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When history matters: The overlooked role of priority effects in grassland overyielding

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Abstract

1. Biodiversity–ecosystem functioning experiments have shown that plant species and functional group richness are important drivers of grassland productivity, but the impact that plant order of arrival (i.e. priority effects) has on grassland overyielding and its drivers (complementarity and dominance effects) has been overlooked so far.
2. Using species-specific plant biomass data collected in mixture and monoculture plots of a grassland field experiment (Jülich Priority Effect experiment) that manipulated the order of arrival of three plant functional groups (forbs, grasses and legumes), we quantified net biodiversity effects (overyielding) as well as complementarity and dominance effects in mixtures one and 2 years after sowing. In this experiment, priority effects were created by sowing one functional group 6 weeks before the two others. First, we tested whether plant order of arrival affected overyielding, complementarity and dominance effects. Second, we investigated whether the magnitude of net biodiversity, complementarity and dominance effects was dependent on the strength and direction of priority effects.
3. We found that complementarity and dominance effects were affected by plant order of arrival during community assembly. In addition, we found that moving from negative to positive priority effects increased grassland overyielding, mainly via increased complementarity effects.
4. These results highlight the need to combine biodiversity and assembly approaches in future ecosystem functioning research, as this will increase the predictive power of community ecology in conservation and ecological restoration.

KEYWORDS
additive partitioning, biodiversity, community assembly, ecosystem functioning, historical contingency, plant order of arrival

1 | INTRODUCTION

Long-term biodiversity–ecosystem functioning (BEF) experiments have shown that communities with a greater plant species or functional group richness are often more productive above-ground (Hector et al., 1999; Marquard et al., 2009; Tilman et al., 1997) and below-ground (Oram et al., 2018; Ravenek et al., 2014). Several mechanisms such as multitrophic interactions, resource partitioning and abiotic facilitation have been proposed to explain these positive biodiversity–productivity relationships, but their relative contributions to grassland overyielding remain unclear (Barry et al., 2018; Eisenhauer, 2012; Weisser et al., 2017). Over the years, the use of statistical methods developed to partition the net effect of biodiversity on ecosystem functioning into two (Loreau & Hector, 2001) or three (Fox, 2005) additive components has allowed researchers to quantify the contribution of niche differences and/or interspecific interactions (complementarity effect) as well as dominance of highly productive species (dominance/selection effect) to the increased functioning of diverse plant communities. Although these additive partitioning methods do not allow a direct identification of the biological processes driving grassland overyielding (Barry et al., 2018; Hector et al., 2009), they largely contributed to a better understanding of the mechanisms behind the patterns observed in BEF experiments (Cadotte, 2017; Cardinale et al., 2007; Fox, 2005; Loreau & Hector, 2001, 2019; Marquard et al., 2009; Oram et al., 2018; Roscher et al., 2005).

Plant species and functional group richness, however, are not the only drivers of ecosystem functioning in natural habitats. Both the order and timing of species arrival during community assembly can also have long-lasting impacts on community structure and functioning (Fukami et al., 2010; Körner, Stöcklin, Reuther-Thiébaud, & Pelaez-Riedl, 2008; Švamberková, Doležal, & Lepš, 2019; Weidlich et al., 2017, 2018; Wilsey, Barber, & Martin, 2015), as well as on the shape of the relationship between biodiversity and productivity (Fukami & Morin, 2003). This phenomenon is referred to as a priority effect and is a biotic component of historical contingency (Fukami, 2015; Grainger, Letten, Gilbert, & Fukami, 2019; Ke & Letten, 2018). Priority effects occur when early arrival of species affects the establishment, growth or reproduction of species arriving later (Eriksson & Eriksson, 1998) and can thus lead to alternative states in vegetation (Fukami, 2010, 2015; Fukami & Nakajima, 2011).

Despite the importance of priority effects for community assembly, we lack an understanding of their importance in influencing the direction and magnitude of the relationship between biodiversity and ecosystem functioning. At a given level of plant species and functional richness, however, it is probable that different sequences of plant species arrival could affect grassland overyielding via its effects on complementarity and dominance effects. For instance, an early arrival of N_2-fixing species (legumes) in the community could favour the establishment of late-arriving species such as grasses and non-N_2-fixing forbs via nitrogen facilitation mechanisms (Temperton, Mwangi, Scherer-Lorenzen, Schmid, & Buchmann, 2007), thus leading to the creation of positive priority effects. This would be in line with the greater net biodiversity and complementarity effect values usually observed in grassland communities containing legumes (Loreau & Hector, 2001; Marquard et al., 2009). Because larger complementarity effect values are expected when species facilitate one another (Fox, 2005; Loreau & Hector, 2001), positive priority effects would then be associated with greater complementarity effect values. An early arrival of species performing well in monoculture plots (e.g. grasses), however, could lead to negative priority effects and larger dominance effect values because early-arriving species might dominate mixtures at the expense of species arriving later during assembly. Therefore, we hypothesize that different sequences of plant species arrival during community assembly would lead to the creation of priority effects affecting the magnitude of net biodiversity effects as well as the relative contributions of complementarity and dominance effects to grassland overyielding.

To test this hypothesis, we used species-specific plant biomass data collected in 2013 and 2014 in a subset of the plots of the Jülich Priority Effect experiment located in Germany (Weidlich et al., 2017, 2018). In this field experiment, the order of arrival of three plant functional groups (PFG: legumes, grasses and non-N_2-fixing forbs) was manipulated to investigate how priority effects affect plant community structure and ecosystem functioning in temperate grasslands. Each PFG arrived either 6 weeks earlier (legumes, grasses or forbs sown first) or at the same time (synchronous) as the other PFGs. For each experimental plot, the net biodiversity effect was quantified as in Loreau and Hector (2001) and was partitioned using the method of Fox (2005) into three additive components: trait-independent complementarity effect, trait-dependent complementarity effect and dominance effect (Table 1). These data were analysed using a two-step approach. First, we investigated whether PFG order of arrival affected overyielding as well as its drivers in assembling grassland communities. Second, we investigated whether the magnitude of net biodiversity, complementarity and dominance effects was dependent on the strength and direction of priority effects. This study provides strong evidence that manipulating plant order of arrival during community assembly can lead to the creation of priority effects of various strengths and directions affecting the magnitude of net biodiversity effects in grassland communities.

2 | MATERIALS AND METHODS

2.1 | The Jülich Priority Effect experiment

We used above-ground plant biomass data collected at the species level in June 2013 and June 2014 from a subset of the plots of the Jülich Priority Effect experiment located in Germany (latitude: 50°53′51.53″N, longitude: 6°25′21.09″E, elevation: 94 m, average air temperature: 10.6°C, average annual precipitation: 704 mm). Detailed meteorological data measured in Jülich from 2012 to 2014 are provided in Figure S1. A detailed description of the experiment can be found in Weidlich et al. (2017). Briefly, this experiment was set up in 2012 using a full factorial and randomized design to study how PFG order of arrival and sown species richness affect ecosystem functioning and plant community structure in temperate grasslands (Weidlich et al., 2017, 2018). Priority effects in community assembly

TABLE 1 Interpretation of the terms of the two-way additive partitioning method of Loreau and Hector (2001) and the tripartite additive partitioning method of Fox (2005)

		Interpretation		
Loreau and Hector (2001)	**Fox (2005)**	**Positive values**	**Zero**	**Negative values**
Net biodiversity effect (NBE) $NBE = \sum_{i=1}^{N} (Y_{Oi} - Y_{Ei}) = \sum_{i=1}^{N} (Y_{Oi} - RY_{Ei} M_i)$		The observed yield in mixture is greater than the weighted average of the monoculture yields (overyielding)	The observed yield in mixture is equal to the weighted average of the monoculture yields (no effect)	The observed yield in mixture is lower than the weighted average of the monoculture yields (underyielding)
Complementarity effect	Trait-independent complementarity effect (TICE) $TICE = \left(\sum_{i=1}^{N} RY_{Oi} - 1 \right) \bar{M}$	Species yields are on average higher than expected under the null hypothesis. Large values are expected if species occupy different niches or facilitate one another	No effect	Indicates interspecific competition (e.g. physical and/or chemical interference) or other processes with the same effect
Selection effect	Dominance effect (DE) $DE = N \operatorname{cov} \left(M, \frac{RY_O}{\sum_{i=1}^{N} RY_{Oi}} - RY_E \right)$	Species with higher-than-average monoculture yields dominate at the expense of species with low monoculture yields. Large values are expected when species occupy similar niches	No effect	Species with lower-than-average monoculture yields dominate at the expense of others
	Trait-dependent complementarity effect (TDCE) $TDCE = N \operatorname{cov} \left(M, RY_O - \frac{RY_O}{\sum_{i=1}^{N} RY_{Oi}} \right)$	Species with higher-than-average monoculture yields dominate, but not at the expense of species with low monoculture yields. Large values suggest that species have nested niches	No effect	Species with lower-than-average monoculture yields dominate, but not at the expense of species with high monoculture yields

Note: In the equations listed in this table, N is the number of species sown in the plots, RY_{Oi} is the observed relative yield of species i (i.e. the ratio between the yield of species i growing in mixture and the yield in its corresponding monoculture), RY_{Ei} is the expected relative yield of species i ($1/N$), and $\bar{M}$ is the average monoculture yield across all sown species.

were created by manipulating the order of arrival of three PFGs: N_2-fixing forbs (legumes), non-N_2-fixing forbs (forbs) and grasses. In synchronous communities, all plant species were sown at the same time during the first sowing event. In forbs-first (F-first), grasses-first (G-first) and legumes-first (L-first) communities, however, all the species from one PFG were sown 6 weeks before the others. Even though this experiment was initially set up using two sown species richness levels (9 or 21 species), we only used data collected from plots in which nine species (three species per functional group) were sown, as monoculture plots were only available for the species present in the 9 species mixtures (see Table S1). In addition, because the plots were set up on two different areas characterized by two different soil types, we only used plant biomass data collected from the plots located on the same area as the monocultures to ensure comparability. In total, data collected from 16 mixture plots (n = 4 for each PFG order of arrival treatment; surface: 16 m^2/plot) and 18 monoculture plots (n = 2 for each species; surface: 4 m^2/plot) were used for this study. Both monoculture and mixture plots were established at the same time when the experiment was set up in 2012.

2.2 | Additive partitioning of net biodiversity effects

For each experimental plot with N species sown, we calculated the net biodiversity effect (NBE) as the difference between the observed yield (Y_O) and the yield that would be expected (Y_E) if each component species growing in mixture produces 1/N of the yield produced in its corresponding monoculture (M). We then used the method of Fox (2005) to partition NBE into three additive components: dominance effect (DE), trait-independent complementarity effect (TICE) and trait-dependent complementarity effect (TDCE) (Equation 1). This tripartite partitioning method is a modified version of the two-way partitioning method proposed by Loreau and Hector (2001) (i.e. the selection effect of Loreau and Hector is exactly equal to the sum of the dominance effect and trait-dependent complementarity effect of Fox). Table 1 summarizes information from the papers of Fox (2005) and Loreau and Hector (2001) to calculate and help interpreting the terms of their additive partitioning methods. All calculations were performed using the *apm* function of the *bef* R package developed for the purpose of this study. This R package is available on GitHub (https://github.com/BenjaminDelory/bef).

$$\mathrm{NBE} = \mathrm{TICE} + \mathrm{DE} + \mathrm{TDCE} \quad (1)$$

2.3 | Quantification of priority effects

In our field experiment, we created priority effects by sowing a group of $N - p$ (N *minus* p) species 6 weeks after a group of p early-arriving species (N is the total number of species sown in the plots). The cost of arriving late during plant community assembly (P, priority effect) for the $N - p$ late-arriving species was calculated using Equation 2, in which Y_{Oi}^{Late} and Y_{Oi}^{Sync} are the observed yields of species i when it arrived later or at the same time as the early-arriving species, respectively. This priority effect index has the same mathematical properties as the additive neighbour-effect intensity index developed by Díaz-Sierra, Verwijmeren, Rietkerk, Dios, and Baudena (2017): it is standardized, symmetric (additive symmetry) and bounded between −1 (competitive exclusion of late-arriving species) and +2 (obligate facilitation of late-arriving species). The direction and strength of the priority effect are given by the sign and absolute value of P, respectively (Figure 1). As we had four replicates for the Synchronous treatment, we calculated four values of P for each F-first, G-first and L-first plot. In Figure 3 and Figure S4, we reported the mean value of P (n = 4) calculated for each plot with a priority effect treatment as well as its 95% confidence interval computed by bootstrapping using the percentile method (10,000 iterations).

$$P = 2\frac{\sum_{i=1}^{N-p}\left(Y_{Oi}^{Late} - Y_{Oi}^{Sync}\right)}{\sum_{i=1}^{N-p} Y_{Oi}^{Sync} + \left|\sum_{i=1}^{N-p}\left(Y_{Oi}^{Late} - Y_{Oi}^{Sync}\right)\right|} \quad (2)$$

2.4 | Statistical analyses

We used two-way ANOVA models to determine whether the PFG order of arrival in assembling communities, the sampling year (1 or 2 years post-seeding) or their interaction affected overyielding and its three additive components (DE, TICE and TDCE). ANOVA assumptions were systematically checked by looking for any pattern in a plot showing the values fitted by the linear model against model residuals. Detailed ANOVA tables are provided in Table S2. Pairwise comparisons using Tukey contrasts were performed on estimated marginal means computed with the emmeans (Lenth, 2018) R package. p-values and 95% confidence intervals were adjusted for multiple comparisons using Tukey adjustment. Sidak's adjustment method was used when Tukey's method was not appropriate. We tested whether the estimated marginal means were significantly different from zero by examining whether their 95% confidence interval contained zero or not. If the confidence interval did not contain zero, we considered that the estimated marginal mean significantly deviated from zero.

For each combination of sampling year and PFG order of arrival, we evaluated the agreement between the observed and expected yields of each component species growing in mixture by examining whether the 95% confidence interval surrounding the average observed yield contained the value expected by the null model or not (see Figures S2 and S3). The confidence intervals were computed by bootstrapping (10,000 iterations) using the percentile method. If the 95% confidence interval of a given species did not contain the yield value expected by the null model, we considered that the observed and expected yields were significantly different from each other.

For each sampling year, the strength of the linear relationship between the priority effect index (P) and overyielding (NBE), trait-independent complementarity effect (TICE), trait-dependent complementarity effect (TDCE), total complementarity effect (CE = TICE + TDCE) or dominance effect (DE) was assessed by calculating Pearson`s product–moment correlation coefficients.

When a significant linear relationship was found between two variables ($p < .05$), standardized major axis regression models were fitted using the smatr R package (Warton, Duursma, Falster, & Taskinen, 2012). Correlation coefficients and model parameters with their 95% confidence interval are provided in Table S3. Results for TICE and TDCE are provided as supplementary material (Figure S4).

Statistical analyses were performed in R 3.5.2 (R Core Team, 2018) with an alpha value of .05.

3 | RESULTS

3.1 | Plant order of arrival during community assembly affects complementarity and dominance effects

One year after setting up the Jülich Priority Effect experiment (data collected in 2013), all mixture plots were overyielding, and the magnitude of this positive biodiversity effect was not affected by the order of arrival of PFG during community assembly (Figure 2a). The mechanisms behind overyielding, however, were strongly affected by PFG order of arrival. While overyielding in synchronous (Sync), forbs-first (F-first) and grasses-first (G-first) communities were simultaneously driven by positive dominance and trait-independent complementarity effects (Figure 2b,c), overyielding in plots where legumes were sown first (L-first) was mainly caused by a dominance effect (Figure 2b). Contrary to our expectations, the trait-independent complementarity effect was the lowest (in fact, not significantly different from zero) when legumes were the first to arrive in the community (Figure 2c). We did not find any significant difference in trait-dependent complementarity effect between PFG order of arrival treatments. As shown in Figure 2d, this effect was either close to (G-first) or not significantly different from zero (Sync, F-first and L-first). The strong dominance effect observed in communities where legumes were sown first was due to the fact that one legume species (*Trifolium pratense*) with higher-than-average monoculture yield dominated the mixtures at the expense of all the other species sown in the plots, except for *Medicago sativa*. In these plots, the yield achieved by *T. pratense* was on average 23% lower than its yield in monoculture (see Figure S2). In plots where grasses and forbs were sown first, all the species that arrived first performed better or as good as what would be expected under the null hypothesis (i.e. for each species *i*, its yield in mixture Y_{Oi} equals its yield in monoculture M_i divided by sown species richness), despite the fact that *T. pratense*

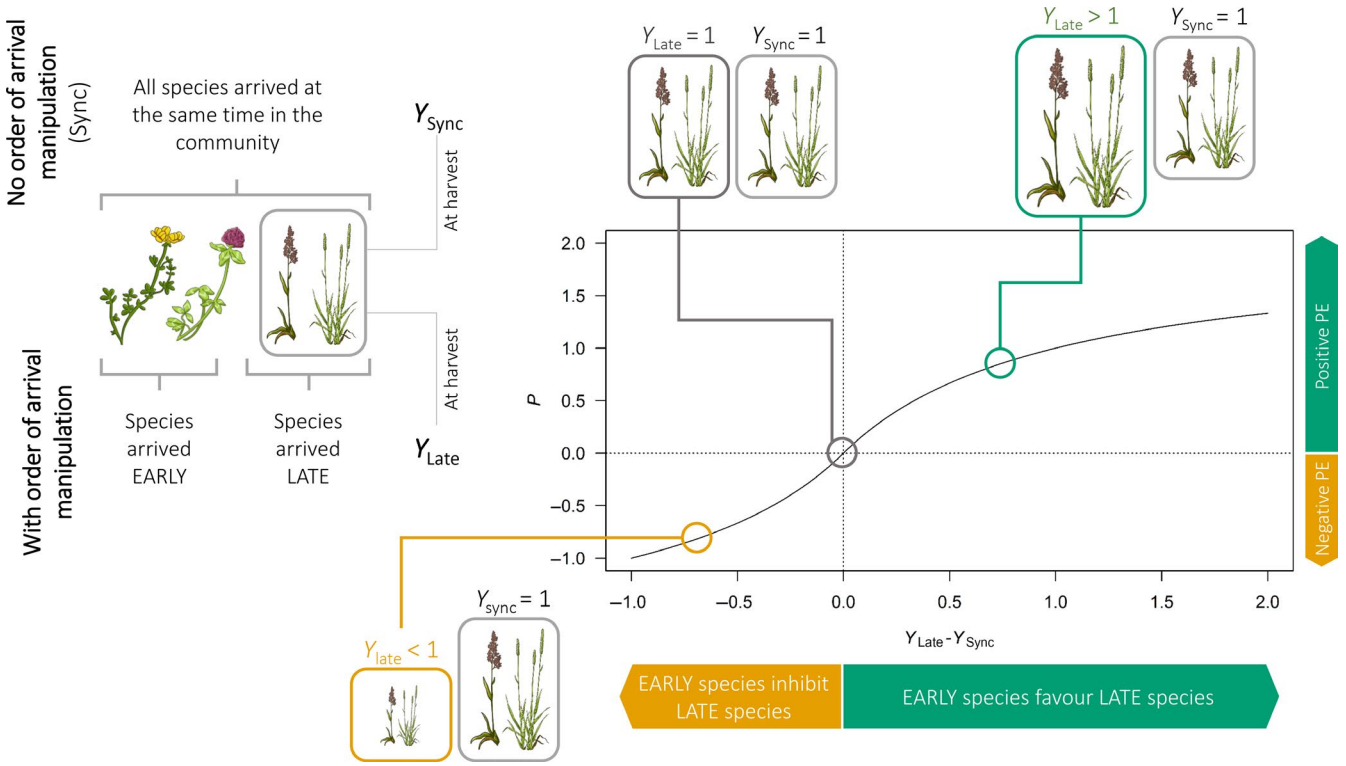

FIGURE 1 Framework for the quantification of priority effects. In our experiment, we created priority effects by manipulating plant order of arrival. To do so, one plant functional group was sown 6 weeks before the two others. A scenario without any order of arrival manipulation (synchronous) was also included in the experimental design. Y_{Late} is the total yield of late-arriving species in the treatment with order of arrival manipulation. Y_{Sync} is the total yield of the late-category species in the synchronous treatment. For each order of arrival scenario, both Y_{Late} and Y_{Sync} are calculated using the same species pool. Y_{Sync} was fixed at 1 unit. The priority effect index (*P*) shares the same mathematical properties as the additive intensity index proposed by Díaz-Sierra et al. (2017): it is standardized, symmetric around zero, and is bounded between −1 and +2

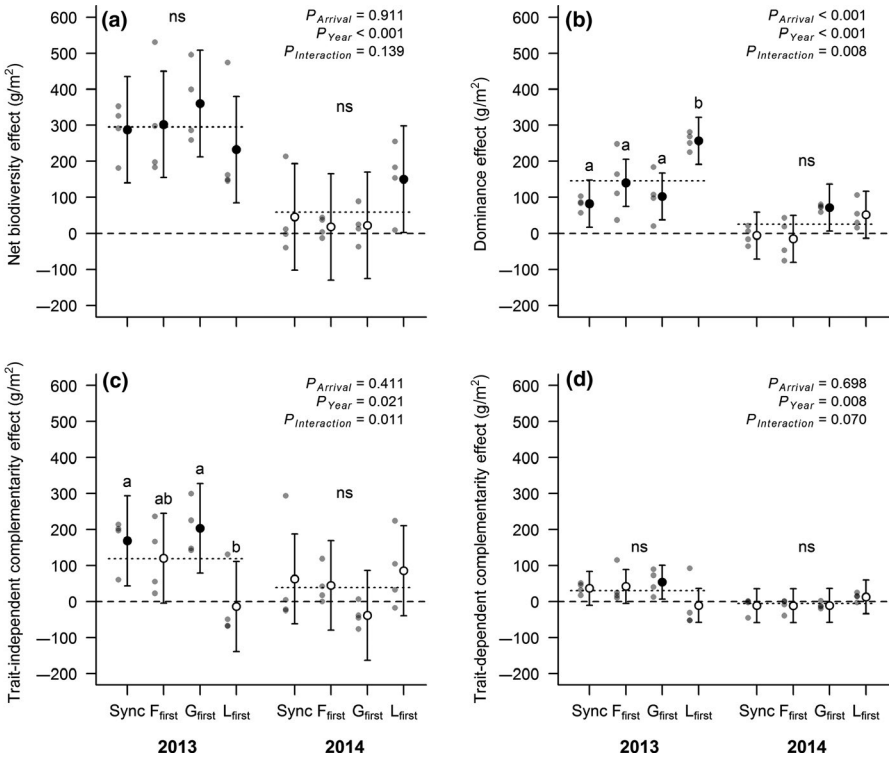

FIGURE 2 PFG order of arrival alters overyielding drivers in the Jülich Priority Effect experiment. The tripartite method of Fox (2005) was used for the partitioning. For each sampling year and each PFG order of arrival treatment, the panels show the net biodiversity effect (a) and its three additive components: dominance effect (b), trait-independent complementarity effect (c) and trait-dependent complementarity effect (d). Values are estimated marginal means ± 95% confidence intervals (n = 4). Individual data points are displayed as grey dots on the left side of each group. For each sampling year, PFG order of arrival treatments that do not share a common letter are significantly different from each other (p < .05). Mean values that are significantly different from zero are shown with a filled dot (p < .05). Means values are otherwise shown with an empty dot (p > .05). Detailed ANOVA tables are available in Table S2

was also dominating the plots (see Figure S2). In plots where all PFG were sown at the same time, however, at least one species of each PFG performed better or as good as what would be expected based on monoculture yields (see Figure S2).

In 2014, overyielding values were 80% lower than in 2013 (Figure 2a). Similarly, the dominance, trait-independent complementarity and trait-dependent complementarity effects measured in 2014 were on average 82%, 68% and 117% lower than in 2013, respectively (Figure 2b–d). Although we did not find any statistically significant difference between PFG order of arrival treatments for all biodiversity effects measured in 2014 (Figure 2a–d), plots where legumes were sown first were the only ones to consistently have positive overyielding values (Figure 2a), and plots where grasses were sown first were all characterized by positive dominance effect values (Figure 2b). For all PFG order of arrival treatments, both trait-independent and trait-dependent complementarity effects measured in 2014 were not significantly different from zero (Figure 2c,d). In all experimental plots harvested in 2014, two grass species (*Dactylis glomerata* and *Holcus lanatus*) consistently performed better or as good as what would be expected under the null hypothesis (see Figure S3). These two species performed remarkably well in legumes-first plots, with *D. glomerata* even having a yield in mixture not significantly different from that obtained in monoculture (see Figure S3). Except for plots where legumes were sown first, the biomass of *T. pratense* measured in 2014 was lower than what would be expected by the null model. The species with the greatest monoculture yield (*Festuca pratensis*) had a low productivity in all experimental plots, except in those where grasses were sown first (see Figure S3), thus explaining the positive dominance effect values measured in grasses-first plots (Figure 2b). In plots where they were the first to arrive, all forb species performed at least as well as what would be predicted by the null model (see Figure S3).

3.2 | Moving from negative to positive priority effects increases grassland overyielding via increased complementarity effects

Overyielding in our grassland experiment was positively correlated to the priority effect index (Figure 3a,b, Table S3). Interestingly, this increase in net biodiversity effect observed when moving from negative to positive priority effects was solely due to an increase in complementarity effects (Figure 3c,d). Both trait-independent and trait-dependent complementarity effects were positively correlated to *P* (see Figure S4 and Table S3), but no relationship was found between dominance effect and *P* (Figure 3e,f). The same pattern was

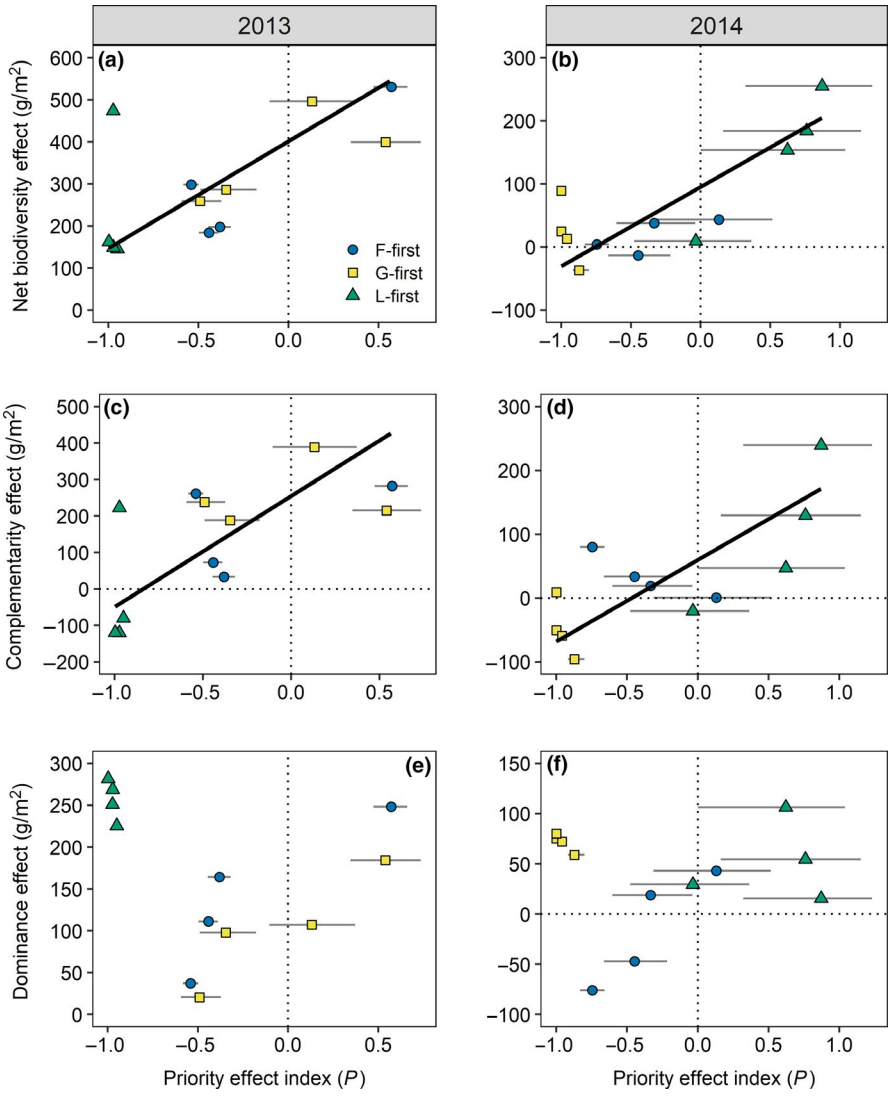

FIGURE 3 Moving from negative to positive priority effects increases complementarity and overyielding in a temperate grassland. The relationship between the priority effect index and overyielding (a, b), complementarity (c, d) or dominance (e, f) is shown separately for each sampling year (left panels, 2013; right panels, 2014). When two variables were significantly correlated ($p < .05$), the regression line (solid line) is shown. Values of *P* are shown as mean ± 95% confidence interval ($n = 4$). The confidence intervals were computed by bootstrapping using the percentile method (10,000 iterations). Pearson's product–moment correlation coefficients (*r*) and regression parameters (slope and intercept) can be found in Table S3. The symbol used for each individual observation refers to the PFG order of arrival treatment (see legend in panel a)

found in both sampling years despite the fact that the priority effect index values calculated for each experimental plot were very different in 2013 and 2014, particularly for plots where legumes or grasses were sown first (Figure 3).

In legumes-first plots, strong negative priority effects (*P* close to −1) were measured in 2013 but, one year later, 75% of these plots were characterized by strong positive priority effects (*P* close to +1) and had the greatest overyielding values. These results strongly suggest that sowing legumes first can lead to the creation of positive priority effects. In plots where grasses were sown first, however, 25% of the plots were characterized by positive priority effects (*P* close to 0.5) in 2013, with only 50% of the plots having negative priority effect values (*P* close to −0.5) on the same year. One year later (2014), all grasses-first plots were characterized by strong negative priority effects (*P* close to −1).

4 | DISCUSSION

Linking BEF research with the field of community assembly is one of the next important steps in ecology, since natural communities experience assembly and are not weeded as BEF experiments are (Bannar-Martin et al., 2018). In order to do this, we believe that assembly processes that are important for the structure and functioning of plant communities, such as historical contingency in plant species order of arrival, have to be considered alongside plant species and functional group richness. This study enabled an important step in this direction within a priority effect experiment that includes natural assembly as well as monocultures. We show that plant order of arrival can affect overyielding drivers, namely complementarity and dominance effects, in the first years of assembly of a temperate grassland. We also provide evidence that the magnitude of complementarity and net biodiversity effects is dependent on the strength and direction of priority effects. More specifically, we showed that the greatest overyielding values were achieved in plots characterized by positive priority effects, and that the main reason for this was increased complementarity effects.

Overall, the net effect of biodiversity on above-ground productivity in the Jülich Priority Effect experiment markedly decreased from 2013 to 2014. This drop in overyielding was paralleled by a

decrease in complementarity (both trait-independent and trait-dependent) and dominance effects. Even though grassland overyielding usually tends to strengthen over time because of increased species complementarity (Cardinale et al., 2007), year-to-year fluctuations have also been observed in other BEF experiments. For instance, in the Jena Main experiment, the net effect of biodiversity on above-ground productivity decreased between the two first years of the experiment (Marquard et al., 2009), although not as strongly as what we observed in our study. This decrease in overyielding was then followed by a constant increase in net biodiversity and complementarity effects up to the fifth year of the Jena Main experiment (Marquard et al., 2009). In the Jena Trait-based experiment, the net effect of biodiversity on root productivity did not change between the first and third year of the experiment. Complementarity and selection effects, however, strengthened over time, but in two opposite directions: while complementarity effect became more positive, selection effect became more negative from 2012 to 2014 (Oram et al., 2018). Unfortunately, we were not able to investigate long-term fluctuations in biodiversity effects in the Jülich Priority Effect experiment because plant biomass data measured at the species level were only available for the second and third growing seasons. Considering that grasses dominated all plots at the end of our experiment (Weidlich et al., 2017), however, it is possible that stabilizing mechanisms favouring the growth of rare species over dominant ones would have contributed to increase the relative abundance of forbs and legumes in the years following 2014 (see Chesson, 2000; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012). Negative biotic plant–soil feedbacks are an example of such mechanism, because the accumulation of specialist pathogens in the rhizosphere of dominant species would promote negative frequency dependence and allow species to coexist (Mommer et al., 2018; Mordecai, 2011). This might then have led to an increase in complementarity and net biodiversity effects in our experimental plots.

Although the biological mechanisms responsible for the greater competitive ability of grass species observed in 2014 is unknown, it explains the strong negative priority effects measured on the third year of the experiment in plots where grasses were sown first. In these plots, grasses competitively excluded forbs and legumes (the total above-ground biomass production of forbs and legumes was on average 94% lower in grasses-first plots than in synchronous plots) (see Figure S3). The reasons behind this strong grass dominance are still unclear, but knowledge gained in other ecosystems, such as Mediterranean grasslands, can help to identify possible environmental drivers favouring grass-dominated transient states. In a field experiment testing the importance of year and site effects on the structure of plant communities in Californian grasslands, Stuble, Fick, and Young (2017) also found good 'grass' years leading to different vegetation states and identified both mean annual temperature and total number of rainy days as likely drivers of plant community dissimilarities. In a different study, Clary (2008) found that the relative abundance of annual and perennial grass species in Mediterranean grasslands was mainly determined by rainfall seasonality, with low summer precipitation levels favouring annual grass dominance. Although we cannot confirm it, the overall warmer and drier conditions during the third growing season of our experiment might have driven the convergence of plant communities towards a grass-dominated state. Our study makes abundantly clear that more research is now needed to improve the predictability of transient community dynamics with regard to weather conditions during plant establishment and plant order of arrival during assembly (Fukami & Nakajima, 2011; Temperton, Baasch, Gillhaussen, & Kirmer, 2016).

Contrary to our expectations, sowing leguminous species before the other PFGs led to a strong dominance of *T. pratense* and created strong inhibitory priority effects for late-arriving species after 1 year. Considering that (a) the leaf area index and light interception by the canopy are high when leguminous species such as *T. pratense* are present (Frankow-Lindberg, 2012; Mwangi et al., 2007), (b) plot invasibility can be negatively correlated with legume abundance (Tilman, 1997), and (c) legumes are able to increase soil N availability via direct N transfer to non-legume neighbours (N transfer) and/or reduced interspecific competition for soil mineral N (N sparing) (Fargione, Brown, & Tilman, 2004; Frankow-Lindberg, 2012; Temperton et al., 2007), it is probable that late-arriving species were more limited by light than nutrient availability in legumes-first plots on the second year of the experiment (DeMalach, Zaady, & Kadmon, 2017; Hautier, Niklaus, & Hector, 2009; Roscher, Kutsch, & Schulze, 2011). For 75% of the plots where legumes were sown first, however, the direction of priority effects shifted towards positive values 2 years after the start of the experiment, and these plots were also those with the greatest overyielding values in 2014. Although our results suggest that increased complementarity probably favoured the establishment of late-arriving species in plant communities (i.e. positive values of our priority effect index were associated with greater complementarity effect values), the ecological mechanisms at play are still unclear and deserve more research attention in the future (Barry et al., 2018; Wright, Wardle, Callaway, & Gaxiola, 2017). Following the framework proposed by Barry et al. (2018), we present three non-mutually exclusive mechanisms that could explain increased complementarity between early and late-arriving species: below-ground resource partitioning, biotic feedbacks (both negative and positive) and abiotic facilitation (physical stress buffering).

Below-ground resource partitioning in space and/or time has been one of the most prevalent hypotheses to explain the positive biodiversity–productivity relationships found in grassland ecosystems (Barry et al., 2018; Loreau & Hector, 2001). However, results from experiments that manipulated plant species richness without manipulating plant order of arrival often did not support this hypothesis (Jesch et al., 2018; Mommer et al., 2010; Oram et al., 2018; Ravenek et al., 2014), thus suggesting that mechanisms other than resource partitioning drive above-ground and below-ground grassland overyielding. If different species arrive at different times during plant community assembly, however, one can expect below-ground niche partitioning to occur as a consequence of soil resource pre-emption and/or niche modification (sensu Fukami, 2015) by early-arriving species. In the Jülich Priority Effect experiment, we found that the root length density in the topsoil layer depended on

the sequence of arrival of PFGs. In 2014, the standing root length density was indeed lower in plots where legumes were sown first in comparison with synchronous and grasses-first plots (Weidlich et al., 2018). Whether this pattern was due to changes in vertical root distribution, total root productivity or both is still unknown, but it is a strong indication that plant order of arrival during assembly can have important consequences for ecosystem functioning, particularly below-ground. Future research using imaging techniques to non-destructively follow root development over time (e.g. minirhizotrons) (Rewald & Ephrath, 2013) as well as molecular or spectral techniques to disentangle the relative contribution of individual plant species to biomass production in different soil layers (Meinen & Rauber, 2015; Mommer, Wagemaker, De Kroon, & Ouborg, 2008) hold much potential to investigate how the sequence of arrival of different species or functional groups affect vertical root distribution and below-ground productivity in temperate grasslands.

Because species arriving first during plant community assembly can alter the biotic and abiotic soil conditions that will be experienced by species arriving later (Baxendale, Orwin, Poly, Pommier, & Bardgett, 2014; Bezemer et al., 2006; Hu et al., 2018), historical contingency effects can arise as a consequence of plant–soil feedbacks, thus affecting plant community assembly (Kardol, Cornips, Kempen, Bakx-Schotman, & Putten, 2007; van der Putten et al., 2013). When the relative abundance of a species is high, as is typically the case in monoculture plots, the accumulation of species-specific pathogens such as bacteria, fungi or nematodes in the rhizosphere can result in negative biotic feedbacks leading to negative frequency dependence (Guerrero-Ramírez, Reich, Wagg, Ciobanu, & Eisenhauer, 2019; Hendriks et al., 2013; Mommer et al., 2018). According to modern coexistence theory (Chesson, 2000; Fukami, Mordecai, & Ostling, 2016), such negative feedbacks act as a stabilizing mechanism allowing species coexistence. They are also thought of as one of the primary mechanisms (alongside N facilitation) behind the increased ecosystem functioning (overyielding) observed in species-rich grassland communities compared to monocultures (Barry et al., 2018; Mommer et al., 2018). Although we did not verify this in our experiment, the build-up of species-specific pathogens in monocultures over time might explain the decrease in average monoculture yield observed from 2013 to 2014, as well as the greater performance achieved by *T. pratense* (2013), *D. glomerata* (2013) and *H. lanatus* (2013, 2014) in synchronous mixtures in comparison with the performance predicted by the null model (see Figures S2 and S3).

Positive biotic feedbacks can result from the accumulation of symbiotic mutualists in the rhizosphere such as N_2-fixing rhizobia and mycorrhizal fungi (Eisenhauer, 2012; Semchenko et al., 2018; van der Putten et al., 2013; Wright et al., 2017). Because these mutualists are able to increase the amount of resources that can be taken up by plants (Barry et al., 2018; Wright et al., 2017), their accumulation in the rhizosphere of early-arriving species could lead to increased establishment of species arriving later during plant community assembly. Although increased soil N availability can be expected as a consequence of legume presence in plant communities (Temperton et al., 2007), we do not think that it played an important role in our experiment for at least two reasons: (a) there was no effect of time and PFG order of arrival on the soil N content (Weidlich et al., 2017) and (b) we did not find evidence for N transfer using N content and $\delta^{15}N$ natural abundance data (see Figure S5). Positive biotic feedbacks favouring the establishment of late-arriving species could also arise via the accumulation of plant growth-promoting rhizobacteria in the rhizosphere of early-arriving species. Although the link between non-resource mutualists and increased ecosystem functioning has been far less studied in comparison with rhizobia and mycorrhizal fungi (Barry et al., 2018), studies have shown that plant growth-promoting rhizobacteria positively impact on plant performance by inhibiting soil-borne pathogens, particularly in species-rich plant communities (Eisenhauer, 2012). In addition, some rhizobacterial strains are known to modulate root development and root system architecture as well as promoting root and shoot growth (Delaplace et al., 2015; Verbon & Liberman, 2016). Despite evidence showing that plant species richness drives the structure and activity of the root-associated microbiota, notably via root biomass and root exudate-dependent mechanistic pathways (Eisenhauer et al., 2017; Lange et al., 2015; Steinauer, Chatzinotas, & Eisenhauer, 2016), the role of historical contingency related to plant order of arrival is currently unclear despite its obvious relevance for the cyclical feedback loops between plants, microbes and soils. In order to gain a better understanding behind the mechanisms driving plant–plant interactions in naturally assembling communities (such as complementarity), we argue that a better understanding of how the sequence of arrival of different plant species or functional groups affects root exudation patterns as well as the soil and plant-associated microbiota is much needed.

Next to resource partitioning and biotic feedbacks, abiotic facilitation via physical stress buffering (or microclimate amelioration) is a mechanism that could have also contributed to increase species complementarity and grassland overyielding in plots characterized by a positive priority effect (Barry et al., 2018). When some species arrive earlier than others, they modify the local environment by providing shade, thus reducing temperature and evapotranspiration as well as increasing air relative humidity and soil water content (Bruno, Stachowicz, & Bertness, 2003; Wright et al., 2017). These modified conditions can then benefit species arriving later during assembly and favour their establishment, thus leading to positive priority effects. To what extent early-arriving species modified the abiotic environment experienced by species arriving later was not investigated in our field experiment, but it certainly deserves more research attention as it would allow us to gain a better understanding of the mechanisms behind the creation of positive priority effects in grasslands.

Because our experimental design did not include monocultures for 12 of the species used in the plots sown with 21 species (high diversity plots in Weidlich et al., 2017), we were not able to measure net biodiversity effects for these plots. Therefore, our results are based on overyielding values measured at one species richness level only (with 9 sown plant species). Whether the findings presented in this study hold true across a species richness gradient still needs to be investigated. Because our results can have strong implications for

restoration settings where the sequence of arrival of different plant species or functional groups can be manipulated to create priority effects that alter community trajectories (Temperton et al., 2016; Wilsey et al., 2015; Young, Stuble, Balachowski, & Werner, 2017), we believe that future research combining both assembly and biodiversity approaches are needed. BEF findings can be applied in the 'real world' either by comparing ecosystems undergoing natural assembly or by including an element of intervention such as is commonly done in ecological restoration where species are added to a system (but usually at the same time) (Jochum et al., 2019; Manning et al., 2019). Further research combining our PFG order of arrival and BEF approach seems very promising, although challenging to design. This is due to the high number of possible treatment combinations associated with the creation of two orthogonal gradients (plant order of arrival × species richness). In addition, these experiments should be designed in such a way that species-specific responses can be separated from functional group responses (Weisser et al., 2017), which was not the case in our study. Nevertheless, we believe that such experiments are now needed to improve our understanding of the functioning of grassland ecosystems and increase the predictive power of community ecology in conservation and ecological restoration.

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CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHORS' CONTRIBUTIONS

E.W.A., P.v.G. and V.M. performed the Jülich Priority Effect experiment and collected the data; B.M. analysed the data, wrote the *bef* R package and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Raw data and R scripts used for data analysis are fully accessible here: https://doi.org/10.5281/zenodo.3366967. The R package *bef* is available on GitHub (https://github.com/BenjaminDelory/bef).

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SUPPORTING INFORMATION

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

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