# An a posteriori species clustering for quantifying the effects of species interactions on ecosystem functioning

**5 authors**, including:

Camille Richon
University of Liverpool
**8** PUBLICATIONS   **18** CITATIONS

Michel Loreau
French National Centre for Scientific Research
**417** PUBLICATIONS   **39,032** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project  Two postdoctoral positions in Theoretical Ecology View project

Project  The eco-mechanics of ecological interactions View project

RESEARCH ARTICLE

Methods in Ecology and Evolution    BRITISH ECOLOGICAL SOCIETY

# An a posteriori species clustering for quantifying the effects of species interactions on ecosystem functioning

Benoît Jaillard[1] 🆔  |  Camille Richon[1]  |  Philippe Deleporte[2]  |  Michel Loreau[3]  |
Cyrille Violle[4] 🆔

[1]UMR1222 Ecologie fonctionnelle et Biogéochimie des Sols et Agrosystèmes (Eco&Sols), INRA, Montpellier, France

[2]UMR1222 Ecologie fonctionnelle et Biogéochimie des Sols et Agrosystèmes (Eco&Sols), CIRAD, Montpellier, France

[3]Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis, France

[4]UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS – Université de Montpellier – Université Paul Valéry – EPHE, Montpellier, France

**Correspondence**
Benoît Jaillard
Email: benoit.jaillard@inra.fr

**Present address**
Camille Richon, Laboratoire des Sciences du Climat et de l'Environnement, CEA Orme des Merisiers, Gif-sur-Yvette, France

## Abstract

1. Quantifying the effects of species interactions is key to understanding the relationships between biodiversity and ecosystem functioning but remains elusive due to combinatorics issues. Functional groups have been commonly used to capture the diversity of forms and functions and thus simplify the reality. However, the explicit incorporation of species interactions is still lacking in functional group-based approaches. Here, we propose a new approach based on an a posteriori clustering of species to quantify the effects of species interactions on ecosystem functioning.

2. We first decompose the observed ecosystem function using null models, in which species diversity does not affect ecosystem function, to separate the effects of species interactions and species composition. This allows the identification of a posteriori functional groups that have contrasting diversity effects on ecosystem functioning. We then develop a formal combinatorial model of species interactions in which an ecosystem is described as a combination of co-occurring functional groups, which we call an *assembly motif*. Each assembly motif corresponds to a particular biotic environment. We demonstrate the relevance of our approach using datasets from a microbial experiment and the long-term Cedar Creek *Biodiversity II* experiment.

3. We show that our a posteriori approach is more accurate, more efficient and more parsimonious than a priori approaches. The discrepancy between a priori and a posteriori approaches results from the way each clustering is set up: a priori approaches are based on ecosystem or species properties, such as ecosystem size (number of species or functional groups) or species' functional traits, whereas our a posteriori approach is based only on the observed interaction and composition effects on ecosystem functioning.

4. Our findings demonstrate that an a posteriori approach is highly explanatory: it identifies who interacts with whom, and quantifies the effects of species interactions on ecosystem functioning. They also highlight that a combinatorial modelling of ecosystem functioning can predict the functioning of an ecosystem without any hypothesis about the biotic or environmental determinants or any information on species functional traits. It only requires the species composition of the ecosystem and the observed functioning of others that share the same assembly motif.

# 1 | INTRODUCTION

Species interactions strongly influence ecosystem functioning (Hooper et al., 2005; Loreau & Hector, 2001). However, quantifying their net impact is puzzling (Balvanera et al., 2006; Duffy, 2009; Huston, 1997; Jiang, Wan, & Li, 2009). Analytical methods have been proposed to separate the net effects of species composition from those of species interactions (Garnier, Navas, Austin, Lilley, & Gifford, 1997; Jiang et al., 2009; Kirwan et al., 2009; Loreau & Hector, 2001; Wilson, 1988). These methods have successfully explained biodiversity effects in several biodiversity–ecosystem functioning experiments (Loreau & Hector, 2001; Reich et al., 2012), but they have not quantified the net effect of species interactions nor identified the species that really interact. The quantification of all possible pairwise species interactions is practically infeasible in species-rich ecosystems because of the curse of dimensionality (McGill, Enquist, Weiher, & Westoby, 2006). The difficulty of this task lies in the fact that myriad different types of positive and negative species interactions can simultaneously occur within ecosystems. Several attempts have been proposed to frame a pragmatic and operational approach to quantify ecosystem-wide species interactions. The trait-based characterization of species' competitive abilities, that is the search for organism traits that can explain how species' functions influence the performance of competing neighbours (Grace, 1990), paved the road to a generic description of species interactions. In the last decade, this approach has been widely used to study species interactions (the "interaction milieu" sensu McGill et al., 2006) through the systematic evaluation of the community-level distribution of interaction traits. However, interaction traits are still unknown in most taxa (Violle, Reich, Pacala, Enquist, & Kattge, 2014).

Even if functional-group approaches simplify reality, they offer an operational and parsimonious way to analyse and model ecosystem functioning. Nevertheless, up to now this approach has mostly relied on a priori clustering based on expert knowledge, as illustrated by the widespread classification of plants into three groups: legumes, graminoids and forbs. An a posteriori clustering may be promising since it will identify functional groups based on realized effects, for instance based on the way interacting species modulate ecosystem functioning. Such clustering has hardly been applied so far. A notable exception is the study of Wright et al. (2006) which searched for the best species clustering to predict ecosystem biomass. More recently, Jaillard, Rapaport, Harmand, Brauman, and Nunan (2014) developed a novel modelling approach to species interactions based on their effects on ecosystem functioning. This model was able to successfully reproduce all the forms of biodiversity–ecosystem functioning relationships reported in the literature but its flexibility remained low because it is based on a priori prevalent assembling rules that determine ecosystem functioning. Here, we extend Jaillard et al. (2014)'s model by proposing

an a posteriori clustering approach to the effects of ecosystem-wide species interactions on a given ecosystem function.

The aim of this study is to quantify the net effects of species interactions on a given ecosystem function. As suggested by Wilson (1988), we first decompose the observed ecosystem function using null models in which species diversity does not affect ecosystem functioning. This allows us to separate the effects of species interactions from the effects of species composition on ecosystem functioning. This separation makes it possible to a posteriori identify functional groups (sensu Díaz & Cabido, 2001 and Lavorel & Garnier, 2002) that have contrasting interaction and composition effects on the ecosystem function. Then, we propose a formal combinatorial framework to describe an ecosystem as a combination of co-occurring functional groups, which we call *assembly motif*, echoing the network motifs in network theory (Milo et al., 2002). Each assembly motif parsimoniously accounts for the observed effects of species interactions and composition on ecosystem functioning. We test this approach using two datasets: one microbial diversity experiment (Langenheder, Bulling, Solan, & Prosser, 2010) and the Cedar Creek *Biodiversity II* experiment (Tilman et al., 2001). We demonstrate that our approach can identify who is interacting with whom, and quantify the effects of species diversity on ecosystem functioning.

# 2 | MATERIALS AND METHODS

## 2.1 | Separating the effects of species interactions and species composition on ecosystem functioning

Consider a set $S = \{1, ..., s\}$ of $s$ species $i$ (Figure 1a). An ecosystem is defined as an assemblage $A$ of individuals that belong to different species:

$$A = \{i \in S\}.$$

A cumulative function $F_{\text{observed}}(A)$ such as primary production, respiration or nutrient recycling is observed for each ecosystem $A$. The function $F_{\text{observed}}(\{i\})$ (with $i = 1, ... ,s$) for monocultures of each species is also observed.

We set two null hypotheses, named $H_0$ and $G_0$, respectively (Figure S1). The null hypothesis $H_0$ describes a situation where the species interactions within an ecosystem do not affect the ecosystem functioning. Under $H_0$, the expected function $F_{\text{expected}/H0}(A)$ of an ecosystem is simply the mean of functions $F_{\text{observed}}(\{i\})$ of all monocultures of co-occurring species $i$ of $A$ (Wilson, 1988):

$$F_{\text{expected}/H_0}(A) = \bar{F}_{i \in A \text{observed}}(\{i\}). \tag{1}$$

The null hypothesis $G_0$ describes a situation where neither the species interactions nor the species composition affect the ecosystem function. Under $G_0$, the expected function $F_{\text{expected}/G0}(A)$ of any

**(a)    Clustering of species**

Original set of species

**(b)    Clustering of ecosystems**

Functional groups of species
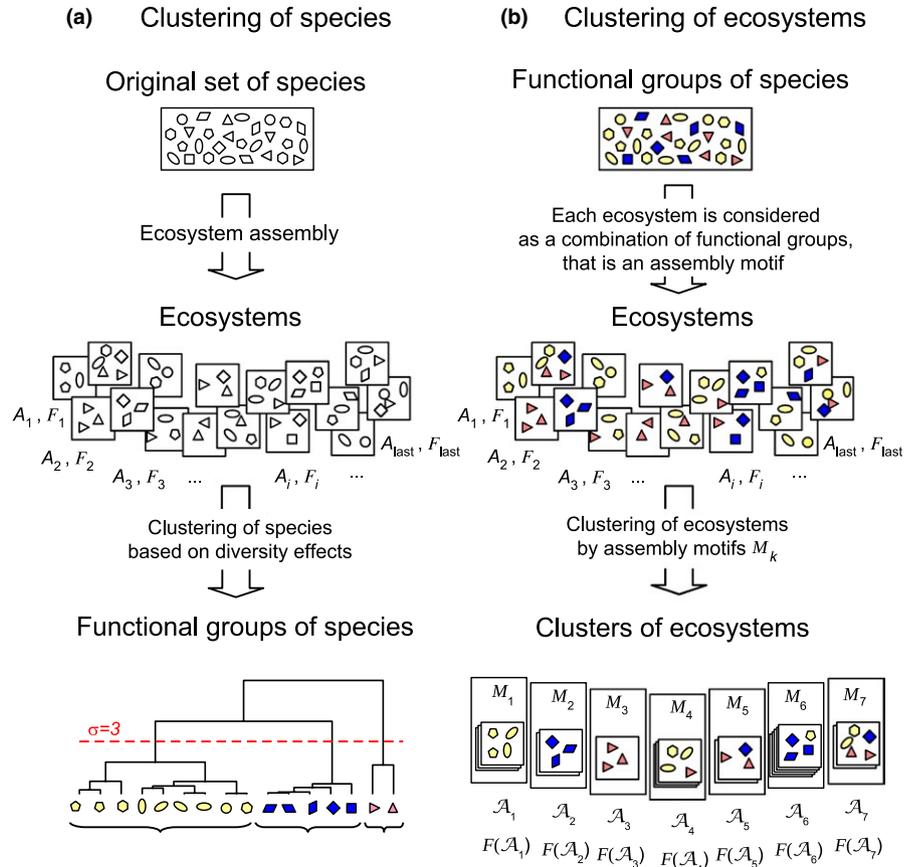


**FIGURE 1** Step-by-step clustering framework to model the diversity effects on an ecosystem function. (a) An ecosystem $A$ is defined as a set of co-occurring species and is characterized by an aggregate function $F$. Species are clustered into functional groups (here $\sigma = 3$ for instance) on the basis of the mean diversity effects of clusters of ecosystems containing a given species. (b) Each ecosystem is then described by a combination of functional groups, that is an *assembly motif* $M_k$ (here, $m = 2^\sigma - 1 = 7$ possible assembly motifs). Ecosystems described by the same assembly motif $M_k$ are grouped into the clusters $\mathcal{A}_k$ and characterized by the aggregate functions $F(\mathcal{A}_k)$ ($k = 1...7$). The goodness of fit of the model clustering is evaluated by its determination coefficient and its robustness by cross-validation

ecosystem is consequently constant. By convenience, we assume that the constant is the expected function $F_{\text{expected}/H0}(S)$ of all the species used in the experiment, that is according to the Equation 1, the mean of functions $F_{\text{observed}}(\{i\})$ of all monocultures of species $i$ of $S$:

$$F_{\text{expected}/G_0}(A) = F_{\text{expected}/H_0}(S) = \overline{F}_{\substack{\text{observed}\\ i \in S}}(\{i\}) \quad (2)$$

The function $F_{\text{observed}}(A)$ of an ecosystem can then be decomposed as follows:

$$F_{\text{observed}}(A) = \frac{F_{\text{observed}}(A)}{F_{\text{expected}/H_0}(A)} \frac{F_{\text{expected}/H_0}(A)}{F_{\text{expected}/G_0}(A)} F_{\text{expected}/G_0}(A).$$

or:

$$F_{\text{observed}}(A) = \alpha(A)\, \beta(A)\, F_{\text{expected}/G_0}(A) \quad (3)$$

with:

$$\alpha(A) = \frac{F_{\text{observed}}(A)}{F_{\text{expected}/H_0}(A)} \quad (4)$$

and:

$$\beta(A) = \frac{F_{\text{expected}/H_0}(A)}{F_{\text{expected}/G_0}(A)}. \quad (5)$$

The quotient $\alpha(A)$ corresponds to the effect of species interactions on the ecosystem function. This *interaction effect* is specific to an ecosystem. It equals one under $H_0$, is lower than one when the species interactions decrease the ecosystem function and is higher than one when the species interactions increase the

ecosystem function. The normalized remainder $\beta(A)$ corresponds to the effect of species composition of the ecosystem on its function. This *composition effect* characterizes the subset of species that belong to the ecosystem, relatively to the whole set of species. It equals one under $G_0$, is lower than one when the species composition decreases the ecosystem function and is higher than one when the species composition increases the ecosystem function. The composition effect is one on average when all the possible ecosystems are tested. Finally, the remainder $F_{\text{expected}/G0}(A)$ is by definition constant: this is a scale factor specific to the species set used in the experiment, that is the function expected with neither interaction nor composition effects. The scale factor integrates all the variations in species functions in the experiment (e.g. variation in environmental conditions across time). It has the dimension of the ecosystem function. Interaction and composition effects are dimensionless.

## 2.2 | Analysing the diversity effects induced by each species on ecosystem functioning

The idea is now to cluster ecosystems on the basis of the ecosystem interaction and composition effects. We denote by $\mathcal{A}$ the set of ecosystems $A$ observed in the experiment. We define $\mathcal{A}_i$ (with $i = 1, ... ,s$) the cluster of ecosystems $A$ that contains at least one individual of the species $i$ of $S$:

$$\mathcal{A}_i = \{A \in \mathcal{A} \text{ such that } \exists\, i \in A\}. \qquad (6)$$

The interaction and composition effects $\alpha(\mathcal{A}_i)$ and $\beta(\mathcal{A}_i)$ induced by each species within the ecosystems are estimated by the mean diversity effects of ecosystems $A$ that contain at least one individual of the species $i$ of $S$, then:

$$\alpha\left(\mathcal{A}_i\right) = \underset{A \in \mathcal{A}_i}{\bar{\alpha}}\left(A\right) \quad \text{and} \quad \beta\left(\mathcal{A}_i\right) = \underset{A \in \mathcal{A}_i}{\bar{\beta}}\left(A\right). \qquad (7)$$

## 2.3 | Introducing the concept of assembly motif: a simple and operational descriptor of the composition of an ecosystem

Each ecosystem is a subset of individuals that belong to different species: it can also be described as a subset of individuals that belong to different functional groups of species. We cluster the species set $S = \{1, \dots, s\}$ into $\sigma$ functional groups $S_j$ (with $j = 1, \dots, \sigma$) on the basis of their interaction and composition effects $\alpha(\mathcal{A}_i)$ and $\beta(\mathcal{A}_i)$ (Figure 1a). The $\sigma$ functional groups $S_j$ allow the assembly of $m = 2^\sigma - 1$ non-empty combinations of functional groups. We term *assembly motif* $M_k$ (with $k = 1, \dots, m$) each combination of functional groups, then:

$$M_k = \{S_j \text{ with } j \in \{1, \dots, \sigma\}\}$$

We associate each ecosystem $A$ with an assembly motif $M_k$ by assuming that each species $i$ of $A$ belongs to a functional group $S_j$ of $M_k$ and that each functional group $S_j$ of $M_k$ is represented by at least one individual of species $i$ of $A$. Then, we define $\mathcal{A}_k$ ($k = 1, \dots, m$) as the cluster of ecosystems $A$ described by the assembly motif $M_k$:

$$\mathcal{A}_k = \{A \in \mathcal{A} \text{ such that } \forall\, i \in A, \exists\, S_j \in M_k$$
$$\text{with } i \in S_j, \text{ and } \forall\, S_j \in M_k, \exists\, i \in A \text{ with } i \in S_j\}.$$

## 2.4 | Modelling the function of an ecosystem according to its assembly motif

An assembly motif characterizes a particular biotic environment. Next, we cluster ecosystems by assembly motifs; that is, we cluster ecosystems that share a similar biotic environment (Figure 1b). We use the ecosystem clustering by assembly motifs to model the ecosystem function. As in Equation 6, we define $\mathcal{A}_{i,k}$ (with $i = 1, \dots, s$) the cluster of ecosystems $A$ of $\mathcal{A}_k$ that contains at least one individual of the species $i$ of $S$:

$$\mathcal{A}_{i,k} = \{A \in \mathcal{A}_k \text{ such that } \exists\, i \in A\}.$$

According to Equation 7, the interaction and composition effects $\alpha(\mathcal{A}_{i,k})$ and $\beta(\mathcal{A}_{i,k})$ of ecosystems $A$ of clusters $\mathcal{A}_{i,k}$ are estimated by:

$$\alpha\left(\mathcal{A}_{i,k}\right) = \underset{A \in \mathcal{A}_{i,k}}{\bar{\alpha}}\left(A\right) \quad \text{and} \quad \beta\left(\mathcal{A}_{i,k}\right) = \underset{A \in \mathcal{A}_{i,k}}{\bar{\beta}}\left(A\right). \qquad (8)$$

According to Equations 3 and 8, the function $F_{\text{modelled}}(A)$ of any ecosystem $A$ is finally modelled as the product of the mean interaction effect, the mean composition effect and the scale factor of ecosystems that contain the same species and share the same assembly motif:

$$F_{\text{modelled}}\left(A \in \mathcal{A}_k\right) = \underset{i \in A}{\bar{\alpha}}\left(\mathcal{A}_{i,k}\right) \underset{i \in A}{\bar{\beta}}\left(\mathcal{A}_{i,k}\right) F_{\text{expected}/G_0}\left(A\right). \qquad (9)$$

## 2.5 | Combinatorics and statistics

The interaction effects $\alpha(A)$ and the composition effects $\beta(A)$ are computed for each ecosystem using its species composition and the monoculture functions of each species (Equations 1–5). The mean interaction and composition effects $\alpha(\mathcal{A}_i)$ and $\beta(\mathcal{A}_i)$ of the clusters of ecosystems containing a given species $i$ of $S$ are computed using all the ecosystems containing the species (Equation 7). The species centroids are then clustered in functional groups using Euclidean distance and Ward's linkage algorithm (functions dist, method = "euclidean," and hclust, method = "ward.D" with R, see the scripts in Supporting Information) on the basis of mean diversity effects $\alpha(\mathcal{A}_i)$ and $\beta(\mathcal{A}_i)$ (Legendre & Legendre, 2012).

The hierarchical tree of species centroids clustering is cut at different levels by increasing step-by-step the number of functional groups (see Figure 1). At each step, that is for a given number of functional groups, all possible assembly motifs $M_k$ are assembled, and the ecosystems are clustered by assembly motifs. For a comparison of different approaches, the species are also clustered by (1) functional groups a priori defined by Tilman et al. (2001) and by (2) size (i.e. number of species in the ecosystem). In the latter case, each ecosystem size is an assembly motif.

The mean diversity effects $\alpha(\mathcal{A}_{i,k})$ and $\beta(\mathcal{A}_{i,k})$ of species in each assembly motif are computed according to Equation 8. The function $F_{\text{modelled}}(A \in \mathcal{A}_k)$ is then evaluated according to Equation 9. The interaction effect is a quotient and thus measures a multiplicative process: the mean of this biodiversity effect is computed according to a geometric formula (Equations 7–9). The composition effect is a remainder and thus measures an additive process: the mean of this biodiversity effect is computed according to an arithmetic formula (Equations 1, 2, 7–9) (Crawley, 2007).

The goodness of fit of each clustering model is evaluated by the coefficient of determination $R^2$ of the relationship between modelled and observed ecosystem functions, that is the ratio between the variance explained by the modelling and the total variance observed in the experiment:

$$R^2 = 1 - \frac{\sum\limits_{A \in \mathcal{A}} \left(F_{\text{observed}}\left(A\right) - F_{\text{modelled}}\left(A\right)\right)^2}{\sum\limits_{A \in \mathcal{A}} \left(F_{\text{observed}}\left(A\right) - \bar{F}_{\text{observed}}\left(A\right)\right)^2}.$$

The robustness of each clustering model is evaluated by cross-validation. Because of the small number of observations in most experiments, we use a leave-one-out cross-validation; that is, each ecosystem function is independently predicted by removing the

ecosystem to predict from the experiment dataset. The prediction accuracy is evaluated by the model efficiency $E$, that is the ratio between the variance explained by the independent predictions and the total variance observed in the experiment (see, e.g., Nash & Sutcliffe, 1970):

$$E = 1 - \frac{\sum_{A \in \mathcal{A}} \left( F_{observed} \left( A \right) - F_{predicted} \left( A \right) \right)^2}{\sum_{A \in \mathcal{A}} \left( F_{observed} \left( A \right) - \bar{F}_{observed} \left( A \right) \right)^2}.$$

When all the possible ecosystems are observed, all the possible assembly motifs are represented at least once. When only a part of possible ecosystems are observed, some assembly motifs are not observed. When an assembly motif is represented by only one ecosystem, the ecosystem function cannot be independently predicted. We define the *predicting ratio* as the number of ecosystems for which the function can be predicted by the clustering model, divided by the number of all observed ecosystems.

All the computations are done using the R-software (R Development Core Team, 2009).

## 2.6 | Biodiversity datasets

We used two datasets to test our approach. The first dataset is based on the observation of all the possible ecosystems assembled with an initial pool of microbial species. Langenheder et al. (2010) designed this experiment to analyse the biodiversity–productivity relationship in bacterial microcosms. They tested all the 63 possible species combinations with a pool of six bacteria: 6, 15, 20, 15, 6 and 1 combinations with 1, 2, 3, 4, 5 and 6 bacteria, respectively. Here, we analyse the xylose oxidation (ecosystem function) after 48 hr for the 63 bacterial ecosystems, of which six are monospecies and 57 plurispecies cultures.

The second dataset is the Cedar Creek *Biodiversity II* experiment dataset (Tilman et al., 2001). This experiment was dedicated to the analysis of the biodiversity–productivity relationship in grasslands. Here, the studied ecosystem function is the yearly plant above-ground biomass per unit area. The experiment contained 88 ecosystems from a pool of 16 prairie species (Reich et al., 2012; Tilman et al., 2001). Diversity treatments consisted of 1-, 2-, 4-, 8- and 16-species plots, each replicated 34 times on average, which corresponds to 168 experimental plots. The species composition in each plot was a random draw from the experimental species pool. All species were grown in monoculture. The 16 prairie species were a priori clustered into four functional groups of four species: legumes, forbs, C3- and C4-grasses. As a case study, here we analyse the above-ground biomass harvested in the 88 ecosystems in August 2004, of which 35 are monospecies and 53 plurispecies plots. Each biomass is the average value of the harvests of three "unsorted" strips.

## 3 | RESULTS

### 3.1 | Species clustering based on the diversity effects on ecosystem functioning

The scale factors $F_{expected/G0}(A)$ are 0.633 xylose oxidation and 114.8 g/m$^2$ of biomass accumulated for a year in the microbial and *Biodiversity II* experiments, respectively. The decomposition of the function of each ecosystem into dimensionless effects of species interactions $\alpha(A)$ and species composition $\beta(A)$ allows the comparison of these two experiments (Figure 2). The mean interaction effect is 1.46 ± 0.23 in the microbial experiment and 2.08 ± 1.18 in the *Biodiversity II* experiment. Even though the interaction effect is significantly correlated with the observed ecosystem function in both experiments, they are more strongly correlated in the
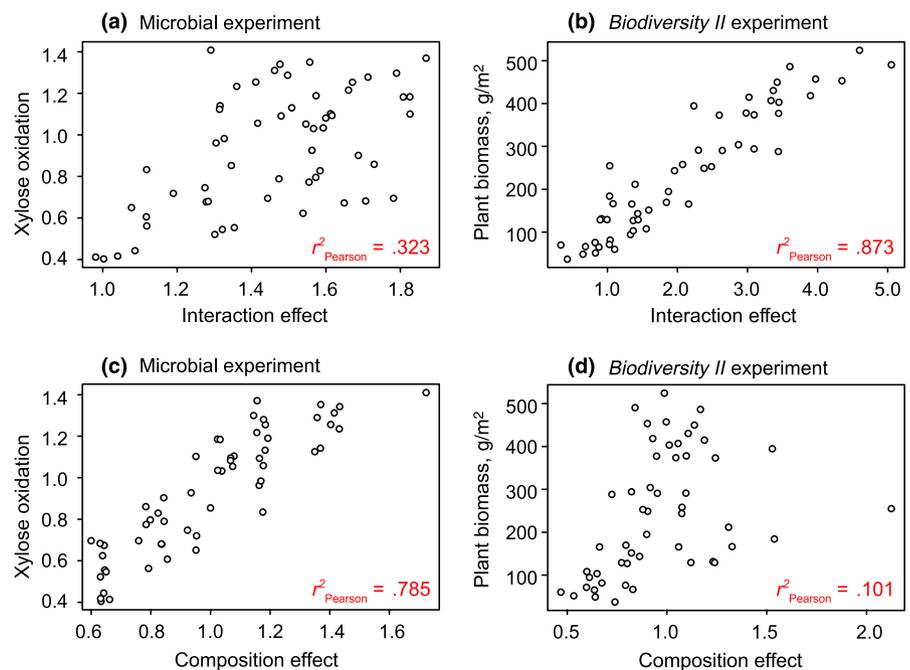


**FIGURE 2** Effects of species interactions and species composition of an ecosystem function. (a) and (b) Ecosystem function vs interaction effect, (c) and (d) Ecosystem function vs composition effect. The coefficient of correlation $r^2_{Pearson}$ of the relationship are indicated: they are significant at $p < .001$

*Biodiversity II* experiment ($p < 10^{-16}$) than in the microbial experiment ($p = 3.9 \times 10^{-6}$) (Figure 2a and b). The mean composition effect is exactly one (1.00 ± 0.27) in the microbial experiment where all the species combinations are assembled. The mean composition effect is close to one (0.97 ± 0.14) in the *Biodiversity II* experiment: it is not significantly different from one ($p < 10^{-16}$). In both experiments, the composition effect is significantly correlated with the observed function. However, composition effect and observed function are more strongly correlated in the microbial experiment ($p < 10^{-16}$) than in the *Biodiversity II* experiment ($p = .007$) (Figure 2c and d). In both experiments, the interaction effect and the composition effect are not correlated ($r^2_{Pearson} = .019$ and $p = .305$ in the microbial experiment; $r^2_{Pearson} = 1.7 \times 10^{-4}$ and $p = .927$ in the *Biodiversity II* experiment) (Figure 3).

A species-centred analysis can be performed when comparing the location of ecosystems containing a given species on the α-by-β space (Figure 3). Overall, such an analysis highlights tremendous differences between species effects. For instance, in the microbial experiment, SL104 belongs to ecosystems with the highest composition effect on xylose oxidation (Figure 3a). The other species belong to ecosystems that are close to each other's (Figure 3c and Figure S2a).

In the *Biodiversity II* experiment, the functional groups defined by Tilman et al. (2001) are not homogeneous in their effects (Figure 3b and d). Among legumes, *Lupinus perennis* (Luppe) and *Lespedeza capitata* (Lesca) belong to ecosystems with the highest interaction effects, whereas *Amorpha canescens* (Amocan) belongs to ecosystems with the highest composition effect (Figure 3d and Figure S2b). Finally, *Petalostemum purpureum* (Petpu) belongs to ecosystems characterized by low interaction and composition effects (Figure 3d and Figure S2b).

The hierarchical clustering (Figure 3e and f) corroborates this explanatory analysis. In the microbial experiment, SL104 is first isolated in a singleton, then SL68 and SL187. Based on a four-group clustering, the functional groups of species are namely: { SL104 }, { SL68 } and { SL187 } in singletons, then { SLWC2, SL106, SL197 } (Figure 3e). This means that, when the three species SLWC2, SL106 and SL197 co-occur with each other inside their functional group, and with species SL104, SL68 and SL187 that belong to singletons, they induce similar diversity effects on the ecosystem functioning. In the *Biodiversity II* experiment, the species are first separated in two groups, then *Lupinus perennis* is isolated from the smallest group. Based on a three-group clustering, the functional groups of species are namely: {*Lupinus perennis*} in a singleton, {*Lespedeza capitata*, *Koeleria cristata*,
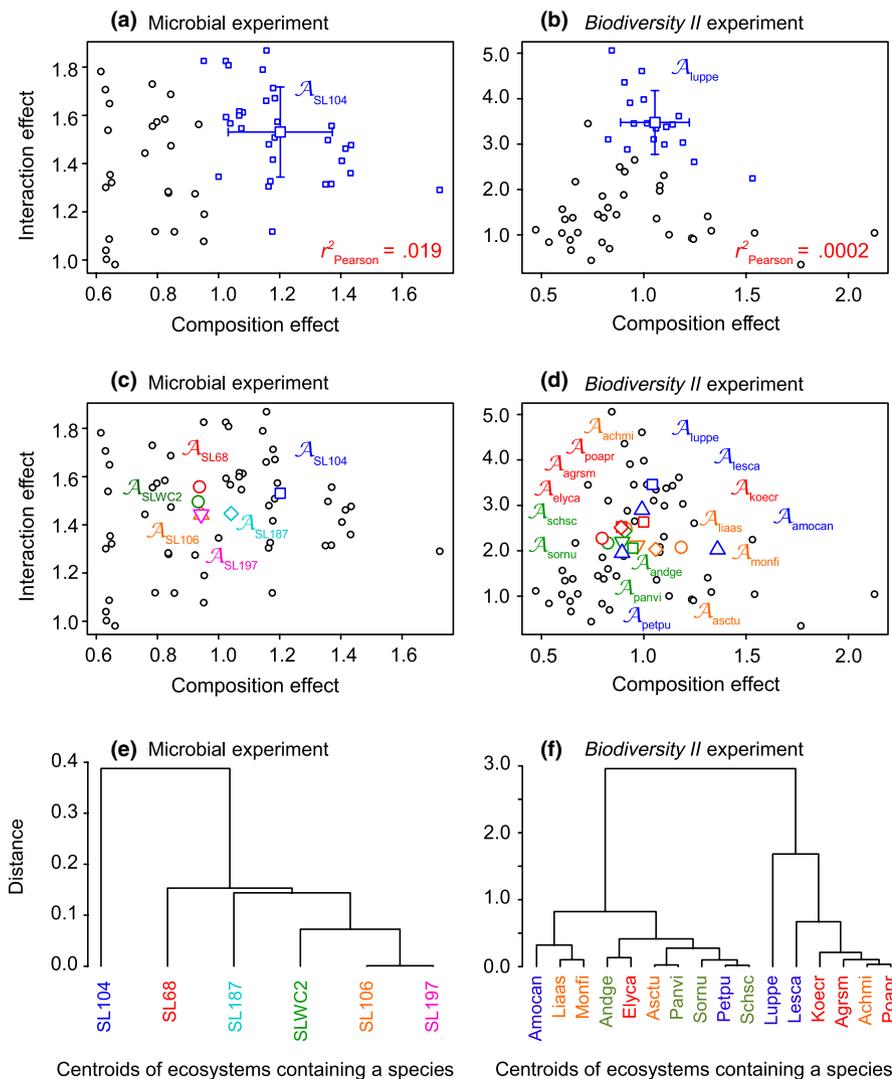


**FIGURE 3** Species clustering based on the mean diversity effects of the clusters of ecosystems containing a given species. (a) and (b) Interaction effect vs composition effect. Example of a cluster of ecosystems containing a given species (SL104 or *Lupinus perennis*). (c) and (d) Interaction effect vs composition effect. Centroids of the clusters of ecosystems containing each species. (e) and (f) Trees of hierarchical clustering of centroids of the ecosystem clusters containing each species. The centroids are clustered using Euclidean distance and Ward's linkage algorithm. In (d) and (f), different colours correspond to different functional groups defined by Tilman et al. (2001), legumes (blue), C3-grasses (red), C4-grasses (green) and forbs (gold)

*Agropyron smithii, Achillea millefolium, Poa pratensis*} and {*Amorpha canescens, Liatris aspera, Monarda fistulosa, Andropogon gerardi, Elymus canadensis, Asclepias tuberose, Panicum virgatum, Sorghastrum nutans, Petalostemum purpureum, Schizachyrium scoparium*} (Figure 3f). Ten species belong to the largest group, that is a C3-grass, two legumes, three forbs and the four C4-grasses. This clustering means that, when the ten species co-occur with each other inside the largest functional group, and with species of other functional groups, they induce similar diversity effects on the ecosystem functioning. Except the C4-grasses, the functional groups a priori defined by Tilman et al. (2001) are split into several clusters: C3-grasses and forbs into two, and the four legumes into three different clusters.

## 3.2 | Modelling the ecosystem functioning based on the ecosystem clustering

Next, we focus on the modelling of ecosystem function based on the ecosystem clustering by assembly motifs, that is the combination of functional groups of species (see Figure 1). We recall that each species clustering in functional groups is a model, which generates a new set of assembly motifs. Consequently, we explore the model quality, accuracy and efficiency, by increasing step-by-step the number of functional groups (Figure 4). The goodness of fit of the model increases from a low value until one when there are as many functional groups as species (Figure 4a and b). The model robustness is evaluated by its efficiency: it also increases, but remains always lower than the goodness of fit of the model. In contrary, the predicting ratio decreases with the number of functional groups, from one when all the ecosystems are clustered together in a singleton (all ecosystem functions are predicted by the mean function of all ecosystems), until zero when

there are as many functional groups as species (no ecosystem function can be predicted because each ecosystem cluster is a singleton) (Figure 4c and d). The best number of functional groups results from a trade-off between the accuracy ($R^2$), the efficiency ($E$) and the predicting ability (predicting ratio) of the model. In the microbial experiment, $R^2$ increases from 1 to 5 functional groups (Figure 4a). However, $E$ presents a maximum for four clusters of species, which corresponds to a predicting ratio of 53/57 ecosystems (Figure 4c). In the *Biodiversity II* experiment, $R^2$ increases, with local maximums for 3, 6 and 8 species functional groups, and the predicting ratio decreases quickly from 1 to 16 functional groups. A species clustering in three functional groups allows to predict the functions of 52 of 53 ecosystems.

For a given species clustering, each ecosystem can be described by a unique assembly motif, and its function can be evaluated by modelling (Figures S3 and S4 for the independent modelling of both diversity effects). In the microbial experiment, all the 63 species combinations are observed. Species richness is the most frequently used metric of diversity in biodiversity–ecosystem functioning research (Hooper et al., 2005; Langenheder et al., 2010; Reich et al., 2012; Tilman et al., 1997, 2001). As a consequence, here we use species number (ecosystem size) as a reference (Figures 5a and b). This modelling leads to dispersed and overlapping diversity effects (Figure 5a), but goodness of fit ($R^2 = .438$, $p = 9.1 \times 10^{-7}$) and efficiency ($E = .245$, $p = 1.8 \times 10^{-3}$) are significant (Figure 5b). Based on a four-group species clustering, the resulting ecosystem clustering by assembly motifs is much more structured (Figure 5c and d). The diversity effects of ecosystems that share an assembly motif are close to each other, confirming the functional redundancy of clustered species (Figure 5c). The goodness of fit is high ($R^2 = .892$, $p < 10^{-16}$), and the efficiency of this modelling remains high and highly significant ($E = .828$, $p < 10^{-16}$) (Figure 5d).
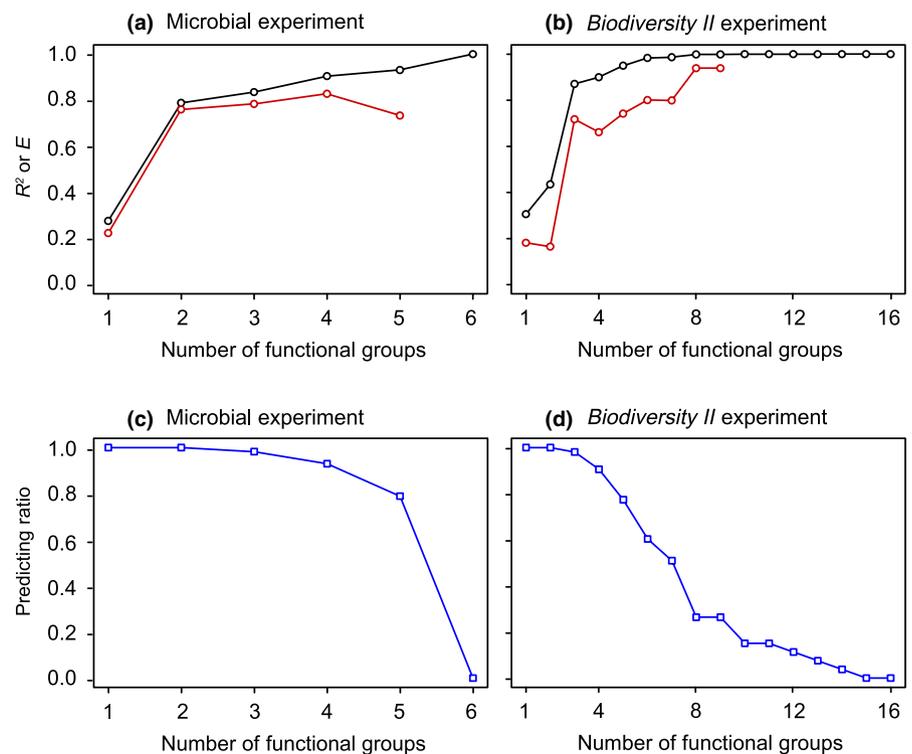


**FIGURE 4** Accuracy, efficiency and predicting ability of modelling vs the number of functional groups. (a) and (b) Coefficient of determination $R^2$ (in black) and efficiency $E$ (in red) of the relationship between the ecosystem function observed vs modelled ($R^2$) or predicted ($E$) by cross-validation. (c) and (d) Predicting ratios, that is the proportion of ecosystems of which the function can be predicted by the clustering model

Microbial experiment

**Modelling outcome of an a priori clustering based on the ecosystem size (number of species)**



**Modelling outcome of an a posteriori 4-group clustering of species**
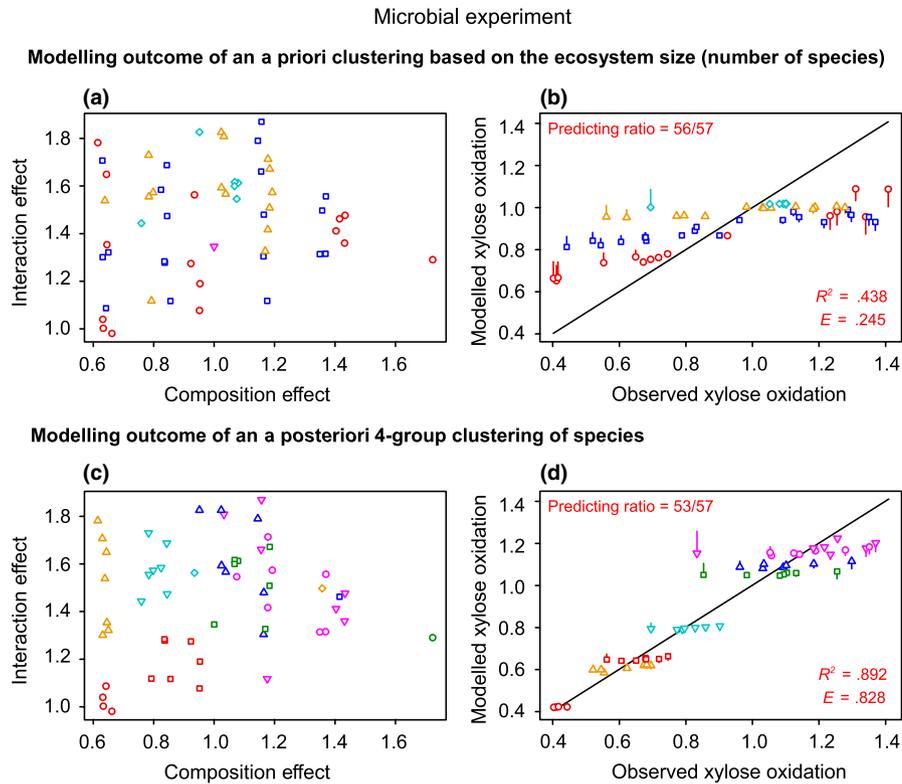
**FIGURE 5** Ecosystem clustering, goodness of fit and efficiency of the clustering model for ecosystem functioning in the microbial experiment (Langenheder et al., 2010). (a) and (b) Modelling based on the ecosystem size (number of species). (c) and (d) Modelling based on an a posteriori four-group species clustering. (a) and (c) Interaction effect vs composition effect. (b) and (d) Relationship between modelled and observed ecosystem functions. Each bar corresponds to the error induced by leaving out the ecosystem to predict. Different coloured symbols correspond to different assembly motifs. Solid black line is the 1:1 line

In the *Biodiversity II* experiment, only 53 of 65519 (65535 - 16 monocultures) plurispecies ecosystems are observed, thus less than 0.1% of all possible species assemblages. The clustering of ecosystems by their size induces dispersed and overlapping ecosystem groups (Figure 6a), a poor goodness of fit ($R^2$ = .489, $p$ = $1.2 \times 10^{-9}$) and a poor efficiency ($E$ = .142, $p$ = $1.2 \times 10^{-3}$) of the modelling (Figure 6b). A four-group clustering based on functional groups a priori defined by Tilman et al. (2001) improves significantly the goodness of fit ($R^2$ = .771, $p$ = $4.4 \times 10^{-16}$), but more weakly the efficiency of the modelling ($E$ = .375, $p$ = $2.7 \times 10^{-8}$), and the predicting ratio equals to 46/53 (Figure 6c and d). An a posteriori species clustering in only three groups improves strongly both the goodness of fit ($R^2$ = .863, $p$ < $10^{-16}$) and the efficiency ($E$ = .717, $p$ = $2.2 \times 10^{-14}$) of the modelling (Figure 6e and f). Moreover, the function of 52/53 ecosystems can be predicted independently.

## 4 | DISCUSSION

### 4.1 | Separating the interaction and composition effects: an alternative proposal

The decomposition of ecosystem functions into diversity effects has been successfully used in the past to analyse biodiversity–ecosystem functioning experiments (Loreau & Hector, 2001; Reich et al., 2012). This method follows an integrative path by computing the covariance between the observed and expected contributions of each species to ecosystem functioning. We here followed the same philosophy but used the ratio between observed and expected yield (so-called relative yield of the mixture, RYM) instead of the covariance, as suggested

by Wilson (1988). Based on this decomposition, we defined two new elementary ecosystem-level diversity effects: interaction and composition effects. Both interaction and composition effects are dimensionless, which allows comparisons between experiments performed in various conditions.

The two experiments that we re-analyse here are very different: bacterial assemblages grown for 48 hr in laboratory (Langenheder et al., 2010) and grassland mixtures cultivated for several years in the field (Tilman et al., 2001). In the microbial experiment, the observed function is strongly correlated to the composition effect. In both experiments, species interactions greatly increase ecosystem function, between 1.4 and 2.1 times, indicating strong complementary interactions (e.g., facilitation, niche differentiation) between species, as suggested by Tilman et al. (2001) and Langenheder et al. (2010). In addition, we found that the covariance between the interaction and composition effects is not significantly different from zero, which corroborates Loreau and Hector (2001)'s results. These findings demonstrate that the interaction and composition effects are independent in both experiments, but the two diversity effects contribute significantly to ecosystem functioning.

### 4.2 | The emerging concept of assembly motifs

We propose to quantify the net effect of species interactions on ecosystem functioning through the lens of *assembly motifs*, that is a combination of co-occurring functional groups within an ecosystem. An assembly motif is a pattern of species composition that reflects a given biotic environment. Our results show that ecosystems described by the same assembly motif display diversity effects on ecosystem

*Biodiversity II* experiment

**Modelling outcome of an a priori clustering based on the ecosystem size (number of species)**



**Modelling outcome of an a priori clustering of species based on 4-functional groups defined by Tilma*n et al.* 2001: legumes, forbs, C3- and C4-grasses**



**Modelling outcome of an a posteriori 3-group clustering of species**
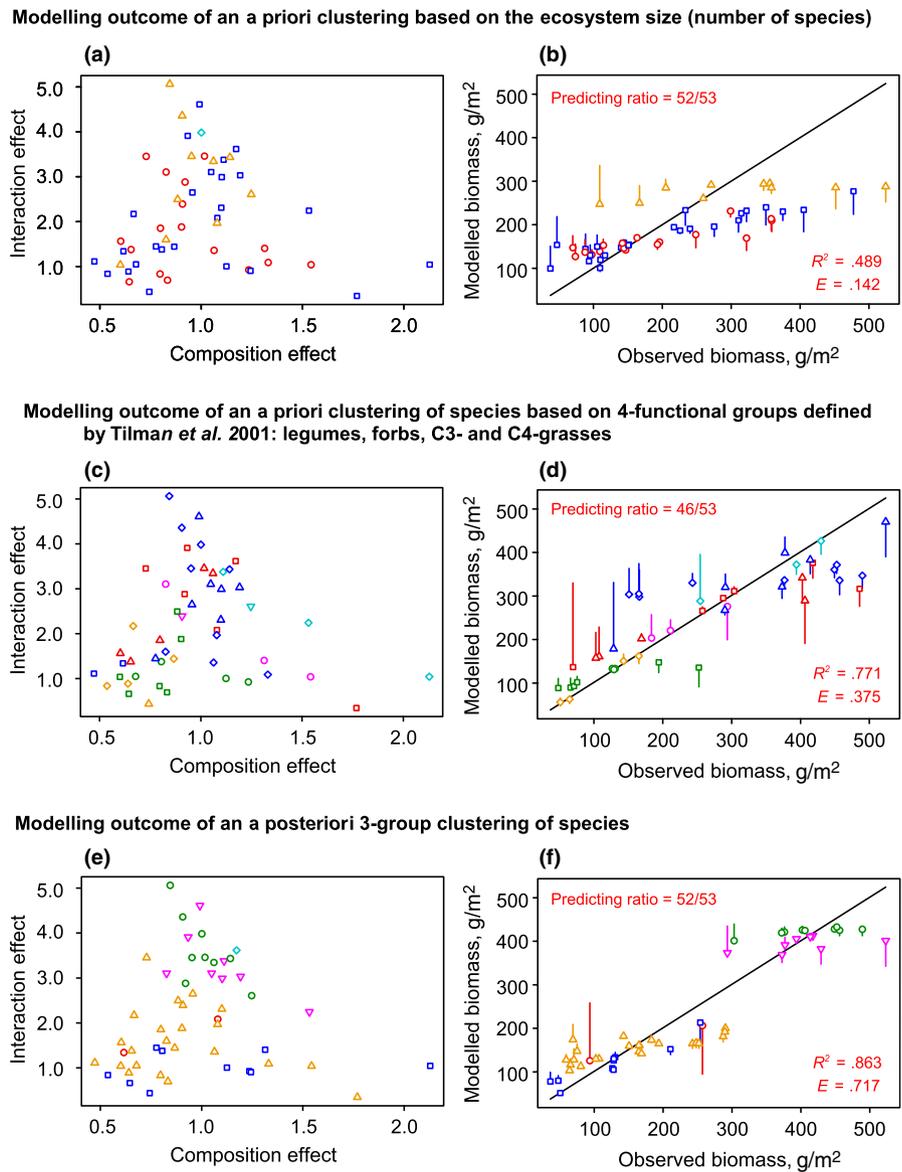


**FIGURE 6** Ecosystem clustering, goodness of fit and efficiency of the clustering model for ecosystem functioning in the *Biodiversity II* experiment (Tilman et al., 2001). (a) and (b) Modelling based on the ecosystem size (number of species). (c) and (d) Modelling based on an a priori four-group species clustering defined by Tilman et al. (2001), that is legumes, forbs, C3- and C4-grasses. (c) and (d) Modelling based on an a posteriori three-group species clustering. (a), (c) and (e) Interaction effect vs composition effect. (b), (d) and (f) Relationship between modelled and observed ecosystem functions. Each bar corresponds to the error induced by leaving out the ecosystem to predict. Different coloured symbols correspond to different assembly motifs. Solid black line is the 1:1 line

functioning similar to each other in terms of interaction and composition effects. An assembly motif therefore describes the biotic environment that regulates the effects of species interactions on a given ecosystem function.

The underlying condition of our modelling framework is that the presence/absence of at least one species from each functional group changes the ecosystem-wide species effect in a similar way (Jaillard et al., 2014). This condition is the simplest and the most commonly used in ecology (Díaz & Cabido, 2001; Hooper et al., 2005). It implicitly assumes that the presence of particular species, thus of particular interactions, is more important than the number of interactions, the number of species or the number of functional groups. Some authors have long pointed out that the composition of an ecosystem, that is the identity of species or functional groups, affects its functioning more than diversity per se (Hooper & Vitousek, 1997). Our results confirm the validity of this hypothesis in both studied experiments.

Our modelling framework is based on combinatorics through combinations and clustering of species, functional groups and ecosystems. Clustering of species or ecosystems is a simplification of the real world. It assumes that clustered species are functionally redundant, which means in our case that they induce roughly the same effects on the ecosystem functioning. However, the functional redundancy, and thus the species clustering, is specific to the considered experiment, to the set of species used and to the ecosystem function observed in the experiment (Loreau, 2004). Species clustering is only a shortcut that should enable a better understanding of reality. The clustering of species based on their diversity effects reduces the range of possibilities to affect the ecosystem functioning. The clustering of ecosystems by assembly motifs reduces the range of effects induced by the species interactions and composition on ecosystem functioning. The variance within each ecosystem cluster is low. The clustering thus enables the a posteriori determination of a likely interacting schema based on parsimonious species clusters and readable ecosystem clusters. It finally

sets up a comprehensive interacting organization of species within ecosystems, without any a priori knowledge of species properties.

## 4.3 │ Identifying and quantifying the interacting roles of species within ecosystems

We clearly showed that an ecosystem clustering based on assembly motifs is much more suitable than the classical clustering based on the ecosystem size, such as the number of species or functional groups. Langenheder et al. (2010) biologically showed that the species SL104 plays a key role on xylose oxidation. Our modelling approach retrieves this key role of SL104 and specifies that the species increases the ecosystem function by composition effect rather than interaction effect. It also shows that the three species SLWC2, SL106 and SL197 are clustered in a same functional group; thus, they induce similar diversity effects by interacting between them and with others.

In the *Biodiversity II* experiment, we highlight that only three a posteriori functional effect groups explain and successfully predict ecosystem functioning. The a priori species clustering based on the number of species as well as the clustering defined by Tilman et al. (2001) are both based on four groups: they explain and predict less accurately the ecosystem biomass than our a posteriori approach. Our a posteriori approach is thus more accurate, more efficient and more parsimonious than both a priori approaches based on ecosystem size and functional groups a priori defined. Surprisingly, the four legumes classically clustered into a single functional group (legume) were found in different functional groups based on our a posteriori clustering. *Lupinus perennis* belongs to the ecosystem cluster with the highest interaction effects. *Lupinus perennis* is a legume, the leaves and fine roots of which have a very short longevity, lesser than 4 weeks, releasing large amounts of nitrogen in soil (Craine et al., 2002). In Europe, the *Lupinus* genus is also known among legumes to produce cluster roots that release citrate and protons and mobilize poorly available nutrients such as phosphorus (Hinsinger, Plassard, Tang, & Jaillard, 2002; Jaillard, Plassard, & Hinsinger, 2003; Lambers, Clements, & Nelson, 2013). The *Lupinus* species from the New World are less studied but Lambers, Bishop, Hopper, Laliberté, and Zúñiga-Feest (2012) reported that *Lupinus lepidus* also produces cluster-like roots. *Lespedeza capitata* is clustered with a forb (*Achillea millefolium*) and three C3-grasses (*Koeleria cristata*, *Agropyron smithii* and *Poa pratensis*). The species cluster has high interaction effects but low composition effects. Note that *Lupinus perennis* and *Lespedeza capitata* are always isolated in small functional groups and have strong structuring effects on the ecosystem function across years (from 2001 to 2007, data not shown). *Amorpha canescens* belongs to ecosystems with the highest composition effects but low interaction effects. Our results confirm that legumes play a key role in ecosystem-level biomass production, as previously highlighted by many authors (e.g. Tilman et al., 1997, 2001), but, as suggested by Craine et al. (2002) and Wright et al. (2006), they also indicate that the "legume" functional group is not homogeneous in the ability of legumes to affect plant biomass.

## 4.4 │ Biodiversity effects: a new conceptual framework

The approach developed here first separates the interaction effect from the composition effect of diversity on an ecosystem function, then clusters species in functional groups on the basis of these diversity effects on ecosystem functioning. However, the novelty is mainly to combine functional groups of species and to assume that any species assemblage, matching to all possible combinations of functional groups; that is, all possible assembly motifs, can significantly affect, positively or negatively, the interaction and composition effects. Jaillard et al. (2014) already showed that a combinatorial approach makes it possible to reproduce all shapes of diversity–ecosystem functioning relationships reported in the experimental literature, suggesting that the multifaceted response of ecosystems to biodiversity changes is driven by effects of assembly probabilities and variations in species properties. We here demonstrate that a combinatorial approach also allows the modelling of ecosystem functioning without any hypothesis about its biotic or environmental determinants, and without any information on species functional traits. We only use the available experimental data, that is the function and species composition of ecosystems, and the function of species in monoculture. Wright et al. (2006) study is the only one to assess random species clustering based on their ability to predict an ecosystem function. The main result obtained by Wright et al. (2006) was that the explanatory powers of a priori and random clustering were not significantly different. In contrast to the conclusion of Wright et al. (2006), our results show that an a posteriori species clustering can be highly explanatory. It even makes it possible to predict with accuracy the functioning of an ecosystem on the sole basis of its species composition.

A posteriori approaches such as ours aim at describing the structure of raw data. In our case, the idea is to determine the functional structure of ecosystems that best accounts for the observed data without attempting to explain the underlying biological processes. This approach allows testing some hypotheses; in particular, it allowed us to challenge the widespread use of the legume–forb–graminoid clustering when investigating the role of biodiversity in regulating ecosystem functioning. It also makes it possible to efficiently predict a given ecosystem function based on a set of ecosystems in which species composition and function have already been observed. Nevertheless, a posteriori approaches remain statistical and phenomenological. They should be complemented by a priori approaches that formulate new explanatory hypotheses based on the findings of a posteriori approaches. For instance, the identification of functional traits associated with different species groups identified by our combinatorial approach could help to reveal the underlying biological processes. Ultimately, a deeper understanding of biodiversity–ecosystem functioning relationships should ideally come from a combination of a posteriori and a priori approaches: the former to explore data and reveal real patterns and the latter to determine the functional traits or biological processes responsible for the observed species patterns. This combination is best suited to providing robust, general, explanatory and anticipatory

predictions of the effects of species diversity on ecosystem functioning (Mouquet et al., 2015).

# 5 | CONCLUSION

We propose a combinatorial model to quantify the net effects of species interactions on ecosystem functioning and an efficient method to fit species clustering to experimental datasets. When applied to two datasets, a microbial experiment and the *Biodiversity II* experiment, we show that assembly motifs, that is patterns of ecosystem assembly that reflect patterns of species interactions, explain a large part of the biodiversity effects on ecosystem functioning. This confirms that the existence of interactions of a certain type is more important than the number of interactions, of species or of functional groups. Our model is based solely on assembly motifs defined as patterns of ecosystem functional structure: it is the first model that characterizes species by their ability to affect ecosystem functioning, without explicitly accounting for their biological properties (e.g. functional traits).

## AUTHORS' CONTRIBUTIONS

B.J. conceived the research; B.J. and C.R. implemented the code; B.J. and P.D. developed the statistics; B.J., C.R., M.L. and C.V. drew the figures and wrote the manuscript.

## DATA ACCESSIBILITY

The R scripts and datasets are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rh4v0 (Jaillard, Richon, Deleporte, Loreau, & Violle, 2017).

## ORCID

*Benoît Jaillard* [iD] http://orcid.org/0000-0002-5156-1866

*Cyrille Violle* [iD] http://orcid.org/0000-0002-2471-9226

## REFERENCES

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, *9*, 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grasslands species. *Functional Ecology*, *16*, 653–574.

Crawley, M. J. (2007). *The R book*. Hoboken, NJ: John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470515075

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, *16*, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Duffy, J. E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, *7*, 437–444. https://doi.org/10.1890/070195

Garnier, E., Navas, M. L., Austin, M. P., Lilley, J. M., & Gifford, R. M. (1997). A problem for biodiversity-productivity studies: How to compare the productivity of multispecific plant mixtures to that of monocultures? *Acta Oecologica*, *18*, 657–670. https://doi.org/10.1016/S1146-609X(97)80049-5

Grace, J. (1990). On the relationship between plant traits and competitive ability. In J. Grace, & D. Tilman (Eds.), *Perspectives on plant competition* (pp. 51–65). San Diego, CA: Academic Press.

Hinsinger, P., Plassard, C., Tang, C., & Jaillard, B. (2002). Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. *Plant and Soil*, *248*, 43–59.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., … Wardle, D. A. (2005). Effect of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3–35. https://doi.org/10.1890/04-0922

Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, *277*, 1302–1305. https://doi.org/10.1126/science.277.5330.1302

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, *111*, 449–460. https://doi.org/10.1007/s004420050180

Jaillard, B., Plassard, C., & Hinsinger, P. (2003). Measurements of $H^+$ fluxes and concentrations in the rhizosphere. In Z. par Rengel (Ed.), *Handbook of soil acidity* (pp. 231–266). New York, NY: Marcel Dekker Inc.

Jaillard, B., Rapaport, A., Harmand, J., Brauman, A., & Nunan, N. (2014). Community assembly effects shape the biodiversity-ecosystem functioning relationships. *Functional Ecology*, *28*, 1523–1533. https://doi.org/10.1111/1365-2435.12267

Jaillard, B., Richon, C., Deleporte, P., Loreau, M., & Violle, C. (2017). Data from: An a posteriori species clustering for quantifying the effects of species interactions on ecosystem functioning. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.rh4v0

Jiang, L., Wan, S., & Li, L. (2009). Species diversity and productivity: Why do results of diversity-manipulation experiments differ from natural patterns? *Journal of Ecology*, *97*, 603–608. https://doi.org/10.1111/jec.2009.97.issue-4

Kirwan, L., Connolly, J., Finn, J. A., Brophy, C., Lüscher, A., Nyfeler, D., & Sebastià, M.-T. (2009). Diversity-interaction modeling: Estimating contributions of species identities and interaction to ecosystem function. *Ecology*, *90*, 2032–2038. https://doi.org/10.1890/08-1684.1

Lambers, H., Bishop, J. G., Hopper, S. D., Laliberté, E., & Zúñiga-Feest, A. (2012). Phosphorus-mobilisation ecosystem engineering: The roles

of cluster roots and carboxylate exudation in young P-limited eco-systems. *Annals of Botany*, 110, 329–348. https://doi.org/10.1093/aob/mcs130

Lambers, H., Clements, J. C., & Nelson, M. N. (2013). How a phosphorus-acquisition strategy based on carboxylate exudation powers the success and agronomic potential of lupines (*Lupinus*, Fabaceae). *American Journal of Botany*, 100, 263–288. https://doi.org/10.3732/ajb.1200474

Langenheder, S., Bulling, M. T., Solan, M., & Prosser, J. I. (2010). Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PLoS ONE*, 5, e10834. https://doi.org/10.1371/journal.pone.0010834

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd ed.). Amsterdam, the Netherlands: Elsevier.

Loreau, M. (2004). Does functional redundancy exits? *Oikos*, 104, 606–611. https://doi.org/10.1111/oik.2004.104.issue-3

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76. https://doi.org/10.1038/35083573

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., … Wardle, D. A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294, 804–808. https://doi.org/10.1126/science.1064088

McGill, B., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Ecology Letters*, 21, 178–185.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, 298, 824–827. https://doi.org/10.1126/science.298.5594.824

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., … Loreau, M. (2015). Predictive ecology in a changing world. *Journal of Applied Ecology*, 52, 1293–1310. https://doi.org/10.1111/1365-2664.12482

Nash, J. E., & Sutcliffe, J. V. (1970). River flow forecasting through conceptual models part I-A discussion of principles. *Journal of Hydrology*, 10, 282–290. https://doi.org/10.1016/0022-1694(70)90255-6

R Development Core Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Retrieved from http://www.R-project.org

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B., & Eisenhauer, N. (2012). Impacts of biodiversity loss escalate through time as redundancy fades. *Science*, 336, 589–592. https://doi.org/10.1126/science.1217909

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–846. https://doi.org/10.1126/science.1060391

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13690–13696. https://doi.org/10.1073/pnas.1415442111

Wilson, J. B. (1988). Shoot competition and root competition. *Journal of Applied Ecology*, 25, 279–296. https://doi.org/10.2307/2403626

Wright, J. P., Naeem, N., Hector, A., Lehman, C., Reich, P. B., Schmid, B., & Tilman, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, 9, 111–120. https://doi.org/10.1111/j.1461-0248.2005.00850.x

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

---

**How to cite this article:** Jaillard B, Richon C, Deleporte P, Loreau M, Violle C. An a posteriori species clustering for quantifying the effects of species interactions on ecosystem functioning. *Methods Ecol Evol*. 2017;00:1–12. https://doi.org/10.1111/2041-210X.12920

---