

Functional identity of dominant species in a predator community prevails over functional diversity in shaping the top-down control of herbivores

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Abstract

1. Decline in species richness as well as changes in community evenness or functional diversity have been hypothesised to jointly affect ecosystem functioning. However, disentangling the relative effects of these changes in community structure is hard as these different aspects often covary with species richness in real-world ecosystems. In this study, we investigated the individual and interactive effects of functional diversity and community evenness of predators on the level of control of herbivorous prey.
2. Using a highly replicated mesocosm experiment, we crossed three levels of functional diversity of arthropod predators with two levels of community evenness while controlling for the effect of species richness. Using this experimental setting, we hypothesised that the effect size of functional diversity of predators depends on community evenness. We expected a positive effect of functional diversity of predators on top-down control at high level of community evenness while we thought that species identity and their associated traits should drive most of the effect on top-down control at low level of community evenness.
3. Our results did not provide any evidence for an interaction between functional diversity and community evenness nor any beneficial effect of increased functional diversity overall on predation rates of herbivorous prey. In addition, our results revealed that species and functional identity drives most of the effects of predator community composition on top-down control of their prey in our study system. Assemblages composed of active hunters with low handling time and no starvation ability tended to have the highest impacts on prey biomass.
4. By indicating that top-down control of herbivorous prey by arthropod predators is mainly driven by species and functional identity and not by functional diversity, our study provides insights into the consequences of ongoing species loss on ecosystem functioning. Future research should now explore the predictability of trophic interactions based on functional traits of predator and herbivorous prey to anticipate the consequences of changes in species composition on ecosystem functioning.

KEYWORDS

biodiversity and ecosystem functioning, evenness, functional diversity, mesocosm, phytophagous insects, predator–prey interactions, species identity

1 | INTRODUCTION

Global changes manifested by short and long-term climate modifications, overexploitation of natural resources, land use changes or habitat destruction deeply affect biodiversity (Ceballos et al., 2015; Leclère et al., 2020). The global decline in species richness erodes the level and the stability of many ecological processes indicating that alteration in community structure have major impacts on ecosystem functioning (Cardinale et al., 2012; Hooper et al., 2005). However, much of our knowledge about biodiversity and ecosystem functioning comes from studies on species richness based on correlative approaches and much of the variability in the biodiversity–ecosystem functioning relationship remains to be explained. Many other aspects of community structure than species richness are important to consider if we are to understand the consequences of environmental changes on ecosystem functioning.

Community evenness, that measures how regular abundances are among species within a community, is an important aspect of community structure significantly affecting ecological functioning (Crowder et al., 2010; Hillebrand et al., 2008). Recent studies even reported stronger effects of community evenness compared to species richness, suggesting a major impact of abundance distribution in communities on ecosystem functioning (Filstrup et al., 2019). Community evenness, or its inverse species dominance, can directly affect ecosystem functioning through species identity and the frequency distribution of traits in the community (Hillebrand et al., 2008; Maestre et al., 2012). Two main hypotheses have been proposed to explain the effect of species trait distribution on ecosystem functioning. First, the ‘mass ratio hypothesis’ states that the extent to which species traits affect ecosystem functioning is proportional to their abundance in the community (Grime, 1998). This hypothesis suggests that the most abundant species are expected to have the most influence on ecosystem functioning independently of the richness of subordinate species. Second, it has been demonstrated that functional diversity, that is the variation in species trait values in the community, promotes nonadditive effects on ecological functioning. This is due to antagonistic or synergistic interactions leading to more efficient use of resources among coexisting species (Cadotte et al., 2011; Díaz & Cabido, 2001; Flynn et al., 2011). These two hypotheses express different aspects of community trait composition but are not mutually exclusive and have been found to significantly explain part of the variation in different ecological processes (Sankoly et al., 2019). They both offer potential mechanistic explanations for the variable effects of species richness or community evenness on ecosystem functioning. If functioning is enhanced by niche complementarity and more equitable distribution of different

functional traits, then a reduction in evenness is likely to reduce ecosystem functioning (Hillebrand et al., 2008). However, if ecosystem functioning is primarily driven by the functional traits of the dominant species, a reduction in evenness could lead to either a positive or a negative effect on a given function, depending on the traits of the species that become more dominant (Hillebrand et al., 2008; Nijs & Roy, 2000). While this clearly suggests that community evenness and trait composition jointly shape ecosystem functioning, how these two major aspects of community structure interact to affect ecosystem functioning remains poorly explored, particularly on arthropods communities (Le Bagousse-Pinguet et al., 2021).

Top-down control of prey by their predators is a key function in ecosystems (Barnes et al., 2020; Dainese et al., 2019). Top-down control usually results from multiple interactions in highly complex food webs that are poorly understood and hard to describe. Despite an overall positive effect of species richness of predators on prey populations, idiosyncratic effects of species richness of predators on prey suppression have been reported (Griffin et al., 2013; Letourneau et al., 2009). Letourneau et al. (2009) indicated that predator species richness enhanced prey suppression in about 70% of the cases and reported high variability in the effects of species richness, suggesting that other aspects of community structure affect the level of top-down control. Both functional diversity and community evenness of predator communities may affect top-down control but how they respectively contribute to explain variability in the relationship between species richness and top-down control remains largely unknown (Crowder et al., 2010; Greenop et al., 2018; Schmitz, 2009). Moreover, species richness, functional diversity or community evenness often covary in real-world ecosystems, especially in highly disturbed ecosystems such as agroecosystems, hindering the evaluation of their individual effect on top-down control and highlighting the need for a proper assessment of their relative effects (Naeem, 2002).

In this study, using a replicated mesocosm experiment, we investigated the relative and interactive effects of functional diversity and community evenness of predators on the level of top-down control of herbivorous prey while controlling for the effect of species richness. We hypothesised that the effect size of functional diversity of predators depends on community evenness and expected a positive effect of functional diversity of predators on top-down control only at a high level of community evenness due to interspecific niche complementarity. Moreover, species identity of the dominant species should drive most of the effect on top-down control at low levels of community evenness (when species dominance is high). In addition, we explored the effects of functional characteristics of multiple assemblages to provide insights into the traits that are potentially involved in species-identity effects.

2 | MATERIALS AND METHODS

2.1 | Study design and community composition

To test how functional diversity modulates the effect of evenness in predator communities on herbivore consumption rates, we set up a mesocosm experiment that crossed three levels of functional diversity of predators with two levels of community evenness. We selected the aphid *Acyrtosiphon pisum* and the leafhopper *Euscelidius variegatus* as the two main herbivorous species for the experiment. This choice was driven by the fact that these species are common prey for predators in agroecosystems that can be easily maintained under experimental conditions, and because their different functional traits and behaviours make the emergence of complementarity effects between predators more likely. For instance, niche complementarity between foliage and ground-dwelling predators preying on *A. pisum* can emerge due to the dropping behaviour of *A. pisum*, which is a defence mechanism against predator foraging in the vegetation (Losey & Denno, 1998). In each mesocosm, we planted four plants of *Vicia faba* and 24 plants of *Trifolium repens* as they are host plant for the two main herbivorous species.

Eleven predator species that are known to prey on aphids and leafhoppers and that are common predators found in grassland or faba bean fields were selected to define predator assemblages used in the experiment. Based on the literature, we selected *Adalia bipunctata*, *Pterostichus melanarius*, *Drusilla canaliculata*, *Anthrenus nemoralis*, *Chrysoperla carnea*, *Forficula auricularia*, *Phalangium opilio*, *Tenuiphantes tenuis*, *Xysticus kochi*, *Xerolycosa minita* and *Pisaura mirabilis* (Allard & Yeagan, 2005; Anderson, 1962; Balog et al., 2013; Blackman, 1967; Dib et al., 2011; Dixon & McKinlay, 1992; Ximenez-Embun et al., 2014). In order to assemble three-species communities that represent three contrasted levels of functional richness, we first characterised these species using six functional traits involved in the predation (Drieu & Rusch, 2017; Schmitz, 2008; Woltz & Landis, 2014; Wootton et al., 2023). We collected information about body size (mm), circadian activity (diurnal, nocturnal), habitat domain (soil, foliage), hunting mode (ambush hunters, active hunters), averaged handling time (low, high) and starvation ability (yes, no) (Table S1). Based on this information, we calculated functional diversity index for each of all possible three-species combinations among the 11 species of predator. We used functional richness (FRic) to assess the functional diversity of predator communities as this index is independent of species abundance and therefore allows to disentangle the effect of functional diversity from the effect of community evenness (Mouchet et al., 2010). Functional richness quantifies the volume of trait space occupied by a species assemblage and is measured using the volume inside the convex hull enclosing all the species of an assemblage (Cornwell et al., 2006; Mouchet et al., 2010; Villéger et al., 2011). We then selected three assemblages among the potential 165 assemblages of three species, each one in each of the third quartiles of the functional richness distribution. This led to combine *A. bipunctata*, *A. nemoralis* and *X. kochi* in the low functional richness level; *A. bipunctata*, *C. carnea* and *P. mirabilis* in the medium

functional richness level; and *C. carnea*, *P. opilio* and *P. mirabilis* in the high functional richness level. *A. bipunctata*, *A. nemoralis* and *C. carnea* were bought at Biobest Company, while *P. mirabilis*, *P. opilio* and *X. kochi* were collected in the fields and maintained in the laboratory.

The two levels of community evenness were designed to have a low evenness modality (Pielou index = 0.79) and a high evenness modality (Pielou index = 1) for all levels of functional richness. The total number of predators in each mesocosm was six individuals so that the low level of evenness consisted in three-species communities composed of four individuals of the dominant species and one individual of the two remaining species, while the high level of evenness consisted in two individuals of each species.

In addition, for the low evenness modalities, we considered each situation of species dominance among assemblages of three species to control for the effect of predator identity. This resulted in four different treatments of evenness for a given level of functional richness: three low evenness treatments with each species dominating, and one high evenness treatment. As we considered three levels of functional richness, we ended up with 12 different treatments crossing each level of functional richness with each evenness treatment (four evenness treatments crossed with three functional richness levels) (Figure S1). For a given round of the experiment, we replicated each treatment at least three times (one round had four replicates) and considered six mesocosm controls with herbivores only. One round of the whole experiment therefore consisted of 42–54 mesocosms. To ensure robustness of the results, we replicated the whole experiment four times between 2016 and 2018 leading to a total of 180 mesocosms surveyed.

In each mesocosm, we introduced 150 aphids and 10 leafhoppers 24 h before the introduction of predators based on realistic densities of these phytophagous species in fields (Ammann et al., 2022; Bosco et al., 1997; Erb et al., 2010). We assessed the number of aphids and leafhoppers after 5 days of predation exposure using a mouth aspirator and careful visual inspections in each mesocosm. The number of prey collected were converted to biomass using average weights of 0.51 and 3.53 mg for *Acyrtosiphon pisum* and *Euscelidius variegatus*, respectively (Lamb et al., 1987; Purcell & Suslow, 1987). Mesocosms were kept in a greenhouse at ambient temperature and water was provided to plants every 2 days. We did not need any permission or appropriate licence to perform the experiment.

2.1.1 | Statistical analyses

We first used linear mixed models to investigate the interactive effects of functional richness and evenness on prey biomass. We ran three different sets of models, two using the biomass of each prey separately as response variables and one model explaining the overall prey biomass as a response variable. Explanatory variables were functional richness levels in interaction with evenness levels. We used replicate of the experiment as a random intercept in the linear mixed models (i.e. $\sim(1|\text{replicate})$). Post-hoc Tukey tests were then used to perform multiple comparisons between levels

of significant factors on prey biomass. Model residuals were inspected to ensure homoscedasticity and normality and response variables were log-transformed to improve normality and variance homogeneity.

To investigate if and how the identity of the dominant predator species affects prey biomass within the low evenness treatment, we ran linear mixed models to examine the effect of dominance identity on prey biomass (by prey species or for both prey species). To do so, we only considered mesocosms under the low evenness treatment for all level of functional richness. We used replicates of the experiment as a random intercept in the linear mixed model. Post-hoc Tukey tests were then used to perform multiple comparisons between levels of dominance on prey biomass. Model residuals were inspected to ensure homoscedasticity and normality and response variables were log-transformed to improve normality and variance homogeneity.

In order to further investigate the potential drivers of top-down control, we ran analyses exploring how other aspects of assemblages than functional richness or community evenness could affect top-down control of herbivores. We specifically focused on functional specialisation (i.e. the weighted mean distance of an assemblage to the centroid of the global species pool), functional originality (i.e. the weighted mean distance of an assemblage to the nearest assemblage) as well as functional identity (i.e. the weighted average position of each assemblage along each axis in functional

space) of each assemblage to investigate traits associated to species identity effects (Magneville et al., 2022). To examine how these factors affect top-down control of herbivores, we ran linear models using either functional specialisation, functional originality or functional identity in trait space (along the main PCoA axes in functional space) as explanatory variable and prey biomass as response variable. Model residuals were inspected to ensure homoscedasticity and normality.

All analyses were performed with R (v. 4.1.2). Linear mixed models were fitted using the *lme4* package (Bates et al., 2015) and multiple comparisons were performed using the *multcomp* package (Hothorn et al., 2008). Functional diversity metrics were calculated using the *mFD* package (Magneville et al., 2022).

3 | RESULTS

3.1 | Effects of functional richness and community evenness on herbivores

We found no effect of functional richness (ANOVA, $F_{2,147}=0.65$, $p=0.51$), community evenness (ANOVA, $F_{1,147}=0.52$, $p=0.46$) and their interactions (ANOVA, $F_{2,147}=0.59$, $p=0.55$) on overall prey biomass as well as on aphid and leafhopper biomass separately (Figure 1; Table S2; Figures S2 and S3). Compared to the control,

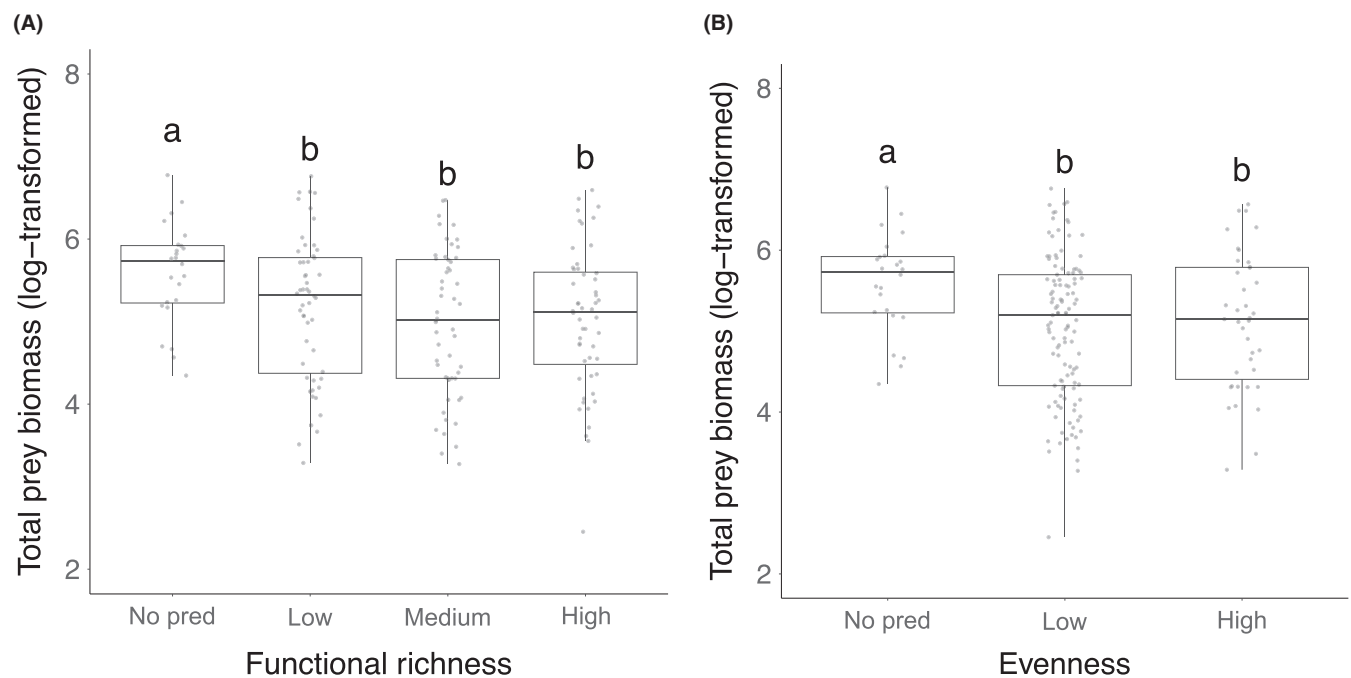


FIGURE 1 Effects of functional richness treatments (left panel—A) and community evenness (right panel—B) of predators on overall prey biomass. Functional richness levels include low, medium and high value based on the functional richness of predator assemblages selected. Community evenness include the low and the high treatment based on Pielou index. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Overall prey biomass was log-transformed and replicate was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

our analyses indicated an effect of predator introduction on prey as lower prey biomass (species considered together or separately) were consistently found in all functional richness or evenness treatments.

3.2 | Effects of predator identity on herbivores

Our analyses revealed a strong effect of the identity of the dominant species in assemblages on overall prey biomass and on aphid biomass while no significant difference of the identity of the dominant species were found on leafhopper biomass (Table 1; Figure 2; Figures S4 and S5). Among the different compositions, we found that assemblages dominated by *A. bipunctata*, *C. carnea*, *P. mirabilis* and *X. kochi* always significantly reduced the total biomass of herbivores relative to controls. Among them, assemblages dominated by *C. carnea* were the most suppressive one (Figure 2).

TABLE 1 Effects of the identity of dominant species in the low evenness treatment on total herbivore biomass (log-transformed).

Predictors	Response variable = Total prey biomass (log-transformed)		
	Estimates	CI	p-values
(Intercept)	5.58	4.80 to 6.36	<0.001
Dominant species [<i>Adalia bipunctata</i>]	-0.49	-0.78 to -0.20	0.001
Dominant species [<i>Anthocoris nemoralis</i>]	-0.18	-0.53 to 0.18	0.323
Dominant species [<i>Chrysoperla carnea</i>]	-0.89	-1.18 to -0.60	<0.001
Dominant species [<i>Phalangium opilio</i>]	-0.20	-0.56 to 0.15	0.256
Dominant species [<i>Pisaura mirabilis</i>]	-0.53	-0.82 to -0.24	<0.001
Dominant species [<i>Xysticus kochi</i>]	-0.43	-0.79 to -0.08	0.018
Random effects			
σ^2	0.27		
τ_{00} repetition	0.58		
ICC	0.68		
$N_{\text{repetition}}$	4		
Observations	141		
Marginal R^2 /Conditional R^2	0.090/0.708		

Note: The table summarises the outputs of linear mixed models (replicate was used as a random intercept) on total prey biomass reporting estimates of each assemblage, the confidence intervals (CI) as well as the *p*-value. The reference level is the control treatment with no predator. Significant *p*-values are in bold.

3.3 | Effects of functional specialisation, originality and identity of predators

Our analyses revealed that functional originality limited the top-down control of herbivores (i.e. total prey biomass increased with functional originality) while functional specialisation did not affect the total biomass of herbivores (Figure 3; Tables S3 and S4). Functional identity of assemblages did not strongly affect total herbivore biomass although a marginal positive effect of the first PCoA axis on total herbivore biomass was detected (Tables S5 and S6). Although marginally significant, the analysis of the functional traits associated with the first PCoA axis suggests that assemblages composed of active hunters with low handling time and no starvation ability tend to enhance the top-down control of herbivores (Table S7; Figure S6). When considering aphid and leafhopper separately, we found a significant positive effect of functional identity along the first PCoA axis for aphid biomass but not for leafhopper biomass (Figures S7 and S8). Aphid biomass was therefore reduced by assemblages composed of active hunters with low handling time and no starvation ability.

4 | DISCUSSION

Our study reveals that predator identity drives most of the effects of predator community composition on the top-down control of herbivorous species in our study system. Our results did not provide strong support for a beneficial effect of increased functional diversity overall as well as community evenness on top-down control of herbivores. More importantly, our results did not provide any evidence of an interaction between functional diversity and community evenness as initially hypothesised.

The results of this study are in support of the mass ratio hypothesis as they suggest that top-down control of the two herbivore species in our system is mainly driven by identity of dominant predator species and not by niche complementarity process. Indeed, the dominant predator species significantly affected overall prey biomass while increased levels of functional richness did not lead to strong negative impacts on overall prey biomass. If niche complementarity effects between predator species would have had a strong effect, then overall prey biomass would have been reduced as the volume of trait space occupied by predator species assemblages increased or as functional originality increased. Our results are in line with several other experimental studies showing that species identity is a key aspect modulating the relationships between predatory diversity and herbivore suppression (Alhadidi et al., 2018; Denoth et al., 2002; Long & Finke, 2014; Schmitz & Suttle, 2001; Sokol-Hessner & Schmitz, 2002; Straub & Snyder, 2006). We found that assemblages dominated by *A. bipunctata*, *C. carnea*, *P. mirabilis* or *X. kochi* were the most efficient to reduce overall prey biomass as well as aphid or leafhoppers separately, while assemblages dominated by *P. opilio* or *A. nemoralis* did not perform better than the

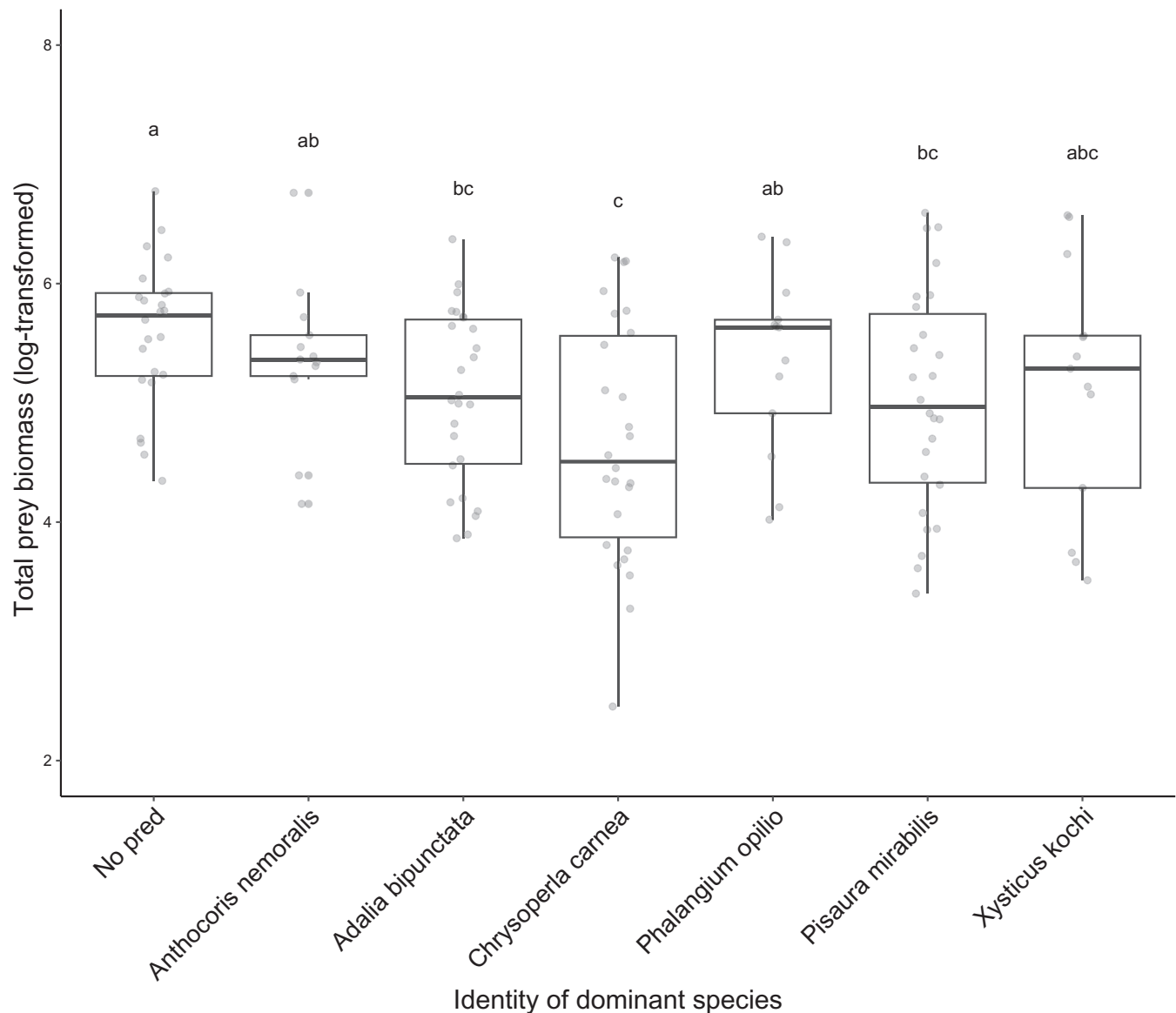


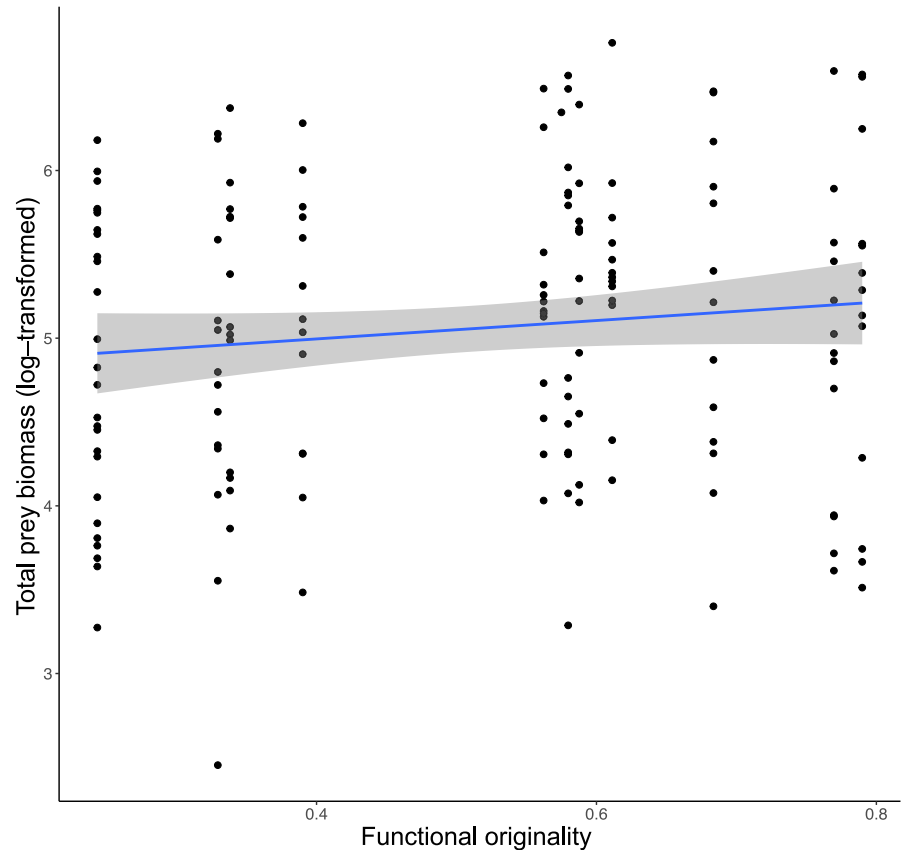
FIGURE 2 Effects of the identity of dominant predator species in the low evenness treatments on overall prey biomass. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Overall prey biomass was log-transformed and was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

control treatment. These results are consistent with previous experimental studies demonstrating the efficiency of some of these species to reduce aphids and leafhoppers (Alhadidi et al., 2018; Griffiths et al., 2008; Wyss et al., 1999).

The strong effect of predator identity on herbivore suppression detected in this study suggests that traits of the most efficient species may explain identity effects more than species diversity (Garibaldi et al., 2015). The analysis of the effect of functional characteristics of assemblages suggests that functional identity of predator communities is indeed related to the top-down control of herbivores. Our data suggest that assemblages composed of active hunters with low handling time and no starvation ability tend to enhance the top-down control of herbivores. When analysing the effect of functional identity separately for

aphids and leafhoppers our results indicated that functional identity supported by the first axis of the PCoA was only significant for aphid biomass but not for leafhoppers. However, other traits that were not considered here might modulate the relationships between community composition of predators and top-down control of herbivores. For instance, metabolic rate, degree of dietary specialisation, attack rates or behaviour of species are traits that might be important to consider to better understand the relationships between trait functional space in predator assemblages and the level of top-down control of herbivores (Wootton et al., 2023). Moreover, in our experimental design the total biomass of predator communities, which is a key parameter of predator prey interactions, was totally confounded with predator identity limiting our ability to separate the effect of overall biomass of predators and

FIGURE 3 Relationship between the functional originality of predator assemblages and total prey biomass (log-transformed). The functional originality is the weighted mean distance to the nearest species from the global species pool. The relationship is statistically significant (estimate of functional originality $FO_{ri}=0.55$, $p=0.02$; Table S4).



predator identity on top-down control of herbivores (Ostaniec et al., 2021; Rusch et al., 2015).

Using mesocosm experiment offers the possibility to test precise hypotheses about the relationships between several facets of community composition of predators and top-down control of herbivores. Indeed, analyses using real-world data are often more complicated to interpret due to the collinearity between multiple aspects of community structure and the difficulties to properly measure top-down control (Ostaniec et al., 2021; Rusch et al., 2015). Despite this advantage, using mesocosms also comes with several limitations that might have an effect on the results of this study. First of all, we deliberately used simplified communities composed of three predator species and two herbivore species and performed our experiment over short time scale (i.e. 5 days). Although our assemblages were realistic compared to assemblages found in the wild, such simplified communities and short time scales may have limited our ability to detect functional diversity effects. Such artificial environment and over-simplified community may affect antagonistic and behavioural interactions between species that might dampen the predation activity of some species (Finke & Denno, 2003). It might be possible that we only detect species identity at such small scale while considering much larger predator and prey communities as well as much longer experiment would allow the detection of complementarity effects in space and/or time (Greenop et al., 2018). In addition, the small area used in each cage may have limited complementarity effects and exaggerated negative behavioural interactions within or between species such as intraguild predation or cannibalism that

might have affected trophic interactions and our ability to detect potential effect of functional richness. Finally, we used a substitutive experimental design that kept total predator abundance constant across levels of functional richness or evenness in order to investigate their relative effects without confounding effects related to changes in the total number of individuals (Sih et al., 1998). One limit of such an approach is that studied assemblages differ from real-world assemblages where larger species are less abundant than smaller species for metabolic reasons (Woodcock & Heard, 2011). Considering these limitations, we advocate for similar experiment holding total predator biomass constant in much larger mesocosms and over longer period to properly assess how functional richness and community evenness interact in real-world ecosystems.

5 | CONCLUSIONS

Our study demonstrates that the top-down control of aphids and leafhoppers by arthropod predators in our system is mainly driven by species and functional identity and not by functional diversity. This result, that is in line with several other studies on different systems, suggests that ongoing species loss non-linearly affects ecosystem functioning and that changes in dominance patterns that emerge before species extinction could dramatically affect ecosystem functioning through the identity of species involved. In addition, our results advocate for a better description of species identity effects mediated by functional traits for most of ecosystem functions

if we are to anticipate how multifaceted changes in communities will affect ecosystem functioning in a global change context.

AUTHOR CONTRIBUTIONS

Adrien Rusch and Lucile Muneret conceived the ideas and designed the experiment. Adrien Rusch, Marie D'Ottavio, Nicolas Hénon, Benjamin Joubard, Denis Thiéry and Lucile Muneret perform the experiment and collect the data. Adrien Rusch and Lucile Muneret analysed the data. Adrien Rusch led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known conflicts of interest that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data supporting the paper are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.ghx3ffbv9> (Rusch et al., 2023).

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SUPPORTING INFORMATION

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

Table S1: Table summarizing the trait values of the six species used in predator assemblages.

Table S2: Summary of the linear mixed models of the effects of functional richness, community evenness and their interaction on overall prey biomass, aphid biomass and leafhopper biomass. The response variables were log-transformed to improve normality and homogeneity of variance residuals. Replicate was used as a random intercept in the linear mixed models.

Table S3: Model output of the effect of functional specialization of all predator assemblages on overall prey biomass. Functional specialization was computed as the weighted mean distance of a given assemblage to the centroid of the global species pool. Table shows the estimates as well as the confidence intervals (CI) and the associated *p*-values. The significant *p*-value is in bold.

Table S4: Model output of the effect of functional originality of all predator assemblages on overall prey biomass. Functional originality was computed as the weighted mean distance from the assemblage to the nearest assemblages from the global species pool. Table shows the estimates as well as the confidence intervals (CI) and the associated *p*-values. Significant *p*-values are in bold.

Table S5: Model output of the effect of functional identity (PC1) of all predator assemblages on overall prey biomass. Functional identity is the weighted average position of each assemblage along each axis in functional space, in this case PC1. Table shows the estimates, the confidence intervals (CI) and the associated *p*-values. Traits associated with PC1 are shown in Table S5 and in Figure S5. The significant *p*-value is in bold.

Table S6: Model output of the effect of functional identity (PC2) of all predator assemblages on overall prey biomass. Functional identity is the weighted average position of each assemblage along each axis in functional space, in this case PC2. Tables shows the estimates, the confidence intervals (CI) and the associated *p*-values. Traits associated with PC2 are shown in Table S6 and in Figure S5. The significant *p*-value is in bold.

Table S7: Table reporting the correlations between functional axes and traits of species. For continuous traits, a linear model was computed and *r*² and associated *p*-value were returned. For non-continuous traits, a Kruskal-Wallis test was computed and *eta*² statistic was returned. Significant or marginally significant correlations are shown in bold. BodySize, body size (mm); Circ, circadian activity (diurnal, nocturnal); Hab, habitat domain (soil, foliage); Hunt, hunting mode (ambush hunters, active hunters); Hand, handling time (low, high); StarvAb, starvation ability (yes, no). Significant *p*-values are in bold.

Figure S1: Figure of the experimental design of the study crossing three levels of functional richness (FRIC) with two levels of community evenness. The total number of predators in each mesocosm was six individuals so that the low level of evenness consisted in three-species communities composed of four individuals of the dominant species and one individual of the two remaining species, while the

high level of evenness consisted in two individuals of each species. For a given round of the experiment, we replicated each treatment three times and considered six mesocosm controls with herbivores only. One round of the whole experiment therefore consisted of 42 mesocosms. To ensure robustness of the results we replicated the whole experiment four times between 2017 and 2019 leading to a total of 168 mesocosms surveyed.

Figure S2: Effects of functional richness treatments on aphid biomass. Functional richness levels include low, medium and high values based on the functional richness of predator assemblages selected. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Aphid biomass was log-transformed and replicate was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

Figure S3: Effects of functional richness treatments on leafhopper biomass. Functional richness levels include low, medium and high values based on the functional richness of predator assemblages selected. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Leafhopper biomass was log-transformed and replicate was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

Figure S4: Effects of the identity of dominant predator species in the low evenness treatments on aphid biomass. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Aphid biomass was log-transformed and replicate was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

Figure S5: Effects of the identity of dominant predator species in the low evenness treatments on leafhopper biomass. Overall abundance of predators was kept constant between treatments except for the no predator treatment (No pred) which is a control treatment with herbivores only. Leafhopper biomass was log-transformed and replicate was used as a random intercept in the linear mixed models. Different letters indicate significant differences between treatments based on multiple comparisons (post-hoc Tukey tests).

Figure S6: Relation between trait values and PCoA axes. BodySize, body size (mm); Hab, habitat domain (soil, foliage); Hunt, hunting mode (ambush hunters, active hunters); Hand, handling time (low, high); Circ, circadian activity (diurnal, nocturnal); StarvAb, starvation ability (yes, no). Correlations between traits and axes are shown in Table S7.

Figure S7: Figure illustrating the positive relationship between the functional identity of predator assemblages and aphid biomass. The functional identity is the weighted average position of assemblages along the first axis of functional space. The low values of the first

axis tend to be associated ($p=0.06$, see Figure S5) with active hunters, with low handling time and no starvation ability, while high value tend to be associated with sit and wait predators, with high handling time and starvation ability (see Figure S5; Table S7). The relationship is statistically significant (estimate of Funct Ide PC1=0.75, p -value=0.04).

Figure S8: Figure illustrating no relationship between the functional identity of predator assemblages and leafhopper biomass. The functional identity is the weighted average position of assemblages along the first axis of functional space. The low values of the first axis tend to be associated ($p=0.06$, see Figure S5) with active hunters, with low handling time and no starvation ability, while high value tend to be associated with sit and wait predators, with high handling

time and starvation ability (see Figure S5; Table S7). The potential relationship is not statistically significant (estimate of Funct Ide PC1 = -0.09, p -value=0.77).

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