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High-resolution distribution of bumblebees (*Bombus* spp.) in a mountain area marked by agricultural decline

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Summary. Since the 1980s, bumblebee species have declined in Europe, partly because of agricultural intensification. Yet little is known about the potential consequences of agricultural decline on bumblebees. In most mountainous areas, agricultural decline from rural exodus is acute and alters landscapes as much as intensive farming. Our study aims at providing a quantitative assessment of agricultural decline through its impact on landscapes, and at characterising bumblebee assemblages associated with land-use types of mountain regions. The studied area (6.2 km²) belongs to the Eyne's valley in the French Pyrenees, known to host the exceptional number of 33 bumblebee species of the 45 found in continental France. We compare aerial photographs from 1953 and 2000 to quantify agricultural decline. We cross a bumblebee database (2849 observations) with land-use types interpreted from aerial photographs from 2000. Comparison of land-use maps from 1953 and 2000 reveals a strong progression of woodland and urbanised areas, and a decline of agricultural land (pastures and crops), except for hayfields. Spatial correlations between low altitude agro-pastoral structure and the occurrence of bumblebee species shows that bumblebee specific richness is highest in agro-pastoral land-uses (pastures and hayfields) and in the ski area, and poorest in woodland and urbanised areas. Urbanisation and agricultural decline, through increased woodland areas, could lead to a loss of bumblebee diversity in the future. To preserve high bumblebee richness, it is crucial to design measures to maintain open land habitats and the landscape's spatial heterogeneity through agro-pastoral practices.

Résumé. Distribution à haute résolution des bourdons (*Bombus* spp.) dans une zone montagnarde affectée par la déprise agricole. Depuis les années '80, les espèces de bourdons régressent en Europe, en partie à cause de l'intensification agricole. Par contre, on en sait peu sur les conséquences potentielles de la déprise agricole sur les bourdons. Dans la plupart des régions montagnardes, la déprise agricole suite à l'exode rural est aiguë et modifie les paysages autant que l'agriculture intensive. Notre étude vise à fournir une évaluation quantitative de la déprise agricole à travers son impact sur les paysages, et à caractériser les assemblages de bourdons associés aux types d'utilisation du sol des régions montagnardes. La zone étudiée (6.2km²) appartient à la vallée d'Eyne dans les Pyrénées françaises, connue pour héberger le nombre exceptionnel de 33 espèces de bourdons sur les 45 présentes en France continentale. Nous comparons les photographies aériennes de 1953 et 2000 pour quantifier la déprise agricole. Nous croisons une base de données de bourdons (2849 observations) avec les types d'utilisation du sol interprétés à partir de la photographie aérienne de 2000. La comparaison des cartes d'utilisation du sol de 1953 et 2000 révèle une forte progression des bois et des zones urbanisées, ainsi qu'un recul des terres agricoles (cultures et pâtures) à l'exception des prés de fauche. Les corrélations spatiales entre la structure agro-pastorale de basse altitude et l'occurrence des espèces de bourdons montre que la richesse spécifique des bourdons est plus élevée dans les types d'utilisation du sol agro-pastoraux (pâtures et prés de fauche) et au développement de la station de ski, et plus pauvres dans les bois et les zones urbanisées. L'urbanisation et la déprise agricole, à travers l'augmentation des zones boisées, pourraient conduire à une perte de la diversité des bourdons à l'avenir. Afin de préserver la haute richesse en bourdons, il est crucial de concevoir des mesures visant à maintenir les habitats ouverts et l'hétérogénéité spatiale du paysage à travers des pratiques agro-pastorales.

Keywords: Pyrenees; habitat preference; land use changes; mountain environment; agro-pastoral practices

For several decades, numerous bumblebee species (*Bombus* spp.) have been regressing in Europe (e.g. Rasmont et al. 2005; Williams 2005; Biesmeijer et al. 2006; Williams & Osborne 2009). This decline results among other things from major changes in land use brought about by intensive

farming (Burel et al. 1998). Habitat fragmentation through loss of wilderness areas (breeding, nesting, and foraging sites) and loss of their connectivity further contributes to the decline of pollinating insects, including bumblebees (Osborne et al. 1991; Steffan-Dewenter et al. 2006; Le Féon et al. 2010), and the decline of biodiversity as a

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whole (Dauber et al. 2003; Fahrig 2003). Changes in land cover and land use adversely affect bumblebee communities by degrading either nesting or foraging sites, or flower resources (Rasmont & Mersch 1988; Kevan 1999). The first cause of land use change evoked to explain the bumblebee decline is agricultural intensification (e.g. Burel et al. 1998; Carvell 2002; Carvell et al. 2006; Le Féon et al. 2010), resulting in a loss of diversity with a rise in the number of generalist species at the expense of rarer species (Burel et al. 1998).

However, little is known about the potential consequences of agricultural decline on the bumblebee fauna. Some studies have estimated the impact of this phenomenon on plants (Dullinger et al. 2003; Uematsu et al. 2010), beetles (Tocco et al. 2012), butterflies and orthopterans (Uchida & Ushimaru 2014), snails (Labaune & Magnin 2002) and birds (Laiolo et al. 2004; Nikolov 2009; Radović et al. 2013), but to our knowledge no quantitative research has been published on the matter for bumblebees. The concept of agricultural decline describes any cessation of the activity of crop or livestock in lands that are no longer profitable for agriculture, which are sometimes converted into more profitable uses (e.g. forestry, recreation; MacDonald et al. 2000) and sometimes abandoned (land abandonment). In mountain environments of Europe, agricultural decline induced by rural exodus began during the First World War and was then intensified after the Second World War (MacDonald et al. 2000). Arguably, this alters landscapes in a similar way to intensive farming. Consequences of land abandonment include landscape disruption by spontaneous reforestation of formerly open land habitats. Grasslands progressively turns into shrub and, finally, to forest. This leads to a decrease in open land habitats and reduces habitat heterogeneity, which therefore constitutes a threat for biodiversity (Burel 1999; MacDonald et al. 2000; Dimböck et al. 2003; Laiolo et al. 2004; Bolliger et al. 2007).

The municipality of Eyne, located within the Eastern Pyrenean region, is a particularly interesting spot. It has been known since the eighteenth century for its faunistic and floristic diversity, but it deserves special attention for its bumblebee diversity and species richness (Iserbyt et al. 2008). Many bumblebee species are well represented in Eyne whereas they are regressing in the rest of Europe (for instance *Bombus confusus* Schenck, *B. cullumanus* (Kirby), *B. gerstaeckeri* Morawitz, *B. humilis* Illiger, *B. ruderatus* (Scopoli), *B. subterraneus* (L.) and *B. sylvarum* (L.) (Rasmont et al. 2005; Iserbyt et al. 2008). After a long period of agriculture (37 farms holdings before the First World War), Eyne experienced a long process of agropastoral abandonment (Davassee & Galop 1997), with a massive decrease in farm numbers (only three farms left in 2008; Discussion with R. Staats; unreferenced). The utilised agricultural area (UAA) in the municipality of Eyne felt from 235 ha in 2000 to 99 ha in 2010 (AGRESTE-DRAAF Languedoc-Roussillon 2011). Is the agricultural

decline a possible explanation for the remarkable species richness observed in Eyne, or is it rather a threat?

This study aims firstly at providing a quantitative assessment of the agricultural decline phenomenon through its impact on landscapes, and secondly at characterising the bumblebee assemblages associated with the different land use types found in Eyne. This will allow evaluation of the potential impact that future agricultural decline could have on the bumblebee fauna.

Material and methods

Studied area

The study was carried out in the low altitude area of Eyne's territory (42°24'36"–42°29'36"N, 2°04'16"–2°08'53"E; Figure 1). It encompasses 6.2 km² and ranges in altitude from 1450 m in the vicinity of the village to 1876 m.

The landscape of this zone is currently shaped by three economic activity sectors: forestry, farming and tourism (CRNC 2002; Staats & Mendez 2012). For the last 60 years there has been a steady recolonisation of the bottom of the valley by an increasingly thicker forest, and a resumption of logging in the south-eastern part of the town (ONF 1996; Davassee & Galop 1997). In addition to the agricultural decline resulting in land abandonment, many other reallocations of agricultural land have occurred. The surfaces that were cropped until the second half of the nineteenth century are now grazing lands or hayfields. As for tourism, a ski resort with several ski slopes was set up in 1970. The development of these three economic sectors strongly influences land use dynamics within the studied area (Staats & Mendez 2012).

Land use data

This study is partially based on the aerial photography (1 m ground resolution) missions carried out in July–August 1953 and 2000 by the French Institut Géographique National (IGN) (IGN 1953 F 2250 1/25,000 – P – Partielle (97%); IGN 2000 FD 66 2000 1/25,000). After digitisation and georeferencing of the aerial photographs, we selected an identical study area for 1953 and 2000 (Figure 2a and b). Comparing the aerial photo interpretation of the low altitude area in 1953 and 2000 enables us to assess the vegetation and land use dynamics. As both photographs were taken during the same season, we could distinguish, with aerial photograph interpretation, the urbanised areas and the various ecological systems (cf. land use types in Results) based mainly on the characteristics of the vegetation mat, and delineated them as polygons. In addition, the quality of the results obtained through photo interpretation was assessed and improved with field validation. Field measurements and landscape survey with local farmers and local authorities took place in July 2002. Each measurement was pinpointed using a GPS locator (Magellan SporTrak Pro, Thales Navigation, San Dimas, CA, USA) with an accuracy of 1–10 m.

Faunistic data

Data origin. We extracted most data of Eyne's bumblebees from the *Banque de Données Fauniques de Gembloux et de Mons* (see Rasmont & Iserbyt 2014). Those data result mostly from sample collection carried out by the Laboratory of Zoology of the

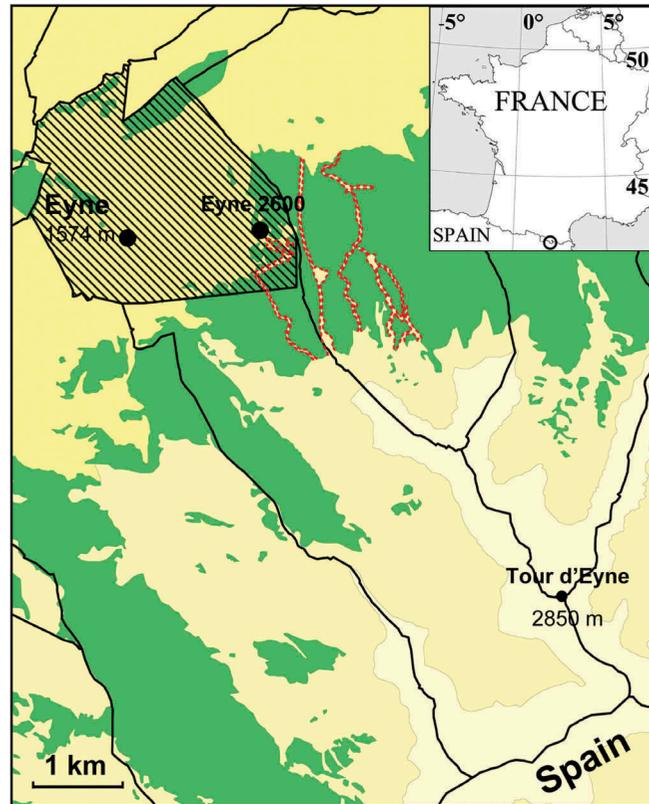


Figure 1. The municipality of Eyne. The shaded zone is the studied area; the dark yellow zone shows the hayfield, crop and pasture area; the green zone is the forested area; the yellow zone shows the subalpine grassland and heathland, and the pale yellow zone the alpine grassland. The red dotted line shows the ski slopes. The village itself is indicated by the black dot on the top left (WGS84, 42° 28'13"N, 02°05'06"E; from IGN 1997; Iserbyt et al. 2008).

University of Mons as part of a faunistic study project (Iserbyt et al. 2008). For analyses of the diversity and richness of bumblebees in each land use type, we only considered GPS-localised data. These were collected during the sampling operations from 1998 to 2008 in the studied area (Figure 1). A total of 2849 observations concerning 29 species and 217 stations were considered.

Data management. Data were managed using the Data-Fauna-Flora software (Barbier et al. 2002). We associated each land use type with its bumblebee species composition by setting up spatially explicit species distribution maps.

Data analysis. Based on CORINE Land Cover data (SOeS – European Union 2011), we assumed that land use did not change between 1998 and 2008 in the municipality of Eyne. We crossed bumblebee information of the period 1998–2008 from the database with land use distribution in 2000. In this way, we obtained a measure of bumblebee diversity and specific richness for each land use type. The presence and abundance of species are related to each land use type.

We computed mathematical indices for diversity and specific richness (Hurlbert expectancy and cumulative rarity index) in order to assess diversity and specific originality respectively. Hurlbert expectancy is the mathematical index used to quantify the specific diversity of a land use type (Hurlbert 1971; Legendre & Legendre 1998). The formula for Hurlbert expectancy used in this work is the simplified version proposed by Rasmont et al. (1990):

$$Es = \sum_i \left[1 - \left(\frac{N - N_i}{N} \right)^S \right] \quad (1)$$

where N_i = number of specimens of the i th species, N = total number of individuals within the station, and S = number of specimens in a random sample. It expresses the expected number of species in a random sample of S specimens (here $S = 40$, corresponding to the rounded minimum number of specimens observed in the sampled stations).

The originality of the land use type is assessed by the cumulative rarity index proposed by Rasmont et al. (1990):

$$R = \sum_i (1/N_i) \quad (2)$$

where N_i = number of individuals of the i th species observed in a reference territory. This index measures (in specimens⁻¹) the richness of each land use type in rare or endemic species compared to a reference territory, here the whole of continental France without the Eyne municipality (Iserbyt 2009).

We compared specific compositions of the various land use types using a nonparametric statistical test: the two-tailed Kolmogorov test (Siegel & Castellan 1988). For each station, we confronted the bumblebee observations (matrix 217 stations × 22 bumblebee species) to the observed land use (matrix 217 stations × seven land use types). In order to measure and describe the relationship between land use types and species' assemblages, we used a linear classification

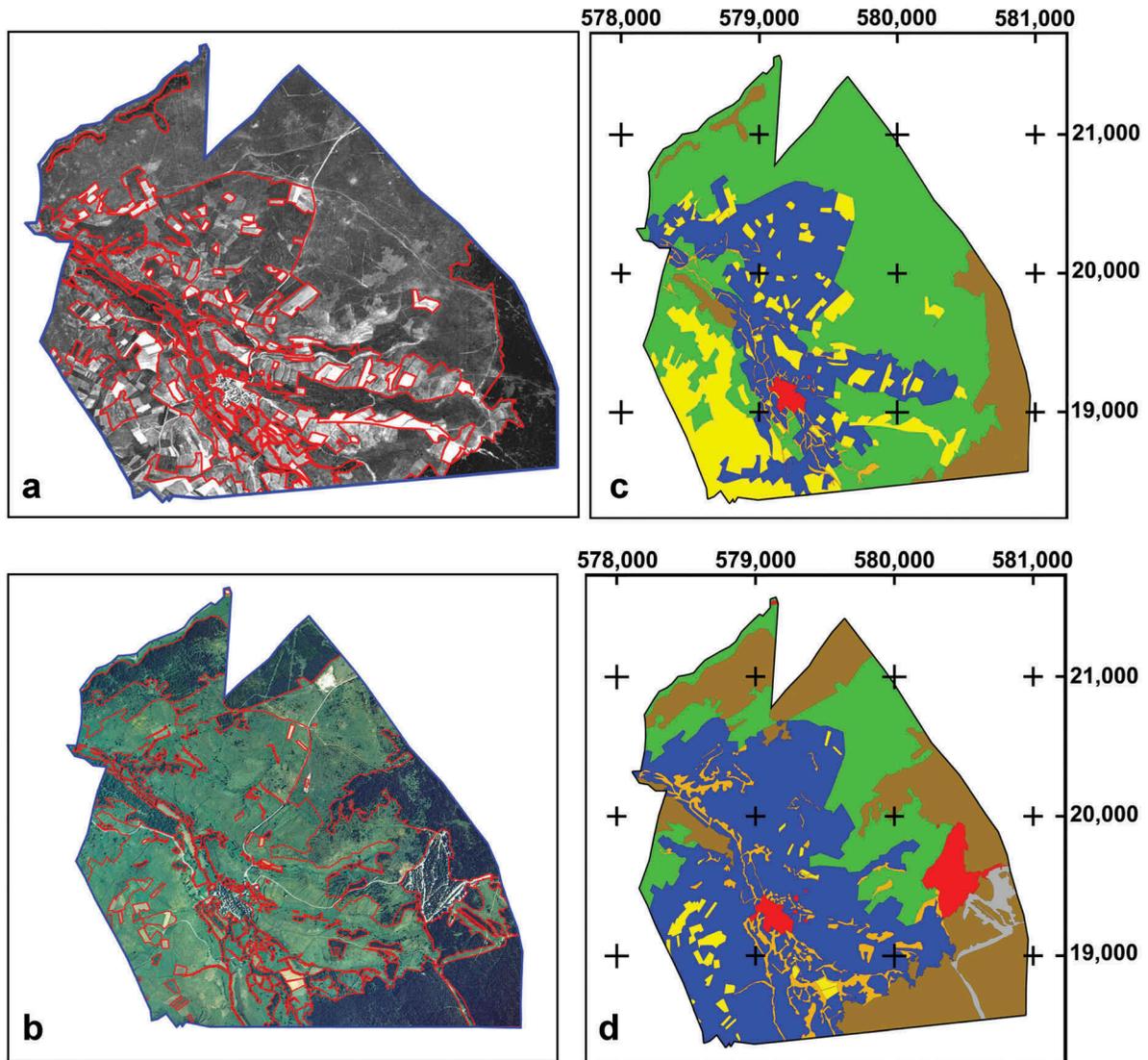


Figure 2. Delimitation of the working zone and land use types in 1953 (a) and 2000 (b). The zone in blue is the studied area, the delimitation of the land use types is shown in red. Identification of the land use types in 1953 (c) and 2000 (d). Yellow corresponds to “crops”; orange colour corresponds to “hedges and banks”; red to “dwellings”; green to “pastures”; blue to “hayfields”; brown to “woodland”; and grey to “pseudo-alpine” land use. The ticks indicate the kilometric grid in the Lambert 3 (south of France) coordinate system (from IGN 1953 and IGN 2000).

technique: canonical correspondence analysis (CCA; Ter Braak & Smilauer 2002). This analysis enables us to calculate the proportion of the bumblebee distribution variance due to land use types. We thus identified the most relevant land use type from a faunistic viewpoint and the relationship between bumblebee species and land use types. CCA enables us to visualise and simplify interactions between the specific distributions and land use types that characterise the stations. The relationship between species and land use types can be represented by projecting species and land use factors onto the canonical axes. Only those species represented by at least five specimens were retained in order to reduce statistical noise in the dataset. CANOCO 4.5 (Ter Braak & Smilauer 2002) was used for this analysis.

Results

Land use classification

By photo interpretation of aerial photographs and field survey, we identified a total of seven simple, consistent land use types: woodlands, crop fields, dwelling areas, hedges and banks, pastures, hayfields, and pseudo-alpine grasslands (Figure 3). The “woodland” type includes reforested zones as well as natural stands and forest edges. The “pseudo-alpine” land cover type is caused directly by human intervention through deforestation of

the subalpine forest to make room for ski slopes (Figure 1). The “crop” type includes all cultivation varieties (e.g. rye, potatoes, and turnips). There is no distinction between “true cropped” land and the field edges,

where most of our samplings for this type were done. The “hedges and banks” type includes hedges, bushes, shrubs, isolated trees, banks and embankments. The “pastures” type refers to grasslands grazed by livestock,

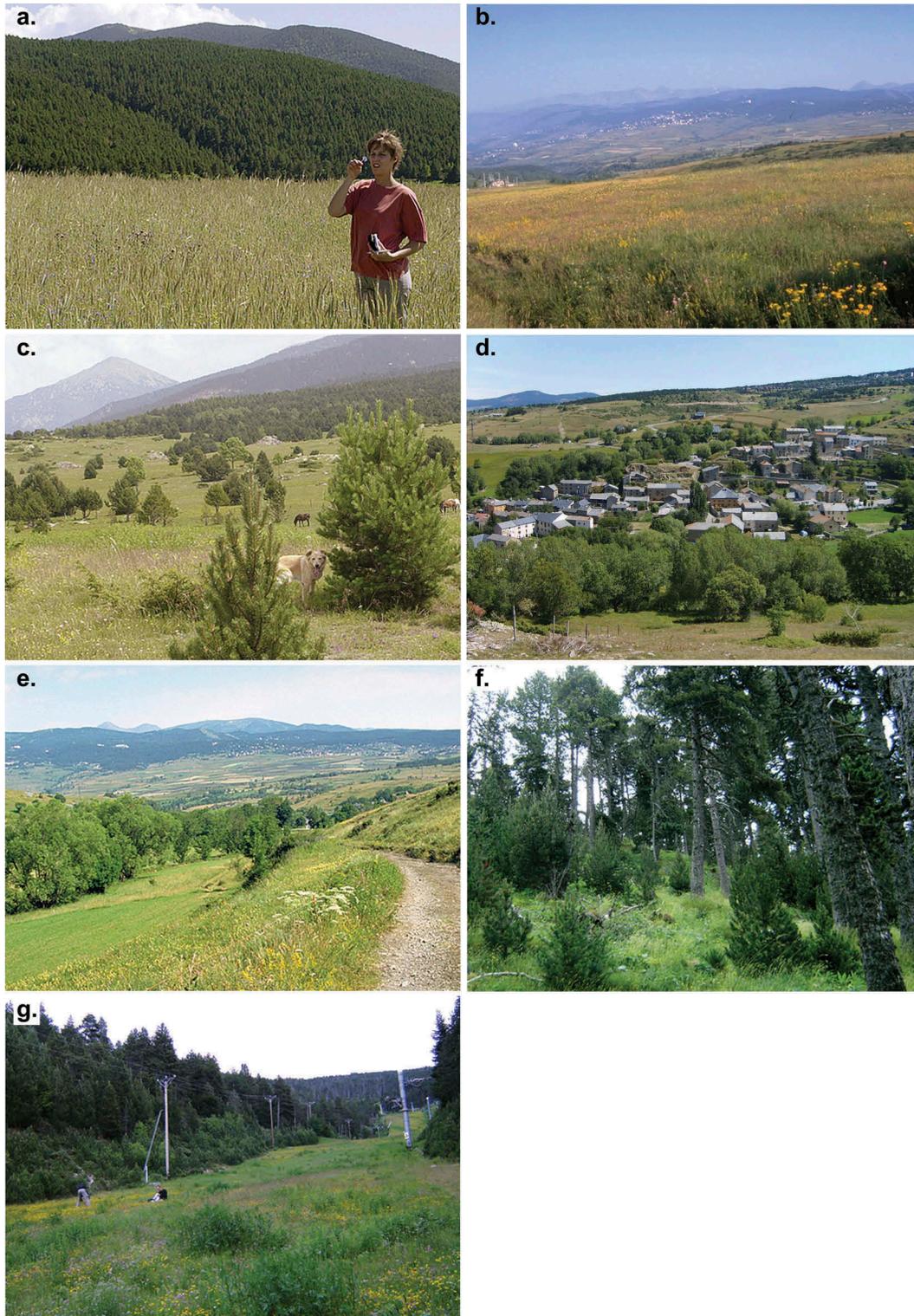


Figure 3. Land use types. From left to right and from top to bottom: (a) crops, rye cultivation (1620 m). (b) Hayfields (1750 m). (c) Pastures, grassland (1560 m). (d) Dwellings, the village of Eyne (1570 m). (e) Hedges and banks, near the village (1600 m). (f) Woodland, pinewood of *Pinus uncinata* Ramond ex DC at the entrance to the Eyne valley (1820 m). (g) Pseudo-alpine, ski slopes (1800 m).

whereas the “hayfields” type to grasslands that are mown for hay.

Land use dynamics

Comparing land cover maps drawn in 1953 and 2000 enables us to understand its dynamics (Figure 2c and d). This comparison reveals the following features (Table 1):

- Strong increase of surfaces covered by woody vegetation. The area covered in woodland rose from 54.1 ha in 1953 to 162.0 ha in 2000.
- Strong increase of surfaces devoted to urbanisation and ski area (“dwellings” and “pseudo-alpine”). The dwelled area rose from 3.9 ha in 1953 to 19.7 ha in 2000; the “pseudo-alpine” area reached 10.6 ha in 2000.
- Increase of surfaces covered by shrubby vegetation. “Hedges and banks” trebled their floor space between 1953 (10.6 ha) and 2000 (32.6 ha) especially downslope from the village (Figure 2b and d).
- Decrease of surfaces devoted to agriculture; the “pastures” fell from 310.6 ha in 1953 to 121.2 ha in 2000 and the “crops” fell from 93.4 to 11.4 ha; except for hayfields that increased from 148.8 ha to 264.4 ha.

Diversity and bumblebee richness per land use type

The specific composition of bumblebees remained almost the same before and after 1998 (Table 2). However, data location before 1998 (before the use of GPS) is not sufficient to allow precise linking of bumblebee data with land use data. This association could only be carried out from 1998 and is presented in this paper.

Table 1. Land use types in 1953 and 2000.

Land use types	Surfaces (ha) in 1953	Surfaces (ha) in 2000	Variation (ha)	Tendency
Woodland*	54.1	162.0	+ 107.9	++
Crops**	93.4	11.4	- 82.0	-
Dwellings	3.9	19.7	+ 15.8	+
Hedges and banks	10.6	32.6	+ 22.0	+
Pastures	310.6	121.2	- 189.4	-
Hayfields	148.8	264.4	+ 115.6	++
Pseudo-alpine	—	10.6	+ 10.6	+

Note: The percentage error when calculating the surface areas is estimated at 1%. *Woodland and its edge; **field edges essentially.

The species list associated to land use types varies both in terms of quantity and quality (Table 2). From the species present from 1998 to 2008 in Eyne’s low altitude zone, only eight are present in all types, and thus represent a typical assemblage of the bumblebee community found at Eyne’s low altitude zone (*B. hortorum*, *B. lucorum*, *B. mesomelas*, *B. pascuorum*, *B. ruderarius*, *B. soroeensis*, *B. subterraneus*, *B. terrestris*; Table 2). The 21 other bumblebee species found at this low altitude zone are rarer or may show more specific ecological preferences, which restricts their habitat to one or two land use types. The proportion of species represented by only one specimen varies considerably according to the land use type. It is very high for the “woodland”, “hedges and banks”, “crops” and “hayfields” types, with respectively 42.1, 35.7, 31.2 and 28% of the total number of species, compared to other types, i.e. “dwellings”, “pastures” and “pseudo-alpine” (respectively 0, 10 and 10%).

The diversity and originality of each land use type based on its bumblebee fauna are presented in Table 3. The diversity and originality indices are very different. The land use type that scores particularly high both in terms of richness and originality is “hayfields”, whereas the “dwellings” type is the one showing the lowest scores. The “pastures”, “hayfields” and “hedges and banks” types have the highest species richness (Hurlbert expectancy). The “hayfields”, “crops” and “woodland” types have a high cumulative rarity index comparable to that of the whole study area. Conversely, the other types show much lower cumulative rarity indices, indicating a more ordinary bumblebee fauna.

Except for “hedges and banks”, land use types differ markedly in their specific composition (Table 4) even for the most abundant species of the study area.

The diversity (Hurlbert expectancy) and originality indices (Table 3) on the one hand, and the correlations between land use types (Table 4) on the other hand, emphasise the strong contrast between land use types. They show a marked difference between the urbanised environment (“dwelling” type), which show a weak diversity, and the treeless or shrubless agrarian environments (“hayfields” type), showing a very high density.

The faunistic differences between the various land use types (Table 4) result from the large proportion of singletons, the low number of generalist species in the study area, and hypothetically the biotopographic preferences of some species.

Bumblebee assemblages associated with the different land use types

The biotopographic preferences of many species are difficult to identify. Stations where *B. humilis* was observed (Figure 4b) seem to indicate that this species prefers open

Table 2. Relative proportion of the number of specimens found for each species, for the studied area before and during the 1998–2008 sampling period, and for each land use type during the 1998–2008 period.

Taxa	Studied area (before 1998)	Studied area (1998–2008)	Woodland*	Crops	Dwellings	Hedges and banks	Pastures	Hayfields	Pseudo-alpine
<i>Bombus barbutellus</i> (Kirby) ** (a)	0.1 (1)	- (1)							
<i>Bombus campestris</i> (Panzer) ** (a)	0.4 (4)	- (1)							
<i>Bombus flavidus</i> Eversmann ** (a)	2.1 (24)								
<i>Bombus gerstaeckeri</i> Morawitz	1.2 (14)					2.0 (1)			
<i>Bombus norvegicus</i> (Sparre Schneider) ^(a)			0.7 (1)						
<i>Bombus quadricolor</i> (Lepeletier) ^(a)	3.4 (39)			0.2 (1)				0.1 (1)	
<i>Bombus cullumanus</i> (Kirby)	0.3 (3)							0.1 (1)	
<i>Bombus magnus</i> Vogt			0.7 (1)				0.5 (2)	0.1 (1)	0.2 (1)
<i>Bombus ruderatus</i> (Fabricius)	0.2 (2)								
<i>Bombus sylvestris</i> (Lepeletier) ^(a)	9.2 (104)							0.1 (1)	0.6 (3)
<i>Bombus mucidus</i> Gerstaecker	1.6 (18)							0.1 (1)	0.6 (3)
<i>Bombus rupestris</i> (Fabricius) ^(a)	2.1 (24)			0.2 (1)				0.1 (1)	
<i>Bombus sichelii</i> Radoszkowski	3.0 (34)							0.4 (5)	
<i>Bombus mendax</i> Gerstaecker	1.8 (20)			0.2 (1)					0.8 (4)
<i>Bombus bohemicus</i> Seidl ^(a)	6.5 (74)						0.3 (1)		
<i>Bombus hypnorum</i> (L.)	0.3 (3)		0.7 (1)				1.4 (5)	0.2 (2)	
<i>Bombus wurflenii</i> Radoszkowski	3.2 (36)		0.7 (1)					0.3 (3)	0.9 (5)
<i>Bombus pratorum</i> (L.)	2.5 (28)		1.4 (2)			2.0 (1)		0.1 (1)	0.8 (4)
<i>Bombus confusus</i> Schenk	0.4 (5)		5.4 (8)		1.8 (4)			0.1 (1)	2.1 (11)
<i>Bombus lapidarius</i> (L.)	3.2 (36)			0.5 (2)				0.9 (10)	2.3 (12)
<i>Bombus monticola</i> Smith	0.2 (2)			3.4 (15)				1.8 (20)	0.6 (3)
<i>Bombus pyrenaicus</i> Pérez	6.5 (74)					2.0 (1)		2.3 (26)	4.9 (26)
<i>Bombus terrestris</i> (L.)	0.2 (2)			0.2 (1)				1.6 (18)	4.7 (25)
<i>Bombus subterraneus</i> (L.)	2.5 (28)			3.9 (17)				1.2 (13)	0.2 (1)
<i>Bombus pascuorum</i> (Scopoli)	2.2 (25)			4.8 (21)				2.0 (22)	2.5 (13)
<i>Bombus hortorum</i> (L.)	4.3 (49)			1.1 (5)				6.1 (68)	6.1 (32)
<i>Bombus mesomelas</i> Gerstaecker	6.9 (78)			0.2 (1)				1.0 (11)	12.0 (63)
<i>Bombus humilis</i> Illiger	1.1 (13)			11.9 (52)				5.4 (60)	3.0 (16)
<i>Bombus soroeensis</i> (Fabricius)	7.5 (85)			16.1 (70)				4.1 (15)	6.5 (34)
<i>Bombus sylvanum</i> (L.)	1.0 (11)			17.7 (77)				8.5 (31)	
<i>Bombus ruderarius</i> (Müller)	20.4 (231)			15.8 (69)				26.0 (95)	
<i>Bombus lucorum</i> (L.)	6.0 (68)			17.7 (77)				9.2 (102)	
Total number of specimens	1135	2849	147	436	218	49	365	1108	526
Total number of species	30	29	19	16	11	14	20	25	19

Notes: *Woodland and its edge; **species absent during the 1998–2008 observation period and not taken into account in this study. (a): Exclusively inquiline species. -: species that are present but with low relative proportions. Between brackets, the number of specimens for each species.

Table 3. Estimation of the bumblebee diversity and originality for the studied area (before 1998 and during the 1998–2008 period) and each land use type (during the 1998–2008 period).

	Number of specimens	Number of species	Hurlbert (Number of species expected in a 40 specimens sample)	Cumulative rarity (Specimens ⁻¹)
Studied area (before 1998)	1135	30	16.2	0.044
Studied area (1998–2008)	2849	29	12.4	0.041
Woodland*	147	19	10.3	0.018
Crops	436	16	9.3	0.018
Dwellings	218	11	8.5	0.005
Hedges and banks	49	14	11.3	0.008
Pastures	365	20	12.3	0.011
Hayfields	1108	25	11.3	0.029
Pseudo-alpine	526	19	10.7	0.011

Note: *Woodland and its edge.

Table 4. Specific composition comparison for the different land use types by a two-tailed Kolmogorov test.

	Woodland	Crops	Dwellings	Hedges and banks	Pastures	Hayfields	Pseudo–alpine
Woodland							
Crops	0.34 (***)						
Dwellings	0.30 (***)	0.11 (NS)					
Hedges and banks	0.18 (NS)	0.19 (NS)	0.20 (NS)				
Pastures	0.36 (***)	0.17 (***)	0.14 (**)	0.21 (*)			
Hayfields	0.19 (***)	0.17 (***)	0.20 (***)	0.07 (NS)	0.25 (***)		
Pseudo-alpine	0.17 (**)	0.30 (***)	0.28 (***)	0.15 (NS)	0.35 (***)	0.14 (***)	

Note: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; NS: non-significant.

habitats and particularly the “hayfields” and “crop” types. Stations where *B. pratorum* was observed seem to indicate that this species prefers closed habitats and particularly the “woodland” and “pseudo-alpine” types. Some species seem to have similar affinities for certain land use types. This is the case, for instance, for *B. monticola* (Figure 4e), *B. pyrenaicus* (Figure 6c), *B. sichelii* (Figure 6h) and *B. wurflenii* (Figure 7e), which seem to show affinity for the “pseudo-alpine” type. Stations where, for instance, *B. confusus* (Figure 4a; 11 stations), *B. lucorum* (Figure 4c; 83 stations) or *B. magnus* (Figure 4d; three stations) were present do not allow for a reliable identification of these species’ preferences. Superficial examination of the specific distribution maps does not allow determination of the species’ biotopographic preferences (Figures 4–7).

Canonical correspondence analysis enables us to calculate the common variance of both matrices [station \times species] and [station \times land use] (Figure 8a and b respectively). This common variance represents the variation in bumblebee distribution that is determined by land use types. Approximately 11% of the variance in the bumblebee

distribution is explained by the seven types. The factors with the highest contribution to the definition of axis 1 are positively related to the degree of closure characterising the land use type analysed (mainly “woodland” and “pseudo-alpine”) and negatively related to its degree of openness (mainly “hayfields”, “crops” and “pastures”). Axis 2 (Figure 8b) shows an opposition between the treeless and shrubless agrarian environments (“hayfields” and “crops” types) and the other land use types. Projecting the species in the plane defined by the first two canonical axes (69.1% of the variance explained) results in distinct groups of species. These divide (axis 1, Figure 8a) into open habitat species and closed habitat species (“woodland”, “hedges and banks” and “pseudo-alpine” types) and split the open habitats (axis 2, Figure 8a) into the treeless and shrubless agrarian types (“crops” and “hayfields”) and the other more or less wooded types (Figure 8a). On the basis of these features the species divide into four groups. Group I encompasses many species: *B. bohemicus*, *B. hortorum*, *B. hypnorum*, *B. monticola*, *B. mucidus*, *B. pascuorum*, *B. pratorum*, *B. pyrenaicus*, *B. sichelii* and *B. wurflenii*

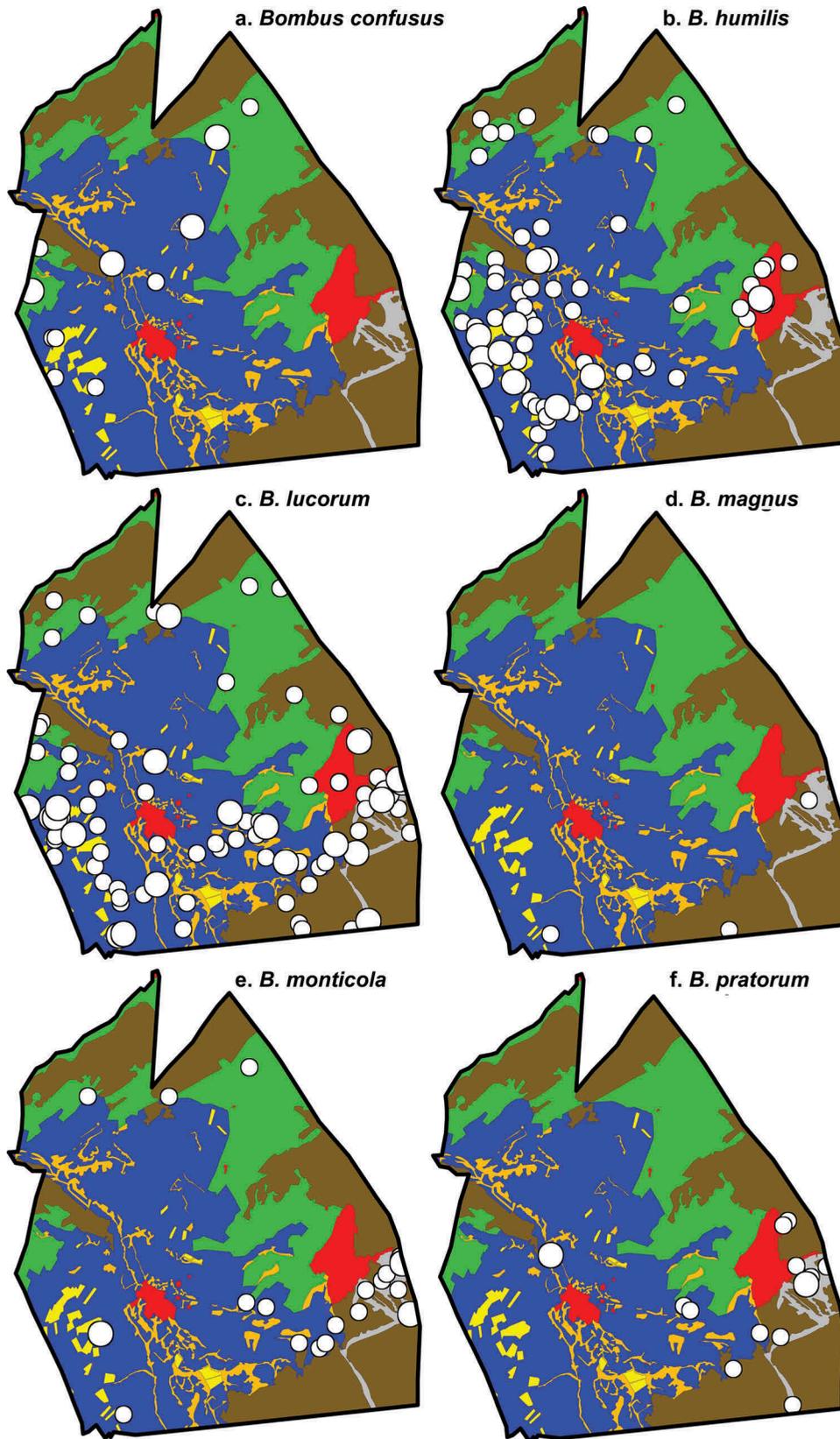


Figure 4. Distribution map of bumblebee species. (a) *Bombus confusus* Schenck (36 specimens, 11 stations). (b) *B. humilis* Illiger (247 specimens, 71 stations). (c) *B. lucorum* (L.) (546 specimens, 83 stations). (d) *B. magnus* Vogt (three specimens, three stations). (e) *B. monticola* Smith (56 specimens, 21 stations). (f) *B. pratorum* (L.) (31 specimens, 14 stations). The data are indicated by dots corresponding to a diameter of either 150 m, when the number of specimens in the station is greater than or equal to five, or a diameter of 75 m, when the number of specimens is less than five.

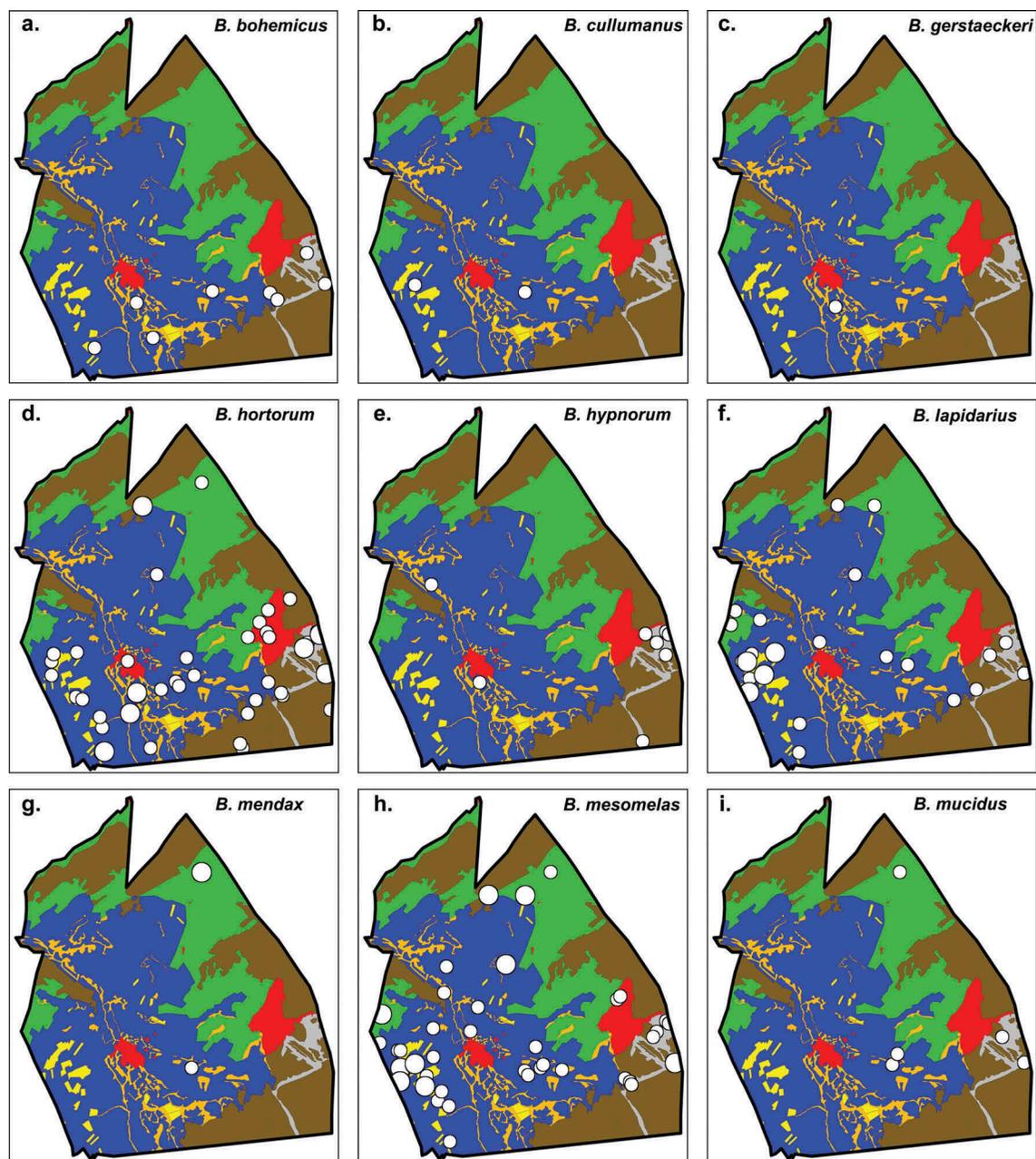


Figure 5. Distribution map of bumblebee species. (a) *Bombus bohemicus* Seidl (10 specimens, eight stations); (b) *B. cullumanus* (Kirby) (two specimens, two stations); (c) *B. gerstaeckeri* Morawitz (one specimen, one station); (d) *B. hortorum* (L.) (145 specimens, 44 stations); (e) *B. hypnorum* (L.) (nine specimens, eight stations); (f) *B. lapidarius* (L.) (51 specimens, 24 stations); (g) *B. mendax* Gerstaecker (seven specimens, two stations); (h) *B. mesomelas* Gerstaecker (162 specimens, 41 stations); (i) *B. mucidus* Gerstaecker (six specimens, five stations). The data are indicated by dots corresponding to a diameter of either 150 m, when the number of specimens in the station is greater than or equal to five, or a diameter of 75 m, when the number of specimens is less than five.

(Figure 8a). This group can be described as showing preference for deforested areas, for skiing facilities (“pseudo-alpine” type) or for areas rich in trees and/or shrubs (“hedges and banks” and “woodland”) (Figure 8b). Two

groups are characterised by biotopographic preferences for open environment. Group II (*B. confusus*, *B. mendax*, *B. terrestris* and *B. sylvarum*) is particularly linked to urbanised and pasture areas whereas group III (*B. humilis*, *B.*

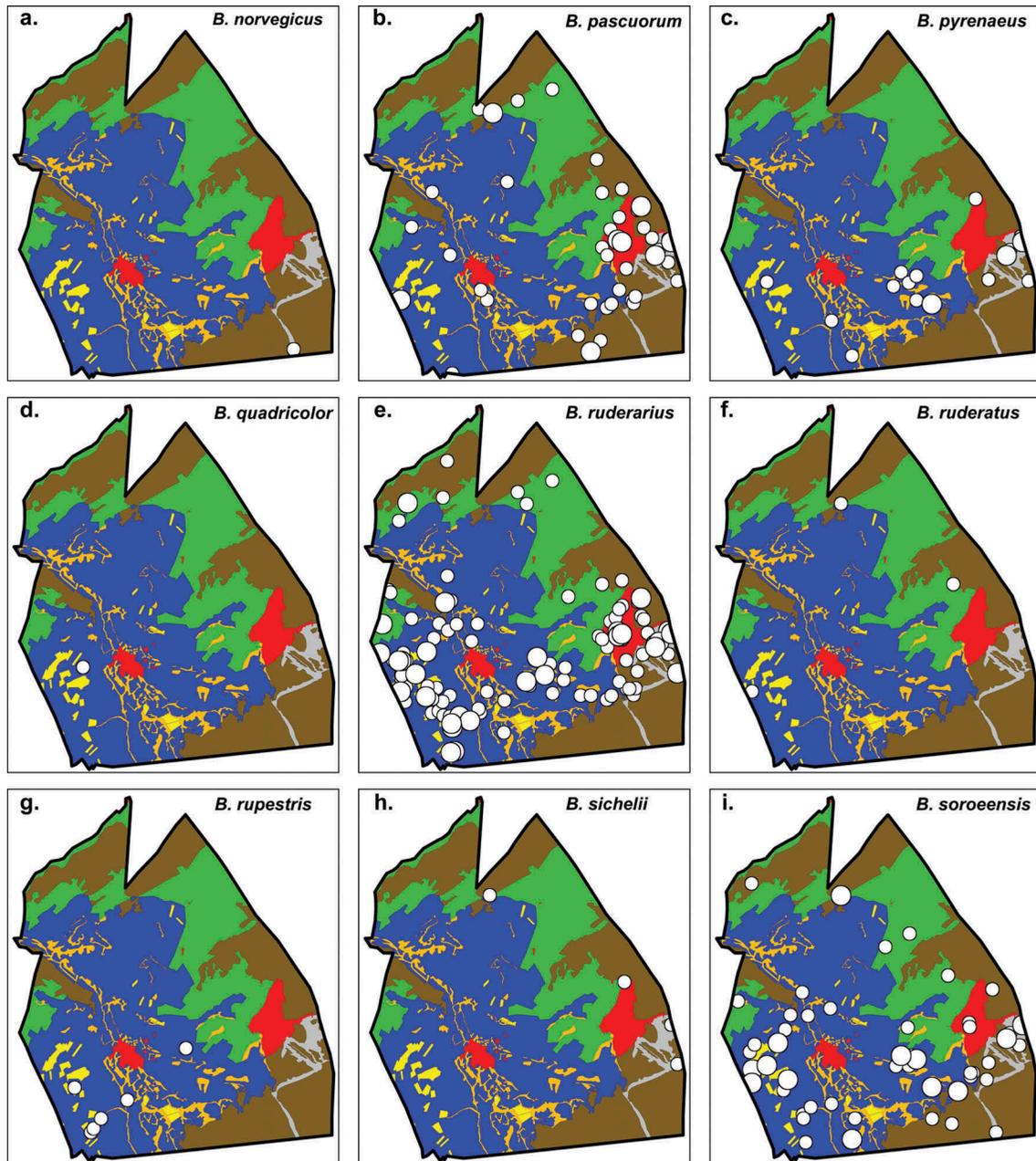


Figure 6. Distribution map of bumblebee species. (a) *Bombus norvegicus* (Sparre Schneider) (one specimen, one station); (b) *B. pascuorum* (Scopoli) (116 specimens, 45 stations); (c) *B. pyrenaicus* Pérez (56 specimens, 17 stations); (d) *B. quadricolor* (Lepeletier) (one specimen, one station); (e) *B. ruderarius* (Müller) (554 specimens, 104 stations); (f) *B. ruderatus* (Scopoli) (four specimens, three stations); (g) *B. rupestris* (Fabricius) (six specimens, six stations); (h) *B. sichelii* Radoszkowski (six specimens, four stations); (i) *B. soroensis* (Fabricius) (254 specimens, 51 stations). The data are indicated by dots corresponding to a diameter of either 150 m, when the number of specimens in the station is greater than or equal to five, or a diameter of 75 m, when the number of specimens is less than five.

lapidarius, *B. mesomelas*, *B. rupestris*, *B. soroensis* and *B. subterraneus*) is mainly associated to agrarian areas (“hay-fields” and “crop” types). The most abundant species (*B. lucorum* and *B. ruderarius*, group IV) tend to be generalist and cannot be characterised according to a particular land use type.

Discussion

Land use dynamics

The agricultural decline phenomenon in the Pyrenees has already been demonstrated in the Quérigut district (France, Ariège; Fabre 1977) and in Eyne’s valley (Davasse & Galop 1997). As in our study, they observed

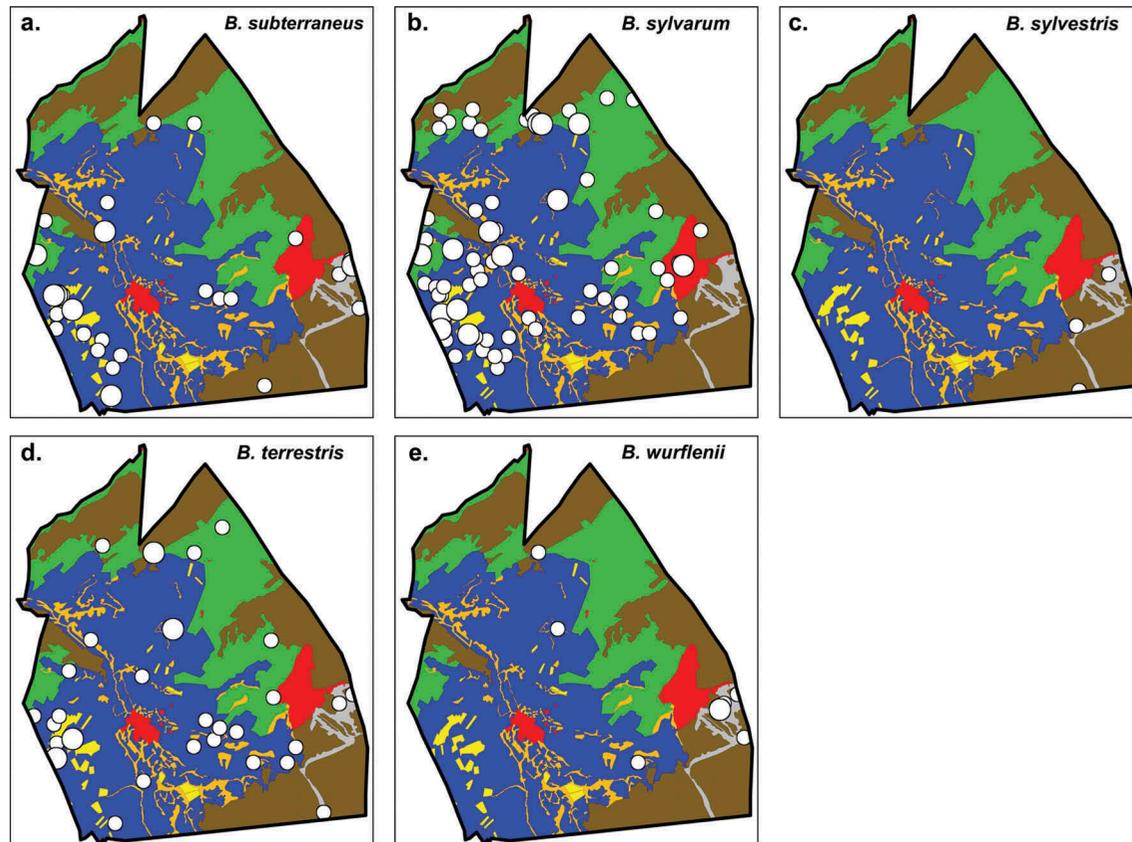


Figure 7. Distribution map of bumblebee species (continuation). (a) *Bombus subterraneus* (L.) (112 specimens, 28 stations); (b) *B. sylvarum* (L.) (332 specimens, 68 stations); (c) *B. sylvestris* (Lepeletier) (four specimens, three stations); (d) *B. terrestris* (L.) (87 specimens, 29 stations); (e) *B. wurflenii* Radoszkowski (14 specimens, seven stations). (See Figure 1d and e for the legend). The data are indicated by dots corresponding to a diameter of either 150 m, when the number of specimens in the station is greater than or equal to five, or a diameter of 75 m, when the number of specimens is less than five.

a continuous trend towards land abandonment and a more extensive use of the remaining agricultural land. Contrary to what takes place in areas undergoing strong agricultural intensification, uncropped plots such as forests, pastures and hedges tend to coalesce. The present agro-pastoral landscape found in Eyne is characterised, among other things, by a dense network of hedges and banks that increases the connectivity between the wooded areas upslope and downslope of the village. Converting the “crops” and “pastures” types into mainly “hayfields” and “woodland” types resulted in a tremendous change in the landscape. The rise of human pressure by urbanisation is clearly noticeable (Figure 2c and d). The dwelling area increased fivefold due to the development of the ski resort and its hamlet “Eyne 2600” (Figure 1). At the same time, ski slopes have been laid out. It is difficult to predict how far this land use type will expand as this is strongly dependent upon economic and touristic contingencies. The current landscape found in Eyne results directly from the overall evolution in land

use induced by agricultural decline and the development of the ski resort and its facilities.

Bumblebee assemblages associated with the different land use types

The apparently low value (11%) of the variance in bumblebee distribution explained by the seven land use types could mainly be explained by the inter-annual species abundance variation. We accumulated the species’ abundance over 10 years without taking into account the large inter-annual variations that occurred (Iserbyt & Rasmont 2012). Moreover, floral resources, microclimates and altitude are also factors that influence the distribution of bumblebees in this region (Iserbyt et al. 2008; Iserbyt & Rasmont 2012).

The specific richness observed in the “woodland” type may result from the merging of the data pertaining to actual forest with the data concerning its edge. Edges often have a higher index of biodiversity, and so the fact that they are included in “woodland” may overestimate the observed

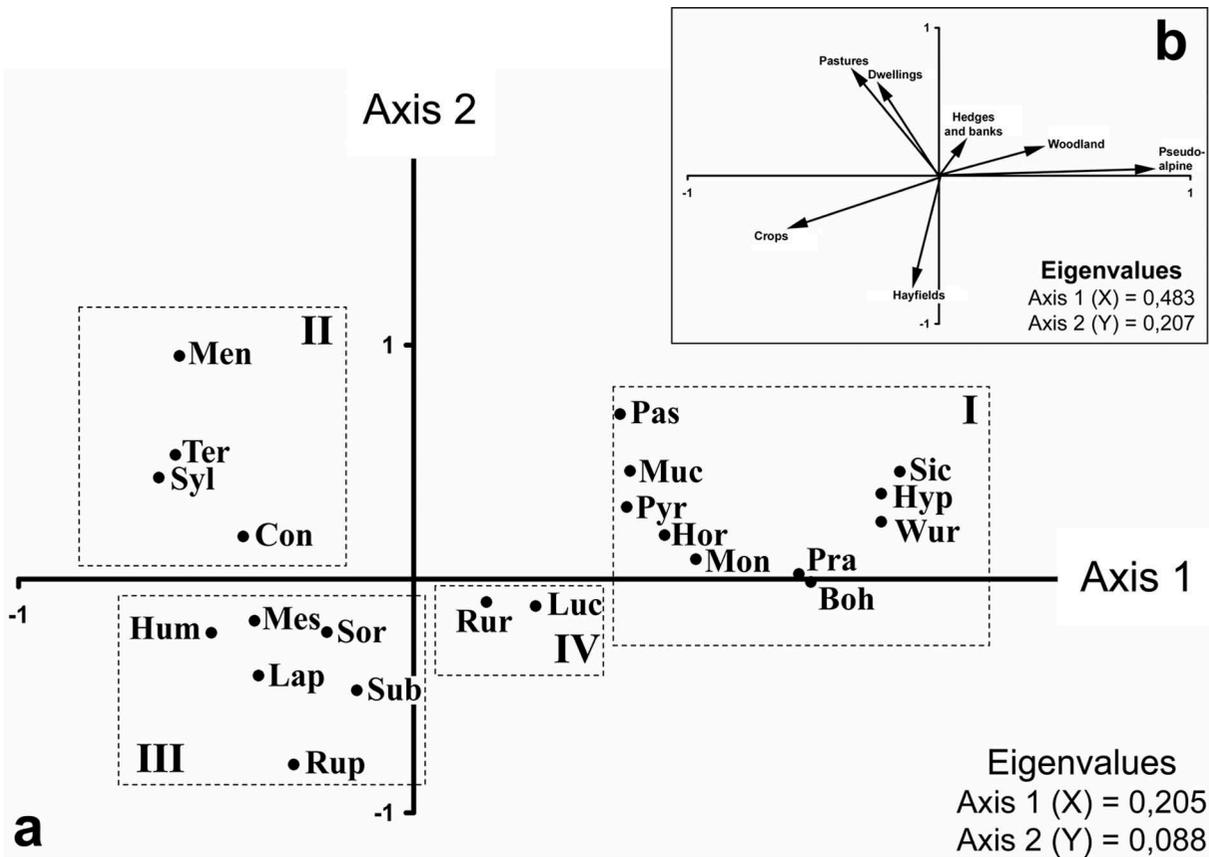


Figure 8. Projection of the species (a) and land use types (b) on the first two axes of the canonical correspondence analysis. The coordinates are indicated in accordance to the scale of eigenvectors. The Roman numerals refer to the biotopographic groups. Abbreviations for the bumblebee species: Boh: *Bombus bohemicus**, Con: *B. confusus*, Hor: *B. hortorum*, Hum: *B. humilis*, Hyp: *B. hypnorum*, Lap: *B. lapidarius*, Luc: *B. lucorum*, Men: *B. mendax*, Mes: *B. mesomelas*, Mon: *B. monticola*, Muc: *B. mucidus*, Pas: *B. pascuorum*, Pra: *B. pratorum*, Pyr: *B. pyrenaicus*, Rup: *B. rupestris**, Rur: *B. ruderarius*, Sic: *B. sichelii*, Sor: *B. soroensis*, Sub: *B. subterraneus*, Syl: *B. sylvarum*, Ter: *B. terrestris*, Wur: *B. wurflenii*. *Obligatory inquiline species.

diversity of this type. The proportion of singletons is relatively high (42.1%) for this land use type. The species represented by a single specimen include *B. sichelii*, *B. subterraneus*, and the obligatory inquiline species *B. bohemicus*, *B. norvegicus* and *B. sylvestris*. As emphasised by Oertli et al. (2005), a high percentage of singletons results either from a weak sampling or from rarity or sometimes a specific vagrancy (i.e. an individual accidentally found outside the range of its species). Few bumblebee species are linked to the forest environment (*B. hypnorum*, *B. pascuorum* and *B. pratorum*; Reinig 1970; Rasmont 1988; Iserbyt et al. 2008).

Between 1953 and 2000 most cropped zones were converted into “hayfields” zones. This evolution may have contributed to the exceptional bumblebee species richness in Eyne (Iserbyt et al. 2008). Hayfields have the highest specific richness of all land use types encountered in the studied area, with high diversity and originality indices (Table 3). The high proportion of singletons in this land use type results from the presence of rare species (*B. cullumanus*, Figure 5b; *B.*

magnus, Figure 4d; *B. rupestris*, Figure 6g) but mostly from the vagrancy – facilitated by the laying out of ski slopes (Figure 1) – of species that are typical of the middle and high altitudes (*B. mucidus*, Figure 5i; *B. wurflenii*, Figure 7e), or the forest (*B. hypnorum*, Figure 5e). The presence in this area, shaped by mountain agro-pastoral activity, of species such as *B. cullumanus*, *B. confusus*, *B. humilis*, *B. ruderatus*, *B. subterraneus* and *B. sylvarum*, generally considered as regressing in Europe as a whole (Rasmont et al. 2005; Xie et al. 2008; UKBAP 2009; Goulson 2010), shows the importance of careful conservation efforts. Eyne is one of the last two places in the world where the presence of *B. cullumanus* has been documented (Rasmont et al. 2005, email from G. Mahé to P. Rasmont; unreferenced).

Estimation of the potential impact of agricultural decline on the bumblebee fauna in Eyne

Having determined the habitat preferences of the different species, and the greater or lesser role of the different land

use types in the diversity of bumblebees, we can evaluate the potential impact that further agricultural decline could have on the bumblebee communities.

As Michel (2006) suggested for small mammals in the Armorican region (France, Ille-et-Vilaine and Manche), in Eyne the current extensification of agriculture, mostly through reallocation of crops to hayfields, could initially contribute to maintaining the specific diversity that has been observed for half a century (Delmas 1976; Iserbyt et al. 2008). Moreover, as described by Oertli et al. (2005) in Switzerland, the main factors explaining a high bumblebee diversity are the coexistence of the different habitat types and the weak intensity of agricultural practices. This is precisely the present situation in Eyne as a whole but more specifically in the low altitude part of its territory.

However, the agricultural decline process leads to a progressive tree and shrub encroachment due to pastoral abandonment (Davasse & Galop 1997). While crops around the town are converted into hayfields, the older and more distant hayfields are used as extensive pastures for a short period in spring and autumn, allowing shrubs and trees to grow. As a result, we are witnessing the progressive emergence of wooded habitats. Subsequent loss of open land habitats is a threat to plant (Dirnböck et al. 2003) and animal diversity (Labaune & Magnin 2002; Laiolo et al. 2004). If these land dynamics are to last, urbanisation, shrub encroachment and reforestation are likely to result in a reduction in bumblebee specific diversity. Indeed, urbanisation has a negative impact on bumblebee gene flows and dispersal (Jha & Kremen 2013). Furthermore, several works showed that bumblebee abundance and specific richness increase proportionally to the extent of pastures and meadows (Hatfield & LeBuhn 2007) and decrease proportionally to the extent of forest (Diaz-Forero et al. 2011 2012). The reforestation process that took place between 1953 and 2000, mostly at the expense of pastures, could induce a reduction of specific richness in the future.

Sooner or later agricultural decline will have a negative impact on grassland bumblebee species (*B. confusus*, *B. cullumanus*, *B. humilis*, *B. ruderatus*, *B. subterraneus* and *B. sylvarum*; according to Rasmont 1988; Benton 2006; Iserbyt et al. 2008) to the benefit of edge-loving species (e.g. *B. hortorum*, *B. pascuorum* and *B. ruderarius*; according to Pittioni & Schmidt 1942; Rasmont 1988; Benton 2006) and forest-loving species (e.g. *B. pratorum* and *B. hypnorum*; according to Pittioni & Schmidt 1942; Reinig 1970; Rasmont 1988; Benton 2006; Iserbyt et al. 2008; Crowther et al. 2014). More specifically, it is likely that the rare species found in Eyne, such as *B. confusus*, *B. cullumanus* and *B. ruderatus*, which are stringently dependent on legume-rich dry grasslands (Rasmont 1988; Benton 2006; Iserbyt et al. 2008), will regress if the current land use dynamics persists (i.e. reforestation and urbanisation). Indeed, the decline of

these bumblebee species as observed among other places in Britain (Goulson et al. 2005), Belgium and France (Rasmont et al. 2005), seems to result from changes in plant communities induced by changes in agricultural practices.

As to species strictly dependent on woodland such as *B. pratorum* and *B. hypnorum* (Pittioni & Schmidt 1942; Reinig 1970; Rasmont 1988; Benton 2006; Iserbyt et al. 2008; Crowther et al. 2014), the current reforestation process should sooner or later enable the dispersal and expansion of these ordinary and already abundant species, which are expanding in the Western Palaearctic (Rasmont 1989; Goulson & Williams 2001; Williams et al. 2009; Crowther et al. 2014).

The linear uncultivated landscape features such as “hedges and banks” or field edges have an important ecological function for bumblebees, as habitats for species with a liking for transitional environments (e.g. *B. hortorum*, *B. pascuorum* and *B. ruderarius* according to Pittioni & Schmidt 1942; Reinig 1970; Rasmont 1988; Benton 2006), as shelters from predation, as nesting sites owing to the numerous possibilities afforded (Svensson et al. 2000), or as corridors for population flows (Steffan-Dewenter et al. 2002; Cranmer et al. 2012). In the UK, some studies showed that hedges do not represent a barrier to the movement of bumblebees (Krewenka et al. 2011), and even that they could facilitate their spatial orientation during travel (Cranmer et al. 2012). However hedges tend to get thicker and bigger during land abandonment process and therefore could act as barriers to the movement of bumblebees. This, coupled with the expansion of woodland areas, could therefore increase the fragmentation of open land habitats. As observed generally in the Western Palaearctic (Williams 1988; Osborne & Corbet 1994; Goverde et al. 2002; Fahrig 2003), habitat loss and fragmentation could in the long run lead to a decrease of Eyne’s bumblebee diversity, at least among species preferring open environments.

Kreyer et al. (2004) did not observe any restriction in the foraging activity of *B. pascuorum* and *B. terrestris* in Hesse (Germany) due to the presence of a forest barrier in a plain. The situation is different in Eyne (Figure 1), where the pine forest makes up a homogenous ecological barrier at an altitude ranging from 1800 to 2100 m. This barrier splits the Eyne valley, with its alpine and subalpine grasslands from the tableland surrounding the village, with its mountain “pastures”, “crops” and “hayfields”. The laying out of ski slopes east of the village has involved the clearing of long strips of forests between subalpine heathlands and grasslands, and the cultivated tableland (Figure 1). It is precisely along these corridors or at their lower end that several bumblebee species normally linked exclusively to alpine and subalpine heathlands and grasslands come to forage (*B. mendax*, Figure 5g; *B. monticola*, Figure 4e; *B. mucidus*, Figure 5i; *B. pyrenaicus*, Figure 6c; *B. sichelii*, Figure 6h; subalpine species according to Pittioni &

Schmidt 1942; Rasmont 1988; Iserbyt et al. 2008). The opening of these ski slopes thus decompartmentalised the vegetation altitudinal zonation and brought high altitude species to the vicinity of the village.

Preserving the spatiotemporal heterogeneity of the landscape through agro-pastoral practices (Marage 2004) is essential to maintain specific diversity; but this is largely contingent on natural and human disruptive patterns (Burel 1999; Lambin et al. 2001).

Nevertheless, the impact of climate change can also significantly affect the population dynamics of bumblebees (Rasmont et al. 2015), especially in mountain environments. Indeed, our previous studies showed that climate is an important driver of changes in bumblebees abundance and diversity in the Eyne valley (Iserbyt & Rasmont 2012), and that bumblebees are highly vulnerable to extreme temperatures, such as heat waves (Rasmont & Iserbyt 2012). The increase of forest cover at the entrance of the Eyne valley could become a barrier and stop low altitude bumblebee communities from moving to higher altitude zones, in response to global warming. This trend is offset by the laying out of ski slopes, which could act as corridors and enable species to disperse to higher altitudes. Moreover, changes in land use may affect local climate because of the modification of solar partitioning. For example, conversion of woodland in open land induces a decrease in humidity and an increase in temperature (Vitousek 1994). Micro-climatic conditions of a landscape depend not only on regional climate, but also on landscape structure and configuration.

Conclusion

In summary, it should be underlined that the land use types favourable for specific diversity and originality in Eyne's bumblebee population are hayfields, pastures, hedges and banks, and cleared corridors (ski slopes). Conversely, the least favourable are forestland and urbanised zones. Urbanisation and reforestation due to agricultural decline cause an extension of this unfavourable area. It is therefore crucial for bumblebee conservation that agricultural policies allow for the maintenance of open land habitats and habitat diversity.

The main limitations of this study are the availability of data, and especially their accuracy. Indeed, data prior to 1998 have not been used because of their lack of precision, which failed to allocate bumblebee species to the different land use types for the period of 1950. Therefore, we have not been able to demonstrate a dynamic of bumblebee species in relation to the land use.

Next steps in this research could involve the development of prospective scenarios of land use change in these mountain regions marked by agricultural decline. In order to assess the impact of these scenarios on bumblebee populations, they should take into account

the socio-economic evolutions related to agriculture (intensification or abandonment) and tourism (e.g. skiing), coupled to climate change.

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