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Farmland biodiversity benefits from small woody features

Clément Vallée^{a,*}, Isabelle Le Viol^b, Christian Kerbiriou^b, Yves Bas^{a,c}, Frédéric Jiguet^a, Karine Princé^a

^a Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, 43 rue Buffon, Paris 75005, France ^b Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, Station Marine, Quai de la Croix, Concarneau 29900, France ^c CEFE, Univ Montpellier, CNRS, EPHE, IRD, 1919 route de Mende, Montpellier 34090, France

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ABSTRACT

Although positive effects on biodiversity of woody features in agricultural landscapes are widely recognized, questions remain as to which landscape context to prioritize their implementation and in what proportion. To investigate the response of farmland biodiversity to small woody features (SWF) density in different landscape compositions (cropland, grassland, mixed), we analyzed fine-resolution data from standardized monitoring schemes on 111 birds, 22 bats, and 25 bush cricket's species, at national scale (relying on 3772, 834 and 727 monitoring points) over the period 2015–2019, in metropolitan France. We used Generalized Additive Mixed Models to analyze population and community responses, through different metrics (abundance, species diversity, and functional composition). We found a positive response exhibited by the three taxa to SWF, more especially in cropland where the SWF density is the lowest relative to grassland and mixed landscapes. Also, our results suggested a non-linear response common to the three taxa, with an increased benefit up to at least 6 % of SWF density in cropland, and beyond for most of the metrics but to a lesser extent (e.g., maximum abundance reached at 7–12 % SWF). We note, however, that some species among farmland bird specialists are negatively impacted by SWF. Overall, we emphasize the benefits to promote woody features in agricultural landscapes, notably in cropland, to support biodiversity and its associated ecosystem functions. Our study provides crucial empirical evidence to the recommendations from previous studies and the relevance of the EU Biodiversity Strategy for 2030 to dedicate at least 10 % of farmland to high-diversity landscape features.

1. Introduction

Agriculture is the most dominant land use in the European Union (39.1 % of the EU-28 area, Eurostats, 2018), and despite some farming types important for supporting biodiversity (such as extensive grazing or traditional orchards; Price, 2013) and 41 types of farmland habitat included in Annex I of the Habitats Directive (Halada et al., 2011), agricultural intensification processes are recognized as a main cause of biodiversity loss and ecosystem degradation (ECA, 2020). Yield maximization is achieved, in fact, at the expense of other services that agroecosystems can provide, such as carbon storage, water purification, pollination, natural pest control, soil productivity (IPBES, 2019). Moreover, a drastic decline of farmland biodiversity has been well documented for the past five decades for several taxa such as birds, bats or insects, especially in Europe (Gregory et al., 2019; Williams-Guillen et al., 2016; Outhwaite et al., 2022), through reductions of species abundance/density (Kleijn et al., 2011), biotic homogenization (Doxa et al., 2012) and species extinctions (Maxwell et al., 2016). These trends have been largely associated with the intensification of agriculture, acting at multiple spatial scales (Butler et al., 2007; Emmerson et al., 2016; Jeliakov et al., 2016) notably through (i) the intensification of farming practices (e.g. soil tillage, fertilizers and pesticides use; Robinson and Sutherland, 2002; Bengtsson, 2015; Humann-Guillemot et al., 2019), (ii) the reduction of crop diversity, (iii) an increase in field size and a decrease in diversity and amount of semi-natural habitats in particular the removal of agricultural landscape features (e.g. hedgerows, ponds, small woodland, fallows, terraces, dry-stone or earth walls; Czucz et al., 2022b).

Among these landscape elements, small woody landscape features (SWF; hedgerows and small patches of trees) are of primary importance to maintain biodiversity in farmland (e.g., birds: Siriwardena et al., 2012; birds and plants: Concepcion et al., 2020). They contribute to

farmland connectivity through dispersal corridors (Davies and Pullin, 2007) utilized by several taxa, including mobile species such as bats (Pinaud et al., 2018) and birds (Mortelliti et al., 2010). SWF also provide or support a number of ecosystem services (e.g. wood production, carbon sequestration, mitigation of soil erosion, pollination, natural pest control; Falloon et al., 2004; Hinsley and Bellamy, 2000).

However, SWF - and hedgerows in particular - have undergone serious decline in Europe for decades (Sklenicka et al., 2009). In France, where agroecosystems cover up to half the territory (Agreste, 2020), 70 % of the linear hedge has disappeared from bocages since the 1950s (de Menthiere et al., 2023), partly due to the increase in plot size to facilitate the mechanization of agriculture and the availability of alternative fencing. Far from being halted, the trend has accelerated in recent years with an average annual loss of “23,571 km/year between 2017 and 2021”, compared with “10,400 km/year between 2006 and 2014” (de Menthiere et al., 2023), not compensated by the only 3000 km being replanted every year. Protecting and increasing these small woody features is therefore a major challenge in reconciling agricultural production and biodiversity conservation (Sklenicka et al., 2009), that policy tries to face through a number of measures and targets in some major EU sectoral policies, such as the Common Agricultural Policy especially through the Eco-Schemes, the EU Biodiversity Strategy to 2030 (EU BDS) and the European Commission proposal for a Nature Restoration Law (NRL) - recently adopted by the European Parliament through a tight vote (in July 12, 2023), and now under negotiations between EU Institutions. However, the effectiveness of AES to secure biodiversity is still under debate across Europe (Kleijn et al., 2011; Prince et al., 2012; Kleijn et al., 2019), and several assessments found that, overall, AES are not fulfilling their goals (Pe'er et al., 2017; Pe'er et al., 2019). The CAP 2023–2027 has a potential to support landscape features through Eco-Schemes (e.g. commitments to create hedgerows, seeded fallows, field margins), Agri-Environment-Climate measures, and under GAEC 8 (Good Environmental and Agricultural

* Corresponding author at: Centre d'Ecologie et des Sciences de la Conservation, Muséum National d'Histoire Naturelle, 43 rue Buffon, Paris 75005, France. E-mail

address: valle.clement@wanadoo.fr (C. Vallée). <https://doi.org/10.1016/j.biocon.2023.110262>

Condition), which prescribes a “minimum share of agricultural area devoted to non-productive areas or features” (either 4 % or 7 % if some productive elements are included), as well as the “retention of landscape features”, a “ban on cutting hedges and trees during the bird breeding and nesting season”, and “as an option, measures for avoiding invasive plant species” (Czucz et al., 2022a). The EU BDS sets as one of its targets to bring back at least 10 % of agricultural area under high-diversity landscape features, and the NRL proposal identifies for Member States the target to achieve an increasing trend at national level of share of agricultural land with high-diversity landscape features, until a satisfactory level is reached. Nevertheless, empirical evidence to the relevance of these policy targets to support multi-taxon biodiversity in agricultural areas are scarce (but see Jeanneret et al., 2021).

At local-scale, benefits from SWF have been shown to be potentially context dependent (Batary et al., 2010; Concepcion et al., 2020). For instance, Besnard and Secondi (2014) found that hedgerows diminished benefits from meadows for grassland passerine birds. On scale, Concepcion et al. (2020) found that tree groups and isolated trees support overall bird diversity only in some regional arable or mixed farming systems, but not in the studied pastures systems. However, conducting exhaustive tests at national or European scales, covering large and multiple landscapes composition areas, is still needed to establish effective recommendations at the scale of application, e.g., eco-schemes and Pillar 2 agri-environment-climate commitments (CAP 2023–2027) in the EU. It is indeed important for prioritization and effectiveness of interventions to be aware that their positive impact may be reduced (or even reversed) depending on landscape context. Farmland biodiversity is also known to respond non-linearly to the complexity of agricultural landscapes (Concepcion et al., 2008; Concepcion et al., 2012). However, the non-linearity of this relationship has rarely been explored. Concepcion et al. (2012) found hump-shaped relationships between the length of semi-natural boundaries and richness of birds, bees, spiders and plants (semi-natural vegetation including woody features along with other features such as grass margins). A specific focus on SWF is still lacking though, probably due to a lack of sufficient high-quality data so far. Defining optimal SWF density thresholds could help practitioners and land managers to prioritize management interventions and ensure that they are as cost-effective as possible. Such optimal density thresholds can also help identify global environmental tipping points (Oliver et al., 2015), but can hide strong intertaxa and intrataxon response differences (Concepcion et al., 2008). First, intertaxa threshold values differences can emerge from various home range-size linked to their respective body weights (Borger et al., 2008). For instance, bush cricket could be affected by SWF on a smaller scale (Reinhardt et al., 2005) compared to bat (Frey-Ehrenbold et al., 2013). The identification of an optimal SWF density value is therefore crucial to define a relevant target (Primdahl et al., 2010), but requires prior confirmation of its relevance to farmland biodiversity, through a multi-taxa study (Batary et al., 2020). Then, intra-taxa differences require consideration of different measures of biodiversity and community composition to highlight if a trade-off between species does not emerge in response to these SWF and if some particular functional traits are involved (Birkhofer et al., 2015). For instance, the average habitat specialization of birds can be expected to decrease with SWF density, as farmland birds specialists has been shown to be negatively impact by SWF (e.g., in regional arable system in Spain, Concepcion et al., 2020), which would not be demonstrated using abundance or species richness measures alone (Filippi-Codaccioni et al., 2010). To help policy makers proposing biodiversity targets and interpreting biodiversity projections in future land use scenarios, and land managers to increase the effectiveness of interventions, it is thus crucial to identify which species pool benefits (or not) from SWF, and to develop a diversity of measures that encompass the different needs of these farmland communities.

To address these important knowledge gaps on the response of farmland biodiversity to SWF, large-scale multi-taxa datasets covering multiple landscape compositions are needed. In this study, we relied on three datasets from nation-wide citizen monitoring schemes covering three different

taxonomic groups: common birds, bats and bush-crickets, representing multiple trophic levels (herbivores, insectivores, predators), functional groups (e.g., pollination and pest control services), species traits (e.g., diurnal/nocturnal activity, body size), and conservation status. In addition, we used a fine-resolution mapping of SWF density at the scale of Metropolitan France, which presents a diversity of agroecosystems (Prince et al., 2012). We analyzed the variation in abundance, taxonomic and functional diversity of the three taxa along a gradient of SWF density, in different agricultural landscapes (croplands, grasslands and mixed landscapes) accounting for the effects of other anthropogenic pressures. Specifically, we expected that the benefit from an increase in SWF density is context-dependent, with a stronger benefit in cropland than in other agricultural landscapes, consistently with the “intermediate landscape-complexity hypothesis” (H1), follows a non-linear relationship with optimal SWF thresholds (H2), that differs among taxa (H3a), and among intra-taxon metrics, possibly reflecting an intrataxon compositional shift mediated by species traits (H3b).

2. Material & methods

2.1. Biodiversity data

We used bird data collected by the French Breeding Bird Survey (FBBS), a standardized monitoring scheme in which observers (volunteer ornithologists with acknowledged expertise) survey breeding birds in randomly selected 2 × 2-km squares (hereafter, FBBS plots), by counting birds at 10-point counts, 5 min each, twice per spring. See Jiguet et al. (2012) and Appendix A for details. We considered abundance data for 111 most common breeding bird species (Table A.1; Appendix A) from 2015 to 2018.

We used activity data for bats and bush-crickets collected through standardized passive acoustic monitoring at “stationary points” by the French

index measures the mean degree of habitat specialization among the individuals forming a local community. It is based on the Species

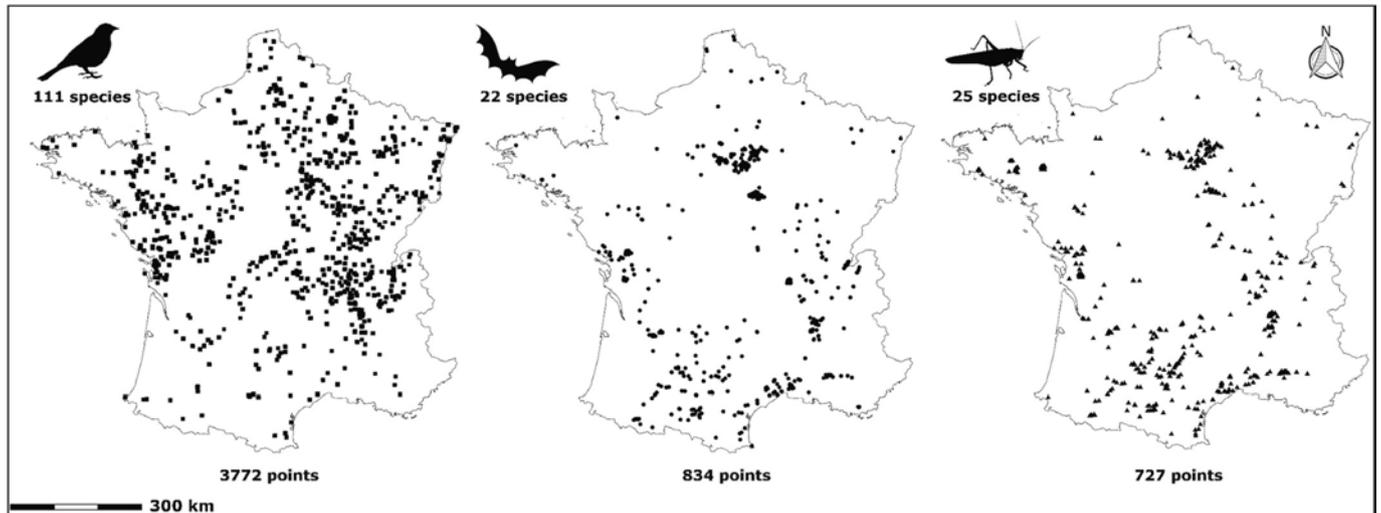


Fig. 1. Spatial distribution of selected monitoring points for common birds, bats and bush-crickets.

Bat and Orthoptera Acoustic Monitoring Programs (Vigie-Chiro and SON). Species recognition was performed using the Tadarida software (Bas et al., 2017). We used activity data (log-transformed) from May to July for 22 bat species, and from mid-June to mid-October (as in Newson et al., 2017) for 25 bush-cricket species over the period 2015–2019. We only retained the recordings for which the weather conditions were favorable (see Appendix A for details). Also, the number of temporal replicates of each monitoring point being too low to efficiently account for pseudo-replication, in case of a repeated temporal sampling from the same point, we kept a single record (the closest from the year 2015; source year of SWF data; see Appendix A for details). As acoustic data activity provides good proxies of relative abundance (Hundt et al., 2012; Mimet et al., 2020), we refer to it as abundance for better readability in the results of the three taxa hereafter.

The focus of analysis being on agricultural areas, we only kept count points surveyed within agricultural habitats at both local level (see Appendix A) and landscape level (see Section 2.4). The final dataset represented a total of 3772 unique monitoring points for birds, and respectively 834 and 727 for bats and bush-crickets (see spatial distribution in Fig. 1).

2.2. Community metrics

To better understand the underlying effects of SWF density on farmland biodiversity (H3), we assessed its effect on taxonomic diversity, using the Simpson diversity index (Simpson, 1949), but also on functional diversity. For this, we relied on the community-level weighted means approach (Lavorel et al., 2008) to compute these functional composition metric:

- 1) *the average trophic level*, with the Community Trophic Index for birds (CTri; Princ'e et al., 2013). The CTri discriminates between communities with more granivorous species (e.g., low trophic level), and communities with more insectivorous and carnivorous species (e.g., high trophic level). Species trophic level is determined on the basis of the three diet proportions (seeds, invertebrates and vertebrates, with weights of 1, 2 and 3, respectively) of each species (BWPI, 2006). For bush-crickets we used the Community Body Length Index (CBLI; based on Bellmann and Luquet, 2009), based on species body length ranging from 13.5 to 35 in mm, as the trophic level was not documented for this taxon, with the assumption of an upper position in the food web for larger species (Whitman, 2008). As all European chiropteran species are insectivorous, we did not calculate a trophic food average level for this taxon.
- 2) *the average habitat specialization*, with the Community Specialization Index for birds and bats (CSI; Julliard et al., 2006; Dubos et al., 2021). This

Specialisation Index SSI (ranging from 0.2 to 3 in birds and 0.8 to 5.4 in bats species) expressed as a coefficient of variation of species' abundance across different habitats, for each species (Filippi-Codaccioni et al., 2010). Homogenization of biotic communities often results in the disappearance of specialist species, thus the higher the CSI, the less homogenized the communities are (Clavel et al., 2011).

These indices were chosen in reference to energy and niche partitioning, with the assumptions that (i) The higher the trophic level of the community, the better the state of biodiversity (Soliveres et al., 2016); (ii) The higher the specialization of the community, the higher the “farmland” community is proportionally composed of species at risk as farmland specialist species are particularly declining (Gregory et al., 2019, see Table A.1 for the list of farmland specialists species). All these four indices were calculated with the R package vegan (Oksanen et al., 2020).

2.3. Small woody features data

To assess the large-scale landscape impact of small woody features, we used the 2015 HRL Small Woody Features (SWF) product from Copernicus Contributing Missions (CCMs, 1:5000 initial resolution across all EEA39 countries).

SWF includes woody linear structures such as hedgerows, scrubs or tree rows along field boundaries, riparian, roadside vegetation and isolated patches of trees and scrub ($200\text{m}^2 \leq \text{area} \leq 5000\text{m}^2$). Specific geometric rules (width, length, compactness and area) are applied to ensure that the selected features are included in this definition (see Appendix A for details). Consequently, this dataset excludes stone walls, drainage ditches, grass margins, field boundaries without hedgerows or trees, roads or artificial tree rows (e.g., vineyards, orchards). Linear or patchy structures within open forest are also excluded. Spatial distribution of SWF gradient over the French territory is presented in Fig. A.1.

We extracted the SWF density (as a percentage) at 500 m around each monitoring point in the main analysis. We also extracted it at 300 m, 1 km and 10 km as sensibility analysis to this buffer size choice (see details in Section 2.6 and Appendix C).

2.4. Agricultural landscape compositions

To assess the effect of SWF density according to the main composition of agricultural landscapes (H1), we distinguished points according to their main agricultural landscape composition: cropland, grassland and mixed. To do so, we relied on a similar methodology as the Landscape Mosaic indicator, a

tripolar classification of a location accounting for the relative contributions of three land cover types (Riitters et al., 2009, 2020). We first extracted the percentage of the 44 land cover classes in a 1-km buffer around each monitoring point using the Corine Land Cover 2018 product with an initial resolution of 250 m; this year was chosen as it was the closest to the temporal coverage of the biodiversity and SWF datasets. We excluded all monitoring points where the joint percentage of agricultural landscapes (CLC Class 2: arable land, permanent crops, pastures, heterogeneous agricultural areas) did not exceed 60 %, (as mentioned in Section 2.1). We then classified each monitoring point according to their dominant agricultural landscape (>60 %) among “cropland” and “pastures” (hereafter referred to as grassland) and classified other monitoring points that did not have specific dominance as “Mixed”. In total, we had three categories of landscape: “cropland”, “grassland” and “mixed”. Spatial distribution of the dominant agricultural landscapes at national level is also presented in Fig. A.1.

For birds, as the number of monitoring plots was higher than for the other two taxa, we were able to identify minor secondary dominance (>20 % cropland or grassland). We considered these two additional categories “dominant cropland and minor grassland” and “dominant grassland and minor cropland” (see Table A.2 for the repartition of points in these categories) for complementary analyses (see Fig. C.1).

2.5. Other environmental data

We extracted several other environmental variables known to influence abundance of birds, bats or bush-crickets. As their populations and communities are known to be influenced by climate conditions (Güzere et al., 2015; Vaughan et al., 1997; Skinner and Child, 2000), we extracted annual mean temperature (min = 10.5, mean = 16, max = 23.1 in degree Celsius; Jiguet et al., 2010) and mean monthly precipitation over the period May–July (min = 0.9, mean = 3, max = 13.2 in mm; Illan et al., 2014), per site, using the European climate raster (E-OBS) provided by ECA&D at 10-km resolution, and the R-package climateExtract (Schmucki, 2022). We also excluded topographical variability (see Appendix A, <500 m monitoring points were excluded).

In addition, we extracted other environmental covariates known to strongly influence the crepuscular and nocturnal activity of bats and bush-crickets: average temperature of the day (min = 7.3, mean = 20.6, max = 30.8 in degree Celsius), wind speed (at 6 p.m. of the survey days, min = 0, mean = 3.9, max = 10 in meters per second), Julian day (Mariton et al., 2022; Froidevaux et al., 2019a, 2019b; Newson et al., 2017). We also used the distance to the nearest water bodies (min = 1, mean = 803, max = 6619 in meters including lakes, ponds, sea, etc.) as a specific important variable for bat communities (De Conno et al., 2018). We also initially used the effect of urban area (in percentages, in a 1 km- buffer size, using 2018 CLC product) and light pollution from Elvidge et al., 2021 as covariates (using the same 1 km-buffer size) to synthesize anthropogenic pressures. As these variables were not significant (or negligible effect that does not affect the detective SWF pattern), we did not include them in the final analysis (but see Appendix B, Fig. B.1).

2.6. Statistical analysis

We used generalized additive mixed models (GAMMs) to study the effects of SWF density on birds, bats, and bush-crickets, as a function of agricultural landscape composition.

GAMMs are particularly suitable for exploring (1) the existence of a relationship between our community metrics and SWF, and (2) illustrating the form of this relationship (linear or nonlinear). To assess the impact of SWF on the three taxa, we fitted models at population (models “A”) and community (models “C”) levels, as follows:

- (1) Model “A”, where the dependent variable is the abundance of each species, per count point. For bird observations, to avoid temporal

pseudo replication associated with a very high computational cost, in case of temporal replicates at the same monitoring point, we averaged the abundances over the period 2015–2018, for each species, at each point. For the three taxa, the species identity was included as a random effect in order to consider variation in abundance among species. For birds, we also included a nested random effect of count point within FBBS plot, to account for hierarchical sampling. For bats and bush-crickets, we included the year as a random effect to account for the temporal structure of the datasets. All models followed a Tweedie distribution adapted to non-integer counts, as in our case with averaged abundances (birds) or log-transform activity (bats, bush-crickets). The name of these models follows this logic: *Abirds*, *Abats*, *Acrickets*.

- (2) Model “C”, where the dependent variable is a community metric (Simpson, CSI, CTrI, CBLI). For birds, as in model *Abirds*, we included a nested random effect of count point within FBBS plot. We also included the year as a random effect to account for temporal pseudo replication. For bats and bush-crickets, we only included Year as a random effect.

These models followed a normal distribution. The name of these models follows this logic: *Cbirds* for (Simpson index), *CSibats* or *CBLIcrickets*.

To assess whether the effect of SWF on biodiversity is context dependent (**H1**), in all models, we considered the interaction between SWF density and agricultural landscape composition (Landscape Mosaic categories), as well as landscape composition alone, as fixed effects. We also explored the potential non-linear effect of SWF within the different agricultural landscapes, by allowing a smooth effect on the interaction (**H2**). We included all environmental variables (see Section 2.5 for details) as smoothed, fixed effects to account for spatial structure of the data (except for distance to nearest water bodies in bats models as we had a strong initial hypothesis with a log link). We used penalized cubic regression splines to compute smooth terms (as this is the most suitable for large datasets; Wood, 2017) with a shrinkage penalty to also perform variable selection by setting zero effect for non-significant variables, using R package mgcv (Wood, 2022).

In the case where the SWF effect was non-linear (**H2**), we computed the value of the breaking point between the predicted values of the metric and the values of SWF density, using the *segmented* function of the package of the same name (Muggeo, 2023). We also measured the maximum predicted value as it can be slightly different from the breaking point (or minimum in case of a negative effect). We computed the SWF density at a 500 m buffer for two main reasons. First, this buffer size has been shown by previous studies to be relevant to assess the impact of semi-natural landscapes features for these taxa (e.g., Concepcion et al., 2008; Concepcion et al., 2012; Froidevaux et al., 2019a, 2019b). Second, we used this buffer size as it is close to the average area of a French farm (69 ha, Agreste, 2020) and thus our results are most easily interpretable in terms of conservation. However, we ensured that the results remain consistent and not sensitive to the buffer size choice (500 m) when considering other scales (300 m, 1 km), as some differences could arise from the range of dispersal or body size among distinct taxa (Concepcion et al., 2008), detailed in Appendix C). Additionally, we tested for the detection of a significant effect of SWF density at a much larger scale, using a 10 km-buffer size (see Appendix C).

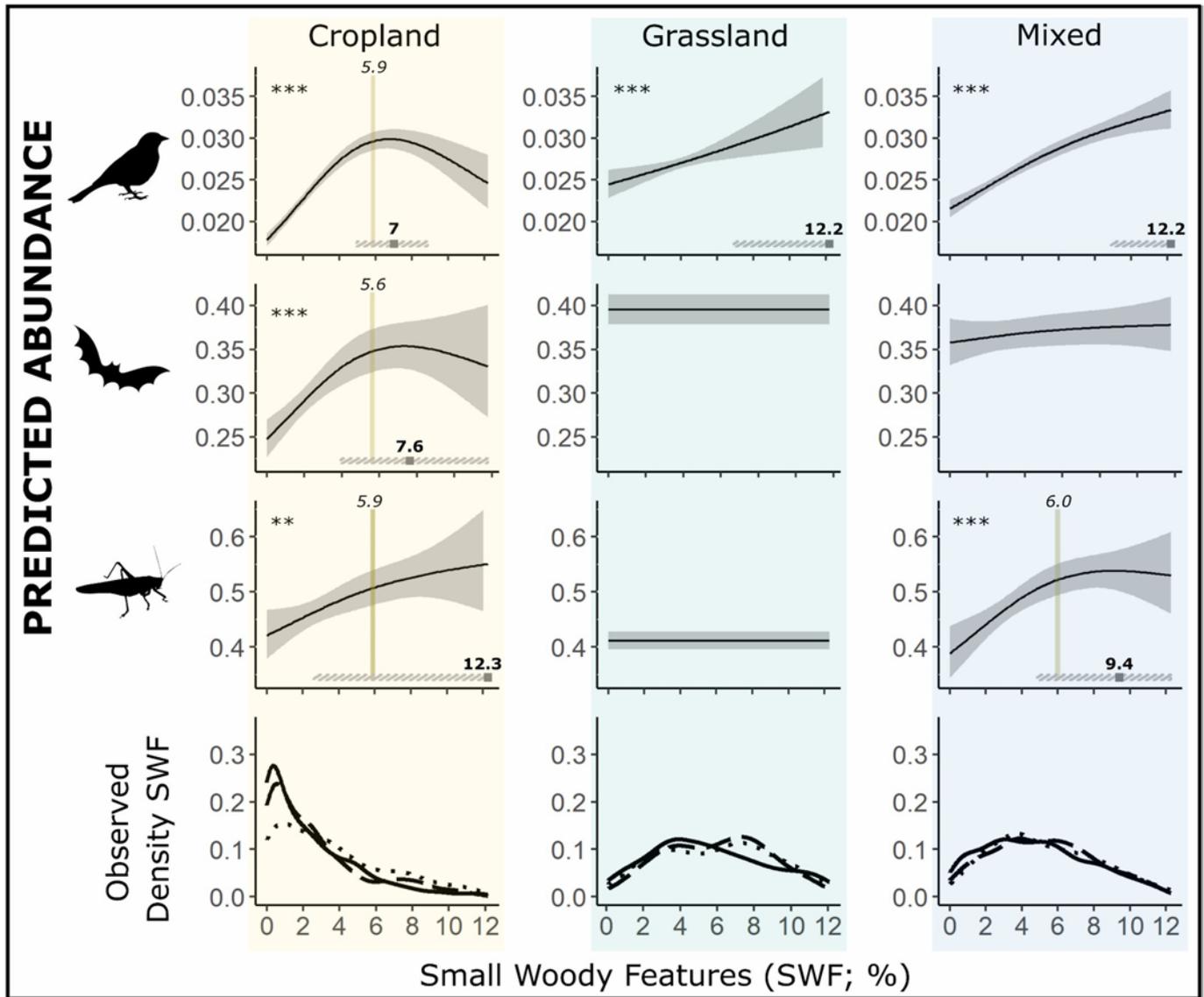


Fig. 2. Predicted abundances of the three taxa as a function of increasing SWF density, in different agricultural landscape compositions. The green-vertical and gray- horizontal lines respectively represent the breakpoint value and the maximum estimated value (and 95 % confidence interval). In observed SWF density plots, line types represent the different datasets (dots = birds, long-dashes = bats, solid = bush-crickets). Estimated effective degree of freedom and linear SWF coefficient with p - values associated are shown in Table C.1–2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

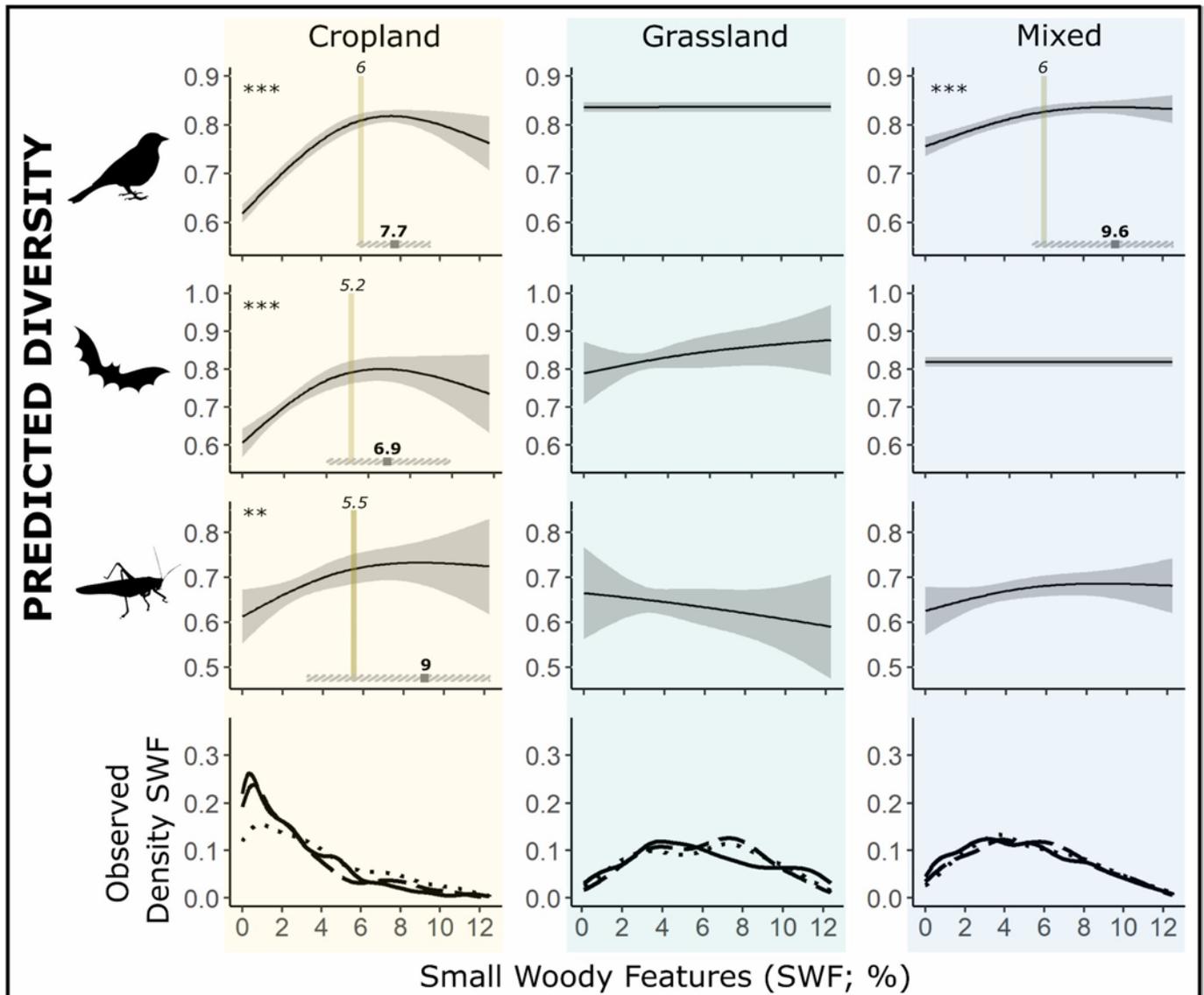
Overall, among the 30 tests of the effect of SWF density on abundance, species diversity and functional composition (CSI, CTrI, CBLI metrics), we detected mostly significant positive linear effects ($n = 12$ out of 30), while significant negative effects were scarce ($n = 3$) (Table C.1). As expected (H1), the benefit from an increase in SWF density is context-dependent with more positive responses in cropland ($n = 7$), to a lesser extent in mixed agricultural landscapes ($n = 4$) and rarely in grassland ($n = 1$). In accordance with our initial hypothesis (H2), non-linear responses were globally more suitable for modeling the responses of the three taxa to SWF (Table C.2; Figs. 2–4; 16 significant non-linear effects detected). Responses to SWF appeared relatively similar among taxa (notably with respect to the direction of the response and the overall shape of the relationship, opposed to H3a) but may be modulated by species traits (H3b).

Since the main source of differences between responses comes from differences between landscapes (H1), namely more effects detected in cropland, below we present the results by landscape type.

In dominant cropland landscapes, we found that abundance and species diversity of the three taxa increase with SWF density, up to an estimated maximum of SWF ranging from 6.9 % to 12.3 % (Figs. 2–3). This increase is

stronger at low values of SWF density (up to ca. 6 %; see exact breakpoints values in Figs. 2–3) leading to a large rise in both abundance and richness (e.g., respectively, up to +67 % and +32 % for birds, see Fig. C.2). At high SWF density, we found weaker responses for most metrics (Figs. 2–3), but also with higher estimate uncertainties especially for bats and bush-crickets (due to data scarcity). Nevertheless, we found that bush-crickets abundance continues to increase for SWF densities above 6 % (Fig. 2), leading to a gain of +28 % abundance at 10 % SWF (Fig. C.3) comparatively to +21 % at 6 % SWF (Fig. C.2). As for the other community metrics, we found positive responses in CSI_{bats} but negative ones in CSI_{birds} (Fig. 4). Looking at the responses of bird species, we found that the abundance of farmland specialists exhibited a similar response pattern to SWF than CSI, i.e., with abundance decreasing as SWF density increases in agricultural landscapes (Fig. C.4). CTrI_{birds} respond positively to SWF density as opposed to CBLI_{crickets}.

Fig. 3. Predicted species diversity (Simpson index) of the three taxa as a function of increasing SWF density, in different agricultural landscape compositions. The green-vertical and gray-horizontal lines respectively represent the breakpoint value and the maximum estimated value (and 95 % confidence interval). In observed SWF density plots, line types represent the different datasets (dots = birds, long-dashes = bats, solid = bush-crickets). Estimated effective degree of freedom and linear SWF coefficient with p-values associated are shown in Table C.1–2. (For interpretation of the references to color in this figure legend, the reader is referred to the web



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differences). It is also noteworthy that the positive effect notably in cropland is still detected up to our largest buffer size tested (10 km, Fig. C.6).

In dominant mixed landscapes, birds and bush-crickets share a common significant positive increase in abundance with SWF density (less important than in cropland for A_{birds} , but more for A_{crickets} ; Fig. C.2). At the community level, only bird metrics were significant, with a positive response of both species' richness and CTI_{birds} to increasing SWF density, but negative response of CSI_{birds} . We also noted that in these landscapes, initial values of the various metrics were generally intermediate between those in cropland and in grassland (but see Fig. C.5).

In dominant grassland landscapes, we found only one significant effect of SWF density, corresponding to a linear positive response of A_{birds} (Table C.3, Figs. 2–4), but leading to a less important increase in bird abundance than in cropland (Fig. C.2). We noted that initial metric values were generally higher than in cropland (Fig. C.5).

Despite the various home-range and mobility traits among taxa that can influence responses to landscape features, we found consistent patterns detected alongside buffers at the landscape level (300 m, 1 km) compared to the buffer used (500 m), highlighting that the choice of these scales did not impact our results (but see the detailed pattern in Fig. C.6–7–8 for slight

4. Discussion

We present a nationwide, quantitative and multi-taxa study of the impact of small woody features on farmland biodiversity in different agricultural landscapes. Using monitoring data on three taxa, we illustrate the relevance of the EU BDS 10 % target on high-diversity landscape features (also including buffer strips, fallow land, field margins, ditches, etc.) providing further information on how it relates to a more general biodiversity support from a land management perspective. We found a strong positive response of the abundance and species diversity of the three taxa, particularly in cropland compared to grassland (H1).

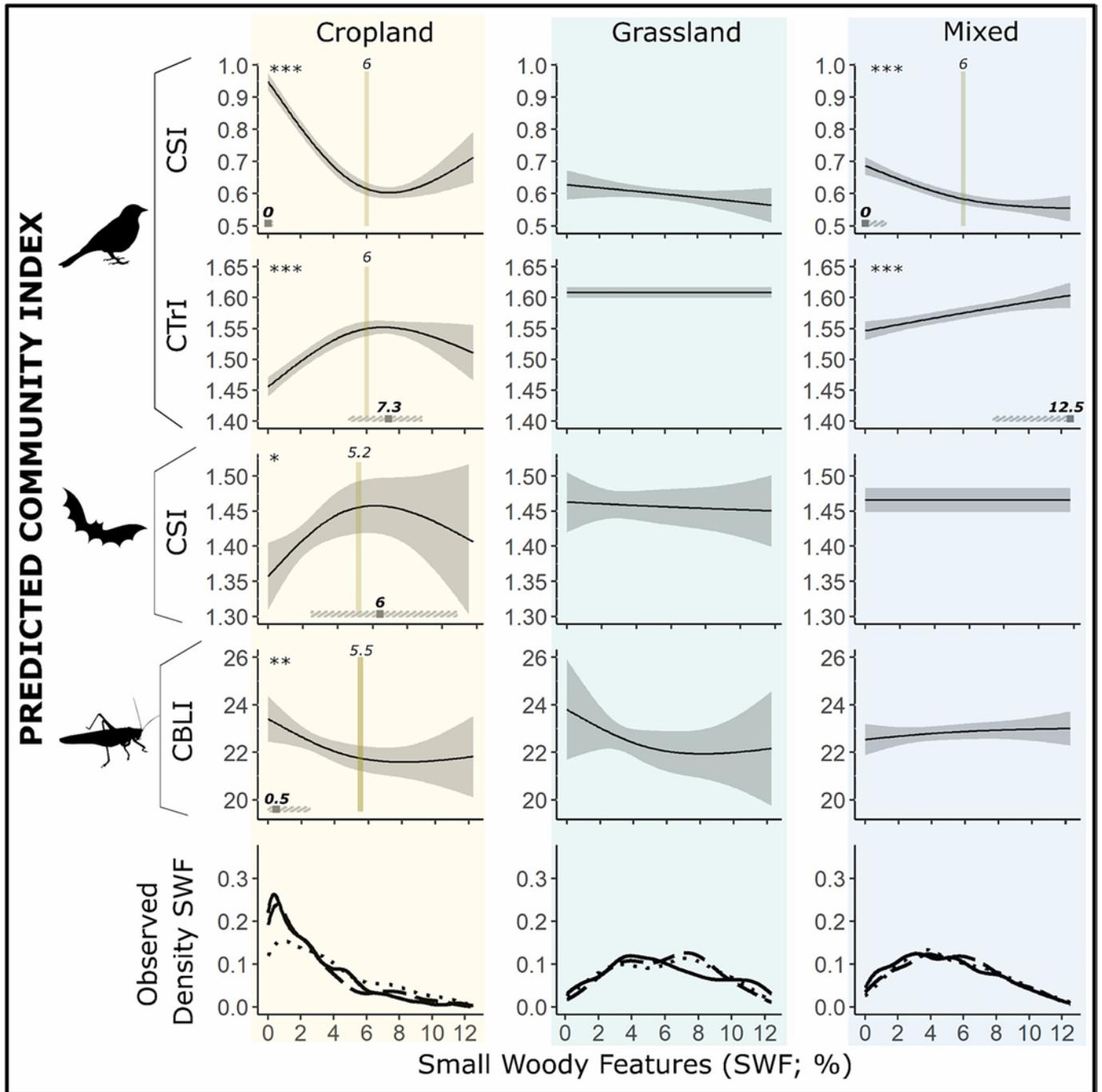


Fig. 4. Predicted community metrics (CSI: Community Specialization Index, CTrI: Community Trophic Index and CBLI: Community Body Length Index) as a function of increasing SWF density, in different agricultural landscape compositions. The green-vertical and gray-horizontal lines respectively represent the breakpoint value and the maximum estimated value (and 95 % confidence interval). In observed SWF density plots, line types represent the different datasets (*dots* = birds, *long-dashes* = bats, *solid* = bush-crickets). Estimated effective degree of freedom and linear SWF coefficient with p-values associated are shown in Table C.1–2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We showed that the relationship is generally non-linear, with maximum abundance and diversity reached at SWF density ranging from 6.9 % to 12.3 % (H2). We also found that a minimum SWF-density breakpoint of ca. 6 % (up to which the benefits are the most important) can greatly support farmland biodiversity. This observation, common to several taxa (as opposed to our initial hypothesis H3a), is particularly important in a context of a limited budget dedicated to the preservation of farmland biodiversity (i.e. the role of the current CAP 2023–2027; Pe'er et al., 2022). We also emphasize that some farmland specialist birds may be negatively affected by SWF (H3b).

4.1. Farmland biodiversity response to small woody features

A first key finding is the increased benefit from SWF in terms of both abundance and species diversity in cropland compared to grassland, common to the three taxa. This is consistent with results from previous studies focusing on either a single taxon (birds: Broughton et al., 2021) or on a specific community metric (Jeanneret et al., 2021). We thus provide unique empirical evidence that SWF density is more beneficial in cropland compared to grassland for biodiversity. This result could arise for multiple reasons. First, the initial lower abundance and species diversity in cropland compared to grassland allow for more room to increase (Fig. C.5). Second, although SWF can act as corridors, this benefit can be diminished when habitat-matrix

differences are smaller, as observed in grassland compared to cropland (Forman, 1995). Moreover, Concepcion et al. (2012) demonstrated greater benefits for diversity in four taxa due to the length of semi-natural elements (including, but not limited to, SWF) in cropland compared to grassland. Then, these increased benefits in cropland inside the same taxa could be due to different requirements of species in each farmland composition (i.e., different community composition between cropland and grassland). Lastly, in grassland the benefits may be reduced due to landscape fragmentation induced by the implementation of hedgerows, as hypothesized by Besnard and Secondi (2014). Our results also highlighted the severe consequences of neglecting such landscape features (SWF) in cropland areas, as abundances and diversity are reduced by up to 67 % and 32 % compared to the values reached at a 6 % SWF density (breakpoint value shared by most metrics, and according to reference value at 0 % SWF density defined by the models). This breakpoint density SWF value is therefore consistent across taxa as opposed to our initial hypothesis (H3a).

These observed nonlinear community responses can reflect species composition shifts such as equilibrium between specialist species and generalist ones (H3b; as discussed by Tscharntke et al., 2005). Accordingly, we found a decrease in the average habitat specialization of bird communities ($CS_{I_{birds}}$) that may reflect the drop in abundance of farmland bird specialists, the only guild of bird species responding negatively to increasing SWF density (Fig. C.4). As shown in previous studies, measures related to increasing such features could not be assumed leading to uniform benefits, and particularly not for species associated with open agricultural habitats, such as the Skylark *Alda arvensis* or Northern Lapwing *Vanellus vanellus* (e.g. Princ'e and Jiguet, 2013). Yet, we conversely found that increasing SWF density increases the average specialization of bat communities. This increase in $CS_{I_{bats}}$ is mainly due to the absence of farmland specialists among bat species. Specialist bat species are mainly forest specialists (Froidevaux et al., 2023), such as *Myotis* specialist group which particularly benefits from SWF, as shown in a case study in England by Froidevaux et al. (2019a). The increase in SWF density tends to increase bat diversity overall, as such an increase in $CS_{I_{bats}}$ could be the reflection of an increase in species diversity, more specifically an addition of specialist species, without loss of species: in open fields with no or few SWF, the community is mainly composed of generalist species such as *Pipistrellus pipistrellus* and *Pipistrellus kuhlii*, species present in almost all sites (respectively 97 % and 70 % of occurrence in the dataset).

Another indicator showing that community composition responds to SWF is the $Ctrl_{I_{birds}}$, whose increase (i.e., communities with higher mean trophic level) may reflect that an increase in SWF is accompanied by an increased presence of prey suitable for insectivorous and raptors, but also provides more habitat for higher trophic level "hedge nesters" (Bas et al., 2009). As for bush-crickets, we expected higher SWF density to lead to increased $CBL_{I_{crickets}}$ through increased energy availability, however we found a negative response to SWF. This finding is consistent with Schirmel et al. (2019) reporting a negative correlation between average body mass of a *Caelifera* community and increased fertilizer inputs in meadows. This counter-intuitive result may be explained by the increased abundance of small-sized species that often exhibit higher densities than larger species, as previously discussed by Whitman (2008). All these results at the community level highlights the need in the future to identify more precisely which species can benefit (or not) from this SWF. Moreover, one limitation of our study is that we did not investigate the SWF response of some taxa in the trophic network (e.g., plants, pollinators) of farmland biodiversity (see Concepcion et al., 2020; Jeanneret et al., 2021).

Focusing on cropland landscapes, we illustrated the robustness of the relationship between biodiversity and SWF to the spatial resolution used to characterize SWF landscape context. Interestingly, despite large differences among and within taxon home range sizes, we still detect a similar positive effect at different spatial scales up to regional level (10 km). Although a threshold of 6 % SWF to get the largest increase of biodiversity abundance and diversity is verified at various landscape-scale buffers (300 m, 500 m and 1 km), we stress that this estimated value comes with its uncertainty,

especially for bats and bush-crickets, for which high densities of SWF were poorly represented within datasets. Therefore, we reiterate that 6 % appears to be a bare minimum threshold up to which the increase is most significant, but higher SWF densities may still lead to a moderate increase in biodiversity depending on the agricultural context.

4.2. Implications for policies impacting landscape features

This large-scale, multi-taxa study highlights the priority of increasing small woody features density to support higher levels of biodiversity in agricultural landscapes, specifically in cropland. We found that maximum abundance and species diversity values were achieved at 6.9 % to 12.5 % SWF density, but a bare minimum of 6 % at the landscape-scale could support the largest part of the positive effects detected with our dataset (corresponding to 4.7 ha of SWF per 78.5 ha farmland landscapes). This information is relevant in the context of the targets set in the EU Biodiversity Strategy to 2030, and especially for the two main pieces of legislation supporting it, the CAP and the Nature Restoration Law (currently under negotiations). Our study results indeed provide some new insights, aiming at increasing the effectiveness of measures implemented on the ground, and provide crucial empirical evidence to the relevance of the recommendations of Kremen and Merenlender (2018) and the EU BDS 2030 to raise this threshold to 10 % of high-diversity landscape features in all agricultural land, which seems more appropriate for biodiversity conservation.

We more specifically support the recommendations of Jeanneret et al. (2021, study on vascular plants, earthworms, spiders, wild bees) by showing that our pool species would also benefit from the implementation and/or enhancement of these features more particularly in cropland. This previous study showed that in addition to being an effective measure to support farmland biodiversity in cropland (Pe'er et al., 2022), preservation of semi-natural elements would likely lead to the lowest decrease in production (compared to grassland) and SWF can enhance pest control, pollination and arable landscape can achieve high yields with them (Martin et al., 2019). Tschumi et al. (2020) also showed that SWF are the most effective features to preserve avian biodiversity compared to other semi-natural elements (buffer strips, ditches, fallow land). It appears as a priority to increase the density of SWF in cropland knowing that in these agro-ecosystems the current mean density is the lowest (2.5 % in our study). We point out that one limitation of the considered remote sensing product is that it only informs on SWF density while other factors, such as height, maturity, vegetation composition and structure, management practices, may modulate its impact (Broughton et al., 2021; Froidevaux et al., 2019b; Hofmeister et al., 2017). Finally, our study focus on major landscape compositions (cropland, grassland, mixed) but it has been shown that SWF impact can be modulated by region and more detailed agrosystem classification (e.

g., intensive cropland vs extensive cropland, Concepcion et al., 2020) and thus balanced decisions about the design of landscape conservation schemes may be adopted according to specific conservation targets in each case (Concepcion et al., 2020; Pe'er et al., 2022).

This last point is exacerbated as our study highlights large benefits from increasing SWF density to enhance farmland community abundance and diversity (and bat specialization) but points out that it will unlikely reverse the decline of farmland birds. Supporting both arable and grassland specialist birds would indeed require implementing multiple strategies and considering regional species pools to maximize the positive responses of farmland biodiversity as a whole (Princ'e et al., 2013; Concepcion and Díaz, 2019). For instance, the spatial configuration of SWF could be adjusted according to the regional species pools; certain birds (mainly forest and ecotones birds species, Concepcion and Díaz, 2019) would gain advantages to implement them within the field by enhancing connectivity and reduced field size offered by these landscape features (in addition to providing shelter and food, Hinsley and Bellamy, 2000). On the other hand, specialized open field birds (e.g., skylark that are currently under threat) could be less negatively impacted by the increased SWF density if they are implemented between fields (and not

within fields) to preserve large open field areas they depend on (Concepcion and Díaz, 2011; Concepcion and Díaz, 2019). Apart from woody features, non woody boundaries such as ditches, grass and flower stripes, can also be important to farmland biodiversity (Siriwardena et al., 2012; Schulte et al., 2017; Scheper et al., 2013). Also, coupling increase in SWF density to farming approaches or measures beneficial to biodiversity, such as chemical input reduction (Chiron et al., 2014), conservation tillage (Barr'e et al., 2018), field size reduction and increase in crop heterogeneity (Sirami et al., 2019), increase in the share of fallow land (that farmland specialized birds particularly benefits, Concepcion and Díaz, 2019; Traba and Morales, 2019), may increase the effectiveness of restoration and conservation actions. Nevertheless, SWF represent highly valuable features to both biodiversity and many ecosystem services that can provide multiple benefits to farmers (Brodt et al., 2009) and thus we agree with Collier (2021) to present these SWF as examples of cost-effective Nature-Based-Solution. **CRedit authorship contribution statement**

Clement Vall'e: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **Isabelle Le Viol**: Conceptualization, Writing – review & editing, Supervision. **Christian Kerbiriou**: Writing – review & editing. **Yves Bas**: Writing – review & editing. **Fred'eric Jiguet**: Writing – review & editing. **Karine Prince**: Conceptualization, 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

The data that support the findings of this study are openly available in Dryad at reference URL [https://datadryad.org/stash/share/wQfHDGVBkCkFiz6gsbzs8Z_Eq6pYjXUpzE1kml0M] number <https://doi.org/10.5061/dryad.6wwpzn3v>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110262>.

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