

# Consistent functional clusters explain the effects of biodiversity on ecosystem productivity in a long-term experiment

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**Abstract.** Biomass production in ecosystems is a complex process regulated by several facets of biodiversity and species identity, but also species interactions such as competition or complementarity between species. For studying these different facets separately, ecosystem biomass is generally partitioned in two biodiversity effects. The composition effect is a simple, linear effect, and the interaction effect is a more subtle, nonlinear effect. Here we used a clustering approach (1) to separately and comprehensively capture all linear and nonlinear effects induced by both biodiversity effects on ecosystem functioning, and (2) to determine the functional composition at the origin of each biodiversity effect. We used data from the long-term Cedar Creek BioDIV experiment carried out over 22 yr, and we partitioned multiplicatively the biomass in composition and interaction effects. Both biodiversity effects were weakly correlated. Our clustering approach accurately explains and predicts each diversity effect over time: each one is modeled by a different functional composition. Even if environmental conditions and the strength of interaction effect strongly varied over time, the functional clusters of species that govern the interaction effect do not change over the 22 yr of the experiment. The functional composition governing the interaction effect is therefore very robust. In contrast, the functional clusters of species that govern the composition effect are less robust and change with environmental conditions. Understanding ecosystem functioning therefore requires that ecological properties are first partitioned by type, then each type of property is analyzed and modeled separately. Approaches without a priori groupings of species, such as functional clustering, appear particularly efficient and robust to unravel the web of species interactions, and identify the role played by species on biodiversity effects.

*Key words:* assembly motif; biodiversity–ecosystem functioning; combinatorial analysis; functional groups; species clustering.

## INTRODUCTION

Explaining and predicting variation in ecosystem properties such as plant biomass across ecosystems remains a challenge for ecology. Biodiversity–ecosystem functioning research has found that the functioning of an ecosystem depends in part on biotic factors, including species composition (Hooper et al. 2005, Balvanera et al. 2006, Isbell et al. 2017). Several studies emphasized the role played by the functional composition of ecosystems, that is, the functional groups of species (Tilman et al. 1997, 2001,

Cardinale et al. 2011, Weisser et al. 2017). They also showed that functional diversity, that is, the number of functional groups, enhances biomass production (Tilman et al. 1997, Hooper and Dukes 2004, Reich et al. 2004, Weisser et al. 2017). Biomass production, however, is a complex ecosystem process that is regulated by several facets of biodiversity, including species composition and species interactions such as competition or complementarity between species. Disentangling the role played by species composition and species interactions has been a major focus of biodiversity and ecosystem functioning research during the past 20 yr (Loreau and Hector 2001, Loreau et al. 2002, Hooper et al. 2005, Cardinale et al. 2007, 2011, Hector et al. 2011). Several questions, however, remain unanswered. In particular, an important question is whether the effects of species composition and

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species interactions are induced by the same species, and if not, which species govern each of these effects. It is also unknown whether the role played by the various species persists over time, or whether it varies with the state of the ecosystem or environmental conditions (Allan et al. 2011, Isbell et al. 2011).

The most common way to separate the effects of species composition and species interactions is to refer to an expected yield based on species monocultures. Two different approaches, however, have been proposed to partition these effects: an additive partition and a multiplicative partition. The additive partition (Loreau 1998, Loreau and Hector 2001) was developed to test whether the selection effect induced by dominant species in mixtures was enough to explain the effects of biodiversity on ecosystem functioning. This approach splits the net diversity effect, that is, the difference between observed and expected yield, into a selection effect and a complementary effect. It has greatly improved our understanding of the biodiversity–ecosystem functioning relationship during the last two decades, notably by showing that dominant species do not often solely explain biodiversity effects (Loreau and Hector 2001, Hector et al. 2002, Cardinale et al. 2011, Reich et al. 2012). The multiplicative partition is older (Wilson 1988). It aims to test the overyielding of a species mixture in regard to the expected yield based on species monocultures. It thus partitions a nonlinear interaction effect from a linear composition effect, both diversity effects being relative and dimensionless. The multiplicative partition is therefore well adapted to identifying species that react similarly to co-occurring species in species mixtures, and hence that contribute similarly to ecosystem functioning (Wilson 1988, Garnier et al. 1997, Jaillard et al. 2018a).

Species that contribute in a similar way to biodiversity effects are assumed to be functionally redundant (Loreau 2004), and are thus clustered into a single functional group (Violle et al. 2007, Garnier et al. 2016). The theoretical corpus of functional ecology distinguishes between effect functional groups, which cluster species that similarly influence ecosystem properties, and response functional groups, which cluster species that respond similarly to changes in biotic and abiotic factors (Díaz and Cabido 2001). Both species clusterings are generally based on species properties that are assumed a priori to play a role in either ecosystem functioning or the response to environmental changes (Lavorel and Garnier 2002). This approach makes two strong assumptions, which may not hold: (1) species interactions can be fully accounted for by species intrinsic properties, and (2) the causal or statistical relationships between species properties and ecosystem functioning are already known, which considerably limits the heuristic ability of a priori species clustering (van der Plas et al. 2019).

In Jaillard et al. (2018a, 2018b), we proposed a clustering approach to determine the functional composition of ecosystems, that is, the functional groups of species whose co-occurrence determines a given ecosystem property, without any a priori knowledge of these species.

This clustering approach searches for the species clusters that best account for the observed variations in the ecosystem property. Importantly, this approach only considers changes in ecosystem properties associated with changes in species co-occurrence, while being blind to the functional traits of species, the processes involved in species interactions, or the shape of the biodiversity–ecosystem functioning relationships, among other information. Such an approach without any a priori information would be particularly valuable to identify the role played by the various species in each effect of biodiversity on each ecosystem property. If a given species were assigned to different functional groups depending on the biodiversity effect under scrutiny, this would suggest that previous attempts to use the same functional groups to explain multiple ecosystem properties are inadequate.

Long-term biodiversity–ecosystem functioning experiments are particularly useful to track variations in the functional composition of ecosystems and the structure of species interactions over time. Seminal studies highlighted changes in biodiversity effects over the course of long-term biodiversity–ecosystem functioning experiments, notably an increase in net biodiversity effects over time (Fargione et al. 2007, Allan et al. 2011, Reich et al. 2012). However, the underlying processes remain unknown given that the physiological mechanisms and functional traits involved were not assessed at each time step in these studies.

Here we examine the respective contributions of the composition and interaction effects of biodiversity on total plant biomass production in a long-term biodiversity experiment (Cedar Creek BioDIV experiment Tilman et al. [2001]) using a multiplicative partition approach. First, we partition biomass production into a composition effect and an interaction effect. Second, we identify the species groups that govern each of the biodiversity effects, and whether these groups of species change through time. Because the composition and interaction effects differ drastically by their nature, they were analyzed and modeled separately to examine the functional composition that governs each of these biodiversity effects adequately. We show that the composition and interaction effects are governed by different groups of species. In particular, the interaction effect is accurately modeled by five functional groups of species. The clustering of species into these five functional groups is very robust over time, despite strong variations in environmental conditions. Clustering approaches without a priori knowledge are simple but very efficient and robust methods to identify the sets of species contributing to each biodiversity effect.

## MATERIAL AND METHODS

### *The BioDIV experiment*

The Cedar Creek BioDIV experiment (also called Biodiversity II and referred as e120<sup>7</sup>) was designed to test

<sup>7</sup><http://www.cedarcreek.umn.edu/research/>

the effects of plant biodiversity on population and ecosystem functioning (see Tilman et al. 1997, 2001, 2002). It is composed of 168 plots assembled from a pool of 16 perennial grassland species. The species composition in each plot was randomly drawn from a 16-species pool. The 16 species were originally clustered into a priori four functional groups: legumes, nonlegume forbs, warm-season C4 grasses, and cool-season C3 grasses (that we denote  $L$ ,  $F$ , 4, and 3, respectively). A strip of each plot was harvested from 1996 to 2017.

The long-term BioDIV experiment encountered a few experimental difficulties over time, as pointed out by Fargione et al. (2007), Reich et al. (2012), and Clark et al. (2018). Detailed information regarding the data used in this study is given in Appendix S1: Section S1. Overall, we analyzed 16 monocultures, 1 by species, and 117 species mixtures containing 2, 3, 4, 6, 7, 8, 14, 15, and 16 species (in 26, 10, 17, 6, 14, 10, 28, 5, and 1 combinations, respectively). Each species was included in  $53 \pm 4$  (mean  $\pm$  standard deviation) out of 117 species mixtures in average. We used yield data derived from “sorted biomass” by species, and thus did not consider the biomass of weed species that appeared over time.

#### *Multiplicative partition of diversity effects*

For a given year, the yield of a species mixture was multiplicatively partitioned (Wilson 1988). First, we obtained the interaction effect by dividing the observed yield,  $Y_{\text{observed}}$ , by the expected yield,  $Y_{\text{expected}}$ .  $Y_{\text{expected}}$  is computed as the average yield of monocultures of species co-occurring in the species mixture. Second, we obtained the composition effect by dividing the expected yield  $Y_{\text{expected}}$  by  $Y_{\text{monocultures}}$  computed as the average yield of all species grown in monoculture used in the experiment (Jaillard et al. 2018a) (Appendix S1: Section S2):

$$Y_{\text{observed}} = \frac{Y_{\text{observed}}}{Y_{\text{expected}}} \frac{Y_{\text{expected}}}{Y_{\text{monocultures}}} Y_{\text{monocultures}}$$

The first quotient of this equation is called the interaction effect, the second quotient is called the composition effect, and the last term is called the scale factor of the experiment for a given year. Composition and interaction effects are species mixture properties. The interaction effect integrates all nonlinear effects induced by interactions among species within a species mixture on ecosystem biomass. Given that the interaction effect is a quotient, its mean is computed using a geometric formula. The composition effect corresponds to linear effects induced by the species composition of a given species mixture: the more productive the constitutive species, the greater the composition effect. By definition, the composition effect equals one in a species mixture composed of all species used in the experiment, here the species mixture containing 16 species. It

must be close to one if the occurrence frequencies of the different species in the experiment are close to each other.

#### *Time analysis of interaction effect, composition effect, and relative yield*

The use of time-series experiments raises the issue of environmental variations over time. Reich et al. (2012) computed an environmental scale factor for each year. This factor was  $Y_{\text{monocultures}}$ , that is, the average yield in monoculture of all species used in the experiment (here the 16 grassland species) for a given year. Reich et al. (2012) defined the relative yield as the ratio between the observed yield  $Y_{\text{observed}}$  and the scale factor  $Y_{\text{monocultures}}$ . The relative yield is therefore the product between the interaction effect and the composition effect (Appendix S1: Section S2). By definition, the interaction effect, composition effect, and relative yield are dimensionless quantities corrected for environmental variations by this environmental scale factor.

The use of time-series experiments also raises the question of pseudoreplications (Hurlbert 1984). The data were first treated as time series to examine trends over time. Next, we treated them as 22 annual pseudoreplications: each annual harvest was separately analyzed, and the reported global statistics are the medians of the annual statistics. In this analysis, each harvest is equally weighted.

#### *Clustering analysis of interaction effect, composition effect, and relative yield*

We separately analyzed biodiversity effects and relative yield using a clustering approach to a posteriori determine the functional composition that governs each of the three species mixture properties throughout the experiment, namely, interaction effect, composition effect and relative yield (Jaillard et al. 2018b).

The clustering analysis over time proceeded in two steps. First, we searched for the species clusters that best account for the species mixture property over the whole time period, each harvest being equally weighted. The species clustering that best accounts for the species mixture property is the one that minimizes the intracluster variance and maximizes the intercluster variance. This condition is measured by the coefficient of determination,  $R^2$ , of the species clustering, that is, the ratio of the variance explained by the species clustering on the total observed variance. The clustering method is top-down, that is, it starts with a single large group of species, which is successively partitioned until there are as many groups as there are species. It provides a hierarchical tree of functional groups of species.

Second, the predictive capacity of species clustering was evaluated by cross-validation at each level of the hierarchical tree and for each annual harvest: we used a leave-one-out cross-validation, that is, each ecosystem

property was independently predicted by removing the ecosystem property to predict from the data set. The predictive accuracy of the species clustering was measured by the model efficiency,  $E$ , that is, the ratio of the variance of predictions on the total observed variance. The Akaike information criterion corrected for small sample size,  $AIC_c$ , of species clustering was also calculated at each level of the hierarchical tree and for each annual harvest. This criterion measures the parsimony of a clustering model. The hierarchical tree of species clustering was then pruned based on two criteria: an increasing  $E$ , then a decreasing  $AIC_c$ . The level of pruning determines the maximum number of functional groups that can be retained without overfitting. The  $F$  ratio and  $P$  value associated to  $R^2$  for the maximum number of functional groups are then computed.

The reported statistics, that is, the model efficiency  $E$  and the maximum number of functional groups, are the medians of the annual statistics. The greater the coefficient of determination  $R^2$  and the efficiency  $E$ , the greater the explanatory and predictive abilities of the model. A high  $E/R^2$  ratio indicates a model with a predictive ability close to its explanatory capability. The number of functional groups has no statistical significance. However, the greater the explanatory and predictive capabilities of the model, the greater the number of functional groups possibly identified.

As a matter of comparison with the a posteriori clustering approach, we also used the four functional groups a priori defined by Tilman et al. (2001) to assess interaction effect, composition effect and relative yield. A hierarchical tree of species clustering was built for each diversity effect and relative yield, by forcing the species tree to go through species clustering into the four functional groups a priori defined (Appendix S1: Section S3).

#### *Robustness of clustering analyses*

The robustness of the a priori and a posteriori species clustering was evaluated by bootstrapping. Clustering analyses were done with 1–21 harvests, randomly resampled from the set of 22 harvests. Each resampling was repeated 100 times, leading to  $21 \times 100$  clustering analyses. Each resulting species clustering, from the trunk to the leaves, was compared to the species clustering obtained with 22 harvests using the Jaccard index. The Jaccard index measures a distance between two clusterings: an index of one indicates a zero distance. The reported statistics were the medians of 100 Jaccard indices computed for each of 21 numbers of removed harvests.

#### *Statistical analyses and clustering computations*

All the computations were performed using the R-software (R Development Core Team 2009). We performed linear regressions using *lm* function. Partition of observed yield into interaction effect, composition effect, and scale factor was done using a R-source script

(Jaillard et al. 2017). We performed the clustering computations using the R-package *functClust* available on the R-CRAN (see Open Research). All other scripts (Jaillard 2021) are available on the INRAE dataverse.

## RESULTS

### *Partitioning ecosystem biomass into interaction and composition effects*

Out of the 22 yr, the interaction effect ranges from 0.01 to 13.4. This means that interactions among species have decreased up to 100 times, or increased more than 13 times, the yield compared to the expected yield (Fig. 1a). The interaction effect is strongly correlated with the relative yield (median Pearson's  $r^2 = 0.713$ , median  $P = 0.012$ ). It equals  $2.43 \pm 1.84$  (mean  $\pm$  standard deviation) in average, and increases over time (by 0.065 per year, Pearson's  $r^2 = 0.061$ ,  $P < 10^{-10}$ ) (Fig. 1b). A detailed analysis shows that the interaction effect increases primarily in species-rich mixtures, with an increase of 0.11 per year for the species mixtures containing from 14 to 16 species, compared to an increase of 0.01 only for the two-species mixtures, for example (Appendix S2: Fig. S1).

The composition effect ranges from 0.03 to 3.1; that means that the expected yield of species mixtures used in the BioDIV experiment ranged from almost nothing to more than three times the average monocultures (Fig. 1c). Its average out of the 22 yr is  $1.02 \pm 0.34$ , which is marginally different from 1 ( $P = 0.009$ ). This means that the different species occur equitably in the BioDIV experiment. The composition effect is weakly correlated with the relative yield (median Pearson's  $r^2 = 0.064$ , median  $P < 10^{-10}$ ). It does not change over time (by  $-0.001$  per year, Pearson's  $r^2 = 0.001$ ,  $P = 0.223$ ) (Fig. 1d). Although formally linked, the interaction effect and the composition effect are weakly correlated (median Pearson's  $r^2 = 0.058$ , median  $P = 0.009$ ) (Fig. 1e).

The scale factor is the annual average yield in monoculture of all species used in the experiment (Fig. 1f). It varies from 53.1 to 103.2 g/m<sup>2</sup> over the whole 1996–2017 period ( $75.3 \pm 17.2$  g/m<sup>2</sup>), and is weakly correlated with the relative yield (Pearson's  $r^2 = 0.024$ ,  $P < 10^{-10}$ ) (Fig. 1f and Appendix S2: Fig. S2). The average yield in monoculture of each species ranges from 8.5 to 199.0 g/m<sup>2</sup> ( $75.3 \pm 17.2$  g/m<sup>2</sup>) (Appendix S2: Fig. S3a). The legumes are among the most productive species, and the C3 grasses among the least productive species in monoculture. The yield in monoculture of all species is correlated with the scale factor, that is, the average yield in monoculture of all species, with an average slope of 1 ( $P = 1.11 \times 10^{-06}$ ). However, a variance analysis shows that the yield in monoculture of four species increased much faster than the scale factor: *Amorpha canescens*, *Lupinus perennis*, *Monarda fistulosa*, and *Lespedeza capitata* (slope = 3.4, 2.3, 2.2, and 1.6, respectively, with a  $P < 0.01$ ) (Appendix S2: Fig. S3b). *Amorpha canescens*,

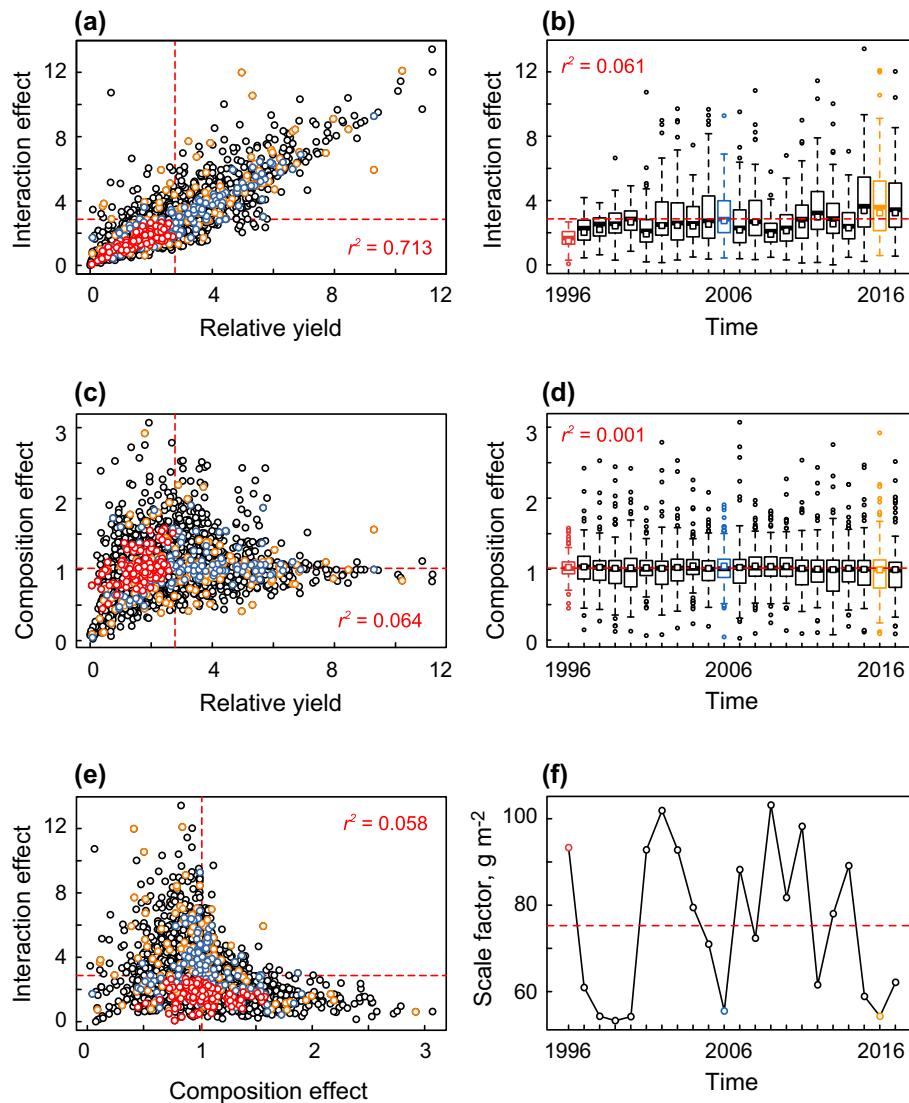


FIG. 1. Interaction effect, composition effect, and scale-factor in the BioDIV experiment from 1996 to 2017. (a) Interaction effect changes across years. (b) Interaction effect vs. relative yield. (c) Composition effect changes across years. (d) Composition effect vs. relative yield. (e) Scale factor changes across years. (f) Interaction effect vs. composition effect. The number of data are 117 species mixtures  $\times$  22 yr. The dotted red lines indicate the mean values on the whole time period. (a), (c), and (e) The Pearson's square coefficient of correlation  $r^2$  between analyzed variable and time is indicated. (b), (d), and (f) The median  $r^2$  of Pearson's square coefficients of correlation between analyzed variables computed year by year is indicated. The years 1996 (in red), 2006 (in blue), and 2016 (in gold) are shown as examples.

*Lupinus perennis*, and *Lespedeza capitata* are legumes, suggesting that legumes in monoculture overresponded to environmental variations.

#### Prediction of interaction and composition effects based on a priori species clustering

The clustering analysis forced by the a priori species clustering and applied to the interaction effect gives a coefficient of determination  $R^2$  of 0.408 ( $F$  ratio = 229.4,  $P < 10^{-10}$ ), and an efficiency  $E$  of 0.285 ( $E/R^2 = 0.698$ ) (Fig. 2a, b). This means that a priori species clustering

explains at best 41% of the total variance of interaction effect and predicts in return 29% of the observed variance on interaction effect; that is 70% of explained variance. The clustering analysis also shows that the optimum number of functional groups is three ( $AIC_c = 66.2$ ). This means that the species clustering into four functional groups overfits the species mixture yield: it explains better the total variance of interaction effect, but it predicts a lower proportion of observed variance for the interaction effect.

The clustering analysis of composition effect gives stronger results:  $R^2$  of 0.547 ( $F$ -ratio = 162.8,  $P < 10^{-10}$ ), and  $E$

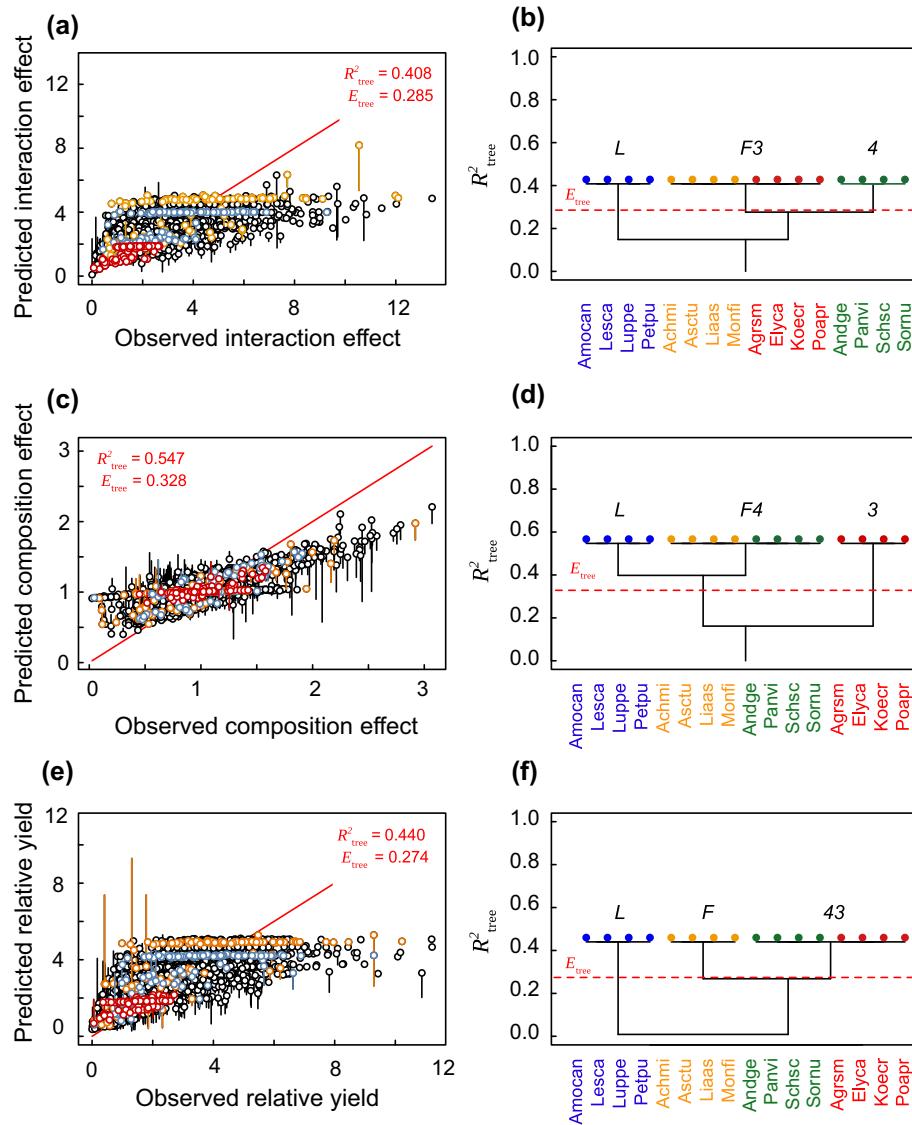


FIG. 2. Modeling of interaction effect, composition effect, and relative yield of ecosystems from 1996 to 2017, forced by a priori clustering of species. (a) and (b) Interaction effect. (c) and (d) Composition effect. (e) and (f) Relative yield. (a), (c), and (e) Modeling of diversity effects based on the hierarchical tree of species clustering. Each bar corresponds to the error induced by leaving out the ecosystem to predict (cross-validation). Solid red line is the 1:1 line. (b), (d), and (f) A priori species clustering. Functional groups are noted *L* for legumes, *F* for forbs, and 4 and 3 for C4 and C3 grasses, respectively. The level of leaves corresponds to the coefficient of determination  $R^2$ . The dotted red line corresponds to efficiency  $E$  of species clustering. The years 1996 (in red), 2006 (in blue), and 2016 (in gold) are shown as examples.

of 0.328 ( $E/R^2 = 0.599$ ) (Fig. 2c, d). However, it also shows that the optimum number of functional groups is three ( $AIC_c = -350.7$ ), rather than four as a priori defined. Yield in monoculture significantly differs among species' functional groups. It is such as: Legumes > (Forbs–C4 grasses) > C3 grasses ( $L > F4 > 3$ , with  $P < 0.001$ ).

The clustering analysis of relative yield based on a priori species clustering gives intermediate results:  $R^2$  of 0.440 ( $F$ -ratio = 384.4,  $P < 10^{-10}$ ), and  $E$  of 0.274 ( $E/R^2 = 0.623$ ) for three functional groups ( $AIC_c = 49.6$ ) (Fig. 2e, f).

Overall, the a priori clusterings issued from the conventional species clustering explain between 41 and 55%

of variance, and predict in return between 27 and 33% of observed variance over the 22 yr. The a priori clusterings have thus a moderate explanatory capacity and a poor predictive ability for both diversity effects, as well as for the relative yield of species mixtures.

*Prediction of interaction and composition effects based on a posteriori species clustering*

The a posteriori clustering analysis applied to the interaction effect over the 22 yr gives a  $R^2$  of 0.669 ( $F$ -ratio = 199.6,  $P < 10^{-10}$ ), and  $E$  of 0.400 ( $E/R^2 = 0.598$ )

(Fig. 3a). The median Akaike information criterion ( $AIC_c = 15.3$ ) indicates an optimum number of five functional groups of species. The five functional groups are:  $A = \{Lupinus\ perennis\}$ ,  $B = \{Andropogon\ gerardi, Elymus\ canadensis\}$ ,  $C = \{Poa\ pratensis\}$ ,  $D = \{Amorpha\ canescens\}$ , and  $E = \{Lespedeza\ capitata, Petalostemum\ purpureum, Achillea\ millefolium, Asclepias\ tuberosa, Liatris\ aspera, Monarda\ fistulosa, Panicum\ virgatum, Schizachyrium\ scoparium, Sorghastrum\ nutans, Agropyron\ smithii, Koeleria\ cristata\}$  (Fig. 3b). The functional groups  $A$ ,  $C$ , and  $D$  are singletons. The

singletons  $A$  and  $D$  are each composed of a legume, *Lupinus perennis* in a singleton and *Amorpha canescens* in another singleton. *Amorpha canescens* is the most productive species. The yield in monoculture of functional groups gives the following ranking:  $D > A \approx E > B > C$  ( $P < 0.001$ ).

The clustering analysis applied to the composition effect gives a  $R^2$  of 0.640 ( $F$ -ratio = 309.7,  $P < 10^{-10}$ ), and  $E$  of 0.498 ( $E/R^2 = 0.778$ ) (Fig. 3c). The median Akaike information criterion ( $AIC_c = -375.1$ ) indicates an optimum number of three functional groups of species:  $A =$

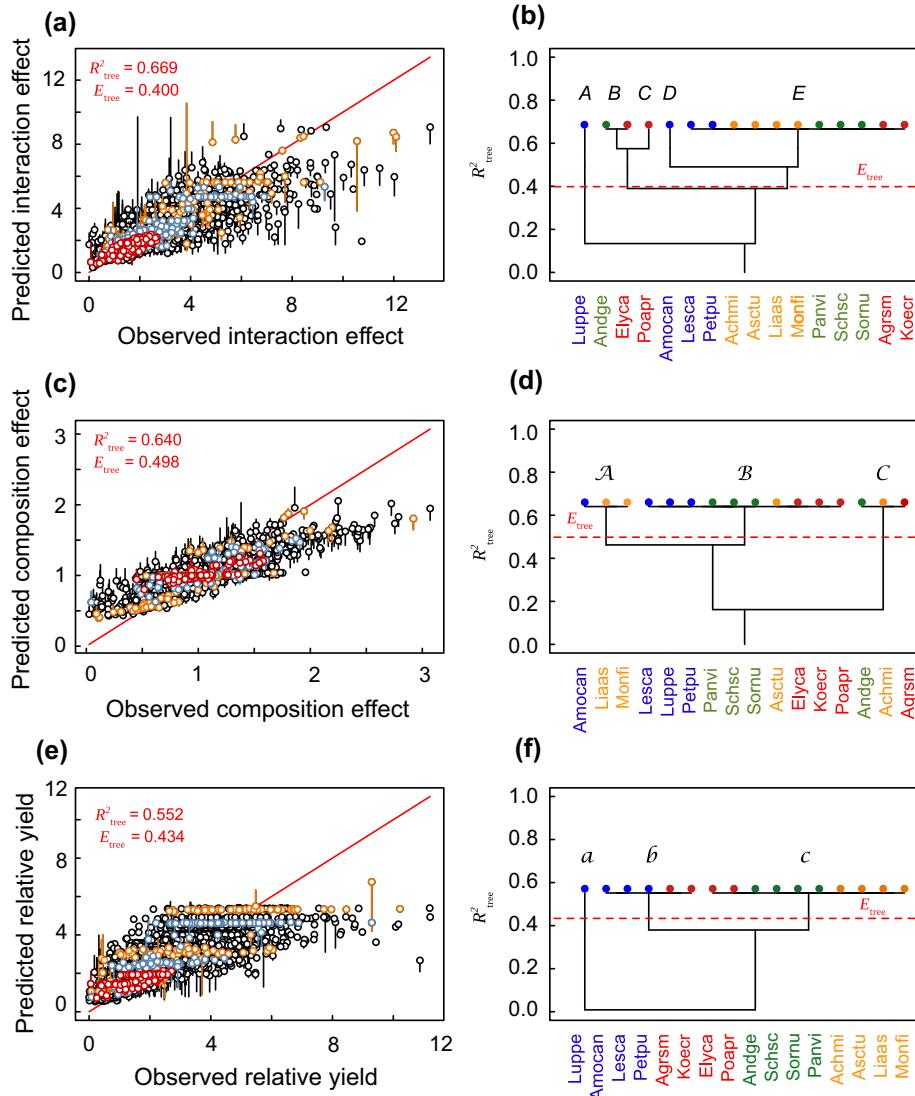


FIG. 3. A posteriori clustering of species for interaction effect, composition effect, and relative yield of ecosystems from 1996 to 2017. (a) and (b) Interaction effect. (c) and (d) Composition effect. (e) and (f) Relative yield. (a), (c), and (e) Modeling of diversity effects based on the hierarchical tree of species clustering. Each bar corresponds to the error induced by leaving out the ecosystem to predict (cross-validation). Solid red line is the 1:1 line. (b), (d), and (f) Hierarchical tree of species clustering. Optimal number of functional groups is indicated by Akaike information criterion  $AIC_c$  corrected for small sample size: It is 5, 3, and 3 for interaction effect, composition effect, and relative yield, respectively. Functional groups are noted  $A$ ,  $B$ ,  $C$ ,  $D$ , and  $E$  for interaction effect;  $A$ ,  $B$ , and  $C$  for composition effect; and  $a$ ,  $b$ , and  $c$  for relative yield. The level of leaves corresponds to tree coefficient of determination  $R^2_{tree}$  at the optimum number of species functional groups. The dotted red line corresponds to optimal tree efficiency  $E_{tree}$ . The years 1996 (in red), 2006 (in blue), and 2016 (in gold) are shown as examples.

{*Amorpha canescens*, *Liatris aspera*, *Monarda fistulosa*},  $B = \{Lespedeza capitata, Lupinus perennis, Petalostemum purpureum, Panicum virgatum, Schizachyrium scoparium, Sorghastrum nutans, Elymus canadensis, Koeleria cristata, Poa pratensis\}$  and  $C = \{Andropogon gerardi, Achillea millefolium, Agropyron smithii\}$  (Fig. 3d). The functional group  $A$  contains the three most productive species in monoculture, and the functional group  $C$  includes three species out of the least productive species in monoculture (Appendix S2: Fig. S3). The yield in monoculture of functional groups gives the following ranking:  $A > B > C$  ( $P < 0.001$ ).

The clustering analysis applied to the relative yield gives a  $R^2$  of 0.552 ( $F$ -ratio = 584.3,  $P < 10^{-10}$ ), and an  $E$  of 0.434 ( $E/R^2 = 0.786$ ) (Fig. 3e). The median Akaike information criterion ( $AIC_c = 17.5$ ) indicates an optimum number of three functional groups of species:  $a = \{Lupinus perennis\}$ ,  $b = \{Amorpha canescens, Lespedeza capitata, Petalostemum purpureum, Agropyron smithii, Koeleria cristata\}$  and  $c = \{Elymus canadensis, Poa pratensis, Andropogon gerardi, Schizachyrium scoparium, Sorghastrum nutans, Panicum virgatum, Achillea millefolium, Asclepias tuberosa, Liatris aspera, Monarda fistulosa\}$  (Fig. 3f).

Overall, the a posteriori clusterings explain between 55 and 67% of variance, and predict in return between 40 and 50% of variance observed in the 117 species mixtures over 22 yr. In addition, their  $AIC_c$  are lower than the  $AIC_c$  of conventional clusterings, indicating that these models are more parsimonious. The a posteriori species clusterings are therefore more parsimonious and have a much better explanatory capacity and predictive ability than conventional clusterings for both diversity effects, as well as for the relative yield of species mixtures.

#### Robustness of a priori and a posteriori species clustering

To be useful, a clustering must be robust. We therefore assessed the robustness of species clustering by randomly removing an increasing number of years (Appendix S2: Fig. S4). As expected, a priori clusterings are very robust, by construction. The a posteriori species clustering for the interaction effect is also very robust: the clusterings into five and four functional groups are only drastically modified after the removal of 10 out of the 22 yr, and the clustering into three functional groups after the removal of 14 out of the 22 yr. This indicates that the functional composition of interaction effect does not change over 22 yr. The a posteriori species clustering for the composition effect appears less robust: the clustering into three, even two functional groups is strongly modified after the removal of a few years only. This suggests that the functional composition of composition effect varies over time. As previously shown, the yield in monoculture of four species increases with scale factor. The shift of yield in monoculture of these species would induce changes in the functional composition of composition effect over time.

#### Association between combinations of functional groups and diversity effects

Our clustering of species into functional groups leads to the sorting of species mixtures into combinations of functional groups, which we termed assembly motifs. By convenience, hereafter we sort the assembly motifs by increasing species mixture property (Fig. 4). In the a priori clustering, the interaction effect is optimally modeled by three functional groups:  $L$ , 4 and  $(F3)$  together. The interaction effect is low when each functional group is isolated (motifs 4,  $L$  and  $(F3)$ ), medium when functional groups co-occur two-by-two (motifs  $(F3)4$ ,  $L(F3)$  and  $L4$ ), and the highest when the three functional groups co-occur together (motif  $L(F3)4$ ) (Fig. 4a). In sum, the interaction effect increases with the number of functional groups.

In the a posteriori clustering, the same trend is observed, but in a more nuanced way. The interaction effect is higher when the functional group  $A$  co-occurs with other groups in assembly motifs:  $ABCE \gg BCE$ ,  $ACE \gg CE$ ,  $ABCDE \gg BCDE$ ,  $ABC \gg BC$ ,  $ABCD \gg BCD$ ,  $ACDE > CDE$ ,  $AC \gg C$ , and  $ACD \gg CD$ . The co-occurrence of  $A$  is associated with a high positive effect. The functional group  $B$  is not associated with a high interaction effect, but the co-occurrence of  $A$  with  $B$  is associated with the highest interaction effects:  $ABCE$ ,  $ABCDE$ ,  $ABC$ , and  $ABCD$  motifs are among the highest interaction effects, and  $ABCE > ACE$ ,  $ABCDE > ACDE$ ,  $ABC > AC$  and  $ABCD > ACD$ . Conversely, when  $A$  occurs with or without  $B$ , the co-occurrence of  $D$  decreases the interaction effect:  $ABCDE < ABCE$ ,  $ABCD < ABC$ ,  $ACDE < ACE$ , and  $ACD < AC$ . The co-occurrence of  $D$  when  $A$  occurs is associated with a negative effect.

The composition effect responds differently to combinations of functional groups (Fig. 4c,d). As expected, combinations of all functional groups (motifs  $L(F4)3$  and  $ABC$ , Fig. 4c,d, respectively) are close to one. The co-occurrence of functional groups is generally associated with a composition effect that is intermediate to those of constitutive functional groups. For instance, in the a priori clustering,  $L > L3 > 3$ ,  $(F4) > (F4)3 > 3$  or  $L > L(F4)3 > (F4)3$  (Fig. 4c), in the a posteriori clustering,  $A > AB > B$  or  $A > ABC > BC$  (Fig. 4d). The only exception is  $L(F4) > L > (F4)$  in a priori clustering, but the composition effect of motifs  $L$  and  $L(F4)$  are not significantly different. The relative yield is the product of interaction effect and composition effect: it responds to the number of functional groups as a trade-off between interaction effect and composition effect (Fig. 4e,f).

## DISCUSSION

#### The interaction and composition effects are distinct biodiversity effects

Although the interaction and composition effects are formally linked, we found that they are weakly correlated. The composition effect, that is, the contribution of

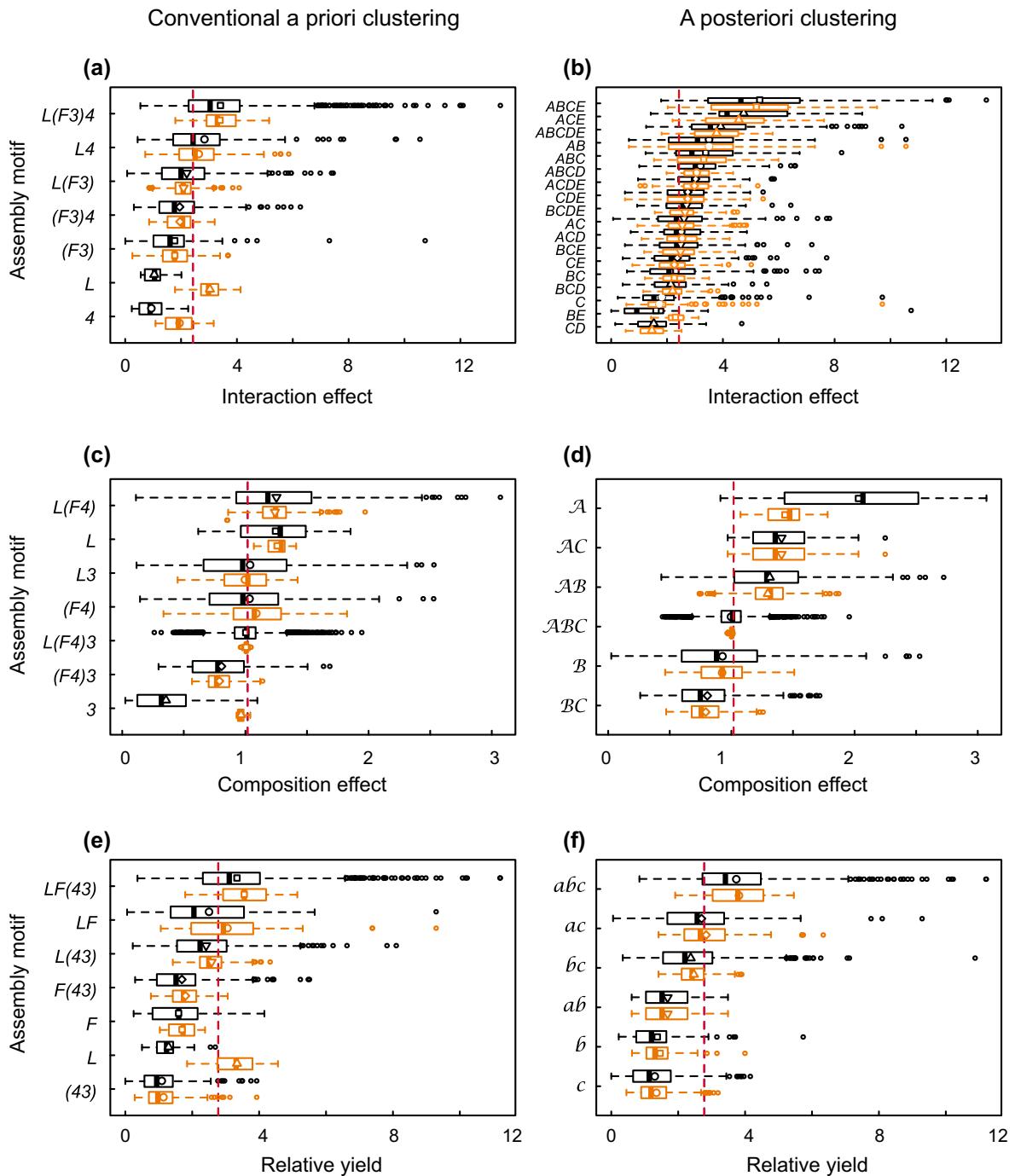


FIG. 4. Assembly motifs vs. diversity effects and relative yield predicted by cross-validation from 1996 to 2017. (a) and (b) Interaction effect. (c) and (d) Composition effect. (e) and (f) Relative yield. (a), (c), and (e) Conventional a priori clustering. (b), (d), and (f) A posteriori clustering. Black and gold boxes are observed and predicted yields, respectively. The blue line corresponds to mean values over 22 yr.

species' intrinsic properties, and the interaction effect, that is, the collective contribution of species interactions, are two distinct biodiversity effects. As previously suggested by Kirwan et al. (2009) and Connolly et al. (2013), it is therefore useful to model them separately and independently.

This result supports the findings obtained by previous authors when separating the selection effect from the complementarity effect in terrestrial, aquatic, and microbial ecosystems. Indeed, a zero selection effect implies a zero correlation between the interaction and composition effects. The deviation from the expected relative

yield of species in mixture is not necessarily positively correlated with their yield in monoculture (Loreau and Hector 2001, Hector et al. 2002, Cardinale et al. 2007, 2011). However, the additive partition, as defined and used by Loreau and Hector (2001), and the multiplicative partition defined by Wilson (1988) are two different approaches that address different issues. The additive partition was designed to test a possible selection effect by using the general theory of selection proposed by Price (1995). The multiplicative partition separates non-linear effects from linear effects at the ecosystem level: It is therefore best suited to identify functionally redundant species, that is, species that react similarly to species interactions, whatever the expected yield of species mixtures (Wilson 1988, Garnier et al. 1997, Jaillard et al. 2018a).

The composition effect is a simple, additive, and linear effect induced by differences in productivity of co-occurring species that compose an ecosystem: the more productive the co-occurring species, the higher the composition effect. It integrates the entire biological variability of species that compose ecosystems. The composition effect is therefore a basic effect that necessarily occurs in all ecosystems. In the BioDIV experiment, the composition effect is close to 1 on average, because the number of ecosystems is large enough, and all species are equitably represented in the experimental design. It does not vary over time because the experimental design did not change over time. Our findings show that the composition effect is well modeled and predicted by the clustering analysis. The model of a posteriori species clustering into three functional groups explains 64% of the variance of the composition effect over 22 yr. This is a high explanatory power over such a long time period. In return, our model can independently predict 70% of the variance explained across the 22 yr. The clustering analysis has a strong explanatory and predictive capacity for the composition effect of ecosystems. However, the model of species clustering is not robust. This suggests that the contribution of each species to the composition effect varies over time. Our results confirm that species in monoculture respond differently to changes in environmental conditions, especially for the legumes. The scale factor, which captures environmental conditions, varies from 1 to 2, meaning that external environmental forces strongly regulate ecosystem productivity. The scale factor integrates the main temporal environmental effects on ecosystems, but the composition effect also integrates a part of environmental effects. Although the compositional effect appears to be a simple effect, its sensitivity to environmental variations impedes its robust modeling by a unique clustering of species.

In contrast, the interaction effect is a collective ecosystem property: it is nonlinear and possibly idiosyncratic. We found that the interaction effect increases steadily over time, especially in species-rich mixtures. We also observed that its contribution to yield predominated. This result is consistent with the findings previously

reported by Fargione et al. (2007) and Reich et al. (2012) for the same experiment. Conversely to the composition effect, the clustering analysis of the interaction effect identified up to five functional groups of species. The species clustering into five groups is very robust. Such an accuracy and stability of the clustering model over such a long period is striking. It demonstrates that the nature of species interactions involved in the regulation of biomass production does not change over time, even if the environmental effect strongly fluctuates, and even if the strength of interaction effect strongly varies over time. This demonstrates that, in the BioDIV experiment, the web of species interactions within ecosystems does not change over the 22 yr. Given the predominance of the interaction effect over the composition one, explaining and predicting ecosystem productivity therefore requires explaining and predicting the interaction effect in priority.

*An a posteriori species clustering explains and predicts accurately ecosystem functioning*

Many authors have shown that ecosystem productivity increases with biodiversity, notably with the number of species (Tilman et al. 1997, 2001, Cardinale et al. 2011, Weisser et al. 2017) and with the number of functional groups (Tilman et al. 1997, Hooper and Dukes 2004, Reich et al. 2004, Weisser et al. 2017). However, in general, the effects identified are moderate, and explain only a small fraction of observed variance. For instance, Tilman et al. (1997) showed that standing yield increases twice from one to five functional groups. Our results showed that this increase is much greater, reaching between three and four times from one to three functional groups. The effect underlined by Tilman et al. (1997) seems moderate in comparison to the one we computed for two reasons. First, the authors referred to conventional functional groups built a priori, usually based on a taxonomic or physiological basis (Hooper et al. 2002). For instance, all Cedar Creek experiments (Tilman et al. 1997, 2001, 2002, Szymstad et al. 1998, Craine et al. 2002, 2003, Reich et al. 2004, 2012) used four functional groups: the group of legumes that share the nitrogen symbiotic fixation in roots, the groups of C3 and C4 grasses differ in their photosynthetic metabolism in leaves, and the group of forbs that includes various nonfixing Dicotyledons. We showed that the legumes in monoculture respond more than other groups to environmental conditions. However, it has been also previously noted that these groups are functionally heterogeneous (Tilman et al. 1997, Reich et al. 2001, 2003, 2004, Craine et al. 2002, 2003). The clustering approach brings together taxonomically and physiologically different species, but the co-occurrence of these in ecosystems has similar effects on the ecosystem property. Second, ecosystem biomass production results from several diversity and environmental effects, whose determinisms are different and independent. The partition of

biomass into interaction effect, composition effect and scale factor makes it possible to isolate each of these contributions: (1) multiplicative, nonlinear and collective contribution of interactions among species via the interaction effect; (2) additive, linear, and specific contribution via the composition effect, (3) and abiotic effects induced by environmental conditions via the scale-factor. We are thus able to analyze which process determines each of these contributions more precisely. The analysis of assembly motifs involved in each diversity effect shows that the drivers that determine composition effect and interaction effect are completely different.

Finally, our findings showed that assembly motifs, that is combinations of functional groups, are highly structuring and very discriminating entities. As several authors have already shown (Hooper and Vitousek 1997, Tilman et al. 1997, Hooper 1998, Hooper and Dukes 2004), assembly motifs are of great interest for explaining variation in ecosystem properties. Obviously, species interactions vary according to patterns of species co-occurrence, inducing different effects on ecosystem functioning. As a consequence, a given species, or functional group of species, responds differently according to the assembly motif to which it belongs, that is, according to the other species with which it co-occurs within the assembly motif. The ecosystem clustering into assembly motifs accounts for both the linearity of response of the composition effect and the nonlinearity of response of the interaction effect to changes in ecosystem biodiversity.

#### *An a posteriori species clustering identifies the main species that govern ecosystem functioning*

The a posteriori clustering greatly improves the explanatory and predictive abilities of species clustering. However, ecosystem biomass results in the same time from both the composition effect and the interaction effect. As previously claimed (Jaillard et al. 2018a), a clustering analysis using observational data, without prior partition, can only identify the main species combinations that govern ecosystem functioning. Our results show that both model accuracy and efficiency for such a species clustering remain high. Nevertheless, this species clustering can only be a trade-off between the species clustering for interaction effect and the species clustering for composition effect. This unique species clustering is a combination of several clusterings: such a species clustering is therefore difficult to interpret in terms of biological processes.

Many studies from the BioDIV experiment have noted the major role played by legumes in the regulation of ecosystem productivity (Szymstad et al. 1998, Tilman et al. 2001, Craine et al. 2002, Fornara and Tilman 2009). Our results further emphasized interactions between *Lupinus perennis*, *Andropogon gerardi*, *Elymus canadensis*, *Poa pratensis*, and *Amorpha canescens*. When *Lupinus perennis* co-occurs with any other species, the interaction effect is high: *Lupinus perennis* increases the

species mixture biomass, likely by improving the biomass of co-occurring species. When *Lupinus perennis* co-occurs with *Andropogon gerardi*, *Elymus canadensis*, or *Poa pratensis*, the interaction effect is the highest: *Lupinus perennis* and *Andropogon gerardi*, *Elymus canadensis*, or *Poa pratensis* have a synergetic effect. When *Lupinus perennis* co-occurs with *Amorpha canescens*, with or without *Andropogon gerardi*, *Elymus canadensis*, or *Poa pratensis*, the interaction effect is lower: *Amorpha canescens* reduces the improving effect of *Lupinus perennis*. Our findings demonstrate that these interaction effects do not change over time.

*Amorpha canescens* and *Lupinus perennis* are legumes that fix nitrogen (Fornara and Tilman 2009). However, one can have large interspecific ecological differences among legumes related to nitrogen fixation (Craine et al. 2002), and nitrogen fixation can be associated with a broad suite of physiological traits. For instance, *Lupinus* mobilizes soil phosphorus in its rhizosphere as a result of organic acid release by roots (Hinsinger et al. 2002, Lambers et al. 2013). Other legumes strongly acidify their rhizosphere and change soil properties (Jaillard et al. 2003). These effects are not captured by functional traits traditionally used to build conventional species clustering. *Amorpha canescens* is the most productive species in the BioDIV experiment. It is clear that *Amorpha canescens* and *Lupinus perennis* act differently, possibly because of the higher competitive ability of *Amorpha canescens* for light or for other resources: when *Amorpha canescens* co-occurs with *Lupinus perennis*, it decreases the positive interaction effect induced by *Lupinus perennis*. *Lupinus perennis* and *Amorpha canescens* are legumes: a clustering that groups together all legumes, thus including both species, hence can have a good explanatory capacity. However, not all legumes release organic substances that mobilize soil phosphorus in the rhizosphere, or grow broadly and produce large amounts of yield in monoculture. A species clustering that groups together *Lupinus perennis* and *Amorpha canescens* consequently fails to predict ecosystem biomass because it confuses the roles actually played by each legume on the ecosystem property. Only an a posteriori clustering of species can faithfully account for the observed functioning of an ecosystem.

#### CONCLUSION

Most ecosystem functions, such as biomass production, respiration and nutrient recycling, result from at least two biodiversity effects, a composition effect and an interaction effect. Here we argue that understanding the drivers of ecosystem functions requires that each biodiversity effect needs to be first separated then analyzed separately. Our findings confirm that both diversity effects are not correlated, and that an a posteriori species clustering accounts for and accurately predicts each diversity effect. Overall, our findings demonstrate that, in the long-term BioDIV experiment, even if environmental conditions

and the interaction effect vary over time, the web of species interactions within ecosystems does not change with time. Clustering analyses without a priori represent a robust approach that is particularly efficient to unravel the web of species interactions.

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## SUPPORTING INFORMATION

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## OPEN RESEARCH

Data sets are available from the University of Minnesota Cedar Creek Data Catalog under the following data set IDs: "ple123: Plant aboveground biomass data"; "pce123: Plant species percent cover data"; "ple120: Plant aboveground biomass data"; "pce120: Plant species percent cover data". The package *functClust* is available on the R-CRAN at <https://CRAN.R-project.org/package=functClust>. The R-codes (Jaillard 2021) used here for computing and drawing the figures are available from Portail Data INRAE at <https://doi.org/10.15454/DD9J5T>.