

Reconsidering the role of ‘semi-natural habitat’ in agricultural landscape biodiversity: a case study

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3

4 **Reconsidering the role of ‘semi-natural habitat’ in agricultural landscape biodiversity: a**
5 **case study**

6

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23

1 **ABSTRACT**

2 Semi-natural habitats are considered as the main source of biodiversity in agricultural
3 landscapes. Most landscape ecology research has focused on the amount (relative surface) and
4 spatial organisation of these habitats. However, these two components of landscape
5 heterogeneity, composition and configuration, are often correlated. Also, landscape structure
6 effects on biodiversity were mostly observed locally, while there is a great need for studying
7 landscape-scale gamma diversity. We conducted a mensurative experiment to determine the
8 independent effects of semi-natural habitat amount and configuration on gamma diversity of
9 carabid beetles and vascular plants. The influence of landscape heterogeneity components
10 were tested on species richness, evenness and composition. Local diversity (species richness
11 and composition) was compared across the various cover types to determine their relative
12 contributions. Only carabid species evenness and composition were influenced by semi-
13 natural habitat amount. Carabid and plant species richness and plant species composition
14 remained unaffected by semi-natural habitats. Local diversity analysis showed that three types
15 of habitats can be distinguished in agricultural landscapes: grasslands (temporary and
16 permanent ones), woody habitats (woodlands and hedgerows) and row crops. These results
17 beg for a re-evaluation of the semi-natural covers. Temporary and permanent grasslands are
18 often similar, probably because of comparable farming management. Permanent grasslands
19 and woody habitats are often combined as semi-natural covers, although they support very
20 different communities. The lack of effect of semi-natural habitat amount and configuration on
21 gamma diversity results from a more complex organisation of biodiversity in landscapes and
22 supports the move from semi-natural vs. farmland to habitat mosaic landscape representations.

23

24 **Keywords:** carabidae, flora, landscape structure, community, MultiModel Inference

1 INTRODUCTION

2 Often used as a surrogate for landscape heterogeneity or complexity (*e.g.* Thies et al.
3 2003; Tschardt et al. 2005), the amount of semi-natural cover in an agricultural landscape, a
4 descriptor of landscape composition, has been shown to exert a positive effect on vascular
5 plants, insects, spiders, birds, and small mammals found there (*e.g.* Benton et al. 2003; Burel
6 et al. 2004; Hendrickx et al. 2007; Billeter et al. 2008). Semi-natural cover types differ from
7 the farmland (crop) covers in that they are relatively permanent, *e.g.* hedgerows, woodlands,
8 and permanent grasslands and pasture. These semi-natural covers are expected to play an
9 essential role in maintaining biodiversity in many cultivated areas by providing over-
10 wintering sites, food resources, refuges, and source populations for re-colonisation of
11 disturbed habitats (Tschardt et al. 2005; Chaplin-Kramer et al. 2011). In addition, an
12 increasing literature underlines the importance of edges between semi-natural covers and
13 crops (landscape configuration), as they have been shown to enhance local animal and plant
14 species movements and spillovers between adjacent patches (Tschardt et al. 2007; Brudvig
15 et al. 2009; Blitzer et al. 2012; Concepcion et al. 2012). These movements, are important for
16 habitat complementation (accessibility of multiple required habitat types), source-sink
17 relationships (Dunning et al. 1992) and re-colonization processes, *i.e.* metapopulation
18 functioning (Hanski 1999). Hence, semi-natural habitats are not only important for their local
19 communities but also contribute to maintain communities of cultivated lands (*e.g.* ‘beetle
20 bank’, MacLeod et al. 2004). Semi-natural habitats of different kinds may not host the same
21 community (*e.g.* permanent grassland vs. woodland) but share the fact of promoting species
22 persistence at the landscape level.

23 An important issue in studying the effect of landscape heterogeneity on biodiversity is
24 the spatial scale (extent) at which diversity is measured. To date, landscape ecology research
25 has mostly used the focal-patch or focal-site approach, where biodiversity is evaluated at the

1 patch, or site, level (alpha diversity - see Thornton et al. 2011 for a review). Such alpha
2 diversity assessment only partially reflects the total diversity of landscapes as different cover
3 types may host different community assemblages (beta diversity). The contribution of beta
4 diversity to the total landscape diversity (gamma diversity) is expected to be dominant over
5 the contribution of alpha diversity (Tschamntke et al. 2012). Hence, biodiversity conservation
6 in agricultural landscapes needs a landscape perspective and the contribution of the various
7 cover types to gamma diversity should be considered.

8 Commonly, studies evaluate the proportion of semi-natural covers – landscape
9 composition – without considering independently its spatial arrangement – landscape
10 configuration – (Millan-Pena et al. 2003; Gabriel et al. 2005; Woodcock et al. 2010). When
11 the configuration of semi-natural covers is explicitly considered (*e.g.* Hendrickx et al. 2007;
12 Holzschuh et al. 2010; Concepcion et al. 2012), the landscape metrics used to measure it (*e.g.*
13 proximity index, or total edge length) are usually correlated with habitat amount (Fahrig
14 2003). Thus, the relative effects of composition and configuration are difficult to estimate
15 independently (Fahrig 2003; Ewers and Didham 2006). However, it is important to identify
16 these independent effects, to determine whether conservation scheme should be aimed at
17 increasing the amount of semi-natural cover in landscapes or at creating a particular spatial
18 pattern of them (Boitani et al. 2007; Lindenmayer and Fischer 2007; Smith et al. 2009).

19 We conducted a mensurative experiment to determine the relative and independent
20 effects of the amount of semi-natural cover (a measure of landscape composition) and the
21 length of edge between semi-natural cover and farmland (a measure of landscape
22 configuration) on biodiversity. We selected twenty 1 km² landscapes in an agricultural region
23 of western France, such that the correlation between the two landscape descriptors was
24 minimized. Within each landscape we surveyed carabid beetle and vascular plant multi-
25 habitat gamma diversity, using a stratified hierarchical sampling design (Crist et al. 2003;

1 Bennett et al. 2006; Diekötter et al. 2008). Local diversity was compared across the various
2 cover types of agricultural landscapes to determine the relative contributions of the different
3 covers to the landscape (gamma) diversity. It has already been shown that carabid beetle and
4 plant richness and composition respond to the amount of semi-natural cover in agricultural
5 landscapes (Jeanneret et al. 2003; Millan-Pena et al. 2003; Aviron et al. 2005; Billeter et al.
6 2008), which make them appropriate species groups for this study.

7

8 **METHODS**

9 **Study area**

10 The study was located in an agricultural area in the Ille-et-Vilaine department (6 775
11 km²), Brittany, western France (Fig. 1). The area is dominated by mixed dairy farming. The
12 farmlands are interspersed with woody elements (woodlands and hedgerows), and are
13 comprised of annual crops (mostly winter cereals and maize), and temporary and permanent
14 grasslands. These hedgerow network (bocage) agricultural landscapes were typical of western
15 Europe (Baudry et al. 2000) until the middle of the twentieth century. Over the past 50 years
16 thousands of kilometres of hedgerows have been removed and crop fields have been enlarged
17 to accommodate agricultural intensification (Meeus 1993; Baudry and Papy 2001).

18

19 **Land-cover data**

20 Land cover maps were originally created from remote sensing data. An object oriented
21 classification from Landsat TM5 imagery (1ha resolution) was the main source, and
22 permanent grasslands were extracted from a temporal series of MODIS images (COSTEL
23 Land-cover map, Hubert-Moy et al. 2012). For the hedgerows we used data from BD Topo ©
24 IGN at 50 cm resolution. The selection of study sites explained below was based on these
25 remote sensing data, but these data were taken in years previous to the actual surveys and had

1 relatively low spatial resolution. Therefore, to obtain an accurate description of each selected
2 landscape, we conducted a field survey, and recorded the current land-covers on ArcGIS 9.2
3 (ESRI). All landscape parameters used in the statistical analyses were then computed from
4 these more precise maps.

5

6 **Landscape selection**

7 The map based on remote sensing data was divided into square moving windows of 1
8 km², using Chloe 3.1 (Baudry et al. 2006), a routine especially designed for landscape
9 heterogeneity analysis and screening (Baudry and Denis 1995). Within each window /
10 landscape we computed the proportion of each cover type based on the number of pixels, and
11 the length of edge between each cover type combination was measured based on the number
12 of pairs of adjacent pixels (excluding diagonal adjacency). From among all candidate
13 landscapes, we selected those with less than 5% of land covered by roads, built-up area and
14 water, and with at least 2% of woodlands and 2% of permanent grassland to ensure that every
15 landscape contained these cover types. We chose landscapes with similar amounts of
16 woodlands and permanent grasslands ($|\% \text{ Woodlands} - \% \text{ Permanent Grasslands}| < 10\%$) to
17 avoid an effect due to the dominance of one or the other. In addition, each selected landscape
18 was embedded within a larger area (3 km × 3 km) with a similar composition (< 10%
19 difference in any cover type), to ensure that landscape effects would be similar at all
20 biodiversity sampling points. Finally, we selected twenty non-overlapping landscapes across
21 which the correlation between the percentage of semi-natural cover and the length of edge
22 between semi-natural cover and crops was minimized, while maximizing the range of values
23 over each of these gradients.

24

1 **Landscape descriptors**

2 Landscape descriptors for the analyses were based on the precise maps based on field surveys
3 during the sampling year (see above). The amount of semi-natural cover (ranging from 18.7 to
4 53.8 %) was used as the landscape composition descriptor and the total length of edge
5 between semi-natural cover and farmland (ranging from 5.5 to 17.3 km) as the landscape
6 configuration descriptor. We defined semi-natural cover as woodlands, hedgerows, and
7 permanent grasslands, following the commonly used categorization of cover types in
8 agricultural landscapes (*e.g.* Bengtsson et al. 2005; Hendrickx et al. 2007; Billeter et al. 2008;
9 Holzschuh et al. 2010). Permanent grasslands were defined as grasslands that are not included
10 in crop rotation for the past 10 years, and identified using time series imaging (see “Land-
11 cover data”). Correlation between the two landscape descriptors was low ($r_s = -0.24$; Fig. 2).

12

13 **Gamma diversity assessment**

14 *Sampling design*

15 Assessing multi-habitat gamma diversity at the landscape scale requires a
16 hierarchically stratified sampling design (Bennett et al. 2006; Diekötter et al. 2008). In each
17 selected landscape, five cover types (woodland, hedgerow, permanent grassland, temporary
18 grassland, and winter cereal) were sampled. Two patches of each cover types were sampled in
19 each landscape, resulting in ten sample points per landscape (Fig. 1). These patches were
20 chosen randomly, but subject to constraints of farmer authorizations to access fields and
21 hedgerows and ease of accessibility.

22

23 *Sampling methods*

24 Carabid beetles were sampled using two pitfall traps per sample point. The traps were
25 positioned 10 m from the patch margins, except for hedgerows. Traps were collected every

1 two weeks, but were only left open for seven consecutive days. There were two sampling
2 seasons: from May to June 2011 (containing four sampling periods), and September 2011
3 (containing two sampling periods), except for winter cereal patches, which were harvested in
4 July. This sampling regime was designed to encompass the two main seasons during which
5 carabid beetles emerge (Kromp 1999). Data from each trapping period were pooled by
6 sampled patch, and carabid species were identified following (Roger et al. 2010).

7 At each patch, plant species were sampled using three quadrats, the total area of which
8 corresponded to the minimal recommended sample area for each cover type (Mueller-
9 Dombois and Ellenberg 1974). These quadrats were distributed along transects from the
10 margin to the centre of the patch, to sample edge and interior species (except for hedgerows).
11 Grasslands and winter cereal crops were sampled using three 2 m × 2 m quadrats, established
12 at 2, 6 and 10 m from the patch margin. Woodlands were sampled using three 5 m × 5 m
13 quadrats separated by 5 m. Hedgerows were sampled using three 5 m × 2 m quadrats
14 separated by 5 m. Data from the three quadrats were pooled for each sampled patch.

15

16 **Diversity measures**

17 *Gamma diversity measures*

18 Data from the 5 cover types (ten sample points in each landscape) were pooled to
19 obtain the total gamma diversity at the landscape level, *i.e.* the multi-habitat gamma diversity.

20 As biodiversity measures, we used species richness, species evenness and Sorensen
21 dissimilarity index, representing respectively three aspects of community diversity: species
22 number, species dominance and species composition. Species evenness was computed on
23 abundance data for carabid beetles. For plants, we used occurrence data, *i.e.* within each
24 landscape we assigned a value to every species from 0 to 10 (0 indicated absent from the
25 landscape, and 10 indicated present in the 10 sampling points). Species composition

1 dissimilarities were assessed using pair-wise Sorensen dissimilarity index between all
2 landscape combinations (190 combinations).

3

4 *Local diversity measures*

5 In addition to gamma diversity, species richness and composition were compared
6 between the 5 sampled cover types (habitat) across the 20 studied landscapes. As two patches
7 of each cover types were sampled per landscapes, these analyses included 40 replicates for
8 each cover types.

9

10 **Statistical analysis**

11 All statistical tests were performed using R software 3.00 with the “MuMin” package
12 for MMI, “Ade4” for multivariate analysis, “vegan” for dissimilarity analysis, and “lme4”
13 package for linear mixed models. All descriptors were standardized to make the effect
14 strength of the coefficients comparable across descriptors (Smith et al. 2009; Smith et al.
15 2011). We checked for normality of descriptors with Shapiro-Wilcoxon tests, Quantile -
16 Quantile and Kernel density plots.

17

18 *Effect of landscape heterogeneity on carabid and plant gamma diversity*

19 We used Multi-Model Inference (MMI) and model averaging to test the effects of the
20 amount of semi-natural cover and the total length of edges between semi-natural cover and
21 farmland on species richness and species evenness. For each analysis there were four possible
22 models, including the null model (see supplements 1 and 2). We computed standardized
23 average linear regression coefficients weighted by the Akaike weights across the “best”
24 models ($\Delta AICc \leq 4$, Burnham and Anderson 2002; Smith et al. 2009; Arnold 2010), and

1 tested their significance using unconditional 95 % confidence intervals (Burnham and
2 Anderson 2002; Smith et al. 2009).

3 Landscape heterogeneity effects on species composition were addressed by correlating
4 the Sorensen dissimilarity matrices with distance matrices calculated for each landscape
5 descriptor (Anderson et al. 2011). Each matrix contained the 190 pairwise combinations of the
6 20 landscapes. The correlations were estimated using the Spearman method as dissimilarity
7 and distance variables were not normally distributed. The correlation significance was
8 determined using a Mantel permutation test (Anderson et al. 2011), which evaluates the null
9 hypothesis of no relationship between distance matrices (based on 9999 permutations).

10

11 *Comparison of the five sampled cover types*

12 Species richness of the five sampled cover types was compared using generalized
13 linear mixed models (GLMM) which included landscape as nested factor. For plants, we used
14 a Poisson distribution because data did not follow a Normal distribution.

15 Species composition of the five sampled cover types was compared using principal
16 components analyses (PCA) on carabid and plant species presence / absence data at the
17 habitat level. The clusters of each of the 5 covers types were then projected on the graphical
18 representation of the two first PCA axes. In addition, a k-means cluster analysis was
19 performed and the obtained classification was compared with the cover types. 5 clusters were
20 looking for as we initially expect a group for each of the 5 sampled cover types.

21

22 **RESULTS**

23 Altogether, 106 carabid beetle species and 278 plant species were found. The number
24 of species per landscape (gamma diversity) varied from 36 to 59 (47 on average) for carabid
25 beetles and from 44 to 102 (70.3 on average) for plants.

1 **Effect of landscape structure on carabid and plant gamma diversity**

2 Our results revealed no significant effects of semi-natural habitats on carabid species
3 richness, as the coefficient confidence intervals of the percentage of semi-natural cover and
4 the length of edge between semi-natural and farmland cover contained 0 (Fig. 3). However,
5 carabid species relative abundance was significantly less even (lower species evenness) with
6 increasing percentage of semi-natural cover in the landscape (Fig. 3). With an increasing
7 difference between the landscapes in their percentage of semi-natural cover the carabid
8 species composition was increasingly dissimilar, *i.e.* higher Sorensen dissimilarity ($r_s = 0.24$;
9 Mantel test p-value = 0.003). The length of edge between semi-natural and farmland cover
10 had no significant effects on carabid species evenness (Fig. 3) or Sorensen dissimilarity index
11 ($r_s = 0.04$; Mantel test p-value = 0.358).

12 We found no effects of either landscape descriptor on plant species richness or species
13 evenness (Fig. 3). Also, the percentage of semi-natural cover and length of edge between
14 semi-natural and farmland cover had no significant effects on species composition, measured
15 as Sorensen dissimilarity ($r_s = 0.01$ and 0.03 ; Mantel test p-value = 0.441 and 0.392
16 respectively).

17

18 **Species richness and species composition across the sampled cover types**

19 For carabids, the highest species richness was observed in winter cereal fields
20 (although they were sampled for a shorter time) followed by permanent and temporary
21 grasslands while the lowest were found in hedgerows and woodlands (Fig. 4). Particularly,
22 carabid species richness in forest was about half that in winter cereal fields. For plants, the
23 highest species richness was found in hedgerows followed by permanent grasslands which
24 contained one third fewer species; woodlands and temporary grasslands; and winter cereals

1 which had the lowest plant species richness at about half the number of species as in
2 hedgerows (Fig. 4).

3 Regarding species composition, the results were similar for carabids and plants (Fig. 5,
4 Table 1). For both taxa, three main types of communities can be distinguished in the the k-
5 means cluster analyses (Table 1). Permanent and temporary grassland samples were classified
6 in the same clusters (clusters 2 and 4 for carabids and clusters 1 and 2 for plants). Similarly,
7 woodland and hedgerow samples were often included in the same clusters (clusters 1 and 3
8 for carabids and clusters 3 for plants). However, for plant, some hedgerows were classified
9 independently from woodland samples (cluster 5). Winter cereal samples were grouped
10 independently for both, carabids and plants (cluster 5 and 4 respectively). These observations
11 are confirmed by the PCA graphical representations (Fig. 5) where grasslands communities
12 (as permanent and temporary grasslands samples overlap), and winter cereal communities can
13 be clearly distinguished. However, hedgerows and woodland samples only partially overlap,
14 especially in the case of plants. Importantly, the two first axes of these PCAs represented only
15 a limited percentage of the total variance, *i.e.* 10.1 % and 8.2 % (cumulated) for carabids and
16 plants respectively.

17

18

19 **DISCUSSION**

20 **Response of gamma diversity to semi-natural covers**

21 We found that carabid species evenness and composition were affected by the amount
22 of semi-natural cover. The reduction of carabid species evenness with the percentage of semi-
23 natural cover was mostly due to a large increase in *Poecilus cupreus* (L.) abundance in these
24 landscapes. This is somewhat unexpected since *P. cupreus* is one of the most common open-
25 field species in Europe (Kromp 1999; Holland 2002). We speculate that this species benefited

1 from an increase in semi-natural cover by using them as overwintering sites. Indeed, *P.*
2 *cupreus* is known to use crop fields and semi-natural field margins as complementary habitats
3 (Griffiths et al. 2007). Regarding species composition, it seems that some species, probably
4 forest species, favoured landscape with more semi-natural cover while open field species
5 favoured landscapes where these habitats were less frequent. This interpretation is consistent
6 with previous studies carried out in the same region (Burel et al. 1998; Millan-Pena et al.
7 2003).

8 Unlike previous studies (Hendrickx et al. 2007; Billeter et al. 2008; Holzschuh et al.
9 2010; Concepcion et al. 2012), we found no effect of the amount or spatial organisation of
10 semi-natural covers on species richness of carabids or plants, and no effect on species
11 evenness or composition of plants. These results may be due to a relatively small gradient in
12 semi-natural amount – from 18.7 to 53.8 % (Ekroos et al. 2010; Eigenbrod et al. 2011)
13 compared to most studies that showed a positive effect of the amount of semi-natural cover
14 (e.g. Billeter et al. 2008). The fact that the whole study region is comprised of the same type
15 of farming system may explain this small gradient. In particular, there are no landscapes in
16 our region with an extremely low amount of semi-natural covers (< 10%). However, for both
17 taxa, gamma species richness varied greatly among landscapes.

18

19 **Re-evaluation of the semi-natural cover type**

20 Our results suggest that perhaps in our region the definition of semi-natural covers
21 should be reconsidered. In particular, we considered permanent grasslands, but not temporary
22 grasslands, to be a semi-natural cover. However, in our region, it is not entirely clear whether
23 the permanent grasslands really differ ecologically from temporary grasslands. We found that
24 permanent and temporary grasslands had similar carabid and plant species composition and
25 the average carabid species richness was not significantly different between these two

1 grasslands types. We hypothesize that this is due to comparable management of the
2 permanent and temporary grasslands. While permanent grasslands are more stable habitats
3 than temporary grasslands as they are not included in crop rotation, in other respects,
4 agricultural practices such as grazing, mowing, fertilisation and over-sowing with seeds of
5 desirable plants are similar for the two grassland types. These practices are known to affect
6 grasslands plant diversity (Roche et al. 2010; Gaujour et al. 2012) and probably affect
7 arthropod communities as well, including carabid beetles (see Le Roux et al. 2008 for a
8 review). Therefore, grazing, mowing, fertilisation and sowing may have stronger effects, or
9 may be at least as important as the permanence of the grassland. We therefore suggest that
10 permanent and temporary grasslands should be included in the same habitat/cover category
11 for the two studied species groups as it has sometimes been done (*e.g.* Aviron et al. 2005;
12 Purtauf et al. 2005; Ernoult et al. 2006). An alternative would be to group individual
13 grasslands according to the farming practices actually used in them (*e.g.* intensive use,
14 intermediate use, extensive use).

15 The definition of semi-natural covers usually combines woody covers (hedgerows and
16 woodland) with permanent grassland. However, from our results (Fig. 4 and 5) it is clear that
17 woody and grassland cover types contribute differently to carabid and plant gamma diversity.
18 Thus, we suggest that woody (hedgerows and woodlands) and grassy (permanent and
19 temporary grasslands) habitats should be considered as separate cover types when testing the
20 effect of landscape composition and configuration on agricultural landscape gamma diversity.
21 For plants, it may also be important to separate hedgerows from woodlands. Hedgerows had
22 higher species richness than woodlands (Fig. 4), and somewhat different species composition
23 (Table 1, Fig. 5), probably because of a more developed herbaceous stratum in the former.

24

1 CONCLUSION

2 Our results contrast with our initial expectation that the amount and the spatial
3 configuration of semi-natural cover would have large effects on agricultural landscape
4 diversity. The use of the ‘semi-natural’ cover type arose initially from a binary habitat/matrix
5 landscape representation, which often dominates in the literature (Fahrig et al. 2011). In this
6 framework, semi-natural covers (suitable habitat) are expected to support biodiversity while
7 farmlands (matrix) are seen as a hostile environment because of the intensity and frequencies
8 of anthropogenic disturbances (Fahrig et al. 2011). However, in the present study, we found
9 three cover types (grassy, woody and winter cereal covers) that represent habitats for different
10 carabid and plant communities, each of them contributing to the total gamma diversity. This
11 suggests that important information about the ecological responses of these taxa to landscape
12 structure is lost if semi-natural covers are grouped together into a single land cover category.

13 Our results support the move to a ‘habitat mosaic’ representation of landscapes (Duelli
14 1997; Fahrig et al. 2011), which considers the diversity of landscape covers, including
15 cultivated ones. For instance, habitat or crop diversity has been shown to increase plant,
16 vertebrate and invertebrate diversity (Robinson et al. 2001; Benton et al. 2003; Poggio et al.
17 2010; Woodcock et al. 2010). Also, this representation allows accounting with the spatial
18 pattern of the whole landscape. For example, the diversity of habitats creates a diversity of
19 edges which potentially have various ecological functions such as facilitation of dispersal and
20 access to complementary habitats (Macfadyen and Muller 2013). Importantly, the ‘habitat
21 mosaic’ landscape representation is adaptable as the categorization of cover types can be
22 define according to their functions, or perception by different species or group of species
23 (Fahrig et al. 2011).

24

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1 REFERENCES

- 2 Anderson M. J., Crist T. O., Chase J. M., Vellend M., Inouye B. D., Freestone A. L., Sanders
3 N. J., Cornell H. V., Comita L. S., Davies K. F., Harrison S. P., Kraft N. J. B., Stegen J. C. &
4 Swenson N. G. (2011) Navigating the multiple meanings of beta diversity: a roadmap for the
5 practicing ecologist. *Ecology Letters* 14: 19-28.
- 6 Arnold T. W. (2010) Uninformative parameters and model selection using Akaike's
7 information criterion. *Journal of Wildlife Management* 74: 1175-1178.
- 8 Aviron S., Burel F., Baudry J. & Schermann N. (2005) Carabid assemblages in agricultural
9 landscapes: impacts of habitat features, landscape context at different spatial scales and
10 farming intensity. *Agriculture Ecosystems & Environment* 108: 205-217.
- 11 Baudry J., Bunce R. G. H. & Burel F. (2000) Hedgerows: An international perspective on
12 their origin, function and management. *Journal of Environmental Management* 60: 7-22.
- 13 Baudry J. & Denis D. (1995) Chloé : Utilitaire d'analyse de l'hétérogénéité d'une image ;
14 (fichiers image IDRISI). Rennes, INRA, SAD-Armorique.
- 15 Baudry J. & Papy F. (2001) The role of landscape heterogeneity in the sustainability of
16 cropping systems. In: *Crop Science—Progress and Prospects* (eds. J. Nösberger, H. H. Geiger
17 & P. C. Struik) pp. 243–259. Cabi Publishing, Oxon.
- 18 Baudry J., Schermann N. & Boussard H. (2006) Chloe 3.1: freeware of multi-scales analyses.
19 INRA, SAD-Paysage.
- 20 Bengtsson J., Ahnstrom J. & Weibull A. C. (2005) The effects of organic agriculture on
21 biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42: 261-269.
- 22 Bennett A. F., Radford J. Q. & Haslem A. (2006) Properties of land mosaics: Implications for
23 nature conservation in agricultural environments. *Biological Conservation* 133: 250-264.
- 24 Benton T. G., Vickery J. & Wilson J. (2003) Farmland biodiversity: is habitat heterogeneity
25 the key? *Trends in Ecology & Evolution* 18: 182-188.
- 26 Billeter R., Liira J., Bailey D., Bugter R., Arens P., Augenstein I., Aviron S., Baudry J.,
27 Bukacek R., Burel F., Cerny M., De Blust G., De Cock R., Diekötter T., Dietz H., Dirksen J.,
28 Dormann C., Durka W., Frenzel M., Hamersky R., Hendrickx F., Herzog F., Klotz S.,
29 Koolstra B., Lausch A., Le Coeur D., Maelfait J. P., Opdam P., Roubalova M., Schermann A.,
30 Schermann N., Schmidt T., Schweiger O., Smulders M. J. M., Speelmans M., Simova P.,
31 Verboom J., van Wingerden W., Zobel M. & Edwards P. J. (2008) Indicators for biodiversity
32 in agricultural landscapes: a pan-European study. *Journal of Applied Ecology* 45: 141-150.
- 33 Blitzer E. J., Dormann C. F., Holzschuh A., Klein A. M., Rand T. A. & Tscharntke T. (2012)
34 Spillover of functionally important organisms between managed and natural habitats.
35 *Agriculture Ecosystems & Environment* 146: 34-43.
- 36 Boitani L., Falcucci A., Maiorano L. & Rondinini C. (2007) Ecological networks as
37 conceptual frameworks or operational tools in conservation. *Conservation Biology* 21: 1414-
38 1422.
- 39 Brudvig L. A., Damschen E. I., Tewksbury J. J., Haddad N. M. & Levey D. J. (2009)
40 Landscape connectivity promotes plant biodiversity spillover into non-target habitats.
41 *Proceedings of the National Academy of Sciences of the United States of America* 106: 9328-
42 9332.
- 43 Burel F., Baudry J., Butet A., Clergeau P., Delettre Y., Le Coeur D., Dubs F., Morvan N.,
44 Paillat G., Petit S., Thenail C., Brunel E. & Lefeuvre J. C. (1998) Comparative biodiversity
45 along a gradient of agricultural landscapes. *Acta Oecologica-International Journal of Ecology*
46 19: 47-60.
- 47 Burel F., Butet A., Delettre Y. R. & de la Pena N. M. (2004) Differential response of selected
48 taxa to landscape context and agricultural intensification. *Landscape and Urban Planning* 67:
49 195-204.

1 Burnham K. P. & Anderson D. R. (2002) *Model selection and Multi-Model Inference. A*
2 *practical information-theoretic Approach*. Springer-Verlag, New York, USA.

3 Chaplin-Kramer R., O'Rourke M. E., Blitzer E. J. & Kremen C. (2011) A meta-analysis of
4 crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14: 922-932.

5 Concepcion E. D., Fernandez-Gonzalez F. & Diaz M. (2012) Plant diversity partitioning in
6 Mediterranean croplands: effects of farming intensity, field edge, and landscape context.
7 *Ecological Applications* 22: 972-981.

8 Crist T. O., Veech J. A., Gering J. C. & Summerville K. S. (2003) Partitioning species
9 diversity across landscapes and regions: A hierarchical analysis of alpha, beta, and gamma
10 diversity. *American Naturalist* 162: 734-743.

11 Diekotter T., Billeter R. & Crist T. O. (2008) Effects of landscape connectivity on the spatial
12 distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*
13 9: 298-307.

14 Duelli, P. (1997). Biodiversity evaluation in agricultural landscapes: An approach at two
15 different scales. *Agriculture Ecosystems & Environment*, 62, 81-91.

16 Dunning J. B., Danielson B. J. & Pulliam H. R. (1992) Ecological processes that affect
17 populations in complex landscapes. *Oikos* 65: 169-175.

18 Eigenbrod F., Hecnar S. J. & Fahrig L. (2011) Sub-optimal study design has major impacts on
19 landscape-scale inference. *Biological Conservation* 144: 298-305.

20 Ekroos J., Hyvonen T., Tiainen J. & Tiira M. (2010) Responses in plant and carabid
21 communities to farming practises in boreal landscapes. *Agriculture Ecosystems &*
22 *Environment* 135: 288-293.

23 Ernoult A., Tremauville Y., Cellier D., Margerie P., Langlois E. & Alard D. (2006) Potential
24 landscape drivers of biodiversity components in a flood plain: Past or present patterns?
25 *Biological Conservation* 127: 1-17.

26 Ewers R. M. & Didham R. K. (2006) Confounding factors in the detection of species
27 responses to habitat fragmentation. *Biological Reviews* 81: 117-142.

28 Fahrig L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology*
29 *Evolution and Systematics* 34: 487-515.

30 Fahrig L., Baudry J., Brotons L., Burel F. G., Crist T. O., Fuller R. J., Sirami C., Siriwardena
31 G. M. & Martin J. L. (2011) Functional landscape heterogeneity and animal biodiversity in
32 agricultural landscapes. *Ecology Letters* 14: 101-112.

33 Gabriel D., Thies C. & Tschardt T. (2005) Local diversity of arable weeds increases with
34 landscape complexity. *Perspectives in Plant Ecology Evolution and Systematics* 7: 85-93.

35 Gaujour E., Amiaud B., Mignolet C. & Plantureux S. (2012) Factors and processes affecting
36 plant biodiversity in permanent grasslands. A review. *Agronomy for Sustainable Development*
37 32: 133-160.

38 Griffiths G. J. K., Winder L., Holland J. M., Thomas C. F. G. & Williams E. (2007) The
39 representation and functional composition of carabid and staphylinid beetles in different field
40 boundary types at a farm-scale. *Biological Conservation* 135: 145-152.

41 Hanski I. (1999) *Metapopulation ecology*. Oxford University Press, New York, USA.

42 Hendrickx F., Maelfait J. P., Van Wingerden W., Schweiger O., Speelmans M., Aviron S.,
43 Augenstein I., Billeter R., Bailey D., Bukacek R., Burel F., Diekotter T., Dirksen J., Herzog
44 F., Liira J., Roubalova M., Vandomme V. & Bugter R. (2007) How landscape structure, land-
45 use intensity and habitat diversity affect components of total arthropod diversity in
46 agricultural landscapes. *Journal of Applied Ecology* 44: 340-351.

47 Holland J. M. (2002) Carabid beetles: their ecology, survival and use in agroecosystems. In:
48 *The agroecology of carabid beetles* (ed. J. M. Holland) pp. 1-40. Intercept Press, Andover,
49 UK.

1 Holzschuh A., Steffan-Dewenter I. & Tschardt T. (2010) How do landscape composition
2 and configuration, organic farming and fallow strips affect the diversity of bees, wasps and
3 their parasitoids? *Journal of Animal Ecology* 79: 491-500.

4 Hubert-Moy L., Nabucet J., Vannier C. & Lefebvre A. (2012) Mapping ecological
5 continuities: which data for which territorial level? Application to the forest and hedge
6 network. *International Journal of Geomatics and Spatial Analysis* 22: 619-640.

7 Jeanneret P., Schupbach B. & Luka H. (2003) Quantifying the impact of landscape and
8 habitat features on biodiversity in cultivated landscapes. *Agriculture Ecosystems &
9 Environment* 98: 311-320.

10 Kromp B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy,
11 cultivation impacts and enhancement. *Agriculture Ecosystems & Environment* 74: 187-228.

12 Le Roux X., Barbault R., Baudry J., Burel F., Doussan I., Garnier E., Herzog F., Lavorel S.,
13 Lifran R., Roger-Estrade J., Sarthou J. P. & Trommetter M. (2008) Agriculture et biodiversité.
14 Valoriser les synergies. Expertise scientifique collective. *Rapport INRA (France)*.

15 Lindenmayer D. B. & Fischer J. (2007) Tackling the habitat fragmentation panchreston.
16 *Trends in Ecology & Evolution* 22: 127-132.

17 Macfadyen S. & Muller W. (2013) Edges in Agricultural Landscapes: Species Interactions
18 and Movement of Natural Enemies. *Plos One* 8.

19 MacLeod, A., Wratten, S.D., Sotherton, N.W. & Thomas, M.B. (2004) 'Beetle banks' as
20 refuges for beneficial arthropods in farmland: long-term changes in predator communities and
21 habitat. *Agric. For. Entomol.*, 6, 147-154.

22 Meeus J. H. A. (1993) The transformation of agricultural landscapes in Western-Europe.
23 *Science of the Total Environment* 129: 171-190.

24 Millan-Pena N., Butet A., Delettre Y., Morant P. & Burel F. (2003) Landscape context and
25 carabid beetles (Coleoptera : Carabidae) communities of hedgerows in western France.
26 *Agriculture Ecosystems & Environment* 94: 59-72.

27 Mueller-Dombois D. & Ellenberg H. (1974) *Aims and Methods of Vegetation Ecology*. Wiley
28 International Edition, London.

29 Poggio S. L., Chaneton E. J. & Ghersa C. M. (2010) Landscape complexity differentially
30 affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields.
31 *Biological Conservation* 143: 2477-2486.

32 Purtauf T., Roschewitz I., Dauber J., Thies C., Tschardt T. & Wolters V. (2005) Landscape
33 context of organic and conventional farms: Influences on carabid beetle diversity. *Agriculture
34 Ecosystems & Environment* 108: 165-174.

35 Robinson R. A., Wilson J. D. & Crick H. Q. P. (2001) The importance of arable habitat for
36 farmland birds in grassland landscapes. *Journal of Applied Ecology* 38: 1059-1069.

37 Roche B., Lanoë E., Le Coeur D., Thenail C. & Martel G. (2010) Diversité des systèmes de
38 polyculture élevage et des modes d'exploitation des prairies : quelles conséquences sur la
39 diversité végétale ? *Rencontres recherches ruminants*
40 <http://www.journees3r.fr/spip.php?article2973>.

41 Roger J.-L., Jambon O. & Bouger G. (2010) *Clé de détermination des carabidés : Paysages
42 agricoles de la Zone Atelier d'Armorique*. Laboratoires INRA SAD-Paysage et CNRS
43 ECOBIO, Rennes, France.

44 Smith A. C., Fahrig L. & Francis C. M. (2011) Landscape size affects the relative importance
45 of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34:
46 103-113.

47 Smith A. C., Koper N., Francis C. M. & Fahrig L. (2009) Confronting collinearity: comparing
48 methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*
49 24: 1271-1285.

1 Thies C., Steffan-Dewenter I. & Tschardtke T. (2003) Effects of landscape context on
2 herbivory and parasitism at different spatial scales. *Oikos* 101: 18-25.

3 Thornton D. H., Branch L. C. & Sunquist M. E. (2011) The influence of landscape, patch, and
4 within-patch factors on species presence and abundance: a review of focal patch studies.
5 *Landscape Ecology* 26: 7-18.

6 Tschardtke T., Bommarco R., Clough Y., Crist T. O., Kleijn D., Rand T. A., Tylianakis J. M.,
7 Nouhuys S. v. & Vidal S. (2007) Conservation biological control and enemy diversity on a
8 landscape scale. *Biological Control* 43: 294-309.

9 Tschardtke T., Klein A. M., Kruess A., Steffan-Dewenter I. & Thies C. (2005) Landscape
10 perspectives on agricultural intensification and biodiversity - ecosystem service management.
11 *Ecology Letters* 8: 857-874.

12 Tschardtke T., Tylianakis J. M., Rand T. A., Didham R. K., Fahrig L., Batary P., Bengtsson
13 J., Clough Y., Crist T. O., Dormann C. F., Ewers R. M., Frund J., Holt R. D., Holzschuh A.,
14 Klein A. M., Kleijn D., Kremen C., Landis D. A., Laurance W., Lindenmayer D., Scherber C.,
15 Sodhi N., Steffan-Dewenter I., Thies C., van der Putten W. H. & Westphal C. (2012)
16 Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological*
17 *Reviews* 87: 661-685.

18 Woodcock B. A., Redhead J., Vanbergen A. J., Hulmes L., Hulmes S., Peyton J.,
19 Nowakowski M., Pywell R. F. & Heard M. S. (2010) Impact of habitat type and landscape
20 structure on biomass, species richness and functional diversity of ground beetles. *Agriculture*
21 *Ecosystems & Environment* 139: 181-186.

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23

1 **TABLES**

2

3 **Table 1**

4 Classification matrix for the five sampled cover-types obtained by k-means cluster analysis.

5 W: woodland, H: hedgerow, P and T: permanent and temporary grassland and C: winter

6 cereal crop

Carabids					
Cover types					
Cluster	W	H	P	T	C
1	14	9	0	0	0
2	0	0	8	15	1
3	25	23	4	0	0
4	0	6	27	25	2
5	1	2	1	0	37
Total	40	40	40	40	40

Plants					
Cover types					
Cluster	W	H	P	T	C
1	0	0	24	9	0
2	0	0	15	31	1
3	40	12	0	0	0
4	0	0	1	0	39
5	0	28	0	0	0
Total	40	40	40	40	40

7

1 **FIGURE CAPTIONS**

2

3 **Figure 1**

4 (a) map of the study area, (b) representation of the hierarchical sampling design for one of the
5 1 km² selected landscapes, and (c) localisation of the study area in France. The sampled cover
6 types are W: woodland, H: hedgerow, P: permanent grassland, T: temporary grassland, C:
7 winter cereal crop.

8

9 **Figure 2**

10 Total length of edge between semi-natural habitat (SNH) and farmlands (km) plotted against
11 the proportion of the landscape in semi-natural habitat. Points are the 20 selected landscapes.
12 Dotted lines represent the least squares relationships (not significantly different from zero: r_s
13 = - 0.24).

14

15 **Figure 3**

16 Linear regression coefficients for the effects of proportion of semi-natural habitat (% SNH)
17 and length of edge between semi-natural habitats and farmlands (SNH – Farmland) on carabid
18 beetle species richness (a) and evenness (b), and vascular plant species richness (c) and
19 evenness (d). Points are the standardized averaged coefficients (weighted by the model's
20 Akaike weight) and error bars are the associated 95% unconditional confidence limits from
21 MMI analysis. Models with $\Delta AICc < 4$ were included in the averaging (all supported models
22 are reported in supplements 1 and 2). Landscape descriptors whose confidence intervals
23 exclude zero can be considered as having a significant positive (above zero) or negative
24 (below zero) effect.

25

1 **Figure 4**

2 Average species richness of carabid beetles (a) and vascular plant (b) in the five sampled
3 cover types (40 replicates for each type). Letters indicate significant differences, calculated
4 from generalized linear mixed models (GLMM) that included landscapes as nested factor.
5 Error bars are standard errors of the means.

6

7 **Figure 5**

8 Graphical representation of the first two PCA axes computed on carabid beetle (a) and plant
9 (b) species presence / absence data. Points are grouped by sampling cover type. W: woodland,
10 H: hedgerow, P: permanent grassland, T: temporary grassland, C: winter cereal crop (40
11 replicates for each type). Numbers represent the percentage of variance explained by each
12 axes.