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Pollinator ecology at a landscape scale

A thesis submitted for the degree of Doctor of Philosophy

June 2016

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Summary

Pollination is a key ecosystem service in natural and agricultural ecosystems which provides benefits to human society. It has been estimated that 87.5 % of angiosperms depend on animal pollinators. The role of pollinators in pollination processes is to pick-up, transfer and deposit viable pollen, this enables seed set and fruit development and reproduction in plants. The pollination process is essential not only for wild plants but also for cultivated plants. However, pollinators and the pollination services they provide are increasingly threatened by the pressures exerted by humans on the environment such as agricultural intensification leading to landscape change. It is within this context that my study aims to understand the effects of landscape and geographic location on pollinator diversity, abundance and the provision of pollination services. A range of different measures and methods were used to characterise the landscape, flower-visiting insect diversity and pollination services.

Using a high-resolution landscape characterisation (i.e. by digitising landscape features identified by aerial photographs and GIS ground-truthed field based surveys), we investigated the effects of landscape structure on flower-visiting insect diversity and insect-flower interaction networks in semi-natural grasslands located in low-intensity agricultural systems. The landscape structure was investigated through its two components: composition (i.e. number and the amount of different habitat type) and configuration (i.e. spatial arrangement of these landscape elements). We found that a higher proportion of semi-natural grasslands, a higher patch shape complexity (i.e. land parcels with more irregular shape) and a larger patch size in the surrounding landscape increased flower-visiting insect species richness and abundance at 500m and 1km scales. Landscape structure and the length of stonewalls in the landscape both correlated with network structure. At 1km scale, a higher complexity of patch shape and higher proportion of semi-natural grasslands seem to be advantageous by improving the robustness of insect-flower interaction networks, but at 500m scale, network properties are related to the length of stonewalls.

In the same sites, we characterised the landscape in another way. We used the European CORINE Land Cover (CLC) to test its suitability as a tool to characterise the landscape structure for pollinator studies. CLC does not have a high resolution as it is based on the photo interpretation of satellite images and involves a series of thematic and spatial generalisations to fit the common European classification and the minimum map unit of 25ha. The landscape characterised with CLC was compared with the high-resolution land cover dataset previously used. Then, this CLC dataset was used to test relationships between land cover and flower-visitor diversity at 500m-5km scales. We showed that despite of processes CLC creation and

the constraints related to the classification of the different CLC habitats, landscape composition using CLC is consistent and shows generally reliable patterns with flower-visitor diversity. However, the classes used in CLC do not capture fine scale habitat diversity (such as different grassland types) which has shown to be important in pollination studies. This means different patterns were in some circumstances more difficult to detect. We highlighted the fact that using CLC must be an informed decision. All users must be aware of the different successive steps of CLC production which leads to spatial and thematic generalisations, and the associated limitations in its application.

Subsequently, I investigated how land use intensification (LUI) and the geographical location have shaped species and functional community change in bee communities visiting oilseed rape and coffee crops. For that, compositional changes were assessed in terms of both richness and turnover. I showed that there is species turnover (coffee crop) and species richness differences (oilseed rape) across geographical locations, but different functional community compositions were also found. LUI decreased species richness for both crop species which resulted in a functional richness difference in the coffee crop and a functional replacement in the oilseed rape crop. These changes in species and functional composition may impact the ecosystem resilience.

Lastly, I investigated the effects of the landscape composition and configuration on the provision of pollination services to wild plants. Relationships between landscape structure and the provision of pollination services did not show any consistent pattern, with contradictory responses from different plant species characterised by similar floral structure. Although there was no observed relationship between the landscape structure and the pollination services in this study, it is possible that the provision of pollination services may be influenced by other factors not taken into account, such as the size of the corresponding plant population, local environmental factors (including soil characteristics), weather conditions and farming practices which may have more influence on the provision of pollination services than surrounding landscape structure.

My study gives some new findings on the relationships between the landscape structure and the pollinator community. It shows the importance of implying conservation measures at a landscape scale but it also highlights the necessity of developing more research on this topic especially on improving the method of landscape characterisation.

To my family

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List of Contents

Declaration II

Summary III

Acknowledgements VI

List of main contributors to each chapter VIII

List of Contents X

List of Tables XIV

List of Figures XVII

List of Appendices XX

1. General Introduction 2

1.1. Biodiversity and the related ecosystem services 2

1.1.1. Biodiversity, a broad concept 2

1.1.2. Alpha, beta and gamma diversity 3

1.2. Pollinators and pollination services 4

1.2.1. Pollinators in Ireland 5

1.2.2. Pollinator declines 6

1.2.3. Pollinator status and conservation measures 8

1.3. Agricultural landscapes 9

1.3.1. Irish landscapes 9

1.3.1.1. Grasslands 10

1.3.1.2. Mass-flowering entomophilous crops 11

1.3.1.3. Field margins and hedgerows 11

1.4. Landscape structure 12

1.4.1. Methods to characterise the landscape and available resources 13

1.4.2. CORINE 14

1.5. Landscape and biodiversity 15

1.5.1. Landscape and pollinator diversity 16

1.5.1.1. Landscape composition 16

1.5.1.2. Linear features 17

1.5.1.3. Landscape configuration 18

1.5.1.4. Scale 18

1.5.2. Landscape and pollinator functional diversity 19

1.5.3. Landscape and plant pollinator interactions 19

1.5.4. Landscape and the provision of pollination services 20

X

1.6.	Research objectives.....	21
2.	Effects of scale and landscape structure on pollinator diversity and plant-pollinator interaction networks in semi-natural grasslands.....	24
2.1.	Abstract	24
2.2.	Introduction	25
2.3.	Materials and Methods.....	29
2.3.1.	Study sites	29
2.3.2.	Transect sampling	30
2.3.3.	Landscape characterisation at different spatial scales	30
2.3.4.	Data analysis	31
2.4.	Results	34
2.4.1.	Pollinator species richness and abundance	34
2.4.2.	Plant pollinator interaction networks	34
2.4.3.	Landscape characterisation	34
2.4.4.	Landscape structure and scale effects	37
2.4.5.	Linear feature length effects.....	43
2.5.	Discussion.....	48
2.5.1.	Landscape composition effects.....	48
2.5.2.	Landscape configuration effects	50
2.5.3.	Linear feature effects	51
2.5.4.	Network size effects.....	52
2.5.5.	Scale effects	52
2.5.6.	Differences between years	53
2.6.	Conclusions	53
3.	Testing the suitability of CORINE Land Cover 2012 as a tool to characterise landscape structure for pollinator studies	56
3.1.	Abstract	56
3.2.	Introduction	57
3.3.	Materials and Methods.....	61
3.3.1.	Landscape characterisation: qualitative	61
3.3.2.	Landscape characterisation: quantitative	61
3.3.3.	Determining landscape scale effects on pollinator diversity	64
3.4.	Results	66
3.4.1.	CLC2012 landscape characterisation from 500m to 5km	66

3.4.2.	Landscape characterisation: qualitative differences between CLC2012 and Fossitt classifications	69
3.4.3.	Landscape characterisation: quantitative differences between CLC2012 and Fossitt classifications	71
3.4.4.	Landscape scale effects on pollinator diversity: 500m and 1km scales.....	74
3.4.5.	Landscape scale effects on pollinator diversity: 2.5 and 5km scales.....	80
3.5.	Discussion.....	83
3.5.1.	Comparison of landscape characterised with Fossitt level 3 and CLC2012 level 3 at 1km scales	83
3.5.2.	Landscape effects using CLC2012 on pollinator diversity at 500m and 1km scales ...	84
3.5.3.	Landscape effects using CLC2012 on pollinator diversity at 2.5km and 5km scales ..	85
3.6.	Conclusions	86
4.	Regional and land use intensification effects on beta taxonomic and functional diversity in bee communities.....	89
4.1.	Abstract	89
4.2.	Introduction	90
4.3.	Materials and methods	92
4.3.1.	Bee community data	92
4.3.2.	Regional and land use intensification	95
4.3.3.	Trait data	96
4.3.4.	Data analyses	96
4.4.	Results	100
4.4.1.	Coffee	100
4.4.2.	Oilseed rape	105
4.5.	Discussion.....	107
4.5.1.	Regional and land use intensification effects on beta-diversity of bee visiting coffee crops.....	107
4.5.2.	Regional and land use intensification effects on beta-diversity of bee visiting oilseed rape crops	109
4.5.3.	Limitation of this study	110
4.6.	Conclusions	110
5.	Effects of landscape structure on the provision of pollination services in agricultural landscape	113
5.1.	Abstract	113
5.2.	Introduction	114
5.3.	Materials and Methods.....	116

5.3.1.	Wild plant pollination – semi-natural grasslands.....	116
5.3.2.	Wild plant pollination - hedgerow habitat.....	117
5.3.3.	Data analysis	119
5.4.	Results	121
5.4.1.	Pollination services	121
5.4.2.	Landscape characterisation	121
5.4.3.	Landscape scale effects on provision of pollination services.....	123
5.5.	Discussion.....	126
5.5.1.	Landscape effects on the deposition of pollen on wild plant stigmas in semi-natural grasslands.....	126
5.5.2.	Landscape effects on the seed set of two hedgerow species surrounding tillage crop or grassland	127
5.6.	Conclusions	128
6.	General discussion	130
6.1.	Synthesis of the findings	131
6.1.1.	Pollinator ecology at a landscape scale	131
6.1.2.	Biogeography of taxonomic and functional components of the bee community	133
6.1.3.	Comparing the different methods of landscape characterisation.....	133
6.2.	Recommendations for future landscape management decisions	135
6.2.1.	Semi-natural grasslands	135
6.2.2.	Patch shape	135
6.2.3.	Linear features	136
6.3.	Reflections for future methods of landscape characterisation	136
6.4.	Suggestions for future research	137
6.4.1.	Pollinator ecology.....	138
6.4.2.	Landscape characterisation	138
6.5.	Final conclusions	139
	References.....	140
	Appendices.....	157

List of Tables

Table 1: Mean, minimum and maximum values of the landscape composition and configuration metrics calculated at the 500m and 1km scales..... 35

Table 2: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (Shannon Evenness Index, Area Weighted Mean Shape Index, Mean Patch Size, proportion of semi-natural grasslands and factor Year). Significant results are showed by differing arrows. Arrow directions (↗↘) represent respectively positive and negative relationships. Smaller and thinner arrow represent a *p-value <0.05, medium arrows a**p-value <0.01 and bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best models (i.e. the model with the lowest AIC). 39

Table 3: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (number of plant species, number of insect species, connectance, nestedness, weighted linkage per insect species, H2', linkage density and weighted linkage per plant species) and the explanatory variables (Shannon Evenness Index, Area Weighted Mean Shape Index, Mean Patch Size, proportion of semi-natural grasslands and factor year). Network size was considered as an additional covariate in the models that tested the landscape sale effects on all the network indices (except for the number of plants species) since some network structure parameters are sensitive to network size. Significant results are shown by differing arrows indicating trends. Arrow directions (↗↘) represent respectively positive and negative relationships. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a**p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. model with the lowest AIC). 42

Table 4: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (stonewalls length, hedgerow length and factor year). Significant results are shown by differing arrows indicating trends. Arrow directions (↗↘) represent respectively positive and negative relationships. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a**p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. with the lowest AIC). 45

Table 5: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (Number of plant species, number of insect species, connectance, nestedness, weighted linkage per pollinator species, H2', linkage density and weighted linkage per plant species) and the explanatory variables (stonewall length, hedgerow length and factor Year). Significant results are showed by differing arrows indicating trends. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a**p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. with the lowest AIC). 47

Table 6 : Fossitt habitat codes (left hand column) and their comparative CORINE classes (right hand column)..... 63

Table 7: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC 2012 level 3) for 500m and 1km scales. 67

Table 8: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC 2012 level 3) for 2.5km and 5km scales. 68

Table 9 : Pearson Product Moment Correlation Coefficients showing the significant linear relationships between insect responses and landscape variables at 500m scales in 2010 and 2011.	75
Table 10: Pearson Product Moment Correlation Coefficients showing the significant linear relationships between insect responses and landscape variables at 1km scale in 2010 and 2011.	76
Table 11 : Relationship between % pasture (231- CORINE) / %semi-natural grassland (GS1-Fossitt) and insect variables (negative/positive significant relationship, * relationship found in both years). 79	79
Table 12: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (%arable, %pasture, %forest and factor Year). Significant results are showed by differing arrows indicating trends. Smaller and thinner arrows represent a *p-value <0.05, medium arrows a**p-value <0.01 and bigger and thicker arrows a ***p-value <0.001. Non-significant covariate is represented by NS and covariate not considered in the best model (i.e. model with the lowest AIC) is a blank value. Shaded cells represent relationships driven by a four data points.....	81
Table 13: Summary of the coffee datasets used in this study.	93
Table 14: Summary of the oilseed rape datasets used in this study.	94
Table 15: P-values and R ² of PERMANOVA for the different components of beta taxonomic and functional diversity between regions, according to the distance to the nearest natural habitat and the interaction between these two variables.	102
Table 16: P-values of the PERMDISPER between the regions and the different components of the beta taxonomic and functional diversity.	102
Table 17 : P-values and R ² of PERMANOVA for the different components of beta taxonomic and functional diversity along a latitudinal gradient and according to the distance to the nearest natural habitat and the interaction between these both variables.	106
Table 18: Lists of the different landscape metrics kept in the analysis for semi-natural habitat and grassland.....	120
Table 19: Mean, minimum and maximum of the number of seeds per fruits of <i>Rosa canina</i> found in the hedgerow surrounding the grassland and arable crops.....	121
Table 20: Mean, minimum and maximum of the total number of seeds per ten fruits of <i>Sambucus nigra</i> found in the hedgerow surrounding the grassland and arable crops.	121
Table 21: Mean, minimum and maximum values of the landscape metrics (Shannon Evenness Index (SEI), Area Weighted Mean Shape Index (AWMSI), Mean Patch Size (MPS), proportion of dry calcareous and neutral grasslands (%GS1)) kept in the analysis calculated at the 500m and 1km scales for the semi-natural grasslands.....	122
Table 22: Mean, minimum and maximum values of the landscape metrics (Shannon Evenness Index (SEI), Mean Shape Index (MSI), Number of patches (NumP), proportion of arable crop (%arable crop), proportion of semi-improved grasslands (GA+)) kept in the analysis calculated at the 500m scales for the hedgerow habitat.....	122
Table 23: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (stigma pollen deposition of six plants species) and the explanatory variables (Shannon Evenness Index (SEI), Area Weighted Mean Shape Index (AWMSI), Mean Patch Size (MPS), proportion of dry calcareous and neutral grasslands (%GS1)). Significant results are shown by differing arrows indicating trends. Smaller and thinner arrow represent a *p-value <0.05, medium arrows a**p-value <0.01. Non-significant covariates are represented by NS and covariates not considered in the best model (i.e. model with the lowest AIC) by a blank value.123	123
Table 24: Results of the Generalized Linear Mixed Models (GLMMs) testing for relationships between the response variables (number of seeds per fruit for <i>Rosa canina</i> and the number of seeds in 10 fruits of an inflorescence for <i>Sambucus nigra</i>) and the explanatory variables (Shannon Evenness Index (SEI), Mean Shape Index (MSI), Number of Patches (NumP), proportion of semi-improved	

grasslands (%GA+), proportion of arable land (%BC1)) and the fixed factor crop. Significant results are shown by differing arrows indicating trends. The smaller and thinner arrow represents a *p-value <0.05. Variable not considered in the final model are represented by a blank value..... 125

List of Figures

Figure 1: Schematic representation of the alpha, beta and gamma diversity measures (the small black circle represents a specific community) based on Fischer (2012)..... 3

Figure 2: The cover of the All-Ireland Pollinator Plan..... 9

Figure 3: Illustration of the two major axes of landscape heterogeneity. Each large square represents a landscape and the different colours are the different cover types within the landscapes (Fahrig et al., 2011). 13

Figure 4: Location of 19 sampling sites in the counties of Roscommon and Offaly (shaded grey) in the north midlands of Ireland. The fields sampled are at the centre of the circles and an example of the surrounding landscape from one site is shown. The two scales studied, i.e. 500m and 1km, are represented by the two concentric circles centred on each sampling site. 29

Figure 5: Selected landscapes at 500 m scale illustrating the landscape compositional and configurational heterogeneity. The landscape composition is measured inter alia by Shannon Evenness Index (SEI) which is a measure of the habitat diversity. Figure (a) represents the highest compositional heterogeneity (Castlesampson $SEI_{500m}=0.873$) and (b) the lowest compositional heterogeneity (Knockrogherry $SEI_{500m}=0.344$). The landscape configurational heterogeneity is measured inter alia by the Area Weighted Mean Shape Index (AWMSI) which is a measure of the complexity of the patch shape in the landscape. Figure (c) represents the highest configurational heterogeneity (Ballyduff $AWMSI_{500m}=1.614$) and (d) the lowest configurational heterogeneity (Turrock $AWMSI_{500m}=1.206$) (BC1: arable crops, BL3: artificial surfaces, ED1: exposed sand gravel or till, FL8: other artificial lakes and ponds, FS1: reed and large sedge swamps, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands, GS4: wet grasslands, HD1: dense bracken, PB1: raised bog, WD1: mixed broadleaved woodland, WD4: conifer plantation and WS1: scrub)..... 36

Figure 6: Selected landscapes at 1 km scale illustrating the landscape compositional and configurational heterogeneity. The landscape composition is measured inter alia by Shannon Evenness Index (SEI) which is a measure of the habitat diversity. Figure (a) represents the highest compositional heterogeneity (Clonmacnoise $SEI_{1km}=0.796$) and (b) the lowest compositional heterogeneity (Ardmullen $SEI_{1km}=0.274$). The landscape configurational heterogeneity is measured inter alia by the Area Weighted Mean Shape Index (AWMSI) which is a measure of the complexity of the patch shape in the landscape. Figure (b) represents the highest configurational heterogeneity (Ardmullen $AWMSI_{1km}=1.783$) and (c) the lowest configurational heterogeneity (Knockrogherry $AWMSI_{1km}=1.275$) (BL3: artificial surfaces, FL3: limestone and marl lakes, FL6: turlough, FS1: reed and large sedge swamps, FW2: depositing lowland rivers, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands, GS4: wet grasslands, PB1: raised bog, WD1: mixed broadleaved woodland, WD4: conifer plantation and WS1: scrub). 37

Figure 7: Main effects of the landscape metrics on the insect species richness from the best model (i.e. model with the lowest AIC) at a) 1km scale, and b) c) and d) at the 500m scale. Points represent observed values. The lines characterise the model predictions and dotted lines the 95% confidence intervals. The different colours symbolize the two years (black: 2010 and red: 2011). All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends. 40

Figure 8: Main effects of the landscape metrics on network indices from the best model (i.e. model with the lowest AIC) for (a) the relationship between the linkage density and SEI (b) between the 1-nestedness and AWMSI, (c) weighted linkage per plant and MPS and (d) linkage density and GS1 at 1km scale. Points represent the observed values. Lines characterise the model predictions

and dotted lines the 95% confidence intervals. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.	43
Figure 9: Relationships between the linear feature metrics and insect diversity from the best model (i.e. model with the lowest AIC), a) bumblebee abundance and stonewall length, b) hoverfly species richness and stonewall length, c) insect species richness and the stonewall length and d) butterfly species richness and stonewall, all at 500m scale. Points represent the observed values. Lines characterise the model prediction and dotted lines the 95% confidence intervals (black represents the data from 2010 and red from 2011). All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.	46
Figure 10: Relationship between linear features (stonewalls) and network indices (linkage density) from the best model (i.e. with the lowest AIC) at the 500m scale. Points represent the observed values, the line the model prediction and dotted lines the 95% confidence intervals.	48
Figure 11 : The three levels of CORINE Land Cover classification (European Environment Agency, 1995).	59
Figure 12 : Comparison of the landscape surrounding three sites using Fossitt habitat classification level 3 at 1km scale (maps on the right; 131: mineral extraction sites, 231: pasture, 243: land principally occupied by agriculture, 412: peat bogs, 511: water course) and CLC2012 level 3 (maps on the left; BC1: arable crops, BL3: artificial surfaces, FS1: reed and large sedge swamps, FW2: depositing lowland rivers, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands; GS4: wet grasslands; PB1: raised bogs; WN6: wet willow and alder ash woodland, WD1: mixed broadleaved woodland; WD4: conifer plantation; WS1: scrub; ED1: exposed sand gravel or till, ED4: active quarries and mines, FL8: other artificial lakes and ponds; HD1: dense bracken) (a/ Carrownalassan, b/Castlesampson, c/Clonmacnoise)	70
Figure 13 : Absolute mean ($\pm$ SE) differences of the landcover classes between the two methods at 1km scale (131: Mineral extraction sites, 142: sport and leisure facilities (grouped with 112: discontinuous urban fabric for "Fossitt classes"); 211: non irrigated arable land; 231: pasture; 243: land principally occupied by agriculture with significant areas of natural vegetation; 311: broadleaved forest; 312: coniferous plantation; 322: moors and heathlands; 324: transitional woodlands and scrubs; 332/333: bare rocks/sparsely vegetated areas; 411: inland marshes; 412 peat bogs; 511: water courses; 512 water bodies). Bars in green represent land cover classes which were not recorded by the CLC 2012 classification and bar in yellow not recorded by Fossitt classification.	72
Figure 14 : Proportions of the different CLC 2012 habitat types in the surrounding landscape at 1km scale for each site.....	73
Figure 15: Proportions of the different Fossitt habitat types assigned to CLC 2012 classes in the surrounding landscape at 1km scale for each site.	73
Figure 16 : Relationships between the insect diversity and the landscape metrics at 500m scale. Graphs a,b,c represent data in 2011. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.	77
Figure 17: Relationships between the insect diversity and the landscape metrics at 1km scale. Graphs a,b,c and d represent data in 2010. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.	78
Figure 18: Main effects of the landscape metrics on the insect diversity from the best model (i.e. model with the lowest AIC). Points represent observed values. The lines characterise the model prediction and dotted lines the 95% confidence intervals. The different colours symbolize the two years (black: 2010 and red: 2011). The graphs a represents data at the 2.5km scale and c, d, e at 5km.	82
Figure 19: Location of the oilseed rape and coffee crop systems.	95

Figure 20: Example of the species composition of two sites (a is the number of shared species, b and c are the species exclusive to each site). This illustration is based on Legendre (2014). 98

Figure 21: Example of a functional dendrogram of the relation between the species A-L. Only vertical branches contribute in the calculation. 99

Figure 22: Relationships between the different components of beta taxonomic diversity (β_{tot} , β_{rich} and β_3) and the region and land use intensification. The graphs (a), (b), (d) represent the average dissimilarity of the respective beta components against the distance to the nearest semi-natural habitat. The distance to the nearest semi-natural habitat is standardized. The graph (c) represents the NMDS ordination accounting for the species replacement (β_3) (the size of the circles is proportional to the distance to the nearest natural habitat: smaller circles – closer to natural habitat, larger ones - further) 103

Figure 23: Relationships between the different components of beta functional diversity (β_{tot} and β_{rich}) and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized. The graph (a) represent the NMDS ordination accounting for the difference in functional composition (β_{tot}) (the size of the dots is proportional to the distance to the nearest natural habitat). The graphs (b) and (c) represent the average dissimilarity of the respective β components against the distance to the nearest natural habitat. 104

Figure 24: Relationship between the average species richness (β_{rich}) per site and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized. 107

Figure 25: Relationships between the average β_{tot} , β_3 and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized. 107

Figure 26: Six plant species used for the collection of the stigma pollen (from the top left to the bottom right: *Potentilla erecta*, *Leontodon saxatilis*, *Lotus corniculatus*, *Prunella vulgaris*, *Trifolium repens* and *Trifolium pratense*) (photos: Sarah Mullen). 117

Figure 27: Infrutescence and fruits of *Sambucus nigra* L. (on the left) and fruits of *Rosa canina* L. hybrid (photos: Aude Delmer and Jane Stout). 118

Figure 28: Location of the 14 and 15 hedgerow sites where fruits of *Rosa canina* hybrid and *Sambucus nigra* respectively were sampled and an example of the landscape mapped at 1km grid (BC1: arable crops, BC2: horticultural land, BL3: artificial surfaces, ED4: active quarries and mines, GA1: improved agricultural grasslands, GSI: semi-improved grasslands, WS1: scrub). 119

Figure 29: Main effects of the landscape metrics on median number of pollen grain per stigma of the corresponding plant species studied from the best model. Points represent observed values. The line characterises the model prediction and dotted lines the 95% confidence intervals. The graphs a and b are related to the 500m scale and the graphs c,d,e and f to the 1km scale. 124

Figure 30: Main effects of the landscape metrics at for a 1km grid scale on number of seeds of *Sambucus nigra* L. from the best model. Points represent observed values. The line characterises the model prediction and dotted lines the 95% confidence intervals. 125

List of Appendices

Appendix 1: Summary table of the 19 semi-natural grasslands on which fieldwork was carried out. The table specifies which site were exclusively dry calcareous and neutral grasslands (GS1) or semi-improved grasslands (GA+) with patches of dry calcareous and neutral grasslands. 157

Appendix 2: Location of the 19 semi-natural grasslands sites according to their ID (Appendix 1). 158

Appendix 3: Formulas and descriptions of all the metrics used to characterise the landscapes with a_{ij} the area (m^2) of patch ij , a_i the area (m^2) of each patch of the same type i , A the total landscape area (m^2), N the total number of patches in the landscape, p_{ij} perimeter (m) of patch ij , P_i the proportion of landscape occupied by patch type (class) i , m number of patches types (classes) present in the landscape, E total length (m) of edge in landscape, f_j length (m) of each linear feature of the same type i 159

Appendix 4: Habitats found in the landscapes surrounding the 19 semi-natural grasslands and their corresponding codes (according to Fossitt 2000). 161

Appendix 5: Definition of network parameters (Dormann et al., 2009). 162

Appendix 6: Pearson Product Moment Correlation Coefficients for 500m and 1km scales showing significant relationships between values for all the landscape metrics (except linear features) and the four variables retained (SEI, AWMSI, MPS and GS1) (chapter 2). This table only presents the significant correlation, the metrics not included showed no significance with SEI, AWMSI, MPS or GS1 (p-value < 0.05 and $r > 0.456$, ** p-value < 0.01 and $r > 0.575$). 163

Appendix 7: List of insect species recorded with the transect sampling across all sites. 164

Appendix 8: Mean, minimum and maximum insect species richness and abundance (including mean species richness and abundance of each insect group) per site for 2010 and 2011. 165

Appendix 9: Mean, minimum and maximum value of each qualitative and quantitative insect-flower network parameter per site and calculated for 2010 and 2011. 166

Appendix 10 : Pearson Product Moment Correlation Coefficients for 2.5km and 5km scales showing where significant differences arise between values of all the landscape metrics (CLC2012 level 2) and the three variables retained (arable land, pasture and forest). This table only presents the significant correlation, the metrics not included showed no significance with arable land, pasture and forest. 167

Appendix 11: Mean and standard error for each landscape metrics calculated at 1km scale for CLC2012 CORINE and Fossitt CORINE. 168

Appendix 12: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC2012 level 2) for 2.5km and 5km scales. 169

Appendix 13: Dendrogram of the functional similarities (based on Petchey and Gaston (2002)) of the species recorded in the coffee crops. 170

Appendix 14 : Contribution (R^2) of the latitude, distance to the nearest natural habitat and their interaction on the overall beta taxonomic (and functional) diversity and independently for their two components (species replacement and difference in species richness) for the coffee crop. This was calculated with adonis (PERMANOVA). 171

Appendix 15: Dendrogram of the functional similarities ((based on Petchey and Gaston (2002)) of the species recorded in the oilseed rape crops. 172

Appendix 16: Contribution (R^2) of the latitude, distance to the nearest natural habitat and their interaction on the overall beta taxonomic (and functional) diversity and independently for their two components (species replacement and difference in species richness) for the Oilseed rape crop. This was calculated with adonis (PERMANOVA). 173

Appendix 17: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (SDI, AWMSI, MPS, MFC and grass) for the oilseed rape crop habitat. This table only

presents the significant correlation, the metrics not included showed no significance with the SDI, AWMSI, MPS, MFC and grass. 174

Appendix 18: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (MSI, NumP, %BC1, %GAI and SEI) with the *Rosa canina*. This table only presents the significant correlation, the metrics not included showed no significance with the MSI, NumP, BC1, GA+ and SEI. 175

Appendix 19: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (MSI, NumP, %BC1, %GAI and SEI) with the *Sambucus nigra*. This table only presents the significant correlation, the metrics not included showed no significance with the MSI, NumP, BC1, GA+ and SEI. 176

Chapter 1

General Introduction

1. General Introduction

1.1. Biodiversity and the related ecosystem services

Biodiversity, defined as the variety of life on Earth, provides ecosystem services which benefit human welfare: these include the provisioning services of food, water, timber, fibre, genetic resources; cultural services like ecotourism, recreation, aesthetic values; and regulating services such as climate regulation, water regulation,... and pollination (Millenium Ecosystem Assessment, 2005). Over the past decades, humans have been changing their environment more rapidly than in any other period of history. Consequently, the biodiversity on Earth has considerably declined, resulting in an accelerated rate of species extinction worldwide (Cardinale et al., 2006). This species loss affects the delivery of ecosystem services (Cardinale et al., 2006).

In response to these ecosystem consequences of biodiversity loss, the Convention on the Biological Diversity (CBD) was established and signed at the United Nations Conference on Environment and Development in 1992 in Rio de Janeiro. The CBD objectives are the conservation and the sustainable use of biological diversity, integrated into a first global concerted effort. In 2010 the Strategic Plan for Biodiversity 2011-2020 was adopted under the Convention, with the vision of a biodiversity valued, conserved restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people by 2050 (Convention on Biological Diversity, 2012).

1.1.1. Biodiversity, a broad concept

To identify the distribution of biodiversity and its rate of extinction, it is essential to find ways to quantify this biological diversity. It is not an easy task as biodiversity is complex multifaceted concept (Pavoine and Bonsall, 2011; Purvis and Hector, 2000). It is commonly considered at three levels: genetic, species and habitats and it can include spatial and temporal scales and different entities such as traits and species (Pavoine and Bonsall, 2011; Purvis and Hector, 2000). Therefore there are different ways of defining and measuring it. Initially biodiversity was described in terms of species richness and abundance (Purvis and Hector, 2000), as these were easy ways to quantify it. But it has been recognised that the functional aspect of the species in ecosystem functioning is crucial, but not captured by these simple metrics (Díaz and Cabido, 2001; Fontaine et al., 2005; Gagic et al., 2015)

Indeed, species are characterised by a range of functional traits i.e. measurable traits that can affect the fitness or performance of the organism (McGill et al., 2006). These traits can characterise different aspects such as the behaviour, morphology, physiology, or phenology (Violle et al., 2007). These functional traits can determine the potential niche of an individual and how individuals interact with each other (McGill et al., 2006), defining the contribution of species to ecosystem function (Cadotte et al., 2011). The value and the range of functional traits from different organisms of a community can be used to assess the functional diversity of a community and so the functioning of an ecosystem (Díaz and Cabido, 2001). Considering both taxonomic and functional diversity have been shown as a good way to predict the biodiversity (Moore, 2001).

1.1.2. Alpha, beta and gamma diversity

Knowing the diversity of a specific place is important, but comparing measures amongst different places can give other information on how species assemble into communities (Purvis and Hector, 2000). Diversity can be measured at different levels (alpha, beta and gamma) based on the spatial scales. This concept has been introduced by Whittaker (1960) with alpha representing species richness within a specific community; beta, the turnover of community composition between two or more communities; and gamma, the species diversity of a range of communities from a sample, a region or a landscape (which takes into account alpha and beta components) (Figure 1).

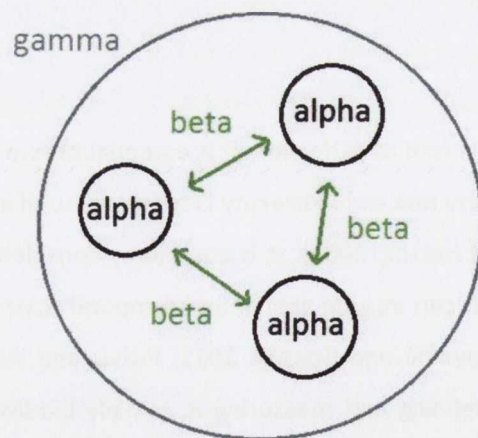


Figure 1: Schematic representation of the alpha, beta and gamma diversity measures (the small black circle represents a specific community) based on Fischer (2012).

Since the introduction of these concepts by Whittaker (1960), the definitions have evolved and now include broader concepts, with different ways of measuring them. Alpha diversity can be

measured as species richness and/or abundance at a site. It can also be estimated with diversity indices (Lande, 1996; Legendre et al., 2005). Alpha diversity has been long used as a referenced measure of biodiversity.

Beta diversity has been studied to identify a range of processes that affect the structure and assembly of communities. Numerous measures have been derived from the original definition of Whittaker to address the objectives of each study (Anderson et al., 2011; Koleff et al., 2003). These measures can be based on species presence/absence or on quantitative abundance data (Koleff et al., 2003; Tuomisto, 2010). Beta-diversity has also been disentangled in two phenomena: (1) species substitution i.e. replacement of species in a site by other species in another site; (2) species loss or gain in richness between sites (Carvalho et al., 2012). However, the second mechanism is not widely recognised. Baselga (2010) suggests that it can result more in a nested process operating along a gradient, with species assemblages of the poorest sites becoming a subset of the richest sites and thereby leading to a nested structure. This nested mechanism does not occur commonly and is instead replaced by a more complex pattern occurring along a gradient (Carvalho et al., 2012).

Finally, gamma diversity is similar to alpha diversity, but at a regional scale. It is measured by pooling the information at a larger scale and it is calculated in the same way as alpha diversity (Legendre et al., 2005).

It is important to study patterns of diversity at alpha, beta and gamma scales. Analysing these patterns at only alpha scale could lead to some lack of information and some misinterpretation of the results as some information will be hidden (Whittaker et al., 2001). Indeed, analyses of the biodiversity at the three spatial scales are important as they considered the contribution of large scale processes to the local (alpha) biodiversity pattern and give information on the connection between local and regional species richness (Gaston, 2000; Nogues-Bravo et al., 2008).

1.2. Pollinators and pollination services

Pollination is a key ecosystem service in natural and agricultural ecosystems (Breeze et al., 2011; Food and Agriculture Organization of the United Nations, 2013). Pollen transfer between flowers can be realised by (1) biotic agents i.e. mammals, bats, birds or insects or (2) abiotic agents i.e. wind, water and (3) self-pollination. Nonetheless, biotic pollination is more common and usually more effective than abiotic (Willmer, 2011). That is generally a combination of

these three processes that occur across vascular plants. Bees are thought to be the most important pollinators among the insects for both natural and agricultural systems (Potts et al., 2010a; Winfree et al., 2008), although non-bee pollinators also play an important role (Orford et al., 2015; Rader et al., 2015). It has been estimated that 87.5 % of angiosperms on earth depend on animal pollinators (Ollerton et al., 2011). Pollen limitation (i.e. reduced female reproductive success as a result of a limitation in pollen supply) has been found in the majority of flowering plant species (Burd, 1994; Knight et al., 2005).

The role of pollinators in pollination processes is to pick-up, transfer and deposit pollen, this enables seed set, fruit development and reproduction (Willmer, 2011). The pollination process is essential not only for wild plants but also for cultivated plants. Seventy-five percentage of most important crop types depend at least in part on animal pollination (Klein et al., 2007). Indeed pollinators are responsible for 35 % of the world crop production (Klein et al., 2007) and the annual economic value of pollination is estimated worldwide at \$232-\$577 billion (Lautenbach et al., 2012) and for Ireland at €53 million (Bullock et al., 2008). These crops are pollinated by managed and wild bees and other animals (Breeze et al., 2011; Ollerton et al., 2012; Rader et al., 2012). Pollinators can also provide another source of food as some species of pollinators, like bees, provide honey and other hive products (Gallai et al., 2009).

1.2.1. Pollinators in Ireland

The main pollinator groups in Ireland are: bees (Hymenoptera; Apoidea) and hoverflies (Diptera; Syrphidae). Ireland has 98 bee species: the honeybee (*Apis mellifera*), 77 solitary bees and 20 species of bumblebee (of which six are cuckoo bumblebees) (Fitzpatrick et al., 2006; National Biodiversity Data Centre, 2015). According to the IUCN red list categorisation, three species are regionally extinct, six critically endangered, ten endangered, 14 vulnerable, 12 near threatened and 38 of least concern (Fitzpatrick et al., 2006). Moreover, 16 were data deficient and three not evaluated (Fitzpatrick et al., 2006).

The most commonly managed pollinator is the honeybee. It has been domesticated for honey production as well as crop pollination globally (National Biodiversity Data Centre, 2015). In Ireland, honeybees are managed mainly for honey production, and it is rare for farmers to introduce honeybees for crop pollination. *Bombus terrestris* is also employed as a managed pollinator across Europe (National Biodiversity Data Centre, 2015). Colonies of this species are imported into Ireland for the pollination of strawberries and tomatoes in glasshouses (National Biodiversity Data Centre, 2015).

In Ireland, 183 hoverfly species have been observed this last century (Speight, 2008). Amongst those species, three are considered extinct as they were not observed for 75 years (Speight, 2008). However, the present Irish hoverfly list is subject to change due to the discovery of an average of one species per year for these last 50 years (Speight, 2008).

Additionally to the bee and hoverfly group, Lepidoptera could be potential pollinators, but there is no direct evidence of that to date. There are 33 resident and regular migrant butterfly species in Ireland (Regan et al., 2010). Of the native Irish butterfly species, one is extinct, six are threatened (endangered or vulnerable) and five are near threatened (Regan et al., 2010) according the IUCN regional red list categorisation. The decline of this pollinator group is most likely caused by declines in habitat quality (Asher et al., 2001).

1.2.2. Pollinator declines

In recent years, a decline in the abundance of many pollinator species but also a reduction of their geographical range has been observed in Europe and North America (Biesmeijer et al., 2006; Potts et al., 2010a; Pywell et al., 2005; Steffan-Dewenter et al., 2005; Williams, 1982). This decline of pollinators can in turn threaten wild and crop plant species and the productivity of agriculture (Food and Agriculture Organization of the United Nations, 2013; Power, 2010; Zhang et al., 2007). In Europe, 9.2% of bees are considered as threatened and 5.2% near threatened according to the European red list (Nieto, 2014). For example, a severe decrease of the bumblebee community evenness has been found in red clover fields in Sweden (Bommarco et al., 2011). Some bumblebee species (mainly late emerging species) are declining in United Kingdom and Ireland, probably due to the common replacement of hay meadows by silage cutting as an agricultural practice (Fitzpatrick et al., 2007). In Denmark, the number of bumblebee species has decreased from 12 to five since 1930 with the longue tongue and late emerging species mainly affected (Dupont et al., 2011). Finally, in the United States, Cameron et al. (2011) showed that the relative abundance of four bumblebee species has decreased by ~96% over the last 30 years, due probably to the infection by the microsporidian pathogen *Nosema bombi* and the reduced genetic diversity. Bumblebee geographical ranges have been also affected by the climate change in Europe and America (Kerr et al., 2015). Biesmeijer et al. (2006) found a decline in bee species richness in many areas in Britain and Netherlands but did not reveal any consistent pattern for the hoverfly community. Thirty one percent of the butterfly species have been shown to be in decline in Europe (Swaay et al., 2010), with 71% of butterfly species declining over a period of 20 years in United Kingdom (Thomas et al., 2004).

Winter losses in managed honeybees have been well documented (Potts et al., 2010b; Stokstad, 1979; VanEngelsdorp et al., 2008).

A range of potential drivers have been identified as (1) agricultural intensification and land use change which results in habitat loss and degradation and habitat fragmentation (Fahrig et al., 2011; Hadley and Betts, 2012; Uuemaa et al., 2009); (2) climate change which can disrupt phenology, abundance, and interaction between plant and pollinator (Hegland et al., 2009; Memmott et al., 2007; Schweiger et al., 2010; Schweiger et al., 2008) and cause range shifts in entire pollinator guilds (Kerr et al., 2015); (3) the introduction of alien plant and pollinator species which compete with native species (Schweiger et al., 2010; Stout and Morales, 2009); (4) the spread of pathogens and parasites (Cox-Foster et al., 2007; Hayes et al., 2008); (5) agrochemical, particularly pesticide use including insecticides and herbicides. Neonicotinoids have been increasingly studied in the last few years to quantify their effects on pollinators and pollination services (Kessler et al., 2015; Rundlöf et al., 2015; Stanley et al., 2015). Neonicotinoids are the most widely used insecticide globally (Goulson, 2013). Sublethal doses of neonicotinoids affect bumblebee colony fitness, honeybee foraging and bee navigating activities (Fischer et al., 2014; Gill and Raine, 2014; Goulson, 2015; Henry et al., 2012; Wright et al., 2015). Moreover bees do not avoid plants treated with neonicotinoids and may even appear to prefer food containing neonicotinoids (Kessler et al., 2015). Effects of neonicotinoids could be widespread: it has been demonstrated that wild bee densities, solitary bee nesting and bumblebee colony growth and reproduction decreased when seed coatings of oilseed rape is treated with neonicotinoids (Rundlöf et al., 2015). Finally, the provision of pollination services can be also altered, Stanley et al. (2015) showed that the provision of pollination services in apple orchard by bumblebee is reduced when they are exposed to the neonicotinoids.

There are many potential drivers of pollinator decline. It is unlikely that environmental drivers act independently of the others (Didham et al., 2007). Interactive effects of drivers, where one driver increases the effect of others, can give more information on the current decline in pollinators (Le Conte and Navajas, 2008; Oldroyd, 2007; Potts et al., 2010b; Settele et al., 2008). Studies to date have generally isolated the impact of one of these drivers. But in reality, these drivers are present simultaneously (Tylianakis, 2008) and thereby knowing their global effects on the pollinator community has become a necessity.

1.2.3. Pollinator status and conservation measures

Despite declines in several pollinator species, there are few pollinator species protected under the European Habitats Directive (92/43/ECC) and no bees or hoverflies are protected nationally by Irish law (National Biodiversity Data Centre, 2012). However, there has been an increasing mobilisation of efforts at different levels to promote pollination management and conservation (Food and Agriculture Organization, 2008). On the global level an International Initiative for the Conservation and Sustainable Use of Pollinators (commonly named the International Pollinator Initiative (IPI)) was established at the 5th Conference of the Convention of Biological Diversity in 2000 (Food and Agriculture Organization of the United Nations, 2013), with regional level actions. The aims of this Initiative are to monitor pollinator decline, its causes and its impact on pollination services; address the lack of taxonomic information on pollinators; assess the economic value of pollination and the economic impact of the decline of pollination services; and to promote the conservation, restoration and sustainable use of pollinator diversity in agriculture and related ecosystems (Food and Agriculture Organization of the United Nations, 2012). More recently, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) carried out its first thematic assessment on pollinators, pollination and food production (to be published in early 2016).

In 2015, Ireland developed a strategy of action, the “All-Ireland Pollinator Plan”, to address pollinator decline and protect the pollination services ((National Biodiversity Data Centre, 2015), Figure 2). Sixty eight governmental and non-governmental organizations joined this initiative and defined 81 actions to promote the pollinators and their services. These actions are based on five main objectives: (1) make Ireland pollinator friendly, (2) raise awareness of pollinators and how to protect them, (3) manage pollinators – support bee keepers and growers, (4) expanding our knowledge on pollinators and pollination services, and (5) collect evidence to track change and measure success. With this plan, Ireland is one of the first European countries to make concrete the establishment of a strategy to protect pollinators and promote pollination services (National Biodiversity Data Centre, 2015).

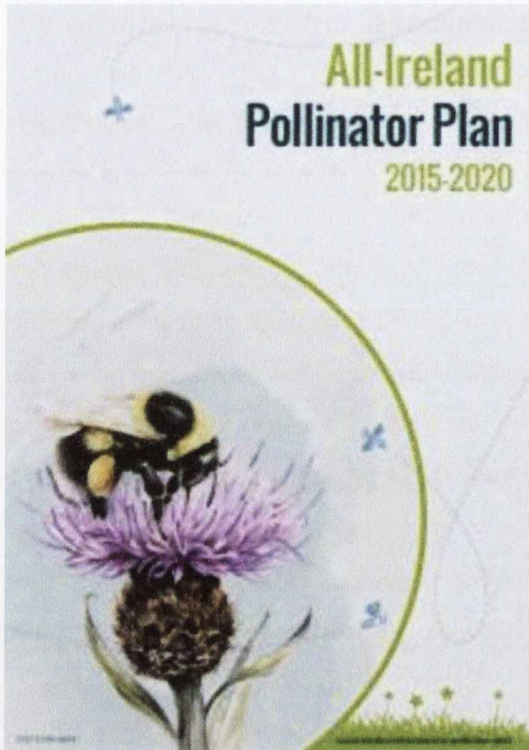


Figure 2: The cover of the All-Ireland Pollinator Plan.

1.3. Agricultural landscapes

Agricultural intensification has been identified as a main driver of biodiversity decline worldwide. Since the Second World War, advances in mechanisation, chemical inputs, genetic research and new agricultural policies led to an intensification of agriculture systems (McLaughlin and Mineau, 1995; Robinson and Sutherland, 2002). As a result, the agricultural environment has undergone many modifications, leading to a simplification of landscape structure, with: (1) modern agriculture focusing on only a small number of crop species (providing a high yield) which dominate the landscape; (2) natural habitats have been converted into crop fields, with lower biodiversity; (3) fields have become larger with a removal of hedgerows to make the harvest easier and quicker (Fahrig et al., 2011; Robinson and Sutherland, 2002).

1.3.1. Irish landscapes

A long history of agricultural practices and policies created the current Irish landscape (Heritage Council and Teagasc). Currently, the eastern area of Ireland is more intensively

managed with arable crops and the west is more composed of small wet fields (Heritage Council and Teagasc). Ireland is endowed with a variety of habitats: arable fields, grasslands, hedgerows, streams, ditches, bogs, lakes, turloughs, rivers, native woodlands and also many maritime areas as Ireland has one of the longest coastlines of Europe (Heritage Council and Teagasc).

Over 60% of the Irish land (i.e. 4.3 million hectares) is devoted to agriculture and 10% to forestry. Most of this agricultural land is grass-based with 14.3 % of semi-natural habitats remaining (Sheridan et al., 2011), and 10 % dedicated to arable crops which occurred mainly in the east and south east (The Heritage Council, 2010).

1.3.1.1. Grasslands

In Ireland, grasslands are mainly “improved” (i.e. intensively managed or highly modified that have been reseeded and/or regularly fertilised and is now heavily grazed and/or used for silage making) with only a small proportion of grasslands classed as semi-natural (Fossitt, 2000; Martin et al., 2007).

The most widely used habitat classification in Ireland (Fossitt, 2000) categorised the improved grasslands into two classes: (1) improved agricultural grasslands (GA1) and (2) amenity grasslands (GA2); and the semi-natural grasslands into four categories: (1) Dry calcareous and neutral grasslands (GS1); (2) Dry meadow and grassy verges (GS2); (3) Dry humid acid grasslands (GS3); (4) Wet grasslands (GS4) (Fossitt, 2000). However, Sullivan et al. (2010) highlighted the importance of considering an intermediate category between improved grasslands and semi-natural grasslands. There is a range of grassland types in Ireland with a graduation of low, medium and high biodiversity. A wide range of fields will be classified using Fossitt (2000) as improved agricultural grasslands, but some are clearly less intensively managed. It is important to identify this intermediate category to allow a better evaluation of the habitat diversity in Ireland but also to monitor further intensification and biodiversity losses (Sullivan et al., 2010).

Dry calcareous and neutral grasslands (GS1), which occur as a result of low intensity agriculture and on free draining mineral soils of various depths, are important habitats for pollinators (Mullen, 2013). These grasslands are typically grazed by livestock (cattle, sheep and horses) and tend to be confined to the steep slopes of esker ridges and moraines in the midlands, and to other areas with shallow and rocky limestone soils (Fossitt, 2000).

1.3.1.2. Mass-flowering entomophilous crops

There are few entomophilous field crops grown in Ireland. The majority of pollinator-dependent species are orchard trees (e.g. apples) and soft fruits (e.g. strawberries, raspberries and blackcurrants). The main entomophilous field crop is oilseed rape (*Brassica napus*). Recently, in the context of tackling global climate change, the Irish Department of Agriculture, Food and the Marine promoted the introduction of bioenergy crops as an alternative fuel source. The main bioenergy crops growing in Ireland are cereals, hemp (annual crop), willow, miscanthus, reed canary grass (perennial crops) and oilseed rape (OSR) which is the most widely grown (CSO, 2012; Department of Communications Marine and Natural Resources, 2007).

Although oilseed rape has been grown in Ireland for many years, its popularity has increased in the past decade due to the increase in price and also because it is a good alternative crop to be integrated in the cereal rotation. Its roots can penetrate deeper in the soil than the cereal which improves the soil structure. There are two types of oilseed rape grown in Ireland depending of their sowing time: spring and winter oilseed rape. However the yields of these two crops are different with an average of 2.2 tonnes per hectare for the spring oilseed rape crop and 4.2 tonnes per hectare for the winter type (Teagasc, 2009).

1.3.1.3. Field margins and hedgerows

Field margins, and more specifically hedgerows, are an integral part of the agricultural landscape in Ireland and have a great importance for biodiversity as they provide food, nest sites, shelter, corridors for movement, and hibernation sites for fauna (Teagasc, 2004). Most of the Irish hedgerows were planted during the 1700's and 1800's as Acts of Parliament were passed requiring landowners to delimit their proprieties with hedgerows (Teagasc, 2004). Across Ireland, hedgerows are composed of 37 species of (native and non-native) shrubs and trees and 105 species of wild herbaceous flora. Hedgerows with the greatest variety of shrubs and trees are probably the oldest (Department of the Environment and Heritage and Local Government, 2007). In intensively managed agricultural landscapes, field margins and hedgerows are generally the only remnants of semi-natural habitat (Marshall and Moonen, 2002).

Currently hedgerows are threatened by agricultural intensification promoting the clearance of hedgerows for the development of land and the agricultural expansion (Department of the

Environment and Heritage and Local Government, 2007) and by the over-cutting of these hedgerows to prevent them growing out into the field and reducing the land available for food production (Natural England, 2007). This technique of management has negative impacts on biodiversity in general, and pollinators in particular, resulting in a loss of nesting sites and a reduction in food resource availability (The National Trust for Ireland, 2011). It is imperative to rethink about the management of hedgerows in the current context of biodiversity loss. Hedgerows are not a protected habitat in Ireland but they do have some protection. Under the Section 40 of Wildlife Act 1976, it is prohibited to cut or trim them from the 1st March to the 31st August.

1.4. Landscape structure

Landscape structure is defined by two components: its composition and configuration. Landscape composition is the number and the amount of the different habitat types, which can be measured inter alia by the proportion of specific habitat, or Shannon's diversity index. Therefore disturbance to landscape composition often leads to a habitat loss. Landscape configuration is the spatial arrangement of these landscape elements, which can be measured by mean patch size, edge density and mean patch shape variability. Disturbance to landscape configuration often leads to a habitat fragmentation (Fahrig et al., 2011; Hadley and Betts, 2012; Uuemaa et al., 2009). Figure 3 represents the two axes of landscape heterogeneity. Two landscapes with the same habitat type richness can have different configurational landscape heterogeneity (Figures 3 a and b): landscape (b) is more configurationally heterogeneous than landscape (a). Two landscapes with the same configuration can differ by their composition (Figures 3a and c). Landscape (c) is compositionally more heterogeneous. Therefore a complex landscape is characterised by a large variety of cover types and more complex spatial patterning of them (i.e. respectively a high compositional and configurational heterogeneity) (Fahrig et al., 2011).

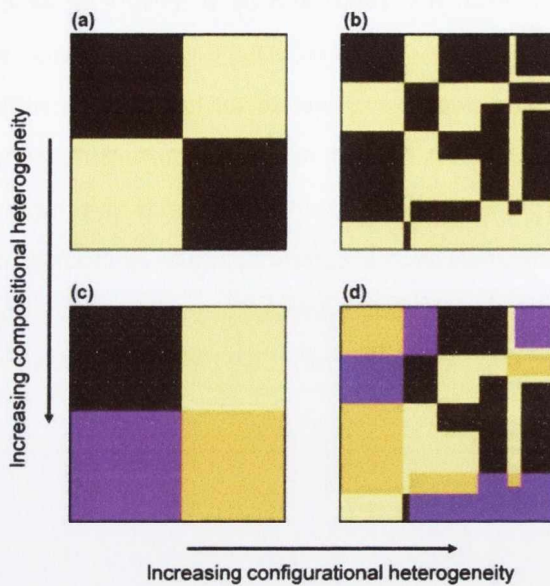


Figure 3: Illustration of the two major axes of landscape heterogeneity. Each large square represents a landscape and the different colours are the different cover types within the landscapes (Fahrig et al., 2011).

In addition to the landscape composition and configuration, habitat quality also defines the landscape. Processes of habitat degradation lead to the gradual deterioration of habitat quality which implies the same habitat type with a reduced level of resources and this can also affect the landscape structure (Mortelliti et al., 2010).

1.4.1. Methods to characterise the landscape and available resources

Current studies use different methods to characterise landscape structure. The interpretation of aerial images is one technique used to allow this characterisation (Dale et al., 1995). In this case, digitalisation of the landscape with Geographical Information System (GIS) software is required to store and represent the landscape. This approach is sometimes completed with information coming from national maps and/or some field work to refine the landscape characterisation (Goulson, 2010; Klein et al., 2012; Meyer et al., 2009; Perović et al., 2015; Stanley and Stout, 2013; Steckel et al., 2014; Steffan-Dewenter et al., 2002; Woodcock et al., 2013).

However land cover (LC) maps produced from remote sensing imagery are commonly used in ecological studies of the relationships between landscape and ecological processes (Lechner, 2010; Wiens, 2002). Datasets derived from satellite images have some disadvantages, such as insufficient resolution to define fine-scale landscape composition and configuration complexity for ecological investigations (Fahrig et al., 2011; McGarigal and Marks, 1995; Sullivan et al.,

2010; Tschardt et al., 2012). However, some advantages are also observed. They can be collected on large scale and for multiple time periods (Dale et al., 1995). Moreover, some of these land cover maps are freely available. That is the case of CORINE land cover (CLC) in Europe which is widely used for a range of ecological studies (Ambarli and Bilgin, 2014; Devictor and Jiguet, 2007; Power et al., 2012; Trichard et al., 2013; Vögeli et al., 2010).

1.4.2. CORINE

CORINE is the abbreviation of Co-Ordinated INformation of the Environment which is a program initiated by the European Commission (European Environment Agency, 1995) in 1985 with the ambition of compiling geospatial environmental databases for all the Member States using a common classification (Lydon and Smith, 2014). It focused on certain environmental topics that are priority for all the Member States to allow a planning policy at a national and European level (European Environment Agency, 1995; Lydon and Smith, 2014). CORINE Land Cover (CLC) is one of the environmental inventories undertaken through this program (Lydon and Smith, 2014).

CLC is based on Photo-Interpretation (PI) of false colour images obtained by satellites (European Environment Agency, 1995). The CLC is a vector map, i.e. based on polygons, with a working scale of 1:100,000 and a minimum map unit (MMU) of 25ha (European Environment Agency, 1995). It provides information on the biophysical cover of the earth's surface, categorising land cover into 44 classes built on a three level hierarchical classification (European Environment Agency, 1995).

Ireland took part to this program and produced firstly the CLC1990 for the whole island. This was undertaken by the cooperation between the Ordnance Survey of Ireland (OSI) and the Ordnance Survey of Northern Ireland (Lydon and Smith, 2014). This was based on data for 1989 and 1990 and allowed the creation of database in a GIS format with a similar nomenclature to the other European Member States at a scale of 1:100,000 (Environment Protection Agency). Subsequently other CLCs were produced i.e. CLC2000, CLC2006 and CLC2012. These following CLCs were managed by the Environmental Protection Agency (EPA) (Lydon and Smith, 2014). CLC2000 was produced by updating the CLC1990, by correcting the database and imagery for geometric and thematic content (considering new technologies and methodologies) and then producing a land cover database using satellite images and available geospatial data for the year 2000 (Environment Protection Agency). CLC 2000 included a level 4 and 5 for its two most abundant classes of level 3, i.e. pasture (231) and peat bogs (412), in

order to fit the national classification (Environmental Protection Agency, 2003). The most recent versions of CLC (2006 and 2012) abandoned this new level of classification and stayed with the common European level 3 of classification. CLC 2006 was built on a significant revision of the previous database (i.e. CLC 2000) (Lydon and Smith, 2014). The last update of CORINE land cover for Ireland is based on the reference year 2012 (CLC2012) (Lydon and Smith, 2014). The process of the production of the CLC2012 incorporated a more complete approach. Indeed a range of high resolution vector and raster databases (that were previously unavailable) were considered in the process of the CLC2012 production. However a process of generalisation was used to homogenize thematically and spatially these ancillary datasets in accordance with the CLC2012 level 3 classification and the 25ha MMU (Lydon and Smith, 2014). Thereby the CLC2012 was created in three steps: (1) preproduction, i.e. data acquisition and preparation, (2) data production, i.e. spectral analysis and photo interpretation of available data, updating of CLC2006 and detection of land cover change between 2006 and 2012 and (3) post-production, i.e. assembly of the data and error checking for the production of CLC2012 (Lydon and Smith, 2014).

CLC databases, as other maps derived from satellites images, should be used with caution. The transformation of the satellites images to these maps involves a series of mechanisms which affect the representation of the landscape and lead to some spatial inaccuracies (Lechner et al., 2013). For example, the minimum map units (MMU) of 25 ha, the thematic classification (i.e. same classes for all Europe) of these output maps can all lead to some error in the landscape representation (European Environment Agency, 1995).

1.5. Landscape and biodiversity

A landscape heterogeneous in compositional and configurational aspects has been considered to support higher biodiversity (Fahrig et al., 2011). It is hypothesised that a landscape with a higher compositional heterogeneity should support a higher species richness as specialist species have more chance of finding their specific resources (Benton et al., 2003) and for other species that need different types of resources for forage, nesting etc., a landscape composed of a higher number of habitat types will be favourable for them (Dunning et al., 1992; Flick et al., 2012). In a similar way, a higher landscape configurational heterogeneity should increase biodiversity because the resources necessary for each species will be found closer to each other and therefore will be easier to reach (Dunning et al., 1992; Flick et al., 2012).

1.5.1. Landscape and pollinator diversity

There is evidence that flower-visiting (pollinating) insects are affected by the landscape at different spatial scales as they are mobile and depend on the availability of flowers and nest sites over a scale of several kilometres (Hadley and Betts, 2012; Tscharntke et al., 2012). These insects need different types of resources to meet their vital needs throughout their lifecycle.

Flower-visiting insects visit in order to collect food resources from flowers. There are differences in the floral preferences between insect taxa, with different flower types attracting different visitors (Fenster et al., 2004). These insects also need many other resources for nesting, overwintering and mating sites (Gathmann and Tscharntke, 2002; Kremen et al., 2007). Bees can nest in a range of habitats including tunnelling in bare ground, using pre-existing cavities, in dead wood, rocks or rodent nests (Goulson, 2010; Kremen et al., 2007). The nesting preferences can be different between species. *Bombus lucorum* and *B. pratorum* nest in pre-existing underground cavities, habitually disused rodents burrows (Goulson, 2010). *Bombus terrestris* and *B. lapidarius* prefer to nest in open terrain and *B. lucorum* and *pascuorum* in forest boundaries (Svensson et al., 2000). Solitary bees can be cavity nesters or ground nesters (Cane et al., 2007; Krombein, 1967). Hoverflies use a range of different habitat types necessary for all the life stage including water bodies as the larvae of some species are aquatic (Speight, 2008). Finally butterflies need different habitat types at different life stage and each species has its own specific need (Bond and Gittings, 2008).

Landscape structure can determine the spatial and temporal distribution of all these resources (Kremen et al., 2007; Steffan-Dewenter et al., 2002). Relationships between landscape structure and pollinator diversity have been documented, but some specific aspects of the landscape have been investigated more largely than other leaving some parts of the relationships unclear. Most studies have generally focused on one specific landscape composition metric to characterise the landscape. However few studies have considered the landscape in its overall complexity with Kennedy et al. (2013) showing the first global quantitative synthesis about the effects of the landscape configuration in combination with the landscape composition on bees.

1.5.1.1. Landscape composition

The presence and abundance of specific habitats in the landscape have been shown to influence pollinator communities. Higher diversity of flower-visiting insects has been found in

landscapes with a higher proportion of semi-natural habitats or in crops grown into organic cultivation (Andersson et al., 2012; Holzschuh et al., 2008; Klein et al., 2012; Morandin and Winston, 2005; Morandin and Winston, 2006; Power and Stout, 2011; Rundlöf et al., 2008). Moreover, agri-environmental schemes (AES) may enhance pollinator species richness in landscapes composed of less than 20 % of semi-natural habitats (Batary et al., 2011). Scheper et al. (2013) showed that the responses of the pollinator community to the introduction of AES are also dependent of the landscape context. The introduction of AES was more beneficial in cropland located in simple landscapes, i.e. characterised by a low variety of cover types and less complex spatial patterning of them. Furthermore different pollinator taxa respond differently to the landscape structure. Different bee taxa respond differently to the landscape composition (Carré et al., 2009). Wild bee species richness and abundance were higher in landscapes with more high quality habitats (Kennedy et al., 2013). A higher bumblebees species richness and abundance were supported by landscapes with a higher proportion of grasslands in comparison with the arable (Rundlöf et al., 2008) and bumblebee densities increased with the availability in the landscape of mass flowering crops (i.e. oilseed rape crops) (Westphal et al., 2003). Nayak et al. (2015) found that bumblebee abundance was positively affected by the cover of semi-natural habitats. *Bombus muscorum* responded specifically to the landscape structure e.g. its occurrence increased in landscapes with a smaller number of trees, a greater proportion of arable lands and higher number of ditches (Diekötter et al., 2006). Higher solitary bee species richness has been found in landscapes composed of more semi-natural grasslands (Steffan-Dewenter et al., 2002; Woodcock et al., 2013). Landscapes with more diversity of habitats had greater butterfly diversity (Weibull et al., 2000). Hoverfly species richness increased in more well-connected landscapes and when there was higher landscape compositional heterogeneity (Burgio and Sommaggio, 2007; Meyer et al., 2009).

1.5.1.2. Linear features

Linear features are also important part of the landscape and may influence pollinators. For example, hedgerows are important for different reasons. Firstly, pollinating insects use hedgerows as nesting and foraging sites (Cranmer et al., 2012). The flowers of hedgerow plants provide food for these insects for much of the year. Secondly, linear features such as hedgerows allow pollinators to navigate between patches of resources (Cranmer et al., 2012). These features are independent of insects foraging needs and are directly related to the physical structure of the hedgerow in comparison to the surrounding habitats (Cranmer et al., 2012; Food and Agriculture Organization of the United Nations, 2012). These structures

influence the flight direction of pollinators and consequently can impact the plant reproductive success of the resource patches depending on their connections via linear features (Cranmer et al., 2012). Other linear features such as stone walls are an important part of the landscape in Ireland. However, to our knowledge no study to date has investigated their impact on pollinator communities.

1.5.1.3. Landscape configuration

Finally, very few studies have examined the effects of landscape configuration on pollinator diversity. Landscapes with more complex patch shapes have been shown to support a higher solitary bee species richness and lower hoverfly abundance (Bourke et al., 2013), whilst butterfly species richness is higher with a higher patch density in the surrounding landscape (Flick et al., 2012) and Perović et al. (2015) reports that lower mean patch size, combined with greater boundary area in the surrounding landscape, supports communities with more vulnerable butterfly species in managed grasslands. Kennedy et al. (2013) showed that the landscape configuration had little impact on the wild bee species richness and abundance.

1.5.1.4. Scale

Moreover differences in responses to landscape structure among taxa may be related to how mobile they are. Pollinating insects use floral resources and nesting/ovipositing sites over scales of several metres to several kilometres (Hadley and Betts, 2012; Tscharntke et al., 2012). It has been found that foraging distances can vary between each pollinator group and species: for example, up to several kilometres for the bumblebees with a variation between each species (Carvell et al., 2012; Knight et al., 2005), an average of 5.5 km for the honeybees (Beekman and Ratnieks, 2000), a maximum of 150 to 600 meters for the solitary bees (Gathmann and Tscharntke, 2002), and very variable for each butterfly species (Cant et al., 2005). Butterflies and hoverflies, unlike bees, are not central-place foragers reliant on returning to provision a nest, and butterfly species vary in the distances they travel (Cant et al., 2005). Little is known about hoverfly foraging distance but Wratten et al. (2003) showed that hoverfly movement can be restricted by barriers such as hedgerows in agricultural landscapes and that they can travel up to 250m to find forage (Cant et al., 2005). Thus the scale at which landscape structure is analysed can influence findings for different pollinating taxa.

1.5.2. Landscape and pollinator functional diversity

The effects of the landscape structure are not the same for all species because they are mediated by species' ecological traits (De Palma et al., 2015; Henle et al., 2004; Newbold et al., 2013). Pollinator species traits may influence the vulnerability of species to aspects of landscape composition and configuration. Only very few studies have started to explore this issue for pollinator communities (De Palma et al., 2015; Williams et al., 2010), but some theories have been discussed in terms of the response of species with particular functional traits to the landscape structure (Henle et al., 2004). For example, sensitivity to isolation from natural habitat should be lower for species with large flight distance (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Steffan-Dewenter et al., 2002). Moreover species with smaller niche breadth are expected to be more affected by habitat fragmentation. Species such as *Apis mellifera* with broad diet and long foraging distances should be less vulnerable with isolation from natural habitat than most solitary bees (Alford, 1975; Beekman and Ratnieks, 2000; Gathmann and Tscharntke, 2002; Steffan-Dewenter and Kuhn, 2003; Steffan-Dewenter et al., 2002). It has been reported that species which nest above ground were negatively affected by isolation from natural habitat and the agriculture intensification, in comparison with the species which nest below ground (Williams et al., 2010). In southern Germany, functional wild bee groups were affected differently by the landscape characteristics. Cuckoo bee richness was positively affected by the patch density in the landscapes and large social generalist species richness and abundance were positively related with the proportion of semi-natural grasslands in the landscape (Hopfenmueller et al., 2014). Moreover a recent study from De Palma et al. (2015) showed that some bee species functional traits (phenology, foraging range, niche breadth and sociality) influence responses to human dominated land use, with different responses among cropland, pastoral and urban habitats.

1.5.3. Landscape and plant pollinator interactions

Insect-flower interaction consists of interactions between communities of plants and insects which is generally a mutualistic relationship as insects visit flowers for food and in return insects carry pollen from one flower to another to allow seed set, fruit development and reproduction (Willmer, 2011). These ecological interaction networks can help us to understand the underlying structure of communities which generally inform on their stability and functioning (Tylianakis et al., 2007). These interactions have been studied using a food web approach (Memmott, 1999) and have been shown to be important to consider in conservation

measure (Kearns et al., 1998). The structure of the network can be measure with a range of qualitative and quantitative parameters which inform about the robustness and stability of the network (Dormann et al., 2009). Network structure has been shown to be affected by phenology, behaviour, physiology and relative abundance of species and thereby might be more informative than simple measures of biodiversity (species richness and abundance) to environmental changes (Tylianakis, 2008). Also changes in network structure might appear before loss in biodiversity and thereby might be good predictors to consider (Tylianakis, 2008).

It is well accepted that insect-flower interaction networks can be also affected by the landscape composition and configuration, but the landscape/pollinator diversity relationship has been studied less often (Ferreira et al., 2013). Moreira et al. (2015) showed that landscape structure affects the plant-pollinator network with a decrease of the nested characteristic of the network with the reduction of habitat quality and landscape heterogeneity. Moreover it has been shown that this network is sensitive to increasing urbanisation (Geslin et al., 2013). Vanbergen et al. (2014) showed that habitat modification caused by a long term livestock grazing alters the flower-insect interaction network and the plant mating system.

1.5.4. Landscape and the provision of pollination services

Landscape features can also affect pollination services. Intensification can cause a disruption of the abundance and composition of plants and pollinators (Sjodin et al., 2008; Steffan-Dewenter et al., 2001; Weibull et al., 2003), which in turn can affect pollination service delivery to both entomophilous crops and wild plants. Seed and fruit production have been shown to be restricted by pollen limitation in many systems (Ashman et al., 2004; Knight et al., 2005) due to an insufficient pollination service delivery, and so disruption of pollination could cause further pollen limitation, and thus reduced seed and fruit set. For example, higher pollination services are found in landscapes with a higher proportion of semi-natural habitats or in a farmland surrounding by more organic crops (in comparison with conventional agriculture) (Andersson et al., 2012; Klein et al., 2012; Morandin and Winston, 2005). An isolation from the natural or semi-natural habitats has an overall negative impact on crop pollination services (Ricketts et al., 2008). However such relationships between landscape structure and the provision of pollination services are poorly documented and focus mainly on crop species.

1.6. Research objectives

This thesis aims to improve our understanding of the impacts of the landscape structure on flower-visiting insect communities and on the provision of pollination services in Ireland. To address this main objective, a range of different methods and measures were used to characterise landscapes, insect communities and pollination services. In addition, insect communities and pollination service data were integrated from different habitat types within Ireland, and on a wider geographical scale. This general objective was addressed by determining:

- (1) How landscape composition and configuration affect the flower-visiting insect diversity and flower-insect visitor interaction network in semi-natural grasslands (chapter 2). For that, I characterised the landscape composition and configuration with a high-precision technique combining different methods (photo interpretation and field surveys) to allow a realistic representation of it. In this chapter, I looked at the relationships between landscape effects and the overall flower-visiting insect community and the different insect groups independently, as different groups can respond differently to landscape structure. By answering this question we wish to show (i) that structurally heterogeneous landscape supports a higher diversity of flower-visiting insect than structurally homogeneous landscape; (ii) that each insect group responds differently to the landscape structure and (iii) that the structure of the flower-insect visitor interaction network varies with the structure of the landscape.
- (2) How good is CORINE Land Cover 2012 to characterise the landscape structure in pollination studies (chapter 3). For that, I compared the landscape information obtained from the chapter 2 and the CLC2012. Moreover, results obtained from the landscape effects using CLC2012 on the insect community were compared with the outputs obtained from the chapter 2. In doing so, we hypothesised that there are some limitation in the use of CORINE Land Cover 2012 in pollinator studies due to the successive steps of the land cover maps production leading to spatial and thematic generalization.
- (3) How land use intensification and geographic location affects the taxonomic and functional community composition (beta-diversity) in bee communities visiting oilseed rape and coffee crops (chapter 4). We hypothesized that similar functional roles are observed in bee community composition in different geographic location. Moreover,

at smaller scales, land use intensification can also drive changes in taxonomic and functional composition and so the relationship between bee communities in crops and the distance to natural habitats was also investigated.

- (4) How the landscape structure affects the provision of pollination services in wild plants (chapter 5). For this, the landscape composition and configuration was related to the stigma pollen grain deposition of six plant species occurring in semi-natural grasslands and the seed set of two hedgerow species. We hypothesised that structurally heterogeneous landscape provides a higher provision of pollination services than homogeneous landscape.

Finally I synthesised the findings from these four data chapters, discussed them and suggested recommendations for future landscape management decisions and for future studies to reinforce our knowledge.

Chapter 2

Effects of scale and landscape structure on pollinator diversity and plant-pollinator interaction networks in semi-natural grasslands

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2. Effects of scale and landscape structure on pollinator diversity and plant-pollinator interaction networks in semi-natural grasslands

2.1. Abstract

During the past 50 years, technological advances and new agricultural policies have led to a simplification of landscape structure in many agricultural ecosystems. This has resulted in the loss and fragmentation of habitats for flower-visiting insects, which play an important ecological and economic role as pollinators of wild and cultivated plants. Semi-natural habitats, important for pollinator communities as they contain high diversity of flowering plants, are often lost in a landscape dominated by intensive agriculture. Although the distribution and amount of semi-natural habitats in a landscape is known to influence pollinator communities in landscapes dominated by arable agriculture, little is known about the impact of landscape structure on pollinator community and on insect-flower interaction network specifically occurring in semi-natural grasslands.

Species richness and abundance of four obligate flower-visiting insect taxa (solitary bees, bumblebees, butterflies and hoverflies) and insect-flower interaction network indices were quantified in surveys of 19 semi-natural grassland sites in the north midlands region of Ireland and related to the composition and configuration of the surrounding landscape at two scales (500m and 1km radius around sampling sites). Landscape structure was characterised by digitising landscape features identified by aerial photographs and GIS ground-truthed using field based surveys.

We found that a higher proportion of semi-natural grasslands, more complexity of patch shape and larger patch size in the surrounding landscape were positive for the overall flower-visiting insect species richness and abundance at the two scales. Landscape structure and the length of stonewalls in the landscape both had both strong relationships with network structure. At 1km scale, a higher proportion of semi-natural grasslands combined with larger patches and greater complexity of patch shape improved the robustness of the network, but at 500m scale, network properties were influenced positively by the length of stonewalls.

These findings can inform landscape management measures to facilitate the conservation of the overall pollinating insect community in areas characterised by a less intensive grass-based agricultural system. Both linear features and landscape structure are important and should be considered in these measures.

2.2. Introduction

Since the Second World War, technical advances and agricultural policies have led to an intensification of agriculture in Western Europe (McLaughlin and Mineau, 1995; Robinson and Sutherland, 2002). As a result, the agricultural environment has become simplified and landscape structure, in terms of its composition and configuration, has become homogenised (Fahrig et al., 2011; McLaughlin and Mineau, 1995; Robinson and Sutherland, 2002). A more heterogeneous landscape is characterised by a large diversity of cover types (compositional heterogeneity) and more complex spatial patterning of them (configurational heterogeneity) (Fahrig et al., 2011). This may influence biodiversity in agricultural landscapes (Fahrig et al., 2011), and it has been hypothesised that a higher heterogeneity of landscape composition should support more species as specialists have more chance of finding their specific resources (Benton et al., 2003), and generalists or those needing different types of resources for forage, nesting etc., will also be favoured in a landscape composed of more habitat types (Dunning et al., 1992; Flick et al., 2012). In a similar way, greater landscape configurational heterogeneity should increase biodiversity because the resources necessary for each species will be found closer to each other (more connectivity in the surrounding landscape) and therefore will be easier to access (Dunning et al., 1992; Flick et al., 2012; Goodwin and Fahrig, 2002).

Pollinators and the pollination services they provide are essential in natural and agricultural ecosystems (Food and Agriculture Organization of the United Nations, 2013; Klein et al., 2007) as they enhance seed and fruit set in many wild and crop plants (Ollerton et al., 2011). It has become increasingly recognised that pollinator abundance and community composition can be influenced by landscape composition and configuration (Hadley and Betts, 2012). The majority of the research to date has studied the effects of habitat isolation or habitat fragmentation of suitable habitat in a matrix of non-suitable habitat on pollinators and pollination (Brittain et al., 2010; Krauss et al., 2003; Lentini et al., 2012; Ricketts, 2001; Steffan-Dewenter, 2003; Steffan-Dewenter et al., 2006). One important finding is that more pollinator species are found in a landscape with more semi-natural habitats or in farmland surrounded by more organically grown crops (Andersson et al., 2012; Holzschuh et al., 2008; Kennedy et al., 2013; Klein et al., 2012; Morandin and Winston, 2005; Morandin and Winston, 2006; Rundlöf et al., 2008) as these habitats provide an abundance of different resources. Moreover, it had been shown that different pollinator taxa can respond differently to the landscape structure (Sjodin et al., 2008) as each pollinator has their own specific need. Although most studies have focused on how

landscape composition affects pollinators, others have examined landscape configuration (Kennedy et al., 2013) and found contrasting relationships with different pollinator groups. Landscapes with more complex patch shapes support higher solitary bee species richness and lower hoverfly abundance (Bourke et al., 2013), butterfly species richness is higher with smaller patches in the surrounding landscape (Flick et al., 2012) and Perović et al. (2015) reports more vulnerable butterfly species in managed grasslands surrounding by this specific landscape configuration. Other features of the landscape may also influence pollinators, for example linear features are used by pollinating insects as nesting and foraging sites (Cranmer et al., 2012; Dover et al., 2000), and allow pollinators to navigate between patches of resources (Cranmer et al., 2012).

Differences in responses to landscape structure among taxa may be related to how mobile they are. Pollinating insects use floral resources and nesting/ovipositing sites over scales of several metres to several kilometres (Hadley and Betts, 2012; Tschardt et al., 2012). Foraging distances can vary between pollinator taxa with bumblebee species foraging between several hundred metres up to several kilometres from their nest (Carvell et al., 2012; Knight et al., 2005). Honeybees can forage up to an average of 5.5 km from their nest (Beekman and Ratnieks, 2000) and solitary bees may fly 150 to 600 meters to forage (Gathmann and Tschardt, 2002). Greenleaf et al. (2007) suggested greater maximum foraging distances for the bee group and showed the dependence of the foraging distances with the body size. Butterflies and hoverflies, unlike bees, are not central-place foragers reliant on returning to provision a nest, and butterfly species vary in the distances they travel (Cant et al., 2005). Little is known about hoverfly foraging distance but Wratten et al. (2003) showed that hoverfly movement can be restricted by barriers such as hedgerows in agricultural landscapes and that they can travel up to 250m to find forage (Cant et al., 2005). Thus the scale at which landscape structure is analysed can influence findings for different pollinating taxa. Moreover, foraging distances are very context dependent, varying with environmental parameters such as the density and distribution of floral resources (Greenleaf et al., 2007).

The way in which insects respond to landscape structure can have knock-on consequences for the interactions between plants and their pollinators (Ferreira et al., 2013). It has been recognised that network pattern are important for our understanding of biodiversity organisation and persistence (Bascompte, 2009) and biotic interaction may affect the resilience of ecosystems to landscape changes (Montoya, 2008). Characteristics of the network such as the asymmetry and nested structure can make the network more robust to changes

(Bascompte et al., 2006; Memmott et al., 2004). Ferreira et al. (2013) highlight a lack of research on the effects of landscape changes on plant-pollinator network and insists on the urgent need to develop research on this topic.

Most of the landscape scale research to date has focused on pollinator communities occurring in orchard, arable land and intensively managed grasslands (Andersson et al., 2012; Holzschuh et al., 2008; Klein et al., 2012; Morandin and Winston, 2006; Power and Stout, 2011; Rundlöf et al., 2008). Thus we focused our study on semi-natural grasslands in areas characterised by a less-intensive agricultural system. Semi-natural grasslands harbour a high diversity of plant species and are an essential habitat type for the pollinator community (Aavik and Liira, 2009; Carvell, 2002; Erhardt, 1985; Williams, 1988). Whilst it is well accepted that a high proportion of semi-natural habitats in intensive agricultural landscapes is beneficial to the pollinating insect community, little is known of how insect pollinator communities of semi-natural grasslands located in less-intensive agricultural area are influenced by landscape structure.

The objective of this research was to study the effects of scale and landscape composition and configuration on insect flower visitor diversity and insect-flower interaction networks in semi-natural grasslands in the north midlands of Ireland, in an area characterised by a less-intensive agricultural system. The impact of surrounding landscape composition and configuration (up to 1km from sampling sites) was studied for the overall flower-visiting insect community. Additionally, to determine whether there are group-specific patterns, these relationships were also studied for each insect group independently. Moreover the effect of landscape structure was also studied on the insect-flower interaction network. We hypothesised that (1) semi-natural grassland habitats in structurally heterogeneous landscapes support higher pollinator species richness and abundance than in homogeneous landscapes, and each insect pollinator group responds differently to the landscape structure: some pollinator groups such as butterflies, solitary bees and bumblebees might be more sensitive to the presence of flower-rich grasslands as they need different plant resources for their life cycle (Erhardt, 1985; Erhardt and Mevi-Shutz, 2009) or have been seen from previous studies to be related positively with semi-natural habitat (Kennedy et al., 2013; Nayak et al., 2015; Rundlöf et al., 2008; Steffan-Dewenter et al., 2002; Woodcock et al., 2013). Other groups such as hoverflies might be more related to a higher landscape compositional heterogeneity as they need a range of micro and macro habitats for larvae and adults (Meyer et al., 2009), (2) that the scale at which landscape structure affects each insect pollinator group in semi-natural grasslands is different due to their differences in size, mobility and life history; we should expect distances up to several

kilometres for the bumblebees and honeybees; few hundred meters for the solitary bees and hoverflies and very variable for the butterfly group, and (3) that the structure of insect-flower interaction networks varies with landscape composition and configuration: responses of the pollinator communities to the landscape structure should give information on their impacts on the structure of the network.

2.3. Materials and Methods

2.3.1. Study sites

This study was conducted in the north midlands region of Ireland in the Counties of Roscommon and Offaly which are characterised by a less-intensive agricultural system. Nineteen sites were selected representing a range of grassland types (Figure 4, Appendix 1 and 2). Fifteen were semi-natural dry calcareous and neutral grasslands sites (GS1, according to the Irish national habitat classification (Fossitt, 2000)) and the rest were semi-improved grasslands (GA+) containing patches of semi-natural dry calcareous and neutral grasslands (GS1). They were chosen to represent a range of flowering plant species richness and to be as similar as possible in their management regime (with no or minimal fertilizer input, not mowed but all grazed). The flowering plant species richness per site varied from 12 to 30. The sites were from 1.6 km to 75 km apart.

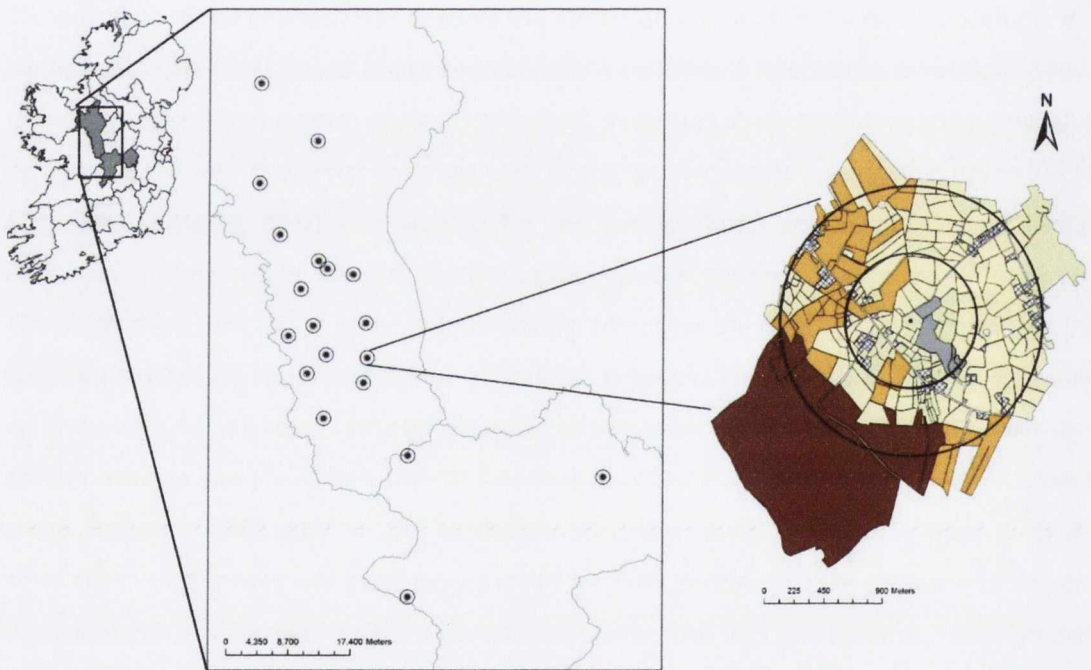


Figure 4: Location of 19 sampling sites in the counties of Roscommon and Offaly (shaded grey) in the north midlands of Ireland. The fields sampled are at the centre of the circles and an example of the surrounding landscape from one site is shown. The two scales studied, i.e. 500m and 1km, are represented by the two concentric circles centred on each sampling site.

2.3.2. Transect sampling

Insect data collection was carried out during 2010 (from late May to late August) and 2011 (from early June to late August; the later start was due to unfavourable weather condition in May). Each year, sampling was conducted in each site once in each of three periods i.e. early summer (May/June); mid-summer (July) and late summer (August) (a total of six surveys per site over the two years). Insect surveys were conducted on dry days, with mean temperature $\geq 10^{\circ}\text{C}$ and wind speed $\leq$ Force 5 on the Beaufort scale. When the weather and time permitted it, two sites were sampled per day, one in the morning and one in the afternoon. Where a site was sampled in the morning on one sampling occasion, it was sampled in the afternoon during the next in order to reduce temporal bias (Mullen, 2013).

In each site, a transect of 250m by 2m was established, divided into 10 equal subunits of 25 m in a zigzag pattern, and walked at a slow steady pace, taking 5 minutes per subunit (50 minutes per transect). In 2011 the transect length was increased to 300m by the addition of two 25m subunits as species accumulation curves in 2010 had not saturated. This made a total walking time per transect of 60 minutes in 2011. On each sampling occasion, all the solitary bee, bumblebee, hoverfly, butterfly and honeybee individuals visiting flowers were recorded along the transect. Flower-visiting insects were identified in the field when possible and if not, frozen in plastic vials and identified later in the laboratory. Hoverflies of the genus *Shaerophoria* were grouped because it was difficult to identify them to species. The flowering plant species on which each flower visitor was foraging was also recorded (Mullen, 2013).

2.3.3. Landscape characterisation at different spatial scales

Around each site, a multi-scale sampling design was set up. Circles of two radii (500m and 1km) were centred on each pollinator sampling site. Pollinators can travel distance from few hundred meters to few kilometres (Greenleaf et al., 2007; Hadley and Betts, 2012; Tscharrntke et al., 2012). Therefore it would be better to characterise the landscape at varying scales up to few kilometres. However, our objective is also to have a landscape which is characterised with a high precision (see details below). According to the resources available for this study, it seems to us more reasonable to characterise the landscape up to 1km. A circle was used in this case as it considers all the landscape elements at an equal distance from the centre of the sampling field. Each landscape element (i.e. each polyline and polygon) was digitised from aerial photographs (Bing Maps and Ordnance survey Ireland (OSI)) with ArcGIS v10. The landscape polygons that partially overlapped with the circle were considered in their entirety

for the landscape configuration analyses. Each landscape element was initially identified by aerial photograph observations and ground truthed with fieldwork according to the Fossitt habitat classification (Fossitt, 2000) and by interviewing farmers.

To provide an overall measure of the landscape structure, different landscape metrics were calculated. All these calculations were made with Patch Analyst 5.1.0.0, an extension of the ArcView GIS system that facilitates the spatial analysis of landscape elements, and were calculated for each of the 19 landscapes. The metrics that characterised landscape configuration and composition were: Shannon Diversity Index (SDI), Shannon Evenness Index (SEI), Area Weighted Mean Shaped Index (AWMSI), Mean Shape Index (MSI), Mean Patch Fractal Dimension (MPDF), Area Weighted Mean Patch Fractal Dimension (AWMPDF), Total Edge (TE), Edge Density (ED), Mean Patch Size (MPS), Number of Patches (NumP), Median Patch Size (MedPS), the landscape proportion of each habitat type and the total length of each linear feature (Appendix 3). The different habitats found in the landscape surrounding the sampling sites are shown in Appendix 4.

2.3.4. Data analysis

Insect species accumulation curves were constructed for each site to determine if saturation was reached or if further sampling at sites would have obtained a greater number of species (Mullen, 2013).

Insect species richness and abundance were pooled by site and per year for all analyses and the factor year (2010 or 2011) was included. The species richness and abundance of the four insect groups (i.e. bumblebee, butterfly, hoverfly and solitary bee) were considered separately. The overall insect (i.e. bumblebee, butterfly, honeybee, hoverfly and solitary bee) and, separately, total bee species richness and abundance were also considered, to enable an overall understanding of the effects of landscape scale on the overall flower-visiting insect community in general, and on bees in particular.

Moreover, we calculated a range of parameters to characterise insect-flower interaction networks using the network level command of the bipartite package (Dormann et al., 2009) in R 3.0.1. Matrices representing the total number of insects of each species visiting each plant species were created by pooling data from all three sampling periods for each site each year. We calculated both qualitative (based on the presence or absence of link i.e. on binary network (Bersier et al., 2002; Dormann et al., 2009)) and quantitative (based on a measure of

interaction strength by involving information on the number of interaction for each link (Bersier et al., 2002; Dormann et al., 2009)) network parameters, including: number of plants (qualitative), connectance (qualitative), nestedness (qualitative), weighted linkage per pollinator (quantitative), complementary specialization (H2') (quantitative), linkage density (quantitative) and weighted linkage per plant (quantitative) (Appendix 5). We calculated these network parameters to have the most complete representation of the network complexity, specialisation and asymmetry. We converted the nestedness value by calculating its inverse, i.e. 1-nestedness. This allows us to have a value which increases with the nested structure of the network. We used this 1-nestedness throughout this study.

To evaluate the impacts of overall landscape structure on pollinating insect species richness and abundance and insect-flower interaction network parameters, we reduced the number of landscape metrics in the models using "Variances Inflation Factors" (VIFs) to assess which variables were highly correlated, and thus removed from the analysis (Zuur et al., 2007). Before including landscape variables in the process of the VIFs tool, some habitat type variables had to be excluded due to their high (>65 %) number of zero values. Thus only two habitat types were considered: GS1 (dry calcareous and neutral grasslands) and GA1 (improved agricultural grasslands), which were the two most abundant habitats and have ecological relevance for pollinators. Additionally to the VIFs tool, the variables retained were chosen also for ecological relevance and to allow possible comparison between the two scales studied. All the metrics with VIFs under 4 were considered, thus at the two scales we included: SEI, AWMSI, MPS and %GS1. At 500m and 1km scales, SEI was negatively correlated with %GA1 (improved agricultural grassland) and MPS was negatively correlated with AWMPFD, ED, NumP and positively correlated with %GS4 (wet grasslands) and %PB1 (raised bogs) (see Appendix 6).

To complete this study, the effects of two linear features (total length of hedgerow (WL1a) and the total length of stone walls (BL1)) on flower-visitor diversity and insect-flower interaction network indices were also analysed.

To assess the landscape structure (and linear features) and scale effects on flower-visiting insect species richness and abundance and network indices, Generalised Linear Models (GLM) with a Poisson distribution were used when the response variables were discrete (count data); a negative binomial distribution was used to deal with overdispersion (Zuur et al., 2007); and a Gaussian error distribution was used for some network indices that were continuous (i.e. connectance, nestedness, weighted linkage per insect, weighted linkage per plant, linkage density and H2'). Year was included as a fixed factor. All these models were simplified by

selecting the optimal model that included the landscape parameters that best explained the data using Akaike Information Criteria (AIC). Separate models were run for each scale (500m and 1km). Once the model was chosen, data were checked for homogeneity, independence, influential observations, and normality by plotting residuals vs. fitted values (Zuur et al., 2007). The four assumptions were verified in greater than 95% of models. Network size was considered as an additional covariate in the models that tested the landscape scale effects on all the network indices (except for the total number of insects and flowers) since some network structure parameters are sensitive to network size (Bengtsson, 1994; Dormann et al., 2009).

2.4. Results

2.4.1. Pollinator species richness and abundance

Species accumulation curves did not fully saturate at any of the sites (Mullen, 2013). A total of 1584 insects were observed in all sites over 2 years (733 in 2010 and 851 in 2011), comprising 78 insect species (59 in 2010 and 60 in 2011) (Appendix 7). The number of insect species ranged from 5 – 24, with 8 to 106 individuals, per site per year. Bumblebees (up to 7 species) and hoverflies (up to 14 species) were found in all sites in 2010 and 2011. But solitary bees and butterflies (a maximum of 4 species of each per site) were only seen in a subset of sites during the sampling period (Appendix 8).

2.4.2. Plant pollinator interaction networks

The total number of plant species in the network per site varied from 3 to 15 in 2010 and from 6 to 17 in 2011. The realised proportion of possible links in the network (connectance) per site ranged from 0.11 - 0.39. Networks were on average less nested in 2010 than 2011. Weighted linkage per insect per site ranged from 1 - 4.24 and weighted linkage per plant varied from 1.250 - 6.57. The specialisation of the network ($H2'$) ranged from 0.13 to 1. Finally linkage density, a diversity index, showed a range of values from 1.78 to 4.39 (Appendix 9).

2.4.3. Landscape characterisation

The landscape compositional heterogeneity calculated, inter alia, by the Shannon Evenness Index (SEI), was variable with a maximum value of 0.87 (Table 1, Figure 5a & b, Figure 6a & b). The landscape configurational heterogeneity calculated by Area Weighted Mean Shape Index (AWMSI) was >1 indicating relatively complex patch shapes (Table 1, Figure 5c & d, Figure 6b & c). Landscapes were dominated by improved agricultural grasslands (GA1), followed by dry calcareous and neutral grassland (GS1) and semi-improved agricultural grasslands (Table 1). The two most common linear feature types in the landscape were hedgerows and stone walls (Table 1).

Table 1: Mean, minimum and maximum values of the landscape composition and configuration metrics calculated at the 500m and 1km scales.

	500 m			1 km		
	Mean (±se)	Maximum	Minimum	Mean (±se)	Maximum	Minimum
Shannon Evenness Index (SEI)	0.65 (±0.03)	0.87	0.34	0.55 (±0.03)	0.80	0.27
Area Weighted Mean Shape Index (AWMSI)	1.36 (±0.02)	1.61	1.21	1.38 (±0.03)	1.78	1.28
Mean Patch Size (MPS)	2.50 (±0.41)	7.41	0.87	2.06 (±0.24)	4.90	1.17
% improved agricultural grasslands (GA1)	45.05 (±4.65)	86.70	15.76	55.47 (±5.03)	87.78	14.77
% semi-improved grasslands (GA+)	16.59 (±3.45)	59.13	0.00	10.57(±2.09)	29.12	0.00
% dry calcareous and neutral grasslands (GS1)	21.44 (±4.31)	63.09	0.00	11.48 (±3.03)	46.95	0.00
Stonewall length (BL1)	5034.12 (±825.04)	14329.49	0.00	16861.26 (±2807.67)	42915.25	0.00
"Natural" hedgerow length (WL1a)	3206.19 (±356.77)	5685.76	423.49	16025.31 (±1430.69)	31426.16	4877.75

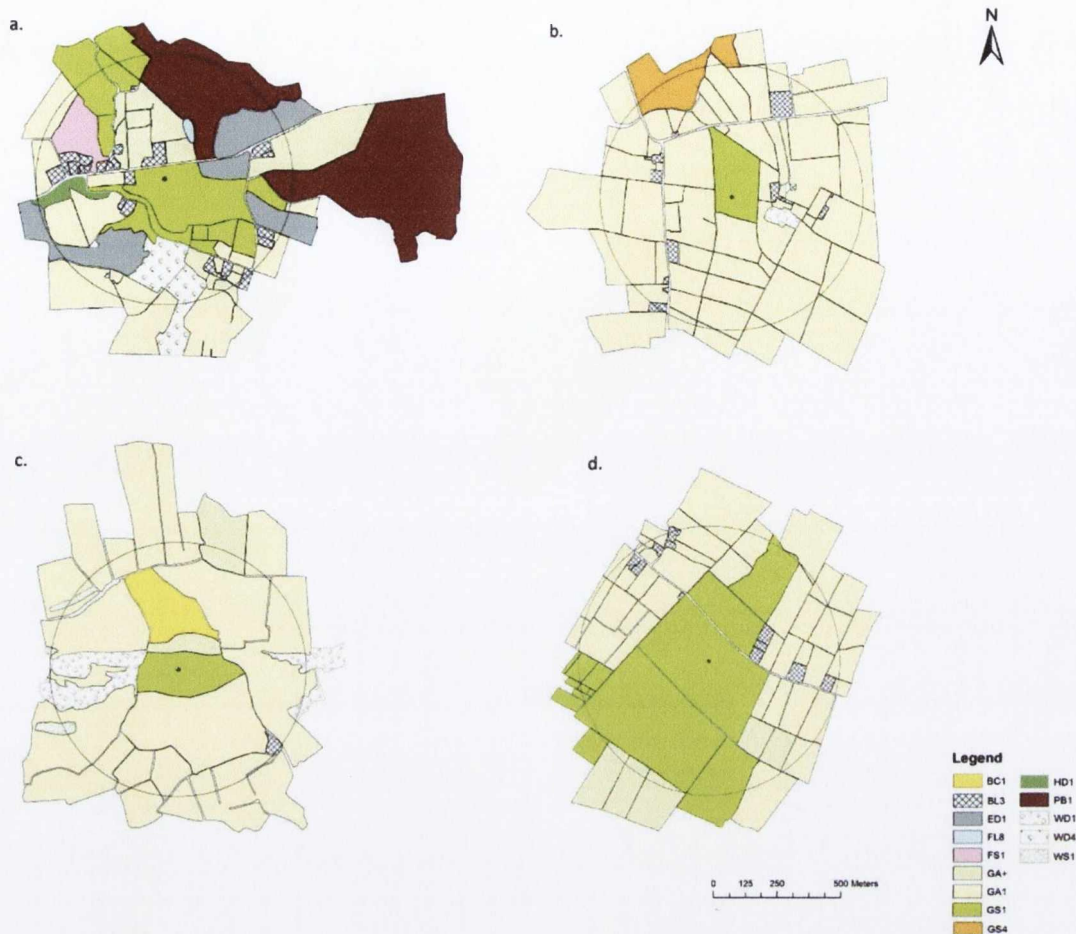


Figure 5: Selected landscapes at 500 m scale illustrating the landscape compositional and configurational heterogeneity. The landscape composition is measured inter alia by Shannon Evenness Index (SEI) which is a measure of the habitat diversity. Figure (a) represents the highest compositional heterogeneity (Castlesampson $SEI_{500m}=0.873$) and (b) the lowest compositional heterogeneity (Knockrogherry $SEI_{500m}=0.344$). The landscape configurational heterogeneity is measured inter alia by the Area Weighted Mean Shape Index (AWMSI) which is a measure of the complexity of the patch shape in the landscape. Figure (c) represents the highest configurational heterogeneity (Ballyduff $AWMSI_{500m}=1.614$) and (d) the lowest configurational heterogeneity (Turrock $AWMSI_{500m}=1.206$) (BC1: arable crops, BL3: artificial surfaces, ED1: exposed sand gravel or till, FL8: other artificial lakes and ponds, FS1: reed and large sedge swamps, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands, GS4: wet grasslands, HD1: dense bracken, PB1: raised bog, WD1: mixed broadleaved woodland, WD4: conifer plantation and WS1: scrub).

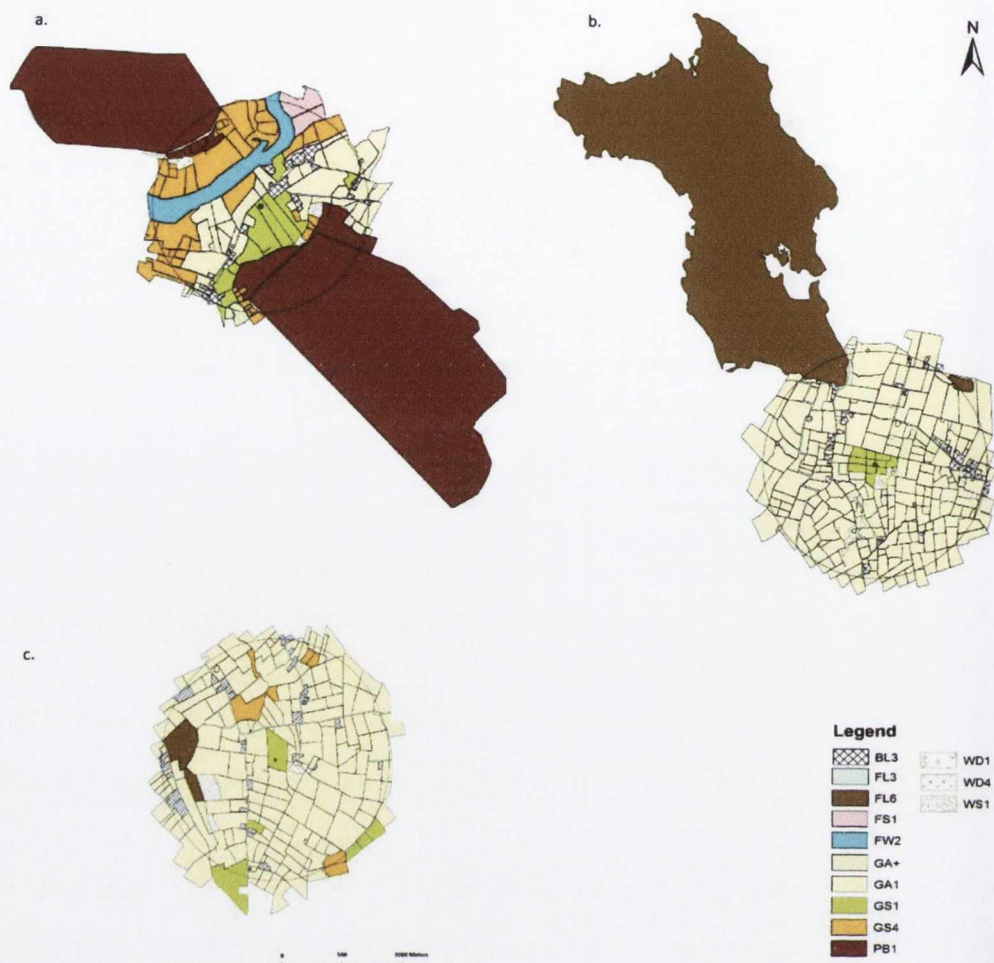


Figure 6: Selected landscapes at 1 km scale illustrating the landscape compositional and configurational heterogeneity. The landscape composition is measured inter alia by Shannon Evenness Index (SEI) which is a measure of the habitat diversity. Figure (a) represents the highest compositional heterogeneity (Clonmacnoise $SEI_{1km}=0.796$) and (b) the lowest compositional heterogeneity (Ardmullen $SEI_{1km}=0.274$). The landscape configurational heterogeneity is measured inter alia by the Area Weighted Mean Shape Index (AWMSI) which is a measure of the complexity of the patch shape in the landscape. Figure (b) represents the highest configurational heterogeneity (Ardmullen $AWMSI_{1km}=1.783$) and (c) the lowest configurational heterogeneity (Knockrogherry $AWMSI_{1km}=1.275$) (BL3: artificial surfaces, FL3: limestone and marl lakes, FL6: turlough, FS1: reed and large sedge swamps, FW2: depositing lowland rivers, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands, GS4: wet grasslands, PB1: raised bog, WD1: mixed broadleaved woodland, WD4: conifer plantation and WS1: scrub).

2.4.4. Landscape structure and scale effects

At the 500m scale, SEI had no relationship with any of the insect variables, but at the 1km scale, it was negatively related to overall insect species richness and abundance (Figure 7a), and with hoverfly abundance (Table 2). All other significant relationships between landscape and insects were positive, with mean patch size and %GS1 having the most significant relationships with insect variables (Figure 7b-d, Table 2). Bumblebee abundance increased

with the proportion of semi-natural grasslands (%GS1) in the landscape at the 1km scale, but neither species richness nor abundance of bumblebees were related to any of the other landscape variables.

At the 1 km scale, AWMSI had a positive relationship with the abundance of bee and butterfly, but at 500m scale, the abundance of butterflies and the species richness of all insects (Figure 7b), hoverflies and butterflies increased with AWMSI. At 500m and 1km scales, insect species richness (Figure 7c) and hoverfly species richness and abundance increased with MPS. Additionally at 1km scale, insect abundance, bee species richness, solitary bee species richness, and butterfly species richness and abundance were positively correlated with MPS. At the two scales studied, %GS1 had a positive relationship with all insect (Figure 7d), solitary bee, and hoverfly species richness and abundance, and bee species richness and abundance. At the 1 km scale only, %GS1 had a positive relationship with butterfly species richness and abundance. Insect species richness, and hoverfly species richness and abundance were significantly different between years at 500m and 1km scales. At the 500m scale only, solitary bee abundance was significantly different between 2010 and 2011.

Table 2: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (Shannon Evenness Index, Area Weighted Mean Shape Index, Mean Patch Size, proportion of semi-natural grasslands and factor Year). Significant results are showed by differing arrows. Arrow directions (↗↘) represent respectively positive and negative relationships. Smaller and thinner arrow represent a *p-value <0.05, medium arrows a **p-value <0.01 and bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best models (i.e. the model with the lowest AIC).

Response variables	500m					1km				
	Landscape metrics				Factor	Landscape metrics				Factor
	SEI	AWMSI	MPS	%GS1		SEI	AWMSI	MPS	%GS1	
Insect Species richness	↗	↗	↗	↗	↗	↘		↗	↗	↗
Insect abundance			NS	↗		↗		↗	↗	NS
Bee species richness				↗		NS		↗	↗	
Bee abundance				↗			↗		↗	
Bumblebee species richness						NS				
Bumblebee abundance				NS		NS	NS		↗	
Solitary bee species richness		NS		↗	NS			↗	↗	NS
Solitary bee abundance	NS	NS		↗	↗				↗	NS
Hoverfly species richness		↗	↗	↗	↗	NS	NS	↗	↗	↗
Hoverfly abundance	NS	NS	↗	↗	↗	↘	NS	↗	↗	↗
Butterfly species richness	NS	↗						↗	↗	
Butterfly abundance		↗		NS	NS		↗	↗	↗	

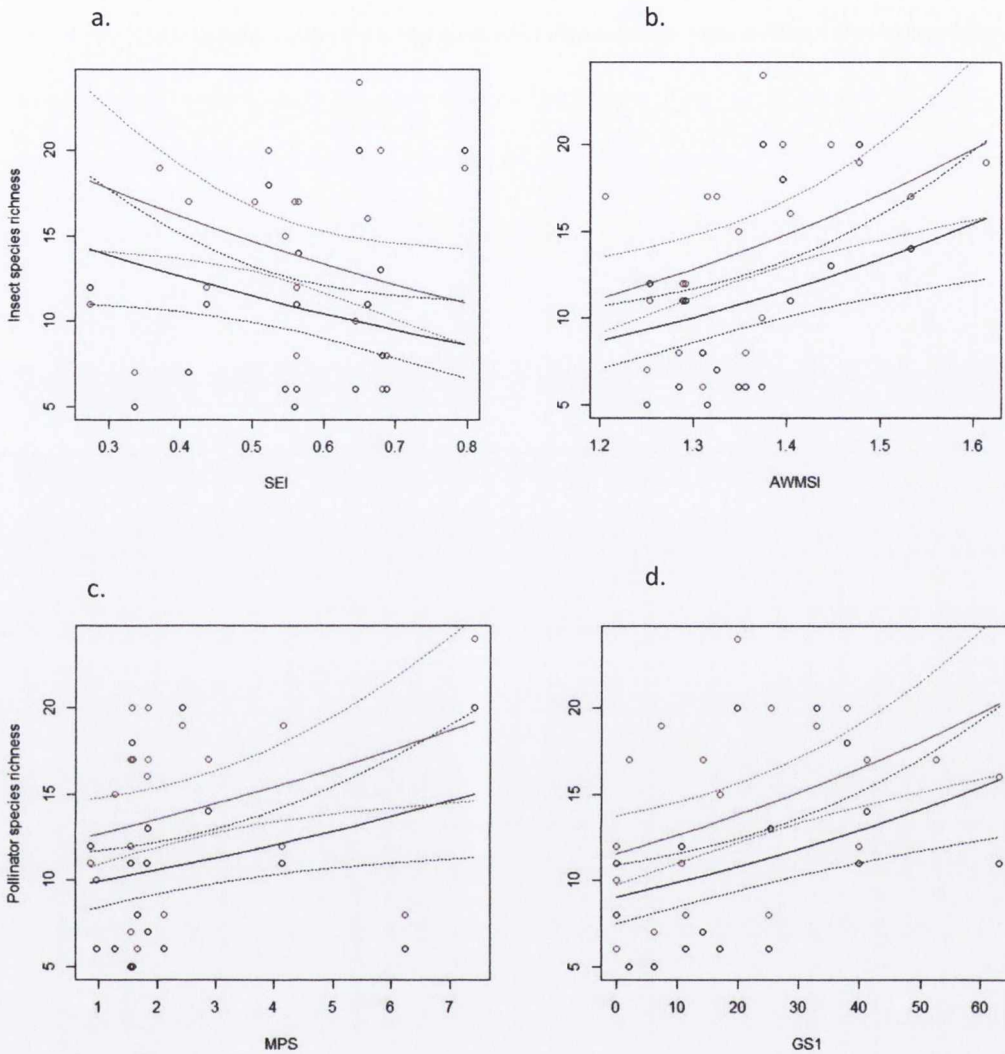


Figure 7: Main effects of the landscape metrics on the insect species richness from the best model (i.e. model with the lowest AIC) at a) 1km scale, and b) c) and d) at the 500m scale. Points represent observed values. The lines characterise the model predictions and dotted lines the 95% confidence intervals. The different colours symbolize the two years (black: 2010 and red: 2011). All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.

Network indices varied in their relationships with the landscape metrics (Table 3). SEI showed only a negative relationship with linkage density at 1km scale (Figure 8a). All the significant relationships with the other three landscape metrics (AWMSI, MPS and %GS1) were positive. At 500m scale, AWMSI was related to the number of plant species and at 1km scale with 1-Nestedness (Figure 8b). MPS was also related to the number of plant species, linkage density and weighted linkage per plant species, but only at the 1km scale (Figure 8c). Number of plant species showed a significant relationship with %GS1 at 500m and 1km scale and %GS1 is positively related with linkage density at 1km scale (Figure 8d). Connectance, 1-Nestedness,

weighted linkage per insect species, linkage density, $H2'$ and weighted linkage per plant species were related to network size at the 500m and 1km scales. At the 500m and 1km scales, number of plants species was significantly different between 2010 and 2011.

Table 3: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (number of plant species, number of insect species, connectance, nestedness, weighted linkage per insect species, H2', linkage density and weighted linkage per plant species) and the explanatory variables (Shannon Evenness Index, Area Weighted Mean Shape Index, Mean Patch Size, proportion of semi-natural grasslands and factor year). Network size was considered as an additional covariate in the models that tested the landscape size effects on all the network indices (except for the number of plants species) since some network structure parameters are sensitive to network size. Significant results are shown by differing arrows indicating trends. Arrow directions (↗ ↘) represent respectively positive and negative relationships. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a **p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. model with the lowest AIC).

	Response variables	500m						1km					
		Landscape metrics			Network			Landscape metrics			Network		
		SEI	AWMSI	MPS	% GS1	Size	Factor Year	SEI	AWMSI	MPS	% GS1	Size	Factor Year
Qualitative Parameters	Number of plant species		↗		↗	/	↗			↗	↗	/	↗
	Connectance					↗						↗	
	1-Nestedness					↗			↗			↗	
Quantitative Parameters	Weighted linkage per insect species			NS		↗						↗	
	H2'			NS		↗						↗	
	Linkage Density					↗				↗	↗	↗	
	Weighted linkage per plant species	NS				↗	NS		NS	↗	NS	↗	NS

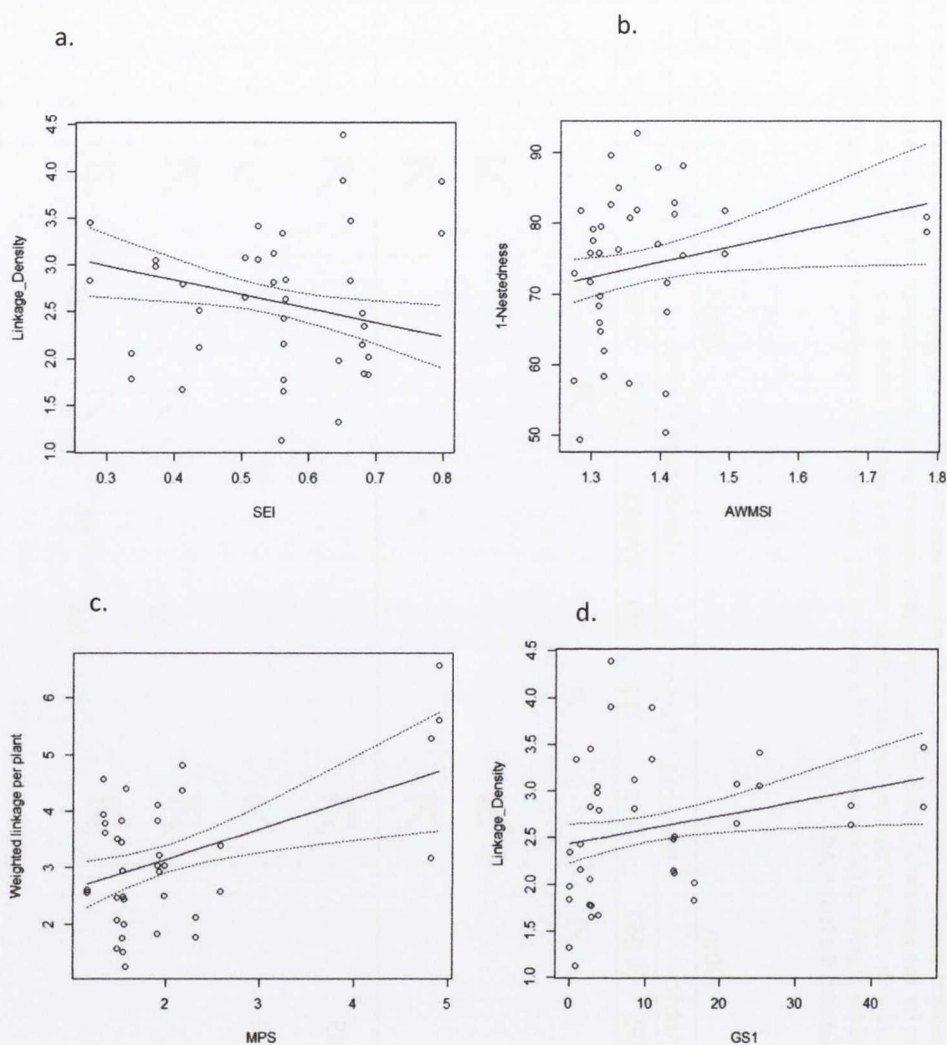


Figure 8: Main effects of the landscape metrics on network indices from the best model (i.e. model with the lowest AIC) for (a) the relationship between the linkage density and SEI (b) between the 1-nestedness and AWMSI, (c) weighted linkage per plant and MPS and (d) linkage density and GS1 at 1km scale. Points represent the observed values. Lines characterise the model predictions and dotted lines the 95% confidence intervals. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.

2.4.5. Linear feature length effects

Stonewall length was related to each of the insect groups differently (Table 4). Insect species richness had a negative relationship with the stonewall length at 500m (Figure 9c) and showed differences between years. Bumblebee abundance increased significantly with stonewall length at 500m (Figure 9a) and 1km scales, as did total bee abundance at the 1km scale. Conversely, hoverfly species richness (Figure 9b) and abundance decreased significantly with stonewall length at the 500m scale. Butterfly species richness showed a negative relationship

at 500m scale with the stonewall length (Figure 9d). At the two studied scales, hoverfly species richness is significantly different between years.

Table 4: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (stonewalls length, hedgerow length and factor year). Significant results are shown by differing arrows indicating trends. Arrow directions (↗↘) represent respectively positive and negative relationships. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a **p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. with the lowest AIC).

Response variables	500m		1km	
	Landscape metrics		Landscape metrics	
	BL1	WL1a	BL1	WL1a
Insect Species richness	↘			
Insect abundance		↗		NS
Bee species richness				
Bee abundance	NS		↗	
Bumblebee species richness				
Bumblebee abundance	↗		↗	
Solitary bee species richness		NS		NS
Solitary bee abundance		NS		NS
Hoverfly species richness	↘	↗		↗
Hoverfly abundance	↘	NS	NS	NS
Butterfly species richness	↘		NS	
Butterfly abundance			NS	

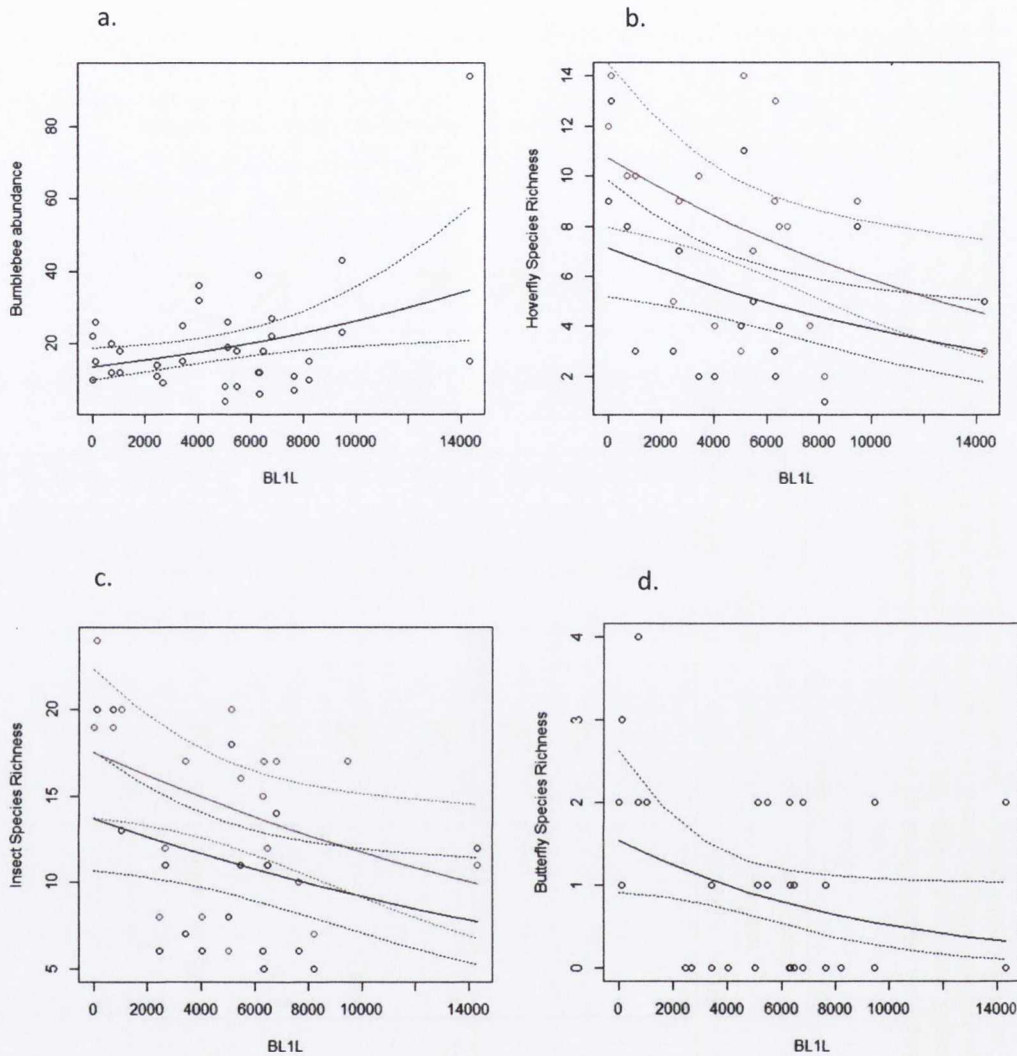


Figure 9: Relationships between the linear feature metrics and insect diversity from the best model (i.e. model with the lowest AIC), a) bumblebee abundance and stonewall length, b) hoverfly species richness and stonewall length, c) insect species richness and the stonewall length and d) butterfly species richness and stonewall, all at 500m scale. Points represent the observed values. Lines characterise the model prediction and dotted lines the 95% confidence intervals (black represents the data from 2010 and red from 2011). All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.

Network indices showed relationships with the linear features at the 500m scale (Table 5). Stonewalls length had a positive relationship with linkage density (Figure 10). The number of plant species in the network was negatively related with the stonewall lengths at 500m and was significantly different in 2010 and 2011. Nested structure, weighted linkage per insect species, linkage density and weighted linkage per plant species were all positively related with network size, whilst connectance and complementarity of specialisation (H2') were negatively related to network size.

Table 5: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (Number of plant species, number of insect species, connectance, nestedness, weighted linkage per pollinator species, H2', linkage density and weighted linkage per plant species) and the explanatory variables (stonewall length, hedgerow length and factor Year). Significant results are showed by differing arrows indicating trends. The smaller and thinner arrow represents a *p-value <0.05, the medium arrow a**p-value <0.01 and the bigger and thicker arrow a ***p-value <0.001. Non-significant covariates are represented by NS and blank cells represent covariates not considered in the best model (i.e. with the lowest AIC).

Response variables	500m				1km			
	Landscape metrics		Network		Landscape metrics		Network	
	BL1	WL1a	Size	Factor Year	BL1	WL1a	Size	Factor Year
Qualitative parameters	↗				↗			
	Number of plant species				↗			
	Connectance				↗			
Quantitative parameters	1-Nestedness				↗			
	Weighted linkage per insect species				↗			
	H2'				↗			
	Linkage Density				↗			
	Weighted linkage per plant species				↗			
					↗			

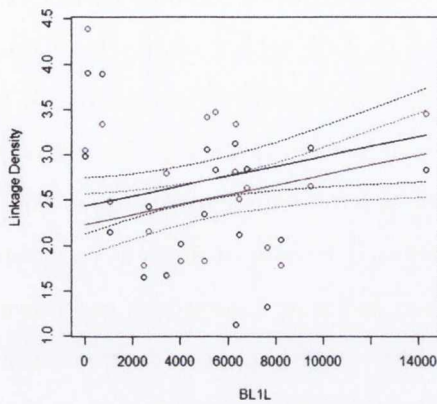


Figure 10: Relationship between linear features (stonewalls) and network indices (linkage density) from the best model (i.e. with the lowest AIC) at the 500m scale. Points represent the observed values, the line the model prediction and dotted lines the 95% confidence intervals.

2.5. Discussion

2.5.1. Landscape composition effects

We found greater insect species richness and abundance, and a higher number of plant species in networks, in sites within landscapes which contained a higher proportion of semi-natural grasslands (%GS1). Since we were sampling in this habitat type, it is perhaps not surprising that landscapes which contain more of the same habitat type, contain more of our focal species. Presumably insect richness and abundance, and plant richness, increases in these landscapes because semi-natural grasslands, and other habitats with high diversity of flowering plants, can support higher flower-visiting insect diversity (Ebeling et al., 2008; Fründ et al., 2010; Hegland and Boeke, 2006; Holzschuh et al., 2007) as they provide an abundance of different foraging resources. Thus when there are more of these habitats in the landscape, larger populations and a greater diversity of insects can persist. Furthermore, via positive feedback, more pollinators may translate into more successful reproduction in a wider diversity of plant species (Fenster et al., 2004). In particular, more semi-natural grassland was correlated positively with species richness and abundance of solitary bees and hoverflies. Woodcock et al. (2013), Kremen et al. (2002) and Steffan-Dewenter et al. (2002), documented similar relationships for solitary bees and Meyer et al. (2009) for hoverflies. Specifically, Meyer et al. (2009) showed that hoverfly species richness is affected by resource heterogeneity (including species richness of flowering plants and area of grassland habitat) which offers a range of

micro and macro habitats for adults and larvae. We also found that landscapes with more semi-natural grasslands supported a higher butterfly species richness and abundance, but only at the 1km scale. Butterflies need to extract nectar from and oviposit on their specific range of plant resources (Erhardt, 1985; Erhardt and Mevi-Shutz, 2009) which may be more abundant when there are more semi-natural grasslands. Bumblebee communities appeared to be the least affected by the surrounding landscape composition at the two scales studied, with only their abundance positively related to the proportion of semi-natural grasslands at 1km scale. This is not surprising as most of the bumblebees we found in these sites can fly relatively long distances and find forage in a range of habitat types, including unimproved and flower rich grasslands (as these habitats provide a continuous supply of ideal plants throughout the flight season) (Edwards, 1998). Moreover a landscape with a higher proportion of semi-natural grasslands was related positively with the weighted mean number of links (linkage density) in the network. This can be explained by the fact that positive relationships have been found between this land cover type and the insect species richness and abundance. A higher density of links makes the network more robust.

Although we would have expected more diverse landscapes to support more flower-visiting insect species (as it was hypothesised that specialist species have more chance of finding their specific resources (Benton et al., 2003)), we actually found the opposite: landscapes with a higher diversity of habitat (i.e. a higher Shannon Evenness Index) had lower insect species richness and abundance, at least when considering landscape up to 1km from the sampling site. This may relate to the local concentration or dilution of pollinators in patches in low and high quality landscape respectively. Moreover this could be due also to a higher proportion of unsuitable habitats or low quality habitats for flower-visitors in more heterogeneous landscapes. Indeed, positive relationships were found between unsuitable habitats (i.e. depositing lowland river (FW2), building and artificial surfaces (BL3), limestone and marl lakes (FL3) and other artificial lakes and ponds (FL8)), low quality habitats (i.e. dense bracken (HD1), raised bog (PB1), conifer plantation (WD4) and exposed sand, gravel or till (ED1)) and Shannon Evenness Index (data not shown). However the suitability of these latter habitats could be discussed as for example lake edges might be suitable habitat for some hoverfly larvae species (Speight, 2008). This specific landscape composition was also negatively correlated with hoverfly abundance at 1km scale, probably for similar reason. Indeed, hoverflies are dependent of the availability of micro and macro habitats for larvae and adults (Meyer et al., 2009) that are less likely to be present in these more heterogeneous landscapes. Additionally, similar relationships were seen with other network parameters. Networks in landscapes with

higher SEI had lower linkage density, suggesting that an increase of low quality habitat for flower-visiting insects in the surrounding landscape makes the network less linked.

2.5.2. Landscape configuration effects

Higher complexity of patch shape (i.e. more irregular shaped patches) with high Area Weighted Mean Shape Index (AWMSI) in the immediate surroundings (500m radius) of the sampling sites was related to higher insect species richness. Landscapes with this kind of structure may promote insect species richness because all the different specific resources necessary for each species will be found closer to each other and will be easier to access. Complexity of patch shapes in the surrounding landscape also influenced butterfly species richness and abundance. Although butterflies are highly mobile, this landscape configuration allows different resources necessary for each butterfly species to be found closer to each other. In the immediate surroundings (500m scale), more irregularity in the patches shape was positively related with the number of plant species in networks, but at the larger scale (1km), this specific landscape configuration reinforced the nested structure of the network. The nested property of a network is characterised by a cohesive structure i.e. a core of generalist species interacting with each other (Bascompte et al., 2003). This specific property offers networks better resistance to perturbations, as loss of a species from the network is unlikely to affect the species it interacts with, as each species is strongly embedded (Bascompte et al., 2003). Moreover, nested structure offers another characteristic to the network i.e. asymmetrical organisation, where specialist species only interact with the most generalised (Bascompte et al., 2003). This allows rare species to have more of a chance persisting in networks (Bascompte et al., 2003).

Finally, we found that landscapes with higher mean patch size contained more insect species (particularly hoverflies, butterflies and solitary bees) and, at the 1km scale, a higher insect abundance. In the relationships where MPS had a significant relationship with insect variables, %GS1 was also significant. Larger patches in the landscape, especially combined with more semi-natural grasslands, means more potential habitats for flower-visiting insects to rely on and so a higher number of visits per plant species. Moreover, the combination of these two landscape metrics may form larger plant population in the landscape and so explained the positive relationships with the number of plant species in the network.

2.5.3. Linear feature effects

Landscapes with more stonewalls had greater bumblebee abundance at 500m and 1km scales. Some species, such as *Bombus lucorum* and *Bombus pratorum* found in this study, nest in pre-existing underground cavities, habitually disused rodents burrows (Goulson, 2010). The specific structure of stonewalls could provide holes and cavities under the walls that can be used by the some bumblebees species. Previous studies revealed that small mammals take refuge during hibernation in stonewalls in UK and Ireland and so bumblebees could benefit from these microhabitats (Haigh et al., 2012). However, overall, landscapes with fewer stonewalls supported a higher pollinator species richness and a higher number of plant species at 500m scales. This relationship is shown also for the butterfly species richness, hoverfly species richness and abundance. This is probably due to the fact that a landscape with more stonewalls means less other linear habitat that are more favourable for the majority of the insect community. Indeed hoverfly adults and larvae need a range of micro and macro-habitats (Meyer et al., 2009), some of which may be less common in landscapes containing more stonewalls. Longer stonewall lengths in the immediate environment (500m scale) were related to greater linkage density in networks.

We found the length of hedgerow in the landscape was not related with any of the insect group and network parameters. Since hedgerows have previously been shown to be beneficial to flower-visiting insects (Cranmer et al., 2012), this is initially surprising. However, several reasons can explain the lack of response of the flowering-visiting insect community to hedgerow length. Firstly previous landscape metrics, such as Area Weighted Mean Shape Index and proportion of semi-natural habitats in the landscape, could act as main drivers of insect response to the landscape at different spatial scales. A higher Area Weighted Mean Shape Index and proportion of semi-natural habitats may result in good connectivity between semi-natural habitats in this area, and hedgerow do not offer any extra significant links through the landscape. Secondly Maudsley (2000) highlights the fact that different factors inherent to the hedgerow can impact the invertebrate community as for example rotational cutting regimes, field edge management, botanical and structural heterogeneity of the hedgerow. Finally, landscapes with a high proportions of semi-natural habitats, which are resource-rich, means that ecological contrast is weak (Kleijn et al., 2011), so hedgerows have little effect.

2.5.4. Network size effects

For most of the network parameters (i.e. connectance, nestedness, weighted linkage per insect species, H_2' , linkage density and weighted linkage per plant species) we considered the network dimension as a covariate as they depend on it. We found that network size was related to all of these indices at 500m and 1km scales, either positively or negatively. Most studies to date have not considered network dimensions, but Dormann et al. (2009) and Bengtsson (1994) highlighted the importance of taking network size into account to understand interaction patterns and thereby allow more sensible ecological conclusions. Indeed in models that do not consider network dimensions, some relationships between network parameters and landscape metrics may appear significant due only to the effects of the missing covariate (Dormann et al., 2009). Network size could also be affected by incomplete sampling effort, but since we have detected differences in response variables according to landscape structure, it is unlikely that incomplete sampling effort is driving patterns. If we did not detect any relationships between landscape and network parameters, it may be that the species poor sites were sampled completely, but the species rich ones were not, which would mean that it would be hard to detect patterns. Moreover Hegland et al. (2010) pointed out that relatively small sampling allows the identification of the functionally most important species in the community.

Since the number of insect and plant species was related to landscape structure, and network size is calculated by multiplying the number of plant species with the number of insect species (which is mainly dominated by the bumblebee), it is perhaps not surprising that we found some landscape metrics were related to network parameters that are affected by network size.

2.5.5. Scale effects

Insect responses to the landscape composition and configuration often showed similar patterns at the two scales studied. In this context, 500m and 1km are probably too close scales to be considered independently in relation to insect diversity responses. Three pollinator taxa groups (i.e. hoverfly, butterfly and solitary bee) showed some significant relationships with the landscape composition and configuration metrics suggesting that 500m and 1km are their scales of interaction. This is in accordance with previous studies showing that solitary bees forage at distance of 150m to 600m (Gathmann and Tschardt, 2002), hoverflies at distance up to 250m (Cant et al., 2005; Wratten et al., 2003), butterflies at variable distance according

to the species (Cant et al., 2005). However the bumblebee group showed the least significant relationships with landscape suggesting that their proper scales of interaction may be above 1km. It has been found that, in general, bumblebee forage larger distance (from several hundred meters up to several kilometres) (Steffan-Dewenter et al., 2002; Westphal et al., 2006) with some species as *Bombus pascuorum* (the most abundant bumblebee species found in our sites) flying sometimes more than 3000m (Chapman et al., 2003). However, considering the linear features, stonewall length showed a relationship with the insect community only at 500m scale, although bumblebee abundance was affected positively at both scales. Interaction network parameters were not related in the same way by the landscape metrics at 500m and 1km scales. At the 1km scale, a specific landscape structure (higher proportion of semi-natural grasslands combined with bigger patches and more complex patch shape) make the networks more robust, and at 500m scale, stonewall length affects the robustness of the network. Therefore distinct landscape structure elements have their specific scale of interaction with the insect-flower interaction network.

2.5.6. Differences between years

Some pollinator responses (mainly the hoverfly group) and plant species richness were significantly higher in 2011 than 2010. This was probably due to the larger sampling effort in 2011 or more favourable weather conditions in this second year. Overall however, the data were remarkably consistent between the two sampling years. Year to year variation in insect numbers is common in studies which examine more than one year (Hatfield and LeBuhn, 2007; Weibull et al., 2000), particularly in systems with annual cropping cycles. The undisturbed grassland sites that we sampled were not disturbed from year to year, and differences between the two years probably represent natural variation in fairly stable systems.

2.6. Conclusions

In general, in this area characterised by less-intensive agriculture, landscapes with more semi-natural grassland were associated with a greater diversity and abundance of flower-visiting insects and insect-pollinated plant species. However, insect communities and interactions with plants were also affected by landscape configurational properties and thus the optimum landscape structure for promoting these insects should include both a high proportion of semi-natural grasslands, larger patches and a greater complexity of patch shape. This landscape structure offers larger areas of suitable habitat for the focal species, as well as relative proximity of different habitat types so that necessary resources are found closer to each other

and are more accessible. The different responses between taxa may reflect their different needs in term of nesting, overwintering, mating and foraging resources. Cavities and holes under stonewalls could provide nest sites for some bumblebee species, but more stonewalls could limit resources for the other insect groups (as hoverflies and butterflies). Landscape structure and linear elements have important effects on insect-flower interaction network structure. At 1km scale a higher proportion of semi-natural habitats combined with larger patches and greater complexity of the patch shape may improve the robustness of the network, but at 500m scale, stonewalls have a contrasting impact on the network.

These findings should be taken into account in future conservation measures to preserve insect communities in areas characterised by a less-intensive agricultural system. However we still need to (1) extend this study to larger scales as we know that some insects can travel several kilometres to find forage and (2) study the landscape scale impact on insect communities in semi-natural grasslands in areas characterised by intensive agricultural systems.

Chapter 3

Testing the suitability of CORINE Land Cover 2012 as a tool to characterise landscape structure for pollinator studies

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3. Testing the suitability of CORINE Land Cover 2012 as a tool to characterise landscape structure for pollinator studies

3.1. Abstract

CORINE land cover (CLC) is a European GIS database providing information on the biophysical cover of the Earth. It was created with the objective of compiling a geo-spatial environmental database for all Member States using a common classification. It is based on the photo interpretation of satellite images and involves a series of thematic and spatial generalisations to fit the common classification with a minimum map unit of 25ha. CLC is widely used in ecology to describe the characteristics of landscapes, especially at larger scales.

The objective of this study was to evaluate the suitability of CLC as a tool to characterise the landscape structure for pollinator studies, which often map the surrounding landscape up to several kilometres around sampling sites (because some pollinating insects can travel up to 5km or more to find the resources they need). For this, we used a dataset generated from CLC for 19 sites located in a low input grassland dominated area of Ireland, and compared this with a high-resolution land cover dataset, based on aerial photographs combined with on the ground habitat classification. The CLC dataset was used to test relationships between the land cover and flower-visitor diversity at 500m-5km scales.

Despite the process of CLC creation and the constraints related to the classification of the different CLC habitats, some consistent patterns were found. CLC cannot be used to characterise landscape configuration at the scale and grain relevant to pollinator communities, but the compositional landscape metrics generated from CLC showed generally similar relationships with flower-visitor diversity as the high-resolution dataset. A landscape with a higher proportion of pasture (mainly composed of flower-poor grasslands) showed significant negative correlation with diversity of some pollinator groups. However the use of CLC must be an informed decision. All users must be aware of the different successive steps of the production leading to spatial and thematic generalisation. The classes used in CLC do not reflect fine scale habitat diversity differences which have been shown to be important in pollination studies. For example, different grassland types (intensive vs. extensive grazing), which vary in term of plant composition, were all categorised in the same CLC class. This means different patterns were in some circumstances more difficult to detect. It is also imperative before reporting CLC classes to understand to which national-level habitat

classification they correspond. Finally, using CLC rather than a high resolution landscape characterisation to investigate patterns of ecological process depends on the research question i.e. if the fine scale information of habitat identifications in the surrounding landscape needs to be considered.

3.2. Introduction

As pollinators are generally highly mobile organisms, utilising resources over potentially very large spatial scales, there has been a lot of interest in understanding how pollinator dynamics are influenced by landscape context (Hadley and Betts, 2012; Tscharntke et al., 2012). Studies investigating the effects of surrounding landscape structure on pollinator communities and pollination services have used diverse approaches to characterise the landscape. Some have based their characterisation on interpretation of aerial pictures (Klein et al., 2012; Perović et al., 2015); others complemented this with national maps (Goulson, 2010; Meyer et al., 2009; Steckel et al., 2014) and/or some field inspection (Stanley and Stout, 2013; Steffan-Dewenter et al., 2002; Woodcock et al., 2013). Others used instead national land-use maps (Andersson et al., 2013; Rundlöf et al., 2008) combined with some ground-truthed observations (Holzschuh et al., 2012; Holzschuh et al., 2008). However, the use of CORINE land cover (CLC) in European studies is not uncommon (Brittain et al., 2010; Carré et al., 2009; Nayak et al., 2015; Power et al., 2012). It is the only available GIS layer which provides a way to compare land cover across studies throughout EU (European Environment Agency, 1995; Lydon and Smith, 2014). It is particularly used at the larger (several km) scale, which is relevant for some pollinator groups, but is difficult to map on the ground. Carré et al. (2009) used the CLC in a study investigating the effect of landscape composition on wild bee communities in different European countries. Others used the CLC as part of national studies on the relationship between the proportion of semi-natural or uncultivated land on pollinators (e.g. Nayak et al. (2015) in UK at a scale up to 3km; Brittain et al. (2010) in Italy at a scale up to 2km). In Ireland, CLC was used to determine landscape diversity in relation to insect-pollinated plant communities (Power et al., 2012) up to 5km from sampling sites.

The CORINE (Co-Ordinated INformation of the Environment) program was initiated by the European Commission (European Environment Agency, 1995) in 1985 with the incentive of compiling geo spatial environmental databases for all the Member States using a common classification (Lydon and Smith, 2014). It focused on certain environmental topics that are priority for all the Member States to allow a planning policy at a national and European level (European Environment Agency, 1995; Lydon and Smith, 2014). CORINE land cover (CLC) is one

of the environmental inventories undertaken through this programme (Lydon and Smith, 2014). Each Member State is responsible for creating their national CLC based on the common European classification. Based on satellite images, it provides information about biophysical cover of the earth’s surface, categorising land cover into 44 classes (Figure 11) at three levels hierarchical classification (European Environment Agency, 1995). The CLC, produced for 2000, 2006 and 2012, is easily accessible and freely available through the European Environment Agency website. As such, it has been used extensively by ecologists (in some cases with other landscape datasets) to characterise landscape to determine how populations (Vögeli et al., 2010), behavior (Lundy et al., 2012), community composition (Ambarli and Bilgin, 2014; Devictor and Jiguet, 2007; Power et al., 2012), and ecosystem services (Trichard et al., 2013) respond to landscape composition and structure (Lechner, 2010; Wiens, 2002).





Figure 11 : The three levels of CORINE Land Cover classification (European Environment Agency, 1995).

Using CLC is advantageous because standardised comparisons can be made across countries within Europe, the data are easily incorporated into GIS mapping and analytical packages, and this approach avoids time-consuming and high-cost field-based mapping. Over time, the quality of the datasets available via CORINE have improved, as national agencies learn from their experience in producing previous versions and by using more advanced techniques and ancillary national datasets (Lydon and Smith, 2014).

However, CLC databases should be used with caution for interpreting ecological patterns and processes. Many studies have considered land cover data as an objective dataset to characterise the landscape structure, but forget the context in which these datasets have been created and for which purpose, which can result in inappropriate use (Comber et al., 2005). With a minimum map unit (MMU) of 25ha (European Environment Agency, 1995), and merging of polygons <5ha, CLC may not have sufficient resolution to define fine-scale landscape complexity for ecological investigations. Moreover, CLC is based on total extent of different landcover types, and does not partition land cover into discrete field-level parcels. Thus, although landcover composition can be quantified in defined areas, the configuration of landcover cannot be calculated (Fahrig et al., 2011; McGarigal and Marks, 1995; Tschardt et al., 2012). Thereby CLC can considerably overlook fine scale features important for local biodiversity (Sullivan et al., 2010). Additionally, CLC does not have the capacity to differentiate similar landcover types such as improved, semi-improved and semi-natural grassland (Sullivan et al., 2010), which vary ecologically but are still classified as the same landcover type (pasture, 231). Another major issue is that these metadata do not describe adequately the landcover categories on which basic classifications have been made (Comber et al., 2005). Moreover CLC measures only land cover but it has been recognised that land use and land function, and relationships between these, are important as they can improve the way of assessing and modelling land changes and so characterising the landscape (Verburg et al., 2009). In contrast to land use, CLC datasets do not give information related to the management (i.e. input use, grazing intensity, etc) (Schuh et al., 2011) which may affect biodiversity. Finally, CLC is renewed roughly every six years thereby land changes operating in between these intervals of time are not reported. Given the high turnover of land use from year to year in agricultural systems which incorporate both pasture and arable crops (Zimmermann et al., in press), studies focusing on ecological process at a specific point in time might not use accurate information if they rely only on CLC.

Here, we use a high-resolution land cover dataset, based on aerial photographs combined with on-the ground habitat classification for 19 sites in the North Midlands of Ireland reflecting a grass dominated system, and compare with an equivalent dataset generated from CLC2012. These datasets are then used to test relationships between land cover and pollinator diversity at 500m-5km scales. The specific objectives are (1) to compare the landscape information obtained in a high resolution methodology to the current CLC2012, (2) to understand the relationship between landscape structure characterised with CLC2012 and pollinator diversity at 500m and 1km scales and identify the pros and cons of using CLC2012 in this context and (3)

extend the study of the relationship between landscape structure and pollinator diversity up to 5km with the CLC2012 database as it has been observed that some pollinator groups can travel distance up to and over 5km scales (Beekman and Ratnieks, 2000; Carvell et al., 2012; Knight et al., 2005).

3.3. Materials and Methods

We used data from the north midlands region of Ireland in the Counties of Roscommon and Offaly which are characterised by a less-intensive agricultural system (chapter 2). The landscape surrounding these sites was characterised in two ways:

1. High-resolution aerial photography and field-mapping: all sites were visited and habitat types were mapped in a 1km radius of the site using Fossitt (2000) national habitat classification scheme (see details in chapter 2).
2. CLC: CLC2012 was downloaded from the website of the Irish Environmental Protection Agency, and then uploaded in an ArcGIS session. Around each site, buffer rings of 500m, 1km, 2.5km and 5km radius were established; CLC2012 was clipped with these buffers to calculate the proportion of each land cover type in the matrix around each site and at each scale. Land cover types were considered at the finest resolution (level 3) of the CLC classification (Figure 11).

Pollinator data in terms of species richness and abundance of the overall flower-visiting insect community and the different insect groups were collected in 2010/11 using a transect-walk method (see details in chapter 2).

3.3.1. Landscape characterisation: qualitative

A qualitative approach was used to investigate the differences between the landscapes characterised with Fossitt level 3 and CLC2012 level 3. Maps created with these two different sources were compared in term of composition and configuration at 1km scales. Surrounding landscapes were divided into different groups representing the main different patterns while comparing the high resolution maps and CLC2012.

3.3.2. Landscape characterisation: quantitative

For each Fossitt habitat code identified in the 19 landscapes, a CORINE class was assigned, based on the definition of the CORINE classes (European Topic Centre on Spatial Information and Analysis, 2009) and personal communication from the national CORINE project co-

ordinator at the Irish Environmental Protection Agency (EPA), Kevin Lydon (Table 6). For some Fossitt codes (ED1, GS1, GS4, BL3 and REPS), two CLC classes were possible. In these cases, both CLC classes were assigned to the Fossitt code, as it was not possible to choose which category represented them best. To compare landscapes characterised by each method, the proportion of land categorised into the Fossitt codes in each landscape were pooled into CLC classes (henceforth “Fossitt class”) and then compared with the proportion of land in each class obtained with the CLC 2012 dataset (henceforth “CLC2012 class”).

Table 6 : Fossitt habitat codes (left hand column) and their comparative CORINE classes (right hand column).

Freshwater		
FL3	Limestone and marl lakes	512
FL6	Turlough	512
FL8	Other artificial lakes and ponds	512
FW2	Depositing lowland rivers	511
FS1	Reed and large sedge swamps	411
Grassland		
GA1	Improved agricultural grasslands	231
GA+	Semi-improved grasslands	231
GS1	Dry calcareous and neutral grasslands	231/243
GS4	Wet grasslands	231/243
Bracken		
HD1	Dense bracken	322
Peatland		
PB1	Raised bog	412
Woodland and scrub		
WN6	Wet willow alder ash woodland	311
WD1	Mixed broadleaved woodland	311
WD4	Conifer plantation	312
WS1	Scrub	324
Exposed rock and disturbed ground		
ED1	Exposed sand gravel or till	332/333
ED4	Active quarries and mines	131
Cultivated and built land		
BC1	Arable crops	211
BL3	Artificial surfaces	112/142
Protection scheme habitat		
REPS	Rural environment protection scheme	231/243

3.3.3. Determining landscape scale effects on pollinator diversity

In chapter 2, we investigated the relationship between insect data and landscape composition and configuration at 500m and 1km radius scale using the high-resolution landscape maps created using the Fossitt classifications. Here we examined the relationship between landscape structure characterised with CLC2012 and insect diversity at 500m and 1km scales. This allowed us to determine differences in pollinator responses according to how landscapes were characterised. The CLC2012 only allowed the calculation of some landscape composition metrics i.e. Shannon Diversity Index (SDI), Shannon Evenness Index (SEI) and the proportion of the different habitat types in the landscape, whereas the high-resolution mapping allows calculation of configurational metrics (see chapter 2), which could not be used here. Moreover, due to the high proportion of landscape composed of one unique patch at these two scales, SDI often had a value of zero and SEI could not be calculated. Therefore, the statistical analysis was based on the calculation of the Pearson product moment correlation coefficients to describe the independent effects of each landscape metric on each insect diversity measure, and this separately for each year (2010 and 2011) and each scale (500m and 1km).

Finally, we extended the study up to 2.5km and 5km scales. At these larger scales, each landscape was composed of more than one habitat according to CLC2012. Therefore the calculation of SDI, SEI and the proportion of different habitat types was possible. However, we do not have high-resolution Fossitt mapping at these scales, and so we could not compare the two methods, but tested whether patterns seen at the smaller scales (500m and 1km), hold at the larger scales (2.5km and 5km). To deal with correlation between landscape metrics, Variance Inflation Factor (VIF) was used to reduce the number of variables to consider in the model. Before including the landscape variables in the VIF process, variables were chosen to be the most relevant in an ecological point of view to the pollinator community. Habitat types including urban fabric (11), mines, dumps and construction sites (13), artificial non-agricultural vegetated areas (14) and continental waters (51), which rarely occurred in the surrounding landscape were not considered. Moreover, variables were chosen to allow possible comparison between 2.5 and 5km scales. After running the VIF on the landscape metrics calculated using level 3 classifications of CLC2012, the variables remaining were not representative of the overall landscape structure. To allow a better representation of the landscape, VIF was run on the CLC2012 level 2. Thereby three landscape composition metrics were retained: arable land (21), pastures (23) and forests (31). In our study area, only non-

irrigated arable land (211) was found in the class “arable land”; “pasture” only included the class 231; and “forest” included three classes: broadleaved forest (311, only at 5km scale), coniferous forests (312) and mixed forests (313) (see Table 8). Arable land was positively related at 2.5 and 5km scales with artificial, non-agricultural vegetated areas (14), and only at 5km scale with urban fabric (11) and mines, dumps and construction sites (13). Pasture was negatively correlated with inland wetlands (41) at 2.5km and 5km scales and with heterogeneous agricultural areas (24) at 2.5km. Finally forest was positively related with scrub and herbaceous vegetated association (32) and urban fabric (11) at 5km scale (see Appendix 10).

Generalized Linear Models (GLMs) with a Poisson distribution were used to test the relationship between landscape and pollinator diversity at 2.5km and 5km scales. A GLM negative binomial was used to deal with 70% of the models that were overdispersed. Year was integrated as a fixed factor. All these models were simplified by selecting the optimal model that included the landscape parameters that best explained the data using Akaike Information Criteria (AIC). Once the model was chosen, they were checked for homogeneity, independence, influential observations, and normality by plotting residuals vs. fitted values (Zuur et al., 2007). The four assumptions were verified in greater than 90% of models.

3.4. Results

3.4.1. CLC2012 landscape characterisation from 500m to 5km

At the 500m scale, a total of six different habitat types were identified in the landscapes surrounding the 19 sites (see Table 7), although four types were rare, and occurred in <5% of the landscape on average. Two additional habitat types were included at the 1km scale. By far the most abundant habitat type at these scales was pasture (231). It was the only habitat type surrounding 10 sites at the 500m scale, although this was reduced to six sites at the 1km scale. The habitat diversity index, i.e. Shannon Diversity Index, was low at both scales (see Table 7).

Shannon Diversity Index (SDI) increased at the 2.5km and 5km scales, when 15 and 17 habitat types were found in the surrounding landscape respectively (Table 8). At least two habitat types were found at all sites at the 2.5km scale, and four at the 5km scale. The most abundant habitat type was still pasture (231) at these larger scales. The second and third most abundant habitats were peat bog (412) and land principally occupied by agriculture with significant areas of natural vegetation (such as wetlands, water bodies, outcrops) (243) (see Table 8).

Table 7: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC 2012 level 3) for 500m and 1km scales.

	500m			1km		
	Mean (±se)	Minimum	Maximum	Mean (±se)	Minimum	Maximum
Shannon Diversity Index (SDI)	0.259(±0.085)	0.000	1.11	0.347(±0.099)	0.000	1.33
Shannon Evenness Index (SEI)	-	-	-	-	-	-
% discontinuous urban fabric (112)	-	-	-	-	-	-
% Industrial and commercial units (121)	-	-	-	-	-	-
% Mineral extraction sites (131)	0.381(±0.381)	0.000	7.24	0.278(±0.278)	0.000	5.29
% sport and leisure facilities (142)	-	-	-	0.010(±0.010)	0.000	0.196
% Non-irrigated arable land (211)	-	-	-	-	-	-
% pasture (231)	85.3(±5.92)	0.000	100	84.3(±5.80)	6.28	100
% complex cultivation pattern (242)	-	-	-	-	-	-
%land principally occupied by agriculture (243)	9.20(±4.26)	0.000	69.3	5.21(±2.29)	0.000	38.9
% broadleaved forest (311)	-	-	-	-	-	-
% coniferous forest (312)	-	-	-	-	-	-
% mixed forest (313)	-	-	-	-	-	-
% natural grassland (321)	-	-	-	-	-	-
% transitional woodland shrub (324)	-	-	-	-	-	-
% inland marshes (411)	2.31(±1.53)	0.000	23.1	3.04(±1.73)	0.000	25.7
% peat bogs(412)	1.92(±1.54)	0.000	29.1	6.42(±2.60)	0.000	34.6
% water courses (511)	0.875(±0.875)	0.000	16.6	0.697(±0.670)	0.000	13.2
% water bodies (512)	-	-	-	0.082(±0.082)	0.000	1.56

Table 8: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC 2012 level 3) for 2.5km and 5km scales.

	2.5km			5km		
	Mean (±se)	Minimum	Maximum	Mean (±se)	Minimum	Maximum
Shannon Diversity Index (SDI)	0.546(±0.093)	0.076	1.38	0.700(±0.060)	0.369	1.26
Shannon Evenness Index (SEI)	0.375(±0.050)	0.069	0.768	0.354(±0.031)	0.174	0.649
% discontinuous urban fabric (112)	0.035(±0.028)	0.000	0.522	0.369(±0.100)	0.000	1.24
% Industrial and commercial units (121)	-	-	-	0.015(±0.015)	0.000	0.281
% Mineral extraction sites (131)	0.197(±0.167)	0.000	3.16	0.178(±0.087)	0.000	1.31
% sport and leisure facilities (142)	0.143(±0.143)	0.000	2.71	0.045(±0.036)	0.000	0.678
% Non-irrigated arable land (211)	0.308(±0.238)	0.000	4.35	0.504(±0.483)	0.000	9.19
% pasture (231)	81.2(±4.414)	30.0	98.6	79.3(±3.39)	33.2	92.7
% complex cultivation pattern (242)	0.106(±0.106)	0.000	2.01	0.125(±0.050)	0.000	0.509
%land principally occupied by agriculture (243)	3.44(±0.963)	0.000	13.6	2.94(±0.626)	0.000	8.52
% broadleaved forest (311)	-	-	-	0.099(±0.060)	0.000	1.03
% coniferous forest (312)	0.082(±0.059)	0.000	0.998	0.629(±0.204)	0.000	3.58
% mixed forest (313)	0.010(±0.010)	0.000	0.199	0.479(±0.175)	0.000	2.39
% natural grassland (321)	0.183(±0.183)	0.000	3.47	0.445(±0.149)	0.000	2.33
% transitional woodland shrub (324)	1.17(±0.403)	0.000	5.66	1.82(±0.352)	0.000	5.11
% inland marshes (411)	2.73(±1.13)	0.000	18.8	1.90(±0.552)	0.000	10.6
% peat bogs(412)	9.69(±3.02)	0.000	39.8	10.7(±2.99)	0.000	47.9
% water courses (511)	0.310(±0.310)	0.000	5.90	0.136(±0.136)	0.000	2.59
% water bodies (512)	0.393(±0.393)	0.000	7.46	0.441(±0.303)	0.000	4.30

3.4.2. Landscape characterisation: qualitative differences between CLC2012 and Fossitt classifications

Several differences were observed between the landscape characterisation using CLC2012 and Fossitt classes. The two main patterns that were found amongst the 19 sites were:

1. In many cases, only one or two habitat types were classified using CLC: In landscapes characterised by a mosaic of small-area habitats and where agriculture was mainly grass based, only one habitat type was identified in six landscapes using CLC2012 classes whereas many patches and habitat types were identified using Fossitt classes. For example, at Carrownalassan (Figure 12a), using CLC2012 classes, only one land cover type (231, pasture) was recognized, whereas using Fossitt classes, this landscape was composed of 238 polygons and 10 different habitats types with most of the landscape composed of improved grassland (GA1) (62.5%), semi-improved grassland (GA+) (14.0%) and dry calcareous and neutral grassland (GS1) (8.5%). Furthermore, for 8 landscapes, using CLC2012 revealed only two habitat types. The most dominant habitat type found in these landscapes was again pasture (231).
2. Large patches of distinctive habitat are captured using CLC: In landscapes with distinct physical features (i.e. large patch of very different habitat), the CLC2012 classification recognised a higher number of land cover classes. For example, at Castlesampson (Figure 12b), the CLC 2012 landscape is divided in 8 polygons and composed of mineral extraction sites (131), pasture (231), land principally occupied by agriculture with significant areas of natural vegetation (243) and peat bogs (412). The two most dominant habitats are pastures (58.4%) and peat bogs (25.1%). Using Fossitt, this same landscape is composed of 213 polygons and 14 different habitat types. The three most dominant Fossitt habitat types are improved agricultural grassland (GA1) (31.3%), raised bog (PB1) (30.5%) and dry calcareous and neutral grasslands (GS1) (13.8%). At Clonmacnoise (Figure 12c), CLC2012 maps showed 6 polygons and 4 different habitats (pastures, inland marshes, peat bogs and water courses), whilst the Fossitt classification resulted in 10 habitat types, dominated by pasture (both wet and improved agricultural), raised bogs and lowland rivers.

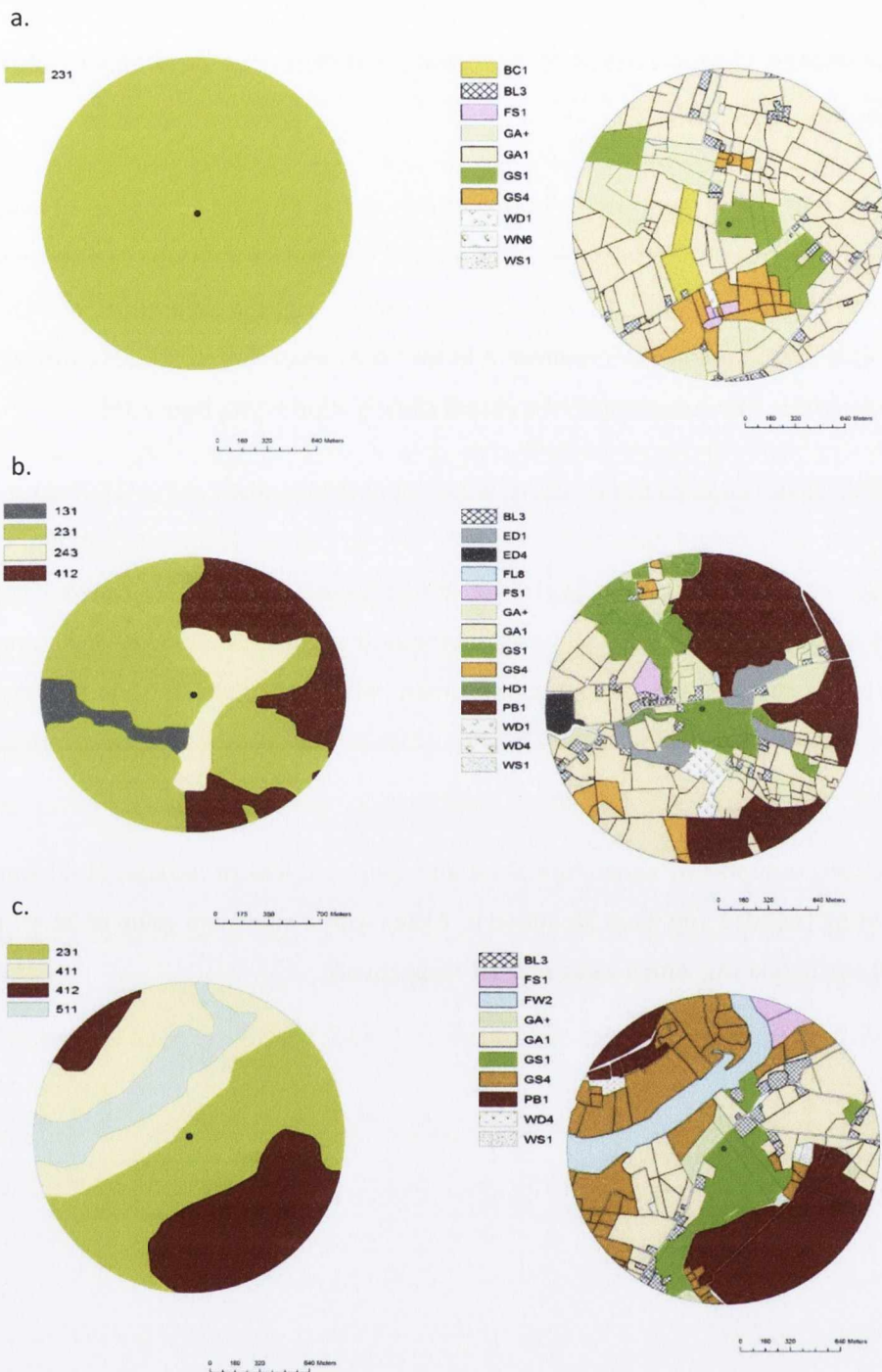


Figure 12 : Comparison of the landscape surrounding three sites using Fossitt habitat classification level 3 at 1km scale (maps on the right; 131: mineral extraction sites, 231: pasture, 243: land principally occupied by agriculture, 412: peat bogs, 511: water course) and CLC2012 level 3 (maps on the left; BC1: arable crops, BL3: artificial surfaces, FS1: reed and large sedge swamps, FW2: depositing lowland rivers, GA+: semi-improved grasslands, GA1: improved agricultural grasslands, GS1: dry calcareous and neutral grasslands; GS4: wet grasslands; PB1: raised bogs; WN6: wet willow and alder ash woodland, WD1: mixed broadleaved woodland; WD4: conifer plantation; WS1: scrub; ED1: exposed sand gravel or till, ED4: active quarries and mines, FL8: other artificial lakes and ponds; HD1: dense bracken) (a/ Carrownalassan, b/Castlesampson, c/Clonmacnoise)

3.4.3. Landscape characterisation: quantitative differences between CLC2012 and Fossitt classifications

Six landcover types were identified by both methods of classification across the 19 landscapes (Figure 13). The principal land use type, pasture (231), was the most different between the two mapping classifications (Figure 14 and 15). The second highest difference was for inland marshes (411). Inland marshes were present in four sites according to CLC2012 (from 0.46% - 25.7%) and in three sites according to the Fossitt classification (< 2%, Figure 15).

Eight habitat types, classified using Fossitt, were not apparent when using CLC (Figure 13). Of these, pasture (231)/ land principally occupied by agriculture (243), discontinuous urban fabric/ sport and leisure facilities (112/142), broad-leaved forests (311) showed the most difference in cover according to the two methods (Figure 13). Pasture/ land principally occupied by agriculture and discontinuous urban fabric/sport and leisure facilities were present in all the sites (2.69% to 49.2% and 1.21% to 5.03%). Broad-leaved forests were present in 16 landscapes (up to 9.38%).

Land principally occupied by agriculture (243) and sport and leisure facilities (142) were only classified using CLC2012 and were identified in 7 sites with a maximum value of 38.4% (Figure 14 and 15) and in one site with a value of 0.2% respectively.

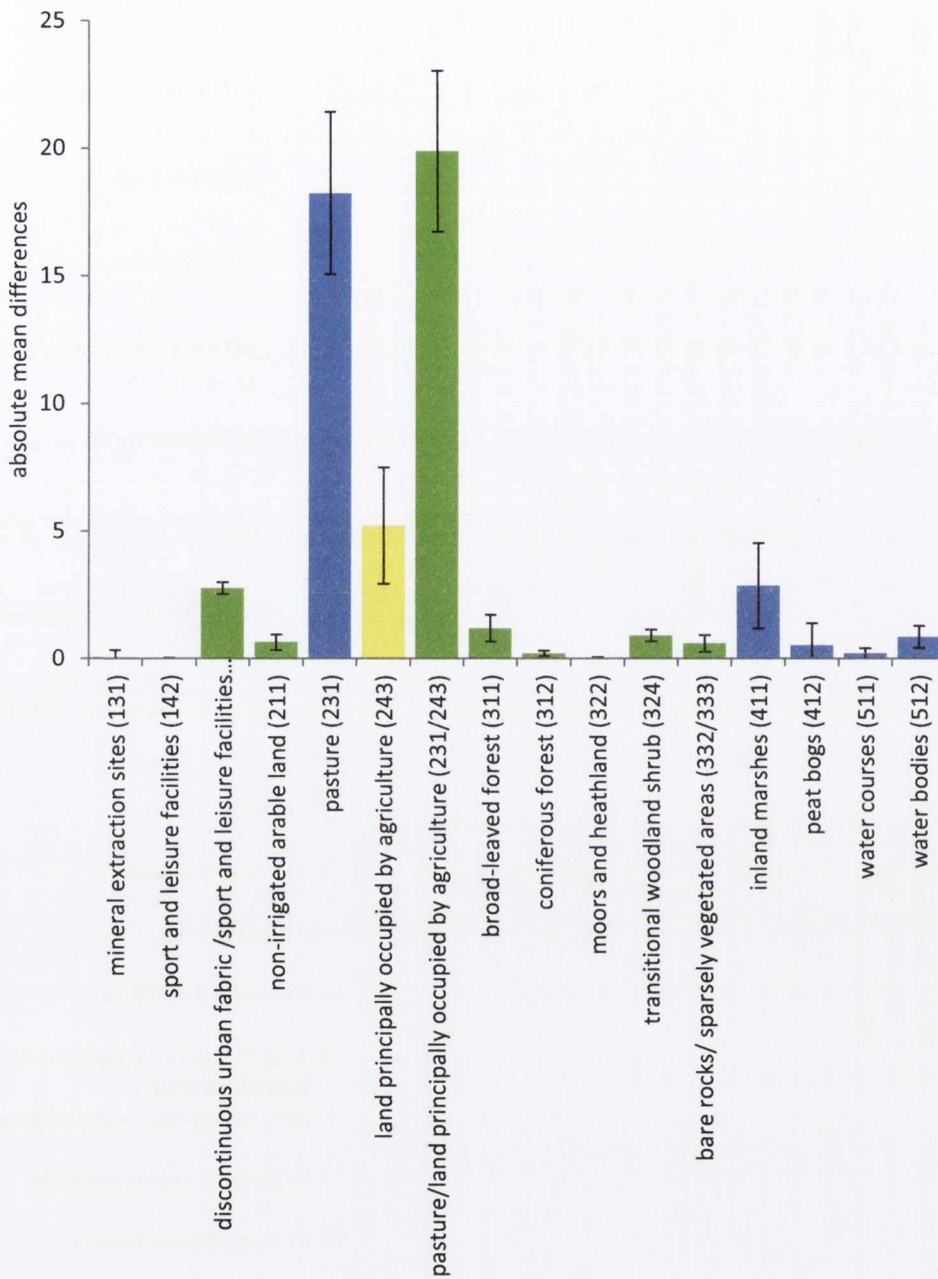


Figure 13 : Absolute mean ($\pm$ SE) differences of the landcover classes between the two methods at 1km scale (131: Mineral extraction sites, 142: sport and leisure facilities (grouped with 112: discontinuous urban fabric for "Fossitt classes"); 211: non irrigated arable land; 231: pasture; 243: land principally occupied by agriculture with significant areas of natural vegetation; 311: broadleaved forest; 312: coniferous plantation; 322: moors and heathlands; 324: transitional woodlands and scrubs; 332/333: bare rocks/sparsely vegetated areas; 411: inland marshes; 412 peat bogs; 511: water courses; 512 water bodies). Bars in green represent land cover classes which were not recorded by the CLC 2012 classification and bar in yellow not recorded by Fossitt classification.

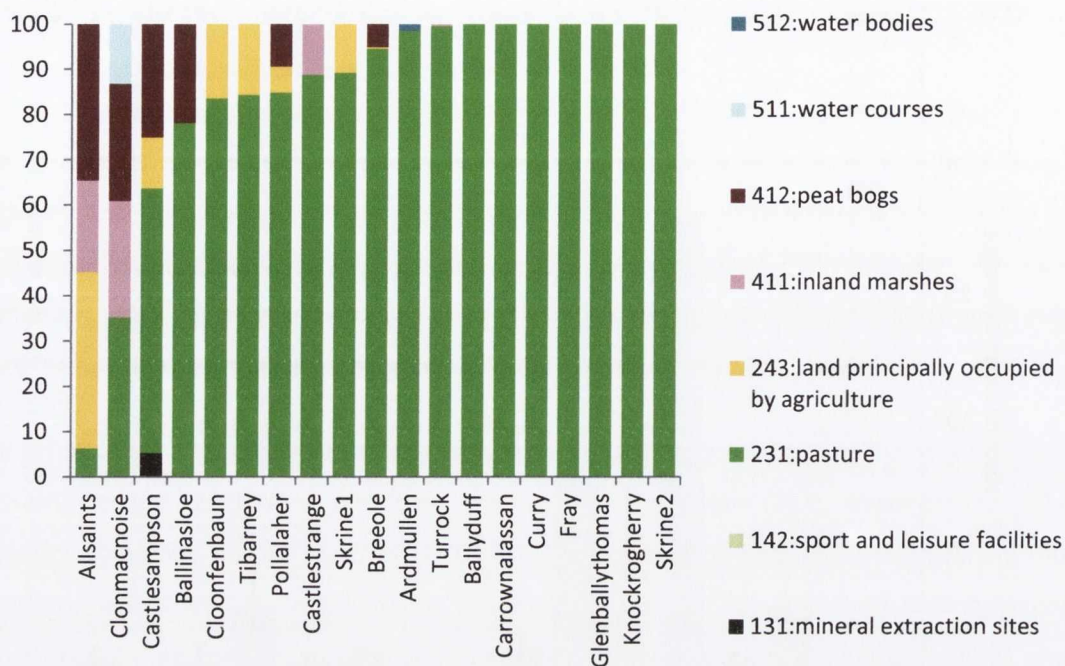


Figure 14 : Proportions of the different CLC 2012 habitat types in the surrounding landscape at 1km scale for each site.

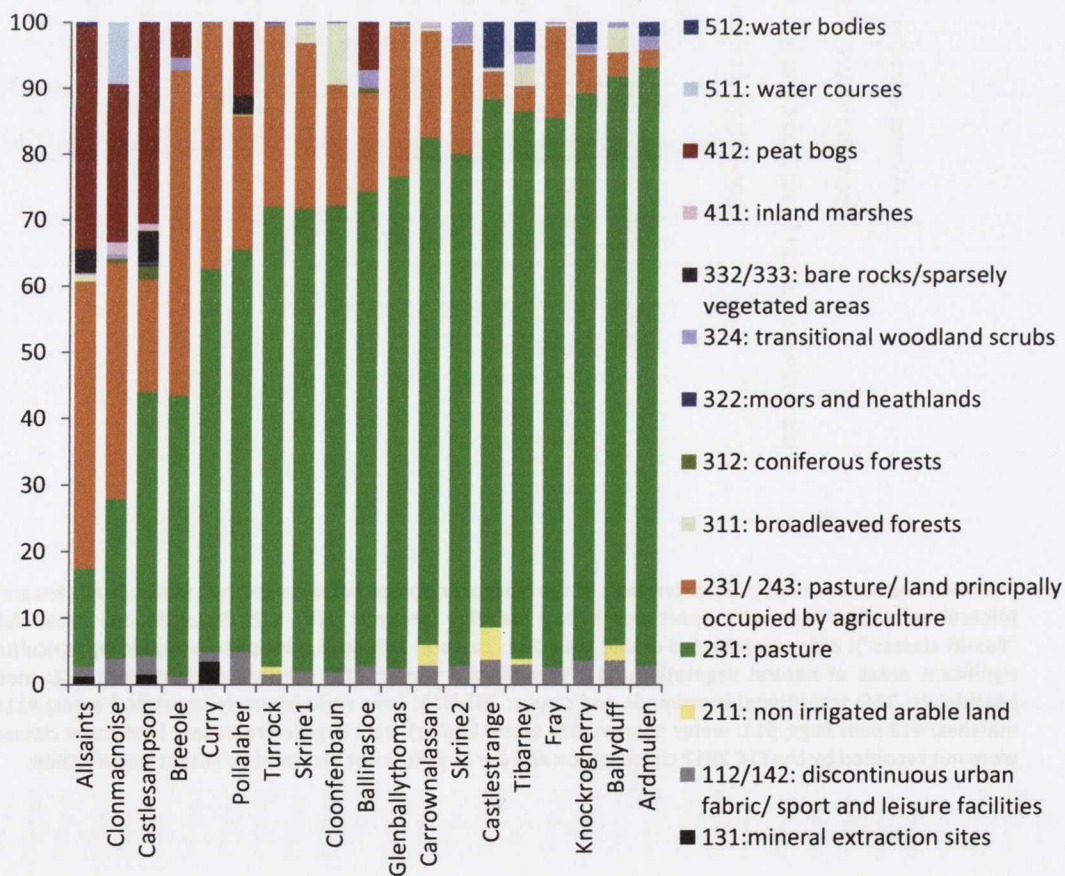


Figure 15: Proportions of the different Fossitt habitat types assigned to CLC 2012 classes in the surrounding landscape at 1km scale for each site.

3.4.4. Landscape scale effects on pollinator diversity: 500m and 1km scales

There were positive relationships between landscape diversity (SDI) and total insect (2011), hoverfly (2011) and butterfly (2010) species richness at the 500m scale (Table 9, Figure 16a) and only with the butterfly species richness (2010) at 1km scale. The proportion of pasture (%231) in the landscape was the only composition metric showing significant negative relationships with insect variables (Tables 9 and 10, figure 16b and 17b). Landscapes with more land principally occupied by agriculture (%243), at 500m scale, were positively related with hoverfly abundance in 2010 and with insect species richness and abundance, butterfly species richness and hoverfly species richness in 2011 (Figure 16c). A landscape with a higher proportion of inland marshes (%411) had a positive relationship with butterfly species richness (500m and 1km) in 2010, with hoverfly abundance (1km) in 2010 (Figure 17c) and with insect species richness and butterfly abundance (1km) in 2011. However, these relationships were driven by the presence of inland marshes in three and four landscapes only at 500m and 1km scales respectively (Figure 17c). At 500m scale, more peat bogs (%412) areas in the surrounding landscape was positively correlated with insect species richness (2010 and 2011), with hoverfly species richness and abundance (2010) and butterfly species richness and abundance (2011). However, these relationships were driven by the presence of peat bogs in three landscapes only. At 1km scale, a landscape with more peat bogs had a positive relationship with butterfly species richness (in 2010) (Figure 17d) and with solitary species richness (in 2011).

Table 9 : Pearson Product Moment Correlation Coefficients showing the significant linear relationships between insect responses and landscape variables at 500m scales in 2010 and 2011.

	Response variables	500m						
		SDI	131%	231%	243%	411%	412%	511%
2010	Insect species richness			-0.484*			0.465*	
	Solitary species richness		0.459*					
	Solitary abundance		0.526*					
	Hoverfly species richness			-0.486*			0.570*	
	Hoverfly abundance			-0.561*	0.477*		0.678**	
	Butterfly species richness	0.556*				0.457*		0.717**
2011	Butterfly abundance							0.662**
	Insect species richness	0.601**		-0.676**	0.593**		0.503*	
	Insect abundance			-0.520*	0.492*		0.498*	
	Solitary abundance		0.772**					
	Hoverfly species richness	0.540*		-0.595**	0.528*			
	Butterfly species richness			-0.565*	0.487*		0.487*	
	Butterfly abundance			-0.488*			0.510*	

* p-value < 0.05 and r > 0.456, ** p-value < 0.01 and r > 0.575; dark shaded cells represent relationships driven by a single data point (i.e. where a particular land cover type was only observed surrounding one site); lighter shaded cells represent relationships driven by 3 data points (i.e. where a particular land cover type was only observed in the surroundings of three sites)

Table 10: Pearson Product Moment Correlation Coefficients showing the significant linear relationships between insect responses and landscape variables at 1km scale in 2010 and 2011.

	Response variables	1km							
		SDI	131%	142%	231%	411%	412%	511%	512%
2010	Insect species richness								0.645**
	Insect abundance								0.868**
	Bee abundance				-0.467*				0.484*
	Bumblebee species richness								0.879**
	Bumblebee abundance								
	Solitary species richness		0.459*						
	Solitary abundance		0.526*						
	Hoverfly abundance				-0.526*	0.514*			
2011	Butterfly species richness	0.552*			-0.472*	0.533*	0.482*	0.717**	
	Butterfly abundance			0.525*				0.662**	
	Insect species richness				-0.507*	0.485*			
	Solitary species richness						0.472*		
	Solitary abundance		0.772**						
	Hoverfly abundance			0.524*					
	Butterfly species richness				-0.474*				
	Butterfly abundance				-0.490*	0.516*			0.542*

* p-value < 0.05 and r > 0.456, ** p-value < 0.01 and r > 0.575; shaded cells represent relationships driven by a single data point (i.e. where a particular land cover type was only observed surrounding one site)

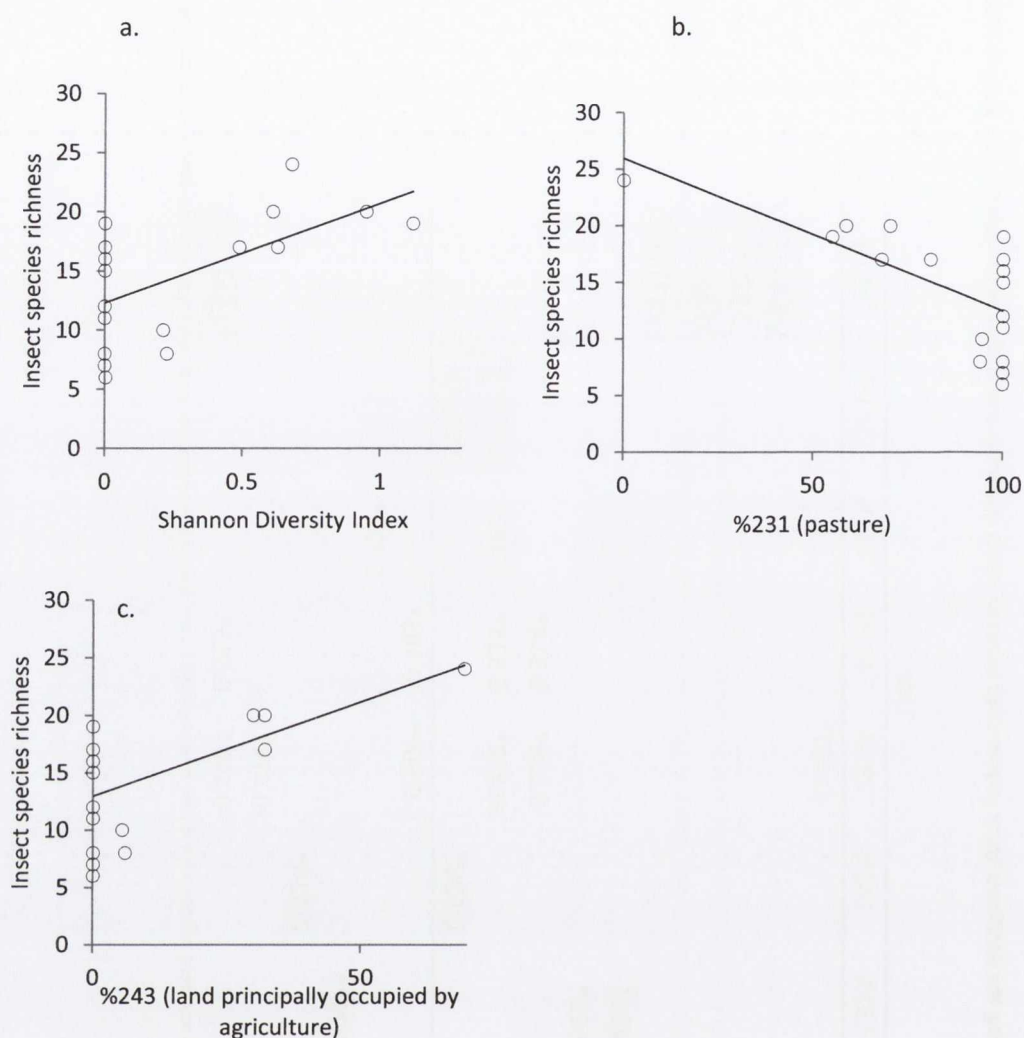


Figure 16 : Relationships between the insect diversity and the landscape metrics at 500m scale. Graphs a,b,c represent data in 2011. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.

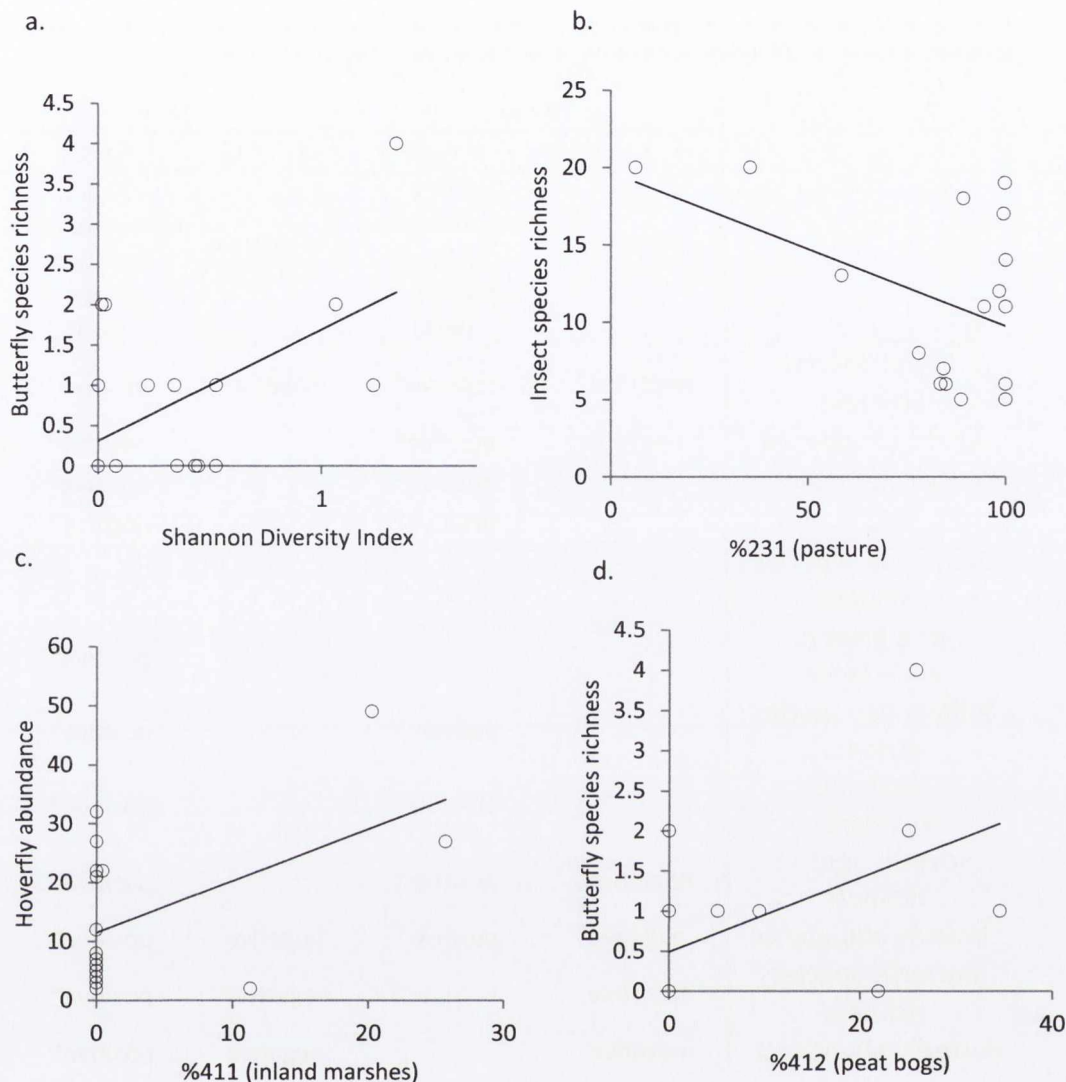


Figure 17: Relationships between the insect diversity and the landscape metrics at 1km scale. Graphs a,b,c and d represent data in 2010. All the significant relationships are not represented, only a few of them are shown to give a general idea of the trends.

These results obtained at 500m and 1km scales were compared with the findings of the chapter 2 (Table 11). While using CLC2012, negative relationships were observed between some of the insect species richness and abundance and the proportion of pasture (231) at 500m and 1km scales. In the previous chapter, only one grassland type, dry calcareous and neutral grassland (GS1), was used in the analysis and showed positive relationships with most of insect abundance and species richness responses.

Table 11 : Relationship between % pasture (231- CORINE) / %semi-natural grassland (GS1-Fossitt) and insect variables (negative/positive significant relationship, * relationship found in both years).

	500m		1km	
	CLC2012	Fossitt	CLC2012	Fossitt
	% pasture (231)	% dry calcareous and neutral grasslands (GS1)	% pasture (231)	% dry calcareous and neutral grasslands (GS1)
Insect Species richness	negative *	positive*	negative*	positive*
Insect abundance	negative	positive*		positive*
Bee species richness		positive*		positive*
Bee abundance		positive*		positive*
Bumblebee species richness				
Bumblebee abundance				positive*
Solitary bee species richness		positive*		positive*
Solitary bee abundance		positive*		positive*
Hoverfly species richness	negative*	positive*		positive*
Hoverfly abundance	negative	positive*	negative	positive*
Butterfly species richness	negative		negative*	positive*
Butterfly abundance	negative		negative	positive*

3.4.5. Landscape scale effects on pollinator diversity: 2.5 and 5km scales

At the 2.5km scale, a higher proportion of arable land was positively related with total insect species richness and butterfly species richness, but there were only two landscapes containing arable land, and it made up <5% of land area (Table 12). At both scales, a high proportion of pasture was negatively related to several insect parameters (Table 12, Figure 18a), except bumblebee abundance (Figure 18b). At the 5km scale only, a higher proportion of forestry in the landscape showed significant positive relationship with the hoverfly species richness and abundance (Figure 18c) and negative significant relationships with bumblebee (and bee) abundance (Figure 18d) and the solitary bee species richness and abundance (Table 12). But again, forestry was uncommon in these landscapes, not exceeding 5% of the surrounding area (Figure 18 c and d).

Table 12: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (insect, bee, bumblebee, solitary bee, hoverfly and butterfly species richness and abundance) and the explanatory variables (%arable, %pasture, %forest and factor Year). Significant results are showed by differing arrows indicating trends. Smaller and thinner arrows represent a *p-value <0.05, medium arrows **p-value <0.01 and bigger and thicker arrows ***p-value <0.001. Non-significant covariate is represented by NS and covariate not considered in the best model (i.e. model with the lowest AIC) is a blank value. Shaded cells represent relationships driven by a four data points.

Response variables	2.5km				5km			
	Landscape metrics		Factor		Landscape metrics		Factor	
	%arable	%pasture	%forest	Year	%arable	%pasture	%forest	Year
Insect species richness	↗	↗		↗	NS	NS		↗
Insect abundance								
Bee species richness		NS					NS	
Bee abundance						NS	↗	
Bumblebee species richness								
Bumblebee abundance			NS		↗		↗	
Solitary bee species richness		↗	NS		↗		↗	NS
Solitary abundance		↗	NS	NS	NS		↗	NS
Hoverfly species richness	NS	NS		↗		↗	↗	↗
Hoverfly abundance	NS	NS		NS		↗	↗	NS
Butterfly species richness	↗	↗			↗			
Butterfly abundance	NS	↗		NS		↗		NS

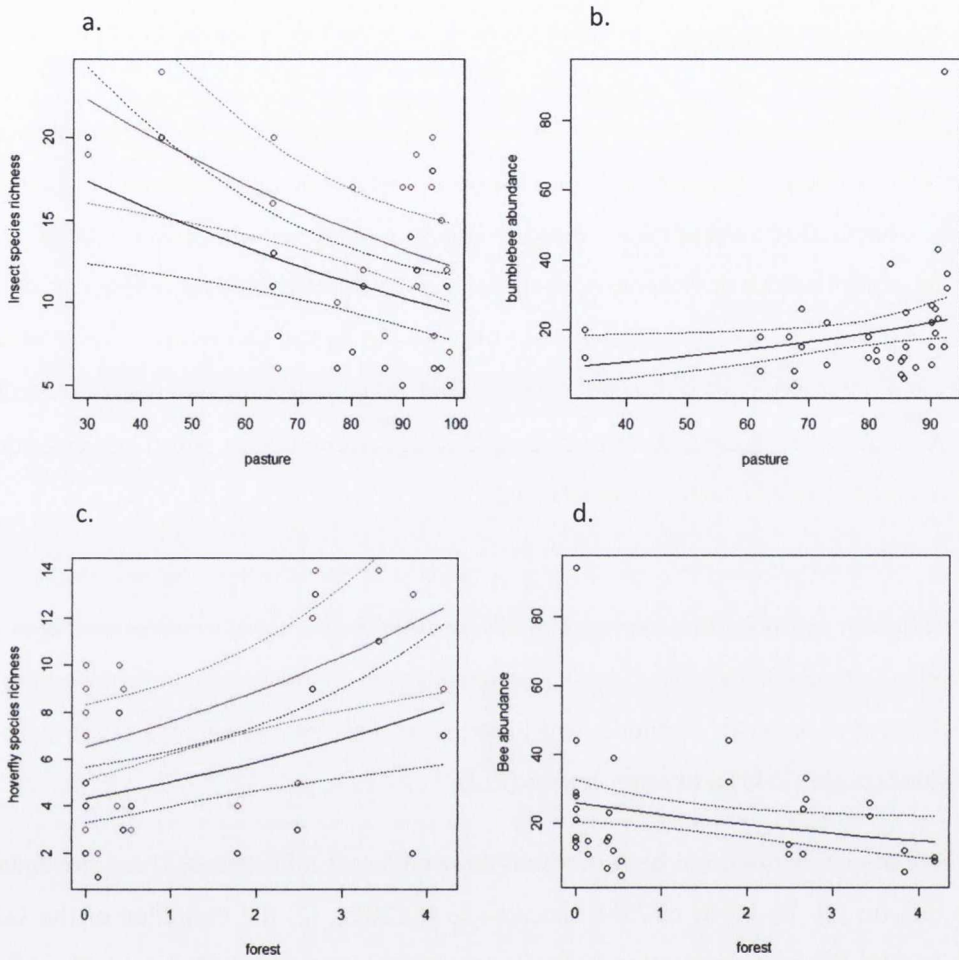


Figure 18: Main effects of the landscape metrics on the insect diversity from the best model (i.e. model with the lowest AIC). Points represent observed values. The lines characterise the model prediction and dotted lines the 95% confidence intervals. The different colours symbolize the two years (black: 2010 and red: 2011). The graphs a represents data at the 2.5km scale and c, d, e at 5km.

3.5. Discussion

3.5.1. Comparison of landscape characterised with Fossitt level 3 and CLC2012 level 3 at 1km scales

As expected, using aerial pictures and ground-truthing to establish Fossitt classification of habitats for landscape characterisation allowed detection of higher resolution land cover patterns. The CLC2012 classification merged adjacent polygons with same CORINE classes, which did not allow the distinction of each polygon in the surrounding landscape. Thus the number of patches in the landscape was not the same using the two methods, and individual patches of habitat were not represented as each individual polygon when using CLC2012, and so it was not possible to calculate the landscape configuration metrics which are dependent of the shape and the size of each individual polygon.

However, CLC2012 allowed the calculation of landscape composition metrics. Habitats with distinct physical features that were generally present over a large continuous area were identified in both classifications. They were relatively well characterized and showed the least mean differences between methods, and included mineral extraction sites (131), peat bogs (412), water courses (511) and water bodies (512).

Other habitats encountered in both methods showed larger differences. These dissimilarities can be due to: (1) the MMU of 25ha allocated to CLC2012; (2) the definition of the CORINE classes and (3) the recategorisation of the Fossitt classes into CLC2012 classes. The MMU of CLC2012 meant that artificial surfaces (112/142), woodland and scrub (including 311, 312, 324), moor and heathland (322), arable land (211), bare rock/sparsely vegetated areas (332/333) were not even detected by CLC2012. The biggest mean difference in area between the two methods was found for pasture (231). The proportion of pasture was generally higher while using the CLC2012 classification in comparison with the Fossitt classification. In Fossitt classification, improved agricultural grassland (GA1) and semi-improved grassland (GA+) were considered as pasture (231). Dry calcareous and neutral grasslands (GS1) and wet grassland (GS4) could be pasture (231) or land principally occupied by agriculture (243) and as it was not possible to choose which category represents them the most, both 231/243 were assigned to the Fossitt code. Thus pasture (231) identified with Fossitt can be underestimated as it did not include the proportion of dry calcareous and neutral grassland (GS1) and wet grassland (GS4). Moreover, some dissimilarities could be due to the widespread prevalence and wide variety of grassland pasture types in Ireland (Sullivan et al., 2010), and the patchy nature of many

pastures which may include other classification types. Different grassland types vary in terms of biodiversity and plant species richness (Sullivan et al., 2010) and those that are flower-rich may have more positive impacts on flower-visiting insect diversity (Edwards, 1998; Meyer et al., 2009). Thus there should be differentiation between these categories in studies of the influence of surrounding landscape on biodiversity and ecological processes.

Inland marshes (411) also showed considerably lower, but noticeable differences between the two methods. The definition of inland marshes (411) is dependent on the level of water present when the remote sensing data are collected (European Topic Centre on Spatial Information and Analysis, 2009). Areas of River Shannon Callows, wet grasslands of turlough basins, poorly drained farmland are included in Fossitt's wet grasslands class (Fossitt, 2000). However, depending on the season, these habitats can be waterlogged to different depths and make it more difficult to distinguish as either inland marsh (411) or pasture/land principally occupied by agriculture (231/243). Moreover, CLC2012 does not report linear features such as hedgerow and stone walls which have been shown to affect pollinator diversity at 500m and 1km scales while using Fossitt level 3 to characterise the landscape. Overall, if not considering the differences due to difficulties of class attribution regarding the grasslands, the differences between the two methods are of ~10% (i.e. the sum of the absolute mean differences of landcover classes between the two methods without considering the differences due to the grassland classification).

3.5.2. Landscape effects using CLC2012 on pollinator diversity at 500m and 1km scales

The proportion of pasture in the landscape showed the most relationships with insect abundance and species richness at the smaller scale, whether using Fossitt (Chapter 2) or CLC2012 (this chapter) to characterise the amount of pasture in the surrounding landscape. For the CLC2012, negative relationships were shown with the proportion of pasture (231) in the landscape. Pasture can be either improved grasslands (GA1), semi-improved grasslands (GA+), dry calcareous and neutral grasslands (GS1) or wet grasslands (GS4). But in our study, pasture (231) replaced in the majority GA1 and GA+ which support less flowering plant species than GS1 (Appendix 11). In chapter 2, positive relationships were revealed between these pollinator responses and the proportion of dry calcareous and neutral grasslands (%GS1). At 500m scale, %GS1 was negatively related with %GA1 ($r = -0.529$), and so negative correlations

between insect abundance and richness and the proportion of 231 (pasture, mostly GA1 and GA+) in this study supports this.

A higher diversity of habitats were positively correlated with the overall pollinator community as well as the two pollinator groups (hoverfly and butterfly) showing the strongest relationships with the landscape metrics. In this study, a higher diversity of habitats was positively correlated with more suitable habitats as mineral extraction sites (131), land principally occupied by agriculture (243), inland marshes (411), peat bogs (412) at 500m and 1km scales.

As shown in chapter 2, all insect groups had relationships with landscape composition metrics up to 1km scale with the bumblebee group presenting the least number of significant correlations.

3.5.3. Landscape effects using CLC2012 on pollinator diversity at 2.5km and 5km scales

Patterns found at 500m and 1km scales were generally consistent using the CLC2012 and Fossitt habitat classifications, and presented similar and justifiable trends regarding the influence of landscape composition on pollinators. We investigated if these patterns can be extended at larger scales by taking into account the foraging distances of each pollinator group, which can vary between pollinator groups and between species. For the solitary bee group, our study showed relationships between landscape composition (in terms of the proportion of pasture and forests) and solitary bee species richness up to 5km scales. The proportion of pasture did not show any relationship with solitary bees at smaller scales, suggesting that solitary bees interact with the landscape more at larger scales. Gathmann and Tscharntke (2002) showed that the foraging distance of the solitary bee group does not exceed 600m, but Greenleaf et al. (2007) suggested greater maximum foraging distance which can explain the scale of interaction of the solitary bees in the context of this study. Woodland can act as an unsuitable habitat for the solitary group when considering surrounding landscape at a larger scale. Similar relationships were found between hoverflies and landscape composition variables at smaller scales and at the larger 5km scale, i.e. there were consistent negative relationships between pasture and hoverfly abundance, and between pasture and hoverfly species richness at the larger scale. Additionally forest showed positive relationship with hoverflies at 5km, confirming what previous studies had investigated that forests are important land use type for the hoverfly community because they offered sites for

overwintering and larval microhabitats (Meyer et al., 2009; Speight, 2011). Butterfly foraging distances vary among species (Cant et al., 2005), and again, there were similar patterns at small as well as larger scales: negative relationships between butterfly abundance and species richness and proportion of pasture extended up to 5km scales. Finally, the bumblebee group was the least related with the landscape composition metric at smaller scale suggesting that they are affected by land cover patterns at a larger scale. This may be explained by the large flight distances of bumblebees: they forage between several hundred meters up to several kilometres from their nest (Carvell et al., 2012; Knight et al., 2005). At larger scales, there was also a negative relationship between bumblebees and the proportion of forest in the landscape. One explanation could be that this landscape element can be an unsuitable habitat for the bumblebee.

3.6. Conclusions

The process of CLC creation implies some mechanisms which affect the representation of the landscape and lead to some spatial inaccuracies (due, inter alia, to the merging of polygons with the same CLC class) and some thematic generalisation to fit the common European classification. Therefore, CLC database cannot characterise the landscape with a high precision and as its name suggests should not be used to characterise the landscape configuration. However, compositional landscape metrics derived from CLC showed, globally, some consistencies with datasets obtained with Fossitt. Classes used in CLC do not report fine scale biodiversity differences which have showed to be important to integrate in ecological studies. In the context of this study, different grassland types varying in term of plant composition were all categorised in the same CLC category. The area of this study was located in a less intensive farming system mostly dominated by grasslands. This means some patterns were in some circumstances more difficult to detect.

Therefore the use of CLC must be an informed decision. It is imperative before reporting CLC classes to understand to which national habitat they correspond and all users must be aware of the different successive steps of the production leading to spatial and thematic generalisation. However, CLC2012 presents some advantages as it does not require a lot of resources to generate and is readily available, which is advantageous for many studies where no national habitat or landcover system is in place.

Finally, the way to justify the use of the CLC in pollinator studies depends on the research question we would like to answer, and this includes consideration of using a high resolution

landscape characterisation. In studies considering the landscape aspect across different European countries, the use of CLC2012 must be preferred as it allows a standardisation of the landscape characterisation. Studies undertaken within a country should preferably work on available national habitat or landcover maps and if possible ground truthed with some fieldwork to allow the detection of fine scale biodiversity features which cannot be identified with CLC2012 but could be important elements of the landscape for the pollinator. However in the case of national studies which cannot afford fieldwork and where national maps are not available, CLC can be an alternative but it should be used cautiously.

Chapter 4

Regional and land use intensification effects on beta taxonomic and functional diversity in bee communities

To be submitted as: Hecq, F., Bartomeus, I., Stout, J. C (and all the data providers). Regional and land use intensification effects on beta taxonomic and functional diversity in bee communities. *Journal of Applied Ecology*.

4. Regional and land use intensification effects on beta taxonomic and functional diversity in bee communities

4.1. Abstract

In natural habitats, similar functional roles are undertaken by different species in different regions of the world. However, this may not be the case for habitats that are highly transformed, like agricultural cropland. For two widely grown crops, we investigated whether similar functional roles are realised, despite pollinator species turnover across different regions. At a landscape scale, it has been observed that land use intensification (LUI) decreases species richness, but species more sensitive to land use intensification are not a random subset of species and some species may even benefit from LUI. The second objective of this study was to investigate if the LUI also affects species turnover and if this results in a functional change in community composition. These two drivers operate simultaneously and we aimed to investigate how LUI and the geographical location have shaped species and functional community change.

We gathered existing data from 13 studies on the species of bees, and their related traits, visiting two crops systems: coffee (*Coffea sp.*) and oilseed rape (*Brassica napus*). Coffee systems were located in two regions (Asia and Central America) and the oilseed rape systems along a European latitudinal gradient (from United Kingdom to North Sweden). Within each system, crops were situated at different distances to the nearest semi-natural habitat: we used this distance as a proxy for land use intensification. We used Permutational multivariate analysis of variance to assess changes in species and functional composition due to the geographic location and land use intensification. Compositional changes (i.e. beta-diversity) were assessed in terms of both richness and turnover.

Our results indicated that there was species turnover (in coffee) and species richness differences (in oilseed rape) across geographical locations, but also different functional roles were realised. LUI decreased species richness for both crop species which resulted in a decrease in the functional breadth of visitors to coffee and in functional replacement in oilseed rape crops. These changes in species and functional composition may impact the ecosystem resilience.

4.2. Introduction

Species composition varies in similar habitat types across geographic locations (Gaston, 2000; Siefert et al., 2013). Despite this, Darwin (1859) suggested that similar functional roles are undertaken by different species in different regions of the world. This pattern has been observed in natural systems (Darwin, 1859) but not in habitat types that are highly transformed, like cropping systems. Many crops benefit from interactions with pollinators (Klein et al., 2007), and widespread crops, grown in many different countries across the world, may be pollinated by distinct species in different regions. In addition, since species richness tends to increase with decreasing latitude for a wide range of taxonomic groups (Gaston, 2000; Qian and Ricklefs, 2007; Qian and Wang, 2015; Tang et al., 2012), we might expect both a change in the identity of species due to the physiological constraints and a change in the total number of species pollinating crops that are grown across a latitudinal gradient. For this study, we will test whether, despite a noticeable pollinator species replacement across different regions, similar functional roles are realised in highly manipulated habitats.

The variation in species composition among communities was described by Whittaker (1960) as beta-diversity. This concept can be used to understand the sensitivity of the community to changing environmental conditions and the interdependency of species associations (Van Dyke, 2008). Beta-diversity is driven by the two phenomena: species replacement (turnover) and the species richness differences (Carvalho et al., 2012). These two components of beta-diversity are the results of different ecological mechanisms (Baselga, 2010; Legendre, 2014). However, diversity measures are not restricted to taxonomy but can also consider the functional aspects of organisms in a community. The diversity of traits, or functional diversity, can determine the potential niche of an individual and how it interacts with individuals from other species (McGill et al., 2006). It also potentially provides information on the contribution of species to the functioning of an ecosystem (Hillebrand et al., 2008; Lavorel et al., 2011; Mokany et al., 2008).

Land use intensification (LUI) is occurring worldwide at a rapid pace (McLaughlin and Mineau, 1995; Turner and Meyer, 1994) and it is known to negatively affect species richness (Weibull et al., 2003). It is frequently assumed that species and functional diversity decline simultaneously with the LUI, but in fact more complex patterns might occur. LUI does not affect all species in the same way: species which are well adapted to anthropogenic modifications of the environment and/or disturbance may benefit, whilst other may lose out (Rader et al., 2014). Thereby LUI affects not only species richness but also species replacement, and this may

influence the functional community composition. LUI may not affect all species in the same way because species are mediated by their functional traits, and some traits may be more vulnerable than others (De Palma et al., 2015; Henle et al., 2004; Newbold et al., 2013). Our study also investigated whether LUI affects not only species richness but also species replacement, and if this is reflected in functional community composition. LUI and geographical location operate simultaneously and we compared both of these effects to characterise how LUI and the geographical location has shaped species and functional community change.

To address these objectives, we focused on bees because they are ecologically important (Ollerton et al., 2011). Although other insects contribute to crop pollination worldwide (Rader et al., 2015), bees are often the most efficient pollinators, and are most commonly studied. To represent the highly transformed habitats, two contrasting crop species were chosen dependent on the datasets readily available: oilseed rape (*Brassica napus* L.) in Europe and coffee (*Coffea arabica* and *C. canephora*) in Central America and Asia. *Brassica napus* L. is increasingly cultivated as a crop in Europe for production of animal food, oil and biodiesel and can self-pollinate, but seed production is increased by visitation from pollen and nectar feeding insects, including wild bees and honey bees (Bommarco et al., 2012; Hayter and Cresswell, 2006; Morandin and Winston, 2005; Sabbahi et al., 2005). *Coffea arabica* is partially self-compatible, whilst *C. canephora* is partially self-infertile (Ngo et al., 2011), but *Coffea* sp. flowers are commonly visited by bees, which can increase fruit set and quality in both species (Ngo et al., 2011; Roubik, 2002b).

4.3. Materials and methods

4.3.1. Bee community data

Flower-visiting insect datasets of coffee and oilseed rape crops were obtained by gathering information from existing studies.

For coffee, the dataset was represented by six different systems located in four countries (Mexico, Panama, Indonesia and India) (Table 13, Figure 19). Each system was composed of at least eight sites and a total of 94 sites were sampled. For oilseed rape, we used datasets from five systems located in four European countries: Sweden, Ireland, UK and Netherlands (Table 14, Figure 19). A minimum of five sites were sampled per system, which resulted in data from a total of 56 sites.

Sampling mostly focused on bees rather than other pollinator groups, and as bees are important pollinators, we limited our analysis to this taxon. As this study was built on available datasets, different methods were used to sample bee communities in different studies. Observations of focal plant species and transect walks were mainly used to sample bees in coffee crops, whilst bees visiting oilseed rape were mainly sampled via transect walks. Since different methods were used in different studies, it was difficult to standardise relative abundance of different bee species, and so we used presence-absence information only.

Table 13: Summary of the coffee datasets used in this study.

Region	Location	Species and variety	Number of sites	Reference
Asia	Indonesia Sulawesi	<i>Coffea arabica</i>	24	Klein (2009)
	Indonesia Sulawesi	<i>Coffea canephora</i>	15	Klein et al. (2003)
	India Kodagu	<i>Coffea canephora robusta</i>	22	Krishnan et al. (2012)
Central America	Mexico, Veracruz	<i>Coffea arabica</i> , Bourbon, Catimor CR-95, Caturra, Mundo Novo, Typica	16	Badano and Vergara (2011)
	Panama	<i>Coffea arabica</i> and catimor, the backcross hybrid of <i>arabica</i> plus <i>canephora</i> to <i>arabica</i>	8	Roubik (2002a); Roubik (2002b)
	Mexico, Chipas	<i>Coffea arabica</i>	9	Jha and Vandermeer (2009)

Table 14: Summary of the oilseed rape datasets used in this study.

Average latitude (WGS1984)	Location	Species and variety	Number of sites	Reference
59.818	Sweden, Upland	<i>Brassica napus</i> var. <i>napus</i> (<i>Stratos</i>)	10	Bommarco et al. (2012)
57.728	Sweden, Vastergötlan	<i>Brassica napus</i> var. <i>napus</i> (<i>Excalibur</i> and <i>Compass</i>)	15	Bartomeus et al. (2014)
52.688	Ireland	<i>Brassica napus</i> var <i>Castille</i> and <i>mixture Castille and Excalibur</i>	5	Stanley and Stout (2013)
52.183	Netherlands	<i>Brassica napus</i>	12	Kleijn et al. (2015)
51.462	United Kingdom	<i>Brassica napus</i> var. <i>napus</i> (<i>Excalibur</i> and <i>Compass</i>)	14	Not published

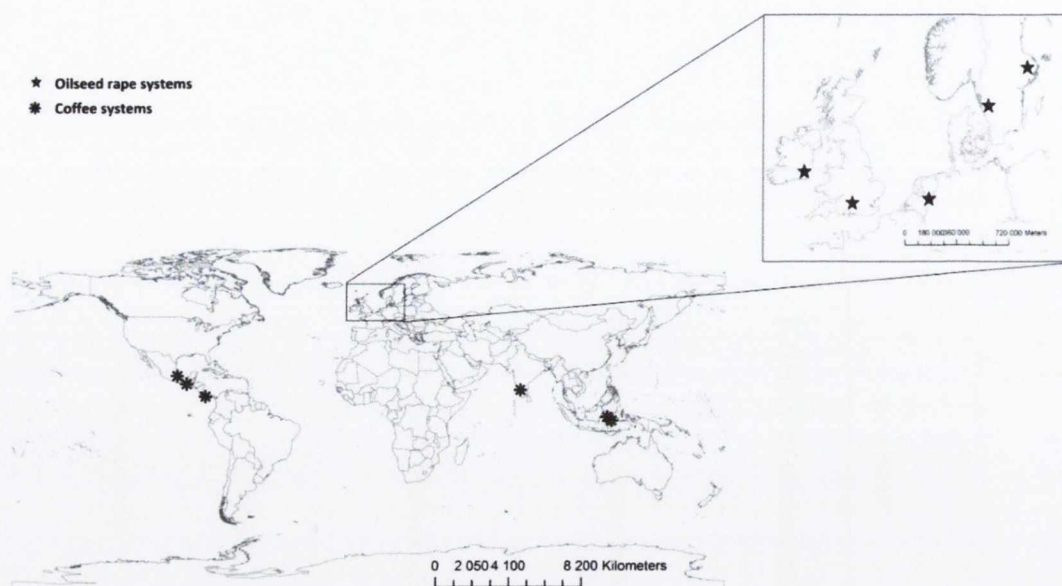


Figure 19: Location of the oilseed rape and coffee crop systems.

4.3.2. Regional and land use intensification

Systems were classified according to their geographic position. Coffee crop systems were grouped in two regions (Central America and Asia) and oilseed rape crop according to a latitudinal gradient in Europe. Additionally, sites within each system were classified according to a land use intensification gradient, which was based on the distance to the nearest natural habitat. We used the distance metric because it was most accessible measure to obtain from all studies. This distance was measured from aerial photographs and/or ground-truthed with fieldwork. We followed the decision from the data owner of each study regarding what constituted semi-natural habitat. For coffee, natural habitat corresponded mainly to the forest. For oilseed rape, semi-natural habitat included woodland, flower-rich grasslands, and hedgerows, depending on whether it was grown in intensive or extensive landscapes.

To account for differences among studies in how the distance to the nearest semi-natural habitat was calculated and because the identity of semi-natural habitat differed between systems, some standardisation among studies was necessary. The distances to the nearest semi-natural habitat were thus standardised to have a mean of zero and a standard deviation of one.

4.3.3. Trait data

Bee species were characterised according to eight traits related to their morphology, behaviour and life history. These traits were chosen as they can be good predictors of pollination efficiency, have been used in previous studies and are easily measured (Albrecht et al., 2012; Garibaldi et al., 2015; Martins et al., 2015). Body size was defined according to the inter-tegular span (ITD) i.e. the distance between the two insertion points (tegula) of the wings of the females (workers in social species) of each species. Thereby body size was classified as tiny (< 1.5 mm ITD, typical foraging distance < 50 m), small (1.5–2.0 mm ITD, typical foraging distance 50–300 m), medium (2–3.3 mm ITD, typical foraging distance 300–1100 m), and large (> 3.3 mm ITD, typical foraging distance > 1100 m) (Greenleaf et al., 2007). Tongue or proboscis length was classified as short (<3mm), medium (3–8mm) and long (>8mm). Sociality (yes vs no) was defined as colony building, including all eusocial as well as primitively social species. Polylectic (yes vs no) included bees visiting a variety of flowers to collect pollen, whereas oligolectic species collect pollen from one or few closely related species of plants. Seasonal activity (complete vs partial) (Junker et al., 2013) referred to whether the pollinator species visits the crop during the whole flowering period or only during early, middle or late stages of flowering. Kleptoparasitic bees (yes vs no) were assumed to be less effective pollinators as they do not actively collect pollen. Buzz pollination (yes vs no) was defined if bees were able to sonicate anthers by vibrating vigorously. Finally, we classified bees according to whether they were central place foragers i.e. consistently return to their nest after foraging (yes vs no).

Traits were measured on specimens when available, if that was not possible, information was found in the literature.

4.3.4. Data analyses

Due to the different sampling methods between systems, abundance data were not comparable, and so taxonomic and functional diversity measures were derived from presence-absence datasets. We calculated the dissimilarity among all pairwise sites for the taxonomic and functional diversity indices. We followed Carvalho et al. (2012)'s approach to calculate taxonomic beta-diversity. This method disentangled the overall beta-diversity (β_{tot}) into species replacement (β_3) and species richness differences (β_{rich}) according the formula:

$$\beta_{\text{tot}} = \beta_3 + \beta_{\text{rich}}$$

These three terms are derived from: a, the number of species common to both communities; and b and c which are the number of species exclusive to site 1 and 2 respectively (Figure19).

Replacement between communities (β_3) corresponds to the substitution of n species in site 1 by n species in the site 2. This was calculated as the minimum number of exclusive species multiplied by two, and expressed as a proportion of the total number of species recorded:

$$\beta_3 = 2 \times \frac{\min(b,c)}{a+b+c}$$

$\beta_3 = 1$ when the exclusive species in both sites are the same and when there are no shared species.

The difference in species richness between communities was calculated as the absolute difference in species richness between two sites and expressed as the proportion of the total number of species recorded:

$$\beta_{\text{rich}} = \frac{|(b+a)-(c+a)|}{a+b+c} = \frac{|b-c|}{a+b+c}$$

β_{rich} approaches 1 when there are large differences in exclusive species between two sites and when there are no shared species.

These two terms lead to the following equation for overall beta diversity:

$$\beta_{\text{tot}} = \frac{b+c}{a+b+c}$$

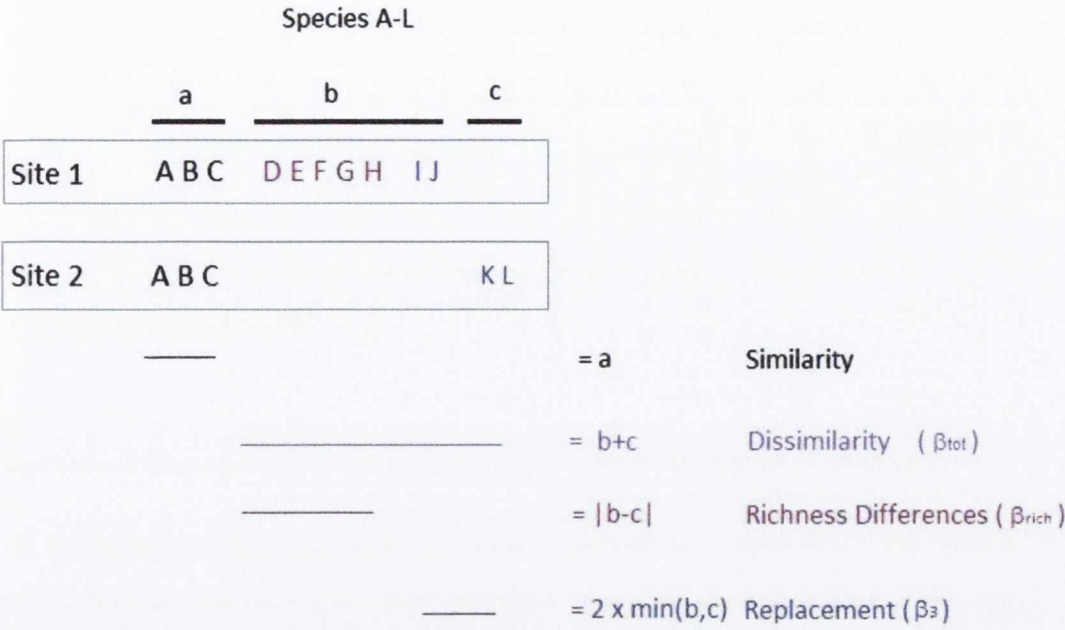


Figure 20: Example of the species composition of two sites (a is the number of shared species, b and c are the species exclusive to each site). This illustration is based on Legendre (2014).

For functional beta diversity, we applied this same framework to the measure of functional diversity developed by Petchey and Gaston (2002). Functional diversity is defined as the sum of the vertical branch length of a functional dendrogram which measures the extent of trait complementarity among species (Petchey and Gaston, 2002). The branches are used to calculate the a, b and c which correspond respectively to the common branches, the branches specific to site 1 and the branches specific to site 2, which are used then as explained above for taxonomic betas (Figure 20).

We developed R script to calculate beta-taxonomic and functional diversity. These codes are publicly-available (<https://github.com/ibartomeus/fundiv>).

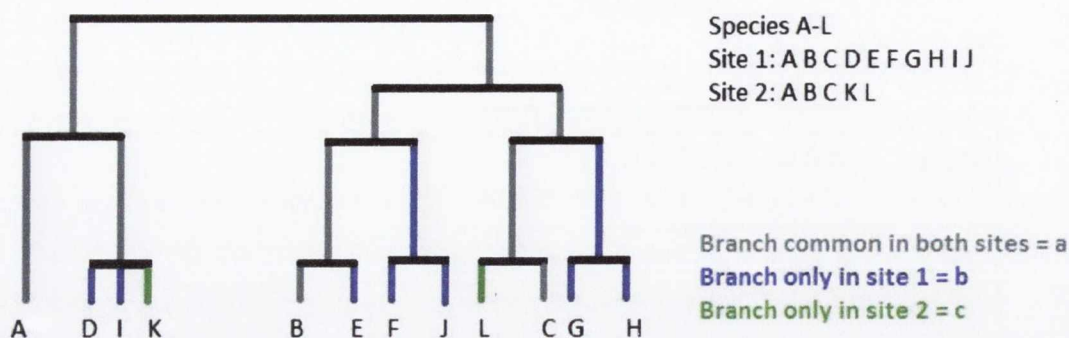


Figure 21: Example of a functional dendrogram of the relation between the species A-L. Only vertical branches contribute in the calculation.

Differences in community composition and function between regions (coffee) and along the latitudinal gradient (oilseed rape), and according to distance from semi-natural habitat, were tested using permutational multivariate analysis of variance (PERMANOVA; (Anderson, 2001)) based on 999 permutations. Additionally, for the categorical variable (region), to test whether one region was more variable than the other one, a permutational analysis of multivariate dispersion (PERMDISP; (Anderson, 2006)) based on 999 permutations was used. PERMANOVA and PERMDISP were performed respectively with the function `adonis` and `betadisper` from the ‘vegan’ package (Oksanen et al., 2007) in R. These tests were also performed separately on the two components (β_{rich} and β_3) of beta-diversity. Non metric multidimensional scaling (NMDS) using the `metaMDS` command (from the package `vegan`) was used to illustrate the differences in taxonomic and functional composition. Additionally, for visualisation purposes, the average taxonomic and functional dissimilarity per site (calculated as the average beta diversity between one site and all the other sites) were plotted against the distance to the nearest natural habitat. All these analyses were also performed on the two components: differences in species richness (β_{rich}) and species replacement (β_3).

4.4. Results

4.4.1. Coffee

A total of 76 bee species were recorded in all the coffee systems (Appendix 13). The number of species found per site varied from one to 24. These species recorded were mainly central place foragers, polylectic, non-kleptoparasitic, non-“buzz” pollinators and visiting the coffee crop during the whole flowering period but presented variation in body size, tongue length and sociality.

Community composition was different between regions and varied with distance from semi-natural habitats (adonis, $F_{1,93}=1.445$, $p=0.026$, $R^2=0.012$, Table 15, Appendix 14). However, the direction of response was different in Asia and Central America, with average compositional dissimilarity per site increasing with distance from natural habitat in Asia but decreasing in Central America (Figure 22a). Moreover the results showed differences in dispersion for the community composition between the two regions (betadisper, $p=0.001$, Table 16), however, it was not possible to visualise the community composition differences in an NMDS because the two regions were completely different.

When the overall differences in community composition were decomposed into species replacement and species richness differences, some significant patterns appeared. In both regions, species richness dissimilarity varied with the distance to the nearest semi-natural habitat (Adonis, $F_{1,93}=4.149$, $p=0.001$, $R^2=0.047$, Table 15 and Appendix 14). Moreover, the average species richness dissimilarity per site decreased with distance from semi-natural habitat (Figure 22b). Species replacement was different between regions and changed with the distance to the nearest natural habitat differently in Asia and Central America (adonis, $F_{1,93}=3.266$, $p=0.013$, $R^2=0.022$, Table 15, Figure 22c, Appendix 14). Moreover, average species replacement per site increased more rapidly with distance from semi-natural habitat in Asia than in Central America (Figure 22d).

The functional composition of the bee community was significantly different in Asia and Central America (adonis, $F_{1,93}=17.923$, $p=0.037$, $R^2=0.162$, Table 15, Appendix 14) and was also affected by the distance to the nearest semi-natural habitat (adonis, $F_{1,93}=3.444$, $p=0.002$, $R^2=0.031$, Table 15, Appendix 13). There were differences in dispersion for the community functional composition between the two regions (betadisper, $p=0.016$, Table 16). NMDS ordination (stress= 0.203, Figure 23a) showed two clear clusters of sites by region. The average functional composition dissimilarity decreased with distance from semi-natural habitat (Figure

23b). The functional richness differences were also affected by the distance to semi-natural habitat (adonis, $F_{1,93}=2.016$, $p=0.042$, $R^2 = 0.021$, Table 15, Appendix 14). The average functional richness dissimilarity per site decreased with the distance to the nearest semi-natural habitat (Figure 23c). Finally, the results showed that functional replacement was significantly variable between regions (betadisper, $p<0.001$, Table 16).

Table 15: P-values and R² of PERMANOVA for the different components of beta taxonomic and functional diversity between regions, according to the distance to the nearest natural habitat and the interaction between these two variables.

	Region		Distance to nearest natural habitat		Region *distance to nearest natural habitat		
	R ²	p-value	R ²	p-value	R ²	p-value	
beta taxonomic diversity	Total	0.209	0.001 ***	0.022	0.001 ***	0.012	0.026 *
	Species richness differences	-0.077	N.S.	0.047	0.001 ***	0.014	N.S.
	Species replacement	0.390	N.S.	-0.025	N.S.	0.022	0.013 *
beta functional diversity	Total	0.162	0.037 *	0.031	0.002 **	-0.006	N.S.
	Functional richness differences	0.063	N.S.	0.021	0.042 *	-0.010	N.S.
	Functional replacement	0.333	N.S.	0.020	N.S.	0.005	N.S.

Table 16: P-values of the PERMDISPER between the regions and the different components of the beta taxonomic and functional diversity.

	Region
	p-value
beta taxonomic diversity	Total
	Species richness differences
	Species replacement
beta functional diversity	Total
	Functional richness differences
	Functional replacement

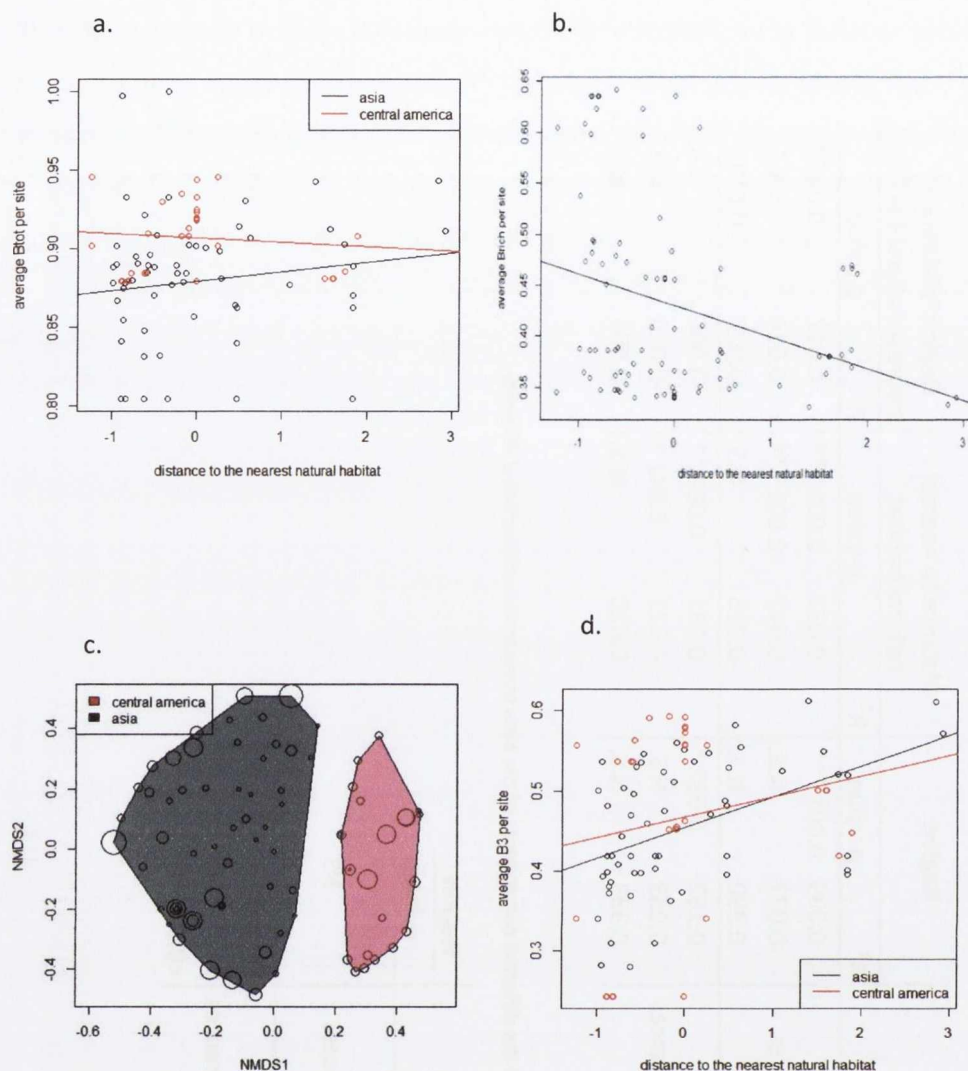


Figure 22: Relationships between the different components of beta taxonomic diversity (β_{tot} , β_{rich} and β_3) and the region and land use intensification. The graphs (a), (b), (d) represent the average dissimilarity of the respective beta components against the distance to the nearest semi-natural habitat. The distance to the nearest semi-natural habitat is standardized. The graph (c) represents the NMDS ordination accounting for the species replacement (β_3) (the size of the circles is proportional to the distance to the nearest natural habitat: smaller circles – closer to natural habitat, larger ones – further)

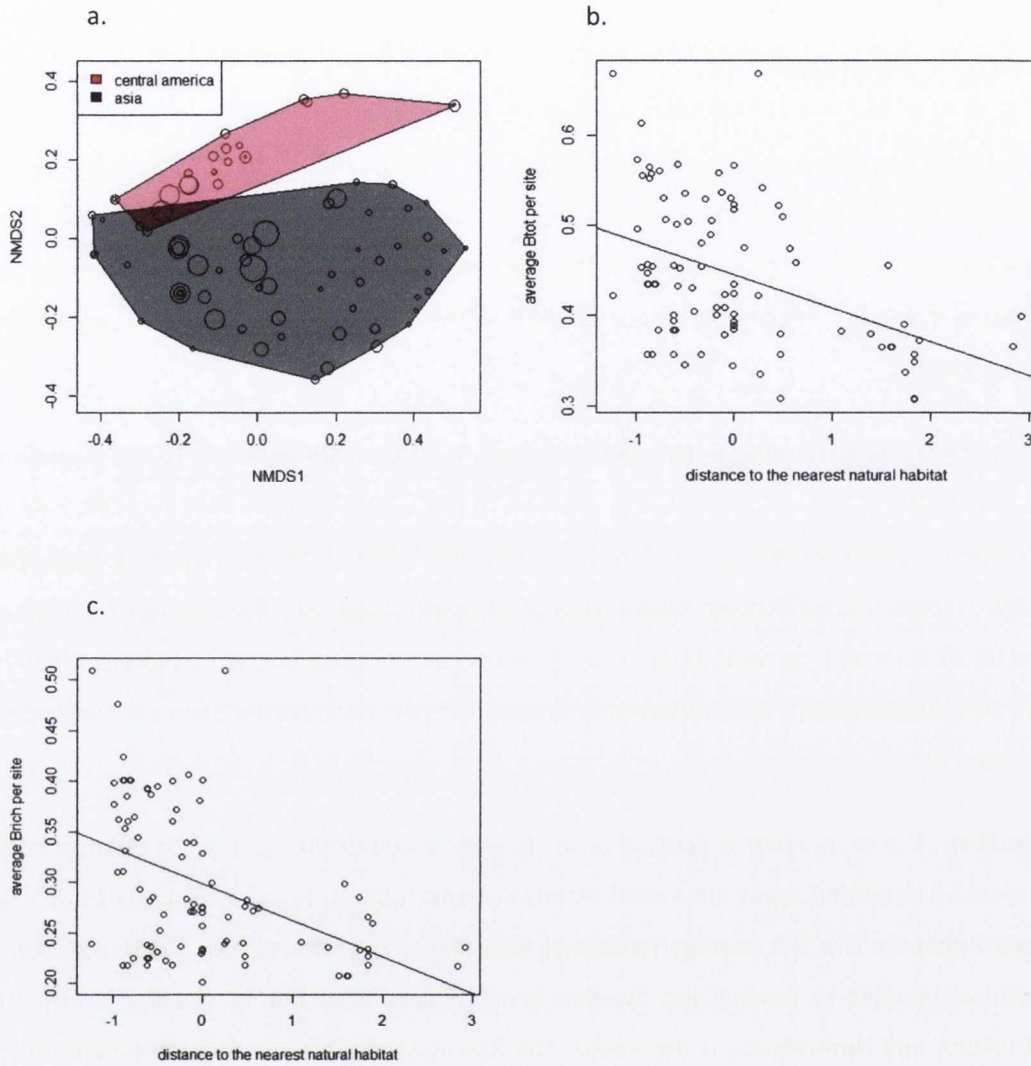


Figure 23: Relationships between the different components of beta functional diversity (β_{tot} and β_{rich}) and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized. The graph (a) represent the NMDS ordination accounting for the difference in functional composition (β_{tot}) (the size of the dots is proportional to the distance to the nearest natural habitat). The graphs (b) and (c) represent the average dissimilarity of the respective β components against the distance to the nearest natural habitat.

4.4.2. Oilseed rape

Forty-eight bee species were observed in the five systems (Appendix 15). The range of species found per site varied from one to ten. The species were mainly central place foragers, polylectic and non-kleptoparasitic and visited the crop during the whole flowering period. However, the bee species presented variation in the body size, tongue length, buzz pollination and sociality.

The species richness difference component was related to the distance to the nearest semi-natural habitat, but the strength and direction of this relationship was not consistent along the latitudinal gradient (adonis, $F_{1,55}=3.421$, $p=0.018$, $R^2=0.060$, Table 17, Figure 24, Appendix 16). The average species richness dissimilarity per site increased with the distance from the semi-natural habitats in the northern latitudes (Sweden and Ireland), but in the more southerly sites (United Kingdom and The Netherlands), species richness dissimilarity decreased with distance (Figure 24).

Similarly, the overall beta functional diversity was related to the distance to the nearest semi-natural habitat and again this varied among systems (adonis, $F_{1,55}=6.817$, $p=0.014$, $R^2=0.096$, and Appendix 16). The average functional dissimilarity per site increased with distance from natural habitats in Ireland and Sweden South (Figure 25a) but in Sweden North, United Kingdom and Netherlands, it decreased. The functional replacement varied significantly with the distance to the nearest natural habitat and differently between latitudes (adonis, $F_{1,55}=116.283$, $p=0.028$, $R^2=0.446$, Table 17 and Appendix 16). The average functional replacement dissimilarity per site decreased in all systems except for Ireland (Figure 25b).

Table 17 : P-values and R² of PERMANOVA for the different components of beta taxonomic and functional diversity along a latitudinal gradient and according to the distance to the nearest natural habitat and the interaction between these both variables.

	latitude		distance to nearest natural habitat		latitude*distance to nearest natural habitat	
	Rsquare	p-value	Rsquare	p-value	Rsquare	p-value
beta taxonomic diversity	Total	0.174	N.S.	0.019	0.022	N.S.
	Species richness differences	-0.007	N.S.	0.040	0.060	0.018 *
	Species replacement	0.294	N.S.	0.008	-0.034	N.S.
beta functional diversity	Total	0.216	N.S.	-0.047	0.096	0.014 *
	Functional richness differences	0.111	N.S.	0.011	0.016	N.S.
	Functional replacement	0.713	N.S.	-0.360	0.446	0.028 *

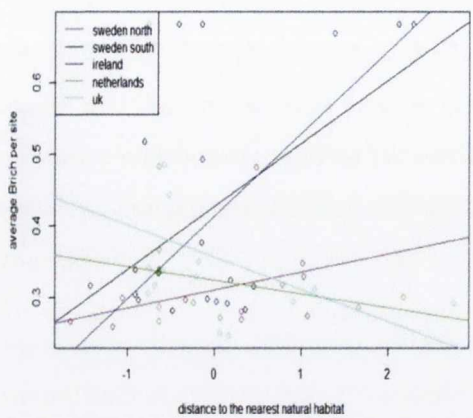


Figure 24: Relationship between the average species richness (β_{rich}) per site and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized.

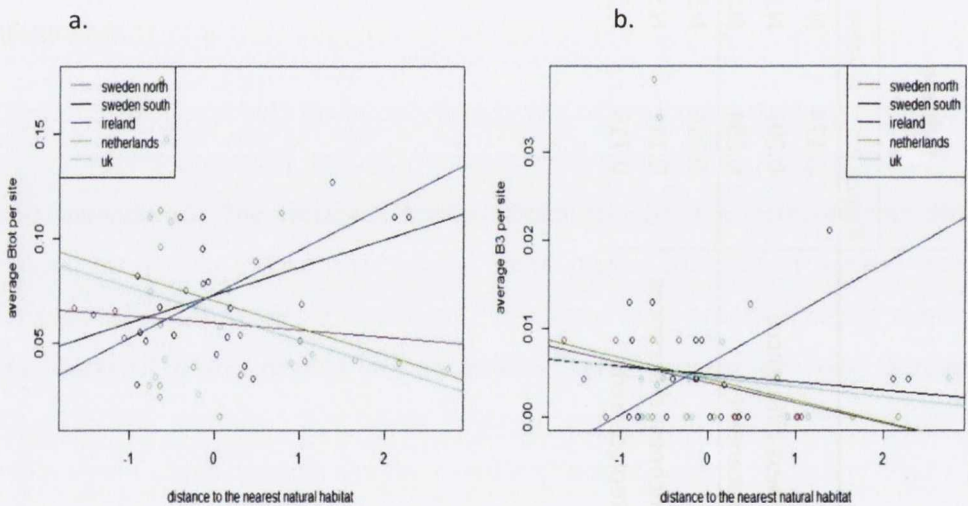


Figure 25: Relationships between the average β_{tot} , β_3 and the distance to the nearest natural habitat. The distance to the nearest semi-natural habitat is standardized.

4.5. Discussion

4.5.1. Regional and land use intensification effects on beta-diversity of bee visiting coffee crops

At the start of this study, we assumed that species composition would be different between regions. Most bee taxa have distributions that do not expand outside the continent level

(Michener, 1979). This explains the differences we found in species composition between the two regions studied. However, different overall functional diversity was also observed between regions. This is initially surprising as we would expect that the different bee communities would provide similar functional roles in both regions. This finding could be explained by the fact that *Coffea arabica* and *C. canephora* both originate from Africa (Clay, 2004; Ngo et al., 2011). It could also be explained by the fact that neither bee communities in Central America or Asia are adapted to forage on coffee. In Asia, bees were mainly solitary and present a range of different body sizes and tongue lengths while in Central America, bees were mainly social and of small size and presented medium tongue length.

Within each region, land use intensification also shaped community composition. The average compositional dissimilarity per site increased with distance from natural habitat (mostly forests) in Asia but decreased in Central America. Therefore sites further from forest were more dissimilar in Asia and more similar in Central America than sites closer to this natural habitat. This trend was mainly due to species replacement. Findings from Bravo-Monroy et al. (2015) showed that the proximity of forests was an important factor in predicting the bee community composition within the coffee crop as the forest could provide new resources essential for some bee species. For example, some honeybees (except *Apis cerana*) and stingless bees have been found nesting in cavities of tall or dead trees (Hayter and Cresswell, 2006; Klein et al., 2003) and thereby might be negatively affected by the land use intensification. Moreover, some species which are well adapted to anthropogenic adaptation of the environment may benefit from the land use intensification (Rader et al., 2014). However, the opposite pattern was found in each region. We had no data on the forest composition and structure in Asia and Central America. But it might be possible that these forests differed structurally and taxonomically between regions and therefore provided different resources for bee communities. This could be responsible for the different trends found in both regions. The effect of land use intensification on the community composition could reflect differences in the species available to visit coffee in each site.

However, land use intensification affected species richness independently of the regions. The average species richness dissimilarities per sites decreased with the distance to the nearest natural habitat. Sites close to the forests were more dissimilar in species richness than the sites further away. There was a tendency to homogenisation of bee communities with increasing distance from forest. This trend was also reflected for the functional richness difference (and the overall functional composition differences). Sites close to forests were

more functionally dissimilar than they were further away. These findings are consistent with the fact that species losses pattern are often mediated by the species functional traits (De Palma et al., 2015; Henle et al., 2004; Newbold et al., 2013). Some specific traits might be more sensitive to the land use intensification. For this study, we noticed that species losses primarily affect bees with social behavior, large body size and shorter tongue (data not shown). These changes in bee functional diversity among sites could have implication for the ecosystem resilience.

These results should be taken with caution as the bee sampling was conducted on different coffee species depending on the system. This can lead to some variation in the bee community composition visiting the coffee flowers.

4.5.2. Regional and land use intensification effects on beta-diversity of bee visiting oilseed rape crops

A latitudinal gradient of species richness differences was observed for the bee community visiting the oilseed rape crops. Depending of the latitude, these species richness differences changed in different ways with the isolation from the nearest semi-natural habitat. The composition and the identity of the natural habitats should vary between latitudes and could be responsible of the different patterns observed. An increase in species richness was observed from polar to equatorial latitude in various studies (Qian and Ricklefs, 2007; Qian and Wang, 2015; Tang et al., 2012) and in temperate countries beta-diversity of a range of taxonomic groups generally decreased with agricultural intensification (Ekroos et al., 2010; Flohre et al., 2011; Vellend et al., 2007). Our results agree with findings from a recent study from Rader et al. 2015 showing that bee (except honeybee) visitations are affected by the isolation from semi-natural habitats. Our findings suggested that latitude and land use intensification only shaped the species richness differences components which did not correspond to a change in the community composition. In this case, we show that two gradients (i.e. a latitudinal gradient and a gradient of land use intensification) may act in synergy on the richness component and create a non-random pattern of species loss.

However, this change in species richness does not provide similar functional role at different latitudes and along a gradient of land use intensification. Bee functional community composition changed with the latitudinal increase. Depending of the latitude, the functional community composition changed as the distance to the nearest natural habitat increased. This

trend was mainly due to functional replacement. Thereby, this implies that these changes in functional diversity among sites could have also implication in ecosystem resilience.

4.5.3. Limitation of this study

Although our results showed that the taxonomic and functional diversity patterns were determined by the region and distance to the nearest natural habitat, much than 50% of the variation (R^2) remains unexplained. Indeed, R^2 values of the effects of the region and distance to the nearest semi-natural habitat are low ($\sim 1\text{-}2\%$). For macro ecological patterns, we should expect these low values as other factors play in the processes such as local management, temporal variation and the connectivity and configuration in the landscape which have shown to affect bee community composition (De Palma et al., 2015; Hopfenmueller et al., 2014; Jha and Vandermeer, 2009; Jha and Vandermeer, 2010; Kremen et al., 2002; Roubik, 2001). Moreover, the distance to the nearest semi-natural habitat is a very indirect measure of overall land use intensification and can be restrictive in its use. It gives an indication of the degree of habitat disturbance locally but is not necessarily related to the intensity of land use and it does not take into account of any other land uses or configuration of patches in the surrounding landscape.

Another key limitation in this study is the use of presence/ absence data which mean a loss of information on relative abundance. Kleijn et al. (2015) showed that it is the abundance of a few common species which drive crop pollination. Therefore, it is not possible to relate the findings of this study to the provision of pollination services.

Finally, for some bee species (*Apis mellifera*, *Apis cerana* and *Bombus terrestris*) it was not possible to make the distinction between the wild and managed species. The latter are likely to reflect beekeeper activities, as well as landscape and geographic location. Therefore results should be taken with caution as some effects might be overestimated, especially for the oilseed rape as the honeybee (*Apis mellifera*) was found in 87% of the sites and account for 20% of the visitation.

4.6. Conclusions

Our results showed that despite a species turnover (coffee crop) or species richness differences (oilseed rape) due to the geographic location, different functional roles were realised regardless of where crops were grown. Land use intensification also shaped species

richness differences for both crop species, in terms of functional richness differences in coffee and to functional replacement in oilseed rape. Our results showed that in temperate and tropical countries, the geographical location and the land use intensification are both shaping, in different ways, species and functional composition of bee communities visiting highly transformed habitats. Our findings may have implication for the resilience of ecosystem.

Chapter 5

Effects of landscape structure on the provision of pollination services in agricultural landscapes

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5. Effects of landscape structure on the provision of pollination services in agricultural landscape

5.1. Abstract

The structure of the surrounding landscape may be important in determining the delivery of pollination services to wild plants. However, the relationship between landscape structure and pollination service delivery are understudied, particularly for wild plants. In this study, stigma pollen deposition of six wild plant species occurring in semi-natural grasslands (*Lotus corniculatus*, *Leontodon saxatilis*, *Prunella vulgaris*, *Potentilla erecta*, *Trifolium pratense* and *Trifolium repens*), and seed set of two wild hedgerow species (*Sambucus nigra* and *Rosa canina*) were used to quantify pollination service delivery in relation to the surrounding landscape composition and configuration at different spatial scales (within 1km of sampling sites). Relationships between landscape structure and the provision of pollination services to wild plants species did not show any consistent pattern, with contradictory responses from different plant species characterised by similar floral structure. Although there may be no relationship, it is possible that large variation in response variables (seed set and pollen deposition) within plant species may have masked patterns. In addition, other factors not taken into account in this study, such as the size of the non-experimental conspecific plant population, local environmental factors (including soil characteristics), weather conditions and farming practices may have more influence on the provision of pollination services than surrounding landscape structure and should be considered in further analysis.

5.2. Introduction

Since the Second World War, the agricultural environment has undergone substantial change as humans have shaped the landscape according to their needs. For instance, modern agriculture promotes a small number of high-yielding crop species, which dominate the landscape: flower-rich grasslands have been converted into crop fields and individual fields have become larger with the removal of hedgerows to facilitate harvesting (Fahrig et al., 2011; Robinson and Sutherland, 2002). This intensification of agriculture has been identified as one of the major threats to biodiversity (Kleijn et al., 2009; Potts et al., 2010a) and the related ecosystem services it provides, including pollination (Hooper et al., 2005; Potts et al., 2010a; Tilman et al., 2001; Vitousek et al., 1997). Intensification can cause shifts in the abundance and composition of plants and pollinators (Burd, 1994; Sjodin et al., 2008; Steffan-Dewenter et al., 2001; Weibull et al., 2003), which in turn can affect pollination service delivery to both entomophilous crops and wild plants. Seed and fruit production have been shown to be restricted by pollen limitation in many systems (Ashman et al., 2004; Knight et al., 2005) due to insufficient pollination service delivery, and so disruption of pollination could cause further pollen limitation, and thus reduced seed and fruit set.

The consequence of landscape-level changes on the provision of pollination services has been explored in some cropping systems (Klein et al., 2007; Ricketts et al., 2008). Although Ricketts et al. (2008) did not find any clear pattern between the distance to natural or semi-natural habitat and the fruit/seed set in a study of 16 crops worldwide, Garibaldi et al. (2011) found that fruit set decreased with distance to the nearest natural habitat in a meta-analysis of 29 studies. Garibaldi et al. (2011) standardised data across the studies and used six additional crops, in comparison with the Ricketts et al. (2008) study, which could be responsible for the different patterns observed. Other studies have found increased crop pollination services in landscapes with a higher proportion of semi-natural habitats or in farmland surrounded by more organic crops (in comparison with conventional agriculture) (Andersson et al., 2012; Klein et al., 2012; Morandin and Winston, 2005). Although this shows the relationships between landscape and crop pollination services have been well studied, the relationships between landscape structure and pollination services of wild plants are less documented. The pollination level, seed set and fruit set of the 16 plant species occurring in dry subtropical forest in northwestern of Argentina have been observed to decline with the effects of forest fragmentation (Aizen and Feinsinger, 1994). Dauber et al. (2010) studied 10 wild plant species from five European countries and showed that the plant patch and population level influence

together the flower visitation and seed set and that the latter increased with patch area and density. Chateil and Porcher (2015) showed that the proximity of semi-natural habitat, but not a higher cover of this habitat in the surrounding landscape, was positively correlated with higher fruit production in *Lotus corniculatus* and Cussans et al. (2010) showed that fruit set of *L. corniculatus* was higher when the plant grows next to oilseed rape crop (in comparison to cereal crop) when the crop is in flower, but little else is known. The findings together showed that we need to consider the composition and the configuration of the landscape in future analysis. Moreover, wild plant species vary hugely in floral structure and rewards, and as a result are pollinated by a variety of different insect groups (Danieli-Silva et al., 2012; Fenster et al., 2004; Wilson et al., 2004). Thus they may be influenced differently by the landscape as different insects groups respond in different ways to landscape structure (see Chapter 2; Sjodin et al., 2008).

In this study, we explored how landscape structure affects the pollination services delivered to wild plants. Both landscape composition and configuration were considered. The objective of this study focused on the effects of landscape structure on stigma pollen deposition and seed set of wild plant species occurring in semi-natural grasslands and hedgerows. The flowers of these plant species are characterised by two different morphological structures: (1) open with the floral reward easily accessible and (2) tubular with the reward more difficult to access (Fontaine et al., 2005).

5.3. Materials and Methods

Pollination services were quantified in two different habitats: wild plant species in semi-natural grasslands and wild plant species in hedgerows surrounding arable and grassland crop fields. This work combined datasets which had already been compiled by other researchers, as well as some novel data collection. Consequently, there were different study designs both for the collection of the pollination services and the landscape characterisation.

5.3.1. Wild plant pollination – semi-natural grasslands

Pollination services were measured at each of the 19 semi-natural grassland sites studied in Chapter 2. Six plant species were chosen: (1) tubular flower species *Lotus corniculatus* L., *Prunella vulgaris* L., *Trifolium pratense* L. and *Trifolium repens* L. and (2) open flower species *Leontodon saxatilis* Lam. and *Potentilla erecta* L. (Figure 26). These plant species were common and occurred across the majority of the sites, in order to have enough sites across which to compare pollen deposition. Stigma pollen grain deposition was used to quantify pollination services. The stigmas from the flowers of the six plant species were collected on all sites where the plant species occurred in 2011. Over a period of two days, the collection of the stigmas was made when the species were flowering. For each species, 10 to 15 stigmas from 10 to 15 separate flowers were collected in each site. In the field, stigmas and styles were placed in vials containing 70% ethanol to fix the pollen grains for later counting in the laboratory. In the laboratory, styles were stained with a Safranin solution (0.5% Safranin in 50% ethanol) and crushed between a slide and a coverslip. The number of conspecific pollen grains was counted with a X10 magnification (Dafni, 1992). Pollen grains were identified using pollen reference collections (see Mullen (2013) for more details). The landscape characterisation method and the calculation of the landscape metrics (at 500m and 1km scales) used were described in the Chapter 2.



Figure 26: Six plant species used for the collection of the stigma pollen (from the top left to the bottom right: *Potentilla erecta*, *Leontodon saxatilis*, *Lotus corniculatus*, *Prunella vulgaris*, *Trifolium repens* and *Trifolium pratense*) (photos: Sarah Mullen).

5.3.2. Wild plant pollination - hedgerow habitat

The hedgerow surrounding two crop types, grassland and arable land, were surveyed in the South East of Ireland in 2013. Two plant species, *Sambucus nigra* L. and *Rosa canina* L. (Figure 27), were chosen as they are commonly part of the hedgerow composition in Ireland and they were commonly present in the field edges of the sites. Twenty fruits from three to five plants of *Rosa canina* were collected in 14 sites (8 grasslands and 6 arable crops). The number of seeds of each fruit were counted and used as the measure to quantify the pollination services. Two to 14 inflorescences from one to five *Sambucus nigra* plants were collected in 15 sites (7 grasslands and 8 tillage crops). The total number of seeds in ten fruits per inflorescence were counted and considered as the measure to quantify pollination services. We used seed set (i.e. seed production per fruit) rather than fruit set (i.e. fruit production per plant) because we did not count flower number at the start of the season, and so had no way to determine how many flowers failed to produce fruits.

There are many hybrids between *Rosa canina* and other *Rosa* species. It was difficult to identify them. Thereby the 'species' considered for this study will be all the hybrids of *Rosa canina*: *R. andegavensis* (*R. canina* X *R. stylosa*), *R. belnensis* (*R. canina* X *R. agrestis*), *R. dumalis* (*R. canina* x *R. caesia*), *R. dumetorum* (*R. canina* X *R. obtusifolia*), *R. scabriuscula* (*R. canina* X *R. tomentosa*), *R. rothschildii* (*R. canina* X *R. sherardii*), *R. toddiae* (*R. canina* X *R.*

micrantha), *R. molletorum* (*R. canina* X *R. mollis*), *R. nitidula* (*R. canina* X *R. rubiginosa*) (Stace, 2010).

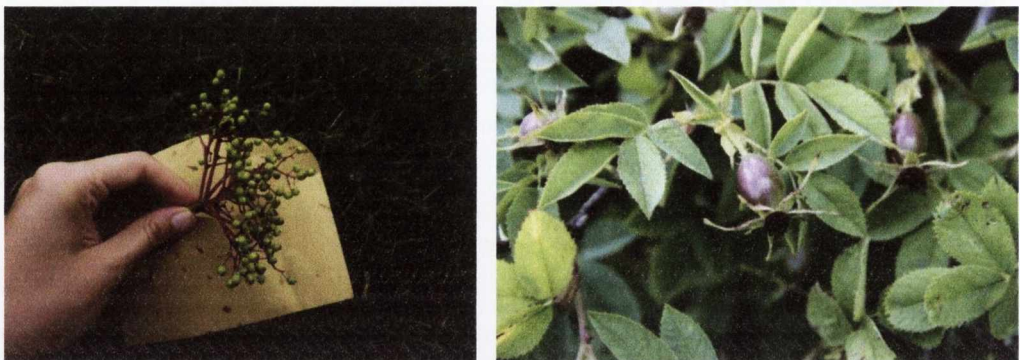


Figure 27: Infructescence and fruits of *Sambucus nigra* L. (on the left) and fruits of *Rosa canina* L. hybrid (photos: Aude Delmer and Jane Stout).

The landscape characterisation was conducted in 2010. A 1km square grid centred on each sampling field was used to characterise landscape structure (Figure 28). Each polygon was digitised from aerial photographs and identified according to the Irish Fossitt habitat classification (Fossitt, 2000) by interviewing farmers and ground-truthed in the field. The landscape polygons that partially overlapped with the square were considered in their entirety for the landscape configuration analyses. For each landscape, we calculated: Shannon Diversity Index (SDI), Shannon Evenness Index (SEI), Area Weighted Mean Shaped Index (AWMSI), Mean Shape Index (MSI), Mean Patch Fractal Dimension (MPDF), Area Weighted Mean Patch Fractal Dimension (AWMPDF), Total Edge (TE), Edge Density (ED), Mean Patch Size (MPS), Number of Patches (NumP), and the landscape proportion of each habitat type (see Appendix 3 for the description of these landscape metrics).

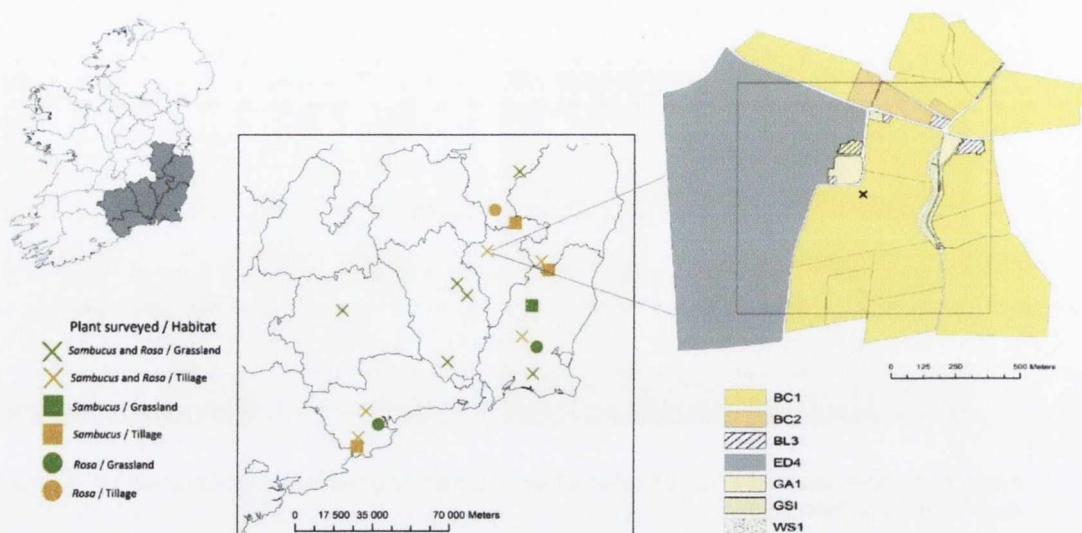


Figure 28: Location of the 14 and 15 hedgerow sites where fruits of *Rosa canina* hybrid and *Sambucus nigra* respectively were sampled and an example of the landscape mapped at 1km grid (BC1: arable crops, BC2: horticultural land, BL3: artificial surfaces, ED4: active quarries and mines, GA1: improved agricultural grasslands, GSI: semi-improved grasslands, WS1: scrub).

5.3.3. Data analysis

To evaluate the overall impact of the landscape structure on each of the pollination services from all the habitat types studied, we reduced the number of variables to integrate in the model using “Variances Inflation Factors” (VIFs) to assess which variables were highly correlated, and thus removed highly correlated variables from the analysis (Zuur et al., 2007). Before including landscape variables in the process of the VIFs tool, some habitat type variables had to be excluded due to their high (>65 %) number of zero values. As well as using the VIFs tool, the variables retained were chosen to allow possible comparison between the two scales studied (for the semi-natural grasslands) or between the two plant species studied from the habitat (for the hedgerow species). The landscape variables retained for each habitat are presented in the Table 18.

Table 18: Lists of the different landscape metrics kept in the analysis for semi-natural habitat and grassland.

Semi-natural habitat	Hedgerow
Shannon Evenness Index (SEI)	Shannon Evenness Index (SEI)
Area Weighted Mean Shape Index (AWMSI)	Mean Shape Index (MSI)
Mean Patch Size (MPS)	Number of patches (NumP)
% dry calcareous and neutral grassland (% GS1)	%arable crops (% BC1)
	%semi-improved grasslands (% GA+)

Different models were used for each habitat type. To study the landscape effects on pollination services in the semi-natural habitats, we decided to calculate the median of the number of pollen grains per site as a high variation in this response variable was observed within sites. Generalised Linear Models (GLMs) with a Gaussian error distribution were applied as the response variable was continuous. In parallel, and for comparison, Generalised Linear Mixed effects Models (GLMM) with a Poisson error distribution were run on the raw datasets i.e. on the 10 to 15 measures of the number of pollen per stigma in each site. Site was considered as a random factor as the response variables in each site are likely to be more related to each other than in other sites. Similar patterns were observed between these two methods and so the results using the medians per site were presented in this study.

Finally, GLMMs with Poisson error distribution were used to study the landscape scale effects on the provision of pollination services of *Sambucus nigra* L. and *Rosa canina* hybrid. Site and plant were considered as random factors and the crop type (tillage versus grassland) was defined as a fixed factor. Mixed models were simplified by removing sequentially the most non-significant explanatory variables until only significant explanatory variables remained. Model validations were applied following the protocol of Zuur et al. (2009).

5.4. Results

5.4.1. Pollination services

In the semi-natural grasslands, pollen grains from 1,081 stigmas were counted. Some stigmas from all plant species were devoid of conspecific pollen grains. The median number of pollen grains found per site varied as follows (maximum and minimum values given): *Lotus corniculatus* (6-362) *Leontodon saxatilis* (40-646), *Potentilla erecta* (5-63), *Prunella vulgaris* (12.5-73.5), *Trifolium pratense* (13.5-161.5) and *Trifolium repens* (13-195.5).

More *Rosa canina* fruits were collected from the hedgerows surrounding grasslands (800) compared to arable crops (560). In samples from both for the grassland and arable habitats, some fruits were devoid of seeds (summary data given in Table 19).

Table 19: Mean, minimum and maximum of the number of seeds per fruits of *Rosa canina* found in the hedgerow surrounding the grassland and arable crops.

<i>Rosa canina</i>	Grassland			Arable crop		
	Mean (±se)	Min	Max	Mean (±se)	Min	Max
Number of seeds per fruit	19.2(±0.207)	0	41	19.0(±0.237)	0	39

A total of 174 and 296 inflorescences of *Sambucus nigra* were collected respectively in the hedgerow surrounding the grassland and arable crop (summary data given in Table 20).

Table 20: Mean, minimum and maximum of the total number of seeds per ten fruits of *Sambucus nigra* found in the hedgerow surrounding the grassland and arable crops.

<i>Sambucus nigra</i>	Grassland			Arable crop		
	Mean (±se)	Min	Max	Mean (±se)	Min	Max
Total number of seeds in ten fruits	29.3(±0.249)	21	53	29.2(±0.175)	13	39

5.4.2. Landscape characterisation

For the semi-natural grasslands, the landscape compositional heterogeneity calculated, inter alia, by the Shannon Evenness Index (SEI), was variable and with a maximum value of 0.873 (Table 21). The landscape configurational heterogeneity calculated by Area Weighted Mean Shape Index (AWMSI) showed value up to 1.78 showing a high complexity of patch shape in the landscape. Mean Patch Size varied from relatively small areas of 0.874 ha to larger areas of 7.41 ha. Some surrounding landscapes did not present any semi-natural grassland at 500m and

1km scales. The maximum proportion of landscape occupied by the semi-natural grasslands was 63.1%.

Table 21: Mean, minimum and maximum values of the landscape metrics (Shannon Evenness Index (SEI), Area Weighted Mean Shape Index (AWMSI), Mean Patch Size (MPS), proportion of dry calcareous and neutral grasslands (%GS1)) kept in the analysis calculated at the 500m and 1km scales for the semi-natural grasslands.

	500 m			1 km		
	Mean (±se)	Min	Max	Mean (±se)	Min	Max
SEI	0.655 (±0.031)	0.344	0.873	0.550 (±0.031)	0.274	0.796
AWMSI	1.36 (±0.023)	1.21	1.61	1.38 (±0.026)	1.28	1.78
MPS	2.50 (±0.41)	0.874	7.41	2.06 (±0.241)	1.17	4.90
%GS1	21.4 (±4.31)	0.000	63.1	11.5 (±3.03)	0.000	46.9

For the hedgerow habitat, Shannon Evenness Index showed a relatively low minimum value of 0.110 and a maximum value of 0.729 (Table 22). The complexity of the patch shape in the landscape varied from 1.25 to 1.55. Up to 83.4% of the surrounding landscape was arable crops, whilst the maximum proportion of semi-improved grassland was 4.47.

Table 22: Mean, minimum and maximum values of the landscape metrics (Shannon Evenness Index (SEI), Mean Shape Index (MSI), Number of patches (NumP), proportion of arable crop (%arable crop), proportion of semi-improved grasslands (GA+)) kept in the analysis calculated at the 500m scales for the hedgerow habitat.

	<i>Sambucus nigra</i>			<i>Rosa canina</i>		
	Mean (±se)	Min	Max	Mean (±se)	Min	Max
SEI	0.552(±0.230)	0.319	0.729	0.501(±0.043)	0.110	0.729
MSI	1.36(±0.021)	1.25	1.55	1.37 (±0.023)	1.25	1.55
NumP	51.3(±4.10)	29	85	49.4 (±3.50)	30	81
% arable crop	46.9(±6.50)	3.27	83.4	38.5(±7.86)	0	83.4
% GA+	0.776 (±0.403)	0	4.47	0.831(±0.428)	0	4.47

5.4.3. Landscape scale effects on provision of pollination services

The number of pollen grains per stigma in *Leontodon saxatilis* was significantly positively related with Area Weighted Mean Shape Index (AWMSI) at 500m scale (Figure 29a-Table 23). At 500m and 1km scales, the number of pollen grains on *Trifolium repens* stigmas was significantly correlated negatively with proportion of semi-natural grasslands (%GS1) (Figure 29b). The number of pollen grains per stigma of *Lotus corniculatus* and *Prunella vulgaris* only showed significant relationships at 1km scale. The proportion of semi-natural grasslands was significantly positively related with number of pollen grains per stigma of *Lotus corniculatus* (Figure 29d). Conversely, pollen deposition on *Prunella vulgaris* showed positive relationship with Shannon Evenness Index (SEI) (Figure 29f). At the 1km scale, pollen deposition of *Lotus corniculatus* and *Prunella vulgaris* were, respectively, positively and negatively related with Mean Patch Size but these relationships were strongly influenced by two outliers (Figures 29c and e).

Table 23: Results of the Generalized Linear Models (GLMs) testing for relationships between the response variables (stigma pollen deposition of six plants species) and the explanatory variables (Shannon Evenness Index (SEI), Area Weighted Mean Shape Index (AWMSI), Mean Patch Size (MPS), proportion of dry calcareous and neutral grasslands (%GS1)). Significant results are shown by differing arrows indicating trends. Smaller and thinner arrow represent a *p-value <0.05, medium arrows a**p-value <0.01. Non-significant covariates are represented by NS and covariates not considered in the best model (i.e. model with the lowest AIC) by a blank value.

Response variable/ Stigma pollen deposition	500m				1km			
	SEI	AWMSI	MPS	%GS1	SEI	AWMSI	MPS	%GS1
<i>Lotus corniculatus</i>		NS		NS	NS		↗	↗
<i>Leontodon saxatilis</i>		↗					NS	
<i>Potentilla erecta</i>		NS	NS	NS		NS		
<i>Prunella vulgaris</i>					↗		↘	NS
<i>Trifolium repens</i>				↘		NS		↘
<i>Trifolium pratense</i>				NS				NS

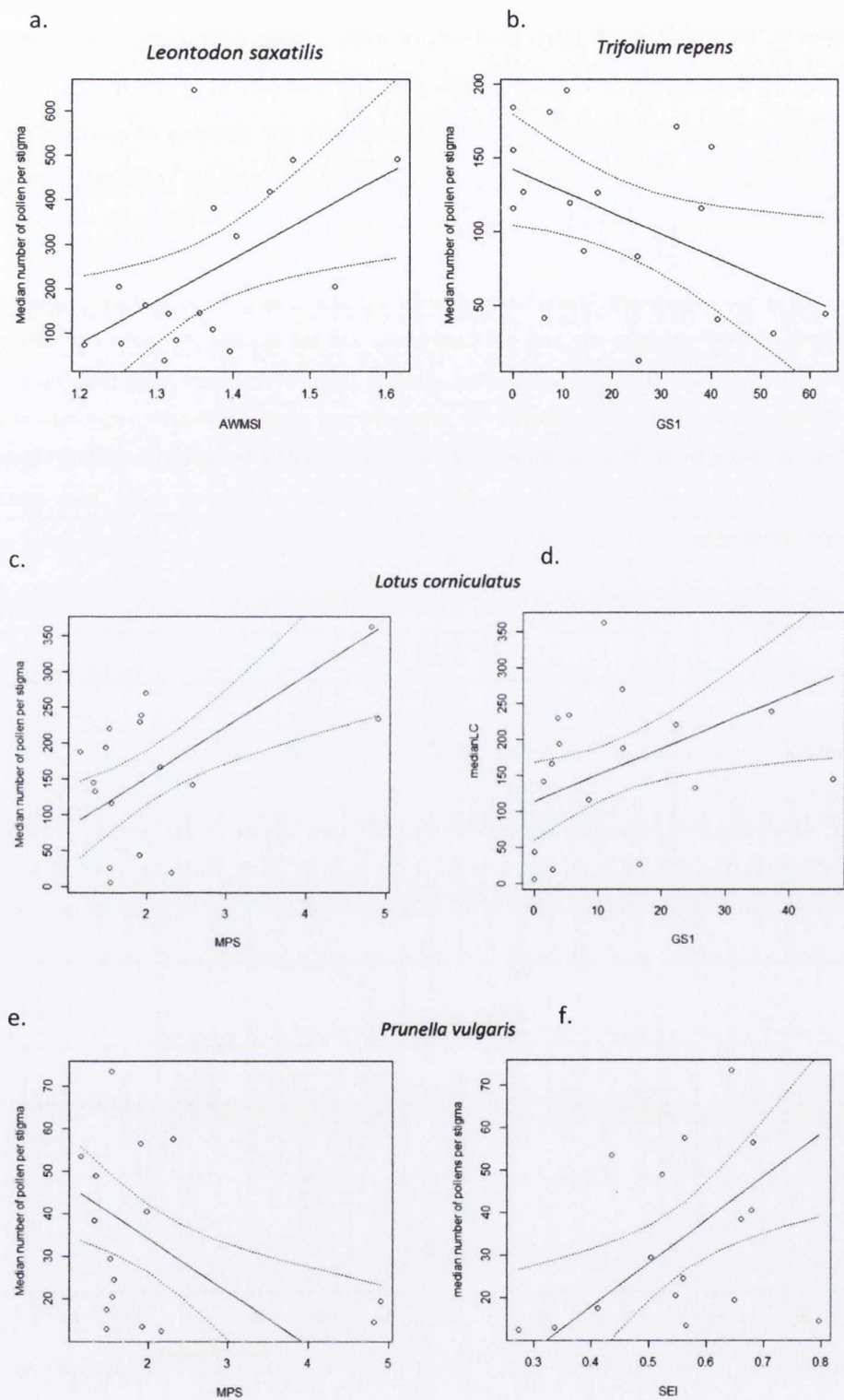


Figure 29: Main effects of the landscape metrics on median number of pollen grain per stigma of the corresponding plant species studied from the best model. Points represent observed values. The line characterises the model prediction and dotted lines the 95% confidence intervals. The graphs a and b are related to the 500m scale and the graphs c,d,e and f to the 1km scale.

In the hedgerow, the number of seeds per fruit of *Rosa canina* hybrid was not significantly related to any of the landscape metrics (Table 24). The number of seeds in ten fruits per inflorescence of *Sambucus nigra* was positively related with the number of patches and the proportion of arable land (Figure 30). For both plant species, seed set was not significantly different in the field margins of the arable or grassland fields.

Table 24: Results of the Generalized Linear Mixed Models (GLMMs) testing for relationships between the response variables (number of seeds per fruit for *Rosa canina* and the number of seeds in 10 fruits of an inflorescence for *Sambucus nigra*) and the explanatory variables (Shannon Evenness Index (SEI), Mean Shape Index (MSI), Number of Patches (NumP), proportion of semi-improved grasslands (%GA+), proportion of arable land (%BC1)) and the fixed factor crop. Significant results are shown by differing arrows indicating trends. The smaller and thinner arrow represents a *p-value <0.05. Variable not considered in the final model are represented by a blank value.

Response variable/ Number of seeds	500m					factor crop
	landscape metrics					
	SEI	MSI	NumP	%GA+	BC1	
<i>Sambucus nigra</i>			↗		↗	
<i>Rosa canina</i>						

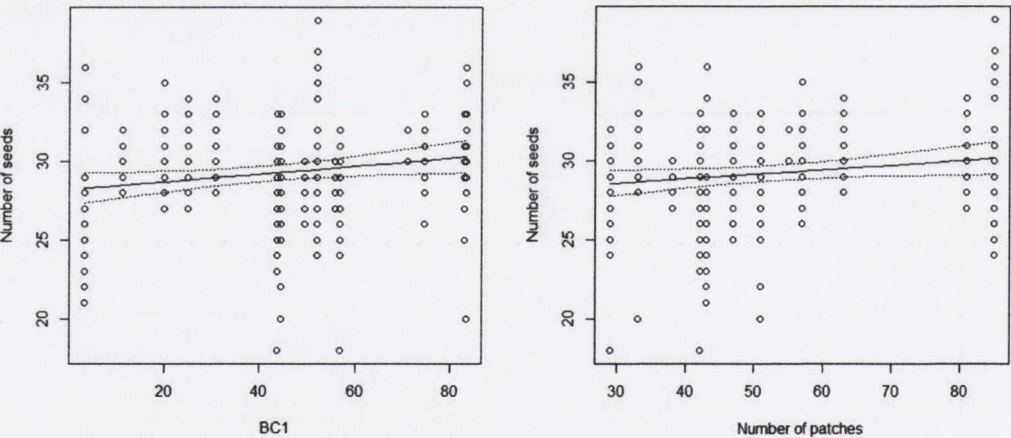


Figure 30: Main effects of the landscape metrics at for a 1km grid scale on number of seeds of *Sambucus nigra* L. from the best model. Points represent observed values. The line characterises the model prediction and dotted lines the 95% confidence intervals.

5.5. Discussion

This study aimed to investigate the effects of landscape structure on the provision of pollination services in agricultural landscapes. To address this objective, landscape-pollination services relationships were studied for different plant species including wild plant species.

5.5.1. Landscape effects on the deposition of pollen on wild plant stigmas in semi-natural grasslands

Different patterns were observed in the amount of pollen per stigma for the different plant species in relation to landscape structure, and also within species with similar flower structure.

For the species with an open flower morphology, pollen deposition on *Potentilla erecta* was not related to any landscape metrics. Conversely, the number of pollen grains per stigma for *Leontodon saxatilis* was higher in landscapes with more complex patch shape at 500m. This landscape configuration metric was also related to various pollinator richness and abundance measures (pollinator species richness, hoverfly species richness and abundance and butterfly species richness at 500m and with the overall pollinator species richness and abundance, solitary bees species richness, hoverfly and butterfly species richness and abundance, see chapter 2). *Leontodon saxatilis*, due to its floral structure, can be pollinated by a range of pollinator species and if pollinators are more common in landscapes with more complex patch shapes, this could lead to an increase in visitation rates and pollen grain deposition. The lack of relationships between the *P. erecta* and the landscape structure could be due to the fact that this plant species offered less favourable resources for the pollinator community in comparison with other plant species. It is also possible that the population size of *P. erecta* is not high in the semi-natural grasslands and in the surrounding landscape which limit the abundance of the pollen donors.

With regards to the species with tubular flower morphologies, different relationships were also found between species. Pollen deposition in *Trifolium pratense* did not relate to any landscape metrics, but pollen deposition in *T. repens* was inversely related to the proportion of semi-natural grasslands in the surrounding landscape. Pollinators with longer mouthpart are more able to extract nectar from these plant species (Fontaine et al., 2005). Moreover *T. pratense* has longer floral structure (Parnell et al., 2012; Wilson and Stine, 1996) and thus more specialised pollination systems than *T. repens*. This might explain the different pattern

found between the pollen grain deposition of these both plant species and the landscape structure. Indeed long-tongued bees found in this study were mainly bumblebees (see chapter 2) which were shown to be the least affected by the proportion of semi-natural grasslands in the surrounding landscape.

At 1km scale, a higher diversity of habitats was related to a higher number of pollen grains per stigma of *Prunella vulgaris*, but a higher number of pollen grains per stigma on *Lotus corniculatus* was found in a landscape with more semi-natural grasslands. *Lotus corniculatus* and *Prunella vulgaris* are pollinated by bumblebees (Harder, 1988; Ollerton, 1993; Proctor et al., 1996), and it has also been shown that the flowers of *Lotus corniculatus* are often visited by butterflies (Ollerton and Lack, 1998). The abundance and species richness of butterfly were positively related to more semi-natural grasslands at 1km scale and only the abundance of bumblebee showed significant relationship at that scale. Whilst this appears to translate into greater pollen deposition in *Lotus corniculatus*, the opposite is true for *Prunella vulgaris*. It is possible that *P. vulgaris* is a less favourable resource and so in the semi-natural grasslands, it is a poor competitor or that in these habitats, *P. vulgaris* is less common and so there are fewer potential pollen donors. However, Chateil and Porcher (2015) observed that the proportion of semi-natural habitats in the landscape had a negative relationships with the fruit set of *Lotus corniculatus* but did not show any pattern with seed set. Inconsistency of patterns between the landscape-pollinator community and the stigma pollen grain deposition can be explained by the intervention of other factors not measured and considered in this study. The population size of each plant species may affect the pollen grain deposition. Lack of replication in pollination service measure might also explain the contradiction in the results.

5.5.2. Landscape effects on the seed set of two hedgerow species surrounding tillage crop or grassland

In our study, seed set of *Rosa canina* was not related to any landscape variables. Fruits were collected on a few *Rosa canina* hybrids with different range of number of seeds produced per fruit (Parnell et al., 2012). The variation in seed set between hybrids could explain the lack of relationship with the landscape characteristic. Contrary to *Rosa canina*, seed set of *Sambucus nigra* showed significant relationships with landscape composition and configuration. The number of seeds per fruit was higher when the landscape was covered by a higher proportion of arable land and when there were more patches in the landscape. One explanation for both of these findings was that hedgerows were common around the edges of fields (a significant

positive correlation was recorded between the number of patches and hedgerow length), and *S. nigra* is a common hedgerow plant. Thus with more arable land and more patches in the landscape, there may be a higher total edge length in the landscape. This may result in larger populations of *Sambucus nigra*, increasing the potential pollen donors and thus seed set. Seed set of *Sambucus nigra* and *Rosa canina* hybrid was not significantly different between field margins of grassland or arable crops, probably because the composition of hedgerows is consistent regardless of crop type. Finally, results should be interpreted with caution as landscape characterisation and pollination service assessment were not undertaken in the same year. Landscape changes had certainly occurred between 2010 and 2013 due to crop rotation and other agricultural practices. Although this could affect both the landscape composition and configuration, it is unlikely to have a great impact as field sizes and shapes are unlikely to have changed, and crop rotation would result in more or less the same crops being grown across the landscape, even if there were differences in individual fields.

5.6. Conclusions

The objective of this study was to have a general overview of potential landscape-level influences on the provision of pollination services. For this purpose, different measures to quantify pollination services of wild plants were used. Lack of pattern and inconsistency in the relationships between landscape and pollination could be explained by factors not taken into account such as the size of the corresponding existing plant population, local environmental factors (soil characteristic), weather conditions, farming practices which may have more influence on the provision of pollination services than landscape structure. Moreover, other plausible reasons may be the lack of replication and the use of non-standardisation of scales, landscape characterisation and metrics, pollination response variables and models. While stigma pollen deposition might be less dependent on surrounding conditions than seed set, some relationships were difficult to explain even with the knowledge of the pattern linking the landscape and the flower visitor species richness and abundance. Landscape structure effects on pollination services studies are far less documented than the ones on the pollinator diversity. This could be due to the difficulty of identifying, measuring and quantifying the different processes that can drive the provision of pollination services.

Chapter 6

General discussion

6. General discussion

In this thesis I aimed to study the effects of landscape structure on pollinator diversity and the provision of pollination services. Different aspects of the landscape structure and the pollination were considered with the objective of reinforcing our current knowledge. Pollinators and pollination services were sampled in different habitat types and in different regions, and with different techniques. Moreover the landscape structure was characterised using different methods and resources available and at different scales. This allows the reliability of different pollination measures and methods to characterize the landscape to be tested.

In the chapter 2, I studied the relationships between landscape composition and configuration, as well as linear features, and the species richness and abundance of flower-visiting insects (bumblebees, hoverflies, solitary bees and butterflies) and flower-insect interaction networks occurring in semi-natural grasslands. In this chapter, the landscape structure was characterised at 500m and 1km scales with a high precision i.e. based on aerial photographs combined with on-the ground habitat classification. Chapter 3 was a methodological study, testing the suitability of CORINE land cover (CLC) as a tool to characterise the landscape in pollinator studies. For this, the landscape characterisation used in the chapter 2 was compared with landscape data obtained with CLC. Then, these CLC datasets were used to test relationships between land cover and flower-visitor diversity at 500m to 5km scales. In chapter 4, I investigated two regional patterns and used different measures of flower-visiting insect diversity to test whether geographical location and land use intensification were shaping the species and the functional composition of pollinator communities. We gathered existing data on the species of bees, and their related traits, visiting two crops systems: coffee (*Coffea sp.*) and oilseed rape (*Brassica napus*). Chapter 5 examined the landscape composition and configuration effects at different spatial scales (within 1km of the sampling sites) on the provision of pollination services of wild plants. Here, I used newly collected data as well as pre-existing landscape and pollination data from other national studies. Finally, in this last chapter, I synthesise my findings and compare them with previous research. I present some recommendations for future conservation measures and finally outline some suggestions for future research.

6.1. Synthesis of the findings

6.1.1. Pollinator ecology at a landscape scale

Flower-visiting insects are affected by the landscape at different spatial scales as they are mobile and depend on the availability of a range of resources such as flowers, overwintering, mating and nesting sites (Hadley and Betts, 2012; Kremen et al., 2007; Tschardt et al., 2012). For example, a more diverse landscape may provide a wider range of feeding, nesting and overwintering sites, therefore providing a higher quality area for flower-visiting insects to live. A range of studies have investigated the effects of the landscape on these insects. One of the most important findings is that a higher proportion of natural and semi-natural habitats in intensive agricultural system has positive impact on flower-visiting insects (Öckinger and Smith, 2007; Steffan-Dewenter et al., 2002; Williams and Kremen, 2007; Woodcock et al., 2013). However, little is known on the impact of the landscape structure on the flower-visiting insects occurring in semi-natural habitats. In the chapter 2, I showed that a higher proportion of semi-natural grasslands was positively related with the diversity of the overall flower-visiting insects occurring in semi-natural grasslands located in a less intensive agricultural system. Moreover I also found that a landscape with a higher proportion of semi-natural grasslands at 1km scale makes plant-pollinator interaction networks more robust by increasing the number of links in the network. Such relationships (between landscape structure and flower insect interaction networks) have been suggested to be of a particular importance as pollination is not only dependent on pollinator diversity but also on the number and type of interactions between plants and pollinators (Memmott, 1999). However, Ferreira et al. (2013) highlights a lack of research on the effects of landscape changes on plant pollinator networks. In this chapter 2, I also studied the effects of the landscape configuration on pollinator communities and the interaction networks. The way land parcels are distributed and shaped in a landscape can also have impacts on flower-visiting insects, and this may be different to the impacts of looking at landscape composition alone. Such relationships have been less investigated, as most studies focus on landscape composition. Throughout chapter 2, I showed that landscape configuration is also an important characteristic and can shape both the flower-visitor community and the plant-pollinator interaction network. Indeed, we observed that a higher complexity of patch shapes in the landscape was positively related with the overall flower-visiting insect species richness and more specifically the butterfly species richness and abundance at 500m and 1km scale. Landscapes with this kind of structure may promote insect species richness and abundance because the probability of any specific resources for each species will be greater. At a 1km scale, this landscape configuration property also was

positively related with the nestedness of the network which thereby makes the network more robust to perturbation (Bascompte et al., 2003).

Finally, linear features such as the stonewalls and hedgerows are also important components of landscape structure (Teagasc, 2004). Although, hedgerows have been recognised for their ecological value for the pollinator community, nothing is really known about this value for the stonewalls (Collier, 2013; Cranmer et al., 2012). I found in the chapter 2 that stonewall length is related with the pollinator diversity as landscapes with more stonewalls at 500m and 1km scales had greater bumblebee abundance. Cavities and holes under stonewalls could provide nesting sites for bumblebee species such as *Bombus lucorum* and *B. pratorum* which have been found to nest in pre-existing underground cavities such as disused rodent burrows (Goulson, 2010), or stonewalls may create sheltered areas where above ground nesters can make their nests. However, details of the relationship between stone walls and pollinator diversity requires further study. Overall, landscapes with fewer stonewalls supported a higher pollinator species richness at 500m scales. This relationship is shown also for the butterfly species richness, hoverfly species richness and abundance. This is probably due to the fact that a landscape with more stonewalls means less length of other linear habitats that are more favourable for the majority of the insect community. Finally, I found no relationship between pollinator group, interaction network, and the length of hedgerow in the surrounding landscape. Hedgerows have previously been shown to be beneficial to the flower-visiting insect but in more intensive agricultural system (Cranmer et al., 2012). To our knowledge, no such relationships have been investigated in a less intensive agricultural area, and these results suggest that a higher complexity of patch shapes and higher proportion of semi-natural habitats may result in good connectivity between semi-natural habitats in this area and hedgerows did not offer any extra link in the landscape. It is also possible that hedgerow management, their botanical and structure composition may offer less resources for the pollinator community. But this has to be verified.

However, the effects of landscape structure are not the same for all species because they are mediated by species' ecological traits (De Palma et al., 2015; Henle et al., 2004; Newbold et al., 2013). Pollinator species traits may influence the sensitivity of species to aspects of landscape composition and configuration. Only very few studies have started to explore this issue for pollinator communities (De Palma et al., 2015; Williams et al., 2010). In chapter 4, I demonstrated that land use intensification (measured as the distance to the nearest natural habitat) shaped the taxonomic, as well as the functional, composition of the bee community visiting two highly transformed habitats: oilseed rape and coffee.

Finally, in chapter 5, similar relationships have been studied with the provision of pollination services of wild plants in intensive and more extensive agricultural systems. Concerning wild plants, the number of pollen grains per stigma as well as the number of seeds per fruits were used as a measure to quantify pollination services. Lack of pattern and inconsistency in the relationships between the landscape and pollination services were observed. This could be explained by the intervention of factors such as the climate, the local population of conspecific, farming practices, soil characteristics which might be more influential on pollination services than the landscape structure, or that landscape structure does not influence wild plant pollination. Alternatively, the design of the study may not have been sufficient to detect any effect.

6.1.2. Biogeography of taxonomic and functional components of the bee community

One common principle in biogeography is that community composition differs between geographic locations (Gaston, 2000; Siefert et al., 2013) and that species richness typically increases with decreasing latitude for a wide range of taxonomic groups (Gaston, 2000; Qian and Ricklefs, 2007; Qian and Wang, 2015; Tang et al., 2012). In chapter 4, I confirmed this principle for bee communities. Our results showed a species turnover in bee communities visiting coffee crops in Central America in comparison to Asia, and species richness differences along a latitudinal gradient for bees visiting oilseed rape crops in Europe. Moreover this change in community composition reflected a change in functional composition. Darwin (1859) already suggested that similar functional roles are undertaken by different species in different regions of the world. This pattern has been observed in natural systems (Darwin, 1859) but not in habitat types that are highly transformed.

6.1.3. Comparing the different methods of landscape characterisation

Ecological studies used different methods to characterise landscape structure. In chapter 2, landscape characterisation was based on the interpretation of aerial pictures completed with some ground-truthing in the field. In chapter 5, I gathered landscape datasets from different studies; overall the landscape was also characterised in the same way as in chapter 2, although some slight differences were observed. In one dataset of the chapter 5, the landscape was characterised on a square grid centred on each sampling site. This method should be avoided and replaced by the characterisation of the landscape on circle centered on the sampling field

because this circular buffer considers all the landscape elements at an equal distance from the centre of the sampling field.

The use of land cover (LC) maps produced from remote sensing imagery are of common used in ecological studies investigating the relationships between landscape and ecological processes (Lechner, 2010; Wiens, 2002). In the chapter 3, I used one of them, the CORINE land cover, which is an European GIS database providing information on the biophysical cover of Europe (European Environment Agency, 1995). This dataset is based on the interpretation of satellite images and uses a common classification of land cover for all of Europe (European Environment Agency, 1995) and is commonly used in ecology to describe the characteristic of the landscape, especially at larger scales. However, some caution is needed for the use of such maps as land cover data used to characterise the landscape structure, was created for different purposes (Comber et al., 2005; Lechner et al., 2013). CLC has some constraints as a common classification of habitats for all European countries and a minimum map unit of 25 ha (European Environment Agency, 1995). Additionally, CLC is based on total extent of different landcover types, and does not partition land cover into discrete field-level parcels. In chapter 3, I tested the suitability of CLC to describe landscape structure in pollination ecology. I confirmed the fact that using CLC should be an informed decision, and that each user should be aware of the different processes leading to the production of these maps. Despite the processes of the CLC creation, some consistency was found in patterns linking landscape composition and pollinator diversity. CLC showed globally similar relationships with flower-visitor diversity as the high resolution dataset. A landscape with a higher proportion of pasture (mainly composed of flower-poor grasslands) showed significant negative correlation with diversity of some pollinator groups. However CLC has some limitations as it does not report fine scale habitat diversity which has been shown to be important in pollination studies. For example, a small hedgerow or patch of semi-natural grassland, too small to be included in CLC, might have an appreciable effect on the local flower visiting insect community. In this study, the sites were located in grass dominated areas. Therefore, different grassland types varying in term of plant composition were all categorised in the same CLC category. This means different patterns were, in some circumstances, more difficult to detect.

All these different methods can lead to different results. The choice of the methods should be dependent of the question we would like to answer leading to consider, inter alia, the use of fine scale landscape characterisation. Some considerations regarding the landscape characterisation are presented in the section '*Reflections for future methods of landscape characterisation*'.

6.2. Recommendations for future landscape management decisions

Pollinators are important for the pollination services they provide; therefore it is a necessary to sustain their populations. My findings can give suggestions of some landscape management measures that could be taken in favour of pollinator communities and their related pollination services. However these recommendations should be taken with caution as they are based on correlations, and not on experimental manipulations that might reveal causation.

6.2.1. Semi-natural grasslands

Results from chapter 2 showed that semi-natural grasslands are important for flower-visiting insects (separately for bumblebees, solitary bees, hoverflies and butterflies) and improve the robustness of plant-pollinator networks in a less intensive farming system mostly dominated by grassland. These semi-natural grasslands are the remnants of past low intensity agricultural practices which have now ceased. Thereby these flower-rich grasslands are now threatened by the abandonment of these management practices which can result in a reversion to scrub, or by the intensification of management which can lead to species poor grassland (Martin et al., 2007). I suggest that the preservation of remaining semi-natural grasslands and re-creation of flower-rich grassland would be beneficial in grass-dominated system for pollinator and pollinator dependent plant community protection. Low-intensity practices could be adopted in the semi-natural grasslands to help maintain pollinator communities. Some semi-natural habitats are protected by the EU Habitat Directive (Martin et al., 2007) but it is important that other semi-natural grasslands should be also protected by law due to their importance for the plant-pollinator communities and wider biodiversity.

6.2.2. Patch shape

More complex patch shapes have been showed to be also very important for pollinators in my study system i.e. a landscape dominated by grassland. Regular shapes of fields are generally the result of a simplification of the landscape structure due to agricultural intensification. Conserving less intensive farming practices might sustain pollinator diversity. Reshaping of fields to have larger areas to make the harvest easier and quicker, to the detriment of existing field boundaries, should be avoided (Fahrig et al., 2011; Robinson and Sutherland, 2002).

6.2.3. Linear features

In my study located in a less intensive farming system mostly dominated by grassland, stonewalls showed contrasting effects on flower-visiting insects, as negative relationships were found with the overall flower-visiting insect community (and independently for the hoverfly and butterfly group) and positive relationships with bumblebees and the robustness of flower-insect interaction networks. Stonewalls could provide holes and cavities under the walls, or shelter, that can be used by the some bumblebees species, but may also replace other linear habitats more favourable for other taxa such butterflies and hoverflies. Other potential linear features (hedgerows, flower-rich strips or tree lines) could be more favourable for the overall pollinator community in a grass-dominated system. It would be interesting to understand which exact resources are provided by the stonewalls to the bumblebee community, and test to see if other linear features could provide these resources in addition to those for other pollinator taxa.

6.3. Reflections for future methods of landscape characterisation

In this thesis, landscape structure was characterised with different techniques. However, all of them defined land cover types according to a human perspective (or remoted sensed device). This did not take explicit consideration of their relevance to the overall pollinator community, or to one specific pollinator taxon. It has been discussed that such maps may be relevant for human observers but may misrepresent the ecological relationships of interest (Addicott et al., 1987; Fahrig et al., 2011). Thereby one alternative is to create a “functional map” which defines land cover based on a function (provision of food, nesting sites) related to the pollinator community. Some cover types that can be distinguished from human perspective are not necessarily different in their function (Fahrig et al., 2011) for the pollinator. For example, areas of open water and artificial surfaces might be equally unsuitable for the bumblebee in term of provision of food. Some land cover types might be redundant if not considered in a functional point of view, and can distort the ecological relationship between the pollinator community and the landscape structure. However, methodological approaches to help produce such maps are still developing (Fahrig et al., 2011). One issue that might slow down the creation of such maps is that the functional cover type depends on the availability of sufficient knowledge of the ecology of the species or species group of interest (Fahrig et al., 2011). While this information is known for a few species or groups, for nearly all pollinator groups and species it is not known yet. Moreover this approach might be time consuming as

each pollinator group (even each pollinator species) has specific needs, thereby individual functional maps should be created for each taxa. Another approach would be to create a 'habitat quality map' by attributing a quality value for each habitat type for each pollinator taxon. This approach has been used by Vogiatzakis et al. (2015) which described a rapid assessment methodology to evaluate land cover quality for birds, plants, butterflies and bees around seven UK Natura 2000 sites. For that, a quality value was assigned to each CORINE land cover class for each taxonomic group. However the quality of land cover will vary with the context such as location, co-occurring species, climate which make the realization of these maps more complex.

Moreover, a patch (i.e. the basic element that makes up a landscape) has been defined differently between studies. From an ecological point of view, a patch is a discrete area of relatively homogeneous environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character (McGarigal and Marks, 1995; Wiens, 1976). However, patches are dynamic and occur at different spatial scales and differ from one organisms point of view to another (McGarigal and Marks, 1995; Wiens, 1976). But what defines the level of homogeneity of a patch? A patch has an internal structure that can present some heterogeneity at finer scale (McGarigal and Marks, 1995). Therefore from an organisms point of view, it is important to know which scale matters (Kotliar and Wiens, 1990; McGarigal and Marks, 1995). In this thesis, patch has been considered also from a human perspective. It was defined as a discrete area of homogeneous environmental conditions, vegetation composition and structure, where the patch boundaries were distinguished by discontinuities in environmental character or physical boundaries (fence, hedgerow, stonewalls, roads, etc...). This representation appears to us the most appropriate, but again this can be discussed. Does a fence, a hedgerow, a stone wall, a road dividing a grassland constitute a fragmenting feature (McGarigal and Marks, 1995) to split the grassland in two different patches? To answer this question, more knowledge on the ecology of each pollinator taxa must be gained first before it will be possible to characterise the landscape in the most optimal manner. However, in the case of this study, it might have been better to not consider the fence as a fragmenting feature and merge polygons with the same habitat type separated by this linear feature.

6.4. Suggestions for future research

Our findings provide new evidence, but also highlight and give rise to new areas of research.

6.4.1. Pollinator ecology

While studying the relationships between the landscape composition and configuration metrics and pollinator diversity and plant pollinator interaction networks in semi-natural grasslands (chapter 2), some significant relationships were observed. I have made a range of suggestions why these relationships were observed, but these suggestions have to be verified; for example whether bumblebees could use the holes and cavities under the stone walls for nesting sites. Specific surveys to confirm our speculations should be undertaken around stonewalls to determine the potential importance of such boundary features. Moreover, as there was no relationships between hedgerow occurrence and any pollinator group, further research on the management, vegetation composition, and structure of hedgerows could be undertaken to understand this lack of response of the pollinator community, and perhaps similar work carried out in an area with a wider gradient of hedgerow length. In general, more “inside” habitat surveys could be carried out to characterise which communities occurred in which habitats, and which resources are taken used by them. As the response of pollinator communities to the landscape structure is dependent on the functional traits of each species, it would be interesting to study landscape composition and configuration effects on community functional diversity, and individually on the relevant functional traits of each species.

Landscape structure and pollination relationships are still largely unstudied, especially for wild plants. The inconsistency of the relationships found in chapter 5 suggest that the landscape may not affect the pollination services, or that factors other than the landscape structure affects the provision of pollination services. Future research could investigate the effects of plant population size, soil characteristics, climate conditions and farming practices on the provision of pollination.

Finally, relationships between landscape and pollinator communities have been investigated up to 1km with a high resolution characterisation. It might be interesting to extend these relationships at larger scales, as some pollinator group such as bumblebees can travel distances up to several kilometers (Beekman and Ratnieks, 2000; Goulson and Stout, 2001).

6.4.2. Landscape characterisation

The study, in chapter 2, could be extended to create functional maps to compare with the high resolution landscape characterisation and see if some similar patterns are observed.

In chapter 3, I compared a high-resolution land cover dataset with the freely available CORINE land cover based on interpretation of satellite images. This study was carried out in less intensive agricultural systems. Similar studies should be undertaken in more intensive agricultural systems, to see if CLC is more reliable in this context.

6.5. Final conclusions

Biodiversity is declining worldwide at a worrying pace (Cardinale et al., 2006). This species loss affects in return the delivery of ecosystem services (Cardinale et al., 2006). Pollinators are also affected by this decline which can threaten in turn wild plant species and the productivity of agriculture (Food and Agriculture Organization of the United Nations, 2013; Power, 2010; Zhang et al., 2007). Since the Second World War, agriculture has increasingly intensified leading to changes in the landscape (McLaughlin and Mineau, 1995; Robinson and Sutherland, 2002). This constant reshaping of the landscape is affecting pollinator communities (Ollerton et al., 2014). Conservation measures at a landscape scale are becoming an increasingly effective tool.

However, more research could be developed in this area to have a more comprehensive view of the relationship linking pollinators to the landscape. This effort to promote a better landscape for pollinator communities should be a global concern where land owners as well as the public have their role to play. The conservation of pollinators is essential, not only as an ecological issue, but also because of many socio-economic consequences.

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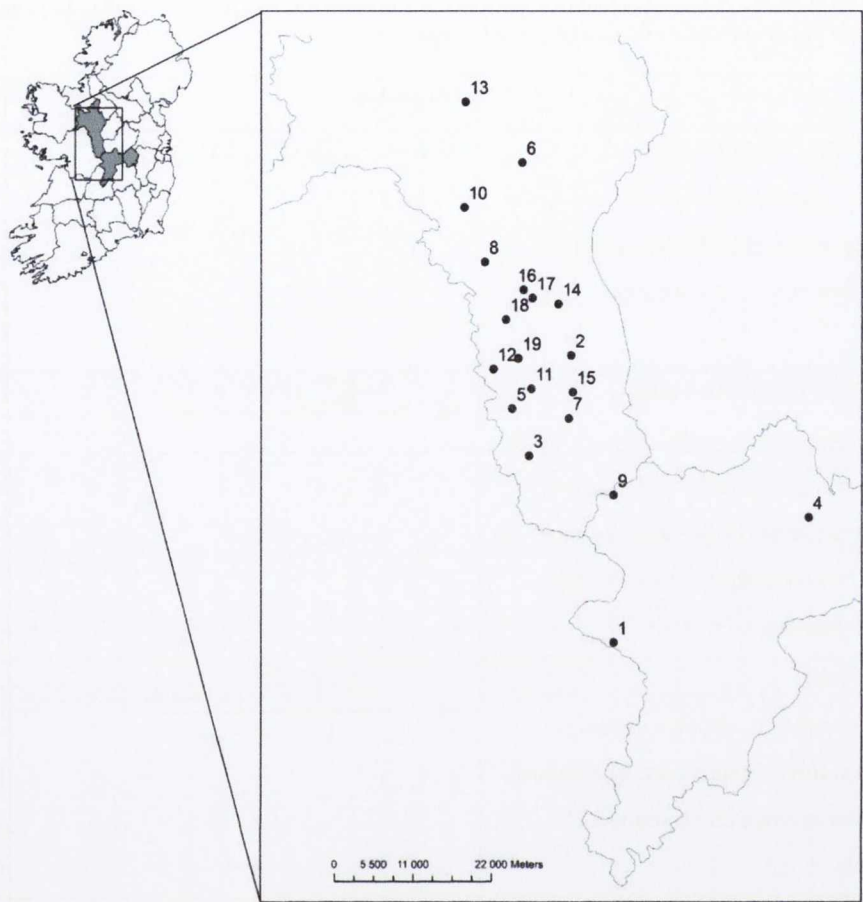
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Appendices

Appendix 1: Summary table of the 19 semi-natural grasslands on which fieldwork was carried out. The table specifies which site were exclusively dry calcareous and neutral grasslands (GS1) or semi-improved grasslands (GA+) with patches of dry calcareous and neutral grasslands.

Site	ID	x-coordinate	y-coordinate	habitat
All Saints	1	600640	710416	GS1
Ardmullen	2	594641	748976	GS1
Ballinasloe	3	588766	735523	GA+ with patches GS1
Ballyduff	4	627931	727332	GS1
Breeole	5	586409	741840	GS1
Carrownalassan	6	587785	774796	GS1
Castlesampson	7	594317	740536	GS1
Castlestrange	8	582557	761495	GA+ with patches GS1
Clonmacnoise	9	600609	730251	GS1
Cloonfenbaun	10	579661	768790	GS1
Curry	11	589080	744504	GS1
Fray	12	583775	747152	GS1
Glenballthomas	13	579835	782939	GA+ with patches GS1
Knockrogherry	14	592832	755857	GS1
Pollalaher	15	594843	744071	GA+ with patches GS1
Skrine1	16	587966	757772	GS1
Skrine2	17	589227	756669	GS1
Tibarney	18	585517	753792	GS1
Turrock	19	587256	748597	GS1

Appendix 2: Location of the 19 semi-natural grasslands sites according to their ID (Appendix 1).



Appendix 3: Formulas and descriptions of all the metrics used to characterise the landscapes with a_{ij} the area (m^2) of patch ij , a_i the area (m^2) of each patch of the same type i , A the total landscape area (m^2), N the total number of patches in the landscape, p_{ij} perimeter (m) of patch ij , P_i the proportion of landscape occupied by patch type (class) i , m number of patches types (classes) present in the landscape, E total length (m) of edge in landscape, f_j length (m) of each linear feature of the same type i .

Names	Formulas	Units
Shannon Habitat Diversity Index A habitat heterogeneity measure accounting for the both habitat richness and evenness. This index is more sensitive to the presence of rare habitat types.	$SDI = - \sum_{i=1}^m (P_i * \ln P_i)$	-
Shannon Habitat Evenness Index A habitat heterogeneity measure accounting for the both habitat richness and evenness. This index is less sensitive to the presence of rare habitat types, heavily weighted towards the most abundant habitat.	$SEI = \frac{- \sum_{i=1}^m (P_i * \ln P_i)}{\ln m}$	-
Mean Shape Index Measures the complexity of patch shape compared to a standard shape (circle or square). Calculated as the average patch shape at landscape level.	$MSI = \frac{\sum_{i=1}^m \sum_{j=1}^n \frac{p_{ij}}{(2\sqrt{\pi * a_{ij}})}}{N}$	-
Area Weighted Mean Shape Index Similar to Mean Shape Index of patches at landscape level, except patches are weighted according to size, i.e. larger patches are weighted more heavily than smaller patches.	$AWMSI = \sum_{i=1}^m \sum_{j=1}^n [(\frac{p_{ij}}{2\sqrt{\pi * a_{ij}}})(\frac{a_{ij}}{A})]$	-
Mean Patch Fractal Dimension A fractal is a geometric form that exhibits structure at all spatial scales. This metric calculates the fractal dimension of each patch using the perimeter-area method, similar to other Shape metrics, quantifying the degree of complexity of the shape. The advantage of fractal analysis is that unlike other Shape metrics, it is scale independent.	$MPFD = \frac{\sum_{i=1}^m \sum_{j=1}^n \frac{2 \ln p_{ij}}{\ln a_{ij}}}{N}$	-
Area Weighted Mean Patch Fractal Dimension	$AWMPFD = \sum_{i=1}^m \sum_{j=1}^n [(\frac{2 \ln p_{ij}}{\ln a_{ij}})(\frac{a_{ij}}{A})]$	-

Similar to the AWMSI, this metric weights the MPFD according to their size.		
Total Edge An absolute measure of total edge length of all patch types (landscape level). Unit = metres.	$TE = E$	m
Edge Density In studies which wish to compare different landscapes (e.g. different sizes), edge density is more appropriate, standardising edge to a per unit area basis.	$ED = \frac{E}{A} 10000$	m/ha
Mean Patch Size Calculates the mean size of all patches in the landscape.	$MPS = \frac{A}{N} (\frac{1}{10000})$	ha
Number of Patches Sums the number of patches in the landscape (either per class or for the entire landscape).	$NumP = N$	-
Median Patch Size Calculates the median patch size in the landscape.	<i>Median</i>	ha
% habitat type Proportion of landscape composed of a specific habitat type	$Ai = \frac{\sum_{j=1}^n a_j}{A} * 100$	-
Total length of linear feature type Sum of the length of each feature type	$Fi = \sum_{j=1}^o f_j$	m

Appendix 4: Habitats found in the landscapes surrounding the 19 semi-natural grasslands and their corresponding codes (according to Fossitt 2000).

Freshwater		Woodland and scrub	
FL3	Limestone and marl lakes	WN6	Wet willow alder ash woodland
FL6	Turlough	WD1	Mixed broadleaved woodland
FL8	Other artificial lakes and ponds	WD4	Conifer plantation
FW2	Depositing lowland rivers ²	WS1	Scrub
FS1	Reed and large sedge swamps	WL1b	Artificial' hedgerow ¹
Grasslands		Exposed rock and disturbed ground	
GA1	Improved agricultural grasslands	ED1	Exposed sand gravel or till
GA+	Semi-improved grasslands with a number of plant species superior of 10	ED4	Active quarries and mines
GS1	Dry calcareous and neutral grasslands	Cultivated and built land	
GS4	Wet grasslands	BC1	Arable crops
Bracken		BL1	Stone walls ¹
HD1	Dense bracken	BL3	Artificial surfaces ²
Peatland		Protection scheme habitat	
PB1	Raised bog	REPS	Rural environment protection scheme

¹: Linear feature habitat

²: Linear feature and polygon

Appendix 5: Definition of network parameters (Dormann et al., 2009).

Qualitative:

Number of plant species in the network

Connectance: Number of links that are in the realized network compared to the total possible links

Nestedness: Characteristic of a network with a core of generalist species that interact closely with each other and a few specialized species that tend to interact with the most generalized species (Bascompte et al., 2003). The nested temperature of a network measures the departure from a perfect nested (0°) to a chaotic structure (1°)

Quantitative:

Weighted linkage per insect species: Weighted mean number of plant species per insect species

H2': Network level measure of specialization based on the difference between the species realized number of interactions and the expected from each species total number of interactions (Blüthgen et al., 2006). It ranges from 0 (no specialization) to 1 (complete specialization)

Linkage Density: Mean number of links of species weighted by number of interaction. It is the average between the weighted linkage per insect species and weighted linkage per plant species in the network

Weighted linkage per plant species: Weighted mean number of insect species per plant species

Appendix 6: Pearson Product Moment Correlation Coefficients for 500m and 1km scales showing significant relationships between values for all the landscape metrics (except linear features) and the four variables retained (SEI, AWMSI, MPS and GS1) (chapter 2). This table only presents the significant correlation, the metrics not included showed no significance with SEI, AWMSI, MPS or GS1 (p-value < 0.05 and r > 0.456, ** p-value < 0.01 and r > 0.575).

	500m				1km			
	SEI	AWMSI	MPS	GS1	SEI	AWMSI	MPS	GS1
SDI	0.855**				0.938**		0.502*	
MSI		0.913**						
MPAR			-0.761**				-0.623**	
MPFD			-0.653**				- 0.486*	
AWMPFD			-0.833**				-0.962**	
ED			-0.915**				-0.938**	
NumP			-0.743**				-0.711**	
MedPS			0.642**					
%FL3					-0.490*	0.859**		
%FL8							0.619**	
%FS1					0.498*		0.504*	
%GA1	-0.806**			-0.529*	-0.895**		-0.603**	
%GS4			0.553*		0.520*		0.806**	
%PB1			0.553*		0.583**		0.717**	
%BL3								-0.630**
%FW2							0.636**	

Appendix 7: List of insect species recorded with the transect sampling across all sites.

Insect species			
<i>Aglais polychloras</i>	<i>Chrysotoxum bicinctum</i>	<i>Hipparchia semele</i>	<i>Platycheirus clypeatus</i>
<i>Anasimyia lineata</i>	<i>Coenonympha pamphilus</i>	Hoverfly sp	<i>Platycheirus granditarsus</i>
<i>Andrena angustior</i>	<i>Cupido minimus</i>	<i>Inachis io</i>	<i>Platycheirus manicatus</i>
<i>Andrena bicolor</i>	<i>Epistrophe grossulariae</i>	<i>Lasioglossum albipes</i>	<i>Platycheirus melanopsis</i>
<i>Andrena cineria</i>	<i>Epistrophe nitidicollis</i>	<i>Lasioglossum calceatum</i>	<i>Platycheirus rosarum</i>
<i>Andrena minutula/semilaevis</i>	<i>Episyrrhus balteatus</i>	<i>Lasioglossum fratellum</i>	<i>Platycheirus scutatus</i>
<i>Andrena sp</i>	<i>Eristalis arbusivus</i>	<i>Lasioglossum leucopus</i>	<i>Platycheirus sticticus</i>
<i>Aphantopus hyperantus</i>	<i>Eristalis arbustorum</i>	<i>Lasioglossum villosulum</i>	<i>Platycheirus tarsalis</i>
<i>Apis mellifera</i>	<i>Eristalis horticola</i>	<i>Lejogaster metallina</i>	<i>Polyommatus icarus</i>
<i>Bombus bohemicus</i>	<i>Eristalis interruptus</i>	<i>Leptidea sinapis</i>	<i>Rhingia campestris</i>
<i>Bombus hortorum</i>	<i>Eristalis intricarius</i>	<i>Lycaena phlaeas</i>	<i>Scaeva pyrastris</i>
<i>Bombus jonellus</i>	<i>Eristalis tenax</i>	<i>Maniola jurtina</i>	<i>Sphaerophoria scripta group</i>
<i>Bombus lapidarius</i>	<i>Eupeodes sp</i>	<i>Melanastoma mellinum</i>	<i>Sphcodes monilicornis</i>
<i>Bombus lucorum</i>	<i>Eupeodes corollae</i>	<i>Melanastoma scalare</i>	<i>Syrpitta pipiens</i>
<i>Bombus muscorum</i>	<i>Eupeodes latifasciatus</i>	<i>Meliscaeva auricollis</i>	<i>Syrphus ribesii</i>
<i>Bombus pascuorum</i>	<i>Eupeodes luniger</i>	<i>Neoaescia podagrica</i>	<i>Syrphus vitripennis</i>
<i>Bombus pratorum</i>	<i>Halictus rubicundis</i>	<i>Nomada ruficornis</i>	<i>Volucella bombylans</i>
<i>Bombus sylvestris</i>	<i>Halictus tumulcrum</i>	<i>Pieris napi</i>	<i>Xanthogramma citrofasciatus</i>
<i>Cheilosia pagana</i>	<i>Heliophilus hybridus</i>	<i>Platycheirus albanus</i>	
<i>Cheilosia sp</i>	<i>Heliophilus pendulus</i>	<i>Platycheirus angustatus</i>	

Appendix 8: Mean, minimum and maximum insect species richness and abundance (including mean species richness and abundance of each insect group) per site for 2010 and 2011.

Insect responses	2010			2011		
	Mean (+se)	Maximum	Minimum	Mean (+se)	Maximum	Minimum
Insect species richness	11.3 (± 1.23)	20	5	14.5 (± 1.18)	24	6
Insect abundance	38.6 (± 5.81)	106	8	44.8 (± 4.20)	82	14
Bee species richness	5.16 (± 0.454)	8	1	5.26 (± 0.404)	8	3
Bee abundance	23.2 (± 4.53)	94	6	21.8 (± 2.48)	44	5
Butterfly species richness	0.789 (± 0.249)	4	0	1.10 (± 0.241)	3	0
Butterfly abundance	1.16 (± 0.407)	6	0	2.16 (± 0.560)	8	0
Hoverfly species richness	5.37 (± 0.769)	13	1	8.10 (± 0.865)	14	2
Hoverfly abundance	14.2 (± 2.96)	49	2	20.8 (± 3.30)	52	3
Bumblebee species richness	4.11 (± 0.332)	7	1	3.58 (± 0.192)	5	2
Bumblebee abundance	21.5 (± 4.58)	94	6	17.4 (± 2.10)	39	4
Solitary bee species richness	1.000 (± 0.242)	3	0	1.53 (± 0.337)	4	0
Solitary bee abundance	1.58 (± 0.467)	6	0	3.21 (± 0.993)	17	0

Appendix 9: Mean, minimum and maximum value of each qualitative and quantitative insect-flower network parameter per site and calculated for 2010 and 2011.

	Response variables	2010				2011			
		Mean (±se)	Max	Min		Mean (±se)	Max	Min	
Qualitative parameters	Number of plant species	8.37 (±0.814)	15	3		10.9 (±0.851)	17	6	
	Number of insect species	11.3 (±1.233)	20	5		14.5 (±1.18)	24	6	
	Connectance	0.213 (±0.016)	0.389	0.130		0.169 (±0.009)	0.250	0.107	
	1-Nestedness	71.9 (±2.35)	85.01	49.5		76.1 (± 2.68)	92.7	50.5	
Quantitative parameters	Weighted linkage per pollinator species	1.91 (±0.171)	4.24	1		2.16 (±0.136)	3.51	1.44	
	H2'	0.594 (±0.050)	1	0.129		0.517 (±0.031)	0.805	0.259	
	Linkage Density	2.49 (±0.179)	3.90	1.12		2.72 (±0.168)	4.39	1.77	
	Weighted linkage per plant species	3.083 (±0.283)	5.61	1.25		3.280 (±0.287)	6.57	1.74	

Appendix 10 : Pearson Product Moment Correlation Coefficients for 2.5km and 5km scales showing where significant differences arise between values of all the landscape metrics (CLC2012 level 2) and the three variables retained (arable land, pasture and forest). This table only presents the significant correlation, the metrics not included showed no significance with arable land, pasture and forest.

	2.5km			5km		
	Arable land (21)	Pasture (23)	Forest (21)	Arable land (21)	Pasture (23)	Forest (21)
Heterogeneous agricultural areas (24)		-0.496*				0.669*
Scrub and/or herbaceous vegetation associations (32)					-0.950*	
Inland wetlands (41)		-0.972**				0.530*
Urban fabric (11)				0.505*		
Artificial non agricultural vegetated areas (14)	0.943**			0.967**		
Mines, dumps and construction sites (13)				0.717**		

* p-value < 0.05 and r > 0.456, ** p-value < 0.01 and r > 0.575

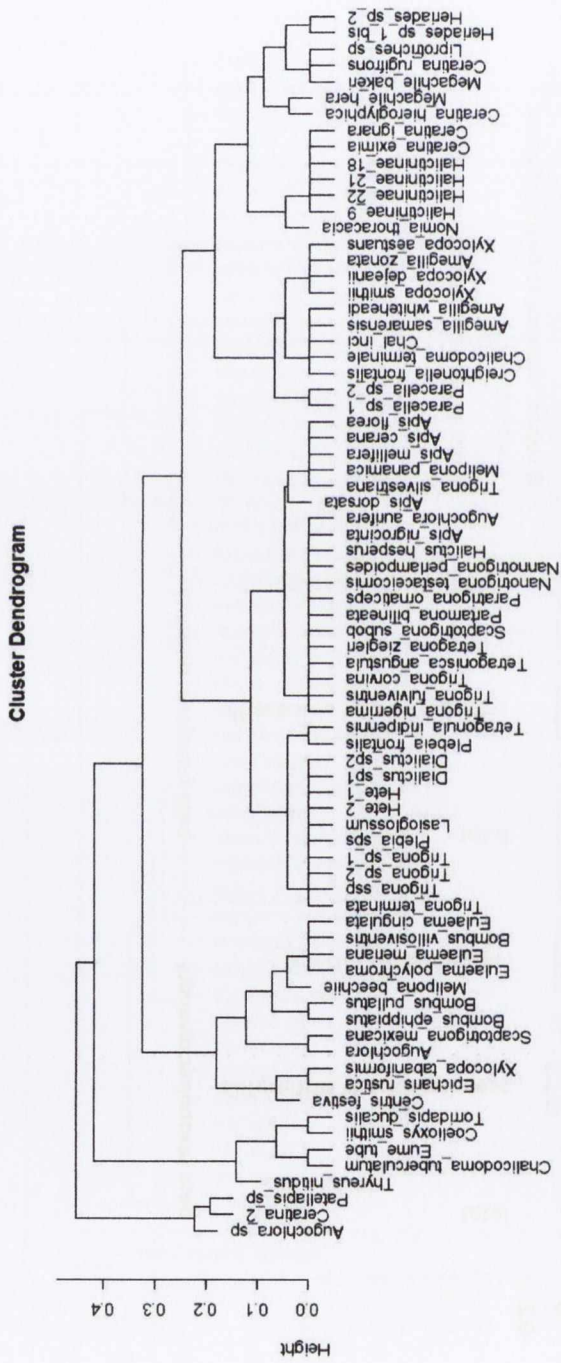
Appendix 11: Mean and standard error for each landscape metrics calculated at 1km scale for CLC2012 CORINE and Fossitt CORINE.

	CLC2012 CORINE	Fossitt CORINE
131	0.278 (±0.278)	0.320 (±0.197)
112/142	0.010(±0.010)	2.75 (±0.228)
211		0.638 (±0.307)
231	84.3 (±5.80)	66.0 (±4.91)
243	5.21 (±2.29)	
231/243		19.9 (3.16)
311		1.18(±0.529)
312		0.193 (±0.113)
322		0.026 (±0.024)
324		0.892 (±0.228)
332/333		0.590 (±0.331)
411	3.036 (±1.73)	0.183 (±0.109)
412	6.42 (±2.60)	5.89 (±2.54)
511	0.697 (±0.697)	0.495 (±0.495)
512	0.082 (±0.082)	0.924 (±0.438)

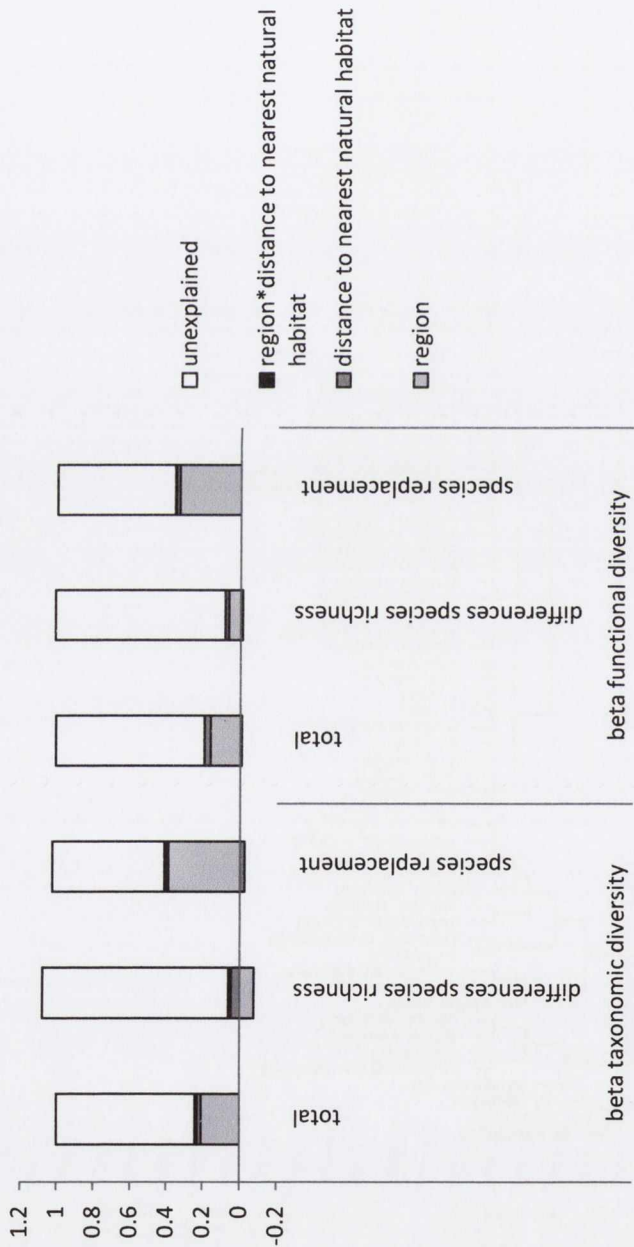
Appendix 12: Mean, minimum and maximum of all the landscape metrics (the different habitat types referred to the CLC2012 level 2) for 2.5km and 5km scales.

	2.5km			5km		
	Mean (±se)	Min	Max	Mean (±se)	Min	Max
Arable land (21)	0.308 (±0.238)	0.000	4.35	0.504(±0.483)	0.000	9.19
Pasture (23)	81.2 (±4.41)	30.0	98.6	79.3(±3.39)	33.2	92.7
Heterogeneous agricultural areas (24)	3.54(±0.961)	0.000	13.6	3.07(±0.624)	0.000	8.53
Forest (31)	0.093 (±0.059)	0.000	0.998	1.21(±0.346)	0.000	4.19
Scrub and/or herbaceous vegetation associations (32)	1.35 (±0.511)	0.000	7.84	2.17(±0.372)	0.000	5.53
Inland wetlands (41)	12.4 (±3.85)	0.000	58.7	12.6(±3.35)	0.120	58.4
Urban fabric (11)	0.035 (±0.028)	0.000	0.522	0.369(±0.100)	0.000	1.24
Industrial, commercial and transport units (12)	-	-	-	0.015(±0.015)	0.000	0.281
Mines, dumps and construction sites (13)	0.197 (±0.167)	0.000	3.16	0.178(±0.087)	0.000	1.31
Artificial non agricultural vegetated areas (14)	0.143 (±0.143)	0.000	2.71	0.045(±0.036)	0.000	0.678
Continental water (51)	0.703 (±0.487)	0.000	7.46	0.577(±0.322)	0.000	4.30

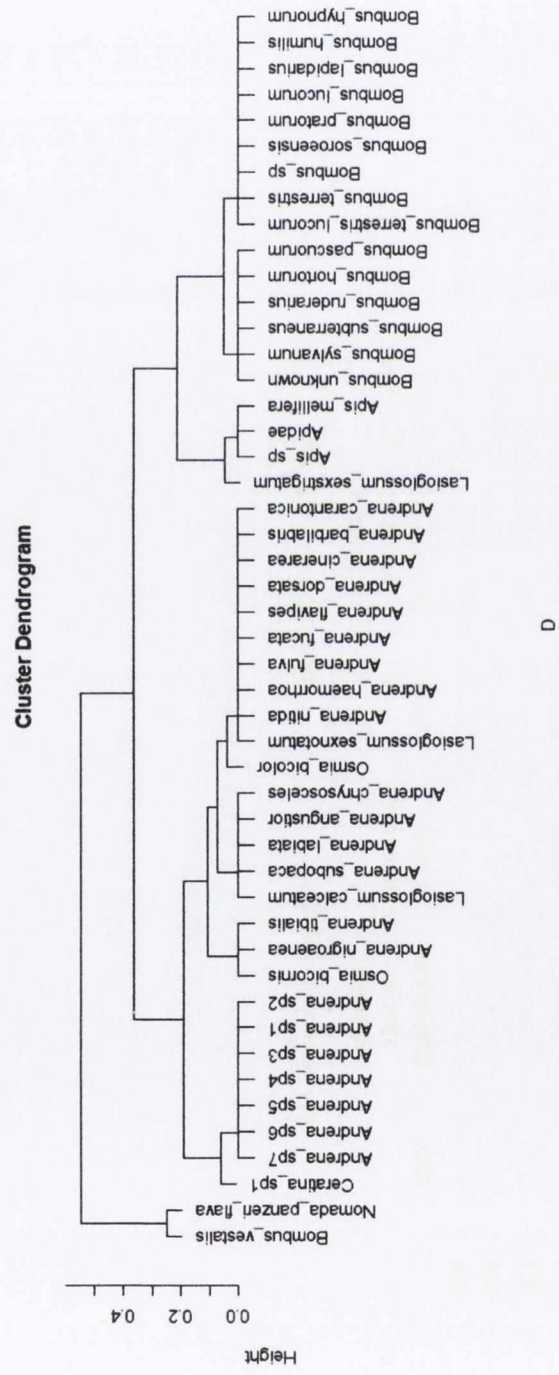
Appendix 13: Dendrogram of the functional similarities (based on Petchey and Gaston (2002)) of the species recorded in the coffee crops.



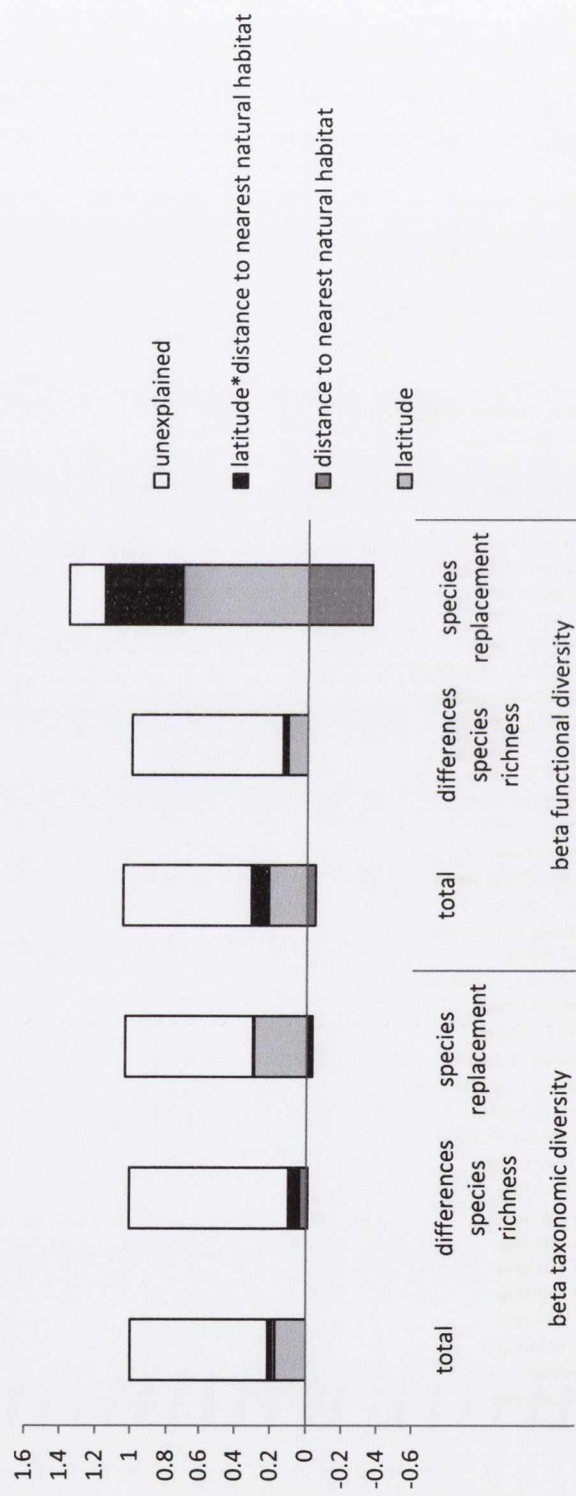
Appendix 14 : Contribution (R^2) of the latitude, distance to the nearest natural habitat and their interaction on the overall beta taxonomic (and functional) diversity and independently for their two components (species replacement and difference in species richness) for the coffee crop. This was calculated with adonis (PERMANOVA).



Appendix 15: Dendrogram of the functional similarities (based on Petchey and Gaston (2002)) of the species recorded in the oilseed rape crops.



Appendix 16: Contribution (R^2) of the latitude, distance to the nearest natural habitat and their interaction on the overall beta taxonomic (and functional) diversity and independently for their two components (species replacement and difference in species richness) for the Oilseed rape crop. This was calculated with adonis (PERMANOVA).



Appendix 17: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (SDI, AWMSI, MPS, MFC and grass) for the oilseed rape crop habitat. This table only presents the significant correlation, the metrics not included showed no significance with the SDI, AWMSI, MPS, MFC and grass.

	SDI	AWMSI	MPS	MFC	grass
SEI	0.905**				
TLA		(-)0.795**			
MSI		0.812**		0.664**	
AWMPFD			(-)0.766**		
TE			(-)0.917**		
MPE			0.958**		
NumP			(-)0.915**		
MedPS			0.707**		
arable		(-)0.708**			(-)0.817**

Appendix 18: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (MSI, NumP, %BC1, %GAI and SEI) with the *Rosa canina*. This table only presents the significant correlation, the metrics not included showed no significance with the MSI, NumP, BC1, GA+ and SEI.

	MSI	NumP	BC1	GA+	SEI
MPFD	0.731**				
AWMPFD		0.747**		0.592*	
TE		0.855**			
ED		0.902*			
MPE		(-)-0.785**			
MPS		(-)-0.851*			
ED4	0.616*				
GA1			(-)-0.937**		
WN5					(-)-0.696**
WN6					(-)-0.696
SDI				0.579*	0.887**

Appendix 19: Pearson Product Moment Correlation Coefficients at 700m scale showing where significant differences arise between values of all the landscape metrics and the five variables retained (MSI, NumP, %BC1, %GAI and SEI) with the *Sambucus nigra*. This table only presents the significant correlation, the metrics not included showed no significance with the MSI, NumP, BC1, GA+ and SEI.

	MSI	NumP	BC1	GA+	SEI
MPFD	0.727**				
AWMPFD		0.696**		0.601*	
TE		0.843**			
ED		0.915**			
MPE		(-)0.795**			
MPS		(-)0.822**			
BC2					0.560*
BL3		0.576*			
ED4	0.666**				
GA1			(-)0.920**		
WD4				0.639*	
WS1		0.556*			
SDI	0.645**			0.538*	0.808**