



# Importance of ground refuges for the biodiversity in agricultural hedgerows



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## ABSTRACT

In most agro-ecosystems, hedgerows provide important habitat for many species. Unfortunately, large scale destruction of hedges has stripped this structure from many landscapes. Replanting programs have attempted to restore hedgerow habitats, but the methods employed often fail to replace the unique microhabitats (complex matrix of stones, logs and roots found along the base of the hedge) that provided key refuges to an array of animal species. We examined the influence of ground refuges on animal diversity in an agricultural landscape. We used non-lethal rapid biodiversity assessments to sample invertebrate and vertebrate taxa in 69 hedges having different levels of herbaceous cover, tree cover, and refuge availability. Co-inertia analyses compared hedge characteristics with the animal biodiversity sampled. We also used a functional index (accounting for body mass, trophic level, and metabolic mode of the species sampled) to compare hedges. In addition, large sedentary predators (e.g. snakes) were used as indicators of shelter presence/quality and as bio-indicators of food web structures. Finally we used unbiased Chao-estimates to evaluate species richness. All results were convergent and show that complexity of the base of the hedge (e.g., bank size and stone abundance) positively influenced biodiversity and predator abundance. Guidelines to restore hedgerows should integrate refuges that can be constructed by retaining the materials that are extracted during the planting of the hedges.

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## 1. Introduction

Hedges are the major elements that sustain biodiversity in many agro-ecosystems (Baudry et al., 2000). Primary used to delimit properties, to protect crops and to contain livestock, hedges play important additional roles. They provide various services (e.g. they supply fodder, fruits, wood, etc.), shelter a wide range of species, and act as corridors for dispersal (Millán de la Peña et al., 2003; Le Viol et al., 2008; Batary et al., 2010). Dense networks of hedgerows have been carefully managed by farmers for thousands of years in Europe, and they have been the focus of many studies (Baudry et al., 2000; Deckers et al., 2005; Lotfi et al., 2010). During the last 50 years, large scale industrialization and intensification of agronomy, especially cereal farming, led to the destruction of immense quantities of hedgerows associated with a strong homogenization of agro-ecosystems (Le Coeur et al., 2002; Baudry and Jouin, 2003; Schäfer et al., 2007; Woodhouse, 2010; van der Zanden et al., 2013). For example in France, more than 1,000,000 km of hedges have

been destroyed in less than 50 years (Pointereau et al., 2001). The destruction of hedge habitats is one of the important causes of the massive biodiversity loss associated with agriculture mediated land use changes in Western Europe (Stoate et al., 2001; Sklenicka et al., 2009; Burel et al., 2013).

The impact of habitat changes in agricultural landscapes is well documented for several animal taxa (either pests or allies; Kromp, 1999; Donald et al., 2001; Aviron et al., 2005). These studies indicate that biodiversity, population declines of various species, or pest outbreaks are influenced by the composition of the plant community (trees, shrubs and herbaceous strips) and by the spatial structuration of the hedgerows (Millán de la Peña et al., 2003; Aviron et al., 2005; Michel et al., 2006; Butet et al., 2010). Current guidelines to restore networks of hedgerows take into account these factors, notably to promote biodiversity, ecosystem functioning and the associated ecological services (Burel et al., 2013).

Hedgerows provide other benefits to animals in the form of the complex structures found at the base of the hedge and formed from roots, stones, logs, and other features that often combine to provide a variety of microhabitats. Many animal species depend on the presence of appropriate refuge structures, notably cryptic organisms that remain sheltered most of the time (Lampo, 1994;

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Murdoch et al., 1996). The various microhabitats found at the base of hedgerows offer types of shelters that can be exclusive for many species. These microhabitats are of greater importance to sedentary organisms, especially those that cannot easily emigrate during harsh climatic periods (e.g., drought, cold winter). To our knowledge, the possible importance of these microhabitats and of ground shelter availability on animal biodiversity in agro-ecosystems has not been investigated. Considering hedgerow destruction rates, assessing the influence of ground refuge availability on animal biodiversity in agro-ecosystems is timely and represents the main objective of this study.

Using a wide range of taxa is preferable over biodiversity estimates based on a single taxon (Van Jaarsveld et al., 1998); but performing multiple surveys poses important methodological and logistic difficulties and thus are rarely carried out. In order to take into account a wide range of taxa, we used a specifically developed approach: non-lethal rapid biodiversity assessments (NL-RBA; Lecq et al., 2015). This approach is derived from rapid biodiversity assessments (RBA; Hammond, 1992; Oliver and Beattie, 1993, 1996a,b) where identification of morphospecies relaxes the logistical constraints associated with classical trap-surveys (e.g. species-level identification in the laboratory). Although taxonomically less precise, RBA are useful tools to estimate local biodiversity (Oliver and Beattie, 1993, 1996a; Obrist and Duelli, 2010). NL-RBA amplifies the advantages of RBA because it does not rely on capturing (and killing) individuals but on immediate identification in the field. Thus, NL-RBA is similar to point counts routinely used for surveying bird species. The identification error rate is low at the morphospecies level (<1%, thereby limiting observer bias) and multiple count sessions can be performed because studied populations are not impacted by removing individuals (Lecq et al., 2015).

Importantly, NL-RBA allows the sampling of a wide taxonomic diversity, including protected species that cannot be easily collected (Haila and Margules, 1996; Van Jaarsveld et al., 1998; Schmeller, 2008). Overall, the lack of taxonomic accuracy for certain taxa (e.g. spiders) is offset by practical and ethical advantages.

The influence of habitat type on functional biodiversity needs also to be examined through ecological features such as life-history traits and trophic relationships (Swift et al., 1996; Folke et al., 2004; Cardinale et al., 2006; Moonen and Bärberi, 2008). For example, because rate of biomass conversion across trophic chains is slow, sustaining apex predators are energetically demanding and thus the status of predator community depends on the status of the underlying trophic levels (Duffy, 2003; Duffy et al., 2007). Top predators are thus often viewed as indicators for the ecological health of the ecosystem (Sergio et al., 2008). Body size and metabolic mode are also important traits to take into account: large endothermic species require much greater absolute amounts of resources compared to small ectothermic animals (Pough, 1980; Woodward et al., 2005). A hedge occupied by a diversity of vertebrate and invertebrate predators is likely sustained by a rich underlying diversity of prey species. Therefore, to assess the influence of ground refuges on hedge biodiversity we incorporated into our analyses the trophic level, metabolic mode and body size of the detected morphospecies. Finally, we also adopted a specific focus on snakes and lizards (i.e. squamates) as indicators of shelter availability, and as food web bio-indicators of the hedges for several reasons. First, being obligate carnivores, most squamates are typically at or near the apex of the hedgerow trophic webs; they depend on the functioning of the underlying trophic levels. Second, they are relatively sedentary and they remain sheltered most of the time, thereby providing accurate spatial information. Furthermore, ophidian populations have declined in agricultural landscapes (Reading et al., 2010) where the network of hedgerows has been severely reduced, suggesting that these predators are sensitive to hedge characteristics (Reading and Jofré, 2009).

By examining terrestrial refuges and cryptic terrestrial species, our main goal was to provide complementary data about the importance of hedges for biodiversity. We predict that the presence of hedges that comprise abundant ground refuges within an agricultural landscape will result in higher biodiversity and more complex trophic webs at those sites. We also aimed to propose practical actions that promote conservation and restoration of these critical habitats.

## 2. Material & methods

### 2.1. Study areas

The two study areas are situated in western central France, in an agricultural landscape that has lost the majority of its hedgerow features. Previously characterized by a network of hedgerows (i.e. 'bocage'), more than 80% of the hedges have been removed from the area during the past 50 years. Traditional farming (e.g. market gardening) has been replaced by intensive industrial cereal farming (e.g. maize, sunflower; Meeus, 1993). Despite this, small patches of densely spaced hedgerows persist in several locations.

We selected 69 field hedgerows in the Deux-Sevres-79 (N = 61 hedges, Chizé; 46°06'58.4N, 0°20'59"3W) and Charente-17 districts (N = 8 hedges, Dompierre-Sur-Mer near the Ocean; 46°10'36.9"N, 1°03'12.3"W). The range of hedgerows selected is representative of the gradient of destruction. Several hedgerows were intact (i.e. traditionally managed over decades; Appendix A) and were notably covered by well-developed trees; others were relictual (i.e. most trees have been removed). Our selection of sites also encompassed a diversity of structures at the base of the hedgerows: either with or without large banks, sometimes with small walls made of stones.

The cultivated fields bordered by the hedgerows were characterised by different crops (meadow, fallow, corn, etc.), different agricultural practices, or connectivity (e.g. dense network of connected hedges versus isolated hedge). These environmental factors likely influence the biodiversity associated with a particular hedgerow. As such, we limited the influence of these factors by haphazardly selecting different types of hedges (e.g., intact versus relictual) across our spatial scale. Moreover, rotating of cultures during the two years of the study (2011–2012) further distributed a possible crop effect across the hedges surveyed. Each species living in a hedge may respond in a particular way to the modifications of agricultural practices in surrounding fields (e.g. differential perturbation caused by pesticides, noise exposure). Implementing all these factors and interactions into the analyses was out of scope of the current study. Therefore, we focused on the availability of ground shelters on a wide range of morphospecies.

### 2.2. Hedge characteristics

We characterized each hedge using two primary features: 1) vegetative cover and 2) base of the hedge that determines ground refuge availability (Appendix B). For each hedge, we measured height and width of the trees and shrubs using a flexible measuring tape. The size of trees >3 m in height was estimated visually. Plants were identified to the lowest possible taxonomic level (e.g., Family or species), and the relative proportion of ground surface covered by vegetation was recorded. This latter measurement included the proportion of the bank covered by grass (e.g., Poace), bramble/shrubs (e.g., *Rubus fruticosus*), and trees (e.g., *Acer campestre*).

For each hedge, we described the bank and other ground refuges. Banks are often made of earth and stones and are generally associated with one or two ditches and a bordering herbaceous strip (Appendix A). Unless the feature was absent from a particular hedge, the characteristics of the bank (height, width), ditch (height,

width, depth), and of the bordering herbaceous strips (width) were measured using a flexible decametre. Larger and higher banks likely contain more materials (e.g. stones, logs) and ground structures (e.g. burrows) and thus should provide more ground refuges than ones having low profiles (MacLeod et al., 2004). In addition, shelter availability was estimated as the number of stones (>10 cm in any dimension) or logs (>10 cm in diameter) in 3 randomly-selected quadrats of 0.25 m<sup>2</sup> in each hedge. To minimize observer bias, all descriptive data were collected by the same person (SL).

We recorded data for 33 variables that described each hedgerow (Appendix B). Many of these variables were auto-correlated (e.g. height and width of a ditch), so we used principal component analyses (PCA) to derive summarizing descriptors of the characteristics of the hedges. PCA is sensitive to the scaling of the initial variables, however, and the analysis can provide an output that cannot be easily interpreted (especially when combining different types of variables). Because our descriptions included various scales of measurement (e.g. stone number, tree height), descriptors derived from PCA were potentially subjected to these biases. Thus, to further assess the influence of plant cover (trees and shrubs), ground refuges, and bordering elements on the sampled biodiversity, we used another approach: hierarchical ascendant classification (Leroy, et al., 2013).

We first calculated Pearson's correlation coefficients ( $r$ ) among the 33 variables. We then computed the distances among them ( $d = 1 - r$ ), and these value were used to construct a hierarchical ascendant classification. Variables that were inter-correlated at a threshold of 0.7 (i.e., distance <0.3) were grouped prior to constructing the classification (Leroy et al., 2013). The resulting hierarchical tree suggested that the groups of variables associated with the base of hedges (e.g., bank size, abundance of ground shelters) clustered separately from groups of variables associated with plant cover (trees and shrubs) and those describing the border of the hedge (herbaceous strip, ditch). Further analyses using the variables associated with bordering elements (e.g., herbaceous strip, ditch) did not contribute significantly to the variation of the sampled biodiversity ( $p > 0.05$ ); therefore these variables were not retained in our final analyses.

Based on this dichotomy, we generated two integrative continuous variables: (1) shelter quality (SQ) was represented by bank height + number of shelters; it provided an index of the quality and quantity of shelters at the base of each hedgerow. (2) Vegetation quality (VQ) was represented by hedge height + ground surface covered by trees + canopy width; it provided an index of the quality and quantity of trees and shrubs. Each hedge was thus characterized by SQ and VQ values. To facilitate comparisons, we classified hedges in three categories (low, medium and high) for each of these variables (SQ or VQ) following the methodology of Marti (1990). Our intent of this categorization was to provide a simple and practical discriminative description of hedges for land managers regardless of the current pattern of land use.

### 2.3. Biodiversity sampling

We used the recently validated NL-RBA (Lecq et al., 2015). This method relies on rapid visual/photo sampling, and thus is appropriate to survey the macro-fauna. It is a cost effective technique that permits to collect large sample sizes without entailing environmental or ethical complications (Lecq et al., 2015). Cryptic species often sheltered into ground refuges can be sampled. For the purpose of this study, we re-analysed the data set used by Lecq et al. (2015) but we used different statistics (see below) to examine a previously untested issue: do vegetative cover and refuge availability influence animal biodiversity?

More precisely, in the current study we focused on terrestrial animals (e.g., arthropods, molluscs, reptiles) that depend on ground

refuges; yet, individuals from many species that do not use ground refuges were also counted (total  $N = 62,382$  observations). The majority of observations ( $N = 40,104$ ) and morphospecies ( $N = 451$ ) were represented by insects and spiders; vertebrates contributed to 2.1% of the individuals and 7.7% of the morphospecies. Most individuals (89.4%) were identified to a relatively precise taxonomic level: species (44.5%), genus (23.1%), or family (28.0%), and were thus accurately assigned to a morphospecies (Oliver and Beattie, 1993, 1996a,b; Kerr et al., 2000; Cardoso et al., 2004; Biaggini et al., 2007). Observers did not overestimate their discrimination capacity; instead they prudently determined less than 50% of the individuals to at the species level and often retained genus or family levels to assign individuals to a given morphospecies. Only 4.6% of problematical individuals required picture examination in the laboratory. Identification errors were relatively low: <6% at species level and less for higher taxonomic level (Lecq et al., 2015). The overall identification error rate remained <1%. To limit observer bias, field workers sampled the different hedges in a random order. Consequently, morphospecies assignment and counting of individuals were likely comparable among the main groups of hedges surveyed.

### 2.4. Functional biodiversity index

To take into account the ecological role and life history traits of the morphospecies sampled, we used a simple index to characterize the ecological rank of the species. To determine that value, we calculated an integrative score that combines body size, diet, and metabolic mode (Appendix C).

- (A) Body mass: We used body mass as a proxy of body size. For most morphospecies, mean values were obtained using published literature and our own data, the latter of which included measurements taken in the field ( $\pm 0.001$  g, Scout Pro SPU-123, Ohaus, USA); individuals were immediately released. Because the values for body mass (BM) ranged widely ( $0.001\text{g} > \text{BM} > 10\text{kg}$ ), they were log-transformed to obtain a linear scale of body size variation (for simplicity, we used the absolute values of all transformations). When body mass was missing, we inferred a surrogate of body mass from the above relationship using body size. Using the body mass of each morphospecies (e.g. 64 morphospecies of spiders; more than 500 morphospecies in total) we did not mix up individuals belonging to contrasted body size (e.g. a small versus a large spider) because they would have been assigned to different morphospecies otherwise. Further, the log transformation of the data strongly limited the influence of assignment imprecision; on a log-scale relatively similar species assigned to a single morphospecies display very similar body masses.
- (B) Trophic level: Diet was based on the documented main prey types of each morphospecies (we excluded anecdotal reports). The trophic level of each morphospecies was ranked as follows: 1 = phytophagous, 2 = necrophagous, 3 = omnivorous, 4 = invertebrate predator feeding on invertebrates, 5 = vertebrate predator feeding on invertebrates, 6 = vertebrate predator feeding on ectothermic vertebrates, 7 = vertebrate predator feeding on endotherms. The rationale for this ranking was to account for the amounts of energy sustaining vertebrate predators and/or endothermic species usually being greater when compared to invertebrate predators and/or ectothermic organisms. This incremental scale (1–7) was conservative because biomass conversion rates across trophic levels are relatively low (<50% in ectotherms, <10% in endotherms) and endothermic prey are usually larger, faster and thus more difficult to subdue compared to ectothermic

prey (thereby requiring additional energy expenditure during capture).

- (C) Metabolic mode: The metabolic mode was categorized as 1 for ectothermic species or 2 for endothermic species. This ranking was very conservative because the average mass specific metabolism of endotherms is at least 10 times greater compared to ectothermic species (Pough, 1980). Using this trait was not in conflict with trophic ranking that also integrated metabolic mode because the differences in energy expenditure between ectotherms and endotherms are not limited to the process of food assimilation.

Overall, the relative mass of larger species, predators, or endothermic species compared to small herbivorous ectotherms was taken into account, but was nonetheless minimized in the analyses through our use of conservative ranking systems. For each morphospecies, we calculated a value of ecological rank by multiplying the three key variables:

2.5.  $Ecological\ rank = \log(body\ mass) \times trophic\ level \times metabolic\ mode$

The resulting values ranged from 1 to 108.4. For instance, we attributed a score of 108.4 to the largest endothermic predator, the red fox, whereas several small phytophagous beetle received a score  $\sim 1$  (e.g., adult *Pyrochroa serraticornis*, <0.01 g that feed on nectar [although larvae are carnivorous]). Conservatively, our index assumes that a fox requires >100 times more energy (actually likely much more) compared to a small beetle and therefore, the underlying trophic and ecological structures to sustain foxes are also more demanding in terms of habitats and energy production.

For each hedge, we calculated the sum of the ecological ranks of each morphospecies observed (“hedge biodiversity score” [HB]). Therefore, the relative abundance of morphospecies was not considered and counting individuals more than once did not influence the analyses. Furthermore, taking the total number of observed morphospecies in each hedge into account did not alter the results; indeed larger predator body sizes and greater biodiversity were usually found in the hedges with large banks (see Results). The distribution of the HB values followed a normal distribution (Shapiro-Wilk test;  $W = 0.98$ ,  $P = 0.26$ ).

2.6. *Analyses of the influence of hedgerow characteristics on biodiversity*

We used four different (complementary) approaches to characterize the hedges and associated biodiversity (Appendix D); enabling us to assess to what extent the results were correlated.

- 1) PCA and co-inertia analyses: co-inertia analyses are appropriate for examining the influence of hedgerow characteristics on biodiversity (Le Coeur et al., 2002; Millán de la Peña et al., 2003; Aviron et al., 2005; Butet et al., 2006). This type of analysis takes into account different elements such as fauna inventories, biodiversity indexes, and other environmental features (Dolédec and Chessel, 1994). Analyses were performed in three steps: 1- Principal component analyses (PCA) on quantitative environmental data that allowed us to classify hedge characteristics; 2- A second PCA on the abundance of each morphospecies in each hedge (thus, grouping morphospecies into descriptive communities); and 3- Co-inertia analyses that projected the two PCAs (environment  $\times$  species) into the same graphical space. Co-inertia analyses provided useful visualization of the interdependence between the structural characteristics of the hedges and the biodiversity they shelter. The statistical significance of the relationship between the characteristics of the hedgerows and

biodiversity obtained from the co-inertia analyses was tested using Monte-Carlo random permutation tests (Dolédec et al., 1997).

- 2) Functional index: The influence of the three hedge categories (low, medium, high) was tested using ANOVAs with the sum of the HB scores as the dependent variable. This analysis was performed considering shelter availability (SD) and vegetation cover (VQ).
- 3) Squamate bio-indicators: Because the calculation of HB values relied on a set of assumptions, we also performed the analyses using exclusively the number of reptiles counted per hedge (four snake and two lizard species). This approach limited confounding elements associated with including morphospecies comprised of a wide range of taxa having different body sizes and life-history traits. In our area, squamates are top predators with sedentary habits and hence suitable bio-indicators. More generally, herpetofauna offers suitable taxa to effectively estimate local biodiversity and ecosystem function (Beaupre and Douglas, 2009; Lewandowski et al., 2010). Although reptilian morphospecies were included in other analyses (i.e., PCA), their relatively low number ( $N = 103$ ) compared to arthropods (>50,000) means that their contribution in the other analyses was limited. Thus, reptile number can be viewed as an independent index to assess the importance of the structures and microhabitats (e.g. refuges, bank, shrubs) situated at the base of the hedges.
- 4) Unbiased richness estimates: NL-RBA allow multiple counting sessions that are required to perform robust species richness analyses (Lecq et al., 2015). We used unbiased Chao estimates to compare the species richness of the different groups of hedges (Colwell and Coddington, 1994).

All analyses were performed with R statistical software (R Development Core Team, 2010) using a multivariate data analysis package (Dray and Dufour, 2007).

### 3. Results

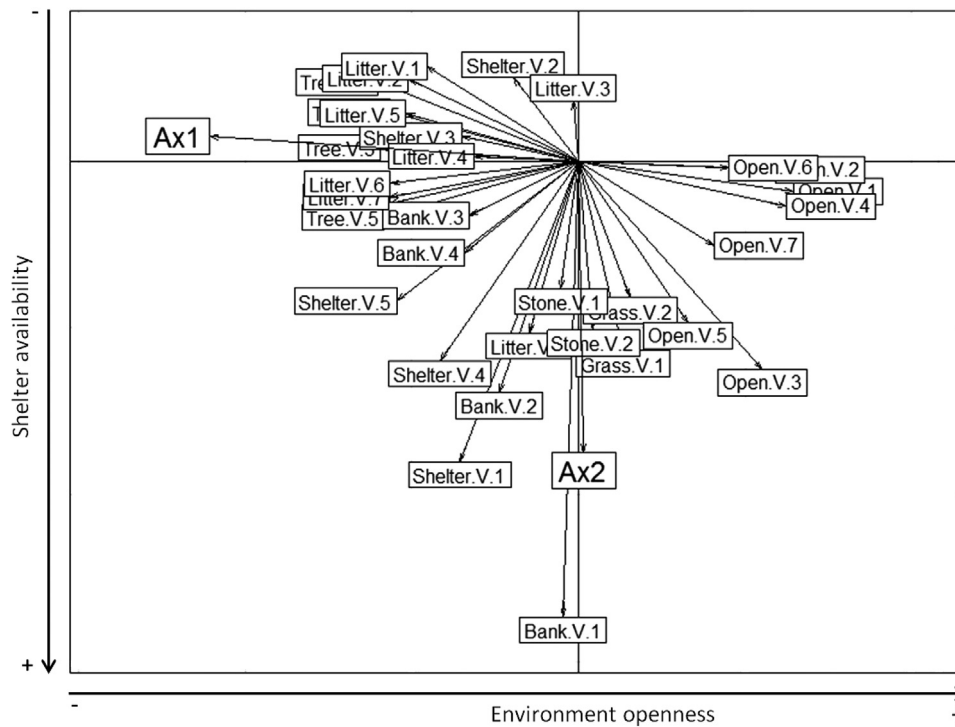
#### 3.1. PCA and co-inertia analyses

The X-axis of the PCA used to characterize hedges accounted for 41.1% of the total variation (Fig. 1). This axis indicated that the gradient of habitat openness could be used to describe the structure of hedges. On the Y-axis, the variables retained in the analysis were associated with a bank (presence/absence, height) and stones, suggesting that this axis was related to a gradient of shelter availability (Fig. 1).

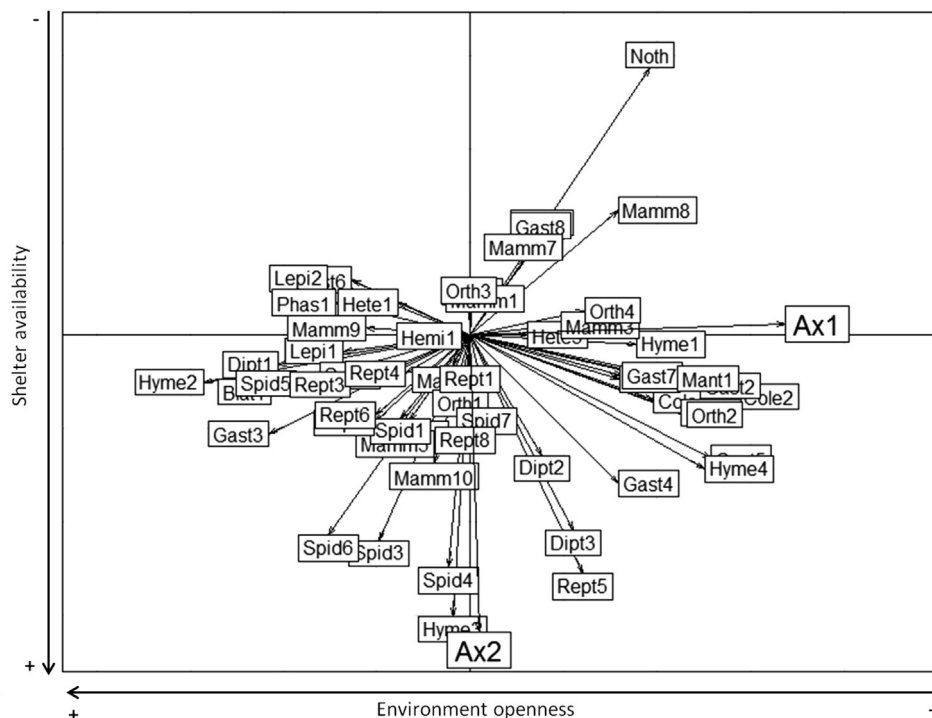
In the analysis performed by implementing the relative abundance of morphospecies, the first PCA axis accounted for 14.1% of the total variation (Fig. 2). The X-axis was mainly defined by morphospecies that were generally observed in open areas (e.g. prey mantis, *Mantis religiosa* [Mant1]) versus morphospecies rather observed in bushy habitats (e.g., stick insect [*Bacillus rossius*; Phas1], red fox [*Vulpes vulpes*; Mam9]). On the Y-axis, morphospecies that depend on ground refuges (e.g. wall lizard [*Podarcis muralis*; Rep4] or hobo spider [*Tegenaria* sp.; Spi6]) were opposed to a set of morphospecies usually found in open habitats (e.g., voles [*Microtus* sp.; Mam8]). Focusing on reptiles (Fig. 2), most species (mainly snakes [e.g. *Vipera aspis*, *Zamenis longissimus*; Rep5, Rep6]) were situated in the same quarter of graphical space as the morphospecies observed semi-open habitats provided with shelters. One lizard species (*P. muralis*) was situated with other morphospecies that are restricted to habitats with abundant shelters (stones, large roots).

Monte-Carlo simulations indicated that the association between environmental (hedge characteristics) and biodiversity (morphospecies abundance) variables was statistically significant ( $P < 0.001$ ).





**Fig. 1.** Result of the PCA performed to characterize 69 hedgerows using various variables. The PCA provides the outcome using environmental variables, notably vegetative cover (e.g. trees, shrubs), herbaceous strip, or shelter availability (e.g. stone count, bank size). The main axes suggest that the degree of openness (% of ground under the shade of trees etc.) versus the availability of ground refuges (e.g. stones) were the main descriptors of the hedgerows. Environmental codes as provided in the [Appendices B and C](#). (note the inverse scale on X and Y axes).



**Fig. 2.** Result of the PCA performed to characterize 69 hedgerows using various variables. PCA performed on animal biodiversity suggest that species were distributed along two similar gradients. “Noth” means that no morphospecies were sometimes observed. Morphospecies codes as provided in the [Appendices B and C](#). (note the inverse scale on X and Y axes).

Both X- and Y-axes of the respective PCAs were almost superimposed in the final co-inertia projection as revealed by the relatively shortness of the arrows (Fig. 3). Overall, the gradients associated with habitat openness and shelter availability obtained with struc-

tural and biodiversity factors were convergent and relatively well superimposed in the co-inertia projection.

Examining the co-inertia plane identified three main groups of hedge/biodiversity associations (Fig. 3). The first group (e.g., hedges



**Fig. 3.** Co-inertia projection using both environmental and animal biodiversity information (Figs. 1 and 2). The length of the arrow corresponds to the residual distance following the combination of the two matrices (first 2 PCAs in Fig. 1). Numbers correspond to hedge number. The small size of the arrows and Monte-Carlo random permutation tests suggest that environmental variables (e.g. ground refuges) were closely associated with animal biodiversity. Three main groups of hedgerows plus two outliers were identified.

#18, 52, 61, 70, 71, 72) was characterized by open habitats with low shelter availability. Another group of hedges was characterized by large banks having limited tree and shrub coverage (e.g. #A1–A3, B1–B3). The last main group was represented by hedges having ample tree and shrub coverage with variable shelter availability (e.g. #36, 50, 53, 78).

### 3.2. Primary hedge categories and biodiversity

HB (hedge biodiversity score) was influenced by both SQ (shelter quality) and VQ (vegetation quality). Higher SQ values (i.e., bank size and shelter abundance) positively influenced HB (ANOVA:  $F_{2,66} = 10.86$ ,  $P < 0.001$ ; Fig. 4A). Tukey's post-hoc tests suggested that the low SQ group differed from the two others ( $P \leq 0.01$ ) whereas the high and medium SQ groups had similar HB values ( $P = 0.16$ ). VQ values were also positively correlated with HB (ANOVA:  $F_{2,66} = 5.26$ ,  $P < 0.008$ ; Fig. 4B). Tukey's post-hoc tests indicated that the low VQ group differed from the two higher VQ groups ( $P \leq 0.05$ ) whereas the high and medium VQ groups were similar ( $P = 0.86$ ).

### 3.3. Squamate bio-indicators

Focusing on reptiles provided similar trends for SQ with a decrease in reptile abundance in the hedge with low shelter availability (Kruskal-Wallis  $\chi^2 = 17.04$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 5A). Using VQ as the independent variable, however, revealed similarities in HB values (Kruskal-Wallis  $\chi^2 = 0.65$ ,  $df = 2$ ,  $P = 0.72$ ; Fig. 5B). The

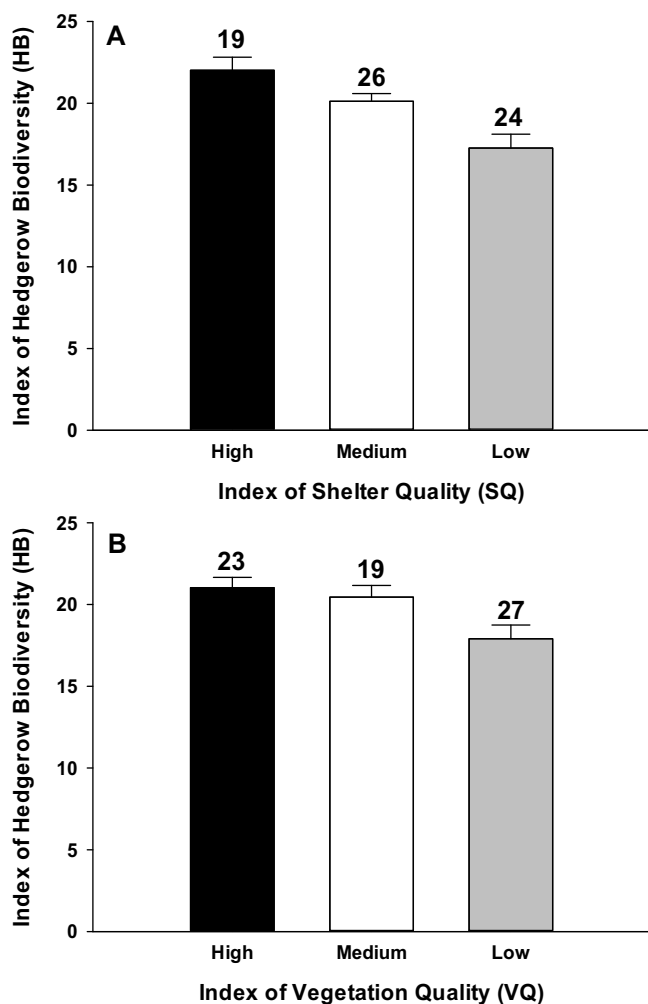
reptiles observed most frequently were *Hierophis viridiflavus* and *Zamenis longissimus*, two large species of colubrids.

### 3.4. Did PCA projections and HB scores provide convergent results?

In PCA, all morphospecies had a similar weight and all individuals were taken into account. Conversely, the HB calculation attributed a specific weight to each morphospecies and the total number of observations of each morphospecies was not taken into account. Therefore, two different approaches were used to describe the biodiversity observed in each hedgerow, and each hedgerow was characterized by different metrics. HB positively correlated with the values provided by the first PCA axis (i.e., degree of vegetation openness;  $R^2 = 0.15$ ,  $F_{1,67} = 12.73$ ,  $P < 0.001$ ,  $N = 69$ , Fig. 6A) and with the second axis (i.e., shelter availability;  $R^2 = 0.26$ ,  $F_{1,67} = 25.04$ ,  $P < 0.001$ ,  $N = 69$ , Fig. 6B, note that removing the outlier [top-right corner of the panel] did not qualitatively change this result). A stepwise regression analysis with HB as the dependent variable suggested that including the two sets of values that describe hedges (X and Y axis) improved the model ( $R^2 = 0.64$ ,  $F_{2,66} = 23.00$ ,  $P < 0.001$ ,  $N = 69$ ), explaining 41% of HB variability.

### 3.5. Specific richness

Unbiased Chao-estimates suggest that (morpho-) species richness was higher in the hedges with high shelter availability (SQ; Fig. 7). The estimated number of morphospecies plateaued under

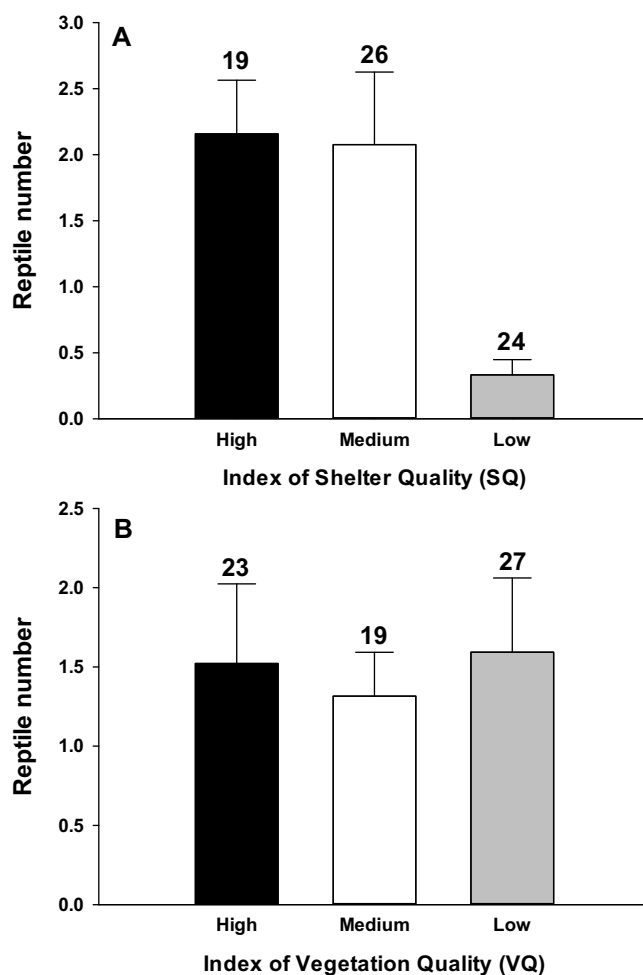


**Fig. 4.** Influence of hedge categories on animal biodiversity (see text for details). Mean values are reported  $\pm 1$  SE (error bars) and sample sizes are given above each bar. A: shelter quality; B: vegetation quality.

230 in the hedges with medium ( $N = 229$ ) and low ( $N = 227$ ) shelter availability, whereas this value reached 280 morphospecies in the hedges with high shelter availability with a constantly increasing trend. These differences were less marked considering the three levels of vegetation quality (VQ), the maximal estimated number of morphospecies ranging from 224 to 256 (Fig. 7).

#### 4. Discussion

This study provided quantifiable evidence that structures along the base of hedges are essential for a wide range of animal species in agricultural landscapes. Ground refuges are notably important for predators from different taxa (including various sizes of invertebrate and vertebrate species), and thus these refuges likely play important roles in the ecological functioning of hedges. Several species targeted in our study are relatively sedentary or exhibit limited dispersal ability; they also largely depend on ground refuges (e.g., adult spiders, lizards or snakes; Gibson et al., 1992; Lelièvre et al., 2010). Therefore indications that the availability of appropriate shelters is crucial for many organisms were predicted; yet this topic has been insufficiently investigated (Griffiths et al., 2008; Bonnet et al., 2013). For instance, to our knowledge, our study reports the first significant effects of various ground refuges on the animal biodiversity sampled in agro-ecosystems. Below we first



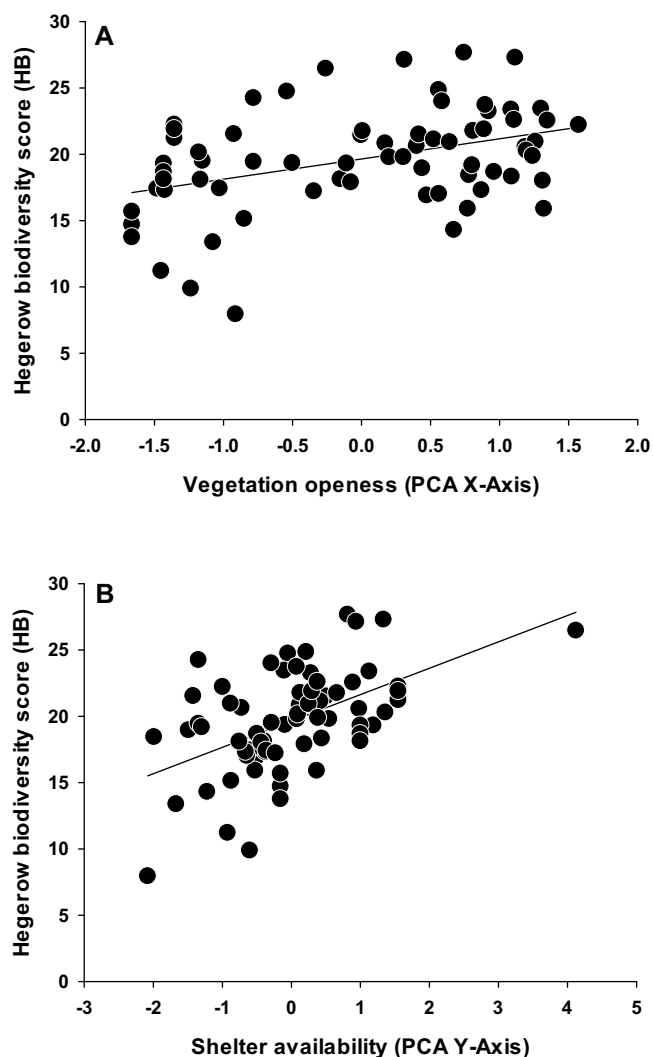
**Fig. 5.** Influence of hedge categories on reptile counts (see text for details). Mean values are reported  $\pm 1$  SE and sample sizes are given above each bar. A: shelter quality; B: vegetation quality.

discuss the advantages and limitations of the method used, then general trends, and finally we propose practical recommendations.

##### 4.1. Advantages and limitations of the method

The main advantages and disadvantages associated with the use of non-lethal RBA have been previously examined (Lecq et al., 2015). Briefly, this approach is cost effective, free from ethical considerations, and thus appropriate to rapidly collect large numbers of observations on a wide range of taxa including protected species. Moreover, using a non-lethal method is essential to perform repeated surveys and unbiased estimations. Taxonomic imprecision represents the main limitation, but depending upon the question addressed, it is compensated by the wide taxonomic diversity sampled.

We used four types of analyses to examine a single central question: do ground refuge availability influence animal biodiversity? Based on different assumptions and procedures the four analytical approaches provided complementary information. PCA and co-inertia are particularly useful to implement disparate information into calculations, and thus to obtain integrated projections that combined hedge characteristics and animal biodiversity (Figs. 1–3). However this method was not designed to take into account the main life history traits (e.g. body mass, diet, metabolic mode) of the animals sampled; thereby missing key ecological and functional aspects of the ecosystem sampled. The functional index we



**Fig. 6.** Correlations between the descriptors of the 69 hedgerow generated by PCA (X and Y axes) and the biodiversity index (HB). A: effect of vegetation openness ( $R^2 = 0.15$ ,  $F_{1,67} = 12.73$ ,  $p < 0.001$ ); B: effect of shelter availability ( $R^2 = 0.26$ ,  $F_{1,67} = 25.04$ ,  $p < 0.001$ ). Discarding the outlier (top right corner panel B) did not change the outcomes (respectively for A & B:  $R^2 = 0.16$ ,  $F_{1,66} = 13.86$ ,  $p < 0.00$ , and  $R^2 = 0.23$ ,  $F_{1,66} = 20.71$ ,  $p < 0.001$ ).

used took into account the main life history traits of the animals (Figs. 4 and 5). But the relative abundance of individuals and the specific richness were not considered. Further, this index involved extremely different organisms (e.g. small insects *versus* large mammals) that are not easily comparable. Using squamate reptile as bio-indicators represented an accurate mean to compare the different groups of hedges: species were precisely identified; their diet, trophic level, and general ecology (e.g. microhabitat use) are well-documented. But using a narrow taxonomic group as a surrogate for broad biodiversity is questionable. Finally, repeated surveys enabled us to take into account the detectability of the morphospecies to produce unbiased Chao-estimates (Colwell and Coddington, 1994), and thus to compare the specific richness of different groups of hedges. Life history traits, ecological characteristics of the sampled organisms along with their possible relationship with the microhabitats were neglected however. Overall, each type of analyses offered specific advantages, strong limitations, and a partial overlapping with the other types of analyses. Importantly, all analyses provided consistent results.

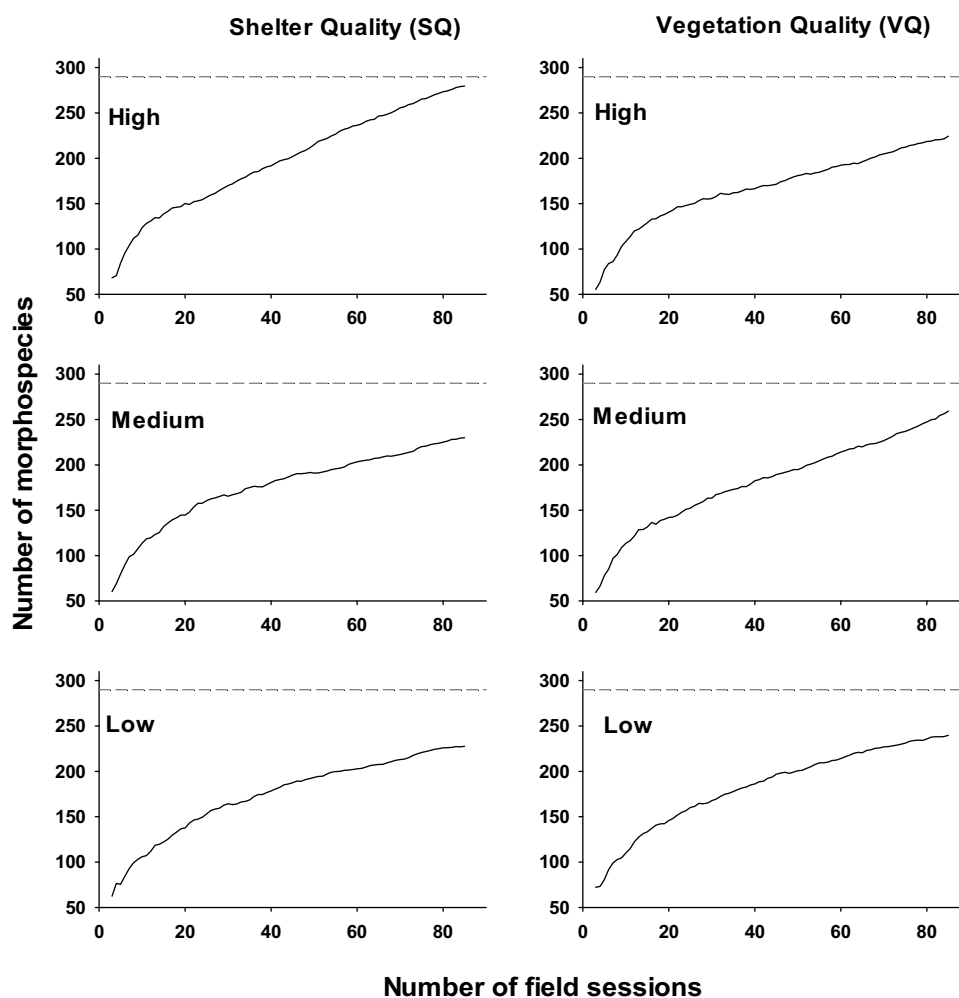
#### 4.2. General trends

The analyses used to characterize plant cover and ground structures of each hedge (PCA) were congruent with the biodiversity index (HB) based on life-history traits (body mass, trophic level, metabolic mode) exhibited by the morphospecies, and with the likelihood to observe large sedentary predator reptiles (Fig. 5). This convergence and the large sample size (69 hedges, more than 50,000 observations of more than 500 morphospecies) indicate that our primary conclusions are robust. PCA and co-inertia analyses revealed that the dimensions of the bank and the availability of shelters influenced the distribution and abundance of the morphospecies observed. Analyses of variance indicated that hedges with larger bank and more ground refuges were more likely to contain larger representatives of each morphospecies that are positioned higher in the trophic web. This conclusion held true when focusing on squamate reptiles. The presence of large snake species and lizards is probably not uniquely correlated with abiotic traits of the hedgerows. Larger bank and more ground refuges likely promote abundance and diversity of squamate prey, and might also offer a wider range of thermoregulatory opportunities. This factor might be crucial because the large species of colubrids sampled exhibit contrasted life styles, thermoregulatory behaviours, but nonetheless heavily rely on ground shelters (Lelièvre et al., 2011, 2012). Finally, species richness estimates suggest that shelter availability positively influenced the diversity of morphospecies. Overall, hedges with a large bank and abundant ground refuges (e.g. stones) harbour a different and more diverse fauna compared to the hedges having a relatively even ground surface.

The persistence of a wide range of predators is essential for the functioning of agricultural ecosystems (Finke and Denno, 2004). For this reason, the influence of networks and characteristics of hedges on bats, birds and many parasitoid arthropods has been studied (Baudry et al., 2000; Burel et al., 2013). Most research efforts focused on connectivity aspects and on the roles of plants (essentially trees). Consequently, practical actions and management recommendations to favour populations of birds, bats and several insect species have been proposed: notably mixing different tree species in hedgerows, promoting sufficient width and elevation of the trees and shrubs, and maintaining an important connectivity in the network of hedges (Batary et al., 2010). Our results indicate that features along the base of hedges also require attention from a management perspective. We suggest that these structures are of equal importance to the trees, shrubs and herbaceous strips in explaining the biodiversity that occupies hedgerow habitat, at least for the rich fauna that intensely uses ground habitats. In France notably, technical guidelines totally neglect the role of shelter availability and the potential importance of bank habitat on hedge-dependent species. In fact, the base of newly planted hedges is systematically cleaned for aesthetic reasons and/or regularly covered with protective films or Ramial wood chips that offer limited refuges.

Further studies are needed to accurately assess the role of the ground refuges for the biodiversity of hedgerows in different agricultural conditions and various landscapes. It is likely, however, that maintaining a diversity of terrestrial microhabitats and substantial shelter availability along the base of hedges will benefit to a wide array of animal species. A change will likely be needed in the management strategies applied to hedges, and their aesthetic value in the landscape. Maintaining suitable microhabitats at the base of hedgerows might also be crucial for dispersal of cryptic and secretive species that are reluctant to cross open areas (Tschamtko et al., 2005). Sedentary species that are typical inhabitants of the hedgerows should be targeted because they frequently use ground refuges rather than the foliage of the trees and shrubs. Successful





**Fig. 7.** Morphospecies richness (Y-axis, unbiased Chao 1 unbiased estimates) was plotted as a function of sampling effort (X-axis, cumulative field sessions) in different hedges (N = 69). The hedges were grouped according to varying availability (high, medium, low, see text) of ground shelters at their base (SQ, shelter quality), or considering the covering vegetation (VQ, vegetation quality). Repeated surveys were performed using a protocol based on non-lethal trapping with corrugated slabs regularly lifted and inspected (see Lecq et al., 2015 for details). For comparison we retained the minimal number of field sessions for all analyses (N = 85). The dashed line indicates the maximal number of morphospecies estimated (280).

simple habitat management actions to promote shrubs (hence shelter availability) and reptile populations in urbanized areas provide encouraging results (Bonnet et al., 2016) suggesting that current guidelines for hedge plantations can be improved and effectively accepted by farmers. Unfortunately, ground refuges and associated microhabitats at the base of hedgerows are currently neglected by conservationists and field managers (Staley et al., 2015); including those that specifically promote the restoration of hedgerows to favour animal biodiversity (Hinsley and Bellamy 2000; Pereira and Rodríguez, 2010).

#### 4.3. Conclusions and practical recommendations

Practically, in agricultural landscapes and for hedge plantations in general, retaining various materials (e.g. stones, logs) to build banks with abundant ground refuges is a simple approach that should be recommended. For example, raw materials extracted by excavation equipment to prepare trenches for tree plantation should be retained, not compacted, and used to form a bank at the base of the hedgerows. The bank might be supplemented by large stones and logs to create various microhabitats. This strategy would simultaneously save time and energy because it minimizes

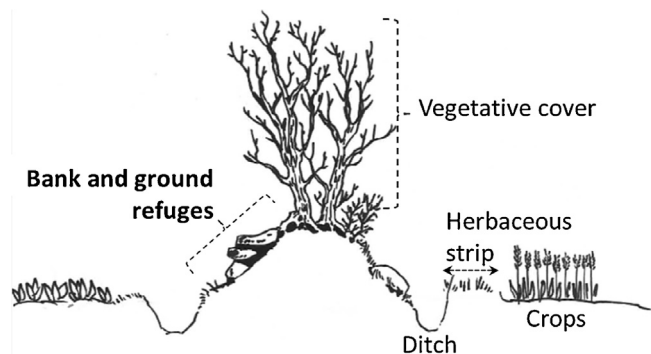
the effort to remove (or compact) excess materials from the site (e.g., earth, stones). Implementing these recommendations into guidelines is important and timely.

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#### Appendix A.

Schematic view (transverse section) of a typical intact hedgerow characterized by a well-developed vegetative cover (>2 m height), a bank with large stones (<20 cm diameter), logs, ditches, and herbaceous strips. This type of hedgerow typically results from traditional agricultural management.



## Appendix B.

Primary variables used to describe the hedgerows. Three main groups were considered: Vegetative cover refers to the trees and shrubs linearly arranged along the main axis of the hedgerow. Tree openness represents the percentage of ground covered by trees and shrubs. Bank and ground refuges refer to the dimension of the bank and to the availability of various ground refuges (e.g. stones, logs, burrows). Others refer to the elements that border the bank, ditches and herbaceous strips notably. Bramble stands for *Rubus fruticosus*, Ivy for *Hedera helix*.

Groupings of variables	Variable	Details	Code
Vegetative cover	Tree coverage	Linear% covered by trees	Tree V.1
	Shrub coverage	Linear% covered by shrubs	Tree V.2
	Tree height	See text	Tree V.3
	Shrub height	See text	Tree V.3
	Canopy width	See text	Tree V.4
	Tree openness	Permeability of the hedge (%)	Open V.1
	Bank and Ground refuges	Bank height	See text
Bank width		See text	Bank V.2
Stone coverage		See text	Stone V.1
Stone height		See text	Stone V.2
Bank openness		% of bank exposed to the open	Open V.2
Grass coverage		% of ground covered by grass	Grass V.1
Grass height		See text	Grass V.2
Ground shelter density		Stones and logs per m <sup>2</sup>	Shelter V.1
Debris coverage		% of ground covered	Shelter V.2
Debris height		Thickness of debris layer	Shelter V.3
Bramble coverage		% of ground covered	Shelter V.4
Bramble height		See text	Shelter V.5
Others		Ditch depth	See text
	Ditch width	See text	Bank V.4
	Herbaceous strip width	See text	Open V.3
	Bare soil coverage	% of bare soil	Open V.4
	Bare soil height	Height of corrugations	Open V.5
	Poaceae coverage	% of ground covered	Open V.6
	Poaceae height	See text	Open V.7
	Litter coverage	% of ground covered	Litter V.1
	Litter height	Thickness of layer	Litter V.2
	Moss coverage	% of ground covered	Litter V.3
	Moss height	Thickness of layer	Litter V.4
	Ivy coverage	% of ground covered	Litter V.5
	Ivy height	Thickness of layer	Litter V.6
	Dicotyledon coverage	% of ground covered	Litter V.7
	Dicotyledon height	Thickness of layer	Litter V.8

## Appendix C.

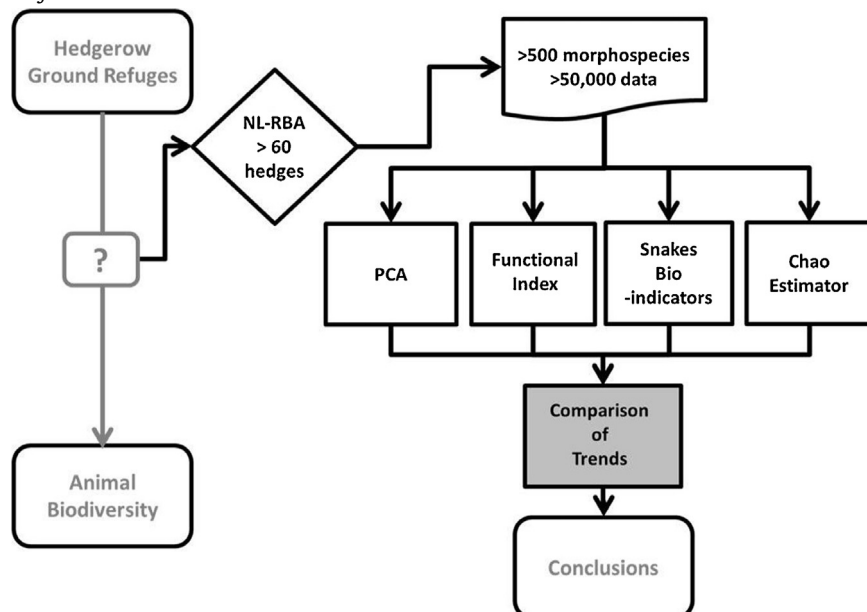
Selected morphospecies frequently observed in the 69 hedgerows sampled among more than 500 morphospecies. This selection was biased toward common species (for conciseness) and reptiles that were also used as bio-indicators (see text). Individuals were identified at the species level, family level, or at a broader taxonomic level. Body mass (g) and metabolic mode were key variables used to calculate the ecological rank (see text). A principal

habitat indicates the main habitat or microhabitat used by the morphospecies. Grass mean herbaceous layer. Foliage includes tree and shrub leaves. Shelter means various refuges like under stones or logs for instance.

Morphospecies	Code	Family	Body mass	Metab. mode	Ecol. rank	Principal habitat
Owl sp. (e.g. <i>Tyto alba</i> )	Aves1	Strigidae	410	Endo	92.59	Trees
<i>Ectobius pallidus</i>	Blat1	Blattellidae	0.03	Ecto	2.48	Litter
<i>Altica</i> sp.	Cole1	Chrysomelidae	0.02	Ecto	2.36	Grass
Cicadellidae	Cole2	Cicadellidae	0.01	Ecto	2.15	Grass
<i>Coccinella septempunctata</i>	Cole3	Coccinellidae	0.04	Ecto	10.41	Foliage
Woodlouse	Crus1	NA	0.09	Ecto	2.97	litter
Crane fly sp.	Dipt1	Tipulidae	0.17	Ecto	3.23	Grass
Mosquito sp.	Dipt2	Culicidae	0.03	Ecto	3.23	Openness
Syrphidae sp.	Dipt3	Syrphidae	0.05	Ecto	2.73	canopy
<i>Arion rufus</i>	Gast1	Arionidae	5.1	Ecto	4.7	Grass
<i>Cepaea</i> sp.	Gast2	Helicidae	0.91	Ecto	3.96	Grass
<i>Clausiliidae</i> sp.	Gast3	Clausiliidae	0.19	Ecto	3	Shelter
<i>Helix aspersa</i>	Gast4	Helicidae	9.21	Ecto	4.97	Grass
<i>Hygromiidae</i>	Gast5	Hygromiidae	0.27	Ecto	3.44	Grass
<i>Pomatia elegans</i>	Gast6	Helicidae	0.45	Ecto	3.65	Grass
Snail sp.	Gast7	NA	NA	Ecto	4.28	Grass
<i>Theba pisana</i>	Gast8	Helicidae	1.22	Ecto	4.05	Grass
Aphid sp.	Hemi1	Aphididae	0.002	Ecto	1.26	Foliage
<i>Graphosoma italicum</i>	Hete1	Pentatomidae	0.09	Ecto	2.79	Foliage
<i>Pyrrhocoris apterus</i>	Hete2	Pyrrhocoridae	0.05	Ecto	7.81	Foliage
<i>Xanthochilus saturnius</i>	Hete3	Lygaeidae	0.03	Ecto	9.94	litter
Ant hill X sp.	Hyme1	Formicidae	0.004	Ecto	5.05	Grass
Ant hill Y sp.	Hyme2	Formicidae	0.02	Ecto	9.21	Trees
<i>Apis mellifera</i>	Hyme3	Apidae	0.11	Ecto	3.04	Openness
<i>Polistes</i> sp.	Hyme4	Vespidae	0.08	Ecto	11.69	Openness
<i>Adela</i> sp.	Lepi1	Coleophoridae	0.03	Ecto	2.46	Foliage
<i>Yponomeuta</i> sp.	Lepi2	Yponomeutidae	0.04	Ecto	2.62	Foliage
<i>Apodemus</i> sp.	Mamm1	Muridae	25	Endo	10.8	Grass
<i>Erinaceus europeus</i>	Mamm2	Erinaceidae	1000	Endo	70.01	Shelter
<i>Martes</i> sp.	Mamm3	Mustelidae	1200	Endo	99.12	Trees
<i>Myocastor coypus</i>	Mamm4	Myocastoridae	6000	Endo	15.56	Bank
<i>Capreolus capreolus</i>	Mamm5	Cervidae	20000	Endo	16.6	Trees
Shrew sp.	Mamm6	Soricidae	8.5	Endo	43.3	Shelter
Micromammal sp.	Mamm7	NA	23	Endo	10.73	Grass
<i>Microtus</i> sp.	Mamm8	Muridae	35	Endo	11.09	Grass
<i>Vulpes vulpes</i>	Mamm9	Canidae	5500	Endo	108.38	Trees
Mantis	Mant1	Mantidae	1	Ecto	16	Grass
<i>religiosa</i>	Orth1	NA	0.14	Ecto	3.14	Grass
Grasshopper sp.	Orth2	Gryllidae	0.5	Ecto	11.17	Shelter
<i>Gryllus campestris</i>	Orth3	Tettigoniidae	0.3	Ecto	10.99	Grass
<i>Tettigonia viridissima</i>	Orth4	Tettigoniidae	0.15	Ecto	10.17	Grass
<i>Bacillus rossius</i>	Phas1	Phyllidae	NA	Ecto	4	Foliage
<i>Coluber</i> sp.	Rept1	Colubridae	205	Ecto	44.19	Shelter
<i>Zamenis longissimus</i>	Rept2	Colubridae	200	Ecto	44.11	Shelter
<i>Lacerta bilineata</i>	Rept3	Lacertidae	36	Ecto	27.79	Shelter
<i>Natrix natrix</i>	Rept4	Colubridae	266	Ecto	38.56	Shelter
<i>Podarcis muralis</i>	Rept5	Lacertidae	8	Ecto	24.52	Shelter
<i>Vipera aspis</i>	Rept6	Viperidae	104	Ecto	42.13	Shelter
<i>Hierophis viridiflavus</i>	Rept7	Colubridae	209	Ecto	44.25	Shelter
Araneidae sp.	Spid1	NA	NA	Ecto	11.72	Shelter
<i>Araneus diadematus</i>	Spid2	Araneidae	0.15	Ecto	12.71	grass
<i>Drassodes cupreus</i>	Spid3	Gnaphosidae	0.14	Ecto	12.59	Shelter
<i>Lycosa</i> sp.	Spid4	Lycosiidae	0.45	Ecto	14.62	Shelter
Salticidae sp.	Spid5	Salticidae	0.02	Ecto	9.14	Grass
<i>Tegenaria</i> sp.	Spid6	Agelemidae	0.22	Ecto	13.37	Shelter
<i>Zelotes</i> sp.	Spid7	Gnaphosidae	0.05	Ecto	10.92	Shelter

## Appendix D.

Flowchart as an overview displaying the main question addressed (left part, grey typescripts), the method used (right part in black typescripts), and the conclusion (bottom right, grey typescripts). The main question of this study was to examine if the availability of ground refuge situated at the base of agricultural hedgerows influence animal biodiversity. We used non-lethal rapid biodiversity assessments (NL-RBA, see Lecq et al., 2015 for details) to sample a wide range of taxa in 69 hedges presenting contrasted characteristics in terms of refuges and plant cover. We collected abundant observations on many morphospecies. We used four complementary analyses to compare the hedges. Principal component analyses and inertia analyses (PCA) based on the diversity of the morphospecies. A functional index accounting for the characteristics of the morphospecies (e.g. body mass, trophic level). We focused on snakes as top predators that intensively use ground refuges. And we estimated (morpho)-species richness through repeated survey to run unbiased Chao-estimator. We then compared the four trends. All analyses suggested that ground refuge availability positively influence the animal biodiversity indexes used.



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