Plant and spider communities benefit differently from the presence of planted hedgerows in highway verges

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ARTICLE INFO

ABSTRACT

Road verges should play a crucial role as a refuge for native flora and fauna in human dominated landscapes. However, the influence of construction choices, such as plantation of woody species, on the biodiversity supported by roadsides has received little attention, although the presence of hedgerows in roadsides is likely to enhance their role as a refuge, notably for woodland species. Using standardised methods, we assessed the impact of planted hedgerows on two taxonomic groups (plants and spiders) inhabiting highway verges within an intensive agricultural landscape. We examined community richness, taxonomic and functional composition in sites with and without planted hedgerows. At the site level, the response of plant and spider communities to the presence of planted hedgerows differed markedly: hedgerows were associated with significantly higher plant richness (higher α-diversity), but similar spider richness. Plant communities in sites without hedgerows appeared as a subset of communities in sites with hedgerows, whereas spider communities in non-planted sites were complementary to that of planted sites (increased β-diversity). The presence of planted hedgerows was also associated with increased taxonomic and functional trait diversity at the landscape level (γ-diversity), through an increased β-diversity in both plants and spiders. Our results thus suggest that a mosaic of planted hedgerows and grassland habitats is crucial for the maintenance of biodiversity at a landscape scale. By providing information for road practitioners and policy makers regarding their potential impact on biodiversity, these results have important direct implications for the management of road networks.

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1. Introduction

Road networks, which have expanded over large areas with human population growth (Watts et al., 2007), are known to influence landscape structure and have major negative impacts on ecosystems dynamics (Trombulak and Frissell, 2000). However, the potential biological value of road verges has also long been recognised (Way, 1977) with possible contribution to the conservation of indigenous flora (Spooner et al., 2004; O'Farrell and Milton, 2006) and fauna (Meunier et al., 2000; Ries et al., 2001). This role as a refuge depends on the surrounding landscape: in natural habitats, generally supporting a high species diversity, road verges may not serve as a refuge (O'Farrell and Milton, 2006) and even have negative

effects, notably by promoting invasion by non-indigenous species (Hansen and Clevenger, 2005; Brown et al., 2006). In contrast, in human dominated areas such as intensive agricultural landscapes, where non-agricultural habitats (e.g. edges) are critical to the conservation of biological diversity and ecological processes (Burel, 1996), road verges should play a crucial role as a refuge and as ecological corridors (Tikka et al., 2001; Smart et al., 2006).

Road verges support intensively managed habitats, which are artificially created on bare soil after road construction (restoration) and subsequently experience frequent mowing. This has direct consequences on the communities they can support and there is a need to identify and promote biodiversity-friendly construction and management practices, in order to optimise the role of road verges as a refuge for wild flora and fauna. As in any habitat, community composition in road verges is controlled by an array of distinct factors acting as filters at both landscape and local scales (Bochet et al., 2007), few of which can easily be manipulated to optimise biodiversity conservation. There have been extensive studies addressing the influence of management on roadside biodiversity, notably mowing frequency and timing (Schaffers, 2002; Jantunen et al., 2007). In contrast, construction choices have received much less attention, with the exception of revegetation with herbaceous species (Matesanz et al., 2006; Leps et al., 2007). In particular, the role of planted trees in the maintenance of diversity in road verges was never considered to our knowledge, even though the presence of hedgerows along roadsides is likely to enhance their role as a refuge, by increasing the diversity of microhabitats. This role of hedgerows as a refuge, however, depends on their ability to receive a significant proportion of the local species pool and of the functional diversity they shelter (Roy and de Blois, 2006). Outside of roadsides, hedgerows appear to be a sustainable habitat and even functional corridors (flora: Corbit et al., 1999; Roy and de Blois, 2008; fauna: Maudsley, 2000; Griffiths et al., 2007; Davies and Pullin, 2007 for a review) even though other authors consider hedgerows as sink habitats (McCollin et al., 2000; Sitzia, 2007).

The aim of the present study is to evaluate the effect of hedgerows on the surrounding biodiversity of highway verges at different spatial scales, and on the distribution of biodiversity within and among sites in the context of an intensive agricultural landscape. Highway verges offer ideal settings to study the influence of hedgerows, because, in contrast to other habitats, the influence of history on community composition is strongly reduced, due to common history of all study sites. To address the impact of hedgerows on biodiversity, we compared the community richness and composition in sites with and without planted hedgerows for two taxonomic groups (plants and spiders), because no single taxon can inform on the ecological behaviour of other groups (Lovell et al., 2007); In addition, in the context of the search for biodiversity indicators, it is of great importance to better assess the characteristics of different taxa (Pearman and Weber, 2007). These two groups differ in their ecological requirements and dispersal capabilities and are likely differentially affected by the presence of hedgerows: plant community composition is expected to be controlled mostly by soil and light characteristics (Schaffers, 2002) whereas spider communities are

known to be highly sensitive to habitat structure and microclimatic conditions (Marc et al., 1999; Entling et al., 2007; see also Beals, 2006) and may exhibit variation on much smaller time scales than plants. By comparing similar grassland habitats in sites with and without planted hedgerows, we specifically examined (1) whether the presence of planted hedgerows influenced the surrounding specific and functional trait diversity, (2) whether plant and spider communities exhibited different environmental patterns, and (3) whether artificial hedgerows resulted in a higher overall biodiversity supported by highway verges.

2. Methods

2.1. Study area

This study was conducted within a 50 km section of highway A11 (1°39′30′′E–48°29′15′′N to 1°03′E–48°14′N) in the Beauce region, an intensive agricultural landscape, West of Paris, France. The Beauce covers about 6000 km² and is characterised by a temperate climate and high base status soils. This study area is a fairly typical modern open-field landscape with a complete absence of hedgerows and very few seminatural habitats, such as remnant woodland patches. Agricultural practices consist mostly of intensive cereal production.

A11 Highway was built 30 years ago and enlarged in 1992. At this time, the newly created verges, devoid of vegetation, were sown with the same seed mixture, including mainly *Leguminosae* and *Poaceae* species (*Festuca rubra*, *Festuca ovina*, *Lolium perenne*, *Festuca arundinacea*, *Bromus inermis*, but also *Medicago lupulina*, *Lotus corniculatus*, *Trifolium arvense* and *Achillea millefolium*), along the whole highway section studied, and were planted with trees at discrete locations (Cofiroute construction company, personal communication). In the following, we define hedgerows as linear patches of planted shrubs and trees longer than 150 m, following the definition of Baudry et al. (2000). Sites with and without planted hedgerows are subsequently referred to as "WT" sites and "WO" sites, respectively. Management practices of highway verges depend on distance from the carriageway edge: all verges receive a visibility cut up to 6 m from the road edge twice a year, but areas behind this safety zone are only cut once a year, whereas vegetation growing under planted trees is seldom, if ever, cut.

2.2. Field sampling and data collection

2.2.1. Field sampling

We selected 25 field sites (Fig. 1) based on the following structural and biological criteria: highway sections were "roadcuts" (resulting from excavation), with edges of the same shape (width = 16.1 m ± 0.7 SE, height = 4 m ± 0.3 SE), slope (30° ± 2.4 SE) and aspect, and were bordered by crop fields. Within the 50 km study area, we selected 11 sites with planted hedgerows (WT) along these criteria, using geomorphic maps, aerial photographs, and field surveys. Hedgerows consisted of mature deciduous trees in the canopy layer, and were on average above 3 m tall and 5 m wide (5.2 ± 0.5 SE, varying between 3 and 8 m). They were generally pluri-spe-
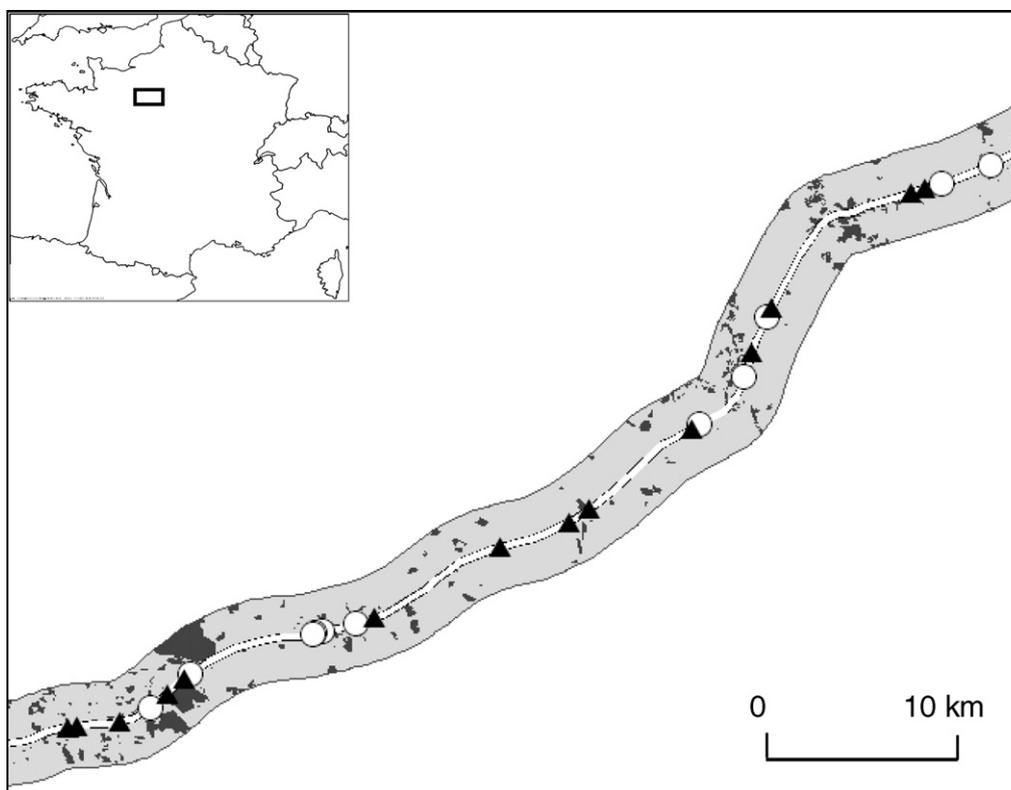
Fig. 1 – Location of the 25 study sites. ▲: sites without hedgerows (WO), O: sites with planted hedgerows (WT); line: A11 highway; grey patches: woodland patches within a 2000 m radius buffer.

cific, including most frequently the following planted species: *Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Alnus cordata*, *Betula verrucosa*, *Betula pendula*, *Carpinus betulus*, *Cornus alba*, *Cornus mas*, *Cornus sanguinea*, *Corylus avellana*, *Cotinus coggygria*, *Fraxinus excelsior*, *Prunus avium*, *Prunus mahaleb*, *Prunus padus*, *Prunus spinosa*, *Quercus sessiliflora*, *Quercus robur*, *Robinia pseudo-acacia*, *Salix caprea*, *Sambucus nigra*, *Sorbus aucuparia*, *Sorbus torminalis*, *Viburnum lantana*, *Viburnum opulus*. When possible, one site without hedgerows (WO) was chosen within 1.5 km of a given site with hedgerows (WT). We thus selected seven pairs of geographically close sites with and without hedgerows and completed this sample with isolated WT ($n = 4$) and WO sites ($n = 7$), for a total of 25 sampled sites (11 WT–14 WO). WO sites were always located at least 50 m from the closest tree.

2.2.2. Data collection
All inventories were performed through a 60 m transect running parallel to the carriageway, located at least 7.5 m from the carriageway edge and at 8.2 ± 0.6 SE from the neighbouring crop field. Such location corresponded to extensive management practices. In WT sites, transects were also located 0.5–1 m from the canopy of planted trees (vertical projection of lower branches), and started and ended at least 50 m away from the end of the hedgerow, to avoid border effects.

For flora, sites were surveyed from May 10th to June 10th 2006. In each site, all vascular plant species were inventoried once in five 1 m^2 quadrats regularly distributed over the 60 m transect. Almost all taxa were identified to species level

according to the International Plant Names Index. A few species that were difficult to distinguish when not in flower or fruit (*Vicia gr tetrasperma-hirsuta* for example) were grouped.

Spiders were sampled using five pitfall traps per site. Traps were placed within 30 cm of each vegetation quadrat on the 60 m transect and were left in place from May 10 to June 10 2006. Each trap was 8.5 cm wide in diameter and 10 cm deep, and contained ethylene glycol, a non-attractive preservative. Two pitfall traps were destroyed and were omitted in the analyses ($n = 123$). Adult spiders were identified to species level following the nomenclature of Platnick (2007). We failed to identify three individuals to species level; nevertheless, because they were obviously different from other species, they were conserved for analyses. Spider juveniles were generally not identifiable to species level and were not considered.

Sites characteristics: sampling design was defined to test impact of hedgerows, so that the variation of other environmental variables was minimised. We recorded sites characteristics and checked the absence of correlation between presence/absence of hedgerows and other environmental factors using Pearson correlations, to check that the effects of hedgerows were not confounded with other environmental factors. For each site, we recorded geographic coordinates, verge width (final variation: 10–20 m), adjacent land use type (crop vs. temporary fallow), slope, distance from crop edge, aspect, and soil nutrient status. The latter was characterised via determination of soil pH, as well as phosphorus (P_2O_5, Olsen%), salt (Na_2O), and total nitrogen (%) concentration in a bulked representative soil sample, taken to a depth of 10 cm

in each of five plots and subsequently mixed. For each site, we also recorded the distance from the nearest woodland patch (411.6 m ± 70.4 SE), as well as the total woodland area within 250 m, 500 m and 1000 m radius buffers, using aerial photographs and the Geographical Information System package ARCGIS 8 (ESRI, 2000). In this open-field system, woodland patches can be considered as the main natural habitat in Beauce. Consequently, we considered that they could be important reservoirs of species compared to others habitats, providing a pool of both plants and spiders from which species were able to disperse and potentially colonise highway verges.

2.3. Species attributes

To address the influence of hedgerows on community functional composition, we characterised species based on readily available functional traits. As such data were analysed using multivariate methods that are highly sensitive to "rare" species or classes, we chose to group some classes to minimise the resulting bias (see caption of Fig. 2). For plants, these functional traits include Raunkier types, maximum adult height, and seed dispersal mode, scored according to a literature review (Supplementary material 1). For spiders, we retained hunting strategies, body size and aerial dispersal behaviour (ballooning vs. non-ballooning species). Hunting strategies (diurnal cursorial hunters, nocturnal cursorial hunters, ambush hunters, and web-builders) and species-specific body sizes were derived from Roberts (1985, 1987). As body sizes usually differ between sexes, the mean value of male and female median sizes was retained. Species exhibiting aerial dispersal using silk (ballooning) are considered species with great dispersal capabilities (Bell et al., 2005 for review) and were defined using the world species list of ballooning Araneomorphae established by Bell et al. (2005). All species that did not appear in this list were considered "non ballooners", which may be incorrect because the list is not exhaustive. However, as we worked with common species frequently found in agricultural landscapes and whose biology is generally well-known, we expect that this bias should be small. For both plants and spiders, a given taxon was assigned attributes only when it was identified to species level and observed in more than four instances (quadrats or traps), which yielded a total of 46 plant species (100% of species observed in more than four quadrats) and 56 spider species (84% of species detected in more than four pitfalls) for which all traits were scored.

2.4. Data analysis

To remove the obvious increase in plant species richness due to the simple presence of planted species and examine solely indirect effects of planted hedgerows on plant community composition, we chose to work with spontaneous plant species only. Hence, unless otherwise stated, shrub or tree species that were observed in the herbaceous strata in a site where they had been planted (as inferred from historical plantation map data, *Cofiroute–Vegetude*) were discarded in subsequent analyses, i.e. they were excluded of this particular site; not, however, that these species were retained in other
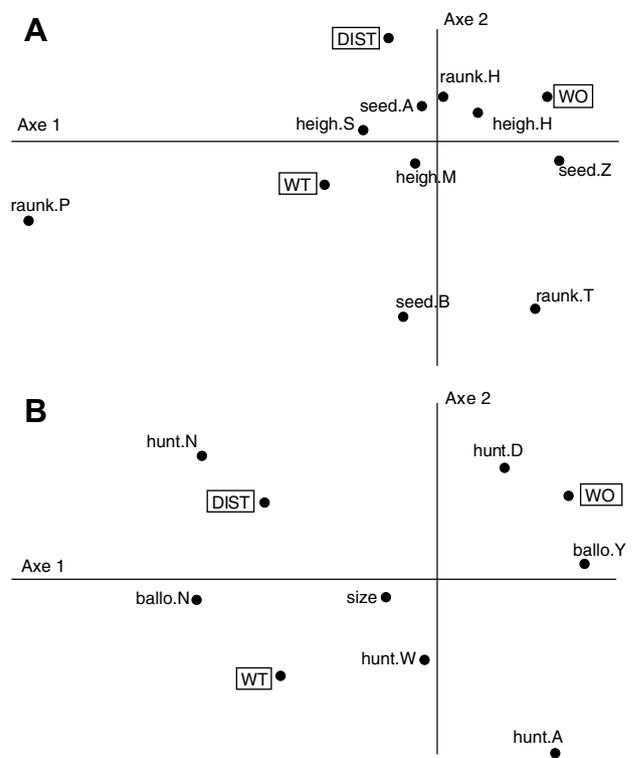

Fig. 2 – RLQ analysis ordination biplot illustrating relationships among environmental and plant species attributes (A) and spider species attributes (B). The analysis is based on presence/absence of species with known attributes that were observed in more than four samples (46 plant species and 56 spider species). (1) *Environmental parameters*. WT: sites with planted hedgerows, WO: sites without hedgerows; dist: distance to the distance to the nearest woodland patch. (2) *Plant traits* (A). rank: raunkier type: H: Hemicryptophytes and Geophytes (28 species), P: Phanerophytes and Chamaephytes (6), T: Therophytes (12); heigh: maximum adult height: S: small (0–45 cm: 9), M: medium (46–100 cm: 19), H: high (100 and more: 18); seed: Seed dispersal: A: anemochory (30), B: barochory and autochory (9), Z: zoochory (7). (2) *Spider traits* (B). ballo: ballooning behaviour: Y: Yes (30), N: No (26); size; hunt: hunting strategies: W: diurnal wandering (18); N: nocturnal wandering (10); W: web-builders (21); A: ambush hunters (7).

sites. In addition, for spider species, we chose to work with presence/absence data only, so that a range of different analyses, some of which valid with presence/absence data only, could be used on the same dataset. With few exceptions, including abundance data yielded very similar results. All analyses were conducted with (R Development Core Team, 2007).

2.4.1. Species richness
To assess the effect of hedgerows at different spatial scales, we considered species richness at the quadrat scale (S_{local}, plants only), at the site scale (S_{site}, in a transect of 60 m, plants and spiders) and at the highway section scale, within

each type of site (S_{type}, within WT or WO types of sites, plants and spiders). For plants, we considered local species richness (S_{local}) within quadrats because we assumed that all species were detected, whereas for spiders, pitfall trapping is known to be influenced by the activity-density of species (Melbourne, 1999). In addition, analysis on local spider richness showed no effect of any environmental variable. Comparing observed species richness across sites and habitats might not be valid in case of unequal species detection probabilities (Boulinier et al., 1998; Nichols et al., 1998). We, therefore, used statistical methods derived from capture–recapture approaches in population or community dynamics to estimate species richness and changes in community composition As in recent studies (Lekve et al., 2002; Doherty et al., 2003; Selmi and Boulinier, 2003; Devictor et al., 2007; Kerbiriou et al., 2008) addressing richness estimation and differences in community composition from species count data, we used the program COMDYN (Hines et al., 1999), based on the jackknife estimator of Burnham and Overton (1979). To estimate species richness at the site level (S_{site}), we used quadrat or pitfall captures as replicates. To estimate richness at type of site level (S_{type} within WT or WO type of sites), we used sites as replicates ($n = 11$): analyses were based on presence–absence data at the site level, pooled across the five quadrats for plants and the five pitfall traps for spiders. As 11 replicates only were available for WT sites, we sampled randomly without replacement 11 sites out of 14 in the WO group; this sampling procedure was performed 15 times. Each of 15 pairs of (1) 11 sampled WO sites plus (2) the 11 WT sites was input into program COMDYN to obtain estimated richness per type of site. The estimated richness in each type of site was then characterised using the mean and standard error of the 15 outputs.

We analysed the combined influence of hedgerows and environmental variables on both local species richness for plants (S_{local}) and estimated richness per site for plants and spiders (S_{site}), using linear models and analyses of variance, as follows: for each taxonomic group (plants and spiders) and dependent variable (S_{local} and S_{site}), we selected the most informative model using a stepwise algorithm based on Akaike Information Criterion (StepAIC, library MASS in R) starting from the most complete model including all environmental variables likely to influence species richness (listed above: see "site characteristics"). Plant richness was included as an additional environmental variable for spiders. Data were log-transformed when necessary to meet normality assumptions; the effects of variables retained by the stepwise algorithm were tested adjusted to others and the nested structure of the data was taken into account (local richness per quadrat nested within site: lme, library nlme in R).

2.4.2. Species composition
We investigated a possible spatial autocorrelation in community composition by performing mantel tests (mantel.randtest, library ade4 in R) to assess the correlation between matrices of geographic vs. specific distances among sites. For plants and spiders, matrices of specific distances across sites were computed with the Jaccard index on presence/absence matrices. This effect was also tested separately within

both types of edges (WT and WO sites). For these analyses, all species were retained.

We also examined the effect of hedgerows on the composition of plant and spider communities in the herbaceous strata using two types of multivariate analyses: Constrained Analysis of Principal Coordinates (CAP) and partial Constrained Correspondence Analysis (pCCA), followed-up by ANOVA-like permutation tests ($n = 999$) to assess significance of effects. CAP (capscale, library vegan in R, see Anderson and Willis, 2003) is an ordination method similar to Redundancy Analysis (RDA), i.e. exploring the relationship between two sets of variables, but allowing non-Euclidean dissimilarity indices. It was used to examine whether species similarity among sites depended on the presence/absence of hedgerows, and on the distance to nearest woodland patch, which was used as a covariable. It was performed on presence/absence matrices across sites, using the Jaccard index. pCCA (cca, library vegan in R, ter Braak, 1986) is an ordination method based on CCA, a constrained ordination method developed to relate community composition to known variation in the environment. It is considered as a good choice if the user has clear and strong a priori hypotheses on constraints. Here, we used pCCA to test whether the presence of some species was associated with the presence or absence of planted hedgerows. We chose pCCA instead of a simple CCA to remove the effect of the distance to the nearest woodland patch, used as a covariable, as in CAP. As both analyses are sensitive to rare species, we only retained species observed in more than four samples, i.e. 46 plant species and 67 spider species.

Third, we examined the complementarity of communities (Nichols et al., 1998) in each type of site (WO type and WT type) using COMDYN with sites as replicates ($n = 11$). In addition to estimating richness within each type of site (S_{type} within WO and WT type of sites), we obtained the following estimators: complement of "extinction probability" between the two types, Φ (i.e. proportion of WT species present in WO), estimated complement of species "turnover", γ (i.e. proportion of WO species present in WT), and "estimated local colonising" species, B (i.e. number of species not present in WT but present in WO). As for richness, we compared the mean and standard error (over 15 re-sampling events) of these estimators between WT and WO types.

2.4.3. Functional trait composition
We investigated whether some species attributes were more likely associated with one type of site and distance to neighbouring woody patch (environmental variables). To this end, we used a multivariate ordination analysis, RLQ, which is an extension of coinertia analysis. RLQ performs a double inertia analysis of two arrays (R, here the environmental array and Q, here the trait array), i.e. measures the adequacy between the two arrays, with a link expressed by a contingency table (L, here the species array: matrix of presence–absence of species across sites) (rlq, library ade4 in R, complete description: see Doledec et al., 1996; for an example: Ribera et al., 2001). The general significance of the relationship between environmental variables and species traits was tested using random permutations test ($n = 999$). We also used only species observed in more than

four samples to limit the potentially strong effects of rare species.

3. Results

Across 25 highway verge sites, we observed a total of 85 plant species and 123 different spider species. For spiders, we captured 8300 individuals, 7862 of which were adults that could be identified to species level. Only eight of the 85 plant species (A. campestre, A. pseudoplatanus, B. pendula, F. excelsior, P. avium, P. padus, P. spinosa, V. opulus) were identical to those planted in the immediately neighbouring hedgerow in WT sites and were excluded from most analyses; note, however, that including them had no effect on the following results.

3.1. Species richness

3.1.1. Influence of planted hedgerows on plant communities
We observed a significant positive effect of the presence of hedgerows (Table 1) on plant richness at the local scale (quadrat level, $n = 125$, $S_{localWT} = 10.20 \pm 0.46$ SE; $S_{localWO} = 8.20 \pm 0.47$ SE, $F_{1,20} = 5.79$, $p = 0.026$). We also found a negative effect of distance from crop edge ($F_{1,20} = 5.75$, $p = 0.026$), as well as tendencies for effects of adjacent land use (higher richness with temporary fallow, $F_{1,20} = 4.15$, $p = 0.055$) and phosphorous rate (negative: $F_{1,20} = 4.00$, $p = 0.059$) on local plant richness. In contrast, no effect of hedgerows or any environmental factor was detected on plant richness at the site level ($n = 25$, $S_{siteWT} = 25.45 \pm 1.66$ SE; $S_{siteWO} = 23.75 \pm 3.12$ SE) and there was no difference in detection probabilities between the two types of sites. However, at the section level ($n = 11$), the estimated plant richness was 139.16 over all WT sites (S_{typeWT}, ± 29.20 SE; detection probability dp $= 0.47 \pm 12.42$ SE) vs. 87.51 over all WO sites (S_{typeWO}, ± 19.43 SE; detection probability dp $= 0.68 \pm$ SE $= 0.12$).

3.1.2. Influence of planted hedgerows on spider communities
We found no effect of the presence of planted hedgerows on spider richness at the site level. Spider richness was significantly affected by distance to the nearest woodland patch (negative effect, $F_{1,18} = 5.94$, $p = 0.025$), site slope (positive effect, $F_{1,18} = 4.65$, $p = 0.044$) and plant richness (positive effect, $F_{1,18} = 6.81$, $p = 0.018$). There was no difference in detection probabilities between the two types of sites. At the section level, ($n = 11$), estimated spider richness was 119.3 over all WT sites (S_{typeWT}, ± 19.6 SE; detection probability dp $= 0.80 \pm 0.10$ SE) and 142.0 over all WO sites (S_{typeWO}, ± 27.15 SE; detection probability dp $= 0.64 \pm 0.11$ SE).

Table 1 – Change in species composition in the herbaceous strata of highway verges in sites without planted hedgerows (WO) vs. sites with planted hedgerows (WT)

	Φ	γ
Plants	0.86 ± 0.11	0.99 ± 0.10
Spiders	0.77 ± 0.09	0.83 ± 0.08

Φ is the proportion of WT sites species still present in WO sites and γ is the proportion of WO sites species still present in WT sites.

3.2. Community composition

3.2.1. Spatial autocorrelation
Using Mantel tests on the full dataset, we found significant spatial autocorrelation in plant communities ($p = 0.001$), but not in spider communities ($p = 0.066$). In contrast, within types of site, spatial autocorrelation was observed in plants (WT: $p = 0.006$; WO: $p = 0.001$) and spiders (WT: $p = 0.007$; WO: $p = 0.028$). However, as WO and WT sites were randomly distributed in space (Fig. 1, autocorrelation should not interfere with our main purpose, i.e. to assess the influence of hedgerows on community composition.

3.2.2. The presence of planted hedgerows influence community composition
Sites with and without planted hedgerows supported significantly different plant and spider communities, as shown by CAP (ANOVA-like permutation tests: plants: $F_{1,22} = 2.26$, $p < 0.001$, inertia explained by hedgerows = 9% and by distance to the nearest woodland patch = 4%; spiders: $F_{1,22} = 1.90$, $p = 0.006$, inertia explained = 7% and 6%, respectively). This effect of hedgerows on plant and spider community composition was confirmed by the pCCA analysis (ANOVA-like permutation tests: plants: $F_{1,22} = 2.13$, $p < 0.01$, inertia explained = 8% and 4% respectively; spiders: $F_{1,22} = 1.81$, $p < 0.005$, inertia explained = 7% and 5%, respectively). This method also identified species that seemed preferably associated with WT sites. For plants, these were A. campestre, B. pendula, Galium mollugo, Centaurium erythraea, Trifolium repens, and for spiders, Panamomops sulcifrons, Maso sundevalli, Walckenaera dysderoides, Ceratinella brevis, and Drassodes cupreus. In contrast, the spider species Tegenaria picta, Ero furcata, and Palliduphantes ericaeus, were preferably associated with WO sites.

3.2.3. Nested vs. complementary communities
We found that the plant community observed in WO sites was a subset of the plant community in WT sites (Table 1). WO sites did not exhibit any private species: we found 99% of WO sites species in WT sites, so that all WO species were expected in WT sites (COMDYN estimator $B = 0$). The reverse was not true: WT exhibited several private species (14%), with only 86% of WT sites species also observed in WO sites. In contrast, spider communities appeared complementary. Respectively 83% (WT) and 77% (WO) of spider species were present in the other type of site, so that each type of sites exhibited private species.

3.3. Relationship between species attributes and presence of hedgerows

For both plants and spiders, there was a significant relationship between species attributes and environmental variables (Fig. 2). RLQ randtest, $p = 0.001$ and $p = 0.001$. For the two taxa, the presence/absence of planted hedgerows was associated with the first axis, which explained respectively 81% and 80% of the total inertia, whereas the distance to the nearest woodland patch tended to be associated with axis 2 (respectively, 19% and 20% of inertia). In spontaneous plant species, Raunkier type was influenced by the presence of hedgerows, with Phanerophytes and Chamaephytes (Rank: P) positively

associated with WT sites (Fig. 2). In contrast, adult height was not significantly associated with site type. Finally, species with no specific means of dispersal (barochory, autochory) tended to be more present in WT sites than in WO sites, whereas animal-dispersed species (zoochory) were more common in WO than in WT sites; wind-dispersed species were not affected by the presence of hedgerows. In spiders, the mode of dispersal (ballooning vs. non-ballooning) was strongly affected by the presence of hedgerows: ballooning species were more likely found in WO sites, and non-ballooning species in WT sites. In addition, web-builders were more common in WT than in WO sites, and diurnal wandering hunters in WO sites. Finally, larger species tended to be more common in WT sites than in WO sites.

4. Discussion

We addressed the effect of the presence of planted hedgerows on neighbouring plant and spider communities of highway verges. We showed that (1) planted hedgerows were associated with higher species richness, i.e. a higher α-diversity ($\alpha_{WO} < \alpha_{WT}$), for plants, but not for spiders. This was due to the fact that plant communities in sites without hedgerows (WO) were a subset of communities in sites with hedgerows (WT), whereas spider communities in WO sites were complementary to communities in WT sites. Below, we argue that such differences are attributable to different ecological characteristics of species, which is supported by the distribution of functional traits, and derive the consequences in terms of roadside management.

4.1. The influence of propagule source vs. local conditions on plant and spider community composition

Following the environmental filter model (Keddy, 1992), two non-exclusive hypotheses may explain the effect of hedgerows on community composition, depending on taxonomic group. Hedgerows could either be a source of dispersers ("source" hypothesis) or could provide microclimatic conditions that affect the presence of some species due to their environmental requirements ("local conditions" hypothesis).

4.1.1. "Source" hypothesis and the effect of hedgerows on plant communities
The dispersal of some species from neighbouring hedgerows into a suboptimal habitat (grassland) would affect community composition in the suboptimal habitat. This phenomenon, known as the edge effect, has been observed in several taxa: contrasted adjacent habitats supporting distinct species assemblages often mix over a few meters on either side of the interface (see for example, Bedford and Usher, 1994). For example, Downie et al. (1996) studying spider community composition across a plantation–pasture ecotone, found that most of the community (70% of species) was formed by the overlap of both pasture and plantation species encroaching across the interface through dispersal or foraging processes. Interface-specialist species were present but contributed less to the interface community content than the other species categories (23% of individuals and 25% of species).

Under the "source" hypothesis, communities are, therefore, expected to exhibit higher species richness in WT vs. WO sites. This was the case for plant communities ($\alpha_{WO} < \alpha_{WT}$), at the quadrat scale, but not at the site level. Another prediction of the source hypothesis is that WO communities should be a subset of WT communities. This was true again for plants: in WT sites, we observed 'private' species which were not supported by WO sites, whereas the reverse was not true. Finally, in the case of a higher effect of dispersal vs. local conditions on species distribution within similar habitats, a distance effect can be expected independently of presence/absence of hedgerows. In plant communities, spatial autocorrelation was in fact detected regardless of the presence of hedgerows. These three observations converge to suggest that dispersal is a major driver of community composition in this group.

The distribution of plant functional traits is consistent with this role of dispersal. We found that Phanerophytes and Chamaephytes were more represented in WT sites, corresponding mostly to the occurrence of the following species: *A. campestre*, *B. pendula*, *Cytisus scoparius*, *F. excelsior* and *P. spinosa*. These species observed in the herbaceous strata most likely originated from seed-bearer trees that grow spontaneously within the otherwise planted hedgerow. Thus, hedgerows offer a sustainable habitat where particular species, and notably woody plants, can grow and reproduce, whereas such species cannot reach maturity within WO sites, due to frequent mowing. The fact that zoochory was more represented in WO sites is, however, not easily interpreted in this framework.

4.1.2. "Local conditions" hypothesis and the effect of hedgerows on spider communities
Microclimatic conditions (influenced, among others, by the neighbouring hedgerows) might be responsible for observed community composition, especially in spiders. For example, spider richness within sites was positively correlated with local plant richness; plant community composition and consequently, the architecture of habitat are well-known predictors of spider community composition (e.g. Beals, 2006). Moreover, woody hedgerows are known to provide particular microclimate conditions in their neighbourhood (Forman and Baudry, 1984) and most authors agree that those are a major factor controlling spider distribution (see, Marc et al., 1999). For example, Downie et al. (1996), examining spider community composition, proposed that close to an interface, the role of vegetation structure is low compared to other factors, including changes in microclimate. Finally, perennial non-crop habitats are known to be used by spiders as overwintering sites and refuges (Oberg et al., 2008). Grassland habitats located next to hedgerows maybe, therefore, provide better conditions than sites without hedgerows for overwintering, with direct consequences on spider community composition. Thus, neighbouring hedgerows may have an environmental filter effect, which leads to the selection of species with particular ecological requirements.

Under the 'local conditions' hypothesis, we expect that sites with and without planted hedgerows support different species. This was the case with spiders: WT and WO communities were complementary instead of nested, thus yielding

similar species richness with or without hedgerows. This implies that some spider species occurring in WO sites were absent from planted sites. As the two types of sites offered the same habitat (grassland with similar percentage cover and dominance of graminoïds), the observed differences are likely be explained by specific microclimatic conditions created by the neighbouring hedgerows. Finally, the role of hedgerow-induced local conditions in spider community composition is also supported by patterns of spatial autocorrelation: the dominant impact of neighbouring hedgerows on spider community composition removed spatial autocorrelation patterns across all sites, whereas spatial autocorrelation remained significant within WT and WO sites.

Despite the significant role of local conditions, spider community composition is also likely affected by dispersal. For example, spider richness within sites was negatively correlated with the distance to the nearest woodland patch. Such effect of distance is well known from the theory of island biogeography (MacArthur and Wilson, 1967) and consistent with results from other field studies: spider species richness in wheat fields has been shown to increase with the proportion of non-crop habitats in the surrounding landscape (Schmidt and Tscharntke, 2005; see also Bianchi et al., 2006 for other groups).

Although the observed distribution of species between site types suggests a major role of local conditions, trait analyses outlined that aerial dispersal capabilities are an important factor explaining the interaction between the presence of hedgerows and spider community composition: species exhibiting ballooning behaviour were more represented in WO sites and the reverse was true for non-ballooning species. This result is comparable to that of Bonte et al. (2004), who found that the distribution of 29 spider species inhabiting fragmented grey dunes depended on their aerial dispersal potential, as well as on the interaction between patch connectivity and area. Ballooning is thought to be more common in species from unstable and ephemeral habitats (Bonte et al., 2003; Bell et al., 2005); moreover, high dispersal capabilities are generally dominant in disturbed habitats (e.g. Nyffeler and Sunderland, 2003 for spiders; Ribera et al., 2001 for beetles), allowing the maintenance of populations in ephemeral agricultural ecosystems (Weyman et al., 1995). We, therefore, suggest that the significantly higher proportion of ballooning species in WO sites may be due to the absence of a neighbouring hedgerow, i.e. of a stable habitat. In contrast, species that do not exhibit this behaviour should be more common in WT sites because hedgerow likely provides more stable conditions, both in terms of management (no mowing) and microclimatic variables. Hedgerows would thus be overwintering refuges (see also, Pywell et al., 2005), from which species colonise the surrounding habitats in spring. Sites without planted hedgerows, which receive a cut, generally in autumn, would be poor refuges that are partly recolonised from more distant sources in spring. Hence, they support a higher proportion of species exhibiting large dispersal capabilities, i.e. "ballooners". Dispersal and local conditions, therefore, appear to drive spider community composition at different temporal scales.

Finally, note that taxonomic differences in composition of spider communities were also associated with differences in

hunting strategies: web-builder were more represented in WT sites possibly due to the greatest heterogeneity of support provided by the presence of neighbouring hedgerow and the higher richness of plant whereas diurnal wandering hunter were more abundant in WO sites.

4.1.3. Conclusions

Planting generally increased the γ-diversity of highway verges, via an increase in both taxonomic and functional trait β-diversity between sites with and without hedgerows, but this positive effect was different in the two taxa considered. For plants, it was mostly due to an increase in taxonomic α-diversity within sites with hedgerows, whereas for spiders it was related to a direct increase of taxonomic β-diversity between the two types of sites. Note that this partition of diversity is likely to vary through time as well (e.g. due to overwintering dispersal patterns in spiders), with different temporal scales in the two taxa, but this was not the focus of the present study. From a theoretical viewpoint, the fact that the partitioning of diversity between α- and β-diversity differed between the two taxa is probably due to the different spatial and temporal scales at which the heterogeneity of interactions between organisms and their environment can be found (see, Loreau, 2000). According to Loreau (2000), "the challenge now is to understand the relationship between α- and β-diversity at multiple scales, and the processes that determine it". In our opinion, comparing the partitioning of diversity among several taxa and functional groups at different spatial scales is, therefore, a promising way to explore the processes that control the distribution of biodiversity.

4.2. Consequences for the management of highway verges

Our findings have direct consequences for the management and conservation of highway verges in agricultural landscapes, where most biodiversity is aggregated in more stable non-crop habitats and field edges (Bianchi et al., 2006). Increasing the botanical and structural heterogeneity of hedgerows by planting is likely to have significant beneficial effects on native flora and fauna (Maudsley, 2000). Obviously, plantation increases species richness both directly (introduction of new species) and indirectly, by providing particular environmental conditions within woody hedgerows and thus contributing to the maintenance of some species (e.g. woody plants) in landscapes where they are poorly represented. But our results suggest that planted hedges may also affect community composition of nearby herbaceous strata, enhancing both taxonomic and functional trait γ-diversity along highway verges.

In practice, our results highlight the importance of creating a mosaic of planted sites alternating with non-planted sites in highly disturbed landscapes. Of course, "natural" dynamics could yield the same results and probably a greater biodiversity as demonstrated by Boutin et al. (2002), who compared natural vs. planted hedgerows. However, in the case of highway verges, natural hedgerows would only arise by recolonisation of the newly created habitats, which involves successional dynamics with intermediate states, and the presence of pioneer species often considered as weeds. In the context of intensive agricultural landscape, where farm-

ers wish to limit weeds in field boundaries as much as possible, planting trees along highways verges appears as a compromise between biodiversity conservation and anthropogenic pressures. The issues of the identity of planted species (which are usually exotic species), of management of hedgerows (Croxton et al., 2004) and of their spatial arrangement along highway verges (to provide effective corridors) remain to be addressed. Given the urge to conserve biodiversity, especially in the context of climate change, road practitioners should consider plantation not only for esthetical reasons but also as a possibility to increase the role of verges as a refuge and, consequently, landscape connectivity.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.04.003.

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