et al., 2006; Frances et al., 2010; Klimek-Kopyra et al., 2020), and that this mortality is not evenly spread across the community but is asymmetric, i.e. impacting least on the species that have the best capacity to compete for the key resources and most on the species that do not (Stevenson et al., 1995; Lawson et al., 2004; Dickson and Busby, 2009; Jaksetic et al., 2017). As a result we explored three core research questions in this study i) does increasing sowing density inevitably accelerate sown grasses eliminating sown forbs? ii) to what extent can initial sowing density influence forb performance in terms of forb abundance, richness and biomass? iii) which subordinate forb species tend to gain advantages in terms of number of seedlings and biomass in the higher sowing density and vice versa?

2. Methods

The field experiment was conducted from May 2017 to August 2019, three growing years, at Manor Top (53°37'82"N 1°43'51"W), Sheffield, UK, on a west facing slope previously used for cultivation with a highly productive clay loam topsoil. Soil nutrient analysis was not available for the site, however as biomass harvesting was a key part of the research methodology and provided a more meaningful measure of potential productivity. Typical peak standing shoot biomass was in the region of 1200 g/m², which corresponds to the upper levels possible in non-wetland sites in both Inner Mongolia, China and Britain (Ni, 2004; Qi et al., 2018). Highly productive soils are common in urban areas and the site represented a worst-case scenario in terms of likely competitive dominance.

Ground preparation work took place in March 2017 to control perennial rhizomatous grasses (herbicide applied twice) and cultivating

the ground. Experimental plots and the sand substrate were installed in May 2017, and the seed mixes were sown in the 23rd May 2017. Sharp sand was used as a “sowing mulch” (see Hitchmough, 2017a) substrate to restrict weed emergence from the soil seed bank and to achieve a high percentage emergence and lower potential productivity in the immediate rooting environment. Sand is often used in urban meadow sowings in practice for these reasons (Hitchmough, 2017a).

The field experiment employed a fully randomised factorial design involving a total of 96 experimental plots. The factorial design and experimental procedures used were similar to that employed by other workers exploring competitive interactions between forbs and grasses in mixed communities, for example; Del Val and Crawley (2005) and Dickson and Busby (2009). In this paper only the effect of sowing density and relevant interactions, rather than the full set of experimental factors, are discussed. Two sowing densities, calculated to achieve approximately 500 or 1000 emerged seedlings/m² were used within the 1 × 1 m plots. These rates are relatively high but were used to ensure that at the various ratios of grasses to forbs present in the study (1:9, 1:1 and 9:1), there would be sufficient minimum numbers of seedlings of all species to analyse. All plots were separated by 1 m wide (downslope) and 0.5 m wide (across slope) weed mat covered cross paths.

Within the communities sown into each plot, there were three categories of forb canopy height (low; medium; tall) to test the significance of light competition and to create meadow communities that were likely to be appealing to people in urban environments. Using the methodology devised by Hitchmough (2017a) seed weight and seed emergence data were used to calculate the amount of seed necessary per plot to arrive at a target number of seedlings per m² (see Table 1). The ratio of emerged seedlings designed into each layer (low: medium; tall) was 4:2:1. This ratio was to reduce the impact of taller species on shorter species in terms of light competition and dominance. These approaches are most effective in practice at ratios > 20:10:1 (Hitchmough, 2017a). These latter ratios could not be used in the experiment because on small plots they require either excessively high overall sowing densities or acceptance of the absence of some species.

The meadow species used in the study involved 15 species which are currently distributed in meadows in both the UK and Inner Mongolia and 14 species only found in Inner Mongolia. The study was designed as two-site research with the experiments replicated in the UK and Inner Mongolia, however due to problems of site management in Inner Mongolia data was not ultimately available from the latter. All forbs were selected based on three criteria of ecological feasibility to the UK environment (a history of cultivation), attractiveness for urban landscape (the appearance and robustness), and availability from commercial suppliers (species selection procedure is shown in Fig. 1). Species are listed in Table 1. *Deschampsia cespitosa* was used as the competitor grass because of its wide distribution in both the UK and Inner Mongolia and its tussock form and capacity to remain structurally intact post flowering. The viability to emerge and establish in cultivations under UK climate conditions were tested in Hitchmough (2010, 2017a).

Species that could not be established from a late spring sowing without winter chilling (*Aconitum carmichaelii*, *Angelica sylvestris* and *Stachys officinalis*) were sown in seed trays and transplanted into the plots according to designed seedling numbers in late November 2017. Due to insufficient seedlings of *Aconitum carmichaelii* and *Angelica sylvestris*, seedling density of these two species were below the designed seedling number.

2.1. Experiment management and data recording

As late spring sowing can lead to low species emergence and establishment due to high temperatures and moisture stress, hessian was stretched over each plot to create approximately 50% shade. Plots were initially irrigated every two days in the absence of rain.

The first year of the experiment was used to establish the communities with data collection (not reported in this paper) commencing two

Table 1

Target numbers of forbs and grasses used in the experiment.

(a) Forb species			Target Seedlings/m ²	
		Species	Low sowing density	High sowing density
Low canopy	Shared	<i>Anemone sylvestris</i>	14	29
		<i>Galium verum</i>	14	29
		<i>Potentilla rupestris</i>	14	29
		<i>Pulsatilla vulgaris</i>	14	29
		<i>Veronica teucrium</i>	14	29
	Mongolian	<i>Dracocephalum rupestre</i>	14	29
		<i>Dracocephalum ruyschiana</i>	14	29
		<i>Thalictrum petaloideum</i>	14	29
		<i>Thermopsis lanceolata</i>	14	29
		<i>Veronica incana</i>	14	29
Medium canopy	Shared	<i>Achillea millefolium</i>	7	14
		<i>Campanula glomerata</i> ^a	7	14
		<i>Origanum vulgare</i>	7	14
		<i>Polemonium caeruleum</i>	7	14
		<i>Stachys officinalis</i>	7	14
	Mongolian	<i>Campanula punctata</i>	7	14
		<i>Delphinium grandiflorum</i>	7	14
		<i>Kalimeris incisa</i>	7	14
		<i>Platycodon grandiflorus</i>	7	14
		<i>Scutellaria baicalensis</i>	7	14
Tall canopy	Shared	<i>Echinops ritro</i>	4	7
		<i>Geranium pratense</i>	4	7
		<i>Sanguisorba officinalis</i>	4	7
		<i>Thalictrum aquilegifolium</i>	4	7
		<i>Veronica longifolia</i>	4	7
	Mongolian	<i>Aconitum carmichaelii</i>	5	9
		<i>Angelica sylvestris</i>	5	9
		<i>Echinops sphaerocephalus</i>	5	9
		<i>Patrinia scabiosifolia</i>	5	9
(b) Grass species				
<i>Deschampsia cespitosa</i>	250	500		

^a Data for *Campanula glomerata* not included in results due to poor emergence (close to zero) in experimental trials

months after the first seedling emergences in June 2017. To retain sown community richness and achieve a relatively uniform starting point for the longer term study, plots were mown (at 50 mm) approximately every 10 days within summer to disadvantage the largest and fastest seedling (mainly *Achillea millefolium*, *Echinops ritro*, *Echinops sphaerocephalus*, *Geranium pratense* and *Deschampsia cespitosa*) and reduce early dominance. This is a standard technique used in landscape practice (Du Gard Pasley, 1990; Schmidthals, and Kühn, 2014). Seedling numbers of *A. millefolium*, *E. ritro* and *E. sphaerocephalus* were then thinned down by hand to the designed seedling numbers. Biomass harvesting of both all species and individual species was used as mean to assess competitive behaviour of species in experimental communities, in line with other research in this field (e.g., Davies et al., 1999; Del Val and Crawley, 2005; Bjørn et al., 2019).

Plots were manually irrigated 3 times in summer 2018 (Met Office,

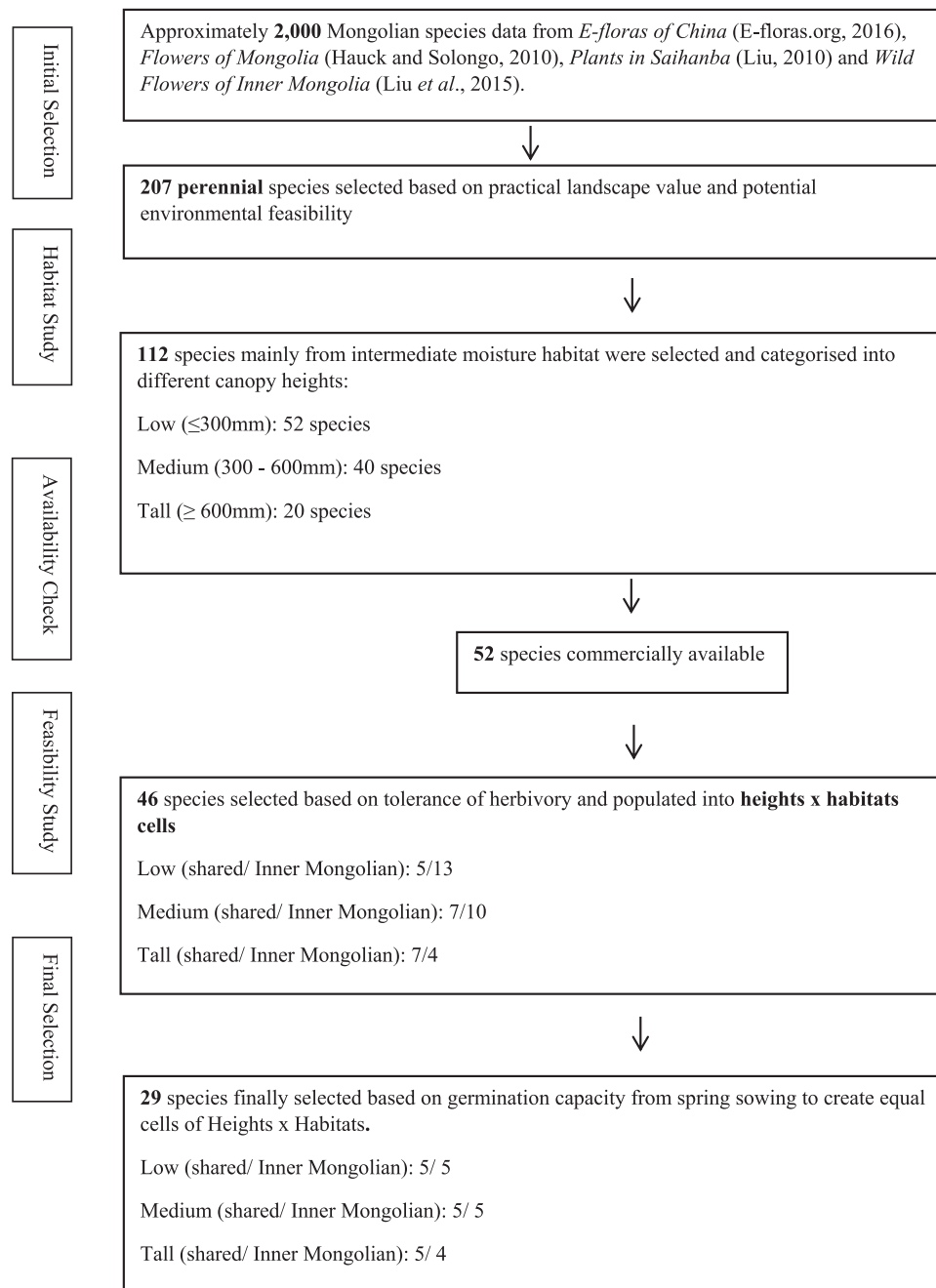


Fig. 1. Forb species selection procedure (E-floras.org, 2016; Hauck and Solongo, 2010; Liu, 2010; Liu et al., 2015).

2018), which was extraordinarily hot and dry. Tall ruderal weed seedlings were removed prior to the commencement of the study in spring 2018. Meadow cutback to about 20 mm above the ground was undertaken prior to the commencement of growth in February 2018. The same practice was applied in August and the cut material was sorted, dried, and weighed to generate biomass data to reflect standard meadow management in practice.

Data was collected from an 800×800 mm permanent quadrat placed in the centre of each plot approximately one year post the first seedling emergents. In April 2018 and 2019, forb seedling numbers present in each plot were counted for each species. Forb and grass cover values in each plot were measured in May in both years. Biomass for each species was collected in August 2018 and 2019. The biomass samples were placed in a drying cabinet at 75 °C for 24 h and left for another 24 h before weighing to achieve some consistency between weighing as

weight increased quickly in the first few hours when moisture from the air was absorbed.

2.2. Statistical analysis

The statistical tests were undertaken with SPSS version 26. Generalized Estimating Equations (the GEEs) were applied to build the 2-level factorial models (i.e. the model tests with all possible 2-factor interactive combination), which included all four designed factors and 'Year' (i.e. to represent the data difference between 2018 and 2019 as Within-subject Variable). Sequential Sidak correction was applied for the comparison of estimated means to obtain the significance levels.

The accumulated biomass data and cover value data in each plot were analysed with the Linear model type within the GEEs, where the tests were valid regarding the standardised residuals and the data size.

Seedling number data were treated as 'counts' and were analysed with Poisson Loglinear type models.

To meet the assumption of data distribution and validate the tests, other model types within the GEEs were applied and data were transformed to optimise normality. Due to the different intrinsic size of species there was a need to standardize the scores. To test the difference of forb biomass between the treatments or years, the mean and standard deviation for each species were calculated as a best guess at the normative behaviour of the species. To standardize the raw scores, the following equation was used to obtain the z-score;

$$Z_{\text{biomass}} = (\text{Sample biomass} - \text{Mean biomass/ species}) / \text{Standard Deviation biomass/ species}$$

This reduced the direct effect of the factor species but still allowed assessment of interaction with respect to species.

3. Results

3.1. Effect of sowing density on forb seedling numbers, forb and grass biomass and cover values in 2018 and 2019

As shown in Fig. 2, high sowing density led to significantly more forb seedlings in both April 2018 ($p = 0.000$) and 2019 ($p = 0.000$) but did not double forb seedling number. The difference of forb seedling number between low and high sowing density had diminished by 2019.

In terms of forb biomass, the high sowing density did not double this but did lead to significantly more forb biomass ($p = 0.015$) in August 2018 (Fig. 3). There was no significant difference by 2019 ($p = 0.710$). This pattern was also reflected in coverage measurements in April for these two years (Fig. 4). There was a significant decrease of forb seedling numbers across this time period in both sowing densities ($p = 0.000$). Mortality was higher in the high sowing density (47.4%) than the low sowing density (40.6%) between 2018 and 2019. In 2018, High density sowings of *Deschampsia cespitosa* supported significantly more forb biomass (1003.40 g), than the low density grass treatment (666.29 g, $p = 0.006$).

In terms of grass biomass, the low sowing density treatment had higher but not significantly higher grass biomass in 2018 ($p = 0.401$). In 2019 grass biomass became significantly ($p = 0.002$) greater in the low sowing density treatment, suggesting the forb dominants were out-competing the grasses. Forb biomass was significantly higher than grass biomass in both sowing densities and both years ($p = 0.000$).

The higher sowing density led to a significantly higher forb ($p = 0.000$) cover value in 2018 (Fig. 4), but this did not increase grass coverage ($p = 0.960$). In 2019, despite forb coverage appearing higher in the high sowing density while grass coverage was higher in the low sowing density treatment, these treatments had no significant effect on

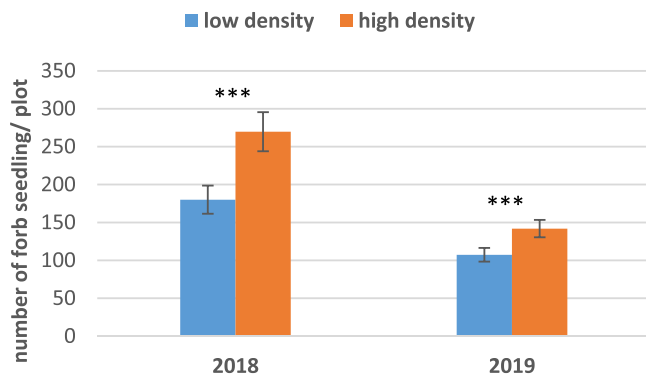


Fig. 2. Effect of sowing density on forb seedling number/ plot in April 2018 and April 2019 (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.000$ and ns=not significant. Error bar = 2 Standard Errors).

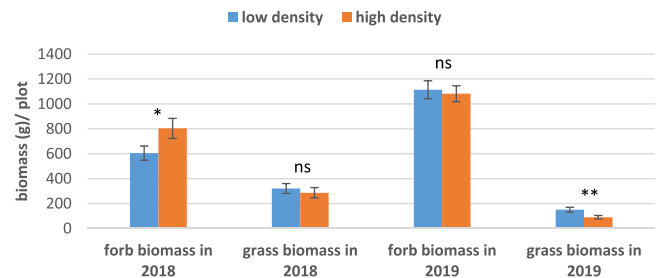


Fig. 3. Effect of sowing density on forb and grass biomass/ plot in August 2018 and August 2019 (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.000$ and ns=not significant. Error bar = 2 Standard Errors).

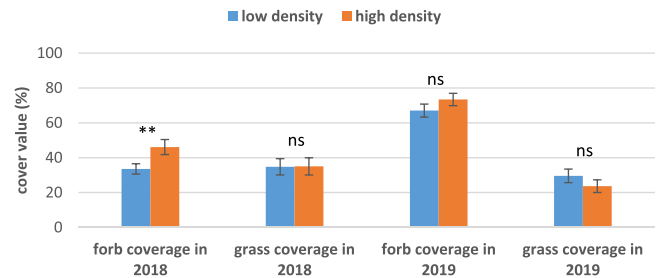


Fig. 4. Effect of sowing density (on forb and grass cover values) in May 2018 and May 2019 (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.000$ and ns=not significant. Error bar = 2 Standard Errors).

the cover values.

3.2. Effect on dominant forbs (*Achillea millefolium* and *Echinops sphaerocephalus*) and subordinate forbs on biomass in 2018 and 2019

Biomass distribution within the community was highly asymmetric for individual species. This pattern is normal in many field experiments and real-life projects. The dominant forbs were mainly *A. millefolium* in 2018 and then both *A. millefolium* and *E. sphaerocephalus* in 2019. The rest of 26 forb species (*Campanula glomerata* is excluded due to no valid data collected) refer to the subordinates in both 2018 and 2019.

High sowing density led to significantly more biomass of *A. millefolium* in August 2018 ($p = 0.004$) but did not significantly increase *A. millefolium* biomass in 2019 ($p = 0.056$), as shown in Fig. 5. The biomass of *E. sphaerocephalus* was not significantly different between the two density treatments in both 2018 ($p = 0.997$) and in 2019 ($p = 0.171$) despite low sowing density leading to greater *E. sphaerocephalus* biomass (467.44 g) than the high sowing density treatment (358.76 g) in 2019. Subordinate biomass showed a similar

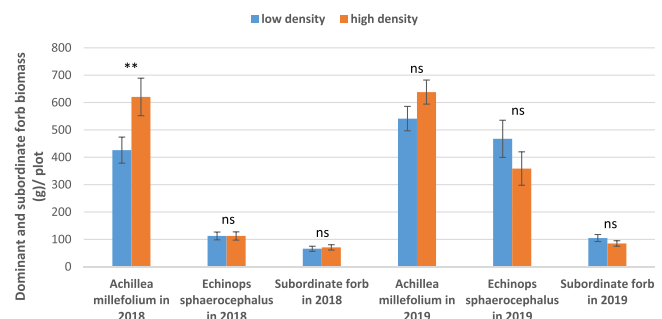


Fig. 5. Effect of sowing density (low and high density) on dominant and subordinate forb biomass/ plot in August 2018 and August 2019 (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.000$ and ns=not significant. Error bar = 2 Standard Errors).

pattern to *E. sphaerocephalus* ($p = 0.622$ in 2018 and $p = 0.139$ in 2019) and showed more biomass in the low sowing density treatment (104.88 g compared with 85.01 g in the high sowing density) despite not being significant (Fig. 5).

High sowing density led to significantly more forb biomass in 2018, mostly because of *A. millefolium*, which comprised most of this forb biomass. Biomass change between the two years, was significantly different for *E. sphaerocephalus* ($p = 0.000$ for both densities). The subordinate biomass was also significantly different ($p = 0.000$) for both low density and high density ($p = 0.019$). Table 2.

3.3. Effect of sowing density on forb seedling richness in 2018 and 2019

In 2018, 18 out of 23 subordinate forb species (data for *Platycodon gradiflorum*, *Scutellaria baicalensis* in both years and *Aconitum carmichaelii* in 2018 was not validated for use in the statistical model) had significantly higher seedling numbers in high sowing density treatments (Table 3). However, in 2019, this went down to 9 out of 24. The effect of increasing sowing density to increase numbers of seedlings was reduced with the passage of time in most of the species especially the lower canopy forb species. Eight low canopy subordinates had more seedlings in high density in 2018 and only 2 species retained this advantage in 2019 (*Potentilla rupestris*, $p = 0.001$ and *Veronica teucrium*, $p = 0.021$).

Overall, six subordinate forb species had significantly higher numbers of seedling in the high sowing density treatment in both 2018 and 2019; *Potentilla rupestris* ($p = 0.003$ in 2018, $p = 0.001$ in 2019), *Origanum vulgare* ($p = 0.000$, $p = 0.007$) *Polemonium caeruleum* ($p = 0.000$, $p = 0.003$), *Kalimeris incisa* ($p = 0.000$, $p = 0.000$), *Stachys officinalis* ($p = 0.000$, $p = 0.000$) and *Thalictrum aquilegifolium* ($p = 0.001$, $p = 0.000$).

3.4. Effect on subordinate forb biomass per species in 2018 and 2019

Increasing sowing density generally had limited capacity to increase subordinate forb biomass for most of the species in both years. As shown in Table 4, *Stachys officinalis* was the only subordinate forb that had significantly more biomass in the high sowing density treatment in 2018 ($p = 0.002$). Low sowing density increased the biomass of *Patrinia scabiosifolia* ($p = 0.032$) in 2018, *Origanum vulgare* ($p = 0.006$) in 2019 and *Dracocephalum rupestre* in both years ($p = 0.018$ in 2018 and $p = 0.005$ in 2019). Despite no statistical difference ($p = 0.106$), *P. rupestris* produced far more biomass in low sowing density (6.17 g) comparing with high sowing density (2.23 g).

4. Discussion

4.1. Does increasing sowing density inevitably accelerate sown grasses eliminating forbs?

Unlike many previous studies (Pywell et al., 2003; Del-Val and

Crawley, 2005; Silvertown et al., 2006), the higher sowing rate did not lead to a larger grass biomass that dominated the community. Grass biomass diminished as a percentage of forb biomass from 2018 on, with the highest grass biomass associated with the low sowing density in 2019 ($p = 0.002$). The grass species used in this study generally showed lower competitiveness than the most competitive forbs that dominated the forb biomass. *Deschampsia cespitosa* is less competitive in terms of relative growth rate than the ubiquitous weedy grasses that invade designed meadow, such as *Arrhenatherum elatius*, *Holcus lanatus* and *Lolium perenne* (Del-Val and Crawley, 2005; Hitchmough et al., 2008). These common highly competitive grasses were eliminated from the site as part of the initial site preparation protocols and the nutrient and moisture stress created by the 150 mm sand mulch treatment, plus the high density sown community inhibited subsequent re-establishment over the three years of this study.

Biomass production of *D. cespitosa* (a species of moist to wet environments) appeared to have been reduced by the sowing mulch relative to the most dominant forb, *A. millefolium*, a relatively aggressive, colonising species (Burton et al., 2006; Bjørn et al., 2019).

This study provides an interesting meadow design model; forbs were not eliminated by grass competition whilst the shade tolerant *D. cespitosa* was able to persist under the summer canopy of the taller forbs and deliver functional benefits, for example early emergence, and quick recovery after late summer cutback to reduce soil exposure. Both sowing density treatments had an extremely low biomass of “weed” species (1.1% and 0.5% of the sown biomass in the low and high sowing treatments in 2018; 0.8% and 0.7% in 2019) after three growing seasons with no weed removal. In the longer term, weedy, more competitive grasses may, in the absence of management, gradually become more abundant in the created meadows. Thus, increasing sowing density does not always accelerate sown grass eliminating forbs, it depends on the relative competitiveness of the grass species in relation to the most dominant forb species.

4.2. To what extent, can initial sowing density influence forb performance in terms of forb abundance, richness and biomass?

In conventional ecological studies, diversity is seen as the key measure of success in meadows creation, however in urban areas, the number of forb seedlings present and their biomass is also important and potentially underpins floral performance as much or more than richness does (Hoyle et al., 2018).

As in many previous studies (Dickson and Busby, 2009; Hitchmough et al., 2017; Lubin et al., 2019), increasing forb sowing density increased the number of forb seedlings present for at least for three years. Having more forb seedlings often leads to more attractive initial appearance and offers greater competition to invading species from an early stage, and provides at least an opportunity for a more sustainable end point (Hitchmough and de la Fleur, 2006; Lauenroth and Adler, 2008; Hitchmough, 2017a). Even if only temporary this is worth having

Table 2
Effect of sowing density on overall results in 2018 and 2019 (SE = Standard Error of Mean).

	2018					2019				
	Low density		High density		P value	Low density		High density		P value
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Forb seedling present number	180.04	18.64	269.71	25.71	0.000 ***	107.35	8.98	141.88	11.54	0.000 ***
Forb biomass (g)	604.34	57.46	803.63	80.64	0.015 *	1113.59	71.84	1081.95	64.27	0.710 ns
Grass biomass (g)	320.70	39.91	286.43	41.47	0.401 ns	150.21	19.39	90.04	13.96	0.002 **
Forb cover value (%)	33.56	2.94	46.08	4.32	0.000 ***	67.02	3.75	73.38	3.54	0.098 ns
Grass cover value (%)	34.79	4.67	35.02	4.93	0.960 ns	29.58	3.88	23.67	3.61	0.139 ns
Bare ground cover value (%)	31.65	3.35	18.90	2.77	0.000 ***	3.63	0.56	2.96	0.51	0.331 ns
<i>Achillea millefolium</i> biomass (g)	426.06	47.77	620.49	68.48	0.004 **	541.27	44.50	638.18	44.00	0.056 ns
<i>Echinops sphaerocephalus</i> biomass (g)	112.56	14.39	112.48	15.00	0.997 ns	467.44	67.95	358.76	61.11	0.171 ns
Subordinate forb biomass (g)	65.73	9.38	70.66	9.67	0.622 ns	104.88	12.75	85.01	10.14	0.139 ns

Table 3

Effect of sowing density on seedling number of each forb species in 2018 and 2019 (SE = Standard Error of Mean; na = not applicable).

	2018				P value	2019				P value
	Low density		High density			Low density		High density		
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Low canopy										
Shared										
<i>Anemone sylvestris</i>	6.63	1.17	9.63	1.36	0.003 **	4.92	0.88	5.00	0.67	0.325 ns
<i>Galium verum</i>	7.44	1.15	11.17	1.64	0.012 *	6.02	0.82	7.75	1.01	0.061 ns
<i>Potentilla rupestris</i>	8.19	1.02	11.19	1.22	0.003 **	5.81	0.60	8.15	0.82	0.001 **
<i>Pulsatilla vulgaris</i>	5.27	0.86	9.85	1.53	0.001 **	2.46	0.47	2.90	0.68	0.363 ns
<i>Veronica teucrium</i>	7.73	1.17	9.65	1.40	0.134 ns	5.33	0.59	6.83	1.02	0.492 ns
Mongolian										
<i>Dracocephalum rupestre</i>	13.21	1.58	19.67	2.24	0.000 ***	4.96	0.80	4.75	0.77	0.393 ns
<i>Dracocephalum ruychiana</i>	9.83	1.54	13.44	2.18	0.017 *	2.42	0.53	2.42	0.47	0.362 ns
<i>Thalictrum petaloideum</i>	8.75	1.08	14.04	1.38	0.000 ***	4.98	0.59	6.94	0.86	0.021 *
<i>Thermopsis lanceolata</i>	5.98	0.89	10.79	1.60	0.000 ***	1.60	0.32	2.19	0.41	0.059 ns
<i>Veronica incana</i>	0.33	0.14	0.54	0.29	0.984 ns	0.00	0.00	0.00	0.00	0.844 ns
Medium canopy										
Shared										
<i>Achillea millefolium</i>	4.27	0.41	8.96	0.81	0.000 ***	4.27	0.41	8.96	0.81	0.000 ***
<i>Origanum vulgare</i>	21.79	2.15	32.42	3.38	0.000 ***	13.60	1.15	17.73	1.38	0.007 **
<i>Polemonium caeruleum</i>	5.54	0.72	8.98	1.05	0.000 ***	2.71	0.45	4.23	0.84	0.003 **
<i>Stachys officinalis</i>	4.33	0.42	9.00	0.83	0.000 ***	2.90	0.34	5.38	0.60	0.000 ***
Mongolian										
<i>Campanula punctata</i>	21.85	2.78	24.65	2.98	0.128 ns	14.27	1.85	14.60	1.90	0.802 ns
<i>Delphinium grandiflorum</i>	11.15	1.58	14.67	1.94	0.002 **	7.67	1.12	9.35	1.46	0.082 ns
<i>Kalimeris incisa</i>	6.52	0.81	14.19	1.58	0.000 ***	3.90	0.53	6.73	0.90	0.000 ***
<i>Platycodon grandiflorum</i>	3.33	0.70	5.33	0.93	na	0.00	0.00	0.06	0.06	na
<i>Scutellaria baicalensis</i>	2.15	0.48	2.29	0.56	na	0.23	0.09	0.15	0.06	na
Tall canopy										
Shared										
<i>Echinops ritro</i>	1.04	0.20	1.92	0.40	0.060 ns	0.48	0.13	1.08	0.28	0.051 ns
<i>Geranium pratense</i>	5.17	0.51	7.67	0.73	0.004 **	5.56	0.61	7.83	0.82	0.039 *
<i>Sanguisorba officinalis</i>	1.52	0.23	3.15	0.49	0.000 ***	1.60	0.23	2.40	0.33	0.040 *
<i>Thalictrum aquilegifolium</i>	5.92	0.68	9.21	1.12	0.001 **	4.67	0.47	7.38	0.75	0.000 ***
<i>Veronica longifolia</i>	2.44	0.46	3.27	0.60	0.210 ns	2.23	0.43	2.46	0.50	0.830 ns
Mongolian										
<i>Aconitum carmichaelii</i>	1.00	0.00	1.00	0.00	na	0.83	0.05	0.83	0.05	0.980 ns
<i>Angelica sylvestris</i>	2.00	0.12	3.00	0.24	0.000 ***	0.75	0.12	0.50	0.09	0.119 ns
<i>Echinops sphaerocephalus</i>	3.75	0.27	5.85	0.41	0.000 ***	2.85	0.31	4.77	0.49	0.000 ***
<i>Patrinia scabiosifolia</i>	2.92	0.36	4.21	0.51	0.001 **	0.33	0.10	0.52	0.32	0.271 ns

especially in very politically contested urban environments, as a sign of initial success. Whether this opportunity leads to longer term success or not, depends on site productivity and management.

Forb seedling number increased, but not linearly with sowing density; and the effect of higher sowing density diminished with the time from the initial sowing because of greater competition leading to greater “self-thinning” (Yoda et al., 1963). Whilst absolute forb seedling numbers in the high sowing density were still higher in the third year (2019, $p = 0.000$) than in the low density, the numbers were likely to become similar in subsequent years, as this is ultimately determined by competition between individuals and species, and herbivory.

In this study, competition for light is believed to be the major factor behind decline in the number of forb seedlings, with many of these being low growing shade intolerant species. ‘Sunscan’ PAR measurements indicated lower solar energy on the soil surface in high sowing density (2.04%, ground solar radiation level/ ambient, watts/m²) than low sowing density plots (2.71%). Earlier in the year cutting and removal of biomass from the meadow or selectively thinning of competitive species would probably have slowed down the loss of forb seedlings.

Mortality of forb seedlings was more marked in this study than in Hitchmough et al. (2008). This was probably because in this study the sowing densities and subsequent emergence were higher, and a greater proportion of the forb species were more sensitive to shade. Although species diversity gradually declined in both sowing density treatments in both 2018 and 2019 (Shannon Wiener index: in 2018; 3.04 in low density, 3.08 in high density; in 2019, 2.94 in low density and 2.97 in high density) differences between densities remained relatively small.

Research in rural herbaceous communities in British Colombia,

shows that doubling sowing density shortens the time taken to reach a forb biomass ceiling (Burton et al., 2006). Higher cover values in spring reduce potential weed invasion and deliver visual evidence of ‘ecological value’ that is of both social and ecological importance (Bergelson et al., 1993; Hoyle et al., 2017a). Increasing sowing density is unlikely to affect grassland community biomass in the long term as it is not possible to override ecological processes such as self-thinning, by adding more seeds. The increase in forb biomass with higher sowing density in this study was primarily due to the increase of *A. millefolium*, the most dominant species. This suggests that increasing sowing density exacerbates asymmetric competition with dominance effects occurring sooner and with subordinate forbs being suppressed or even eliminated in a short time period. The greater biomass of *A. millefolium* in the high sowing density was likely to be the main cause of low grass and subordinate forb biomass (Dwyer, 1958). In this study, *A. millefolium* fundamentally adopted the ‘weedy grass role’ and suppressed the subordinates through similar mechanisms to grass competition.

Subordinate forb biomass was greater in the low sowing density in 2019 despite the difference being non-significant ($p = 0.139$). This was presumably because there were fewer *A. millefolium* to intercept light resources in this treatment. Stevenson et al. (1995) recommended a lower sowing density to be used in unproductive conditions and where competitive perennial grasses are both less productive and present at lower density. If too low a seed density is sown, the impact maybe too limited in closely viewed urban landscapes.

The substantial basal foliage and leafy stems of *E. sphaerocephalus* allowed it to take the role of second dominant. Since light competition is the major process by which dominants suppress subordinates in the

Table 4

Effect of sowing density on biomass of each subordinate forb species in 2018 and 2019 (SE = Standard Error of Mean).

	2018					2019				
	Low density		High density		P value	Low density		High density		P value
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Low canopy										
Shared										
<i>Anemone sylvestris</i>	0.08	0.02	0.06	0.02	0.536 ns	0.06	0.04	0.04	0.02	0.481 ns
<i>Galium verum</i>	2.34	0.73	3.69	1.20	0.243 ns	6.76	1.34	8.52	2.09	0.391 ns
<i>Potentilla rupestris</i>	3.70	1.09	2.35	0.46	0.190 ns	6.17	2.61	2.23	0.58	0.106 ns
<i>Pulsatilla vulgaris</i>	0.18	0.06	0.13	0.04	0.429 ns	0.03	0.02	0.05	0.03	0.672 ns
<i>Veronica teucrium</i>	1.21	0.27	1.42	0.49	0.664 ns	2.32	0.66	1.64	0.48	0.305 ns
Mongolian										
<i>Dracocephalum rupestre</i>	2.94	0.49	1.84	0.31	0.018 *	0.16	0.05	0.03	0.01	0.005 * *
<i>Dracocephalum ruychiana</i>	1.07	0.23	0.66	0.13	0.066 ns	0.43	0.22	0.09	0.05	0.091 ns
<i>Thalictrum petaloideum</i>	0.00	0.00	0.00	0.00	na	0.00	0.00	0.00	0.00	0.140 ns
<i>Thermopsis lanceolata</i>	1.13	0.40	1.22	0.27	0.839 ns	0.30	0.14	0.60	0.22	0.214 ns
<i>Veronica incana</i>	0.00	0.00	0.00	0.00	0.400 ns	0.00	0.00	0.00	0.00	1.000 ns
Medium canopy										
Shared										
<i>Origanum vulgare</i>	20.15	3.59	15.84	3.10	0.257 ns	52.53	7.19	31.63	4.89	0.006 * *
<i>Polemonium caeruleum</i>	0.56	0.26	2.01	0.86	0.056 ns	0.77	0.24	1.66	0.65	0.142 ns
<i>Stachys officinalis</i>	0.26	0.05	0.54	0.10	0.002 * *	0.76	0.16	1.57	0.51	0.102 ns
Mongolian										
<i>Campanula punctata</i>	2.21	0.58	1.64	0.56	0.415 ns	1.24	0.39	0.84	0.61	0.545 ns
<i>Delphinium grandiflorum</i>	2.26	0.62	2.59	0.85	0.713 ns	2.01	0.73	2.18	0.97	0.875 ns
<i>Kalimeris incisa</i>	15.66	3.31	22.33	4.31	0.111 ns	10.85	3.34	10.21	2.98	0.866 ns
<i>Platycodon grandiflorum</i>	0.10	0.03	0.07	0.01	0.315 ns	0.02	0.01	0.00	0.00	0.068 ns
<i>Scutellaria baicalensis</i>	0.73	0.26	0.50	0.17	0.392 ns	0.10	0.04	0.08	0.05	0.609 ns
Tall canopy										
Shared										
<i>Echinops ritro</i>	2.71	0.85	4.84	1.54	0.199 ns	2.73	1.05	3.71	1.47	0.564 ns
<i>Geranium pratense</i>	3.66	0.63	3.48	0.82	0.847 ns	11.87	2.14	13.65	3.77	0.636 ns
<i>Sanguisorba officinalis</i>	2.48	0.62	2.90	0.92	0.678 ns	3.55	0.96	4.36	1.25	0.575 ns
<i>Thalictrum aquilegifolium</i>	0.08	0.02	0.07	0.02	0.674 ns	0.07	0.03	0.02	0.01	0.077 ns
<i>Veronica longifolia</i>	1.14	0.46	1.87	0.77	0.369 ns	1.53	0.48	1.04	0.41	0.402 ns
Mongolian										
<i>Aconitum carmichaelii</i>	0.29	0.05	0.22	0.03	0.231 ns	0.42	0.10	0.24	0.05	0.087 ns
<i>Angelica sylvestris</i>	0.02	0.01	0.03	0.02	0.741 ns	0.08	0.03	0.55	0.52	0.329 ns
<i>Patrinia scabiosifolia</i>	0.78	0.20	0.37	0.10	0.032 *	0.10	0.04	0.06	0.02	0.363 ns

seedling stage in urban meadows (Köppler and Hitchmough, 2015) increasing seedling density of the subordinate species is probably less effective than reducing the density of sown dominants such as *A. millefolium* and *E. sphaerocephalus* where weed biomass is low. Dickson and Busby (2009) argued that spatial separation is an effective way to encourage the growth of less competitive species in a community but this is not feasible in meadow-like vegetation.

4.3. Which subordinate forb species tend to gain advantages in terms of number of seedlings and biomass in the higher sowing density?

For most of subordinate forbs, increasing sowing density increases the number of seedlings but was unlikely to enhance their biomass in 2018 and 2019 in this study. Hitchmough et al. (2017) found the same patterns. Morphological abilities to access light resources through early emergence or taller leafy foliage are essential to survive the more intense competition from dominants. Tall, and native species with presumed superior fitness were more likely to maintain higher numbers of surviving seedling in the higher sowing density in the longer term. Increasing sowing density was least likely to enhance the number of survivals of low canopy forb species.

Although the competition of grasses and the dominant forb *A. millefolium* was greater at the higher sowing density, this treatment retained most of the subordinate forb species (18 out of 23) in 2018. Although a few species such as *Veronica teucrium* and *Campanula punctata* did not show a statistically significant difference, seedling numbers were initially higher at the high sowing density. Beneficial effects of sowing density on subordinate seedling number were greatly reduced in 2019. Only 9 species still had significantly more seedling numbers in the

high-density treatments. Seven species, out of these 9, were native to the UK suggesting that species with native distributions were potentially more adapted and more persistent in the UK climate. This may be also because the shared species have a wider geographically distribution implying adaptiveness to a more generalist habitat conditions, which tend to make them more able to survive in semi-natural grasslands (Pywell et al., 2003). More importantly, most native species had the advantages of greater light competitiveness from the seedling stage due to earlier emergence (*P. rupestris* and *P. caeruleum*), rapid seedling growth (*O. vulgare*) or advantages in architecture, for example, long petioles (*G. pratense*), tall leafy stems (*Sanguisorba officinalis*), or clambering stems as in *Galium verum*.

Sowing density was largely ineffective as a means of increasing subordinate forb biomass. In 2018, 11 species increased their biomass in the high sowing density while 13 species decreased. In 2019, 10 species increased their biomass and 14 species declined in terms of biomass, with *Thalictrum petaloideum* and *V. incana* poorly represented in both years. *Stachys officinalis* was the only species that had a significant increase of biomass among the subordinates. Due to seed dormancy problems, *Stachys officinalis* was one of the species established in the experiment by planting, so they were larger than some other subordinate forbs in the plots, and this may have helped them to cope with shading stress generated by dominant species. The biomass of this species almost increased linearly within the high density treatment in both years. Transplanting did not improve the growth of all species established in this way. For example, *Angelica sylvestris* remained very small (0.02 and 0.03 g in low and high sowing density treatments). This species is largely associated with wet sites (8 on the Ellenberg scale for moisture) and the experiment was probably too dry for this species to establish. Lack of

ecological adaptiveness to the community appears more important than means of establishment.

There was evidence that low sowing density could benefit subordinates that have poor capacity to compete for light. *Dracocephalum rupestre* and *Patrinia scabiosifolia* showed a significantly negative response to the doubling of sowing density. Where competitive pressure was lower, they produced more biomass in 2018. *Dracocephalum rupestre* has short basal foliage and relatively slow growth placing it at a disadvantage when competing for light in taller vegetation. Although differences were not statistically significant, species such as *P. rupestris* or *C. punctata* which also have short foliage also showed a negative response to increased sowing density. *Patrinia scabiosifolia* is also a late emerging species, forcing it to compete for light with already actively growing species, and hence was sensitive to high sowing density. Enhanced ability to access light resources improves the likelihood of subordinate species survival but does not increase their biomass under the competition with more dominant species. This is an important finding for how meadows might be perceived by the public in practice, enhance survival is unlikely to be perceived positively if those seedlings are too small to be flower or even to be perceived as being present.

5. Conclusion

Sowing density is one of the relatively few “levers” available to practitioners to try to design meadow communities with a specific preferred initial composition. To practitioners with a horticultural world view, it seems intuitive that having more plants of a desired species post sowing is a good thing, and likely to be a positive in the future development of the community. The actual benefits of higher sowing density are mostly associated with how the developing meadow community is perceived in the first and second year. More seedlings resulting from higher sowing densities confer a sense of success, and are likely to result in a florally enhanced display in the second year.

Higher sowing densities inevitably result in increased intra and interspecific competition leading to more rapid onset of dominance from within the sown cohort, and a gradual loss of species diversity, and the loss of the slowest growing and most shade intolerant subordinate species in particular. Sown species with tall leafy stems, or other means of competing for light were best able to persist at high sowing densities.

These effects became evident particularly rapidly in this study because both sowing rates were relatively high (in order to reduce missing values for subordinate species) with mean established densities of forb seedlings of 180 (low sowing rate) and 270 per m² (high sowing rate) in the second year (2018), a decline from approximately 500 and 1000 respectively in the first growing season. The direction of travel for forb density was clearly to decline more rapidly at higher sowing densities. The increase in observed biomass of some subordinate species at low sowing density took place under conditions in which sand mulching essentially eliminated weed emergence and competition from the soil seed bank. Where these mulches are absent low density sowings will generally experience greater competition from weeds emerging from the soil seed bank. This may lead to low sowing density meadows having low sown forb densities than those achieved with higher sowing densities. The effect of sowing density is hence highly contingent on local conditions and practices. The most appropriate designed sowing densities need to be based on assessment of these local factors, in order to balance positives and negative outcomes as best as is possible for specific site conditions.

CRediT authorship contribution statement

Mingyu Jiang: Conceptualization, Methodology, Software, Data curation, Visualization, Investigation, Writing – original draft. **James D Hitchmough:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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