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## Original article

## Landscape heterogeneity as an ecological filter of species traits

Rémi Dufлот<sup>a,b,\*,1</sup>, Romain Georges<sup>a,1</sup>, Aude Ernoult<sup>a</sup>, Stéphanie Aviron<sup>b</sup>, Françoise Burel<sup>a</sup><sup>a</sup> CNRS, UMR 6553 Ecobio, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France<sup>b</sup> INRA, UR 980, SAD-Paysage, 65 Rue de Saint Brieuc, CS 84215, 35042 Rennes Cedex, France

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## ABSTRACT

Landscape heterogeneity is a major driver of biodiversity in agricultural areas and represents an important parameter in conservation strategies. However, most landscape ecology studies measure gamma diversity of a single habitat type, despite the assessment of multiple habitats at a landscape scale being more appropriate. This study aimed to determine the effects of landscape composition and spatial configuration on life-history trait distribution in carabid beetle and herbaceous plant communities. Here, we assessed the gamma diversity of carabid beetles and plants by sampling three dominant habitats (woody habitats, grasslands and crops) across 20 landscapes in western France. RLQ and Fourth Corner three-table analyses were used to assess the association of dispersal, phenology, reproduction and trophic level traits with landscape characteristics. Landscape composition and configuration were both significant in explaining functional composition. Carabid beetles and plants showed similar response regarding phenology, i.e. open landscapes were associated with earlier breeding species. Carabid beetle dispersal traits exhibited the strongest relationship with landscape structure; for instance, large and apterous species preferentially inhabited woody landscapes, whereas small and macropterous species preferentially inhabited open landscapes. Heavy seeded plant species dominated in intensified agricultural landscapes (high % crops), possibly due to the removal of weeds (which are usually lightweight seeded species). The results of this study emphasise the roles of landscape composition and configuration as ecological filters and the importance of preserving a range of landscape types to maintain functional biodiversity at regional scales.

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## 1. Introduction

Agricultural landscapes occupy approximately 75% of Europe (Robinson and Sutherland, 2002), and support a high amount of plant and animal total biodiversity (Benton et al., 2003). Agricultural intensification and land-use changes represent major causes of biodiversity decline in agricultural landscapes (Strijker, 2005). Since the 2000s, maintaining biodiversity in agricultural landscapes has become an important social and economic issue, with a focus on preserving ecosystem functioning and ecosystem services

provision (Kleijn and Sutherland, 2003; Le Roux et al., 2008; Millennium Ecosystem Assessment, 2005).

Spatio-temporal landscape heterogeneity strongly influences the species richness and composition of communities, and is consequently an important parameter that should be considered in biodiversity conservation (Fahrig et al., 2011; Huston, 1995; Turner, 1987). In agricultural landscapes, short-term (crop rotation) and long-term (agricultural intensification) temporal changes represent important drivers of biodiversity (Ernoult et al., 2006; Le Feon et al., 2013). Diversity is also influenced by spatial heterogeneity, which is defined as a combination of two components, compositional and configurational heterogeneity (Duelli, 1992; Fahrig et al., 2011). Landscape composition affects diversity as habitat diversity influences plant, vertebrate and invertebrate diversity (Benton et al., 2003; Poggio et al., 2010; Robinson et al., 2001; Woodcock et al., 2010). Landscape configuration which can be measured from the length of edges (or boundaries), influences species movements and spillovers (Blitzer et al., 2012; Brudvig et al., 2009; Concepcion et al., 2012; Tschardt et al., 2005). However, high landscape heterogeneity may also increase fragmentation *per se* and have negative effects on biodiversity. Hence, biodiversity is expected to

\* Corresponding author. CNRS, UMR 6553 Ecobio, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France. Tel.: +33 223 236 663; fax: +33 223 235 026.

E-mail addresses: [duflot.remi@gmail.com](mailto:duflot.remi@gmail.com) (R. Dufлот), [romaingeorges@live.fr](mailto:romaingeorges@live.fr) (R. Georges), [aude.ernoult@univ-rennes1.fr](mailto:aude.ernoult@univ-rennes1.fr) (A. Ernoult), [stephanie.aviron@rennes.inra.fr](mailto:stephanie.aviron@rennes.inra.fr) (S. Aviron), [francoise.burel@univ-rennes1.fr](mailto:francoise.burel@univ-rennes1.fr) (F. Burel).

<sup>1</sup> These authors contributed equally to this work. RD and RG designed the experiment, collected data, performed statistical analyses, and wrote the manuscript. Other authors participated in designing the experiment, data collection and writing the manuscript.

peak at intermediate levels of heterogeneity. Yet, it remains unclear which ecological processes drive species response to landscape heterogeneity components in agricultural areas (Fahrig et al., 2011).

It is generally accepted that functional traits control species responses to landscape heterogeneity gradients (Barbaro and van Halder, 2009; Vallet et al., 2010), and are readily linked with ecological processes (Diaz and Cabido, 2001). Dispersal traits are considered to be the main traits affected by landscape heterogeneity (Hendrickx et al., 2009; Piessens et al., 2004). The phenology (Silvertown and Charlesworth, 2001; Tremlova and Munzbergova, 2007) and longevity (Lindborg, 2007) of plants are also highly sensitive to landscape fragmentation. Therefore, in addition to local abiotic and biotic factors, landscape heterogeneity may be considered as an ecological filter (Tonn et al., 1990), which selects or excludes species from the regional pool according to particular functional traits (Keddy, 1992; Lomba et al., 2011). The species filtered by landscape composition and configuration represent the landscape species pool, with species being further selected by habitat type and local factors to form local species composition and diversity. Hence, it is essential to obtain knowledge about the landscape scale to describe the processes that govern ecological communities from the regional to the local scales.

In recent literature, some studies investigated the effect of landscape heterogeneity on gamma diversity, i.e. the “whole” diversity measured at a landscape scale (Bennett et al., 2006). Traditionally, the dominant “focal patch” approach has been used, which only tests the influence of landscape heterogeneity on a single site/patch (for a review see Thornton et al., 2011). In contrast, the assessment of gamma diversity allows the resulting overall diversity to be viewed, rather than the response of only one patch (Bennett et al., 2006). However, most existing studies that have used this approach, are focussing on a single habitat (Grasslands: Dauber et al., 2003; woodlands: Radford et al., 2005; hedgerows: Ernoul and Alard, 2011; Millan-Pena et al., 2003; crops: Concepcion et al., 2012). Such gamma diversity measures may be referred as “single-habitat gamma diversity”. However, landscapes are mosaics of different habitats, supporting communities of varying species composition. Therefore, single-habitat

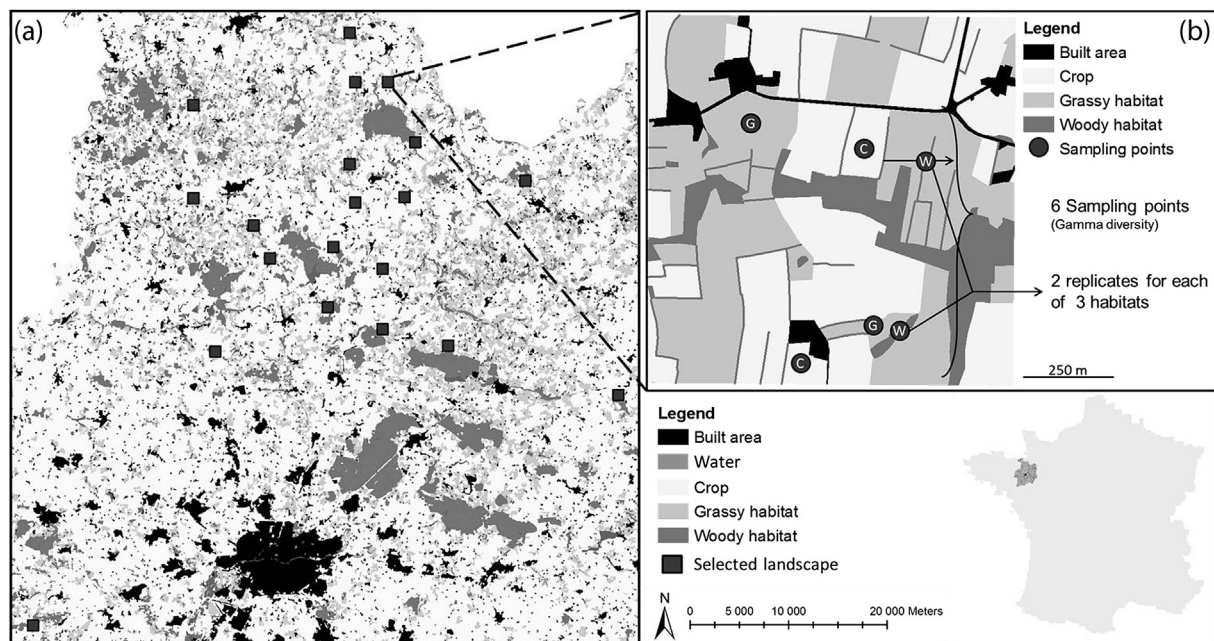
gamma diversity only partially reflects overall landscape diversity, with the study of total landscape scale diversity being required to consider the diversity of multiple habitats, which we termed “multi-habitat gamma diversity”. Such measure of landscape-level gamma diversity hierarchically depends on local diversity (alpha) and beta diversity among patches of the same habitat types (beta patch) and among habitat types (beta habitat) (Crist et al., 2003; Diekötter et al., 2008). Although mosaic-level diversity monitoring is important from a conservation and landscape planning perspective, there are limited studies using this approach (but see Liira et al., 2008).

Here, we investigated the distribution of dispersal, phenology, reproduction and trophic traits for carabid beetles and herbaceous plants along a gradient of spatial heterogeneity in typical western European agricultural landscapes. We evaluated multi-habitat gamma diversity, including crop habitats, to determine i) whether landscape heterogeneity (composition and configuration) serves as an environmental filter for species, ii) which functional traits are affected by the landscape heterogeneity, and iii) whether the observed response patterns could be extended to different species groups (i.e. across taxa).

## 2. Materials and methods

### 2.1. Study area

The study was conducted in hedgerow network agricultural landscapes located in the west of France (Fig. 1). These landscapes are typical of western Europe (Baudry et al., 2000) and have been subject to major modifications since the middle of the twentieth century because of agriculture intensification (Baudry and Papy, 2001; Meeus, 1993). The study area is located in a region where dominant agriculture is mixed dairy farming. The farmlands contain annual crops (mostly winter cereals, but also corn), along with temporary and permanent grasslands, and are separated by woodlands and hedgerows (termed woody elements here). These two types of grasslands are comparable in this area, as they are often similarly managed (Roche et al., 2010).



**Fig. 1.** Map of the study area showing the 20 × 1 km<sup>2</sup> selected landscapes (a) and the hierarchical sampling design of one of these landscapes (b). The sampled cover types are W: woody habitat, G: grassland and C: winter cereal crop.

## 2.2. Sampling design

Twenty square-shaped landscape sites of 1 km<sup>2</sup> were selected to maximise landscape compositional and configurational heterogeneity (Fig. 1). From a regional habitat map derived from remote sensing data (COSTEL Land-cover map, Hubert-Moy et al., 2012), landscapes were selected based on the percentage of semi-natural covers (composition) and the length of edges between semi-natural covers and farmland (configuration).

Within each studied landscape, we sampled carabid beetle and plant communities in the three characteristic habitats of the study area: crop, grassy, and woody habitats. Two patches of each habitat type were sampled in each landscape, i.e. two patches of the most abundant crop (winter cereals), two patches of grassland, and two patches of woody habitat. The variability in the types of woody habitat was addressed by sampling one hedgerow patch and one woodland patch. A total of 120 patches were sampled (6 in each landscape, Fig. 1). The sampled crop, grassland and woodland patches had an average area of 37.8 ha, 9.5 ha and 3.4 ha respectively. The sampled hedgerows were, on average, 132 m long.

Carabid beetles were sampled using two pitfall traps per patch. The traps were positioned 10 m from the patch margins. Traps were collected every two weeks, after being open for seven consecutive days. There were two sampling seasons: from May to June 2011 (containing four sampling periods), and September 2011 (containing 2 sampling periods), except for winter cereal patches, which were harvested in July. This sampling regime was designed to encompass the two main seasons during which carabid beetles emerge (Kromp, 1999). Data from each trapping period were pooled by sampled patch, and carabid species were identified following Roger et al. (2010).

Herbaceous plant species were sampled using three quadrats, the total area of which corresponded to the minimal recommended area of each habitat type (Mueller-Dombois and Ellenberg, 1974). These quadrats were distributed along transects from the margin to the centre of the patch to sample edge and interior species. Grasslands and winter cereal crops were sampled using 2 m × 2 m quadrats, established at 2, 6 and 10 m from the patch margin. Woodlands and hedgerows were sampled using respectively 5 m × 5 m and 5 m × 2 m quadrats, which were separated by a distance of 5 m. Data from the three quadrats were pooled for each sampled patch.

We pooled data from the three habitats for every landscape to obtain the multi-habitat gamma diversity. We used specific occurrence within each landscape site, with every plant and carabid species being assigned a value from 0 to 6 (0 indicated absent from every cover type, and 6 indicated present in the two patches × three cover types). Occurrence was the selected measure because it allows the diversity of habitats to be considered.

## 2.3. Species traits

We selected four carabid beetle life-history traits (Table 1) that are associated with vital functions (breeding phenology, diet and dispersal). First, we removed rare carabid species (less than 5 individuals found across all sampling sites, following Barbaro and van Halder, 2009). We then extracted the selected trait values from previous studies (Barbaro and van Halder, 2009; Ribera et al., 2001), and from a database currently under construction (BETSI, 2012). Finally, we checked that no trait categories contained too few species to avoid any statistical bias. Sixty-two carabid beetle species were included in the analyses, which represented 84.9% of the total sampled carabid species.

For plants, we extracted trait values from existing databases (the Bioflor database, Kuhn et al., 2004; the LEDA traitbase, Kleyer et al.,

**Table 1**

Categories of life history traits used for carabid beetle species.

Vital function	Carabid species traits	Categories	Code
Trophic level	Diet	Generalist predators <sup>a</sup>	D_pred_g
		Specialist predators <sup>a</sup>	D_pred_s
		Phytophagous	D_phyto
Dispersion	Wing system	Apterous	W_apt
		Dimorphic	W_dim
		Macropterous	W_macro
	Body size (length in mm)	Very small (<6 mm)	BS_VS
		Small (6–7.9 mm)	BS_S
		Medium (8–9.9 mm)	BS_M
		Large (10–11.9 mm)	BS_L
		Very large (>12 mm)	BS_VL
Phenology	Breeding season	Spring	BrS_spr
		Summer	BrS_sum
		Autumn	BrS_aut

<sup>a</sup> The “Generalist predators” diet category refers to carabid species which are opportunist predators and have a wide diet, while “Specialist predators” refers to species that feed only/mostly on collembola.

2008) to describe nine plant life-history traits that included phenology, reproduction and dispersal (Table 2). Species for which trait data were not available were excluded from the analyses. We analysed 153 herbaceous plant species, representing 88% of the total sampled herbaceous species. This ratio was consistent with Romermann et al. (2009), who retained at least 80% of the species pool. To avoid statistical bias, categories with too few species were merged with the closest ecological category (Barbaro and van Halder, 2009).

## 2.4. Landscape descriptors

Descriptors of landscape heterogeneity were computed from detailed land-cover maps of each 1 km<sup>2</sup> landscape with Chloe 3.1 software (Baudry et al., 2006). Six landscape descriptors were computed to quantify variability in landscape composition and configuration. Composition was estimated using the percentage coverage in woody (woodlands and hedgerows), grassy

**Table 2**

Categories of life history traits used for herbaceous plant species.

Vital function	Plant species traits	Categories	Code
Dispersion	Seed mass Dissemination	Continuous trait	Seed_mass
		Anemochory	D_an
		Barochory	D_ba
		Zoochory	D_zoo
		Other dispersal mode	D_other
Phenology	Seed bank longevity	Transient	SBL_trans
		Short term	SBL_short
		Long term	SBL_long
	Age of first flowering	Within 1 year	AOF_early
		More than 1 year	AOF_late
	Life span	Annual and biannual	LS_a
		Perennial	LS_p
	Beginning of flowering	[January–March]	BOF_early
		[May–June]	BOF_med
		[July–September]	BOF_late
Reproduction	Duration of flowering (nb. of months)	Very short (<3)	DOF_VS
		Short ([3–4])	DOF_S
		Long (>4)	DOF_L
	Type of reproduction	Only by seed	TR_s
		Mostly by seed, rarely vegetatively	TR_ssv
	Pollen vector	By seed and vegetatively	TR_sv
		Insect	PV_in
		Selfing	PV_se
		Wind	PV_wi
		Various pollen vectors	PV_var



(permanent and temporary grasslands) and crop habitats. Landscape spatial configuration was evaluated using the length of the three edge types among the three habitat categories ('woody.crop', 'woody.grassy', 'grassy.crop').

### 2.5. Statistical analyses

Two complementary types of three-table analysis method were conducted to associate carabid and plant traits with landscape descriptors (Dziock et al., 2011; Dray et al., 2014). Specifically, we used RLQ analysis (Doledec et al., 1996) to obtain a graphic display, and Fourth Corner analysis (Dray and Legendre, 2008) for statistical power. All analyses were computed using the 'ade4' package in R 3.00 software.

RLQ analysis was used to provide simultaneous ordination, and to analyse the joint structure of the three datasets: R (landscape descriptors), L (carabid beetles and plant occurrence data) and Q (species traits). First, all tables were analysed separately using the appropriate ordination method. Correspondence Analysis (CA) was used to analyse the L-species table. The R-landscape descriptors table was analysed using Principal Component Analysis (PCA), with the CA site scores being used as row weighting to couple R and L. The Q-trait tables for carabid beetles and plants were analysed respectively by Multiple Correspondence Analysis (MCA), and by a Hill Smith PCA, which combines quantitative and qualitative variables, using CA species scores as a column weighting to couple Q and L. Subsequently, RLQ analysis was used to combine the independent analyses in a simultaneous ordination. We tested the significance of the relationship between species traits and landscape descriptors (significance level at  $\alpha = 0.05$ ) using a Monte Carlo test (999 permutations). To determine which traits influenced the most the species distributions across landscapes, correlation ratios were calculated between traits and species ordination along the first and second RLQ axes (Doledec et al., 1996; Barbaro and van Halder, 2009).

Fourth Corner analysis was used to quantify and test the correlation between each trait category and each landscape descriptor. Two permutation tests were applied to determine correlation significance (Models 2 and 4, as recommended by Dray and Legendre,

2008). First, we tested the null hypothesis that "species assemblages are randomly attributed to sites, irrespective of the site characteristics" using 9999 permutations of site vectors (rows of L). Then, we tested the null hypothesis that "species are distributed irrespective of their traits" using 9999 permutations of species vectors (columns of L). From these two randomisation models, the largest  $p$ -value was selected to establish significant correlations. The use of multiple landscape descriptors in the R-landscape descriptors table required Bonferroni correction. Furthermore, because two permutation models were used, we used the square root of this corrected alpha level (Dray and Legendre, 2008; Dziock et al., 2011). Therefore, the alpha value used to determine statistical significance in the Fourth Corner analysis was  $\alpha < 0.091$ .

### 3. Results

#### 3.1. Global effects of landscape heterogeneity on species trait distributions

RLQ analysis showed that carabid beetle and plant functional compositions were significantly related with landscape descriptors (permutation test,  $p$ -value = 0.020 and 0.019 respectively). The two first RLQ analysis axes accounted for 91.4% of total carabid community variance (75.2 and 16.2%, respectively; Fig. 2a), and 82.5% of the total plant community variance (42.4 and 40.1%, respectively; Fig. 2b).

For both taxa, landscape composition and configuration descriptors correlated significantly with the first two RLQ analysis axes (Fig. 2). For carabid beetles (Fig. 2a), the first ordination axis of functional traits distribution contrasted more forested landscapes to open ones, dominated by grasslands and crops. The second axis differentiated landscapes with large areas of grassland from landscapes supporting other habitat types (crops and woodlands). For plants (Fig. 2b), on the first axis, landscape descriptors associated with functional trait distributions were the descriptors associated to grasslands versus descriptors associated to crops. The second axis differentiated landscapes supporting increased woody habitats area from open landscapes with many grasslands and crops.

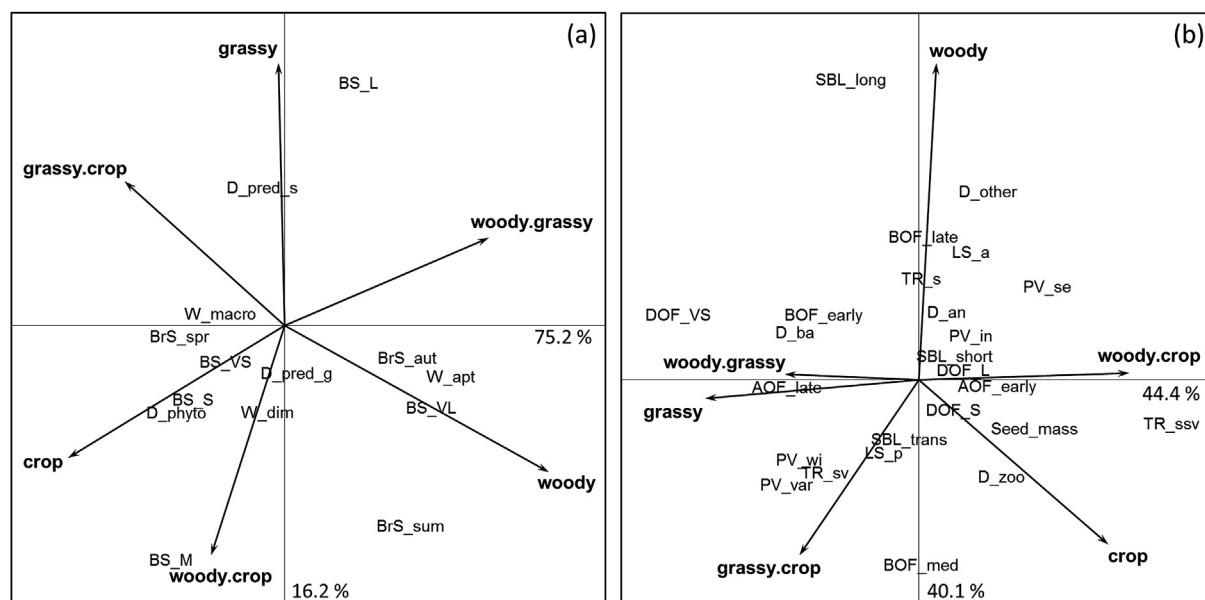


Fig. 2. Ordination of landscape descriptors and species trait categories along the two first axes of the RLQ analysis, for carabid beetles (a) and herbaceous plants (b). Numbers represent percentages of variance explained by each axes. See Tables 1 and 2 for trait category codes.

The highest correlation ratios between RLQ analysis axes and species traits were obtained for carabid beetle body size, wing system and breeding season (Table 3). The plant traits showed a weaker association to the RLQ analysis axes (Table 3). Plant seed mass, seed bank longevity, beginning of flowering and type of reproduction were associated with one of the two RLQ analysis axes. In addition, plant dissemination and pollen vector were equally correlated with the two axes (Table 3).

### 3.2. Relationships between trait categories and landscape descriptors

The results of the RLQ analyses were combined with Fourth Corner analysis. The latter showed significant correlations for landscape descriptors with carabid beetle and plant trait categories ( $p$ -value < 0.091, Tables 4 and 5). The traits that were associated to the RLQ analysis axes were also significantly associated to the landscape descriptors in Fourth Corner analyses, except for plant dissemination and pollen vector. Therefore, these traits were not considered to be affected by landscape heterogeneity.

In wooded landscapes, carabid communities were dominated by apterous species, along with summer and autumnal breeders. In comparison, landscapes supporting a lower amount of woody habitats contained more spring breeders and macropterous species (Table 4). These results are supported by the distribution of these traits along the first axis of the RLQ analysis (Fig. 2a). Regarding body size, medium-sized carabid beetles were significantly less common in landscapes with more 'woody.grassy' edges (Table 4). In addition, the RLQ analysis showed that 'very large' and 'large' sized carabid species were associated with wooded landscapes. In comparison, medium and small sized species were associated with landscapes characterised by higher crop percentages and greater lengths of 'grassy.crop' edges (Fig. 2a).

For plants, landscapes with increased edge lengths between grasslands and crops enhanced species that have an intermediate flowering period. In comparison, late flowering species favoured woody landscapes (Table 5; opposite responses to 'grassy.crop' and 'woody'). Species that primarily reproduce with seeds and that have high seed bank longevity were associated with woody landscapes. In comparison, species that mostly used vegetative reproduction and that have transient seeds were less common in these landscapes (Table 5). The trends observed from the Fourth Corner analyses were consistent with the trait distributions along the second axis of the RLQ analysis (Fig. 2b). In addition, plant species with lightweight seeds were associated with landscapes supporting a high proportion of grassy habitats ('grassy'), whereas heavy

seeded species were associated with highly cultivated landscapes ('crop') and greater 'woody.crop' length edges (Table 5). These results match the variation in seed mass that was observed along the first axis of the RLQ analysis (Fig. 2b).

## 4. Discussion and conclusions

### 4.1. Landscape composition and configuration: two drivers of functional composition

This study shows that landscape heterogeneity acts as an ecological filter on the functional composition of landscape-level diversity. We found that the two landscape heterogeneity components (i.e. composition and configuration) contributed in the selection of species based on their phenology, reproduction and dispersal traits. Previous studies have already reported such landscape filtering on carabid wing systems (Hendrickx et al., 2009; Wamser et al., 2012), breeding season (Purtauf et al., 2005) and body size (Kotze and O'Hara, 2003), in addition to plant seed mass (Tremlova and Munzbergova, 2007; Westoby et al., 1996), beginning of flowering (Silvertown and Charlesworth, 2001) and seed bank longevity (Tremlova and Munzbergova, 2007). However, these studies focused on one particular habitat (e.g. grasslands or crops), whereas the current study detected these relationships for multi-habitat gamma diversity. Thus, we show that the dominance of a given trait category in a given landscape type indicates that all local community types tend to contain a greater frequency of species from a considered group, irrespective of habitat type. This observation implies that such species selection does not only occur within each habitat type, but also at the landscape scale.

There is a limited number of studies that addressed the question of landscape filter effects on multi-habitat gamma diversity (but see Liira et al., 2008; Lomba et al., 2011). However, we used different traits compared to the previous studies; for instance, the mentioned studies did not include dispersal traits (dissemination type and seed mass). Hence, our study provides novel information about the landscape filtering effects on dispersal, which is a major landscape-level ecological process. In addition, the type of statistical analysis used by the previous studies did not explicitly quantify which traits caused the greatest species response to landscape heterogeneity gradients. In the current study, we used RLQ and Fourth Corner analyses to overcome this limitation, leading us to identify the reproduction period and dispersal capacity as the main traits that are affected by landscape heterogeneity.

Our results highlight the importance of taking compositional and configurational landscape heterogeneity into account, as both components played a significant role in landscape filtering effects. However, landscape composition and configuration had different effects and relative importance on carabid and plant diversity, showing, as discussed below, that distinct mechanisms drive the response of these two taxa (Fahrig et al., 2011). The importance of considering both landscape components was particularly noticeable for carabid and plant dispersal traits. Indeed, experimental-based and theoretical-based literature usually considers a major influence of landscape configuration on dispersal (see e.g. Hendrickx et al., 2009 for carabids or Piessens et al., 2004). However, the present study showed that the two landscape heterogeneity components influenced dispersal traits selection at the landscape level (gamma diversity). This may be due to correlations between descriptors of composition and configuration, but, as all descriptors were included, their relative importance in driving functional composition could be identified (Smith et al., 2009). For instance, prior studies showed that landscape configuration had an effect on plant dispersal (Tremlova and Munzbergova, 2007; Westoby et al., 1996); however, the current study showed that

**Table 3**  
Correlation ratios (CR) between carabid beetle traits (a) or herbaceous plant traits (b) and the two first axes of RLQ analysis. Traits with highest correlation ratio are in bold.

	Species trait	CR axis 1	CR axis 2
(a) Carabid beetles	Diet	0.03	0.02
	<b>Wing system</b>	<b>0.13</b>	0.01
	<b>Body size</b>	<b>0.18</b>	0.10
	<b>Breeding season</b>	<b>0.24</b>	0.01
(b) Herbaceous plants	<b>Seed mass</b>	<b>0.03</b>	0.01
	<b>Dissemination</b>	<b>0.02</b>	<b>0.02</b>
	<b>Seed bank longevity</b>	0.00	<b>0.04</b>
	Age of first flowering	0.02	0.00
	Life span	0.00	0.03
	<b>Beginning of flowering</b>	0.00	<b>0.07</b>
	Duration of flowering	0.02	0.00
	<b>Type of reproduction</b>	<b>0.03</b>	0.02
	<b>Pollen vector</b>	<b>0.02</b>	<b>0.02</b>

**Table 4**

Fourth Corner analysis of the effects of landscape descriptors on carabid beetle traits. + and – symbols correspond to positive and negative correlations between the considered trait category and landscape descriptor. Only the significant correlations ( $p$ -values < 0.091, see methods section for explanation) are reported, empty cells represent non-significant correlations. See Table 1 for trait codes. In bold are the traits that were correlated with RLQ axes and showing significant correlation with Fourth Corner.

		Woody	Grassy	Crop	Woody.Grassy	Grassy.Crop	Woody.Crop
Diet	D_pred_g						
	D_pred_s						
	D_phyto						
<b>Wing System</b>	W_apr	+					
	W_dim						
	W_macro	–					
<b>Body Size</b>	BS_VS						
	BS_S						
	BS_M				–		
	BS_L						
	BS_VL						
<b>Breeding Season</b>	BrS_spr	–					
	BrS_sum	+					
	BrS_aut	+					

compositional heterogeneity was the main factor influencing plant dispersal traits. The functional composition of the plant community at the landscape level (i.e. for all considered habitats) might largely depend on the dominant habitat type. Therefore, changes in habitat dominance along the composition gradient are expected to have a major influence on total functional composition, including dispersal traits.

#### 4.2. Landscape stability: an ecological filter of carabid beetles and herbaceous plants

This study showed that two landscape heterogeneity gradients influenced the functional composition of carabid beetle and plant communities in the studied landscapes. Some traits were selected along a gradient of increasing landscape openness (opposing woody landscapes to landscapes dominated by open habitats). In comparison, other traits were distributed along a gradient of increasing agricultural use (grassland vs. annual crops). These

gradients may be considered as gradients of landscape stability. Indeed, open landscapes tend to be more disturbed due to intensified farming, whereas woody landscapes support greater amounts of stable habitats and less intensified farming systems (Baudry and Papy, 2001; Meeus, 1993). In addition, farming practices (such as ploughing and pesticide use) are more frequent in annual crops, which also have a faster turnover due to crop rotation compared to grasslands. These inter- and intra- annual disturbances alter the stability of landscapes that have greater amounts of open habitats and where the annual crops dominate over grasslands. Hence, landscape stability, representing a measure of temporal heterogeneity, seems to exert a selective pressure on both carabid and plant species according to their phenology and dispersal capacity. This relationship between landscape openness and landscape stability should be tested by analysing land cover time series and surveying agricultural practices. Further research is also needed to better determine biodiversity response to temporal heterogeneity.

**Table 5**

Fourth Corner analysis of the effects of landscape descriptors on herbaceous plant traits. + and – symbols correspond to positive and negative correlations between the considered trait category and landscape descriptor. Only the significant correlations ( $p$ -values < 0.091, see methods section for explanation) are reported, empty cells represent non-significant correlations. See Table 2 for trait codes. In bold are the traits that were correlated with RLQ axes and showing significant correlation with Fourth Corner.

		Woody	Grassy	Crop	Woody.Grassy	Grassy.Crop	Woody.Crop
<b>Seed mass</b>	Seed_mass		–	+			+
Dissemination	D_an						
	D_ba						
	D_other						
	D_zoo						
<b>Seed Bank Longevity</b>	SBL_long	+					
	SBL_short						
	SBL_trans	–					
Age of First Flowering	AOF_early				–		
	AOF_late				+		
Life Span	LS_a	+					
	LS_p	–					
<b>Beginning Of Flowering</b>	BOF_early						
	BOF_late	+				–	
	BOF_med	–				+	
Duration Of Flowering	DOF_L						
	DOF_S						+
	DOF_VS						–
<b>Type of Reproduction</b>	TR_s	+					
	TR_ssv						+
	TR_sv						
Pollen Vector	PV_in						
	PV_se						
	PV_var						
	PV_wi						

The gradient related to landscape openness selected early reproductive species for both carabid beetles and plants (breeding season and beginning of flowering). In the more disturbed landscapes, these species may reproduce before the onset of the main agricultural disturbances (e.g. mowing, grazing, pesticide spraying and harvest), resulting in higher reproductive success and persistence. This hypothesis is supported by local-scale studies showing that spring breeding carabid species are more abundant in open landscapes (Barbaro and van Halder, 2009; Purtauf et al., 2005) and that early flowering plants are selected in managed and disturbed sites (Ollerton and Lack, 1992; Silvertown and Charlesworth, 2001). Landscape openness also selected plant species with vegetative reproduction and transient seeds. In unstable open landscapes, transient seeded species might benefit their quick emergence rates, enabling them to develop before destruction or predation. Vegetative-reproducing species are adapted to disturbances, as they are able to reproduce and continue developing even when cut (harvest, mowing) or grazed. The similar trends observed for these two ecologically different taxonomic groups (herbaceous plants and carabid beetles) indicates that strong landscape filtering on the reproduction period at the scale of gamma diversity could be generalised to other taxonomic groups.

Carabid beetles and plant species experienced contrasting filtering effects on their dispersal traits with respect to landscape stability gradients. Carabid beetle dispersal traits were mainly selected by the landscape openness gradient. Landscapes dominated by annual crops and grasslands selected highly mobile carabid species (small, macropterous), which are able to adapt to rapidly changing spatial distributions in resources (Holland, 2002). In these landscapes, a high amount of edges between grasslands and annual crops may favour movement between highly disturbed crops and more stable grasslands, which act as temporary refuges or permit complementation (Purtauf et al., 2005). Low mobility species (large, apterous) were associated with stable landscapes, where they probably benefited from higher amounts of woody habitats (Kromp, 1999). These species that often need a combination of both woody and crop habitats might also benefit from edges between woody habitats and crops in these landscapes (Tscharntke et al., 2005). In contrast, plant dispersal traits (i.e. seed mass) were selected by the gradient of agricultural use (grasslands vs. crops). Landscapes with increased amounts of more stable habitats (grassland) favoured lightweight seeded species. In comparison, heavy weight seeded species were favoured in landscapes with an increased proportion of annual crops and 'woody.crop' edges length. These landscapes are subject to higher herbicide use, and are characterised by a low diversity and abundance of arable weeds (Storkey et al., 2012), which largely support lightweight seeds. Moreover, farmers commonly use herbicides on the adjacent hedgerows or woodlot edges of crop fields to reduce colonisation by non-crop plants (Jamoneau et al., 2011). These practices reduce the quantity of weeds, and explain the effect of 'woody.crop' edges. Plant dispersal modes were not influenced by landscape structure, which contradicted most previous studies (Piessens et al., 2004; Tremlova and Munzbergova, 2007), except a recent one (Alignier et al., 2012). Our results may be due to the fact that dispersal is not a limiting factor at the scale (1 km<sup>2</sup>) or in the landscape type (hedgerow landscapes) of the study. Also, as we studied several traits simultaneously, it is possible that the landscape heterogeneity filtering of plant species according to their dispersal mode was hidden by much stronger effects on other traits (e.g. phenology).

#### 4.3. Conclusions

We used multi-habitat gamma diversity to study variation in plant and carabid beetle functional composition across a landscape

heterogeneity gradient. As a result, we demonstrated the role of landscape stability as an ecological filter of carabid beetles and herbaceous plants in relation to their dispersal and phenology traits. We suggest that future work focused on studying the role of landscape as ecological filter of gamma diversity, should compare the response of multiple taxa by grouping ecological traits within shared ecological functions. Such research would help identify general rules about species responses to landscape heterogeneity, in addition to linking these effects to ecosystem functioning. We found that different landscapes support different sets of functional groups, indicating that all functional groups cannot be preserved at the same time, which is an important issue for conservation management. Hence, it seems that it is necessary to preserve a diversity of landscape types to preserve functional biodiversity at a regional scale.

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