

Activity of European common bats along railway verges



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ABSTRACT

Linear infrastructures such as railways and roads are known to have major negative impacts on species and ecosystem dynamics, modifying landscape structure through artificialization, habitat changes, alteration and fragmentation. Nonetheless, infrastructure verges have also been shown to provide refuges or corridors to a large number of taxa.

Here we examine the potential use by bats of railway verges crossing woodland patches within an agricultural matrix as foraging/commuting habitats. We tested whether (i) at a large scale (national level), railways lines were globally an appreciated foraging/commuting habitat for common bats species, and (ii) at a local scale (landscape level), woodland-railway edges have an effect on bat activity compared to other habitat types like woodland-field edges, woodland habitats and field habitats. At local scale, we also looked for a pre-eminent influence of landscape composition on bat activity over habitat types.

Our results show that the presence of railway verges does not influence significantly the foraging/commuting activity of common bats, except for specialist species like the ones from the *Myotis* group, for which the effect is negative. In several cases (for *Pipistrellus pipistrellus* and *Nyctalus leisleri* at large scale and for *Nyctalus* ssp. at local scale), railway verges even seem to be a significant habitat in an intensive agricultural landscape where semi-natural elements, in particular linear structures like hedgerows, tend to disappear.

In a context of rapid biodiversity decline, our results suggest that railway verges should be considered by managers and engineers not only as a side aspect of the railroad, but also as elements having a potential role in maintaining common biodiversity, especially in human-dominated landscapes such as agricultural systems. In order to contribute to the maintenance of biodiversity, the management of these verges is crucial and some simple rules are considered. Nevertheless, we stress that further studies are needed to better assess the roles, both positive and negative, of railway verges, in order to propose more precise technical design and management recommendations.

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1. Introduction

Land-use changes are important drivers of biodiversity loss (MEA, 2005). Linear infrastructures such as roads and railways play a particular role in this process. These are known to have major negative impacts on species and ecosystem dynamics, modifying landscape structure through artificialization, habitat changes, alteration and fragmentation (Trombulak and Frissell, 2000). They in turn affect community richness, composition and species interactions (Fahrig, 2003). Linear infrastructures can form barriers for

connectivity (Jackson and Fahrig, 2011) and have strong impacts on populations (Fahrig and Rytwinski, 2009). They are also considered as corridors for invasive species (Brown et al., 2006). Linear infrastructures have strongly expanded over large areas associated with human population growth (Watts et al., 2007).

Infrastructure verges have nonetheless been shown to provide refuge or corridors to a large number of taxa (Merriam and Lanoue, 1990; Hodkinson and Thompson, 1997; Penone et al., 2012). They can ensure structural and functional connectivity when they penetrate artificial areas such as dense urban areas or agricultural-intensive landscapes (Tikka et al., 2001; Penone et al., 2012). In addition, they can be substitution habitats for grassland plants and insects (Saarinen et al., 2005; Wehling and Diekmann, 2009), hence contribute to the conservation of indigenous flora (O'Farrell and Milton, 2006) and fauna (Ries et al., 2001).

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The role of infrastructure verges as refuges/corridors may depend on their surrounding landscape. In natural habitats, infrastructure verges do not provide relevant habitat to threatened local species (O'Farrell and Milton, 2006), hence can even have negative effects (Brown et al., 2006). By contrast, in human-dominated areas such as intensive agricultural landscapes, where non-agricultural habitats are sparse and critical to the conservation of biological diversity and ecological processes (Burel, 1996), infrastructure verges are a relevant habitat, having a positive role in the conservation of biodiversity (Le Viol et al., 2008, 2012). Recently, the European Union's environmental policy has promoted this idea by considering such linear elements as potentially relevant pieces of a *Pan-European Ecological Network* (Council of Europe, 2000).

Among studies examining the effects of linear infrastructure verges, very few focused on railway verges, the majority concerning roadside verges (Forman et al., 2003). Indeed, compared to roadside verges, railway verges are less important when considering their total length. Nevertheless, railway verges have at least two peculiarities worth considering compared to roadside verges. Their potential impact on biodiversity may be significant in human-dominated areas such as intensive agricultural landscape due to their greater width margins. In addition, with regards to management, railway lines of most countries are managed by one unique manager, allowing to reach large effects of realistic biodiversity friendly management (see Section 4).

A species group which might be especially sensitive to the presence of railway verges are bats.

Studies have shown that bat activity and species richness decrease when approaching a motorway (Berthinussen and Altringham, 2012). Some studies stressed particular negative effects, such as road casualties (Lesinski et al., 2010). Other studies found that a road formed a strong barrier to the movements of bats within the landscape (Bach et al., 2004; Kerth and Melber, 2009; Abbott et al., 2012).

Yet very few studies have focused on the potential positive effects of linear infrastructures such as railway verges while we know that some bat species fly along such features when commuting from roosts to foraging areas because these linear elements could constitute commuting paths away from predators and wind (Limpens and Kapteyn, 1991). In addition some species forage regularly along linear elements (Verboom and Huitema, 1997). Indeed, foraging activity is facilitated close to these features because of greater abundance of some preys (Verboom and Spoelstra, 1999).

These contrasting behaviours among species may be linked to their specific foraging ecology (Kerth and Melber, 2009). Currently, the impacts of roads and moreover railways on bats are barely known, despite the wealth of grey literature and management/mitigation guidelines on this taxa relating to linear infrastructures in Europe (Limpens et al., 2005; National Roads Authority, 2006; Highways Agency UK, 2011). Studies have mainly focused on 'natural' linear elements such as hedgerows and forest edges (Morris et al., 2010; Boughey et al., 2011b). A few studies have focused on the role of more artificial elements, such as forest tracks in logged and unlogged forests (Webala et al., 2011). Far fewer studies have been led on how proper roads or railways may affect bat activity other than negatively (Kerth and Melber, 2009; Berthinussen and Altringham, 2012).

We hypothesized that some species, particularly gleaner species generally linked with forest habitat (such as species from the *Myotis* genus) are impacted negatively by railway verges. These species could perceive railway verges as an inadequate habitat and in addition could be impacted by the fragmentation effect of these verges. On the opposite, aerial hawking species that generally forage in more open habitats, such as species of the genus *Pipistrellus*, *Nyctalus* or *Eptesicus*, could benefit from the edge effect of railway

verges, using them as a commuting/foraging habitat. To test this hypothesis, we examined the potential use by bats of railway verges crossing woodland patches within an agricultural matrix as foraging/commuting habitats. We tested whether (i) at a large scale (national level), railways lines were globally an appreciated foraging/commuting habitat for different common bats species, and (ii) at a local scale (landscape level), woodland-railway edges had an effect on bat activity compared to other habitat types like woodland-field edges, woodland habitats and field habitats. At local scale, we also looked for a pre-eminent influence of landscape composition on bat activity over habitat types.

2. Methods

2.1. Study sites

The study was conducted along two recent high-speed railway lines (commissioned in 1994 and 2007) in the east and south-east of the Paris Ile-de-France region, France (Fig. 1). Although densely populated, with 20% of the national population and spreading urbanization, the Paris Ile-de-France region is still predominantly rural, with intensive farming covering 50% of the territory, woods and natural land more than 25%, and urban areas and transport infrastructures covering about 25% (DRIAAF-IAURIF, 2004).

Railway verges studied here vary from 10 m-wide to 20 m-wide and are composed of herbaceous species and shrubs. No vegetation management plan existed for these verges. Clearcutting of trees and mowing were applied on a case-by-case basis, when presenting threats for train security, e.g. risk of tree falling on overhead lines (personal communication from Réseau ferré de France). The railway traffic was quite insignificant during the night: starting from 9:30 pm (earliest hour of activity recording), only one train ran on the first high-speed line and a maximum of five ran on the other, depending on the day.

2.2. Experimental design

We identified ten sites chosen via aerial photographs and field visits in order for them to be the most similar: each site consisted of a portion or railway of 600 m to 2 km long fragmenting a woodland patch within a matrix of farmland. In each site, bat activity was sampled at ten sample points according to four different detector locations, called 'site types' below: 3 points on the sides of and parallel to railway tracks-woodland edges (railway edge); 3 points on the sides of and parallel to crop open field-wood edges (field edge); 2 points in plain woodland (wood); 2 points in open fields (field). Woodland and open field points were at least 100 m from hedgerows or forest edges. Points were further than 100 metres from each other (Fig. 1).

2.3. Bat sampling

We used two distinct sets of data. 'Local-scale' data from railway sites were sampled in summer 2010 following a similar protocol to the one designed for the French Bat Monitoring Programme (FBMP), from which we used 'large-scale' (national) data collected from 2006 to 2011. The protocol consists of a square of 2 km-side randomly chosen (by the Museum) in a radius of 10 km from the observer's home, within which ten points are chosen by the observer with at least five points representative of the habitats of the square, the other being located in 'favourable' places for bats such as river banks and wood edges, etc.

For both local-scale and national data sets, bat calls were detected using a Tranquillity Transect Bat detector (Courtspan Design Ltd., UK) and recorded over 6 min on a Zoom H2 digital

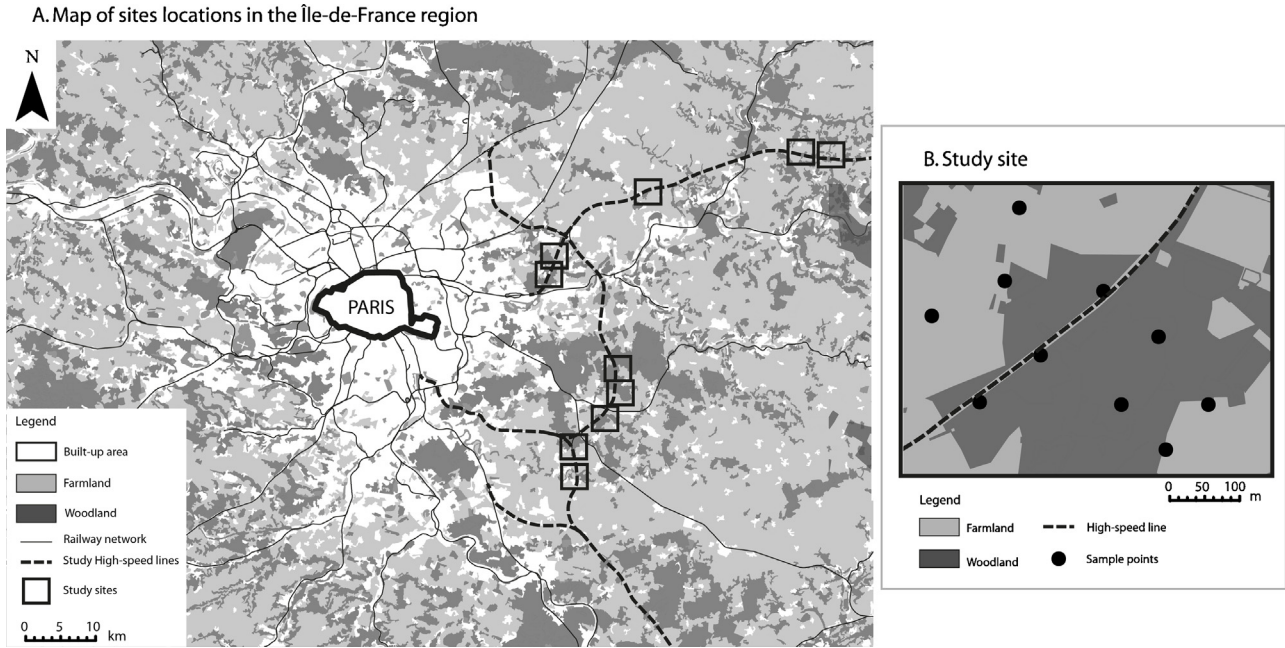


Fig. 1. (A) Map of site locations in the Ile-de-France region, showing the ten study sites along two railway lines. (B) Design of one site with the ten sample points classified in four 'site types': 3 along railway edges, 3 along field edges, 2 in open fields and 2 in woodland.

recorder (Samson technologies, USA) at a sampling rate of 96 ks/s from the two possible outputs of the detector: time expansion (t_{exp}) and high frequency (t_{hf}). Each point is monitored twice: once during the period between June 15 and July 31, during which females are expected to give birth and feed their offspring; second, during the period between August 15 and September 31, during which young are flying and individuals are expected to be less dependent on their reproductive roost. The ten points were sampled during the same night. Habitat characteristics were collected in a radius of 100 m around the sampled point, using a detailed habitat classification (Kerbiriou et al., 2010). The observers begin their sampling 30 min after dusk, in the same order for each visit (from season to season, and from year to year). Observers sampled bats only when weather conditions were favourable (no rain, temperature higher than 12 °C and wind speed less than 5 m/s).

Species calls were identified using Syrinx software version 2.6 (Burt, 2006) for spectrogram analyses. For the local scale data, identifications were made by authors. For the national data, identifications were made by voluntary observers and then validated by Museum's scientists. The majority of volunteers involved in the bat monitoring had participated in training courses organized since 2006, allowing high homogeneity in the identification criteria. For more details on methods (sampling design, bat calls identification, see Appendix S1).

2.4. Statistical analysis

2.4.1. Large scale analysis

In a first assessment of the importance of railway verges as foraging/commuting habitats for bats, we compared 36 sample points realized within railway verges (26 located within railway verges crossing woodland plus 10 within railway verges crossing various habitats) with points in common habitats present in France taken from the FBMP database. Four hundred and eighty-five points were extracted from 10 different habitats, all situated in the Atlantic biogeographical region: arable land (AL, $n=48$), scrubs and heathland (SH, $n=10$); standing water (SW, $n=36$); coniferous forest (CF, $n=19$); broad-leaved forest (BF, $n=84$); discontinuous artificial

surfaces (DA, $n=24$); continuous artificial surfaces (CA, $n=244$); marsh (M, $n=10$); pasture and grassland (PG, $n=24$); and river (R, $n=21$). We conducted compositional analysis (Pearson's Chi-squared test) for the 5 most common taxa of our data set: Common pipistrelle (*Pipistrellus pipistrellus*), Kuhl's pipistrelle (*Pipistrellus kuhlii*), Lesser noctule (*Nyctalus leisleri*), Common noctule (*Nyctalus noctula*) and the myotis group (*Myotis* spp.). Given that recordings of the FBMP are done on a time-expanded format, we used the time expansion (t_{exp}) outputs of the detector for comparison with the FBMP data.

We assessed potential differences in bat activity among habitats using Generalized Additive Mixed Models (GAMM; Wood, 2006, R package mgcv) with a Poisson error distribution. GAMM are able to handle nonlinear relationships between the response and some predictive variables such as *days in season*, a variable expected to respond non-linearly. According to the hierarchical structure of our sampling design (same sites were sampled year to year), we treated the *site* variable as a random effect, while the other explanatory variables (*days in season*, *hours of sampling*, *temperature*, *years*, *habitats* and *quadratic effect of hours and temperature*) as fixed effects (Zuur, 2009). In addition, we hypothesized that close bat call recording plots are more likely to have a similar bat population density due to similar climatic conditions or large-scale landscape compositions. Thus, all models incorporated the spatial correlation structure through the equation $x + y + x^2 + y^2$, where x and y were the geographical coordinates of recording plots (following the approach of Doxa et al., 2010)

2.4.2. Local scale analysis

For the local scale analysis, we used high frequency (t_{hf}) outputs, which allow more accurate information on bat activity, because it considers the duration of bat call passes. With the aim of assessing at a site scale the effect of railway verges on bat activity, we used 89 sample points from the 10 sites classified in four site types: 26 'railway edge' points, 27 'field edge', 17 'wood' points and 19 'field' points.

In addition to this qualitative approach, we assessed the influence of local habitat on bat activity through land cover, comparing

Table 1
Model selection for local scale analysis, including habitat variables and characteristics of sampling conditions: intensive arable land (*arable*), railway lines (*railway*), discontinuous rural fabric (*rural*), broad-leaved woodland (*woodland*), poplar culture (*poplar*), temperature (*temp*) and hour (*hour*). (²) indicates a quadratic effect.

Species	Habitat variables Selected model	Family	Site type variable Selected model	Family
Reproduction period				
<i>Pipistrellus pipistrellus</i>	Ab ~ railway	Negative binomial	Ab ~ type	Negative binomial
<i>Nyctalus</i> ssp.	Ab ~ railway + arable + rural + hours ²	Negative binomial	Ab ~ type	Negative binomial
<i>Myotis</i> ssp.	Ab ~ railway + rural	Zero inflated with negative binomial	Ab ~ type + hour + temp	Zero inflated with negative binomial
Post-reproductive period				
<i>Pipistrellus pipistrellus</i>	Ab ~ railway	Negative binomial	Ab ~ type	Negative binomial
<i>Nyctalus</i> ssp.	Ab ~ railway + woodland + poplar + rural + hour + temp	Negative binomial	Ab ~ type + temp	Zero inflated with negative binomial
<i>Myotis</i> ssp.	Ab ~ railway + woodland + arable + poplar + rural + hour + temp	Zero inflated with negative binomial	Ab ~ type	Zero inflated with negative binomial

railway cover with other types of habitat covers. We built circular 200-metre radius buffers around each sample point using GIS (ARCGIS 9.3/ESRI). For each buffer, we calculated the surfaces of the different habitat cover types using a regional, detailed and geo-referenced land use database of landscape features, with a resolution of 25 m (IAURIF, 2003). Following a correlation test among habitat covers using Spearman's rho, we retained five major non-correlated habitat covers ($|\text{rho}| < 0.5$; Freckleton, 2002): intensive arable land (*arable*); railway lines (*railway*); discontinuous rural fabric (*rural*); broad-leaved woodland (*woodland*); and poplar culture (*poplar*). However, as expected, independence tests between quantitative and qualitative habitat variables using Kruskal–Wallis tests underlined obvious correlations. We thus ran separate modelling. At a local scale, with a restricted data set, we paid special attention to potential zero inflation and overdispersion problems in our data, applying different modelling (Poisson, negative binomial, truncated Poisson or truncated negative binomial; R package pscl, Zuur et al., 2009). The best models were selected using both AIC value and a residuals pattern (Zuur et al., 2009) (Table 1).

3. Results

3.1. Large-scale

The 485 localities of the FBMP allowed to collect 8544 contacts for 5 bat taxa (*Myotis* ssp., *N. leisleri*, *N. noctula*, *P. kuhlii* and *P. pipistrellus*, see Appendix S2), which represent about 524,000 bat calls.

3.1.1. Compositional analysis

Compositional analysis indicates significant differences between railway verges and the other main habitats ($\chi = 52.290$, $df = 4$, $P < 0.001$). Residuals indicate proportionally less *Myotis* ssp., *N. leisleri*, *N. noctula*, *P. kuhlii* and more *P. pipistrellus* in railway verges than in the other main habitats (see Appendix S2).

3.1.2. Variation of bat activity between railway verges and other habitats

As expected, bat activity varied among habitats and between species (Fig. 2). For *P. pipistrellus*, activity was significantly greater in standing water and rivers than in railway verges, while activity in railway verges was significantly greater than in the 7 other habitats (Fig. 2A). For *P. kuhlii*, activity was significantly greater in 6 of

the 10 habitats tested and in none of them was lower than in railway verges (Fig. 2B). Few differences were detected in activity of *N. leisleri* between railway verges and other habitats: differences were greater in discontinuous artificial surfaces than in railway verges and lower in continuous artificial surfaces (Fig. 2C). For *N. noctula* activity is low in railway verges. Few differences in activity between railway verges and other habitats were detected, but activity was greater in aquatic habitats (Fig. 2D). For the *Myotis* ssp. group, among the 10 habitats tested, 4 had greater activity than in railway verges (pasture and grassland, marsh, standing water, river), and for the 6 other we were not able to detect any significant difference (Fig. 2E).

3.2. Local scale

89 points were sampled on railway verges and around and allowed us to collect 33,986 bat calls (see Appendix S2).

Species diversity is as follows: *P. pipistrellus* (82.8%), *N. leisleri* (6.7%), *N. noctula* (2.7%), *Myotis natterii* (2.4%), *P. kuhlii* (1.6%), *Myotis mystacinus* (1.0%), *Eptesicus serotinus* (0.9%), *Myotis daubentoni* 0.6%, *Plecotus* ssp. (0.2%) and bat ssp. (<0.01%).

It was not possible to properly analyze species with a too low occurrence, thus we restricted our analysis of variations in activity to the following taxa: *P. pipistrellus*, *Nyctalus* ssp. and *Myotis* ssp. These last two groupings are justified by their convergent foraging biology: *N. leisleri* and *N. noctula* are aerial hawking bats, whereas *M. natterii*, *M. mystacinus* and *M. daubentoni* are mainly gleaner bats (Dietz et al., 2007).

At site scale, bat activity on railway edges was quite similar to that in neighbouring site types (field edge, wood, field). Only 3 differences were detected. During the reproductive period, activity was significantly greater along field edges than in railways verges for *Myotis* ssp. During the post-reproductive period, the activity of the *Nyctalus* ssp. group was greater in railway verges than in woods and, for the *Myotis* ssp. group, activity was greater along railway edges than in fields (Table 2, right).

In terms of influence of 'local habitat' areas on bat activity (Table 2, left), we detected a significant negative effect of railways areas on the activity of *Myotis* ssp., regardless of the season considered, and a positive effect of this habitat on *Nyctalus* ssp. during the post-reproductive period.

Besides the specific effects of railways areas, we also detected significant effects of other habitats: arable land influences also,

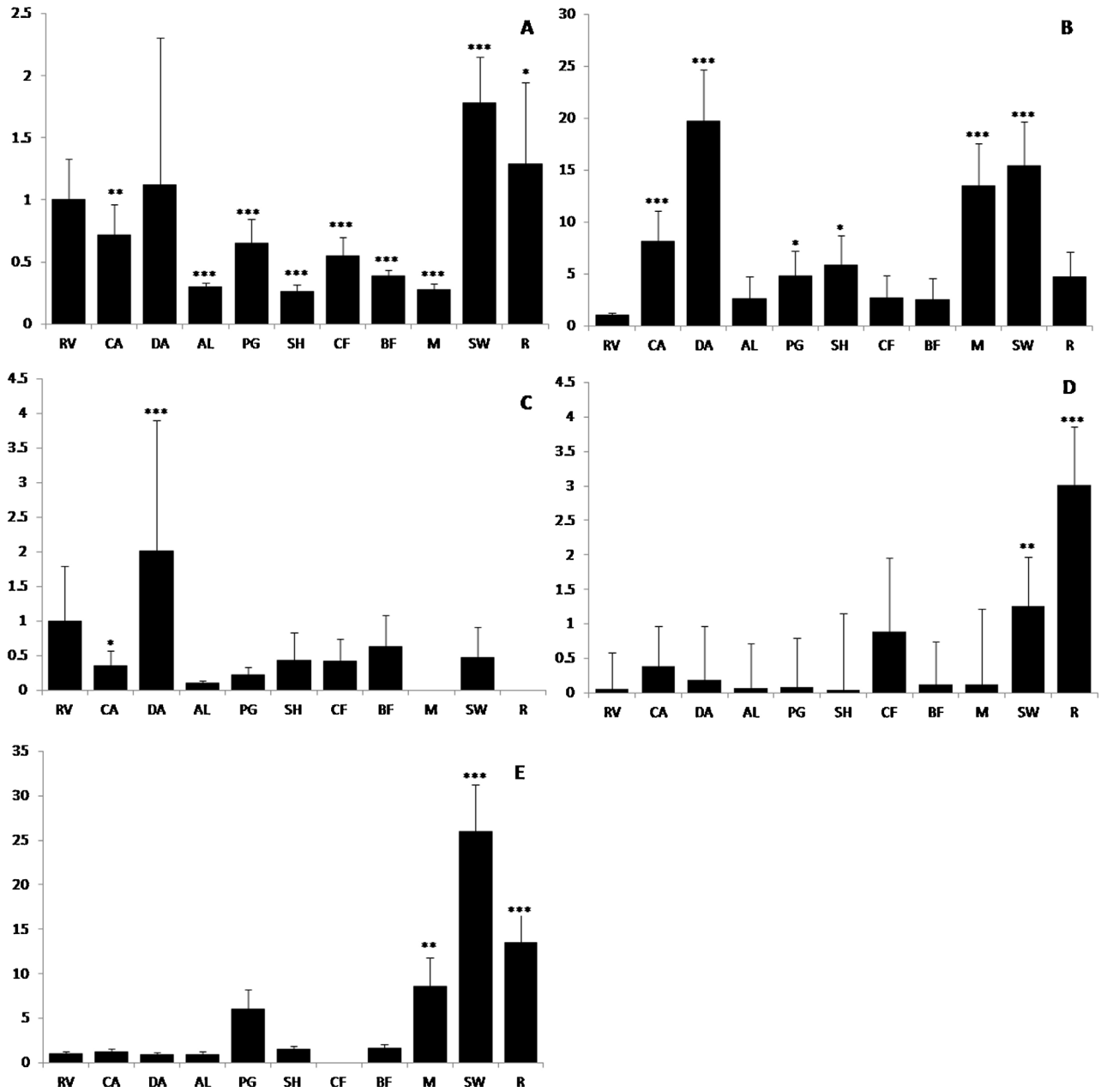


Fig. 2. Relative importance of bat activity (A, *Pipistrellus pipistrellus*; B, *Pipistrellus kuhlii*; C, *Nyctalus leisleri*; D, *Nyctalus noctula*; E, *Myotis* spp.) in railway verges (RV) compared to the main habitats present in France: continuous artificial surfaces (CA); discontinuous artificial surfaces (DA), arable land (AL), pasture and grassland (PG), scrubs and heathland (SH), coniferous forest (CF), broad-leaved forest (BF), marsh (M), standing water (SW) and river (R). With the aim of allowing simple comparisons, bat activity is arbitrarily fixed to 1 for railway verges. Significant differences of bat activity between railway verges and other habitats are indicated with an asterisk. *** indicates a p -value $p < 0.001$; ** indicates a p -value between 0.001 and 0.01; * indicates a p -value between 0.01 and 0.05.

negatively, *Myotis* spp. activity during the post-reproductive period, while *Nyctalus* spp. appears to be influenced positively by arable land during the reproduction period. Woodland influences positively both *Myotis* spp. and *Nyctalus* spp. in the post-reproductive period. On the contrary, rural fabric areas influence negatively *Myotis* spp. in both reproductive and post-reproductive periods, while it influences *Nyctalus* spp. negatively in the reproductive period but positively in the post-reproductive period. Finally, poplar culture influences negatively *Nyctalus* spp. and positively *Myotis* spp. during the post-reproductive period.

4. Discussion

Surprisingly, our results suggest that, in altered landscapes such as intensive agro-systems, artificial structures such as railway verges may contribute to sheltering a similar abundance of common bats as the main other habitats present in these landscapes. After commenting on these results below, we wish to discuss their consequences, in particular the value of adopting biodiversity-friendly management measures for these verges, which could promote biodiversity in such landscapes.

Table 2
Influence of habitat area and site type on bat activity. As habitat area is a continuous variable, given estimates are the slope of the relation between species abundance and habitat area adjusted to co-variable selected (see Table 1), and thus *p*-value informs on the significance of the slope, whereas for site type (categorical variable), the given estimate is the average estimate abundance for each site type considered adjusted to co-variable selected (see Table 1), and thus *p*-value informs on the significance of the test between foraging abundance in railway edge vs other site types (field edge, wood and field). (****) indicates a *p*-value $p < 0.001$; (***) indicates a *p*-value between 0.001 and 0.01; (*) indicates a *p*-value between 0.01 and 0.05; ns: variable not selected for model selection.

Species	Habitat area					Site type			
	Railway	Arable	Woodland	Rural	Poplar	Railway edge	Field edge	Wood	Field
Reproduction period									
<i>Pipistrellus pipistrellus</i>	-0.27 ± 0.15	ns	ns	ns	ns	4.80 ± 0.49	5.87 ± 0.69	5.20 ± 0.78	3.92 ± 0.75
<i>Nyctalus ssp.</i>	-0.06 ± 0.26	1.04 ± 0.29***	ns	-0.64 ± 0.29*	ns	2.05 ± 0.86	2.91 ± 1.21	2.38 ± 1.37	3.83 ± 1.78
<i>Myotis ssp.</i>	-0.34 ± 0.14*	ns	ns	-0.31 ± 0.18	ns	3.44 ± 0.43	4.67 ± 0.52*	3.61 ± 0.75	3.95 ± 0.96
Post-reproductive period									
<i>Pipistrellus pipistrellus</i>	-0.06 ± 0.14	ns	ns	ns	ns	4.93 ± 0.49	5.11 ± 0.68	4.95 ± 0.76	4.64 ± 0.75
<i>Nyctalus ssp.</i>	0.05 ± 0.01***	ns	0.09 ± 0.02***	0.05 ± 0.01**	-0.27 ± 0.02***	3.92 ± 0.50	4.76 ± 0.61	1.74 ± 0.97**	4.50 ± 0.81
<i>Myotis ssp.</i>	-0.63 ± 0.25*	-1.35 ± 0.36***	2.00 ± 0.74***	-1.76 ± 0.59**	1.49 ± 0.39***	4.00 ± 0.49	3.85 ± 0.84	3.57 ± 0.69	0.10 ± 0.96**

4.1. Variation of activity across habitats

At large scale, we found that activity of common bats in railway verges was of the same order of magnitude as in other habitats, except for aquatic habitats which are known as key habitats for numerous European bats species (Russo and Jones, 2003; Nicholls and Racey, 2006). Furthermore, we found that activity was even greater in railway verges than in some other habitats for two aerial species: *N. leislerii* and *P. pipistrellus*. For *P. pipistrellus*, a very generalist species (Russ and Montgomery, 2002), activity in railway verges was greater than in 7 other habitats (Fig. 2). Overall, bat activity among railway verges was not inferior to the activity in highly modified habitats such as continuous artificial surfaces, discontinuous artificial surfaces and arable land, this for 4 of the 5 taxa studied (Fig. 2).

Furthermore, activity was even greater in railway verges than in some other habitats for *P. pipistrellus* and for *N. leislerii*.

At local scale, we found a negative effect of railway areas on the *Myotis ssp.* for the two sample periods and a positive effect on *Nyctalus ssp.* for the post-reproductive period (Table 2). When focusing the analysis on the site type, we detected few obvious significant differences in bat activity between the edges of railways and the three other site types (field edges, plain field and plain wood). The significant difference for *Nyctalus ssp.* during the post-reproductive period (lower activity in woods than on railway edges, Table 2) may seem contradictory with the positive effect of surrounding areas of wood for *Nyctalus ssp.* at the same period. The foraging ecology of these aerial hawking bats could explain these results, *Nyctalus ssp.* being a species that forages mainly in forest edges. They could be less present in the heart of woodland, while the amount of woodland habitat in the landscape would have a positive effect. It must be noted that except for the *Myotis ssp.* group in the reproductive period, we detected no difference between the edges of railways and those of fields. This result seems to indicate a similar functioning role for railway edges on bats than for other linear edges, particularly on common aerial hawking bats (Verboom and Huitema, 1997).

Our results show that the presence of railway verges does not influence significantly the foraging/commuting activity of common bats, except for species like those from the *Myotis* group, a group including mostly gleaner species, less generalist species (Dietz et al., 2007) and some threatened species (Temple and Terry, 2007).

In several cases (for *P. pipistrellus* and *N. leislerii* at global scale and for *Nyctalus ssp.* at local scale), railway verges even seem to be a significant habitat in intensive agricultural landscape where semi-natural elements, in particular linear elements like hedgerows, tend to disappear.

Railways, along with other artificial linear infrastructures, may thus contribute to maintaining common bat populations in such landscapes.

4.2. Interest for biodiversity-friendly management of railway verges

In a context of rapid biodiversity decline, our results suggest that railway verges should be considered by managers and engineers not only as a side aspect of the railroad, but also as elements having a potential role in maintaining biodiversity, especially in human-dominated landscapes.

In order to contribute to the maintenance of biodiversity, the management of these verges is crucial, as shown by previous studies (Noordijk et al., 2010). However, considering bats might be difficult, as many management criteria are already taken into account: enhancing visibility; minimizing security risks for

vehicles; maintaining the stability of the railroad; provide an aesthetically pleasing view for passengers.

As a consequence, the following management rules should be considered: (1) during the construction phase, plants favourable to bats and other biodiversity communities should be included in the revegetation process, (2) the relationship between the network of these linear features and the overall landscape connectivity should be considered (Karim and Mallik, 2008; Boughey et al., 2011a), (3) finally, during the exploitation phase of the railroad, management decisions could take bats into account through a move from clearcutting to more extensive management (e.g. selected cutting and late-mowing), enabling the maintenance of some linear structures and allowing the reproduction of many insect species that constitute the bats' preys (Verboom and Huitema, 1997).

These management propositions must nevertheless be adapted to each environmental context. Indeed, in human-dominated landscapes (i.e. highly intensive agriculture areas or urban areas) this strategy could be successful as it could favour mostly bat species considered as common and generalist in terms of foraging habitat due to their foraging ecology. Indeed, these species have been shown to be less sensitive to the negative impact of artificial linear infrastructure, such as the barrier effect and the risk of collision (Kerth and Melber, 2009). However, the strategy of rendering railway verges attractive for bats would be less relevant in a more natural landscape, where the species association is composed of more specialist species linked to woodland and of gleaner-type. Indeed, studies have shown that these species have stronger reactions to linear infrastructure, and a similar phenomenon has also been observed for rainforest bird species (Kerth and Melber, 2009). In the case of railways, the negative impacts on gleaner bats would be somehow less important than in the case of highways and roads due to the very weak train traffic (at least in France) at night during bat activity. This strategy would also be irrelevant in the case of heavy train traffic at night. Nevertheless, apart from some dense urban areas, this is far from being the case for most of European countries' railway networks.

In this study, we showed that railway verges in human-dominated landscapes could play a role in the foraging/commuting activity of aerial hawking bats. Nevertheless, we stressed that further studies are needed to better assess the roles, both positive and negative, of railway verges. In particular, it now appears necessary to have more information, using trajectory studies, on the tri-dimensional spatial use of artificial linear infrastructures such as roads and railways, in order to better understand the potential role of barrier of these infrastructures.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoeng.2013.12.025>.

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