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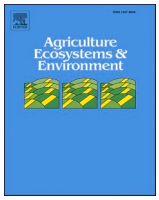

Agricultural practices shape beetle communities in field margins directly and through indirect effects driven by plants

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ABSTRACT

The presence of field margins in agricultural landscapes increases plant and animal diversity, providing food resources and shelter. Margins also increase ecosystem services' delivery by hosting a diverse insect fauna. Beetles, in particular, are important contributors, acting as auxiliaries, decomposers and pollinators. However, these habitats are threatened by agricultural intensification, representing potential traps for biodiversity due to pesticide and fertilizer drift. In this work we aim at understanding the unintended effects of agricultural practices on beetle diversity, abundance and composition in agricultural field margins, at a national scale. More precisely, we investigated which agricultural practices directly impact beetles and which ones indirectly impact them through their effects on plants. Here we used data from a national standardized monitoring network in metropolitan France where both plants and beetles were identified to the species level in more than 300 different field margins, representing the main crops (cereals, vineyards and market gardening) and a gradient of agricultural intensification practices at the national level. We ran structural equation modeling (SEM) to disentangle the direct and indirect effects of management on beetles. We showed that intensive agricultural practices such as high pesticide pressure and fertilization are mostly associated with a decrease in beetle diversity and abundance, as well as in the proportion of floral visitors, while increasing the proportion of pests in each community. We also showed that many of these impacts are mediated by plant diversity and traits. These results suggest that managing composition and structure of field margin vegetation, as well as reducing agricultural intensification both at the regional and at the field-margin level, are key to guarantee high beetle diversity and optimal ecosystem services such as pollination and pest regulation in the field margins.

1. Introduction

Plant and arthropod populations in agricultural landscapes have sharply declined during the last decades (Carmona et al., 2020; Emmerson et al., 2016; Raven and Wagner, 2021), but agro-ecological infrastructures can help to mitigate those losses. Agricultural field margins, defined as the area located between the cultivated field and other adjacent landscape elements, play a key role for maintaining biodiversity (Marshall and Moonen, 2002). This habitat is less disturbed and more stable than the agricultural field itself, and can potentially harbor twice as many plant species as the field core (Munoz et al., 2020). However, field margin biodiversity is still impacted by agricultural practices that take place within the field (Fried et al., 2018; Poinas et al., 2025). For example, nitrogen fertilization and herbicides applied in the field core are known to affect margin vegetation through simple drift (Henckel et al., 2025). Therefore, while field margins can represent a refuge for biodiversity, they also present a risk of becoming ecological traps (*sensu* Heale & Swearer, 2016) with high levels of pesticide and fertilizer contaminations.

Only a few studies have focused on how agricultural practices within fields affect field margin arthropod diversity and composition. Beetles (Coleoptera) are the most diverse insect order, composed of more than 400,000 known species worldwide (McKenna et al., 2019), including many predators, decomposers, flower-visiting or phytophagous species (feeding on leaves, seeds, roots, etc.) that provide important and diverse ecosystem services and functional roles for agriculture, but that can also

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cause important yield losses. Knowledge gaps regarding their biology and the lack of ability to identify beetles at the species scale have therefore contributed to a bias in agroecosystem studies where some families are much better represented than others. A large body of research exists regarding large ground beetles (Carabidae) for example, mostly for the ability of a few species to regulate weeds via seed consumption (Kulkarni et al., 2015). Predator beetles, including ground beetles, rove beetles (Staphylinidae), tiger beetles (Cicindellidae) and most ladybirds (Coccinellidae), have also been studied for their potential to regulate pest species (Crowther et al., 2023; Maisonhaute et al., 2010; Mei et al., 2021; Ostandie et al., 2021; Wu et al., 2024). A few studies have considered beetles for their pollinating role in agroecosystems (e.g. Kehinde and Samways, 2014; Ostandie et al., 2021), but pollination studies have traditionally focused on bees (Anthophila) rather than on coleopterans (Rader et al., 2016; Potts et al., 2016). Finally, a variety of other studies have focused on the presence or damage caused by some beetle pest species, such as in click beetles (Elateridae) (Hermann et al., 2013; Schallhart et al., 2009), or for some weevil species (Hanavan and Bosque-Pérez, 2012), but have not looked at the richness, composition or functional diversity of the whole beetle communities present in the same ecosystem. As a consequence, we are lacking a general characterization of beetle diversity in agricultural landscapes, both because some groups were under-studied but also because one single family can bear very high intra-familial functional diversity.

The relationship between beetle and plant diversity in agroecosystems is also poorly known. Plant diversity in agroecosystems is very well described and studied, including either functional or taxonomic diversity, and in both annual and perennial cropping systems (Bopp et al., 2025; Bourgeois et al., 2019; Fried et al., 2024). Plant richness is notably negatively impacted by intensive management, including high fertilization quantity, pesticide use or tillage (Carmona et al., 2020; Winter et al., 2018). The individual responses of weed traits at the community scale to a wide range of agricultural practices has been explored, showing that intensification favors short-statured ruderal species, with higher specific leaf area, with a rapid germination and with smaller seeds (Fried et al., 2012, 2019; Gaba et al., 2017). Leaf, seed, floral or root traits could all be linked to beetle richness and abundance, because they deliver key resources for them. The relationships between plants and beetles depends strongly on the studied beetle groups. Phytophagous species, such as the Chrysomelidae or Curculionidae, are expected to respond to plant abundance because plants are their food source, but also to plant diversity because most phytophagous beetle species are specialist, with both a trophic specialization on specific parts of plants and a limited set of host-plants. Flower-visiting beetles will also depend directly on plant resources, first to the presence of entomogamous species and also to floral traits, such as colors or inflorescence type (Lanuza et al., 2023). On the contrary, predators are expected to respond mostly to plant structure, such as plant height and heterogeneity of the habitat, creating hunting grounds (Langellotto and Denno, 2004). If plant and beetle diversity are related in agroecosystems (Boutin and Martin, 2009; Meek et al., 2002; Pakeman and Stockan, 2014; Poinas et al., 2025), the well-known impacts of agricultural practices on plants (Carmona et al., 2020; Fried et al., 2018) could also have indirect effects on beetle diversity. However, agricultural predictors are not the only, or, depending on the scale, the most structuring, factors affecting biodiversity in field margins (Poinas et al., 2023). Landscape variables also play a crucial role to shape arthropod communities because of their mobility, but also because vegetation is highly structured in agroecosystems (Courson et al., 2022, 2024; Gaigher et al., 2024; Gallé et al., 2019). Therefore, when we aim at understanding plant-beetle relationships in agricultural landscapes it is necessary to take into account both local practices and landscape variables.

Finally, beetle communities in agricultural ecosystems are mostly studied at a landscape or local scale, especially when focusing on a single taxonomic group (Aguilera et al., 2020; Maisonhaute et al., 2010; Schallhart et al., 2009; Wu et al., 2024). Studies focused at the national scale are often limited to a few regions, resulting in clustered sites that do not represent the full range of variability at large scale (Gallé et al., 2019). A few meta-analyses with larger geographic extents exist regarding beetles, but they extract data created with non-standardized protocols, they scarcely collect detailed agricultural practices (Kulkarni et al., 2015; Triquet et al., 2025), and most of the time focus on species richness-only. In our current work we studied beetle richness, abundance and four main functional groups (predators, phytophagous species, flower visitors, and pest species) at a nationwide scale, in more than 300 different field margins scattered across metropolitan France to represent diverse agricultural crops and practices. Alongside beetle data, we collected detailed field margin vegetation variables, field core and margin management, and landscape composition variables. This represents a unique study given its standardized protocol and wide taxonomic, agronomic and geographic extent.

Our goal in this study was to understand how agricultural practices, alongside with landscape diversity, impact beetle communities in field margins and to what degree there are direct and indirect effects that can help orient management recommendations at a national scale in the future. More specifically, we aim to understand (1) which agricultural practices directly impact beetle richness, abundance and composition; (2) which ones affect them indirectly by modifying plant communities in terms of structure, as well as taxonomic and functional diversity; (3) which plant traits are linked with beetle communities in field margins and (4) how do landscape variables play a role in these relationships between management and biodiversity. We hypothesized, first, that agricultural practices involving high chemical or mechanical lethality to insects - such as insecticide application or field margin mowing - will have direct negative impacts on beetle richness and abundance. Second, we supposed that the practices impacting more the vegetation composition and structure, such as herbicides, fertilization or mowing, will have indirect effects on beetles through their impacts on plants. Herbicides and mowing can reduce the available biomass, thus negatively affecting beetle populations. Fertilization can, on the contrary, increase plant biomass and resource availability for phytophagous beetles. However, it may also reduce plant community diversity by favoring a limited number of nutrient-demanding species, thereby reducing resources for specialized phytophagous or for flower-visiting insects. We also expected that beetles would respond differently depending on their diet, and that beetle composition would also be affected by plant traits and agricultural practices. For example, we assumed that floral traits would be crucial for flower-visiting beetles, while structure and vegetation height would affect predator beetles more, for which vegetation represents a habitat and not a trophic resource. This means that we expect a positive relationship between plant height variance and proportion of predators and a negative one with margin width, as wider margins tend to host more abundant vegetation, where prey hunting is more complicated. Finally, we expected landscape diversity to positively impact richness and abundance of both plants and beetles because of the higher number of species that can colonize the margins from these habitats.

2. Materials and methods

2.1. Study sites and biodiversity sampling

In this work we use the word “beetles” to designate all insects from the order Coleoptera. We used data from the French 500 ENI monitoring network, a national program for monitoring biodiversity and agricultural practices using standardized protocols coordinated by the French Ministry of Agriculture (Andrade et al., 2021). Field margins were defined as a distinct habitat separated from both the cultivated field and the adjacent habitat, usually representing a more or less narrow strip of herbaceous vegetation and managed through mowing. Although the network follows nearly 500 sites yearly starting in 2012, here we focused on a smaller subset where beetles were identified to the species

level (Table 1). For this analysis, we therefore used data collected between 2020 and 2023, during which plant and beetle communities in field margins were surveyed across 313 sites (Table 1), as well as agricultural practices inside the agricultural field and in their field margin.

Field margin vegetation was surveyed once a year at the vegetation peak (end of April to beginning of July), using ten 1 m^2 quadrats, recording presence/absence of the plants identified to the species level. The frequency of each species in the 10 quadrats was used as a proxy for abundance, ranging from 1 to 10 per sample. This abundance proxy is strongly linked to real plant abundance, as verified in a complementary dataset (figure S1). Field margin beetles were sampled by sweep-netting, sampling preferentially flying coleopterans with this method, thrice a year in the same field margins and quadrats, between April and June, only under favorable conditions, meaning a sunny and not windy weather. Beetles were identified to the species level using HAMI, a methodology that combines COI metabarcoding with optimized parataxonomic validation (Penel et al., 2025). The human validation of beetle species allowed to correct for metabarcoding errors, reducing false positives and false negatives, and to add abundance information to each sample. Further details regarding the sampling methods can be found in Andrade et al. (2021). We extracted from this sampling two variables linked to beetle communities: beetle richness and abundance, which were respectively the total number of identified species and individuals, per field margin per year, merging the different sampling dates of one year.We used seven variables reflecting agricultural management, five of which represent in-field practices and two represent field margin management practices. These variables were selected because previous studies have demonstrated that they play a significant role shaping plant communities in this system (Poinas et al., 2023). Due to missing data on certain agricultural practices for specific years, we used the average values of the available practices between 2020 and 2023. This approach is justified by longitudinal analyses of the dataset, which has shown that agricultural practices remain relatively stable from year to year on the same sites on a 5 year period, with far greater variation occurring between different sites rather than over time (Poinas et al., 2025). For the in-field practices, we used nitrogen fertilization dose per year, number of insecticide and herbicides applications per year, number of tillage events per year, and depth of tillage per year. We acknowledge that a number of applications may not always be as relevant as indicators using the actual dose of pesticides (as farmers could spray several low-dose applications versus few large-dose applications). In our dataset, however, the Treatment Frequency Index (TFI) and the number of applications were highly correlated (Pearson's R for herbicides: 0.8 ***; for insecticides: 0.86*** and for non-herbicide pesticides: 0.58 ***)(Figure S2). We then decided to use the number of applications of pesticides at the local site level. For field margin practices, we used the number of mowing events per year and margin width. We added two variables describing pesticide use at the municipality level (i.e, the "commune", which is the smallest administrative unit in France): herbicide Treatment Frequency Index (TFI) and pesticide TFI (sum of herbicide, fungicide and insecticide TFIs) (Solagro, 2022, see: https://solagro.org/nos-domaines-d-intervention/agroecologie/carte-pesticides-adonis). TFIs were calculated as the cumulative ratio of the pesticide dose applied divided by the recommended dose, and is commonly used as an index of intensity of pesticide use (Halberg, 1999).

Finally, we collected two landscape variables in a 1-km radius around each field margin: the % of semi-natural habitats (including: grasslands, forests, hedges, margins and natural mineral areas) and the Shannon index of crop diversity. Spatial data were treated using QGIS v. 3.14.16 and R v. 4.0.1 with the package ALM (Allart et al., 2021). Spatial data sources consisted on freely accessible databases: the French Land Parcel Identification System (RPG) from the common agricultural policy (CAP) (see: https://www.data.gouv.fr/fr/datasets/registre-parcellaire-graphique-rpg-contours-des-parcelles-et-ilots-culturaux-et-leur-groupe-de-cultures-majoritaire), the BD TOPO database of the French National Institute of Geographic and Forest Information (IGN) (see: https://geoservices.ign.fr/documentation/donnees/vecteur/bdtopo), and the OSO Land Cover from Theia (see: https://artificialisation.developpement-durable.gouv.fr/bases-donnees/oso-theia).

Table 1
Number of sampled field margins according to region, crop type and year.

	n
Region	
Temperate	258
Mediterranean	55
Crop type	
Cereals	230
Market gardening	31
Vineyards	52
Total (number of different fields)	313
Year	
2020	28
2021	148
2022	234
2023	89
Total samples	499

2.2. Plant and beetle traits

Six plant traits were collected and/or synthesized from Baseflor (Julve, 1998): life form (perennial *vs* annual), plant type (forbs *vs* graminoids), pollination type (entomogamous *vs* not entomogamous), flowering duration in months, and Ellenberg's nitrogen index (EIV-N), ranging between 1 and 9 which is linked to plant preference for nitrophilous habitats. Maximum plant height in cm was extracted from Flora Gallica (Tison & de Foucault, 2014). For beetles, we used their diet and their pest status to define each species as "predator", "non predator", "pest" or "flower-visiting", where each species can be included in several categories (e.g. flower-visiting and pest). A species was considered as "predator" if it was omnivorous or zoophagous at either larval or imago stage, "phytophagous" if it was phytophagous at either larval or imago stage, and "pest" if it is considered as a main pest of any crop species or if it has already caused yield losses on any crop. Finally, a species was considered as "flower-visiting" if it eats pollen or nectar, potentially contributing to the visited plant pollination. Beetle diet was obtained through a thorough literature search and expert entomologist consultations, which allowed characterizing 375 of the beetle species, out of 732.

For the quantitative traits (plant height and flowering duration) we calculated the Community Weighted Means (CWM) and Community Weighted Variance (CWV) (Sonnier et al., 2010). For the qualitative traits (plant life form, plant type, and beetle diet) we calculated the proportion for each category based on species relative abundance in each community. We ended up with 12 plant variables: plants species richness, abundance, proportion of forbs, proportion of annuals, height CWM and CWV, flowering duration CWM and CWV, Ellenberg's N CWM, entomogamous species proportion, abundance and richness; and five beetle variables: beetle species richness, abundance, proportion of predators, proportion of pests, proportion of flower-visitor.

2.3. Statistical analyses

To identify direct and indirect relationships between environmental variables and plant and beetle diversity, we ran a structural equation model (SEM) using the 'psem' function from the piecewisesem package (Lefcheck, 2016). The SEM was composed of a combination of mixed linear models to quantify the relative direct and indirect effects of a variable, considering the field identity as random variable. Correlations between predictors was tested using the variance inflated factors (VIF), following Hair et al. (2010) we considered VIF values of 10 or higher as revealing severe multicollinearity issues. However, none of our variables

were above 5 and almost all were below 3, except for richness and abundance that scored between 3 and 5. In our model we tested the impacts of all agricultural and landscape variables on all plant and beetle variables, and of all plant variables on beetle variables (Fig. 1). We also tested the effects of crop type and region on all beetle, plant and agricultural practices variables. All the variables were scaled to a mean of 0 and standard deviation of 1, to be able to compare their relative effects. When the residuals were not normally distributed the variables were transformed, either using the log + 1 or a square root transformation (Table 1). We tested the significance of the regression path coefficients associated with each causal relationship. Standardized regression path coefficients were considered to have a strong effect on the variable when they were above 0.8, moderate effect between 0.2 and 0.8, and small effect below 0.2 (Shipley et al., 2009). However, for the two factors (crop type and region) we did not get the standardized path coefficient so we could only compare their effects within each target variable.

3. Results

In this sampling we identified 714 beetle species. Among them, 216 were represented only by one individual, 79 by two individuals, and 51 by three individuals. The five most abundant species —by order of abundance, *Brassicogethes aeneus* (Nitidulidae), *Tytthaspis sedecimpunctata* (Coccinelidae), *Psilothrix viridicoeruleus* (Melyridae), *Rhagonyca fulva* (Cantharidae) and *Cordylepherus viridis* (Melyridae) — together accounted for almost 30% (29.2) of all collected individuals. The mean beetle species richness and abundance per sample were 16.4 ± 8 and 65.7 ± 54, respectively. We identified 449 plant species. Among them, 55 were found only in one quadrat, 53 in two quadrats, and 31 in three quadrats. The five most abundant plant species -by order of abundance, *Lolium perenne* (Poaceae), *Dactylis glomerata* (Poaceae), *Convolvulus arvensis* (Convolvulaceae), *Plantago lanceolata* (Plantaginaceae) and *Bromus hordeaceus* (Poaceae)- together accounted for 22% of the identified plants. The mean plant species richness and abundance were 17.5 ± 8 and 73.5 ± 31, respectively.

3.1. Direct effects of crop type and region on agricultural practices, landscape variables, plants and beetles

When significant, crops and/or region were the most structuring variables for plants and beetle communities (Table 2). Regarding beetle communities, crop type only impacted pest proportion and beetle richness. Crop type also impacted plant abundance, richness, Ellenberg's N score, and all the significant agricultural practices on either beetles or plants, except for margin width. It also impacted the Shannon index of crops, but not the % of semi-natural habitats. Region impacted all proportions of beetle groups, plant abundance, richness, and Ellenberg's N score. It also impacted herbicide TFI in the municipality, but did not impact any other abiotic predictor (Fig. 2).

Mediterranean field margins were characterized by richer and more abundant plant communities, with lower CWM of Ellenberg's N index, and with lower herbicide TFI. Regarding beetles, the proportion of pests and flower visitors were lower in the Mediterranean than in the temperate region (Fig. 2), while those of predators was higher.

Cereal crops were characterized by lower pesticide TFI and higher nitrogen fertilization. Vineyards were characterized by higher pesticide TFI, more tillage and mowing events and lower herbicide TFI, nitrogen fertilization and number of herbicide applications. Plant communities in vineyard margins were richer and more abundant, and had lower

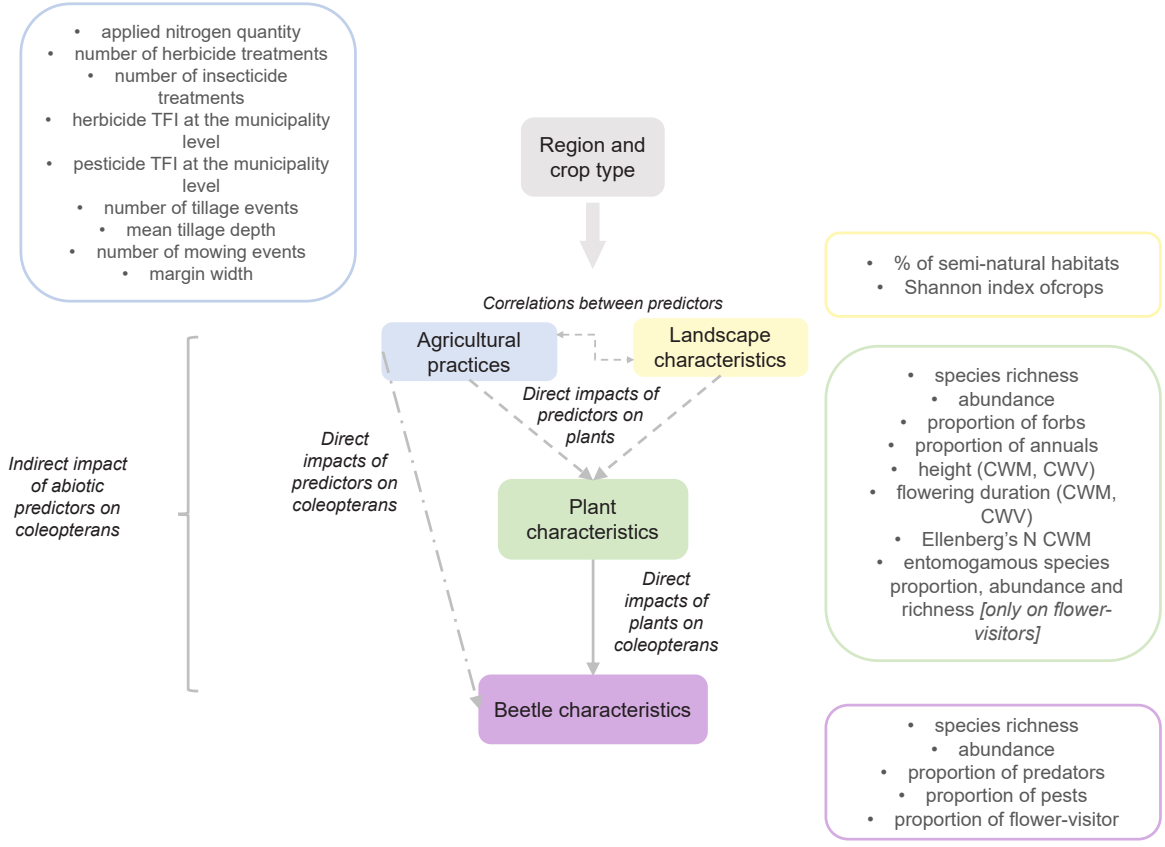

Fig. 1. Conceptual model of the relationships between tested variables. The region and crop type impacts are tested on each agricultural practices, landscape, plant and beetle variables. The relationships between agricultural practices, plants and beetles were all tested in order to detect direct and indirect impacts of agricultural practices on beetles. The solid line represents direct impacts of plants on beetles, the dashed lines represent direct impacts of abiotic predictors on plants, and the dot and dashed lines represent direct impacts of abiotic predictors on beetles.

Table 2
Significant relationships between each response variable and predictor according to the sequential equation modeling with standardized path coefficient estimates, standard error and p-value. SE = standard error, R^2m = marginal R^2, R^2c = conditional R^2.

Response	Predictor	Estimate	SE	p	signif	R2m	R2c
Beetle richness	crop = cereals	−0.03	0.08	> 0.05	ns	0.21	0.56
	crop = market gardening	0.57	0.17	0.002	**		
	crop = vineyards	0.29	0.2	> 0.05	ns		
	number of herbicide treatments (sqrt)	0.17	0.07	0.016	*		
	pesticide TFI at the municipality level (log+1)	−0.29	0.08	< 0.001	***		
Beetle abundance *(log+1)*	CWM of Ellenberg's N score	−0.18	0.07	0.018	*	0.16	0.42
	pesticide TFI at the municipality level (log+1)	−0.16	0.08	0.046	*		
	% of semi-natural habitats (sqrt)	−0.13	0.07	0.047	*		
Proportion of predators in beetle communities (sqrt)	applied nitrogen quantity (log+1)	0.17	0.06	0.003	**	0.11	0.12
	margin width (log+1)	−0.11	0.05	0.025	*		
	region = medit	0.34	0.16	0.033	*		
	region = temp	0	0.08	> 0.05	ns		
Proportion of pests in beetle communities	crop = cereals	−0.12	0.07	> 0.05	ns	0.22	0.22
	crop = market gardening	−0.36	0.15	0.017	*		
	crop = vineyards	−0.66	0.07	< 0.001	***		
	number of tillage operations (log+1)	0.1	0.05	0.037	*		
	plant abundance (sqrt)	0.26	0.1	0.009	**		
	plant richness	−0.18	0.097	0.040	*		
	region = medit	−0.78	0.15	< 0.001	***		
	region = temp	0.02	0.07	> 0.05	ns		
Proportion of flower-visitors in beetle communities	CWV of flowering duration (log+1)	0.18	0.08	0.026	*	0.15	0.32
	margin width	−0.15	0.05	0.002	**		
	proportion of annuals in plant communities	0.14	0.06	0.015	*		
	region = medit	−0.47	0.17	> 0.05	ns		
	region = temp	0.03	0.08	0.005	**		
Plant abundance (sqrt)	crop = cereals	0.12	0.09	> 0.05	ns	0.15	0.6
	crop = market gardening	0.34	0.19	> 0.05	ns		
	crop = vineyards	0.67	0.20	< 0.001	***		
	pesticide TFI at the municipality level (log+1)	−0.20	0.08	0.013	**		
	region = medit	0.80	0.17	< 0.001	***		
	region = temp	−0.05	0.09	> 0.05	ns		
Plant richness	crop = cereals	0.16	0.08	> 0.05	ns	0.2	0.6
	crop = market gardening	0.48	0.18	0.007	**		
	crop = vineyards	0.66	0.19	< 0.001	***		
	pesticide TFI at the municipality level (log+1)	−0.22	0.08	0.006	**		
	region = medit	0.92	0.17	< 0.001	***		
	region = temp	−0.05	0.08	> 0.05	ns		
Proportion of annuals in plant communities	herbicide TFI at the municipality level (log+1)	−0.22	0.11	0.042	*	0.11	0.62
	number of mowing interventions (sqrt)	−0.15	0.06	0.007	**		
	pesticide TFI at the municipality level (log+1)	0.25	0.08	0.002	**		
CWM of Ellenberg's N score	crop = cereals	−0.05	0.09	> 0.05	ns	0.18	0.73
	crop = market gardening	0.03	0.19	> 0.05	ns		
	crop = vineyards	−3.79	0.09	< 0.001	***		
	% of semi-natural habitats (sqrt)	−0.16	0.07	0.021	*		
	applied nitrogen quantity (log+1)	0.18	0.07	0.007	**		
	region = medit	−0.53	0.18	0.003	*		
	region = temp	0	0.09	> 0.05	ns		
CWV of flowering duration (log+1)	number of tillage operations (log+1)	0.16	0.06	0.009	**	0.06	0.54
Applied nitrogen quantity (log+1)	crop = cereals	0.19	0.07	0.007	**	0.05	1
	crop = market gardening	−0.18	0.15	> 0.05	ns		
	crop = vineyards	−0.33	0.11	0.003	**		
Number of herbicide treatments (sqrt)	crop = cereals	0.11	0.07	> 0.05	ns	0.07	1
	crop = market gardening	−0.46	0.15	0.002	**		
	crop = vineyards	−0.48	0.10	< 0.001	***		
Pesticide TFI at the municipality level (log+1)	crop = cereals	−0.22	0.05	< 0.001	***	0.06	1
	crop = market gardening	−0.12	0.12	> 0.05	ns		
	crop = vineyards	0.46	0.08	< 0.001	***		
Herbicide TFI at the municipality level (log+1)	crop = cereals	−0.12	0.05	0.024	*	0.23	1
	crop = market gardening	−0.22	0.12	> 0.05	ns		
	crop = vineyards	−0.72	0.08	< 0.001	***		
	region = medit	−0.75	0.08	< 0.001	***		
	region = temp	0.04	0.06	> 0.05	ns		
Number of mowing interventions (sqrt)	crop = cereals	−0.05	0.05	> 0.05	ns	0.01	1
	crop = market gardening	0.17	0.12	> 0.05	ns		
	crop = vineyards	0.17	0.08	0.043	*		
Number of tillage operations (log+1)	crop = cereals	−0.04	0.05	> 0.05	ns	0.03	1
	crop = market gardening	0.34	0.12	0.006	**		
	crop = vineyards	0.32	0.08	< 0.001	***		

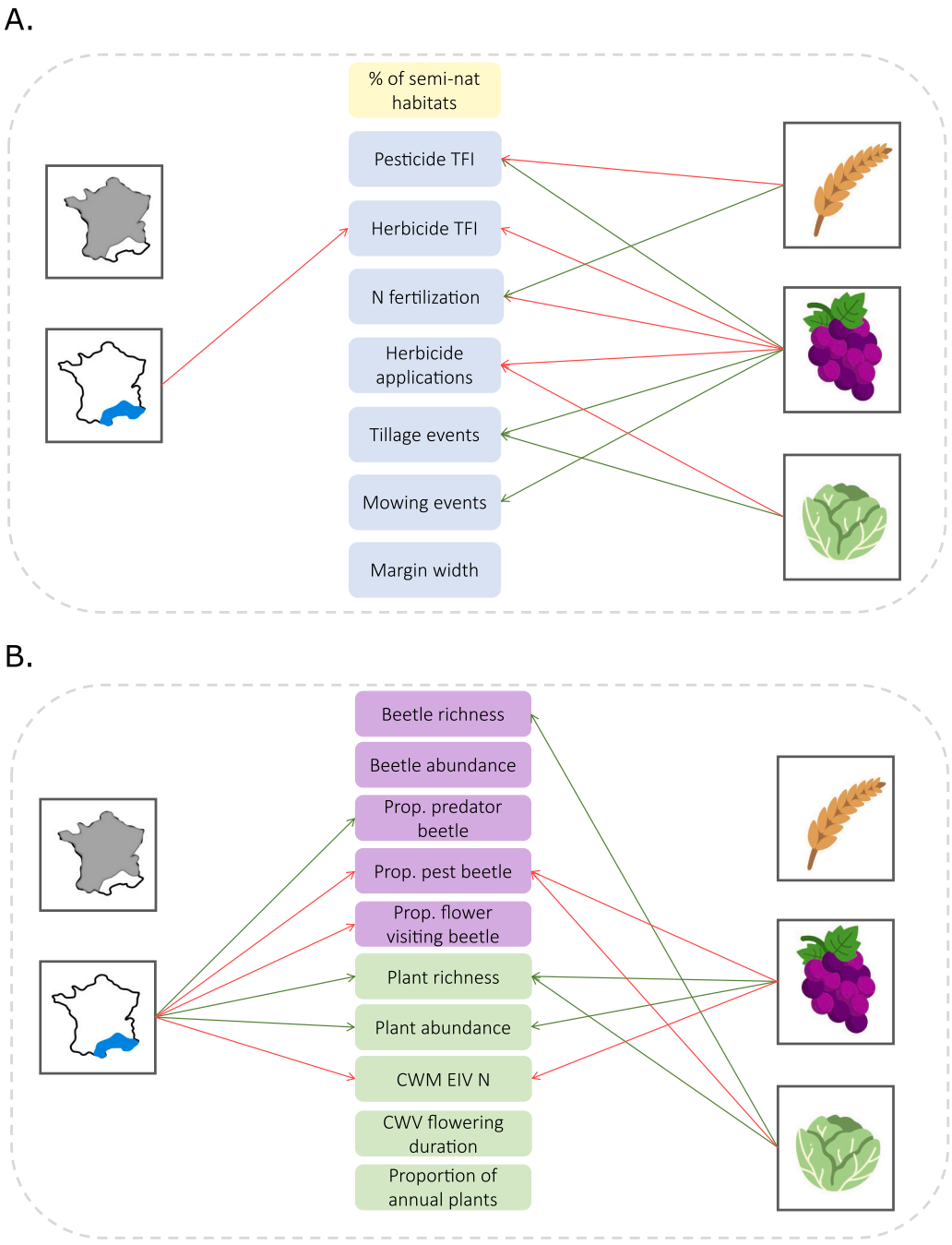

Fig. 2. Impact of crop type and region on A. management and landscape predictors, B. beetle and plant predictors. Only the predictors with at least one significant effect found in the sem model are represented. A green arrow means that the predictor is higher in this region or crop type and a red arrow means that the predictor is lower in this region or crop type. The coefficients corresponding at each arrow can be found in Table 2.

Ellenberg's N index values. Beetle communities in vineyard margins were composed of less pests. Finally, market gardenings were characterized by lower herbicide applications and more tillage events, and were located in landscapes with higher Shannon index of crop diversity. Both plant and beetle richness were higher in market gardening margins, while the proportion of pests was lower (Fig. 2).

3.2. Relationships between plants and beetles

The five direct effects of plants on beetle variables were considered small or moderate, ranging between 0.14 and 0.26 (Table 2). Beetle richness and the proportion of predators were not modified by any plant variable (Table 2, Fig. 3A and C). Beetle abundance was negatively related to CWM of plants Ellenberg's N score (−0.18) (Fig. 3B). The proportion of pests decreased with plant richness (−0.18) while it increased with plant abundance (0.26) (Fig. 3D). The proportion of annual plants in the field margin and the CWV of flowering duration increased the proportion of flower-visiting species (0.14 and 0.18, Fig. 3E). The proportion of forbs in the community, CWM of flowering duration, CWM and CWV of plant height did not affect any beetle variable.

3.3. Effects of agricultural practices and landscape on plants and beetles

All the direct effects of agricultural practices on plants and beetles were small or moderate, between 0.1 and 0.29 (Table 2).

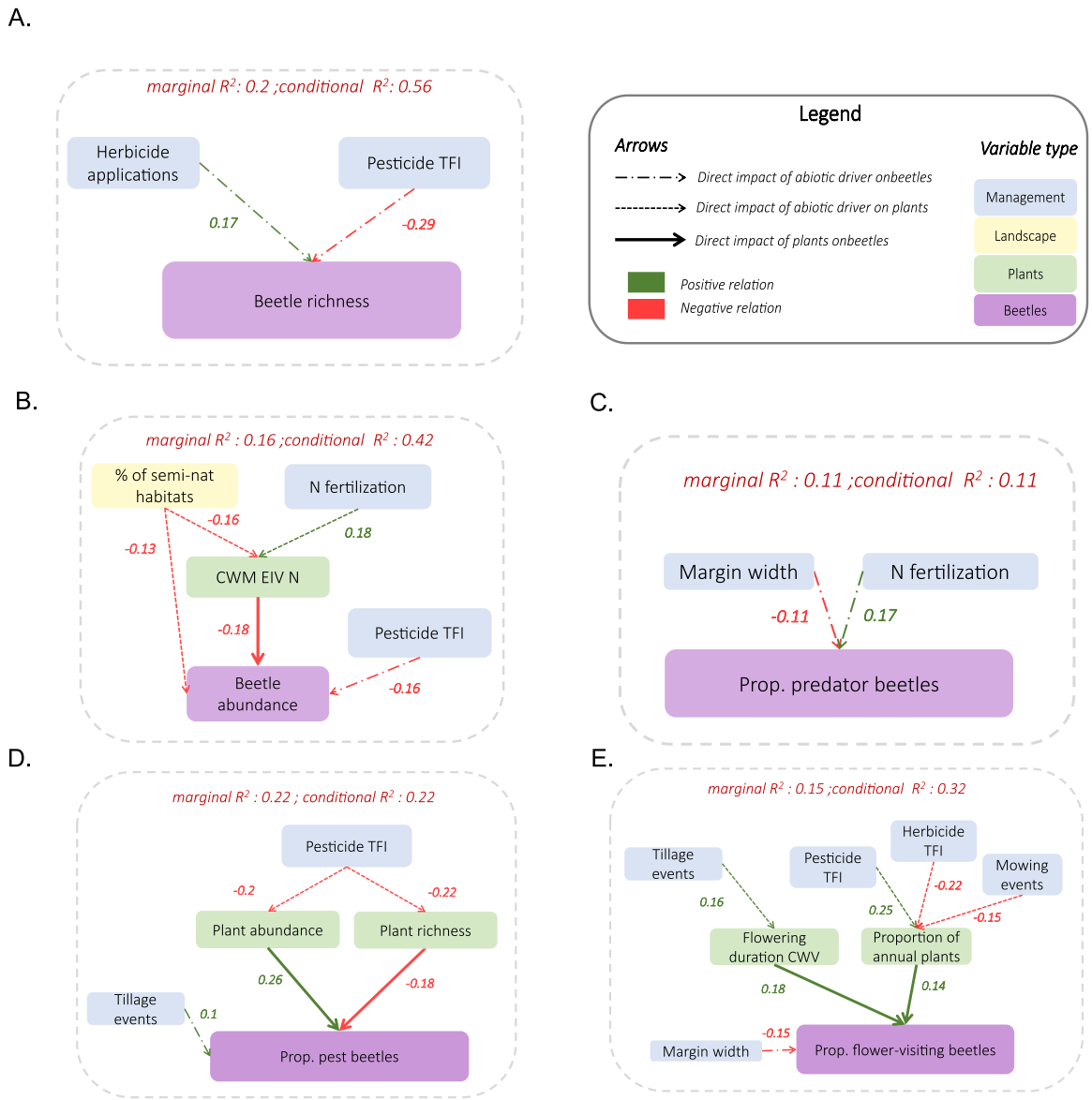

Fig. 3. Relationships between agricultural practices, landscape, plant and beetle variables. For all models the field identity was used as the random variable. Marginal R^2 does not integrate the random effect, while the conditional R^2 includes both random and fixed effects.

The number of herbicide applications and the margin width directly influenced beetle communities but not plant characteristics related to beetles. The number of herbicide applications per year was positively related to beetle richness (0.17). Margin width was negatively associated with the proportion of predators (−0.11) and flower-visitors (−0.15) (Table 2, Fig. 2).

Nitrogen fertilization, number of tillage operations, pesticide TFI at the municipality scale and the % of semi-natural habitats were linked to both plants and beetles. Nitrogen fertilization was positively linked with the proportion of beetle predators (0.17). There was also a positive relationship between nitrogen fertilization and CWM of Ellenberg's N (0.18), thus indirectly having a negative influence on beetle abundance. Pesticide TFI had direct effects on beetles, as well as indirect effects through plant characteristics. It decreased beetle species richness (−0.29) and abundance (−0.16) as well as plant richness (−0.22) and abundance (−0.2), but increased the proportion of annual plants (0.25). Thus, it was indirectly linked to pest and flower-visitor proportions. The number of tillage operations was positively linked with the proportion of pests (0.1). It also positively affected the CWV of flowering duration, thus indirectly increasing the proportion of flower-visiting beetles. Finally, the % of semi-natural habitats was both directly and indirectly positively linked with beetle abundance. Shannon index of crop diversity did not affect any plant or beetle variable (Fig. 3, Table 2).

The number of mowing events and herbicide TFI did not affect beetle communities directly, but were negatively related with the proportion of annuals (−0.15 and −0.22), thus indirectly decreasing flower-visitors' proportion (Fig. 3E, Table 2). Finally, the number of in-field insecticide applications and tillage depth did not affect any plant or beetle variables in the margins.

4. Discussion

Our study provides a comprehensive overview of the aboveground beetle communities in French agricultural field margins at a national scale. This ambitious sampling allowed us to compare beetle communities in the margins of three major crop types, but also in the temperate *vs* Mediterranean regions of France, across a wide variety of agricultural practices and landscapes, along with an exploration of plant-beetle relationships. We showed that agricultural practices have significant impacts on surrounding vegetation, and multiple direct and indirect effects

on beetle communities. Our results also demonstrate that agricultural practices are the most important drivers of field margin beetle communities, but that plants also play a key role in shaping beetle communities. As for plant communities (Fried et al., 2018, 2024; Henckel et al., 2025; Henckel and Fried, 2025; undefined), crop type and region play a key role in structuring field margin beetle communities composition. We also found that pests represent a lower proportion in terms of abundance in vineyards and market gardening margins, which is coherent with the results of Courson et al. (2022). Here, cereal fields are mostly located in landscapes dominated by arable crops. Regarding the region, Mediterranean beetle communities were composed of more predators but less pests and flower-visiting beetles, suggesting a trade-off for beetles between different services. Overall, agricultural intensification decreases beetle communities' diversity and ability to deliver ecosystemic services. We discuss the importance of these direct and indirect effects in more detail below.

4.1. Impacts of agricultural practices and landscape on plants and beetles

We found that intensive agricultural practices were mostly deleterious to plant and beetle communities and therefore to ecosystem delivery potential from the margins, even if it only targets the crops. Pesticide use and fertilization in-field decreased both plant and beetle richness and abundance on the margins, and also drove disturbed plant communities composed of more ruderal plants. This is very coherent with previous results investigating the impacts of agricultural intensification either specifically on plants (Fried et al., 2022), beetles or other arthropods (Basu et al., 2024; Desneux et al., 2007; Geiger et al., 2010; Lichtenberg et al., 2017; Ward et al., 2022), and in both annual (Maisonhaute et al., 2010) or perennial crops (Fried et al., 2019), regarding in-field (Geiger et al., 2010) or margin (Poinas et al., 2025) biodiversity. Results showed unequivocally that pesticides and fertilization have overall direct negative impacts on field margin diversity, both in the Mediterranean region and elsewhere in France, and in the margins of three main French crops. Our study is based on sites distributed at a large geographical scale, with a standardized sampling and with high taxonomic resolution for both plants and coleopterans, showing that these results are consistent despite regional and climatic heterogeneities at the national level. Most of the negative impacts were due to pesticide TFI at the municipal scale, rather than pesticides at the site. This indicates that for mobile organisms such as beetles, the field scale is not sufficient to understand the impacts of pesticides on the communities. On the contrary, the impacts of fertilization were evaluated at the field scale, because the retained variable was the nitrogen quantity applied in the field per year. Both scales are indeed necessary to understand the relationships between management, plants and insect communities in agroecosystems.

Both direct and indirect effects of herbicide TFI and fertilization negatively impacted beetle communities, respectively flower visitors and beetle abundance, through their impacts on the proportion of annual plants and on the community weighted mean of N value. However the indirect impact of pesticide TFI was neutral on pests and positive on flower visitors, through effects on plant abundance and richness (which cancelled each other) in the first case, and on the proportion of annual plants, in the second case. It is interesting because, for both variables, there was no direct impact of pesticide use, indicating that they do not directly affect beetle communities but that they do impact plant communities. Beetles have a higher dispersal capacity than non-mobile organisms like plants, especially flower visitors that all have wings. This suggests that they may not necessarily be directly exposed to pesticides during application, either because they can escape the field and its margins when spraying occurs, or because they were simply located elsewhere in the landscape at the time of treatment. Another result is interestingly contrary to our hypothesis: the positive impact of the number of applied herbicides on beetle richness. This is surprising because herbicide was mostly known to decrease beetle richness, either for carabids or for phytophagous beetles (Iglay et al., 2012; Kraus and Stout, 2019; Trager et al., 2013). However, when the field is intensively weeded, the margin could represent an even more crucial refuge for hosting biodiversity that can almost no longer survive in the field, thus artificially increasing richness in the margin compared to less intensively weeded fields, where beetles could be more diluted between the field and the margin. This result highlights the importance of sampling both in-field and margin plant diversity when we aim at understanding the interplay between management, plants and arthropods in farmlands.

The direct impacts of local and mechanical management are not as clearly detrimental as those of pesticide use and fertilization. In-field tillage was linked with more pests, maybe due to the killing of many -beetle or non -beetle (Poinas, 2023) predators in the soil, reducing the pressure on beetle pests (Jacobsen et al., 2022), which is very detrimental to ecological regulations. However, it also increased the variability of flowering duration, maybe by selecting more ruderal species (Kazakou et al., 2016), whose presence increase in the margins that are typically composed of more grassland species, and thus increase its functional diversity. Margin mowing only impacted plants, driving a lower proportion of annual plants. These impacts on plants indirectly affect beetle communities, with tillage driving a higher proportion of flower-visiting beetles and mowing a lower one.

4.2. Relationships between plants and beetles in field margins

Our main findings regarding relationships between plants and beetles is that plant diversity strongly supports communities with a lower proportion of pests, but that plant abundance did not. This means that plant abundance, contrary to plant richness, is not a positive indicator regarding beetle pest regulation in agroecosystems. Three of the five beetle response variables were directly linked to at least one plant variable. Plant richness was negatively linked with pest proportion, which is a very interesting relationship, indicating that richer spontaneous plant communities support ecological regulation of pests. This has been described before (Judt et al., 2023; Paiola et al., 2020; Winter et al., 2018), but it is interesting to note that Dassou and Tixier (2016) showed with a meta-analysis that there is a positive response of predator arthropods to plant diversity, but no response of pests, which are all phytophagous insects. Here, we found the contrary: plant richness is linked to less pest pressure, even if it does not support more beetle predators. It is possible that plant richness supports more predators in general, not specifically beetle predators. For example, if most pest regulation is being carried out by insectivorous birds, bats, or other groups that we did not monitor but could be affected by margin vegetation (Henckel et al., 2019; Vallé et al., 2023), we would not have detected effects on beetle predators. Another possibility is that pest regulation is being carried out by competition and network stability rather than by predator-prey interactions.

Plant abundance, on the other hand, increases pest proportion, indicating that spontaneous vegetation presence *per se* is not enough to deliver services: it depends on the diversity of these plants. Beetle abundance was negatively linked to the mean (CWM) of Ellenberg's N index, high values of which are typical of more disturbed ruderal habitats (Bourgeois et al., 2019). These communities probably offer poorer shelters and less diversified plant resources for beetles in general. They are probably also more homogenous and dominated by fewer very weedy species, which are less able to support higher beetle abundance.

Finally, the proportion of flower-visiting beetles increased with those of annual plants. This could be due to the higher year-round heterogeneity created by the presence of annual plants. Margins with a higher proportion of annual plants might be able to deliver a wider variety of resources, both between and within years, and to feed different cohorts of flower visitors. On the contrary, perennial plants would be adapted more specifically to some species only. This is supported by the positive link between flower-visitors and variance of flowering duration in the plant community: more diverse periods of flowering are key to support

flower consumers, because those communities can offer flowers during a longer period. The mean (CWM) of flowering duration was negatively linked to pollinator species richness and visitation in Uyttenbroeck et al. (2017) study, but positively to their evenness. More studies directly focused on the relationship of phenological traits variances are needed to uncover more precisely their role.

As stated in our hypotheses, we expected that beetle communities would either respond to plant structure (i.e. CWM and CWV of plant height, annuals), to plant resource delivery (i.e. abundance, Ellenberg's N, floral resources) or to plant diversity (i.e. species richness). However, only few of our hypotheses were verified. Only five plant variables out of the 12 tested were related to any beetle characteristics. Contrary to most results found in the literature (Lichtenberg et al., 2017; Mei et al., 2021; Poinas, 2023), we did not find any relationship between plant and beetle richness and abundance. These studies were either focused on smaller taxonomic groups (weevils, rove beetles, ground beetles) or on arthropods in general. Maybe these different taxonomic scales can be an explanation of these different results, meaning that some impacts can be due to the local degraded landscapes and biodiversity, and others are directly due to the drift of the applied substances to the margins. This could also be due to missing plant variables, not included in our study. Indeed, including all relevant plant traits, like seed or floral resources traits, needed to fully understand plant-beetle functional relationships is a real challenge.

Agricultural intensification and poor plant communities are globally unfavorable to plant and beetle diversity and specifically to pest regulation and flower visitors. However, there is a wide room for improvement. Indeed, our model describing the response of pests to plants and practices is the only one with a conditional R^2 equal to the marginal one, indicating that the site variance itself is not very explicative and that pest presence is mostly ruled by the abundance and the type of resources and by agricultural practices. This indicates that adapting practices and managing vegetation in order to reduce pest pressure is achievable, and that pest regulation could be positively impacted by reduced tillage and pesticide pressure in the landscape, thus allowing natural enemies to develop and regulate pests.

Author contributions

LG writing – original draft (lead); formal analysis (lead); review and editing (lead); conceptualization (equal). **GF** funding acquisition (equal); project administration (equal); review and editing (lead); conceptualization (equal); data curation (equal); investigation for plant traits dataset (equal). **BP** review and editing (equal); investigation for beetle identification (equal); data curation (equal). **CM** review and editing (equal); investigation for beetle traits dataset (equal). **AB** investigation for beetle identification (lead). **JH** investigation for beetle identification (equal) and beetle traits dataset (equal). **GJK** review and editing (equal); investigation for beetle identification (equal). **LB** investigation for beetle identification (equal). **ALC** investigation for beetle identification (equal). **CNM** funding acquisition (equal); project administration (equal); review and editing (lead); conceptualization (equal); data curation (equal); investigation for beetle traits dataset (equal). All authors have read and validated the manuscript.

CRediT authorship contribution statement

Anne-Laure Clamens: Investigation. **Laure Benoit:** Investigation. **Christine N. Meynard:** Writing – review & editing, Validation, Project administration, Data curation, Conceptualization. **Benoit Penel:** Writing – review & editing, Investigation, Data curation. **Guillaume Fried:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Léa Genty:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Gael J. Kergoat:** Writing – review & editing, Investigation. **Julien Haran:** Writing – review & editing, Investigation. **Axel Bourdonné:** Investigation. **Cyril Marty:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christine N Meynard reports financial support was provided by French National Research Agency. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110640.

Data availability

All data and code available at https://github.com/leagenty/indirect_effects_practices_coleo

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