Using priority effects for grassland restoration: Sequential sowing can promote subordinate species

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Received: 23 February 2023 | Revised: 25 July 2023 | Accepted: 24 August 2023

DOI: 10.1111/avsc.12748

Applied Vegetation Science IAVS

RESEARCH ARTICLE

Using priority effects for grassland restoration: Sequential sowing can promote subordinate species

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Funding information
Association Nationale de la Recherche et de la Technologie; CIFRE; RTE

Abstract

Aims: The influence of priority effects on plant community succession is increasingly discussed in community ecology. However, most grassland restoration approaches involving seed addition transfer all target species at the same time. Our objective was to tackle the question: does the order of arrival influence the establishment of restored communities?

Location: La-Bâtie-Neuve, Southern Alps, France.

Methods: We applied sequential sowing using two groups, one set of dominant species and one set of subordinate species, each comprising three different perennial plant species. We tested four sowing treatments: control (without any sowing), two sequential sowing treatments (dominants first or subordinates first) and synchronous sowing. We analysed plant cover each year for three years after sowing and calculated priority and earliness indices (the third year) for each group and each sown species.

Results: Manipulating the order of arrival shaped community composition and trajectories. Some species of both groups were positively affected by being sown first compared to being sown synchronously. However, dominant and subordinate groups differed in their earliness index, showing a significant benefit for subordinates to be sown first. The subordinate species *Onobrychis viciifolia* and *Plantago lanceolata* established only when they were sown first, while *Festuca cinerea* showed greater establishment when sown first and simultaneously, compared to late sowing. The dominant *Anthyllis vulneraria* was not affected by date or type of sowing. However, the cover of the most dominant *Bromopsis erecta* was lower when being sown second, allowing a control of its dominance by delayed sowing.

Conclusion: The strength of priority effects differs between species, which may depend on niche characteristics or microenvironment, influencing (negatively or positively) the establishment of late-arriving species and affecting their competitive abilities. Our study provides evidence that plant community assembly was influenced by the order of arrival, but demonstrated a strong species-specific response to priority effects.

Co-ordinating Editor: Péter Török

KEYWORDS
community assembly, early-arriving species, ecological restoration, late-arriving species, mesophilous grassland, niche modification, stepwise sowing, time-advanced

1 | INTRODUCTION

Priority effects occur when the order of species arrival in a habitat changes biotic and abiotic properties of the microenvironment and thus affects the recruitment, establishment, growth and/or reproduction of late-arriving species (von Gillhaussen et al., 2014; Temperton et al., 2016; Weidlich et al., 2018). Priority effects can be either positive (i.e., facilitative; Bertness & Shumway, 1993) or negative (i.e., inhibitory, competitive; Cole, 1983; Fukami, 2015). Most of the studied priority effects, however, show that a competitive advantage for the first-arriving species prevails because of their greater size or density compared with late-arriving species (i.e., size-asymmetric competition; Grman & Suding, 2010; Wainwright et al., 2012). Many other mechanisms may drive priority effects, such as niche pre-emption or niche modification (Fukami, 2015; Helsen et al., 2016), plant–soil feedbacks and soil legacies (Bever, 2003; Grman & Suding, 2010; Fukami & Nakajima, 2013; van der Putten et al., 2013) or allelopathic effects (Levine et al., 2003). Furthermore, the strength of priority effects can be mediated by both biotic and abiotic factors, such as species identity (von Gillhaussen et al., 2014; Cleland et al., 2015; Wilsey et al., 2015; Stuble & Souza, 2016; Werner et al., 2016) or overlapping niches (Vannette & Fukami, 2014), predation pressure (Chase et al., 2009) and habitat size or productivity (Fukami, 2004; Orrock & Fletcher Jr., 2005; Chase, 2010; Kardol et al., 2013). In productive environments, priority effects may be very strong, resulting in alternative stable states (Chase, 2003; Hobbs & Norton, 2004; Kardol et al., 2013; Weidlich et al., 2017). Priority effects are, however, poorly studied in less productive environments (Wilsey, 2020). Finally, priority effects do not only influence the early community assembly but also shape the potential community trajectories, including their species composition and associated functions (Grman & Suding, 2010; von Gillhaussen et al., 2014; Werner et al., 2016; Stuble & Young, 2020).

Translating the concepts of community assembly and trajectories into relevant methods to drive ecosystem dynamics is a core approach in restoration ecology (Temperton et al., 2016). If an ecosystem has been degraded, damaged or destroyed, restoration managers try to assist its recovery; this can include the recovery of species composition and ecosystem functions (Gann et al., 2019). Changing initial biotic or abiotic conditions and species pools may help to accelerate restoration toward the reference plant community (Garrouj et al., 2019). Despite growing evidence of the importance of priority effects in early plant succession and ecological restoration (van der Putten et al., 2013; Vaughn & Young, 2015), their long-term consequences (Fukami, 2004; Švamberková et al., 2019; García-Girón et al., 2022) and their potential to improve target species establishment (Young et al., 2001, 2017; Fukami & Nakajima, 2011; Werner et al., 2016), most restoration approaches use a simultaneous transfer of target species (Török et al., 2018).

Consequently, there is an increasing number of field and greenhouse studies testing priority effects as a restoration tool. Testing priority effects involves sequential sowing of different species or species groups in order to analyse their influence on plant community dynamics. Species groups may be based on their origin (native vs exotic, Goodale & Wilsey, 2018; Grman & Suding, 2010; Hess et al., 2022; Ploughe et al., 2020; Yu et al., 2020), on their life cycle type (annual vs perennial, Schantz et al., 2015; Vaughn & Young, 2015), or on their functional group (grasses vs legumes vs non-legume forbs; Delory et al., 2019; Stuble & Souza, 2016; Stuble et al., 2017; von Gillhaussen et al., 2014; Weidlich et al., 2017, 2018). Other studies examined priority effects by mixing these groups (Cleland et al., 2015; Lang et al., 2017; Mason et al., 2013; Schantz et al., 2018; Stuble & Young, 2020; Werner et al., 2016; Wilsey, 2020; Young et al., 2017). Alternatively, species may be assigned to groups according to their importance in reference plant communities, for example in distinguishing dominant (species frequently occurring in high abundance) and subordinate species (frequently occurring in low abundance; Grime, 1998). Dominant species are expected to play more important functional roles in communities due to their relative abundance, but subordinate species may also contribute significantly to community diversity and represent impactful ecosystem functions, like N fixation (Mariotte et al., 2013; Mariotte, 2014), particularly in semi-natural grasslands (Gibson, 2009; Werner et al., 2016). For example, subordinate species can increase plant community resistance against drought (Mariotte et al., 2013), probably via mycorrhizal fungal associations that improve plant productivity and positive plant–soil feedback (de Vries et al., 2012, 2018; Mariotte et al., 2012). Contrary to dominant species, subordinate species are expected to show, on average, a low competitive response (tolerance to competition by other species) and lower competitive effect (competition pressure exerted on other species; Goldberg & Landa, 1991; Keddy et al., 2002; Wang et al., 2010). Such competitive properties may explain why subordinate species may be more sensitive to priority effects than dominant species (Sarneel et al., 2016). Delaying the arrival of dominant species may thus improve the establishment of less abundant subordinate species (Mariotte et al., 2012; Young et al., 2017). Historically contingent coexistence has recently been described as possible assembly dynamics that allows coexistence: the coexistence of species A and B is only possible if B is introduced after A in the community whereas only B persists if A and B are introduced together or if A is introduced after B (Song et al., 2021). These assembly dynamics have not only been described theoretically but also experimentally in spider mite communities: the coexistence of the two species was

only possible when the weakest species was introduced first, otherwise only the strongest survived (Fragata et al., 2022). Our objective was to test sequential sowing of dominant and subordinate grassland species and its effect on the restored community assembly.

Plant dominance (relative abundance) in communities may be determined by plant cover or frequency in vegetation surveys. We first identified sets of dominant or subordinate species in our study area using abundances in vegetation surveys of undisturbed semi-natural grasslands. Then we tested priority effects by sowing dominants and subordinates both at the same time and sequentially. Temporal changes in dominance are supposed to occur through autogenic processes involving competitive interactions between plants, depending on life history and adaptive strategies (Grime, 1973; Huston & Smith, 1987). We therefore hypothesised that the order of arrival of the dominants and subordinates changes the species composition of the plant community. More specifically, as dominants have a strong competitive ability (both competitive effect and response), we expected that sowing dominants first or together with subordinates would lead to reduction in of cover, or competitive exclusion of subordinates. In contrast, sowing subordinates first should favour their establishment without preventing the establishment of dominants (Figure 1). We further expect that the sowing treatment affects community assembly and spontaneous species establishment.

2 | MATERIALS AND METHODS

2.1 | Site description

The experiment was carried out in a degraded montane grassland at La-Bâtie-Neuve, in the upper Durance valley ('Haute-Durance') of the Southern French Alps (44°57′93″ N, 6°20″77′ E). The site is located at 1270 metres above sea level (a.s.l.), on an approximately 20° west-facing slope. The average annual precipitation is 947 mm. July is the warmest month with an estimated average temperature of 15.5°C, and January is the coldest with an average temperature of −3°C (estimated from Chorges meteorological station, 863 m a.s.l., 10 km from La-Bâtie-Neuve). Frost can occur from September to May. The soil is stony on calcareous bedrock. The grasslands in this area are extensively grazed by cattle. The recent construction of a high-voltage transmission line in the valley involved a degradation of the soil structure (and vegetation) affected by stripping, compacting and decompacting the soil to create transitory access tracks and construction platforms. At the end of the work, the stockpiled soil was moved back to recreate the original slope.

2.2 | Experimental setup

To test the effect of the order of species arrival on the community assembly, we applied sequential sowing using two groups of perennial plant species according to their frequency of occurrence in 54 plots of typical undisturbed grasslands of the 'Haute-Durance' valley (Durbecq et al., 2020). Both groups included contrasting functional types represented by three plant families: Poaceae, Plantaginaceae and Fabaceae. The first group includes the 'dominant species' of each family, that is the most abundant species family in the studied grasslands. The second group represents the 'subordinate species', that is, the less abundant species in each of the studied families (Table 1). Dominant species were thus defined within plant families and may thus be less abundant than subordinates of another family. All these species are common in grasslands belonging to the habitat type "Semi-natural dry grasslands of *Festuco-Brometalia* and scrubland facies on calcareous substrates" (N6210, EU directive habitat 92/43/EEC, Calaciura & Spinelli, 2008).

2.3 | Experimental design

The experiment included four treatments on bare soil:

(i) Control (without any sowing: it allowed us to estimate the importance of spontaneous colonisation)
(ii) S + D: synchronous sowing (the six species were sown together in 2018 = year 0)
(iii) D1st: dominant species (D) were sown in year 0 and subordinate species (S) in 2019 = first year
(iv) S1st: subordinate species were sown in year 0 and dominant species in first year.

Each treatment was replicated in ten spatially randomised plots (total $n = 40$; Appendix S1). The 2018 sowing date was 19th October, and the 2019 sowing date was 9th October. Autumn sowing was chosen to allow dormancy breaking by cold stratification. Seeds of local origin according to the French label 'Végétal local' (Malaval et al., 2015) were obtained from a local seed company (Phytosem, Gap, France). The number of sown seeds was adjusted to a potential density of 100 individuals/m^2 for each sown species, based on seed producer expertise (Table 1). Plot size was 2 m × 2 m, separated by unsown margins of 50 cm. To prepare the seed bed, the plots were manually raked before and after the first sowing in year 0 to favour seedling recruitment. The experimental site was fenced to prevent seedling damage by cattle grazing. The plots were neither watered nor fertilised.

The dominant Plantaginaceae *Plantago media* did not establish in any treatment of the first year and was also absent the next three years. We therefore removed this species from the analyses.

2.4 | Data collection

Plant community surveys were carried out on all plots. The percentage cover of all vascular species was visually estimated in subplots of 1 m × 1 m placed in the centre of each experimental plot ($n = 40$; Appendix S1) in June 2019, 2020 and 2021 (first, second and third years; Appendix S2).

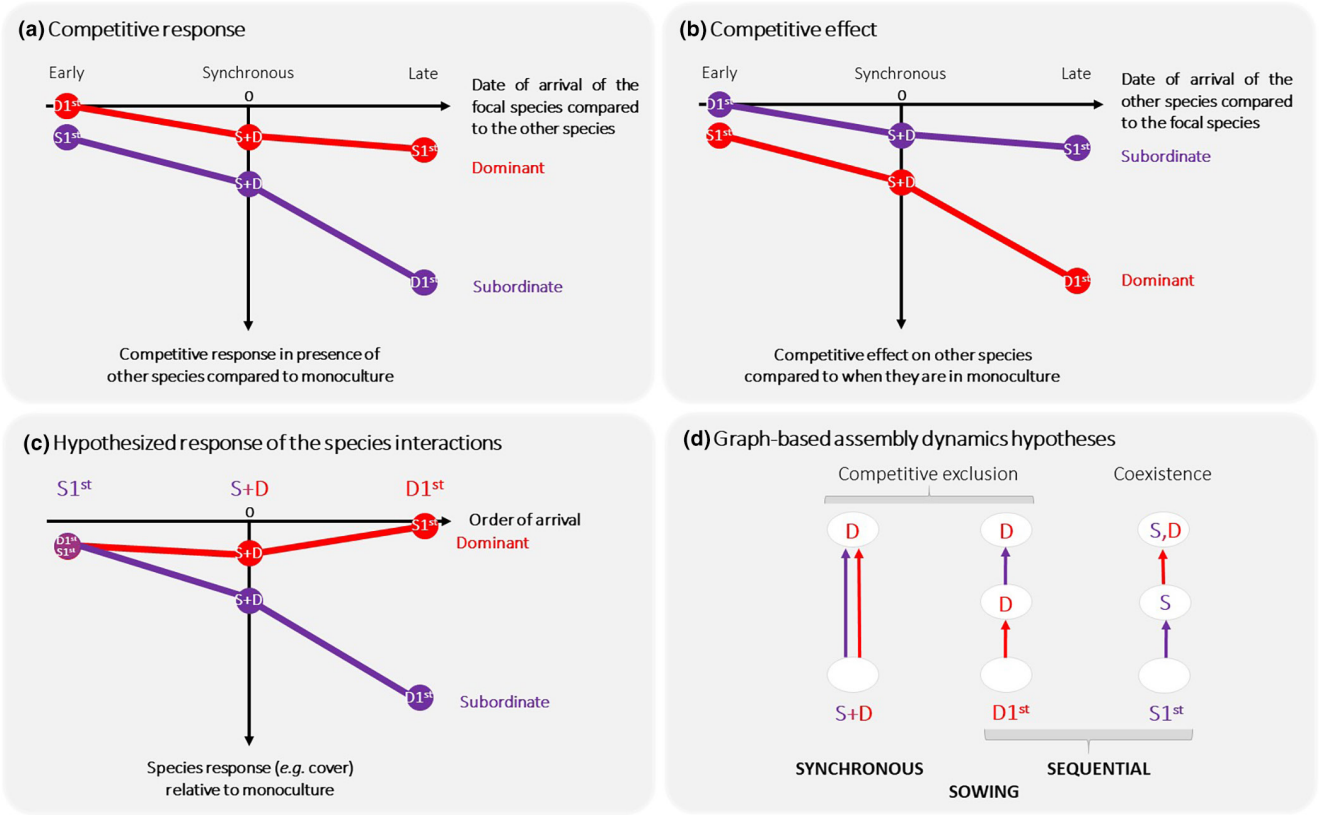

FIGURE 1 Hypothesised patterns of priority effects. Plant interactions depending on which species arrives first (1^{st}), dominants (D), subordinates (S) or when they are sown synchronously (S + D), resulting in (a) competitive response and (b) competitive effect (Goldberg & Landa, 1991). (c) Hypothesised response of species interactions when subordinates are sown first ($S1^{st}$), when subordinates and dominants are sown synchronously (S + D) and when dominants are sown first ($D1^{st}$). (d) Assembly dynamics showing three types of potential assembly dynamics in our study using the graph-based approach suggested by Song et al. (2021). Dominants are shown in red and subordinates in purple. Competitive response (proportion of focal species cover when grown with other species compared to monoculture) and effect (i.e., proportion of other species cover when grown with the focal species compared to monoculture) are displayed according to the hypotheses drawn for each species group (dominant or subordinate). Hypothesis 1: subordinates show a weak competitive effect and therefore do not or hardly affect other species regardless of arrival date (a, purple line). Hypothesis 2: subordinates show a weak competitive response and therefore establish less well in pre-established communities (assuming that pre-established species are already well developed and therefore exert higher resource pre-emption), but resist when sown first (b, purple line; assuming that they are already well developed and able to withstand resource pre-emption). Hypothesis 3: dominant species show a strong competitive effect and therefore strongly affect other species when arriving first, but to a lesser degree when arriving later (a, red line; because at least in a first phase they are less developed than the early-arriving species). Hypothesis 4: dominant species show a highly competitive response and are therefore not affected by other species, even if sown later (b, red line).

2.5 | Statistical analyses

In order to compare the plant community composition of the four treatments, Non-Metric Multidimensional Scaling (NMDS) was performed based on Bray–Curtis distances (Borcard et al., 2011) using R package *vegan* (Oksanen et al., 2020). A permutation multivariate analysis of variance (PERMANOVA, Anderson, 2017) with 9,999 permutations was used to analyse whether the community composition was significantly different between treatments (R package *vegan*).

To explore the effect of sequential sowing on community assembly, linear models (LM) were fitted with sowing treatment (D + S, $D1^{st}$, $S1^{st}$) as fixed effect and total plant species cover (i.e., community) as response variable. We tested the significance of the LM by an *F*-test using the 'Anova' function of the R package *car* (Fox & Weisberg, 2019). As unsown species cover did not comply with the assumptions of LM (normal distribution, homoscedasticity), we ran generalised linear models (GLM) using a quasibinomial distribution to reduce overdispersion. In case of a significant treatment effect, multiple least-square mean comparisons were run using a Tukey adjustment in order to test differences between treatment levels (*emmeans* package, Lenth, 2022).

We further tested for each sown species the difference between being sown one year before other species and being sown synchronously. The proportion of individual species cover to total plant cover was used as response variable. Relative cover was used to correct for great differences in total cover that may bias dominance evaluation. Since data did not comply with the assumptions

TABLE 1 Characteristics of the dominant and subordinate species sown

TAXA	Composition group	Frequency of occurrence	Average cover (%)	CSR strategy	No. of seeds/m^2
POACEAE					
Bromopsis erecta	Dominant (D)	0.93	32.13	S/SC	555
Festuca cinerea	Subordinate (S)	0.26	21.51	S/SR	2000
PLANTAGINACEAE					
Plantago media	Dominant (D)	0.68	5.42	C/CR	1250
Plantago lanceolata	Subordinate (S)	0.40	1.22	C/SC	533
FABACEAE					
Anthyllis vulneraria	Dominant (D)	0.28	3.07	CS/CSR	400
Onobrychis viciifolia	Subordinate (S)	0.14	1.04	CS/CSR	710

Note: Competitive (C), stress-tolerant (S) and ruderal (R) strategies according to Erschbamer (2007), Grime (1977), and Pierce et al. (2013). Number of sown seeds per m^2 adjusted according to seed producer expertise on field germination (Phytosem SAS, Gap, France). Frequency of occurrence and average cover according to Durbecq et al. (2020) ($n = 18$).

of LM, differences between the three sequential sowing treatments were analysed using GLM with quasibinomial distribution to reduce overdispersion.

We used two indices to assess historical contingency processes. The priority index (PI – equation 1) measures priority effects sensu stricto (effect of early species on late-arriving species) and the earliness index (EI – equation 2), which indicates the benefit of arriving early compared to synchronous arrival with other species. Similar to the additive neighbour effect intensity index (Díaz-Sierra et al., 2017), these indices are standardised, symmetric (additive symmetry), and bounded between −1 (competitive exclusion of late-arriving species [PI] or by species sown synchronously [EI]) and +2 (obligate facilitation by early-arriving species [PI] or by species sown synchronously [EI]; Díaz-Sierra et al., 2017; Delory et al., 2019). The combination of both indices provides information on the symmetry of biotic interactions according to sowing time as suggested by Cleland et al. (2015), where PI is very close to their *secondary effect* and EI to their *priority effect*.

$$PI_{n,i} = 2\frac{Y_{n,i}^{Late} - \overline{Y_n^{Sync}}}{\overline{Y_n^{Sync}} + \left|Y_{n,i}^{Late} - \overline{Y_n^{Sync}}\right|} \quad (1)$$

$$EI_{n,i} = 2\frac{Y_{n,i}^{Early} - \overline{Y_n^{Sync}}}{\overline{Y_n^{Sync}} + \left|Y_{n,i}^{Early} - \overline{Y_n^{Sync}}\right|} \quad (2)$$

$Y_{n,i}^{Early}$ and $Y_{n,i}^{Late}$ are the cover of a species (Figure 5c,d), or a group of species (Figure 5a,b), sown early and late in plot i, respectively, n years after being sown. Y_n^{Sync} is the average cover of that same species, or group of species when sown synchronously. As the time between sowing events is one year, we used plant cover of the same age and not necessarily that of the same year. This may result in a bias if environmental factors such as meteorological conditions differ between years. This bias is, however, lower than using plant cover of the same year but different age.

We tested whether the estimated means were significantly different from zero by graphically analysing 95% confidence intervals. We then analysed for each index the differences between the species and between the two groups of species (dominants vs subordinates) using GLM for PI with Gamma distribution (log-link function) and LM for EI. All analyses were performed using R 3.5.3 (R Core Team, 2021).

3 | RESULTS

3.1 | Community assemblages

The NMDS ordination showed a clear separation of the community composition between the four treatments (df = 3; $F = 9.321$; $p < 0.001$, Figure 2), even after three years. Along the first axis of the NMDS, the three sequential sowing treatments were characterised by the sown species on the far right, while ruderal species, such as *Lactuca serriola* L., *Taraxacum* sp., *Medicago lupulina* L. and some mesophilous grassland species, such as *Coronilla minima* L., *Lotus corniculatus* L., *Poterium sanguisorba* L. and *Hippocrepis comosa* L. dominated the control on the left. The second axis separated the three sowing treatments, placing the synchronous sowing (D + S) in the middle of the two sequential sowing treatments with S1st on the upper and D1st on the lower part of this axis.

3.2 | Effect of sequential sowing on vegetation cover

In 2021, three years after the first sowing, the three seed addition treatments increased total plant cover and limited the development of species emerging from the soil seed bank or seed rain (Appendix S2, Appendix S3). Total cover contribution of unsown

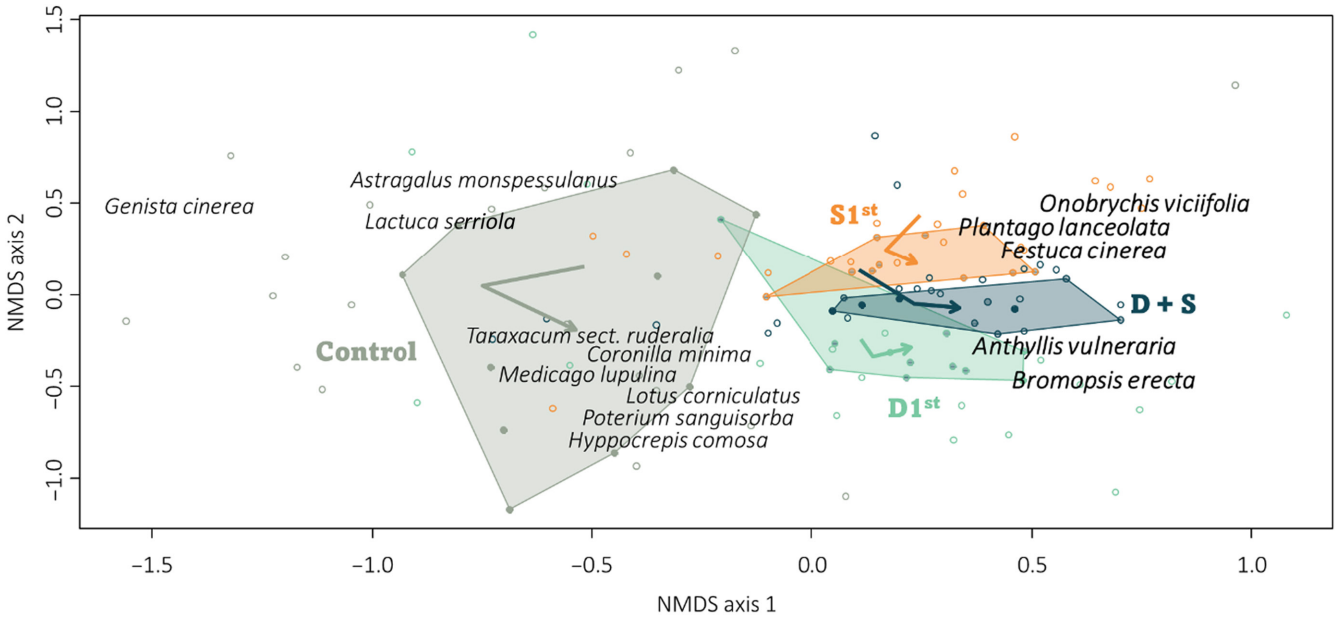

FIGURE 2 Plant species composition according to different sowing sequences using NMDS (NMDS stress: 0.24). Green, orange, blue and grey colour indicates D1st, S1st, Synchronous and Control sequences respectively. Arrows indicate changes in the position of the plot barycentre according to year (2019, 2020 and 2021). The third-year plots are shown as full dots and polygon group for each treatment. Only the 14 species of which cover is most correlated with plot position are shown and sown species are in bold.

species was 30% in the control and was much lower in D + S, D1st and S1st treatments (8%; Figure 3). The two Poaceae (both the relatively dominant and the relatively subordinate) and the subordinate *Onobrychis viciifolia* dominated the synchronous sowing (D + S). In the D1st treatment, the dominant *Bromopsis erecta* represented more than half of the total community cover whereas the cover of both the dominant *Anthyllis vulneraria* and the three subordinates was much smaller (<5%). As expected, subordinates best developed when sown first (S1st). In particular, the covers of the subordinate species *Plantago lanceolata* and *Onobrychis viciifolia* were considerably higher in the S1st than in other treatments.

In the third year, the total cover of the dominant Poaceae *Bromopsis erecta* was significantly higher in both D + S and D1st treatments with an average cover of 34%, compared to its cover in the S1st treatment being approximatively 5% (Figure 4, Appendix S4). There was no significant difference in *Bromopsis erecta* cover between D + S and D1st treatments. No significant treatment effect was found for the dominant Fabaceae *Anthyllis vulneraria*. The three subordinate species (*Festuca cinerea*, *Onobrychis viciifolia* and *Plantago lanceolata*) performed significantly better in S1st than in D1st. However, the cover of the subordinate Poaceae *Festuca cinerea* was not significantly different between S1st and D + S. Additionally, the cover of *Onobrychis viciifolia* and *Plantago lanceolata* was significantly lower in D + S than in S1st (when first sown).

3.3 | Priority and earliness indices

The priority index (PI) and the earliness index (EI) showed that the establishment of both dominants and subordinates was affected by

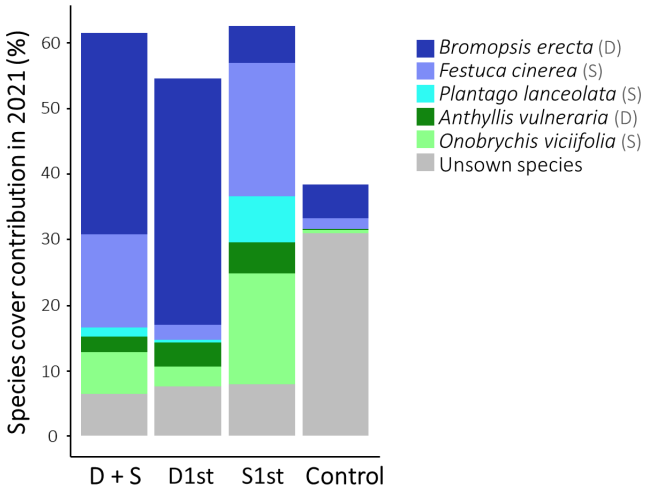

FIGURE 3 Species cover contribution to the total cover in the four treatments, in the third year. D, dominant species; S, subordinate species. D + S, dominant and subordinate species sown synchronously; D1st, dominant species sown first (subordinates second); S1st, subordinate species sown first (dominants second) and Control (no sowing). *Plantago media* did not germinate.

sequential sowing (Figure 5). Dominant and subordinate groups significantly differed in their EI (df = 1, $F = 16.16$, $p < 0.001$) but not in their PI (df = 1, $F = 0.18$, $p = 0.677$). PI was negative for both groups of species (Figure 5a) indicating that the early sown species induced negative effects on later sown species. A PI significantly different from zero would show that both the dominant *Bromopsis erecta* and the subordinates *Onobrychis viciifolia* and *Plantago lanceolata* were negatively affected when arriving late, but PI did not significantly differ between species (Figure 5c). Accordingly, over all dominants

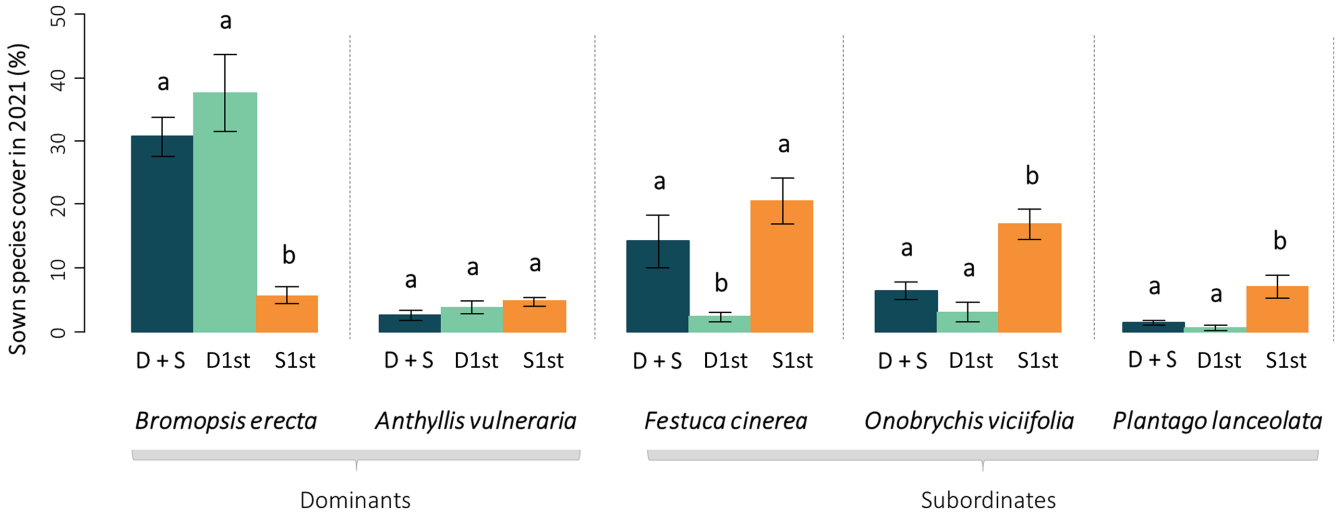

FIGURE 4 Sown species cover in the third year in the three sequential sowing treatments with: D + S, dominant and subordinate species sown synchronously; D1st, dominant species sown first (subordinates second); and S1st, subordinate species sown first (dominants second). Error bars are ±SE and a common letter indicates the absence of significant differences between treatments. Details in Appendix S1.

and subordinates, the PI was significantly negative but there was no significant difference between the two groups (Figure 5a). The EI of the subordinates, in particular of *Festuca cinerea* and *Plantago lanceolata*, was significantly different from zero whereas the EI of the dominants was not (Figure 5b,d, df = 4, $F = 5.10$, $p < 0.01$). The EI was significantly higher in subordinates than in dominants indicating that they benefited more from being sown first.

4 | DISCUSSION

We tested priority effects applied in grassland restoration using synchronous and sequential sowing with a one-year time difference. Manipulating the order of arrival influenced the community composition and trajectories three years after the first sowing. Both dominant and subordinate species showed a reduced cover when sown secondly compared to being sown synchronously. Being sown first, however, increased cover compared to being sown synchronously only for subordinates. The two Poaceae showed the same treatment response: the dominant *Bromopsis erecta* and its relative subordinate *Festuca cinerea* better established when sown first compared with both other treatments (sown later or synchronously).

We hypothesised that sowing subordinate species first not decrease the establishment of the dominant species, but we showed the opposite. The most abundant dominant species *Bromopsis erecta* is known to be a stress-tolerant competitor (Grime, 1979) and showed a significant disadvantage when sown second. This result suggests that *Bromopsis erecta* was affected by direct competition or indirect effects of already established vegetation. The competitive response of *Bromopsis erecta* depended on the time of arrival in a community (Cleland et al., 2015). The relative susceptibility of *Bromopsis erecta* to competition has already been highlighted under different environmental constraints (Corcket et al., 2003; Liancourt et al., 2005). The abundance of this dominant species in dry grasslands is also related to stress tolerance (Corcket et al., 2003; Liancourt et al., 2005). The second hypothesis, that subordinate species are favoured by being sown first, was partly supported by our results. *Onobrychis viciifolia* and *Plantago lanceolata* established well only when sown first. However, the subordinate *Festuca cinerea* was not favoured by sowing first compared to synchronous sowing. These priority effects may have been due to the stronger competitive effect of the dominants, in particular of *Bromopsis erecta* (hypothesis 3). Similar patterns were found in another study on *Onobrychis viciifolia*, showing a particularly weak competitiveness when sown after exotic species (Hess et al., 2020). Additionally, a priority effect experiment in riparian communities showed that subordinate species were more affected by the strength of priority effects (Sarneel et al., 2016). Furthermore, priority effects both favoured subordinate species when sown first, as shown by their highest EI, and hampered the growth of the most dominant species, *Bromopsis erecta*, allowing a higher level of species coexistence in the community. In this paper we differentiated dominant and subordinate species by their relative abundances within each functional group, not overall. For instance, *Festuca cinerea* has a lower average cover than *Bromopsis erecta* but also has a higher average cover than the other dominants (*Plantago media* and *Anthyllis vulneraria*). This may explain why its cover is not different when sown synchronously or when it is sown first. In the same way, we expected the communities resulting from sowing simultaneously and dominants first to be more similar if the 'dominants' were competitively dominant across all species.

The different response of species to the order of arrival may be explained by the niche components hypothesis (Vannette & Fukami, 2014), which states that the strength of priority effects depends on niche components (overlap, impact and requirements). Niche requirements differ between species and may influence (negatively or positively) their recruitment and/or establishment when

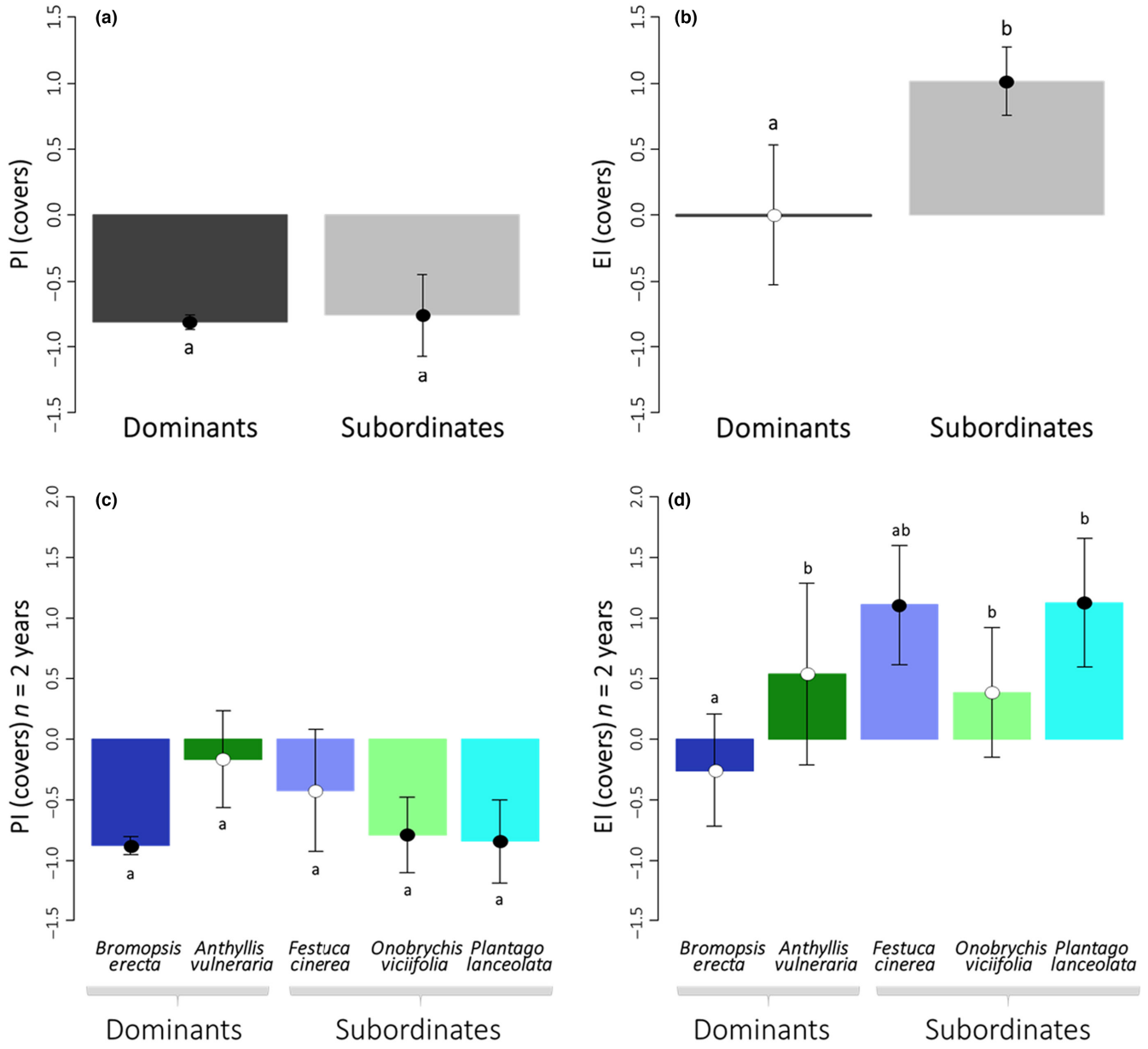

FIGURE 5 (a) Priority Index (PI) and (b) Earliness Index (EI) calculated for the cover of dominants (*Bromopsis erecta* + *Anthyllis vulneraria*) and subordinates (*Festuca cinerea* + *Onobrychis viciifolia* + *Plantago lanceolata*) after two years. (c) PI and (d) EI calculated for the sown species cover in 2021. For each species, values are estimated marginal means ±95% confidence intervals ($n = 10$). White dots indicate that confidence intervals included zero, black dots indicate that there was no overlap between confidence intervals and zero. A letter in common between two bars indicates the absence of significant differences between dominant and subordinate groups, or between two species ($p < 0.05$).

arriving late. Our results showed a lower performance of late-arriving species that were probably hampered by niche modification and size-asymmetric competition of the pre-established vegetation (Vannette & Fukami, 2014; Wilsey, 2020), or by niche pre-emption (Fukami, 2015). Hypotheses three and four were partly validated since the dominant *Bromopsis erecta* had a negative effect on the development of other sown species. The cover of the dominant Fabaceae *Anthyllis vulneraria* was not affected by the sowing treatments or was potentially negatively affected by being sown together with *Bromopsis erecta*, and was thus not higher when the species was sown first. *Anthyllis vulneraria* is a dispersal-limited, late-successional but fast-growing species that may benefit from being sown in a pre-established plant community (Erschbamer, 2007; Marcante et al., 2009). Furthermore, its roots are longer and deeper than those of the sown subordinate Fabaceae *Onobrychis viciifolia* and of the other sown species (Jungk, 1993), thus avoiding competition for soil resources. In our study, *Anthyllis vulneraria* was not negatively affected by the pre-established community when sown after subordinate species (PI close to zero), which confirms a high recruitment capacity in established vegetation (Vannette & Fukami, 2014),

unless it was affected by *Bromopsis erecta*. Positive effects of already established vegetation on the recruitment niche (e.g., living cover protecting young seedlings and improving water retention; Donath et al., 2006; Durbecq et al., 2022; Wright et al., 2014) may have favoured the dominant *Anthyllis vulneraria* when sown second or synchronously. Alternatively, plant–soil feedback such as interactions with rhizobia may have contributed to the priority effects (de Vries et al., 2012, 2018; Fry et al., 2017; Fukami, 2015; Fukami & Nakajima, 2013; Goldstein & Suding, 2014). The mechanisms of underlying priority effects need to be better understood, with a particular focus on plant–soil feedback and below-ground interactions (Bever, 2003; Fry et al., 2017; Fukami & Nakajima, 2013; Hess et al., 2020; Weidlich et al., 2018). Plant–soil interactions are species-specific (Bezemer et al., 2006; van der Voorde et al., 2011) and the strength of priority effects depends on both the order of arrival and species identity (Cleland et al., 2015; Stuble & Souza, 2016; von Gillhaussen et al., 2014; Wilsey et al., 2015; Werner et al., 2016). Therefore, an advance of a particular species of one year may change soil biota and nutrient status, as well as productivity by niche modification (Vannette & Fukami, 2014).

In conclusion, regardless of underlying mechanisms, our study provides evidence that plant community assembly was influenced by the order of arrival, potentially changing community composition and trajectories. In several cases, coexistence may need sequential arrival in a community (Fragata et al., 2022; Song et al., 2021). Thus, the order of species arrival may be a useful tool to optimise seed-sowing approaches in ecological restoration. Our results were in agreement with those of other studies indicating strong variations between species and thus highly species-specific priority effects (Cleland et al., 2015; Stuble & Souza, 2016). The next step in the use of priority effects in restoration ecology would be to obtain a better understanding of the predictability of priority effects (Song et al., 2021) and to identify the need for sequential sowing which may differ depending on species and environmental characteristics. Our distinction between relatively (within each family) dominant and subordinate species was a first attempt to categorise species that would need to be sown sequentially and those that are competitive in simultaneous sowing. A more specific categorisation based on functional traits of species, especially traits related to germination and early-stage survival and growth may provide more results (Torrez et al., 2017). To be applied in ecological restoration, further studies are needed to assess priority effects of target species in different habitat types with different plant communities. Furthermore, a higher number of species of different functional groups needs to be tested to evaluate a potential application in ecological restoration. Such knowledge would allow practitioners to establish lists of species that need to be sown first, second or synchronously in order to develop the plant community structure toward identified references.

AUTHOR CONTRIBUTIONS

Aure Durbecq, Armin Bischoff, Elise Buisson and Renaud Jaunatre conceived the project and conducted the field surveys; Aure Durbecq and Renaud Jaunatre analysed the data and drafted the manuscript. All authors (Aure Durbecq, Renaud Jaunatre, Armin Bischoff, Elise Buisson and Emmanuel Corcket) improved the text and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Alice Dupré-La-Tour, Daniel Pavon, Julien Planche, Margaux d'Ambly, Léo Rocher, Chloé Malik, Gaëlle Carrière, and François-Marie Martin for their assistance. We also thank Benjamin Delory for the discussion on priority effects and the three reviewers for their suggestions.

FUNDING INFORMATION

Financial support was provided by the environmental consultancy ECO-MED (Ecologie & Médiation), RTE (Electricity Transmission Network) and ANRT (National Agency of Research and Technology via the grant CIFRE N°2017/0478).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

Code and data are publicly available at https://forgemia.inra.fr/renaud.jaunatre/durance_pe.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Experimental design with the 40 plots including the ten replicates of the four randomly distributed treatments: D+S: dominant and subordinate species were sown synchronously; D1st: dominant species were sown first (subordinates second); S1st: subordinate species were sown first (dominants second); and Control (no sowing).

Appendix S2. Total species cover and unsown species cover (species from the seed bank/seed rain) in the four treatments in 2019, 2020 and 2021.

Appendix S3. Percentage mean cover of spontaneously emerging plant species.

Appendix S4. Effect of the sowing treatments on sown species cover in 2021 (Figure 4).

How to cite this article: Durbecq, A., Bischoff, A., Buisson, E., Corcket, E. & Jaunatre, R. (2023) Using priority effects for grassland restoration: Sequential sowing can promote subordinate species. *Applied Vegetation Science*, 26, e12748. Available from: https://doi.org/10.1111/avsc.12748