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# Effects of hedgerows on bats and bush crickets at different spatial scales

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#### ABSTRACT

Biodiversity is threatened by the loss and fragmentation of habitats. The role of hedgerows in maintaining biodiversity is well established, but few studies have addressed the importance for biodiversity of the intrinsic characteristics of hedgerows and the quality of hedgerow networks along a spatial scale. We examined three quality indices providing information at different territorial levels: density in the landscape, structural diversity and wood production. We performed an acoustic survey in a grassland to estimate the species abundance and community composition of bats (9 taxa) and bush crickets (11 species). Using an approach based on species and traits, we assessed how hedgerow quality influenced the activity of these taxa at different spatial scales (from 50 to 1000 m) and focused on three types of traits: bush cricket mobility ability, bat foraging strategy and habitat specialization. In general, our results showed the importance of hedgerow quality for bats and bush crickets, but the strength of the association between taxa and hedgerows varied substantially among the species and the spatial scales. Although it depends on the taxa, the production, density and structural diversity of hedgerows each had an overall positive effect. Our results suggested that these effects were generally more important at large scales. The scale effect of the production index is the best predictor of activity for bat and bush cricket taxa and traits. Our results showed the importance of hedgerow quality for the ecology of bat and bush cricket communities and could be used to improve conservation management.

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#### 1. Introduction

Over the last century, agricultural intensification, particularly the increase in agricultural parcel sizes, has had severe consequences for biodiversity (Robinson and Sutherland, 2002). At the landscape scale, one consequence of such intensification is the widespread removal of linear landscape elements in Europe (Robinson, 1997; Sklenicka et al., 2009) and also of large patches of semi-natural habitats, such as forests and grasslands, even though the ecological importance of hedgerows and linear landscape elements has been known for decades (i.e., Burel, 1992; Beier and Noss, 1998; Bennett, 2003). Hedgerows play a role in the control of water flow, water level and water quality (Mérot, 1999; Baudry et al.,

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http://dx.doi.org/10.1016/j.actao.2016.01.009 1146-609X/© 2016 Elsevier Masson SAS. All rights reserved. 2000). They provide breeding habitat, food resources and dispersal pathways for many species of birds (Hinsley and Bellamy, 2000), amphibians (Scribner et al., 2001; Rosenberg et al., 1998; Brown et al., 2006), mammals (Henderson et al., 1985; Pardini et al., 2005) and invertebrates (Burel, 1992; Hannon, 2009).

However, to our knowledge, the effects of the quality of linear elements, such as hedgerows (e.g., their diversity of structure and wood production), at different scales, on biodiversity have been poorly considered in previous studies, except in Pywell et al. (2004) and Dainese et al. (2015). Nevertheless, these effects are of interest because many agri-environmental schemes provide financial support for environmentally sensitive hedgerow management. The effectiveness of such initiatives in terms of both financial costs and biodiversity gains can be improved through a better understanding of the benefits provided by different types of hedgerows in different landscape contexts (Boughey et al., 2011).

In this paper, we present a study of bats and bush crickets, both of which are known to take advantage of the presence of hedgerows, and which have been detected and identified based on their





calls, recorded by detectors. Bats (Chiroptera) and bush crickets (Orthoptera) represent complementary ecological indicators of biodiversity quality. Bazelet and Samways (2011) identified bush crickets as good bioindicators for the assessment of the habitat quality of ecological networks because they respond strongly to management practices, such as grazing intensity (Jauregui et al., 2008) and mowing regime (Gardiner and Hassall, 2009). Bush crickets belong to an invertebrate group that is abundant in grasslands, have a short life cycle and are at a low level in the food chain (mainly herbivore species and some omnivores) compared to bats. Although the importance of linear landscape elements is poorly understood for bush crickets, they have nevertheless been described to be useful for their dispersal behavior (Berggren et al., 2002) and colonization success (Berggren et al., 2001). Thus, we hypothesized that bush crickets could be sensitive to hedgerows at small spatial scales in accordance with Reinhardt et al. (2005). Bat species have a long life cycle relative to bush crickets. In the study areas, bats are all nocturnal insectivores at the top of the food chain (Dietz et al., 2009). They are considered to be bioindicators (Jones et al., 2009) because they react to several stressors, including the loss of landscape elements, which impacts their abundance, distribution and activity (e.g., Boughey et al., 2011). Moreover, all bat species are protected in Europe (IUCN, 2011). The primary predictor of bat abundance is the quality of the habitat, which is positively related to the availability of vegetation corridors (Walsh and Harris, 1996; Hein et al., 2009) and to the density of linear elements (Verboom and Huitema, 1997). Based on the size of the foraging home range of the bat (see Davidson-Watts and Jones, 2005; Perez-Jorda and Ibañez, 1991), we hypothesized that bats could be sensitive to hedgerows at large spatial scales, in accordance with Bellamy et al. (2013) and Frey-Ehrenbold et al. (2013).

Many studies have been performed on the effects of the density and connectivity of linear landscape elements on the movement and dispersal of species (Erickson et al., 2013; Berggren et al., 2001, 2002; Diekötter et al., 2007; Boughey et al., 2011). However, little is known about how the quality of linear elements affects their use by bats because the only studies that show such effects are 'Boughey et al. (2011) and Verboom and Huitema, 1997', and even less is known about bush crickets; thus, we need to better understand the relationship between biodiversity and the quality of linear landscape elements (Hein et al., 2009).

To study linear element quality, we examined three hedgerow characteristics: (1) density within the landscape (density) (2) potential wood production (production) and (3) structural diversity (diversity). Indeed, each of these three indices provides information at different land levels and involves different stakeholders. Density reflects the history of successive agricultural policies (changing the division of lands) at the landscape scale, whereas production and structural diversity are more linked to local farming practices. Thus, these three indices provided information on the management of the land at different scales, which is important because spatial processes are known to influence the structure and dynamics of animal populations and communities (Cottenie, 2005).

In this study, we used two approaches: 1) a species approach in which we tested the effects of the linear element quality on the activity of the species and 2) a trait based approach in which we tested the same effects on several traits (e.g., habitat specialization, bat foraging strategy and bush cricket mobility ability). The trait approach can provide information on the mechanisms involved in the use of different types of hedgerows by bat and bush cricket communities. Such information is essential for developing effective conservation plans and can be used to improve forest and agriculture management strategies.

#### 2. Materials and methods

#### 2.1. Study area

The study was conducted in western France, in the Loire delta, between the cities Nantes and Saint-Nazaire, in a European network of the protected area "Natura 2000" (Fig. 1). The site is mainly composed of extensively managed grassland grazed by cattle and surrounded by a dense network of hedgerows. The grassland was identified as having a high nature conservation value by Veen et al. (2009).

#### 2.2. Sampling design and scale approach

We employed a random stratified design in which 51 point counts were sampled in the grassland, the dominant habitat in the studied site. The point counts were positioned according to two criteria: 1) more than 50% of grassland in the 500 m buffer and 2) at three classes of distance from the hedgerow: 23 point counts at 0 m (i.e., in the hedgerow), 17 at 25 and 11 at 50 m from the hedgerow. These two criteria, "proportion of grassland in the buffer" and "distance to the hedgerow", were not correlated (rho = 0.09, p value = 0.378) and were therefore included as covariables. To measure the effects of the characteristics of the linear landscape elements at different scales, we used ArcGIS 9.3 and a local landuse database (Geffray, 2010). Previous studies linked environmental variables at a few spatial scales with the abundance of bush crickets (Batáry et al., 2007; Braschler et al., 2009; Diekötter et al., 2007; Penone et al., 2013b) and bats (Bellamy et al., 2013; Lookingbill et al., 2010; Dixon, 2012; Hale et al., 2012), and we defined 11 circular buffers (radii of 50 m and every 100 m until 1000 m) around each point count that defined our sampling plots (a correspondence scale of areas depending on the buffer size used in this study and areas obtained with a doubling of surfaces is provided in Appendix C). Within these circular buffers, we extracted landscape



**Fig. 1.** Positions of point counts in the study site (A) and an enlargement showing the 3 distances from the hedgerow (0 m, 25 m and 50 m) (B).

characteristics: the proportion of semi-natural habitat area (grasslands) in each plot (for 500 m buffers around the 51 point counts, mean =  $73.6\% \pm 1.6\%$  SE) and the 3 indices of the quality of linear landscape elements in each plot: 1) the density, i.e., length per unit of studied area, 2) the structural diversity and 3) the wood production.

#### 2.3. Linear landscape element and hedgerow indices

We calculated the three indices for each study plot. To describe the density of linear elements, we calculated the sum of their lengths in meters within the buffer zones. To describe the structural diversity, we used Shannon's diversity index (Shannon and Weaver, 1949) and a database (Geffray, 2010) that described the linear landscape elements in six categories: (1) alignment of trees, (2) riparian vegetation, (3) shrub hedgerows with only shrubs, (4) wooded hedgerows without the presence of shrubs, (5) threestrata hedgerows (tree, shrub and herb). The production index is a measure of the wood volume contained by the linear element (in m3). Hereafter in this study, linear landscape elements will be termed hedgerows in accordance with Baudry and Jouin (2003), who defined a hedgerow as a line of trees and/or shrubs. The production index is calculated from the length of the hedgerow and a coefficient of density for the woody elements given by the database (Geffray, 2010) (see Appendix A). The diversity is not correlated with the production (for 500 m buffer: rho = 0.124, p value = 0.215) or the density (for 500 m buffer: rho = 0.117, p value = 0.241), whereas there is a correlation between density and production (for 500 m buffer: rho = 0.961, p value < 0.001), which makes sense because the more trees present in an area, the greater the timber production. The high value of the last correlation implies the necessity of performing separate analyses of hedgerow indices.

#### 2.4. Bat sampling

Bat activity was assessed by recording bat calls using a Tranquility Transect Bat detector (Courtpan Design Ltd., Cheltenham, UK) with direct and continuous recording on a Zoom H2 digital recorder (Zoom Corporation, Tokyo, Japan) at a sampling rate of 96 ks/s in.wav format. From the two possible outputs of the detector, time expansion and high frequency, we only used the second output, which did not include a trigger on sound volume. We placed one detector at each station at a height of 1.50 m above the ground and facing away from the hedgerow. Each station was monitored twice in 2011. The first monitoring session was from June 15th to July 31st, during which female bats are known to give birth and to feed their offspring. The second monitoring session was performed from August 15th to September 30th, during which the young are flying and individuals are suspected to be less dependent on their reproductive roost. For each station, we recorded two 30-min sound samples (one per session). This sampling occurred during the bat activity peak, which begins 30 min after sunset and spans 4 h (Roche et al., 2005). Correlation between sampling point characteristics (density/diversity/production) and covariables are presented in Appendix D. The sampling was only performed when weather conditions were favorable, i.e., no rain, low wind speed and temperature higher than 12 °C. Hourly cloud cover, temperature and wind speed data were retrieved from a local weather station (Météo France, 2012). We studied bat calls within bat passes (Thomas et al., 1989). Species calls were identified at the species level by the authors using Scan'R (Binary Acoustic Technology, 2010) to isolate each bat vocalization and automate the measurement of relevant parameters and Syrinx software version 2.6 (Burt, 2006) for spectrogram analyses (for more details see Appendix E and Lacoeuilhe et al., 2014); exceptions included vocalizations of *Plecotus austriacus* and *Plecotus auritus*, which were pooled as *Plecotus spp.*, and those of *Myotis myotis, Myotis daubentonii, Myotis mystacinus, Myotis nattereri* and *Myotis bechsteinii*, which were pooled as *Myotis* spp., due to their very low occurrence and some uncertainties in identification. We used the number of calls per 30 min as a proxy for the measure of bat activity. We distinguished two guilds according to their foraging traits: "gleaning bats" which include *Myotis* and *Plecotus* species that mainly eat diurnal brachyceran Diptera and non-volant arthropods, such as weevils, lepidopteran larvae, harvestmen and spiders (Audet, 1990; Swift and Racey, 2002; Dietz et al., 2009), and "aerial hawking bats" which include *Pipistrellus* species, *Eptesicus serotinus* and *Nyctalus* species that mainly search the sky for prey (Schnitzler et al., 2003; Holderied and von Helversen, 2003) (Appendix B1).

#### 2.5. Bush cricket sampling

Because bush crickets produce mating calls (Ragge and Reynolds, 1998), it is possible to collect large standardized data sets using recording devices (Penone et al., 2013a). Bush cricket calling songs have a role in pre-mating isolation, and their structure is an important component of their mate recognition system (Paterson, 1985). Therefore, the analysis of calling songs may allow identification to the species level (Ragge and Reynolds, 1998) and even provide reliable information on species abundances (Fischer et al., 1997). Nevertheless, it does not give an exact estimation of species abundances mainly because only adult males stridulate. However, this method can provide relative measures of abundance (rather than absolute abundance), which is adequate for detecting spatial changes in species abundances and for detecting anthropogenic pressures on bush cricket communities (Penone et al., 2013b). For species with uninterrupted calls such as Tettigonia viridissima, Ruspolia nitidula, Metrioptera roeselii and Phaneroptera falcata, it was not possible to determine a value of abundance because their syllables are emitted at a continuous and quick rate (10-100 per second), which does not allow the easy distinguishing of several individuals singing simultaneously. Thus, we only noted their presence/absence, while for other species, with interrupted calls, we counted the number of calls of each species in each sample point as a proxy for relative measures of their activities.

We detected 11 species from the Tettigoniidae community and distinguished two mobility traits according to Reinhardt et al. (2005) and Marini et al. (2010): mobile (mostly with wings) and sedentary (Appendix B2).

#### 2.6. Mean trait community index

#### 2.6.1. Habitat specialization index

Each species was characterized for habitat specialization through the calculation of a Species Specialization Index (SSI) following the Julliard approach (Julliard et al., 2006). To define habitat specialization for bush crickets, we used the SSI indices assessed by Penone et al. (2013a). For bat SSI calculation, we used an independent data set provided by the national biodiversity monitoring scheme coordinated by the French National Museum of Natural History (http://vigienature.mnhn.fr/; for more details on the data set used, see Appendix F). The SSI was calculated for each species using the coefficient of variation of the species' abundance across habitats (Appendices B1, B2, and F). We calculated the Community Specialization Index (CSI) as the arithmetic mean of the SSI of the detected species weighted by the abundances (Julliard et al., 2006) (see Appendix F). Because of the lack of SSI for some species, CSI values were calculated on 85% of the total of bush cricket calls, whereas for the bats, all calls contribute to the assessment of CSI.

#### 2.6.2. Mobility trait

For dispersal ability of bush crickets, according to Reinhardt et al. (2005) and Marini et al. (2010) we conducted analyses by summing, on the one hand, the abundances of mobile species, and on the other hand, the abundances of sedentary species. Two species (*P. albopunctata* and *M. roeselii*) had intermediate dispersal ability; thus, they were removed from the analyses on this trait, but they represented only 14.4% of the total calls.

#### 2.6.3. Foraging strategy trait

Based on Dietz et al. (2009), we conducted analyses by summing, on the one hand, the abundances of aerial hawking species, and on the other hand, the abundances of gleaner species. As *B. barbastellus* (only 0.9% of total calls) had a mixed foraging type, this species was removed from the analyses of this trait.

For the bat community approach (foraging strategy trait and CSI), we corrected the bat activity by their distance of detection (see coefficients of detection in Barataud, 2012) before calculating the community indices.

#### 2.7. Statistical analysis

## 2.7.1. The influence of hedgerow characteristics on bat and bush cricket species

We assessed the influence of the three indices of hedgerows (density, diversity and production) on bat and bush cricket species using a generalized linear model (GLM).

The response variables were (i) abundance of bush crickets' stridulations (n = 11 species) or bat foraging calls (n = 9 taxa) and (ii) community traits (for bush crickets: species dispersal abilities and CSI and for bats: foraging type and CSI) per site (n = 51).

In our model, the explanatory variables were density, structural diversity and potential of wood production. Because wood production and density are correlated (see 2.3), we constructed a model of each explanatory variable.

We considered a set of covariables, date, temperature, wind speed, and time after sunset (in minutes), because they could also influence bush cricket or bat activities. To test the effect of hedgerow characteristics in taking into account the landscape structure, we also included in the model the distance of each station to the nearest hedgerow and the proportion of seminatural habitat within the 11 buffer zones described above. We took into account the influence of covariables to study the hedgerows' characteristic variables. First, we systematically evaluated the correlations among explanatory variables using Spearman's rho for quantitative variables (Crawley, 2009) (see Appendix D) to detect obvious correlation. Secondly, we performed varianceinflation factor (VIF) on the full models (Fox and Monette, 1992); all variables had VIF<5, indicating no problem of multicollinearity in the explanatory variables of our models. To account for spatial autocorrelation, we added an autocovariate (i.e., a distanceweighted function of neighboring response values; Dormann et al., 2007) with the autocov\_dist function in R (package spdep, Bivand, 2011).

Thus, for each species of bat and bush cricket and for each of the 11 buffer zones, our full statistical models were structured as follow:

$$[species activity]_i \sim date + time after sunset + temperature$$

- + wind speed
- + *distance to the nearest hedgerow*
- + proportion of grassland<sub>i</sub>
- + hedgerow characteristic<sub>i</sub> + autocovariate<sub>i</sub>

where *i* is the buffer size considered (from 50 m to 1000 m radii) and *hedgerow characteristic* is the characteristic considered (density, structural diversity or potential of wood production).

Because of the expected non-normal distribution of bat and bush cricket species calls, and the possible high frequency of zero, we followed Potts and Elith (2006) and Vandevelde et al. (2014) performing four GLMs according to the nature of the response variable (count of bat and bush cricket calls) for each tested species: one with a Poisson error distribution (GLM-P), one with a negative binomial distribution (GLM-NB) and two with a zero-inflated GLMs (Zuur et al., 2010): one with a Poisson error distribution [ZAP] and one with a negative binomial [ZANB]; (R package pscl, Jackman et al., 2012). The zero inflated models were hurdle models (ZAP and ZANB) that consider presence and absence data (with a binomial function) and analyze the presence data in a second step with a count model (Poisson or a negative binomial) (Zuur et al., 2009). Finally, based on the patterns of residuals (as recommended by Zuur et al. (2009) to choose the appropriate modeling), we selected ZANB for all species, except for Plecotus spp., the gleaner group and community specialization indices, for whish we used GLM-NB (see Appendix G). For all species, we used the count model (Zuur et al., 2009) of the ZANB to account for their activity; for species with uninterrupted calls (Appendix B2) and species with a very low occurrence (Barbastella barbastellus), we focused on the presence/ absence and used the binomial model of the ZANB (Zuur et al., 2009). From the full model, using a buffer size of 500 m, we performed a backward selection based on Akaike's information criterion (AIC). The final models for each species and community are presented in Appendix G; note that, exploratory treatment indicate that the procedure of covariable selection is not sensitive to buffer size. Finally, based on the foraging or mobility traits for each bat and bush cricket species and community, we tested the same model taking into account the covariables and measures of hedgerow quality in the landscape (density, diversity and productivity). We can compare the different explanatory variables (indices) using AIC comparisons.

# 2.7.2. Effect of hedgerow characteristics at different landscape scales

2.7.2.1. Step 1: calculation at a given scale. For a given species and for each of the eleven buffer sizes, from 50 m to 1000 m, we used the same final model to test the effect of each hedgerow index (density, diversity or production) on the activity of each species or the community index (forage, mobility and CSI), taking into account significant co-variables. Because we used the same model to test the effect of each index at all scales, we were able to directly compare the value of the estimate of the effect or goodness of fit of model (AIC) of indices for one species or community between different spatial scales. However, we could not perform direct comparisons between species or communities (see Appendix G).

2.7.2.2. Step 2: calculation across scales. Next, we tested whether the slope of the relationship between the dependent variable (species activities and community traits) and the hedgerow indices changed with the scale. Thus, we tested the effect of the buffer sizes on estimates from previous models using a GLM with a normal

error structure because the response variable was normally distributed (hereafter referred to as 'scale analysis') (see Appendix G3). Following the approach of Penone et al. (2013a), we assigned the response variable (i.e., estimate of slope) different weights according to the associated standard error (1 per SE<sup>2</sup>) obtained from the previous analysis. Buffer size effects were adjusted to variables using a type II ANOVA. When we did not detect a linear effect across the buffer size range (from 50 to 1000), we used the exploratory approach of broken-line models. Broken-line models are regression models in which the relationships between the response and explanatory variables are piecewise linear, represented here by two straight lines connected at unknown values: these values are usually called breakpoints (Package segmented, Muggeo, 2008) (see Appendix H). All p values were corrected for potential overdispersion according to the Faraway (2006) approach. All analyses were performed with R software (R Development Core Team, 2011).

#### 3. Results

A total of 35,263 bat calls belonging to 14 species were recorded at the 51 point counts during the two periods. The majority of echolocation calls from the 14 bat species came from three *Pipistrellus* bats (*Pipistrellus pipistrellus* (48.5%), *Pipistrellus kuhli* (24.4%) and *Pipistrellus nathusii* (21.2%)). For bush crickets, we detected 101,419 calling songs belonging to 11 species from the Tettigoniidae family (Appendix B2). For more details on average activities of bats and bush crickets, see Appendix I.

#### 3.1. Effect of the wood production of hedgerows

#### 3.1.1. The effect of the wood production of hedgerows on bats

We obtained 104 positive estimates of which 44 were significant and 28 negative estimates of which 3 were significant (see Appendix J3). The activity of bat species was generally positively correlated with the wood production of hedgerows, as shown in Fig. 2, and the effect was stronger at larger spatial scales (see Appendix J3). Considering the aerial bat species (Fig. 2e), we found that 1) for example, with the 1000 m buffer, their activity is positively (i.e., above zero) correlated with the wood production of the hedgerow (the estimate reported from the modeling at 1000 m – with its standard error), and this effect is significant, as indicated by the asterisk; and 2) the scale effect, obtained from the linear regression, from 50 m to 1000 m, was significant and is shown by the dotted line.

Thus, the activity of aerial bat species was significantly and positively correlated with the wood production in a 1000 m buffer. The scale effect obtained from linear regressions was significant and there is a positive scale effect for these communities (above zero). When we did not detect a linear scale effect, we assessed a potential breakpoint value (see also Appendix H).

# 3.1.2. The effect of the wood production of hedgerows on bush crickets

We obtained 108 positive estimates, of which 16 were significant and 56 negative estimates of which 15 were significant (see Appendix J3). The wood production of hedgerows had a positive influence on the activity of all bush cricket species (see Fig. 3) and the influence was greater when the spatial scale was large, except for the sedentary species and *Uromenus rugosicollis*, for which results were the inverse of the other species: wood production was negatively correlated with their activities and this effect was stronger when the spatial scale was large (see Appendix J3).

#### 3.2. Effect of the density of hedgerows

#### 3.2.1. The effect of the density of hedgerows on bats

The density of hedgerows had a generally positive effect on the foraging activity of the studied bat species and communities based on the studied traits. Among the 132 estimates ( $(9 \tan 4 + 3 \text{ community indices}) \times 11$  buffer sizes) we generated for bats, we obtained 106 positive estimates, of which 33 were significant, and 26 negative estimates, of which only 4 were significant (see Appendix J1). The greater the hedgerow density around the point count, the more numerous were the bat calls. We observed this effect at almost all the spatial scales we studied. Moreover, we found that the larger the scale, the stronger the effect (observed in 9 out of 12 cases, see Table 1 and Appendix J1); therefore, we suggest that the density of hedgerows significantly and positively influenced the activity of the bat species and the two guilds at increasingly large spatial scales (see Appendix K1).

#### 3.2.2. The effect of the density of hedgerows on bush crickets

The effect of density on bush crickets' activity was less marked than for bats and depended on the species studied and on their mobility. Among our 154 estimates (((11 taxa +4 community indices)-(1 non-convergent model)) x 11 buffer sizes), we obtained 96 positive estimates, of which 15 were significant and 68 negative estimates, of which 11 were significant (see Appendix J1).

Moreover, the obtained positive effect increased at a large scale (>500 m) for *T. viridissima*, *R. nitidula* and *Pholidoptera griseoaptera*, whereas the effect was negative and became stronger at a large scale for *U. rugosicollis*. Two contrasting patterns were observed for the two communities based on their mobility traits. The activity of mobile species of bush crickets appeared to increase with the density of the hedgerows and to increase more strongly at large scales, whereas the opposite effect was observed for sedentary species whose activity decreased in the presence of high-density hedgerows, especially at large scale (see Appendix K2).

#### 3.3. Effect of the diversity of hedgerows

#### 3.3.1. The effect of the diversity of hedgerows on bats

We obtained 91 positive estimates, of which 30 were significant and 41 negative estimates, of which 12 were significant (see Appendix J2). This effect was weaker at larger scales and had a break point at approximately 500 m (see Appendix L1 and J2). Moreover, we obtained contrasting and opposing patterns for aerial and gleaner species. The latter showed decreased activity with increasing hedgerow diversity at all scales, whereas the activity of the aerial species increased until 500 m and then decreased at larger spatial scales. Unlike other gleaner species, the activity of *Myotis* spp. increased with hedgerow diversity, especially at large spatial scales (see Appendix J2 and L1).

#### 3.3.2. The effect of the diversity of hedgerows on bush crickets

Among the 110 estimates (((11 taxa + 4 community indices) – (5 non convergent models)) × 11 buffer sizes), we obtained 88 positive estimates, of which 12 were significant, and 72 negative estimates, of which 24 were significant (see Appendix J2). *T. viridissima* and *U. rugosicollis* activities increased with diversity at scales larger than 500 m (see Appendix L2). However, the activities of *R. nitidula* and *P. griseoaptera* decreased with hedgerow diversity at all spatial scales, and the effect was stronger at large spatial scales (see Appendix L2). Hedgerow diversity had a positive effect on the activity of the mobile species, but the effect decreased and became negative for buffers of 800 m and larger, whereas the activity of sedentary species increased with the diversity of hedgerows, and this effect was stronger at large spatial scales (see Appendix L2).



### **Buffer size (meters)**

Fig. 2. Effect on bats of the production of hedgerows at different spatial scales. On the Y-axis: estimates of the relationships between production and activity of 4 different species and activity of aerial and gleaner species. 6 graphs are presented: 4 species (a, b, c, d) with various ecologies and 2 traits (e, f). Asterisks indicate significance. The dotted line shows the scale effect obtained from linear regressions.



Fig. 3. Effect on the bush crickets of the hedgerow production at different spatial scales. On the Y-axis: estimates of the relationships between production and activity of 4 different species, community specialization and activity of mobile and sedentary species (see also Appendix H).

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 Table 1

 Spatial scale effect of density, diversity and productivity (estimate of GLM) and the significance of the GLM (anova, F test) at each spatial scale from 50 to 1000 m.

			Hedgerow density			Hedgerow diversity				Hedgerow production							
		Species	Estimated GLM	SE GLM	P value ANOVA	F ANOVA	AIC GLM	Estimate GLM	SE GLM	P value ANOVA	F ANOVA	AIC GLM	Estimate GLM	SE GLM	P value ANOVA	F ANOVA	AIC GLM
Bush crickets	Continuous calls	T. viridissima R. nitidula	0.028 0.005	0.015 0.034	0.093 0.884	3.52 2.25E- 02	96.10 114.00	0.001 -0.004	0.001 0.001	0.492 0.012	0.51 9.82	34.70 38.20	2.65E-06 8.49E-08	4.63E-07 1.30E-06	<0.001 0.950	32.80 0.00	-132.00 -110.00
		M. roeselii P. falcata	0.082 0.003	0.026 0.043	0.013 0.947	9.64 4.62E- 03	109.00 120.00	0.004 0.007	0.002 0.002	0.069 0.010	4.27 10.40	49.00 48.80	2.75E-06 -1.92E-06	1.34E-06 1.96E-06	0.071 0.352	4.20 0.97	-109.00 -99.30
	Non-continuous calls	P. griseoaptera U. rugosicollis P. nana	0.394 -0.662 0.052	0.072 0.050 0.097	<0.001 <0.001 0.610	30.10 175.00 0.282	133.00 114.00 127.60	-0.012 0.005 -0.050	0.004 0.002 0.014	0.009 0.070 0.005	10.80 4.24 13.61	68.40 56.80 90.79	2.47E-05 -4.21E-06 8.93E-06	5.80E-06 1.59E-06 7.43E-06	0.002 0.026 0.260	18.20 7.04 1.44	-74.60 -103.00 -72.85
		L. punctatissima P. albopunctata C. dorsalis	0.094 1.076 -0.032	0.022 0.487 0.039	0.002 0.069 0.428	18.50 4.87 0.69	108.00 131.14 115.00	$-0.009 \\ -0.074 \\ -0.002$	0.001 0.010 0.002	<0.001 0.020 0.416	48.70 49.50 0.73	41.00 19.00 48.40	4.54E-06 6.02E-05 -7.70E-07	7.57E-07 4.18E-05 1.29E-06	<0.001 0.188 0.565	35.90 2.07 0.36	-118.00 -30.05 -112.00
	Orthoptera mobility trait	P. tessellata Mobility Sedentary	-0.070 0.022 -0.066	0.017 0.001 0.020	0.003 <0.001 0.008	16.10 1610.00 11.40	96.90 31.00 103.00	0.015 -2.64E-04 0.001	0.004 1.71E-04 0.001	0.007 0.158 0.021	12.70 2.37 7.74	60.40 -0.25 19.20	-6.15E-06 1.27E-06 -6.15E-06	1.27E-06 4.81E-08 8.36E-07	0.001 <0.001 <0.001	23.30 700.00 54.10	-105.00 -176.00 -119.00
Bats	Bat foraging trait	Intermediate CSI B. barbastellus	-0.036 0.018 0.158	0.027 0.009 0.044	0.208 0.088 0.006	1.84 3.65 12.90	108.57 85.33 120.00	-0.001 4.51E-04 0.001	0.001 3.51E-04 0.001	0.38 0.23 0.188	0.86 1.65 2.03	40.54 9.59 35.23	-2.05E-06 6.10E-07 7.13E-06	1.12E-06 4.98E-07 1.96E-06	0.100 0.251 0.005	3.35 1.50 13.18	-112.95 -131.38 -100.17
		Myotis spp. N. noctula P. pipistrellus P. kublii	0.450 0.064 0.051 0.134	0.052 0.018 0.007 0.030	<0.001 0.006 <0.001	73.60 12.50 52.80 20.10	113.00 99.50 78.30	0.017 -0.001 0.003 0.003	0.003 0.002 0.001	<0.001 0.411 0.060 0.043	23.20 0.74 4.64 5.55	64.62 50.37 39.20	2.13E-05 2.45E-06 3.03E-06	2.16E-06 6.14E-07 3.75E-07 6.02E-07	<0.001 0.003 <0.001	97.83 15.91 65.20 258.00	-93.06 -125.13 -138.00
		P. nathusii Plecotus spp.	0.154 -0.003	0.030 0.008 0.031	<0.002 <0.001 0.920	411.00 1.07E- 02	81.60 113.48	-0.005 -0.004	0.001 0.002 0.002	0.043 0.047 0.057	0.05 4.74	50.90 48.16	8.11E-06 -2.85E-06	2.64E-07 3.31E-06	<0.001 <0.001 0.412	946.00 0.74	-120.00 -144.00 -88.43
		E. serotinus N. leisleri Aerial Gleaner	-0.056 -0.121 0.218 0.273	0.026 0.034 0.015 0.084	0.060 0.006 <0.001 0.010	4.63 12.60 220.30 10.60	113.00 114.00 95.75 133.69	0.006 0.008 0.003 -0.007	0.001 0.001 0.002 0.002	<0.001 <0.001 0.161 0.019	93.70 46.40 2.33 8.15 0.24	30.60 41.20 46.28 53.11	-8.08E-07 -4.28E-06 1.11E-05 1.17E-05	1.47E-06 1.46E-06 2.88E-07 3.23E-06	0.596 0.017 <0.001 0.005	0.30 8.57 1495.18 13.22	-103.00 -108.00 -142.59 -90.37

#### 3.4. Comparison between the indices

According to the AIC value (Table 1), the best model, for each bat and bush cricket species and for communities based on foraging, mobility and habitat specialization, was the model with the productivity index.

#### 4. Discussion

To our knowledge, our study is the first to assess the influence of hedgerow quality using three characteristics (density, structural diversity and potential of wood production) on the activity of bats and bush crickets, as well as on communities, based on foraging, mobility and habitat specialization. The results of the present study demonstrate the importance of hedgerow quality for bats and bush crickets, but the strength of the association between taxa and hedgerows varied greatly among species and spatial scales. From management and conservation perspectives, we need to understand the characteristics of hedgerows and spatial scales that must be considered to assess the hedgerows' quality for conservation of the different taxa. Indeed, many European bat species use linear features of the landscape for commuting and foraging (Downs and Racey, 2006; Entwistle et al., 1996; Limpens and Kapteyn, 1991; Glendell and Vaughan, 2002), and thus the density of hedgerows was particularly correlated with the activity of bats such as Pipistrellus spp. (Verboom and Huitema, 1997; Boughey et al., 2011). Some studies have shown that occupancy of bat species was positively associated with corridor overstory height (Hein et al., 2009). Merckx et al. (2012) showed that in agricultural landscapes, trees in hedgerows increase the diversity of nocturnal Lepidoptera — which are some of the prey of certain European bats - and can also provide microhabitats, such as dead wood, that also increase invertebrate abundance and diversity (DEFRA, 2010; Winter and Möller, 2008). Moreover, production reflected richly structured habitats with microhabitats (Regnery et al., 2013), that are preferred by many bat species such as P. pipistrellus (Davidson-Watts et al., 2006) and especially by highly specialized and threatened species such as B. barbastellus (Kusch et al., 2004). Moreover, to reach hunting grounds, species such as M. daubentonii forage and commute along wood edges and hedgerows and avoid crossing open areas (Limpens and Kapteyn, 1991). Our results were congruent with the literature but showed this relationship at different spatial scales for 9 bat taxa. We also identified a positive effect on groups based on foraging traits, mobility and habitat specialization. However, concerning bush cricket activity, few studies have documented hedgerow effects (Berggren et al., 2002). For this group, there were nearly as many significantly negative indices as significantly positive indices. The species we studied included species predicted to prefer grasslands and others predicted to prefer forest, which may explain this result.

However, our study has several potential limitations. The ultrasound recording time per site may be relatively short for identifying accurate absolute animal activity or abundance. Sampling using recording throughout the entire night would be more appropriate but also more time-consuming. Still, our design focus on the beginning of the night occurred during the bat and bush cricket activity peak. Moreover, our sampling design allows unbiased measurement of animal activity among the hedgerow characteristics tested.

#### 4.1. Scale effect

Based on the intensities of bat calls and bush cricket stridulations and on the technical characteristics of the microphones, we did not expect to detect individuals at a distance greater than 100 m from the recording point. However, in our study, the strengths of the correlations tended to be strongest at large scales, suggesting that hedgerows could exert an influence at the scale of the landscape. However, it is worth noting that the influence of hedgerows on activity seems to vary depending the index characterizing the hedgerows and the species, most likely because several processes may be involved at different spatial scales (Bellamy et al., 2013). In fact, as already shown by Hale et al. (2012) for bats, the organisms are sensitive to landscape composition and structural connectivity at multiple spatial scales, and the impact of forest harvesting on habitat use by foraging bats varies with spatial scale (Grindal and Brigham, 1999).

Based on homerange studies of bats using radio-tracking methods (see ref. Drescher, 2004), we expected to detect an effect of hedgerow quality at large spatial scales, and this is what we found. For instance, the positive effect of a hedgerow network was detected in buffers whose radii ranged from 400 m to 1000 m, a range that is comparable to the home range of some individuals of *P. pipistrellus* (Davidson-Watts and Jones, 2005) and, *E. serotinus* (Perez-Jorda and Ibañez, 1991) or to the mean distance between roost and feeding sites for species such as *P. nathusii* (Flaquer et al., 2009) and *E. serotinus* (Robinson and Stebbings, 1997).

In addition, our results showed that gleaner species were significantly influenced by the potential production of hedgerow at small scales (see Fig. 2 and Appendix J3), whereas the effect for aerial species was significant only at large scales (Fig. 2 and Appendix J3). Boughey et al. (2011) showed that hedgerows of all types were associated with a similar increase in *P. Pipistrellus* incidence; it is interesting to note that in our study, density and production indices had a positive increasing influence with spatial scales on the activity of the aerial hawking guild and the gleaning guild except for the diversity index for this last group (Table 1).

Based on habitat area requirements and the individual bush crickets' perception of the landscape, we hypothesized that the bush crickets were more sensitive to small-scale changes. Arak and Eiriksson (1992) found that males of *T. viridissima* were regularly spaced with a mean distance of 6 m between nearest-neighbors. However, our results showed that the bush cricket species (i.e., abundances) and community indices were also influenced by landscape structures at large scales (Fig. 3 and Table 1).

In addition, we did not identify thresholds beyond which the scale effect no longer increased. This result was congruent with Penone et al. (2013a) and With and Crist (1995) who showed that some bush cricket species were sensitive to large-scale effects. We obtained a contrasting effect for the two bush cricket communities based on mobility: a significant positive scale effect of the production index on the activity of mobile species and a significant negative effect on the activity of sedentary species (See Appendix J and Fig. 3e and Table 1).

The habitat of specialized species appeared to benefit from the density of hedgerows composed of old and large trees. For bush crickets and bats, we detected a positive scale effect of the density and production indices on the two communities based on indices of habitat specialization (CSI), whereas the effect of the structural diversity index was not significant (Table 1). The comparison of the AIC of the models, for each quality index and for each species or community, showed that the scale effect of the potential wood production best explained the activity of the bats and bush crickets we studied.

For some taxa (i.e., *N. noctula*, Fig. 2) and communities (i.e., gleaners, Fig. 2), we detected a slope change of approximately 600 m with the scale analysis. This change may be specific to our study site and could be linked to the landscape structuring at the regional scale linked to the Loire River. A non-exclusive hypothesis could be linked to specific biological features of the taxa studied,

indicating scale variations of landscape perception, which emphasizes the need to confirm this observed trend with future studies.

## 4.2. Comparison among the 3 indices: density, structural diversity and wood production

We showed that from the landscape perspective, the quality of the hedgerow network was better represented by the potential wood production that generally positively influenced the activity of bush crickets and bats. Concerning bats, the production index showed a frequent significant positive effect on bat activity. Concerning bush crickets, the production index showed a more frequent significant positive effect (see Appendix J) than the density or diversity indices. We assumed two non-exclusive hypotheses to explain the differences in the patterns observed in Fig. 3 between the mobile and sedentary species (Figs. 2f and 3e.). First, the community of a mobile species would be more related to forest edges (i.e., T. viridissima), whereas the community of a sedentary species (C. dorsalis, U. rugosicollis) would be more related to the open areas such as grasslands (Voisin, 2003). Thus, we would have congruence between the traits mobility and habitat selection. Second, the hedgerows may contribute to colonization success in the grasslands, and therefore play a functional role, as Berggren et al. (2001) showed in the case of M. roeselii, which showed higher activity in landscapes with more hedgerows. This result was congruent with our results showing that the activity of this species was influenced positively by the density, diversity, and productivity indices and increased with spatial scale.

Through the diversity index, our study provided new evidence regarding the importance of hedgerows. The diversity of the structure of the hedgerows reflected from an ecological perspective, the heterogeneity of habitats in the hedgerows and thus the heterogeneity of ecological niches. Although this index shows a generally positive effect on the activity of bats and bush crickets compared to the two other indices (see Appendix J), its influence appeared to be less linear: few linear scale effects were detected (see Appendix L) and broken line analysis indicated a change at approximately 400-600 m. These patterns may be linked to the nature of this variable: the diversity index is calculated using a Shannon index (see 2.3). Indeed, the effects of the diversity index can be reversed according to the scales considered. At a small scale, a high structural diversity indicates a strong heterogeneity of the hedgerow types at a given location, whereas at larger scales, high structural diversity implied a good spread of different hedgerows types and a large quantity of each type.

#### 4.3. Conclusion and implications for conservation

If habitat is the primary predictor of bat abundance (Müller et al., 2012; Walsh and Harris, 1996), hedgerows may play a role in optimal foraging by promoting the dispersal of individuals because, they improved the general quality of habitats by improving the access to resource areas and the dispersion between roosts (particularly maternities) and foraging sites. To manage protected areas and to maximize management efforts (the latter point often focuses on the preservation of habitat patches), efforts should focusing more on the preservation of connected habitats (Lookingbill et al., 2010). Mimet et al. (2013) and Pellissier et al. (2012) suggested that, for land use management, both the composition and the configuration of habitats must be taken into account to maintain suitable conditions for biodiversity and Zeale et al. (2012) underline the need to improve the quality and the numbers of ecological corridors. Optimizing the biodiversity gain provided by linear features will maximize the effectiveness of these schemes (Boughey et al., 2011). We showed that the wood production index positively influences the variation in the activities of bats and bush crickets. According to Geffray (2010), the wood production index is potentially correlated to tall and old trees and also to a potential ecosystem service of high timber production for land managers and farmers. Moreover, hedgerows provide habitats for auxiliary crops (Van Emden and Dabrowski, 1994), shelter against the wind and cold for crops, and wood production for firewood (linked to the European and French energy transition) (Château and Rossetti di Valdalbero, 2011). Thus, hedgerows play important roles in the ecosystem and provide many ecosystem services (Altieri, 1999). They reconcile agricultural practices and biodiversity. Moreover, tree-filled hedgerows could provide substitute environments for forest species; thus, in grassland habitats, such as our study site, we need to encourage hedgerows with large and old trees.

Usually, it is recognized that hedgerow density is a heritage of old historical agricultural practices that shaped this landscape structure. Although agricultural practices have been largely modified, this network of hedgerows persists today. Currently, this network is influenced by regional, national and even European common agricultural policy (CAP). The wood production of hedgerows, however, is linked to management by local farmers. Thus, territorial policy decisions or local practices could influence the state of biodiversity. The present study examined different scales and different hedgerow indices and its results suggest that landscape planning should be considered both:1) at large scales because they are the ones that are guided by agricultural policies that can increase the density of hedges and 2) at small scales, such as the agricultural parcel level, because it is at this scale that agroecosystem schemes offer subsidies or/and financial tax shelters that could be distributed to farmers and landowners to create, conserve and manage hedgerows to promote longer cutting cycles for old trees with high production. The distribution of common agricultural policy (CAP) may be conditional on the hedgerow quality, rather than simply their presence.

However, the current European context, with its political pressure regarding wood energy, may not be favorable to shortening cutting cycles for large timber. Because hedgerows provide valuable habitat for many species (Boughey et al., 2011), the diversity index reflected the different types of hedgerows and therefore must be linked with AEM for management. The reintroduction of structural elements to increase habitat heterogeneity should become part of agro-ecosystem schemes (Frey-Ehrenbold et al., 2013). Our study site, as many other sites, was in spaces with multiple purposes including agriculture, hunting, and wood production through which hedgerows contribute to ecosystem services (Baudry et al., 2000).

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#### Appendix A. Supplementary data

Supplementary data related to this article can be found at http:// dx.doi.org/10.1016/j.actao.2016.01.009.

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