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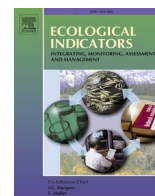
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## Hedgerows are more multifunctional in preserved bocage landscapes

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### ABSTRACT

Hedgerows are key wildlife habitats in agricultural landscapes, with presumably high multifunctionality – that is the capacity to provide multiple ecological, agronomic or cultural functions. However, knowledge gaps remain regarding the drivers of hedgerow multifunctionality and potential synergies and trade-offs between functions. In particular, it is unknown in which landscapes hedgerows best support a range of taxa and associated functions. We assessed the effects of hedgerow features, adjoining farming systems, landscape context, and their interactions on hedgerow multifunctionality based on four ecological functions – biodiversity conservation, potential pollination, potential predation, and pest colonization. We estimated these functions by the abundance and diversity of plant and arthropod taxa in 40 hedgerows, in Brittany (France). Results support previous studies showing the beneficial effects of flower cover, margin width, adjacent organic farming, and other variables related to hedgerow structural complexity on individual taxa or proxies of functions. Most importantly, our study reveals that hedgerows are more multifunctional in landscapes with dense hedgerow networks (so-called ‘bocage’ landscapes), which is likely the result of greater habitat amount, connectivity, and environmental heterogeneity. In addition, we find weak correlations between proxies of functions, and more synergies than trade-offs in response to the explanatory variables, indicating that there is considerable scope for improving the ecological value of hedgerows. We draw attention to the fact that ongoing destruction of hedgerow networks, including wide and structurally complex hedgerows, might lead to long-term or irretrievable loss of associated species and ecological functions, jeopardizing restoration and replanting efforts.

### 1. Introduction

Hedgerows are key habitats for biodiversity conservation, supporting a wide range of plant, animal, and fungi species (Wolton, 2015) and delivering multiple ecosystem services in agricultural landscapes (Montgomery et al., 2020). Consequently, the objective of the European Union Biodiversity Strategy for 2030 is to bring back 10% of agricultural area under high diversity landscape features, including hedgerows and other semi-natural habitats (European Commission, 2021). Agroecological systems often rely on the preservation and restoration of hedgerows to enhance major ecological functions, such as pollination and predation of crop pests (Dover, 2019). As semi-natural habitats can also harbour pest species, another objective is to reduce the potential risk of pest colonization in adjoining crop fields (e.g., Raatz et al., 2021). To date, however, most studies considered one or two functions of hedgerows, but rarely more. Similarly, studies on the biodiversity of

hedgerows and other linear semi-natural habitats generally focused on a limited number of taxa or functional groups (but see Ekroos et al., 2013; Šálek et al., 2015; Lecq et al., 2017; Segre et al., 2019). Very few studies have measured hedgerow multifunctionality – that is the capacity of hedgerows to provide multiple ecological, agronomic or cultural functions (Hörling et al., 2019). Several studies found that hedgerows harbour more abundant or diverse communities of natural enemies, but also fewer pests, compared with herbaceous field margins or crop fields (Boutin et al., 2009; Gareau et al., 2013; Morandin et al., 2014, but see Fusser et al., 2016; Tougeron et al., 2022). On the other hand, other studies found evidence for trade-offs between the promotion of invertebrate natural enemies (dominant in hedgerows) and pollinators (dominant in herbaceous habitats) (Bartul et al., 2019; Rosas-Ramos et al., 2019; Bishop et al., 2023, but see Dainese et al., 2015). Recently, Couthouis et al. (2022) provided evidence that hedgerows have higher multifunctionality than crop fields, based on four functions:

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biodiversity conservation, potential pollination, potential predation, and pest colonization. Beyond the overall ecological benefits of hedgerows compared to other habitats, we have less information regarding the drivers of ecological functions and multifunctionality in hedgerows, and the mechanisms that lead to potential synergies and trade-offs between these functions. Such information should provide key insights for successful hedgerow restoration and replanting.

At local scale, the management, structure and composition of vegetation layers – which can be highly variable among hedgerows – affect hedgerow biodiversity and ecological functioning. Mature and structurally complex hedgerows more likely support high level of biodiversity (Dainese et al., 2015; Garratt et al., 2017; Lecq et al., 2017; Graham et al., 2018). Woody plants, ditches, and earth and stone banks provide important trophic and habitat resources for arthropods, including pollinators and natural enemies of crop pests (Maudsley, 2000). Dense and complex hedgerows are also less likely to harbour common arable weeds that might compete with crops (Cirujeda et al., 2019; Boinot and Alignier, 2023). In addition, intensive farming practices in the adjoining crop field can have detrimental impacts on hedgerow biodiversity (Boutin et al., 2008). Hedgerows adjoining conventional farming fields intercept large amounts of pesticides, which can cause direct mortality in both plants and arthropods (Otto et al., 2009). The drift of chemical fertilizers also causes soil eutrophication and acidification, which favour nitrophilous grasses and reduce resources for flower-visiting arthropods (David et al., 2019; Boinot and Alignier, 2022).

Beyond local factors, there are key processes operating at the landscape scale that determine the level of biodiversity and ecological functioning in habitats. These include the spillover of organisms between habitats in diversified landscapes and species coexistence through greater environmental heterogeneity (Tscharntke et al., 2012). Yet, most studies that measured ecosystem multifunctionality did not consider landscape-scale processes. Evidence for the type of landscape in which hedgerows best support a range of taxa is lacking, which might hinder the successful implementation of hedgerow policies (Staley et al., 2023). Land consolidation programs have led to massive removal of hedgerows and decreased connectivity between wooded habitats in the landscape, with potential negative impacts on hedgerow biodiversity and ecological functioning (Haddad et al., 2015; Moreno et al., 2018). Studies have shown that the preservation of hedgerow networks is beneficial to forest plant and carabid species (Millán de la Peña et al., 2003; Roy and de Blois, 2008) as well as pollinators (Cranmer et al., 2012; Dainese et al., 2017). However, significant gaps remain in the impacts of landscape context on hedgerow biodiversity (considering a wider range of taxa), that is the influence of semi-natural habitats but also the crop mosaic and associated farming practices that can lead to additional heterogeneity of ecological importance (Vasseur et al., 2013).

The objective of this study is two-fold: (1) determine the local and landscape-scale drivers of hedgerow multifunctionality, based on four ecological functions (biodiversity conservation, potential pollination, potential predation, pest colonization) estimated by the abundance and diversity of plant and arthropod taxa in hedgerows, and (2) assess potential synergies and trade-offs between these functions. We are also interested in exploring interaction effects between drivers, which are still given limited attention in agroecological studies despite their apparent importance. For example, it is known that the landscape context can affect the effectiveness of agri-environment schemes such as the creation of field boundaries or the conversion to organic farming. Vice-versa, local habitat management intensity can determine the strength of landscape effects (Tscharntke et al., 2005; Stein-Bachinger et al., 2022). At local scale, we assess the effects of both hedgerow features (e.g., hedge height, canopy width, tree cover, flower cover) and adjoining farming system (conventional farming CF vs organic farming OF). We hypothesize that (1) taller, wider, and structurally more complex hedgerows (with higher woody species diversity) are more multifunctional, because they likely have greater local environmental heterogeneity and more colonization events over time (Graham et al.,

2018), and (2) hedgerows adjoining OF fields are more multifunctional given the reduction of agricultural disturbances such as agrochemical drifts (Boutin et al., 2008). At landscape scale, we assess the effects of total habitat diversity (Shannon index), cover of semi-natural habitats, hedgerow density, crop diversity and OF cover. We hypothesize that (3) hedgerow multifunctionality increases in more complex and diversified landscapes, presumably owing to increased habitat amount, environmental heterogeneity and connectivity between habitats (e.g., Zirbel et al., 2019 in restored grasslands), and (4) hedgerow multifunctionality increases in landscapes with higher OF cover, given the enhancement of resources and the reduction of agricultural disturbances at landscape scale (e.g., Rundlöf et al., 2008; Rundlöf et al., 2009). Finally, (5) we expect mostly synergies between the ecological functions because increased environmental heterogeneity and reduced agricultural disturbances should promote biodiversity conservation, including pollinators and predators of crop pests. On the other hand, crop pests are less likely to benefit from such conditions owing to increased predation (the “enemies hypothesis”), but also reduced crop abundance and increased habitat diversity (the “resource concentration hypothesis”) (Root, 1973). We might however expect a trade-off between the potential pollination and predation functions as suggested in the literature (i.e., open hedgerows with abundant flower cover benefiting pollinators vs structurally complex hedgerows benefitting predators).

## 2. Material and methods

### 2.1. Study site

We conducted the study in the southern part of the Zone Atelier Armorique, a Long-Term Socio-Ecological Research (LTSER) site in Brittany, France (47°59'35 N, 1°45'12 W). Dense hedgerow networks (Fig. 1) and crop-livestock farming systems characterize this region. Wheat and maize fields and temporary grasslands dominate agricultural lands. Hedgerows are generally composed of oak *Quercus robur* or chestnut *Castanea sativa* trees planted on earth and stone banks and pruned for firewood every 9–12 years. When present, the shrub layer is generally dominated by hazel *Corylus avellana*, hawthorn *Crataegus monogyna*, blackthorn *Prunus spinosa*, spindle *Euonymus europaeus*, broom *Cytisus scoparius* or gorse *Ulex europaeus*. We selected 40 hedgerows with an average length of  $150 \pm 66$  m, half adjoining organic farming (OF) fields and half adjoining conventional farming fields (CF) (Fig. S1). Hedgerows were located along two independent landscape gradients of hedgerow density (total length) and OF cover (Figs. S2–S5). CF fields were grown with winter cereals ( $n = 20$ ), whereas OF fields were grown with winter cereals ( $n = 10$ ) or winter cereal-legume intercrops ( $n = 10$ ). This design is representative of the practices of farmers in the study area, where intercrops are more frequent on OF farms. There were no significant differences in management practices (number of interventions, fertiliser input and ploughing) between OF cereal crops and OF intercrops (Couthouis et al., 2022).

### 2.2. Plant and arthropod survey

To estimate the ecological functions of hedgerows (biodiversity conservation, potential pollination, potential predation, and pest colonization), we sampled herbaceous vegetation, flower-visiting insects, predatory arthropods, and pests in hedgerows. In June, we sampled herbaceous vegetation in 10 quadrats ( $1 \times 1$  m) at 5 m intervals along 50 m long transects in each hedgerow. We identified plant species using the Flora Europaea (Tutin et al., 1993) and visually estimated the percent cover of each species. In addition, we classified species into non-weedy species versus common arable weeds, based on the French reference book *Mauvaises herbes des cultures* (Mamarot and Rodriguez, 2014) to compute the total abundance of common weeds. We counted the number of flower-visiting insects three times in May, June and July 2020, by walking along each 50 m long transects at a slow pace for 5





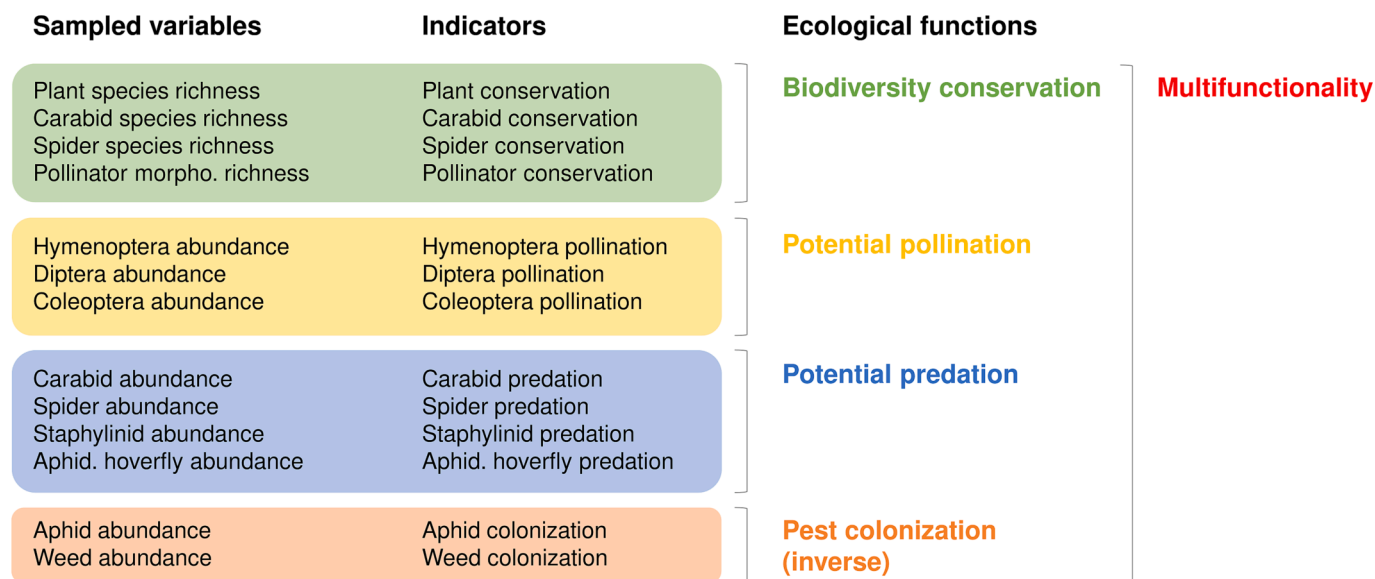
Fig. 1. Bocage landscape and diversity of hedgerows in the Zone Atelier Armorique, a Long-Term Socio-Ecological Research (LTSER) site in Brittany, France. Source: ©Air Papillon (bocage), A. Alignier and S. Boinot (hedgerows).

min. We assigned flower-visiting insects to the following morpho-groups: honeybees, *Bombus terrestris* agg., *Bombus lapidarius*, *Bombus pascuorum*, solitary bees < 1 cm, solitary bees > 1 cm, aphidophagous hoverflies, non-aphidophagous hoverflies, butterflies, other Diptera, other Coleoptera and other Hymenoptera. We also counted the number of aphidophagous hoverflies (foraging, flying or resting adults) in hedgerows, that we used as a potential surrogate for the number of larvae (aphid predators). Finally, we sampled predatory arthropods (carabids, spiders, staphylinids and ladybirds) and insect pests (aphids) twice, in May and June 2020, using a vacuum method (D-vac, 12.5 cm diameter) with a series of five aspirations performed through the vegetation and down to the ground level at 10 m intervals along each 50 m long transect (Brook et al., 2008). Each aspiration consisted of twenty aspirations of 10 s. We identified carabid and spider species following Roger et al. (2010), Roberts (1985), Roberts (1987) and Oger (2020). All in all, we collected 13 variables (abundance and diversity of each taxon) that we used to estimate ecological indicators and corresponding functions (Fig. 2).

### 2.3. Ecological functions and multifunctionality

We estimated ecological functions based on the abundance and species or morpho-group richness of the corresponding taxa (Fig. 2). Arthropod abundances were summed across all sessions. We used a square root transformation for both arthropod and weed abundances to reduce the influence of extreme values. Then, we standardized all sampled variables by their maximum value to obtain 13 indicators on the same scale (0–1). Further, indicators were averaged to estimate the four ecological functions: plant, carabid, spider and pollinator conservation (based on species or morpho-group richness) were averaged into ‘biodiversity conservation’; hymenoptera, diptera and coleoptera pollination (based on the abundance of flower-visiting individuals) were averaged into ‘potential pollination’; carabid, spider, staphylinid and aphidophagous hoverfly predation (based on abundance) were averaged into ‘potential predation’; and aphid and weed colonization (based on abundance) were averaged into ‘pest colonization’. We distinguished the function of potential predation from the function of pest colonization to assess the “enemies” vs “resource concentration” hypotheses. Butterfly and ladybird abundances were not included in the functions of





**Fig. 2.** List of sampled variables and corresponding indicators (0–1 scale) averaged into the four ecological functions, in turn averaged to provide an estimate of hedgerow multifunctionality. We inverted pest colonization values so that positive values indicate higher levels of function.

potential pollination and predation respectively, since their occurrence was very sporadic. We inverted pest colonization values (1 – pest colonization) so that positive values indicate higher levels of function.

We used two approaches to estimate the multifunctionality of each hedgerow; the averaging and the multiple threshold approach (Byrnes et al., 2014). The averaging approach provides a straightforward measure to assess the capacity of (agro-)ecosystems to support multiple functions. We averaged the four ecological functions (biodiversity conservation, potential pollination, potential predation, and inverse pest colonization) to measure hedgerow multifunctionality. On the other hand, the multiple threshold approach provides information on the number of functions simultaneously performing at high levels, by considering the number of functions exceeding a given threshold (i.e., a percentage of the maximum observed value of each function). For each hedgerow, we calculated the number of functions that performed higher than a given threshold (considering all thresholds between 10% and 90% of the maximum value of each function).

#### 2.4. Local factors

We measured eight variables related to hedgerow features, namely hedgerow height (mean of three measurements), canopy and margin widths (on the side where we sampled plant and arthropod taxa), tree and shrub covers (visual estimations), Hill-Shannon diversity of woody species ('Woody diversity'), total flower cover (including herbaceous and woody species), and presence-absence of earth and stone banks in each 50 m transect. In addition, we considered the farming system adjoining each hedgerow (CF vs OF). A generalised pairs plot of hedgerow features and farming systems is provided in Fig. S6. Finally, we measured local climatic parameters with an environmental multi-meter during arthropod sampling, namely temperature (both for pollinators and predators), wind and light (only for pollinators). Climatic parameters were averaged across all sessions in subsequent analyses.

#### 2.5. Landscape factors

We used a multiscale approach and described the landscape context within circular buffer radii of 250 m, 500 m, 750 m and 1000 m around each hedgerow. Land-cover maps of the landscape sites were digitised in Arcgis 10.8.1 (Environmental Systems Research Institute, 2020) using aerial ortho-photographs from BDOrtho® and field surveys. Kermap

(<https://kermap.com/en/>) generated hedgerow mapping, using Computer Assisted Photo-interpretation based on the IGN orthophotograph of 2017. We also mapped land-cover types (woodland, hedgerows, grassland, herbaceous strips, crop types, water and urban area). In addition, we mapped farming systems (OF vs CF) based on existing data obtained for the same study area (Puech et al., 2015) and updated information from interviews with farmers. Then, we rasterized vector maps with a resolution of one pixel for 5 m × 5 m to compute landscape variables using Chloé software (Boussard and Baudry, 2017). We considered five landscape variables, namely the total cover of semi-natural habitats ('SNH cover'), Shannon habitat diversity ('Habitat diversity'), total hedgerow length ('Hedge density'), Shannon crop diversity ('Crop diversity'), and total organic farming cover excluding focal fields ('OF cover'). The following habitats were included in 'SNH cover': woodland, hedgerows, fallows, permanent grassland (>5 years), herbaceous strips and water. The following categories were included in 'Habitat diversity': 1 = woodland/hedgerows/fallows, 2 = perennial crops/permanent grasslands, 3 = temporary grasslands/herbaceous strips, 4 = annual crops, 5 = water. The following categories were included in 'Crop diversity': 1 = maize, 2 = other cereals, 3 = oilseed rape, 4 = temporary grassland, and 5 = other crops. We excluded 'SNH cover' from further analyses as it was highly correlated with 'Habitat diversity' ( $r = 0.912$  within a circular buffer radius of 1000 m). Generalised pairs plots of landscape variables for each buffer radius are provided in Figs. S2-S5.

#### 2.6. Statistical analysis

We analysed the effects of hedgerow features, adjoining farming systems, landscape variables and pairwise interactions on the 13 indicators, four ecological functions, and multifunctionality (both averaged multifunctionality and the number of functions exceeding given thresholds). We also included climatic parameters as covariates, that is temperature, wind and light for all indicators and functions that include pollinator sampling, and only temperature for those based solely on predator or aphid sampling. As we are interested in exploring interaction effects, and given the large number of explanatory variables ( $n = 28$  univariate variables + their pairwise interactions), we used interaction forests to select the most influential variables (and pairwise interactions). Interaction forests are a variant of random forests that not only measures univariate variable importance, but also explicitly models

interaction effects in bivariable splits performed by the trees constituting the forests (Hornung and Boulesteix, 2022). Interaction forests provide ‘effect importance measures’ (EIM) that allow for ranking of univariate variables and covariate pairs with respect to their importance to prediction. Interaction forests also provide information on the type of interaction, either quantitative (the strength of the effect of variable A depends on the value of variable B, but the direction of that effect does not change depending on B) or qualitative (the direction of the effect of variable A changes depending on the value of variable B). Besides, like random forests, interaction forests are a useful statistical tool to identify appropriate spatial scales of landscape predictors measured within various buffer sizes (Bradter et al., 2013). Since there are no significance tests or predefined selection thresholds for EIM values, we considered the top variables or interactions (whose EIM values set themselves apart from the others) for subsequent regression analyses. Interaction forests assess the effects of all possible pairwise interactions, including those that are not necessarily of interest from a biological or ecological point of view. Therefore, our selection procedure for interactions is as follows: (1) considering only relevant and interpretable interactions based on the literature and our expertise, but disregarding interactions that are more difficult to interpret (e.g., interactions between two landscape predictors that are not measured within the same buffer size), (2) visualising the bivariate influence of candidate interactions to check the quality of gradients (e.g., the absence of outliers driving the interaction effect, see Fig. S7). We followed the guidelines provided in Hornung and Boulesteix (2022) and used the R package ‘diversityForest’ to perform interaction forests and plot bivariate influence graphs. We used 20,000 trees per forest, and we performed 10 repetitions of interaction forests to obtain the mean and standard deviation of EIM values.

Once we selected a set of explanatory variables and interactions, we used generalized additive models (GAMs) to assess their effect on indicators, functions, and averaged multifunctionality. GAMs are very useful to assess the nonlinearity of relationships (e.g., the intermediate landscape complexity hypothesis; Tschamntke et al., 2012). We included explanatory variables using splines with a limited degree of freedom ( $k = 5$ ) to avoid overfitting (e.g., Fried et al., 2018; García-Navas and Thuiller, 2020). Explanatory variables were standardized (z-transformation) to facilitate parameter estimation. We checked the degree of collinearity between variables using variance inflation factors (VIFs). All VIF values were lower than 3, indicating that collinearity was not an issue (Zuur et al., 2013). Using the ‘spline.correlog’ function from the R package ‘nfc’ (Bjørnstad, 2020), we did not detect any spatial

autocorrelation in model residuals. Given that response variables are bound between 0 and 1, we computed Beta GAMs using the R package ‘mgcv’ (Wood, 2017). The significance of interactions in GAMs were tested by comparing the AIC (Akaike Information Criterion) of models with and without interactions (Zuur, 2013). We considered the interaction significant only if the model with interaction had an AIC that is 2 units lower than the model without interaction.

Finally, for predictors with a significant effect on averaged multifunctionality, we followed the methodology provided by Byrnes et al. (2014) and used the R package ‘multifunc’ (Byrnes, 2022) to analyse the impact of these predictors on the number of functions reaching a performance threshold (i.e., from 10% to 90% of the maximum observed value of each function). We performed quasi-Poisson GLM and plotted regression lines, parameter estimates of the predictors and their confidence intervals at each threshold level.

### 3. Results

There were no strong pairwise correlations between ecological functions of hedgerows ( $|r| < 0.2$ ). An overview of the results of interaction forests and generalized additive models (GAMs) assessing the effects of local and landscape factors on the four ecological functions and the multifunctionality of hedgerows is given in Fig. 3. Full results of interaction forests and GAMs are provided in Figs. S8-S25 and Tables S1-S18, respectively.

#### 3.1. Biodiversity conservation

Biodiversity conservation was higher in hedgerows with wider margins or adjoining OF systems (Figs. 3, 4A & 4B; Table S1). Specifically, plant conservation increased in hedgerows adjoining OF systems (Figs. S26 & S27A; Table S2). Carabid conservation was higher in hedgerows with wider canopies and higher diversity of woody plant species (Figs. S26; S27B; Table S3). Spider conservation increased with temperature, but only in hedgerows adjoining OF systems (Figs. S26, S27C; Table S4). Pollinator conservation increased with flower cover before reaching a plateau, and was higher for intermediate values of wind speed (hump-shaped effect) (Fig. S26, 27D, Table S5).

#### 3.2. Potential pollination

Potential pollination in hedgerows increases with hedge density

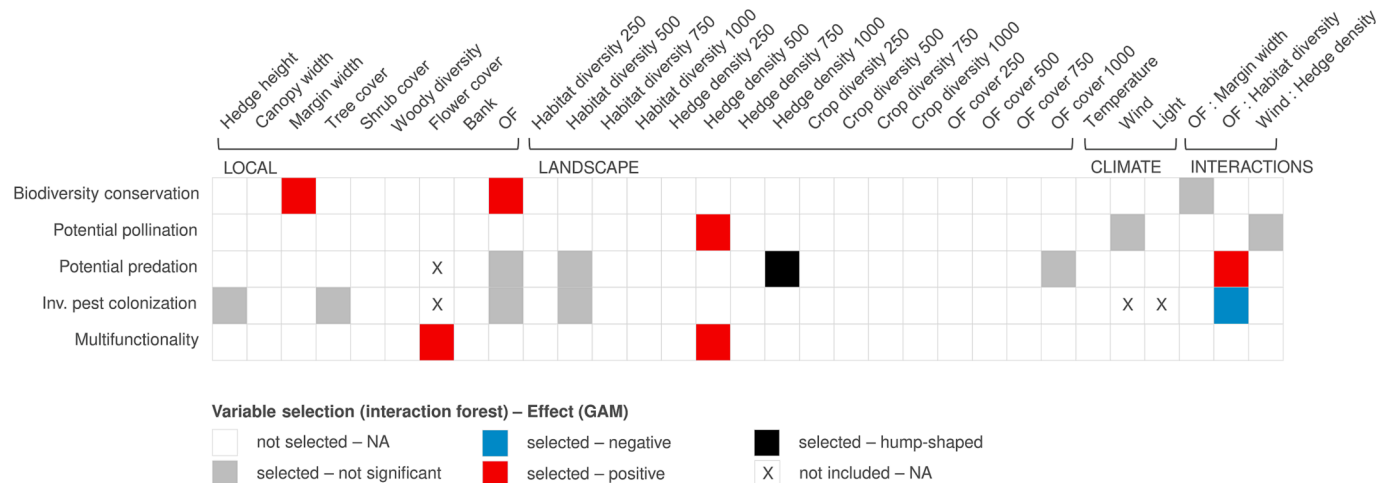
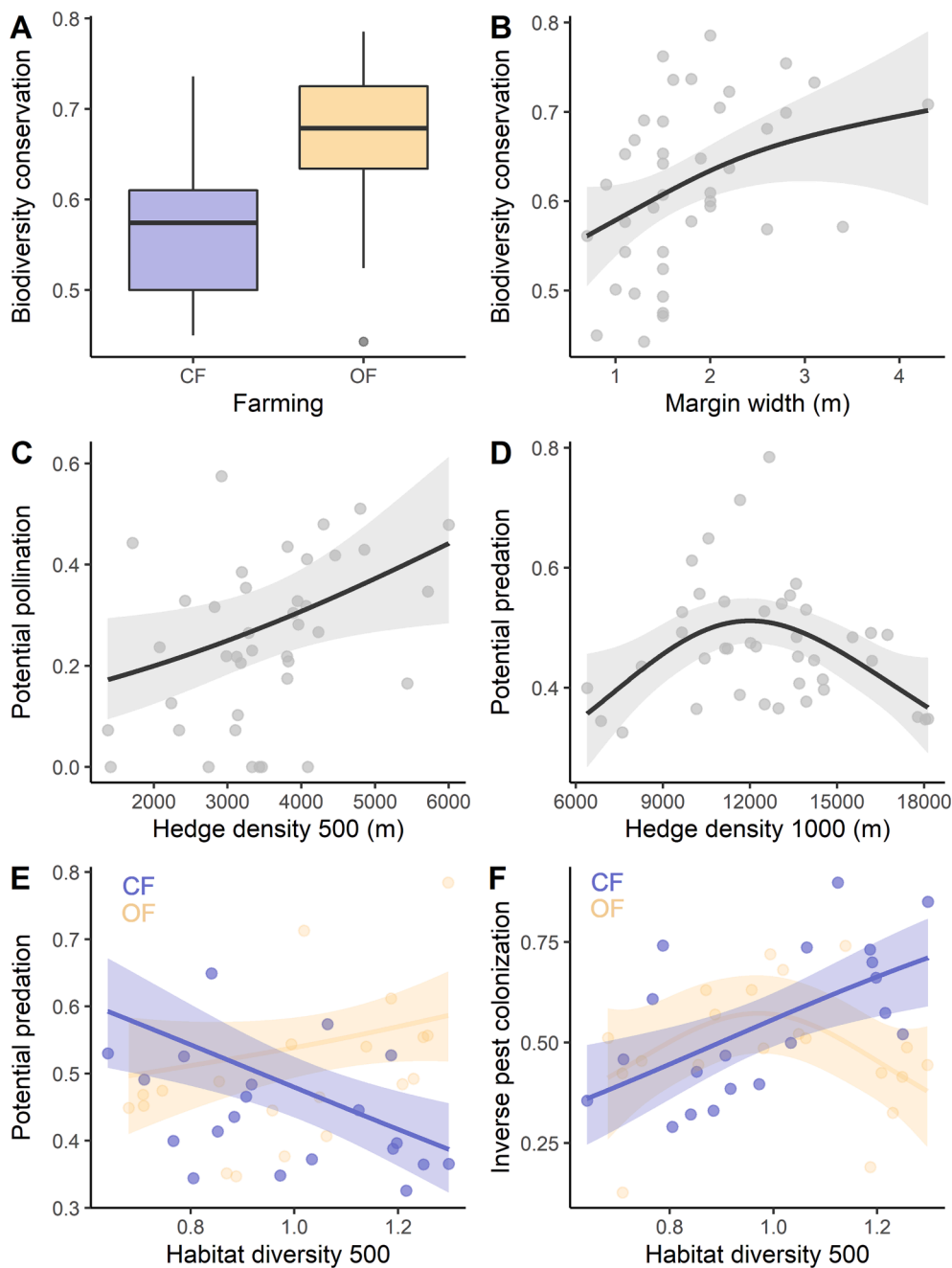


Fig. 3. Overview of the results of interaction forests and generalized additive models (GAMs) assessing the effects of hedgerow features, adjoining farming system (conventional farming CF vs organic farming OF), landscape variables, climatic parameters and interactions on the four ecological functions and the multifunctionality of hedgerows. Crosses in white squares indicate that the explanatory variable is not included in the interaction forest analysis (not measured for the corresponding taxa or no a priori hypothesis). For plotting purposes, we only represent interactions that have been selected by the interaction forest procedure for at least one ecological function.





**Fig. 4.** Drivers of the four ecological functions of hedgerows based on the results of generalized additive models (GAMs). **A)** Biodiversity conservation is higher in hedgerows adjoining organic farming (OF) systems, and **B)** in hedgerows with wider margins. **C)** Hedge density within a buffer radius of 500 m increases potential pollination. **D)** Potential predation is higher for intermediate values of hedge density within a buffer radius of 1000 m. **E)** Habitat diversity within a buffer radius of 500 m decreases potential predation, but only for hedgerow adjoining conventional farming (CF) systems. **F)** Habitat diversity within a buffer radius of 500 m linearly increases inverse pest colonization, but only for hedgerow adjoining CF systems. Raw data are represented by the dots. Shaded areas around regression curves represent 95% confidence intervals. CF = conventional farming, OF = organic farming.

within a buffer radius of 500 m (Figs. 3 & 4C; Table S6), especially Coleoptera potential pollination (Fig. S26 & S28D; Table S9). Hymenoptera potential pollination increased with canopy width and flower cover (Figs. S26, S28A & S28B; Table S7), but decreased by OF cover within a buffer radius of 250 m (Figs. S26 & S28C; Table S7). We did not find significant drivers regarding Diptera potential pollination (Fig. S26; Table S8).

### 3.3. Potential predation

Potential predation was higher for intermediate values of hedge density within a buffer radius of 1000 m (hump-shaped effect) (Figs. 3 & 4D; Table S10). Habitat diversity within a buffer radius of 500 m decreased potential predation in hedgerows adjoining CF systems, whereas it tended to increase potential predation in hedgerows adjoining OF systems (Figs. 3 & 4E; Table S10). Specifically, carabid

potential predation increased with hedgerow height (Figs. S26 & S29A; Table S11). Spider potential predation was higher in hedgerows without earth and stone banks, but increased with crop diversity within a buffer radius of 1000 m (Figs. S26, S29B & S29C; Table S12). Staphylinid potential predation was higher in hedgerows adjoining OF systems (Figs. S26, S29D; Table S13). Habitat diversity within a buffer radius of 500 m increased staphylinid potential predation, but only in hedgerows adjoining OF systems (Figs. S26, S29E; Table S13). Aphidophagous hoverfly potential predation decreased with tree cover (Figs. S26 & S29F; Table S14). On the hand, aphidophagous hoverfly potential predation was higher for intermediate values of hedge density within a buffer radius of 1000 m (hump-shaped effect) (Figs. S26 & S29G; Table S14).

### 3.4. Pest colonization

Inverse pest colonization increased with habitat diversity within a buffer radius of 500 m, but only for hedgerow adjoining CF systems (Figs. 3 & 4F; Table S15). We did not find significant drivers regarding aphid colonization (Fig. S26; Table S16). Weed colonization was lower in hedgerows with wider canopies (Figs. S26 & S30A; Table S17). Habitat diversity within a buffer radius of 250 m decreased weed colonization, but only for hedgerows adjoining CF systems (Figs. S26 & S30B; Table S17).

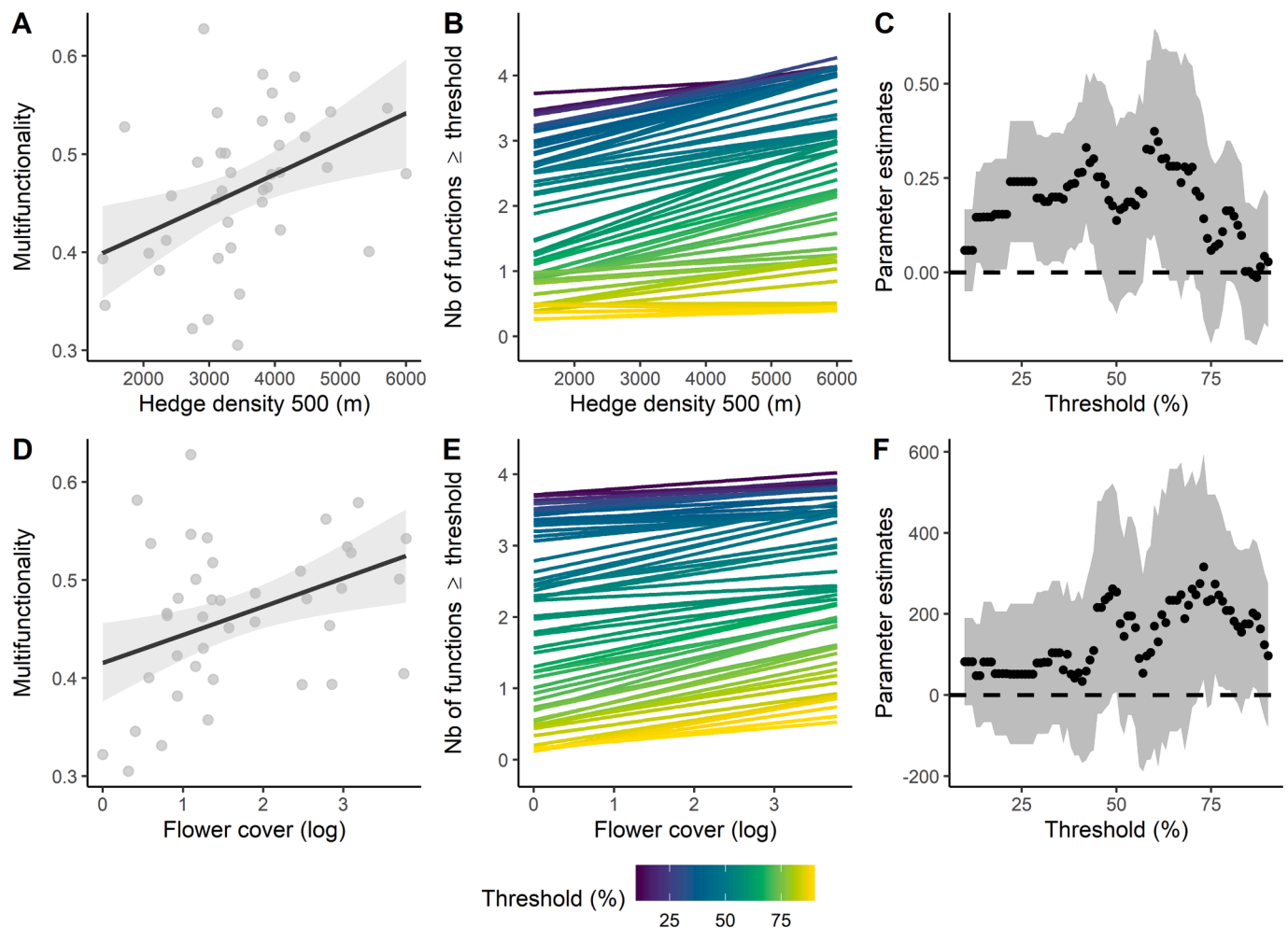
### 3.5. Multifunctionality

Averaged multifunctionality increased both with hedge density within a buffer radius of 500 m and flower cover (Figs. 3, 5A & 5D; Table S18). In addition, the multiple threshold approach indicated that hedge density increased the number of high-performing functions, especially for thresholds between 10% and 50% of the maximum observed value of each function (Fig. 5B & 5C). On the other hand, flower cover had no significant effect on the number of high-performing functions, except considering a threshold around 75% (Fig. 5E & 5F).

## 4. Discussion

### 4.1. Local variables affect individual functions of hedgerows more than their multifunctionality

We did not confirm hypothesis n°1 that taller, wider, and structurally more complex hedgerows are more multifunctional owing to increased local environmental heterogeneity and colonization events over time. Among local factors related to hedgerow features, only flower cover in hedgerows (including both herbaceous and woody plant species) stood out as a driver of hedgerow multifunctionality. However, the multiple threshold approach revealed that increased flower cover in hedgerows does not necessarily lead to increased number of high-performing functions. The effect of flower cover on hedgerow multifunctionality is rather due to its positive and saturating impact on a few indicators, namely pollinator conservation and Hymenoptera potential pollination, in line with previous studies (Alison et al., 2022; Aviron et al., 2023). Nonetheless, hedgerow features – especially those related to width and density – did affect ecological functions and indicators. In line with studies reviewed by Graham et al., 2018, margin width increased biodiversity conservation in hedgerows, likely owing to increased habitat amount and buffering of agricultural disturbances such as agrochemical drifts. Canopy width increased Hymenoptera potential



**Fig. 5.** Drivers of hedgerow multifunctionality based on the results of generalized additive models (GAMs) and multiple threshold approach. **A)** Hedge density within a buffer radius of 500 m increases hedgerow multifunctionality (averaged), and **B)** the number of functions that performs higher than a given threshold (between 10% and 90% of the maximum value of each function). **C)** Parameter estimates (slopes and 95% confidence intervals) of the relationship between hedge density and the number of functions reaching given thresholds. The relationship is significant mostly for thresholds between 10% and 50% (confidence intervals do not overlap with 0). **D)** Flower cover increases hedgerow multifunctionality (averaged). **E)** On the other hand, the effect of flower cover on the number of high-performing functions is low and generally **F)** not significant. Raw data are represented by the dots. Shaded areas around regression curves represent 95% confidence intervals.



pollination and reduced weed colonization, probably by improving plant-pollinator networks. Indeed, hedgerows with wider canopies provide enhanced habitat and trophic resources in space and time for Hymenoptera pollinators (Donkersley, 2019), and environmental conditions that favour rarer plant species over common weeds (Boinot and Alignier, 2023). Further, carabid conservation increased in hedgerows with wider canopies and higher diversity of woody plant species, and carabid potential predation increased in hedgerows with tall trees. More complex hedgerows could provide a diversity of environmental conditions (e.g., shade, moisture, microhabitats) for carabid species with different ecological preferences (Maudsley et al., 2002; Précigout and Robert, 2022). In addition, complex hedgerows are probably more ancient, making colonization events more likely over time (Gruttko and Kornacker, 1995), especially regarding carabid species with poor-dispersal abilities (Griffiths et al., 2007). On the other hand, hedgerow features had little influence on spiders and staphylinids, probably because we did not sample predatory arthropods in shrub and tree layers where they can be dominant (Pollard and Holland, 2006). Therefore, we most likely underestimated the abundance and diversity of these predators in complex hedgerows.

We could not confirm hypothesis n°2 that hedgerows adjoining organic farming (OF) fields are more multifunctional owing to reduced agricultural disturbances such as agrochemical drifts (chemical fertilizers and pesticides). However, adjacent OF affected some ecological functions and indicators. Notably, OF increased biodiversity conservation in hedgerows, especially plant conservation as shown by previous studies (Aude et al., 2003; Boutin et al., 2008; Boinot and Alignier, 2022). Spider conservation also reached highest values in hedgerows adjoining OF systems combined with warmer temperatures during sampling, probably owing to higher plant diversity providing web-building habitats and decomposer or phytophagous prey (e.g., Haughton et al., 1999; Diehl et al., 2013). These results show that agricultural disturbances have a strong negative impact on the diversity, more than the abundance, of plants and arthropods in hedgerows. In some cases, agricultural disturbances can even increase arthropod abundance, given that agrotolerant species are often r-strategists with high fecundity (Jeschke et al., 2008; Bohn et al., 2014).

#### 4.2. Landscape variables related to semi-natural habitats are key to hedgerow functioning

We could partly confirm hypothesis n°3 that hedgerow multifunctionality increases in more complex and diversified landscapes. Indeed, hedgerow density in the landscape increased both averaged multifunctionality and the number of high-performing functions in hedgerows. This is likely the result of various ecological processes. First, a greater density of hedgerows in the landscape provides a greater amount of habitat for associated species. Second, hedgerow density is probably related to the connectivity between hedgerows (and other habitats) in the landscape, which provides ecological corridors for the dispersal and reproduction of individuals (e.g., Petit and Burel, 1998; Mony et al., 2022). Third, landscapes with dense hedgerow networks are characterized by greater abiotic and biotic environmental heterogeneity (Forman and Baudry, 1984; Moreno et al., 2018), a key driver of biodiversity favouring coexistence between species (Stein et al., 2014). Hedgerow density in the landscape increased hedgerow multifunctionality notably through increased potential pollination (especially for Coleoptera). This result supports previous studies showing that the preservation of hedgerow networks promotes pollinator colonization and persistence (Ponisio et al., 2019), and could provide suitable microclimatic conditions for those insects (Le Féon et al., 2013). On the other hand, we found that potential predation was higher in landscapes with intermediate values of hedgerow density (especially for aphidophagous hoverflies), which suggests that highest densities prevented the movement of some predators (a barrier effect as evidenced by e.g., Mauremooto, 1995) or homogenise their distribution across the

landscape (i.e., a dilution effect). Increased predation by higher trophic taxa such as birds could also explain this hump-shaped effect (e.g., Martin et al., 2013).

Other landscape variables did not impact hedgerow multifunctionality, but did affect individual functions. Interestingly, habitat diversity in the landscape (highly correlated with the cover of semi-natural habitats) reduced potential predation in hedgerows adjoining CF fields. Other semi-natural habitats in diversified landscapes were probably more attractive for predators than hedgerows with chemical disturbances and low plant diversity (Otto et al., 2009; Boinot and Alignier, 2022). On the other hand, habitat diversity tended to increase potential predation in hedgerows adjoining OF fields, especially for staphylinids, indicating that predators benefiting from diverse semi-natural habitats more efficiently colonized hedgerows adjoining OF fields. Simultaneously, habitat diversity reduced pest colonization in hedgerows adjoining CF fields (same trend for weeds and aphids), providing support for the “resource concentration hypothesis” (Root, 1973). Most likely, semi-natural habitats in diversified landscapes act as barriers to the dispersal of main crop pests (O’Rourke and Petersen, 2017), and may even mitigate agrochemical drifts, thereby limiting the establishment of nitrophilous and herbicide-tolerant plant species (Fried et al., 2018; Boinot and Alignier, 2023).

We could not confirm hypothesis n°4 that hedgerow multifunctionality increases in landscapes with higher OF cover, which had little influence on ecological functions and indicators. On the contrary, we found that OF cover reduced potential pollination in hedgerows. This could be explained by resource dilution in the landscape and spillover from hedgerows towards OF crop fields that harbour more abundant and diverse floral resources at the time of sampling (e.g., weeds, legumes intercropped with cereals) (Ragué et al., 2022). All in all, we found that landscape variables related to semi-natural habitats (hedgerow density, habitat diversity) more than those related to farming practices (crop diversity, OF cover) are important drivers of local hedgerow functioning. However, we suspect farming practices at landscape scale can have a strong impact on the multifunctionality of the whole hedgerow network, but only studies using mosaic-level sampling could provide information in this regard (e.g., measuring beta- and gamma-diversity at the landscape scale) (Bennett et al., 2006).

#### 4.3. More synergies than trade-offs between the functions of hedgerows

We could partly confirm hypothesis n°5 that there are mostly synergies between the ecological functions of hedgerows. We found weak correlations between the four ecological functions of hedgerows (biodiversity conservation, potential pollination, potential predation, and pest colonization), and overall few drivers in common. Only hedgerow density in the landscape increased both average multifunctionality and the number of high-performing functions. We also find some synergetic responses regarding ecological indicators. For example, hedgerows with wider canopies had higher potential pollination by Hymenoptera and lower weed colonization. Flower cover in hedgerows increased both pollinator conservation and potential pollination by Hymenoptera. OF at local scale promoted plant conservation and potential predation by staphylinids. The absence of strong trade-offs implies that we can use different levers to enhance individual functions of hedgerows and ultimately their multifunctionality. The only trade-off we observed was between potential predation and pest colonization. As discussed in the previous section, landscape habitat diversity reduced pest colonization, but also potential predation, in hedgerows adjoining CF fields. Predator-prey cycles might explain the mutual reduction of pest and predator abundances. However, it is also possible that increased presence of diverse semi-natural habitats changed the distribution of predators (reduction of local abundance but better representation at landscape scale), whereas it reduced pest colonization at both local and landscape scales through the reduction of source habitats (crop fields) and agricultural disturbances.

#### 4.4. Future research on hedgerow multifunctionality

The multifunctional approach has proven to be very useful in detecting important variables that may not be apparent using single-taxon approaches. We found contrasted responses of taxa to hedgerow features, highlighting that we cannot describe hedgerow quality with a single environmental descriptor or biodiversity indicator, in line with previous multi-taxon studies on herbaceous field boundaries (Ekroos et al., 2013) and farmland-forest edges (Sálek et al., 2015). Nonetheless, we found evidence that more complex, wider and probably more mature hedgerows support higher level of biodiversity, benefit some pollinator and predator taxa, and can mitigate weed colonization. Most importantly, we show that the preservation of hedgerow networks is key to hedgerow multifunctionality based on ecological functions. This result suggests that restoration and replanting programmes are more likely to succeed if newly planted hedgerows are inserted into existing hedgerow networks. Unfortunately, ongoing hedgerow loss jeopardizes restoration and replanting efforts. In France, the destruction of hedgerows has even accelerated in recent years, with an average annual erosion of 23.500 km between 2017 and 2022, compared with 10.400 km between 2006 and 2014 (de Menthière et al., 2023). Recently planted and isolated hedgerows (often along roadsides) are unlikely to compensate for mature and well-connected hedgerows and established biodiversity, at least for decades provided that populations or species and associated ecological functions are not irretrievably lost. Importantly, higher density of hedgerows in the landscape should also promote belowground biodiversity of prime importance for nutrient cycling, carbon storage and water regulation, owing to the local formation of litter, humification, soil porosity and fertility (e.g., van Vooren et al., 2017; Holden et al., 2019; González Fradejas et al., 2022), but also through the favourable modification of pedoclimatic variables at the landscape scale (Forman and Baudry, 1984; Benhamou et al., 2013). In addition, hedgerow landscapes are known for their agronomic functions (e.g., sheltering for domestic animals, timber wood and fruit production) and cultural services (e.g., aesthetic value, education, arts, sports) (Forman and Baudry, 1984; Moreno et al., 2018; Montgomery et al., 2020). On the other hand, a higher density of hedgerows requires more management work and associated costs (Groot et al., 2010). There is a need to go beyond the evaluation of local and ecological functioning, by assessing the effects of the density and quality of the whole hedgerow network on landscape-scale multifunctionality (Boinot et al., 2022), including agronomic and cultural functions.

Another major issue is to determine how hedgerows affect agro-ecological functioning in adjoining crop fields. Many studies have described the effects of hedgerows (considered as one habitat category) on ecological functions in adjoining crop fields, often with contrasting results as reviewed by Précigout and Robert (2022). We show that not all hedgerows are identical in their functionality, which depends on a diverse list of factors – from hedgerow features to landscape contexts. Future studies assessing the effects of hedgerows on cropland biodiversity or functioning should account for such variability. Our results also call for a more integrative approach using mosaic-level sampling to better understand the ecological processes at play at the landscape scale, i.e., the processes driving the movements of organisms between hedgerows and other habitats, and the relationships between hedgerow and cropland multifunctionality.

#### CRedit authorship contribution statement

**Sébastien Boinot:** Formal analysis, Visualization, Writing – original draft. **Audrey Alignier:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. **Julien Pétilon:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Aurélien Ridet:** Investigation, Writing – review & editing. **Stéphanie Aviron:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing

– review & editing, Supervision.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

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