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The shape of the predator biomass distribution affects biological pest control services in agricultural landscapes

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Abstract

1. Understanding how community composition of service-providing organisms affects ecosystem functioning is a key challenge in ecology. Although it has been proposed that taxonomic diversity and functional traits mediate this relationship, how several facets of community structure affect the delivery of key ecosystem services remains to be explored.
2. In this study, we investigated how abundance, taxonomic richness as well as the shape of biomass distribution in predator communities affect biological pest control services in vineyard landscapes. Our analyses were based on a dataset combining samples of arthropod predators, measures of predation rates of grape pests and characterization of environmental covariables for 42 fields located in South-Western France.
3. We found that beside the abundance or the taxonomic richness of predators, the shape of biomass distribution (mean, variance, skewness and kurtosis of the distribution) influences the level of biological control. Predator communities largely dominated by low biomass species provided the bulk of biological control services. Lower levels of predation resulted from increased proportions of large biomass species and more evenly distributed biomass values in the communities.
4. Our results indicate that the top-down control provided by low biomass species decreases as the relative proportion of large biomass species increases in the predator community. This suggests that biological control may be affected by negative interactions (e.g. intraguild predation, behavioural interactions) between predators arising from the recruitment of large individuals in the community.
5. Our study revealed that the shape of biomass distribution is a major aspect of functional diversity in predator communities providing insights into the mechanisms that link biodiversity and ecosystem services. While our study focuses on biomass, considering other traits involved in trophic interactions may increase our ability to predict the level of biological control in ecosystems.

KEYWORDS

biomass, ecosystem functioning, ecosystem services, functional ecology, intraguild predation, organic farming, pest control, predator community composition

1 | INTRODUCTION

Multiple lines of evidence show that there is a positive relationship between biodiversity and ecosystem functioning (Cardinale et al., 2012). Research has been dominated by studies focussing on species richness and much variation in the relationship between biodiversity and ecosystem functioning remains to be explained (Balvanera et al., 2006; Gagic et al., 2015). Only focusing on species richness ignores the potential impact of dominant species or the variation of traits between organisms in the community (Enquist et al., 2015; Gagic et al., 2015; Hillebrand et al., 2008). Considering other aspects like species dominance and functional diversity should improve our mechanistic understanding of the relationship between biodiversity and ecosystem functioning (Craven et al., 2018; Hillebrand et al., 2008; Le Bagousse-Pinguet et al., 2019). However, the relative importance of these key aspects of community structure on ecosystem functioning remains poorly explored.

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 suggests that the most abundant species are expected to have the most influence on ecosystem functioning independently of the richness of subordinate species. While this hypothesis has been validated for several ecosystems and functions (Garnier et al., 2004; Kleijn et al., 2015; Smith & Knapp, 2003), recent works indicate that rare species can also substantially contribute to ecosystem functioning highlighting the need to thoroughly evaluate the effect of trait distributions within communities (Dee et al., 2019; Leitão et al., 2016; Soliveres et al., 2016). In this context, examining how the overall shape of the trait distribution in communities, characterized by the central moments including mean, variance, skewness and kurtosis, affect ecosystem functioning should provide key information about the ecological mechanisms in play (Enquist et al., 2015; Gross et al., 2017).

The four moments describing trait distribution depict ecological interactions through both horizontal and vertical diversity effects (Duffy et al., 2007; Schneider et al., 2016). Mean and skewness reflect patterns of trait dominance and indicate whether dominant traits are located in the bulk of the trait distribution or at the extreme, while variance and kurtosis represent the dispersion and the evenness of trait distribution (Gross et al., 2017). First, if a given ecosystem function is driven by the most dominant trait value in the community, then the mean and the skewness of the distribution would significantly explain ecosystem functioning. Negative or positive values of the skewness occur when distributions are respectively strongly left or right tailed, with most abundant species that have extreme trait values compared with the bulk of the distribution (Enquist et al., 2015; Gross et al., 2017). The direction of skewness effects on a given ecosystem function provide information on the degree of asymmetric competition at a single trophic level or on potential trophic cascades (e.g. omnivory or intraguild predation) across trophic levels (Gross et al., 2017; Schneider et al., 2012, 2016). Secondly, if a function is best explained by horizontal diversity effects mediated by niche complementarity (Balvanera et al., 2006), then the variance as well as the kurtosis of trait distribution more than the mean and the skewness values would strongly affect the level of ecosystem functioning (Diaz et al., 2007; Gravel et al., 2016). High variance indicates a large range of trait values and a large dispersion of their abundance and high kurtosis indicates uneven trait distribution with a large number of species possessing similar traits in the community (i.e. peaky distribution; Enquist et al., 2015). If the function results from trait complementarity between species in the community, we could expect that high variance and low kurtosis in trait distribution would enhance ecosystem functioning (Enquist et al., 2015). However, how the shift in trait distribution characterized by these different moments affect ecosystem functioning remains poorly investigated for a large range of functions and ecosystems.

Biological control of phytophagous arthropods by their predators is a key function in ecosystems (Dainese et al., 2019; Rusch et al., 2010; Walker & Jones, 2001). Biological control usually results from multiple interactions in highly complex food webs that are poorly understood and hard to describe (but see Roubinet et al., 2018). 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 in the literature (Griffin et al., 2013; Letourneau et al., 2009). For instance, Letourneau et al. (2009) reported in their meta-analysis that predator species richness enhanced prey suppression in about 70% of the cases while it reduced prey suppression in about 30% of the cases. Such results clearly highlight the need for a more mechanistic understanding of the processes that shape the relationship between predator diversity and prey suppression. Negative relationship may emerge from negative interactions between predators, such as intraguild predation or behavioural interferences (Letourneau et al., 2009; Rusch et al., 2015; Schmitz, 2007). These negative interactions are common in complex food webs and can strongly limit the emergence of positive biodiversity effects mediated by niche complementarity. However, how trait distributions among predator community influence the emergence of negative interactions in food webs remains poorly understood.

Recent advances in food web ecology documented the importance of biomass to understand local food web structure (Brose et al., 2019; Moretti et al., 2017; Schneider et al., 2012). Biomass of a species often determines its trophic position in food webs and body-mass ratios between predators and prey are good predictors of the strength and direction of trophic interactions (Curtsdotter et al., 2019; Jonsson et al., 2018; Rusch et al., 2015; Schneider et al., 2012). Moreover, biomass is a major trait of organisms very often correlated with other functional traits such as dispersal ability, metabolic rates, handling time or ingestion rates (Brown et al., 2004; Digel et al., 2011; Gámez-Virués et al., 2015). Examining how environmental changes affect biomass distributions in local food webs should therefore help to understand the mechanisms driving direct and indirect interactions between predator communities and prey. However, while such information is crucially needed to understand ecosystem functioning, no studies have explored how changes in biomass distributions of predators affect the level of prey control.

In this study, we investigated how abundance, taxonomic richness as well as the shape of the biomass distribution in predator communities affect the delivery of biological pest control services in vineyard landscapes. Our study focuses on communities of generalist predators, including spiders, harvestmen, earwigs or lacewings, suspected to be the main predators of the grape berry moth *Lobesia botrana*, a major pest in vineyards. Because such food webs involve multiple species with complex trophic and non-trophic interactions within and across trophic levels, we hypothesized that the shape of biomass distributions in predator communities would help in deciphering the processes influencing biological control of pest populations. We particularly predicted that: (a) the shape of the biomass distribution among predators better explains biological pest control services than predictors based only on their abundance or taxonomic diversity as it integrates information about allometric constraints in trophic interactions; (b) predator communities with higher proportions of large biomass species tend to decrease predation rates of the prey because of the emergence of negative interactions among predators related to intraguild predation or behavioural interactions.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Our study sites were located in a vineyard-dominated region in south-western France (44°81′0°14′W). Our study design consisted of 21 pairs of organic and conventional vineyards (42 fields). The pairs were selected along two uncorrelated landscape gradients: a gradient of proportion of organic farming (ranging from 2% to 25%) and a gradient of proportion of semi-natural habitats (ranging from 1% to 75%) in a 1-km radius around the centre of the field. Such an experimental design allows to disentangle the relative effects of local farming systems from the proportion of semi-natural habitats and farming systems at the landscape scale. Landscape variables were calculated using ArcGIS 10.1 (ESRI).

2.2 | Predator community sampling

Predator communities of the vineyard foliage were sampled three times in 2015 (between June and September; $N = 124$: 3×42 vineyards and two plots with missing values). At each sampling date, predators were sampled by beating 30 vine stocks in each vineyard (Muneret, Auriol, Bonnard, et al., 2019). All predators were stored in 70% ethanol and individuals were identified at the lowest possible taxonomic resolution. Araneidae and Opiliones were identified at the species level while Dermaptera and Neuroptera were identified at the family level.

2.3 | Community metrics

Several metrics were calculated to characterize each predator community at each date: the overall abundance of individuals, the taxonomic richness as well as the four moments of the biomass distribution. Biomass distribution of the community was obtained by multiplying the number of individuals of each taxonomic unit by its average dry biomass (hereafter biomass distribution refers to the weighted biomass distribution). To calculate average values of dry biomass for each taxonomic unit, stage (adult or juvenile for spiders) and sex (for adult spiders and harvestmen), we randomly selected 10 individuals among all the individuals sampled (all sampling dates combined) and measured their dry biomass. For spiders with a dry body mass lower than 0.01 mg, we estimated the dry body mass using length–mass regression of the form: body mass = exp ($a + b \times \log$(length of cephalothorax)) (Barnes et al., 2016, see Figure S1). When the abundance of each taxonomic unit, stage and sex was lower than 10 individuals, we measured all the specimens available to calculate the average biomass values. For each vineyard and sampling date, the mean, variance, skewness and kurtosis of each biomass distribution, were calculated following the formula in Gross et al. (2017). All the four moments were calculated on log-transformed data for each field at each sampling date.

2.4 | Biological pest control service

We used a sentinel approach to measure levels of biological pest control at three dates in 2015 concomitantly with the predator sampling (Birkhofer et al., 2017). Sentinel cards consisted of 10 eggs of the grape berry moth, *L. botrana*, which is the most damaging insect pest in the studied region. Eggs of *L. botrana* laid on parchment paper (1 × 3 cm card previously glued on felt) by laboratory-reared females were cut and glued on plastic cards (1 × 8 cm). Each card was attached to a vine shoot on one vine stock. In each field, 10 sentinel cards were exposed to predation for 4 or 5 days, depending of the sampling date. All the cards were settled at least 10 m away from the edge or from any other card. At the end of the 5-day exposure, the cards were collected ($N = 1{,}207$) and the number of remaining eggs per card was assessed using a microscope (Muneret, Auriol, Thiéry, et al., 2019). We then estimated predation rates for each card as the ratio of the number of eggs predated to the total number of eggs initially exposed. In very few cases, eggs were damaged due to climatic conditions and the ratio was therefore calculated on the number of eggs initially exposed minus the number of damaged eggs. This variable was used as a proxy for biological pest control services.

2.5 | Statistical analysis

To examine how the structure of predator community influences the level of biological pest control and how organic farming and semi-natural habitats in the landscape modulate this relationship, we applied a piecewise SEM approach (Lefcheck, 2016). We developed four conceptual models (SEM1, SEM2, SEM3, SEM4) to examine the direct and indirect paths between the environmental variables, the structure of predator communities (considering overall abundance, taxonomic richness and each of the four moments of the biomass distribution) and the level of pest control (see Figure S2). SEMs only differed in the variable used to assess how the shape of the biomass abundance distribution affected biological pest control: SEM1, SEM2, SEM3 and SEM4 respectively considered the mean, the variance, the skewness and the kurtosis of the biomass distribution. All SEMs included overall abundance and taxonomic richness as covariables describing the predator community. We developed four SEMs to reduce over-parametrization and limit collinearity between predictors: the mean, variance, skewness and kurtosis of biomass distribution were correlated (see Figure S3). In each SEM, we fitted four different Generalized Linear Mixed Models (GLMMs) with a Gaussian error distribution (Figure S2). Each GLMM corresponded to a model fitted to explain: (a) predator abundance by local (organic or conventional management) and landscape variables (proportion of organic farming and semi-natural habitats), (b) taxonomic richness of predators by local and landscape variables as well as predator abundance, (c) one out of the four moments of the biomass distribution among predator communities by local and landscape variables, predator abundance and taxonomic richness, and (d) biological pest control by local and landscape variables, predator abundance, taxonomic richness and one of the four moments of the biomass distribution among predator communities (Figure S2). Because of our experimental design, we used 'field' nested in 'site' as random effects in all GLMMs (one site being one pair of organic and conventional fields). As we used three correlated metrics (predator abundance, taxonomic richness and one moment of the biomass distribution) in each of the four different models, collinearity was checked in all models using Variance Inflation Factor (all VIFs were lower than 2). Predator abundance and taxonomic richness were log $(x + 1)$ transformed, the kurtosis of the biomass distribution was log transformed and landscape variables were scaled by the mean and the standard deviation to improve model fit. To avoid over-parametrization and reduce overall model complexity, we performed manual stepwise selection (based on AIC) for each GLMM and some explanatory variables were removed before running the SEMs (see Figure S2). We used the d-separation test to evaluate whether the non-hypothesized independent paths were significant and whether the models could be improved with the inclusion of any of the missing paths (see Section 3). The strength of an indirect path between two variables was obtained by multiplying path coefficients belonging to this path and total effects are the sum of direct and indirect pathways. Conditional and marginal R^2 were extracted from the summary of the piecewiseSEM. The residuals of the models were checked for normality and homoscedasticity using the DHARMA package (Hartig, 2017) and we detected no spatial autocorrelation among the residuals using bubble plots and Moran's test. GLMMs were fitted using the LME4 package (Bates et al., 2015) and the SEMs were fitted using the PIECEWISESEM package (Lefcheck, 2016).

3 | RESULTS

3.1 | Predator community structure and biological pest control

Overall, we caught 7,201 individuals composed of 5,462 Araneae (21 families, 77 genus, 70 species), 520 Dermaptera (one family), 245 Neuroptera (one family) and 974 Opiliones (two families, two genus, two species). Among Araneae, 1,521 spiders were identified at the species level (27.8%), 2,045 at the genus level (37.4%), 1,870 at the family level (34.2%) and only 26 spiders were identified at the order level (<1%). Spiders consisted of 4,784 juveniles (87.6%), 79 sub-adults (1.4%) and 599 adults (11%). The most abundant taxa were *Clubiona* sp. (9.94%), *Oxyopes* sp. (4.98%), *Xysticus* sp. (4.80%), *Salticus scenicus* (4.25%), *Tenuiphantes tenuis* (4.19%) and *Nuctenea umbratica* (4.12%). Opiliones were composed of 705 adults (72.4%) of *Phalangium opilio*, 268 juveniles belonging to the genus Phalangiidae (27.5%) and only one individual of *Leiobunum blackwalli*. The dry biomass of the predators ranged from 0.05 mg for *Microlinyphia pussila* at the juvenile stage to 15.68 mg for Dermaptera, with a mean biomass of 1.61 mg ± 2.35 (*M* ± *SD*; see Figure S5). The three heaviest taxa were Dermaptera (15.68 mg), *Araneus diadematus* at the adult stage (12.80 mg) and *P. opilio* (11.70 mg). Mean predation rates on sentinel cards were 0.48 ± 0.50 (*M* ± *SD*).

3.2 | Direct effects of organic farming and semi-natural habitats on predator communities and biological control

The four SEM models exploring the direct and indirect effects of local and landscape variables on the structure of the predator community and biological pest control fitted the data well (SEM1: Fisher's $C = 1.257$, $df = 6$, $p = 0.974$; SEM2: Fisher's $C = 4.381$, $df = 6$, $p = 0.625$; SEM3: Fisher's $C = 1.795$, $df = 6$, $p = 0.938$; SEM4: Fisher's $C = 3.094$, $df = 6$, $p = 0.54$) and no significant path was missing in the models. The results of each best-fitted SEM are presented in the Table S1. All SEMs revealed that organic farming at the local scale directly increased predator abundance which implied indirect changes in community structure and egg predation rates (see Figure 1; Figure S4). At the landscape scale, neither the proportion of organic farming nor that of semi-natural habitats influenced the predator community structure or the level of biological pest control.

3.3 | Direct and indirect effects of changes in predator abundance on the shape of the biomass distribution

Changes in predator abundance lead to direct effects on the mean, variance and skewness of the biomass distribution (not on the kurtosis) as well as indirect effects mediated by taxonomic richness on the mean, variance, skewness and kurtosis of the biomass distribution

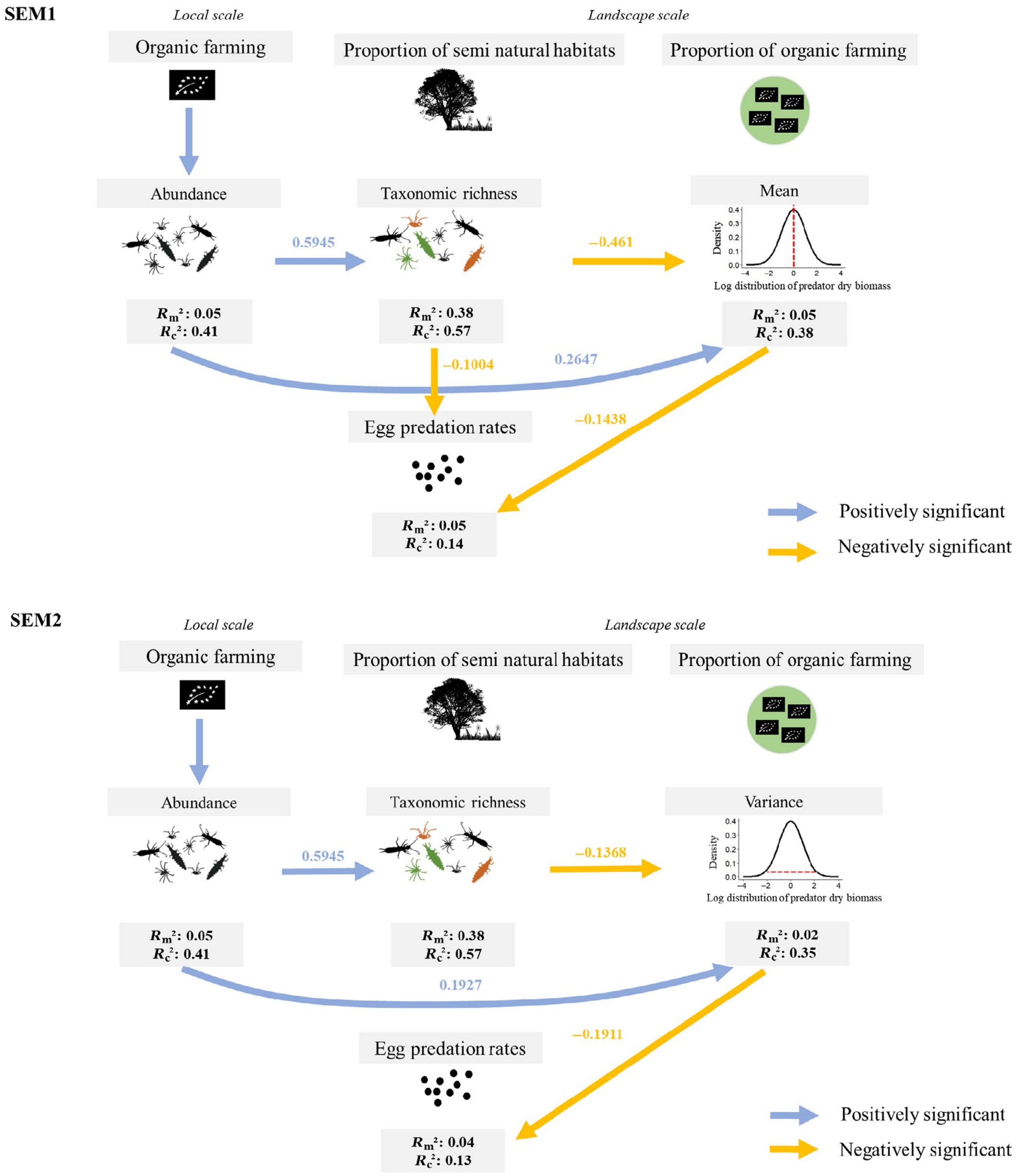

FIGURE 1 Results of the four structural equation models (SEM) used to investigate how different biodiversity attributes (abundance, taxonomic richness, mean, variance, skewness and kurtosis of biomass distribution) within predator communities affect egg predation rates of pest species in vineyard landscapes. Only significant paths are represented. SEM1, SEM2, SEM3 and SEM4 respectively represent the SEMs with the mean, variance, skewness or kurtosis of biomass distribution. R^2_m is the marginal *R*-squared and R^2_c is the conditional *R*-squared

(Figure 1; Table S1). In all SEMs, predator abundance had a significant direct positive effect on taxonomic richness (Standardized Estimate, SE = 0.5945; Figures 1 and 2). SEM1 revealed that the mean of the biomass distribution directly increased with predator abundance (SE = 0.2647) but indirectly decreased via changes in taxonomic richness (indirect SE = −0.274; Figures 1 and 2). The total effect of

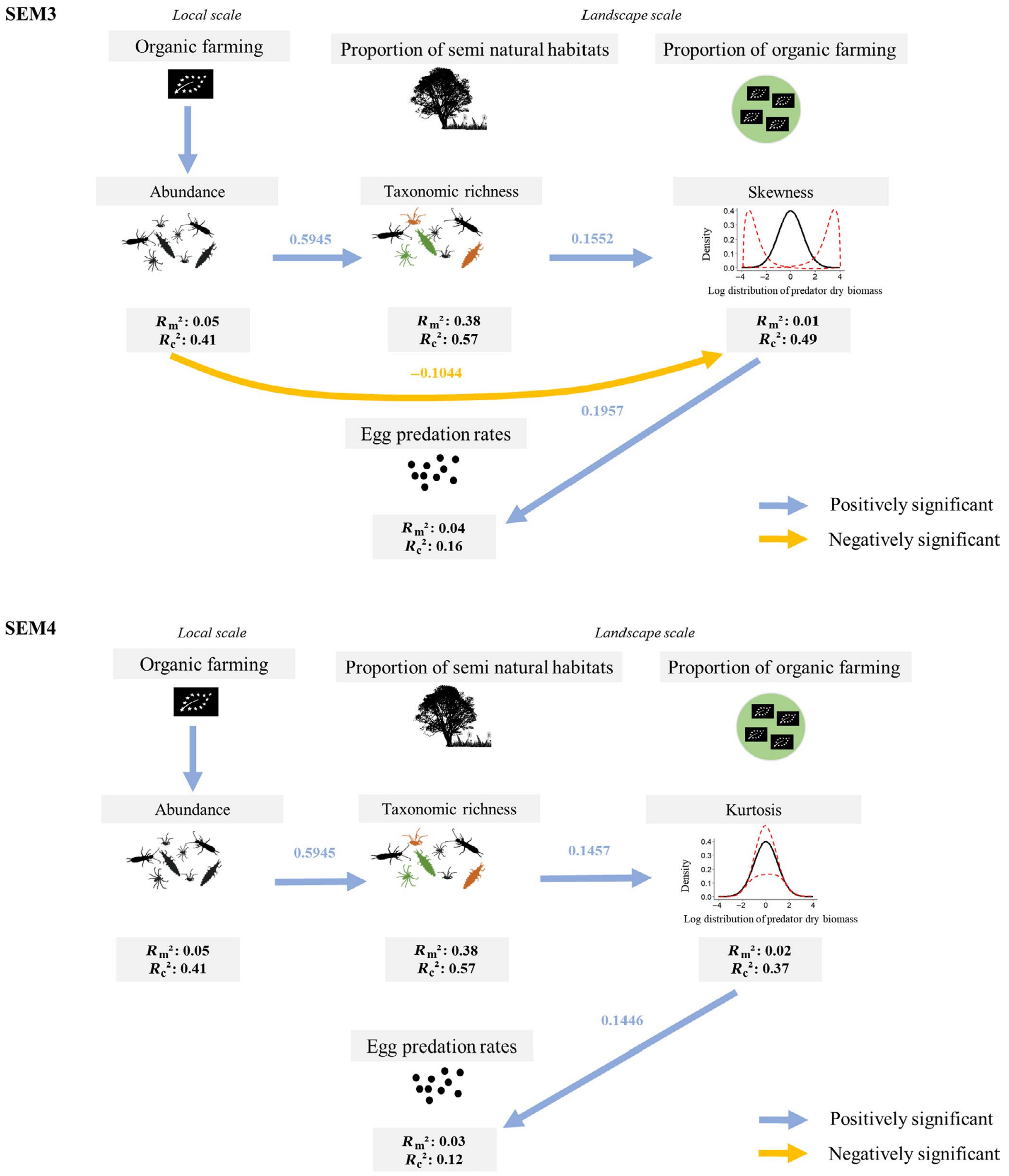

FIGURE 1 (Continued)

changes in predator abundance on the mean of the biomass distribution was weak (total SE = 0.009). SEM2 revealed that the variance in biomass distribution directly increased with predator abundance (SE = 0.1927) but indirectly decreased via changes in taxonomic richness (indirect SE = −0.081; Figures 1 and 2). SEM2 indicated a positive total effect of changes in predator abundance on the variance of biomass distribution (total SE = 0.1117; Figures 1 and 2). SEM3 revealed that the skewness of biomass distribution directly decreased with predator abundance (SE = −0.1044) and indirectly increased through changes in taxonomic richness (indirect SE = 0.09;

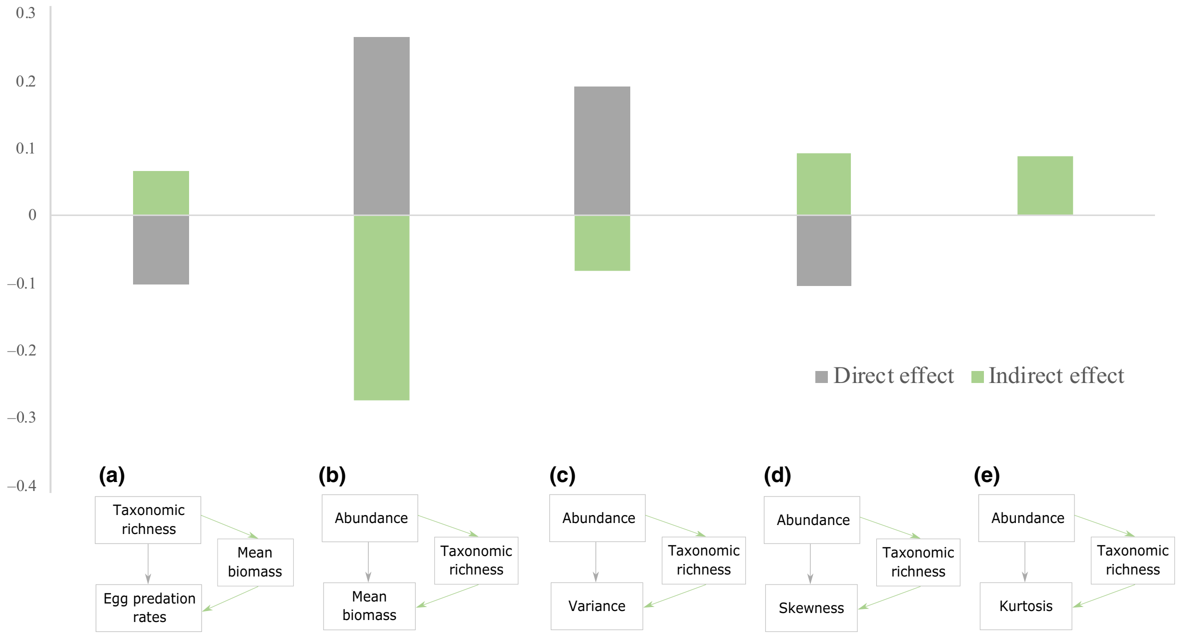

FIGURE 2 Strength of direct and indirect effects of taxonomic richness or abundance on pest control and parameters describing biomass distribution in predator communities. Direct and indirect effects are based on path coefficients found in Figure 1. Indirect effects are mediated through the mean of biomass distribution (a) or by the taxonomic richness (b–e)

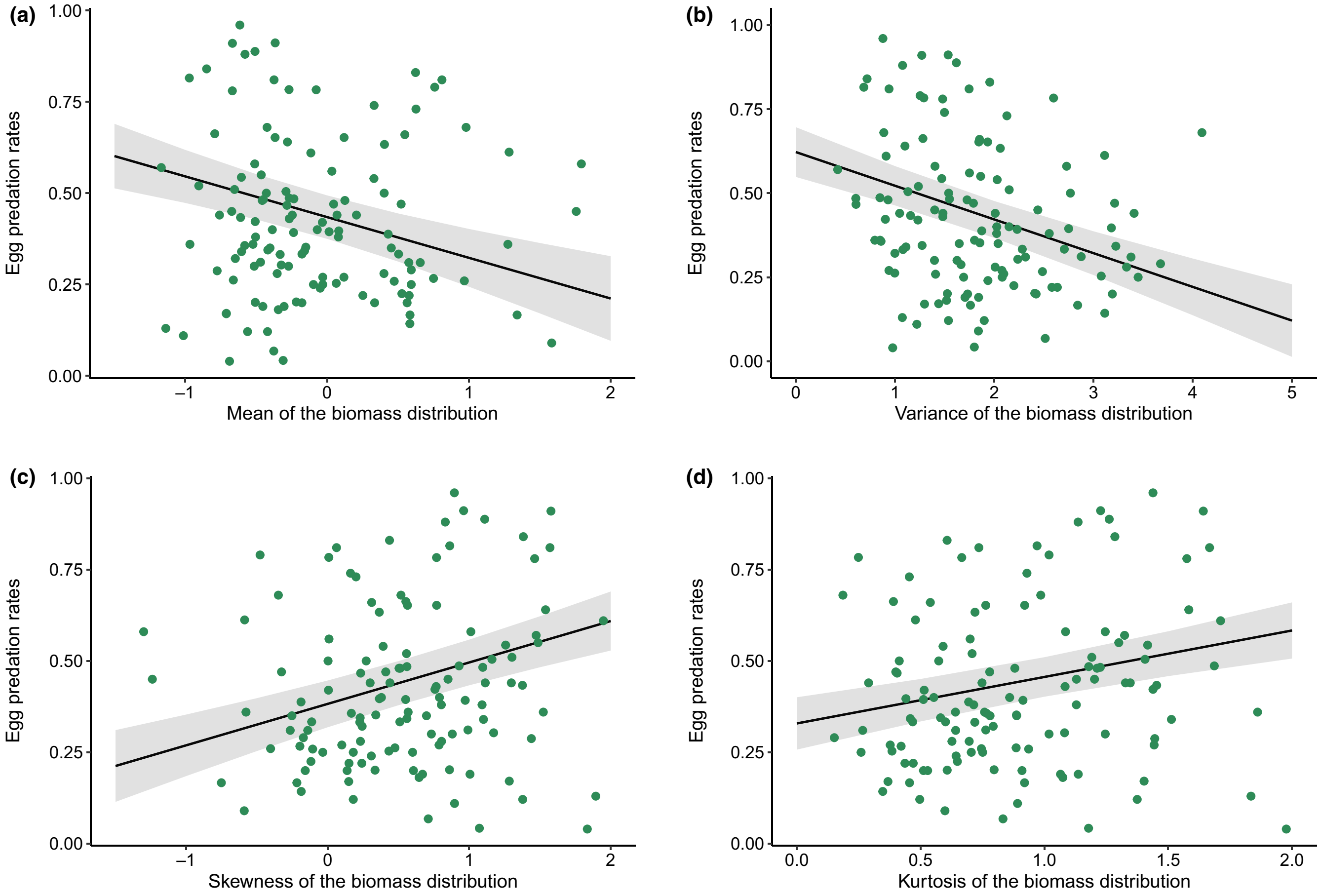

FIGURE 3 Effects of (a) the mean, (b) the variance, (c) the skewness and (d) the kurtosis of the biomass distribution on biological pest control (egg predation rates) in vineyards. Dark green dots represent the mean predation rates per vineyard ($N = 124$). Dark grey lines show predictions from a mixed model adjusted on all predation rates ($N = 1{,}207$), and the light grey part represents the confidence interval of the model

Figures 1 and 2). SEM 3 indicated a small negative total effect of changes in predator abundance on the skewness of biomass distribution (total SE = −0.0144; Figures 1 and 2). SEM4 revealed that the kurtosis of biomass distribution did not directly respond to changes in predator abundance but only indirectly increased through changes in taxonomic richness (indirect SE = 0.0866; Figures 1 and 2).

3.4 | Direct and indirect effects of changes in predator community structure on biological control

Our analyses revealed that egg predation rates were always directly affected by each of the four moments of the biomass distribution (Figure 1; Table S1). Egg predation rates decreased with the mean and the variance of the biomass distribution (respectively, SE = −0.1438 and SE = −0.1911; Figures 1 and 3), indicating lower levels of biological control when the mean or the range of variation of biomasses among predators were higher. Moreover, egg predation rates increased with both the skewness and the kurtosis of biomass distribution (respectively, SE = 0.1957 and SE = 0.1446; Figures 1 and 3), indicating higher levels of biological control when biomass distribution of predators was left-skewed or unevenly distributed (Figures 1 and 3).

Among the four SEMs, egg predation rates were only indirectly affected by predator abundance and predator taxonomic richness except in the SEM1. SEM1 revealed a direct negative effect of taxonomic richness on egg predation rates (SE = −0.1004; Figures 1 and 2) and an indirect positive effect of taxonomic richness via changes in the mean biomass of predators on egg predation rates (indirect SE = 0.066; Figures 1 and 2).

4 | DISCUSSION

By examining how several aspects of the biomass distribution of predator communities affect egg predation rates, our study provides key information about the mechanisms shaping the delivery of biological pest control. We found that predator communities largely dominated by low biomass species (biomass distribution with lower mean, lower variance, positive skewness and high kurtosis) provided the bulk of biological control of grape moths in vineyard landscapes. Lower levels of predation rates resulted from increased proportions of large biomass species and more evenly distributed biomass values in the communities (biomass distribution with higher mean, larger variance, negative skewness and lower kurtosis). Our results also indicate that organic farming directly enhances predator abundances, which affects the shape of their biomass distribution and in turn levels of biological control services.

Our results suggest that biological control is affected by both horizontal and vertical diversity effects within predator communities, confirming previous results obtained in other ecosystems and on other functions (Duffy et al., 2007; Srivastava & Bell, 2009; Zhao et al., 2019). In the horizontal dimension, our results provide support for the mass-ratio hypothesis as we found that dominance pattern in biomass distribution, and not functional complementarity, is driving egg predation rates (i.e. direct positive effect of skewness on egg predation rates). Our data do not provide evidence for functional complementarity between predators as high diversity in biomass values (i.e. high variance) and more evenly distributed biomass values (i.e. low kurtosis) both reduced egg predation rates. Moreover, we found that egg predation rates decreased as the proportion of larger biomass species in the community increases (i.e. higher mean, negative skewness and low kurtosis), indicating a release of the top-down control exerted by predators as larger predators appear in the community. Such indirect negative effects can be due to intraguild predation or behavioural interactions (e.g. physical aggression, avoidance, territorial signalling) between predators as reported in several empirical and theoretical studies (Finke & Denno, 2005; Grether et al., 2017; Jonsson et al., 2018; Rusch et al., 2015; Wang et al., 2019). Our study suggests that vertical diversity effects mediated by these processes emerge in the community as the relative abundance of large body mass species increases (Finke & Denno, 2005; Wang et al., 2019). Emergence of vertical diversity effects come from the fact that metabolic rate of organisms increases with the average biomass of individuals leading to a predator–prey biomass power law across terrestrial and aquatic ecosystems (Brown et al., 2004; Hatton et al., 2015). Due to interactions between horizontal and vertical diversity effects, motifs within the network may have therefore changed from exploitative competition to intraguild predation as larger species appear in the community because of metabolic demand and allometric constraints related to biomass (Brose, 2010; Duffy et al., 2007; Wang et al., 2019). Such switch mediated by body-mass structure of the predator community has been reported in other studies on much simpler food webs (Schneider & Brose, 2013; Schneider et al., 2012). Our results therefore suggest that interactive effects between horizontal and vertical diversity may be at work in more complex communities involving multiple trophic and non-trophic interactions.

The larger predator species in the community may have consumed smaller predators (smaller biomasses) instead of moths' eggs because smaller predators are more optimal prey from a metabolic perspective (Holt & Polis, 1997; Schneider et al., 2012). Species composition along the biomass distribution revealed that individuals with a small biomass largely came from three taxa-stages: juveniles of the families Thomisidae and Araneidae and juveniles of *Oxyopes* sp. (see Figure S6). Many studies on spiders demonstrate that these taxa are predators of Lepidopteran eggs (Miliczky & Calkins, 2002; Pfannenstiel, 2008; Pfannenstiel & Yeargan, 2002). Harvestmen and earwigs are the taxa with the largest biomass in the predator communities of our study area (see Figure S6). While they are able to feed on lepidopteran eggs (Pfannenstiel & Yeargan, 2002; Pinto-da-Rocha et al., 2007), these species are also intraguild predators that feed on intermediate predators such as spiders (Pinto-da-Rocha et al., 2007 and references therein). These results support our hypothesis on increased levels of negative interactions between predators when species with larger biomasses are present in the community. Although it was the only model in which it was detected, SEM1 indicated a direct negative effect of taxonomic richness on predation rates. This suggests that there might be negative interactions that contribute to limit predation rates that are non-mediated by the mean biomass and trophic interactions but by other functional traits and non-trophic interactions (Schmitz et al., 2015). Evidently, other processes such as changes in behaviour of predators due to avoidance or interference may also contribute to the release of top-down control of pests when large biomass species are present in the community (Michalko & Pekar, 2017; Soares & Serpa, 2007).

Our results are in line with recent studies demonstrating that trait-based metrics best explain ecosystem functioning compared with taxonomic or abundance metrics on a large variety of plant or animal groups (Gagic et al., 2015; Gross et al., 2017; Le Bagousse-Pinguet et al., 2019; Rusch et al., 2015). Our study demonstrated that considering the shape of trait distribution in particular allows a more mechanistic understanding of the relationship between community structure and a given ecosystem function (Le Bagousse-Pinguet et al., 2019). Abundance, taxonomic richness as well as functional structure are complementary facets of community structure. Our interpretations about the potential mechanisms in play are based on a single-species perspective and on a single trait of predators. Considering the whole prey community and analysing how the shape of biomass distribution of both predators and prey would affect the net effects of predators on basal prey may have revealed other important mechanisms (Schneider et al., 2016). For instance, while our results provide evidence for mass-ratio effects due to higher levels of predation in predator communities dominated by low-biomass species, functional complementarity between predators might emerge if we would have considered the whole range of prey. Moreover, considering other traits such as behavioural, morphological or physiological traits of both predators and prey (i.e. trait-matching) that are known to shape trophic interactions may have provided complementary information about how horizontal and vertical diversities affect ecosystem functioning (Schmitz, 2008; Schmitz et al., 2015). Ultimately, integrating other traits should increase the predictive power of community metrics which was pretty low in our study (Gagic et al., 2015).

The direct positive effect of organic farming on predator abundance is in line with a large number of studies that show increased abundance of a large variety of functional groups in organic fields (Bengtsson et al., 2005; Tuck et al., 2014). This effect can be attributed to more favourable habitat conditions resulting from several farming practices, such as the absence of synthetic pesticides, higher levels of soil organic matter, higher prey availability, higher diversity of primary producers or more complex habitat structure (Birkhofer et al., 2008; Rusch et al., 2014). However, our results suggest that there is no direct positive effect of organic farming on biological pest control services, but rather an indirect negative effect mediated by the biomass distribution of predators. Our study therefore offers an explanation for the variability of results found in studies examining the effect of organic farming on insect pest control and highlights the need to investigate the effect of functional composition of the predator community to understand or even predict the levels of biological control services.

5 | CONCLUSIONS

Several studies have recently proposed to examine how community structure affects ecosystem functioning using a trait-based approach (Deraison et al., 2015; Gagic et al., 2015). Our study contributes to the development of trait-based approaches to understand ecosystem functioning using a key function in agroecosystems, biological pest control. Overall, we demonstrate that using the different moments of the biomass distribution in predator communities provides a more mechanistic understanding of the processes determining predation than approaches based on taxonomic richness or abundance only. Our results suggest that multiple mechanisms related to both horizontal and vertical diversities, involving mass-ratio effects and negative interactions between predators, are affecting the delivery of biological pest control services. From an applied perspective, our study also provides key information about the identity as well as the functional aspects of key predator species that support biological pest control in vineyards. We notably highlighted that the small predators favour egg predation while the big predators limit egg predation suggesting negative interferences within the predator community. Exploring how the distribution of multiple traits affects trophic interactions across multiple levels in food webs, including larger communities of predators and prey, remains to be explored.

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AUTHORS' CONTRIBUTIONS

N.O., L.M., B.G., D.T. and A.R. conceived the ideas and designed methodology; N.O. and L.M. collected the data; N.O. and L.M., A.R. analysed the data; N.O. and A.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.95x69p8hq (Ostandie et al., 2020).

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SUPPORTING INFORMATION

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