POLLINIS
ONG INDÉPENDANTE ET SANS BUT LUCRATIF QUI AGIT
EXCLUSIVEMENT GRÂCE AUX DONS DES CITOYENS
POUR LA PROTECTION DES ABEILLES DOMESTIQUES
ET SAUVAGES, ET UNE AGRICULTURE RESPECTUEUSE
DE TOUS LES POLLINISATEURS.

ASSESSING POLLINATOR DIVERSITY IN THE PARC NATIONAL DE LA VANOISE, FRANCE

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ABSTRACT

The Vanoise National Park (French: Parc national de la Vanoise) in France is located in the French Alps and was created in 1963. Combined with the Gran Paradiso National Park in Italy which adjoins it the area make up the largest contiguous alpine protected area covering over 1200 km^2. The Vanoise park represents an area of outstanding natural beauty as well as a reserve for nationally significant population of native wildlife. This includes communities of insects that play a critical role in maintaining pollination ecosystem functions maintaining reproductive success and population viability of many flowering plants. These insects, which include both social and solitary bees, as well as hoverflies and other insects, are in themselves a diverse assemblage that represent an important contribution to native biodiversity. The Vanoise park contains a wide range of land uses that extend from urbanised areas abutting protected areas, agricultural pasture, extensively managed semi-natural pasture, and un-managed natural areas within the main park. All have the potential to support insect pollinator communities. Here we undertake detailed quantification of the insect pollinator communities associated with these four different land uses using a variety of methods including transect based walks and pan traps, as well as detailed quantification of insect-plant mutualistic foraging interactions, i.e. what insects pollinate which plants. Key findings are that urban and agricultural pasture within the park have significant potential to support pollinator biodiversity, especially is managed under sympathetic management that maximises floral diversity. There is a strong suggestion that there is a net decline in the abundance of pollinators along an intensification gradient from urban to natural land uses. However, only semi-natural pasture systems were identified as driving differentiation in the pollinator community structure relative to the other land uses. This report discusses these findings in relation to the four land use classes considered within the national park with the goal of identifying their relative role in maintaining pollinator biodiversity.

INTRODUCTION

The Park Nationals de la Vanoise represents areas of outstanding natural beauty and a potentially irreplaceable example of natural and semi-natural managed alpine habitats within France. This area, and areas like it, help support landscape scale species pools of native wildlife, of which insect pollinators represent a significant part of this biodiversity (DeWalt and South, 2015; Roland and Schmidt, 2015; Burkle *et al.*, 2016). This is particularly important in response to increasing evidence of worldwide declines in insect pollinators driven by habitat destruction, intensification of agriculture land use including pesticides, as well as the impact of pests, parasites and invasive species (IPBES, 2016). In France alone there are some 874 species of wild bees wich play a functionally significant role within the reserve and the wider region by maintaining the provision of key pollination services to both wild plants and economically significant crops (Potts *et al.*, 2010; Khalifa *et al.*, 2021). Land use within the reserve is characterised by a patchwork of historical and ongoing land use management characteristics that have the potential to support pollinator diversity and pollination services as well as acting as a population sources facilitating recolonization through sink-source dynamics (García *et al.*, 2018; Matsushita *et al.*, 2018; Engström *et al.*, 2020; Vasiliev and Greenwood, 2020; Bascompte and Scheffer, 2023). Within the park different land uses are exposed to a wide range of social and environmental pressures resulting from both their location as well as their wider cultural and economic role within the communities (Potts *et al.*, 2010; Vanbergen *et al.*, 2013). This results in a wide range of environmental drivers affecting both community structure of pollinators that interact in given locations with surrounding land uses, amenity use by park visitors, and longer term impacts that include climate change or invasive species (Potts *et al.*, 2010). Within complex land use systems such as those in the Vanoise park and surrounding area gradients of habitat management intensity have been shown to impact on the underlying trophic interactions between communities of insect pollinators and the plants on which they feed. This can directly affect community resilience in response to species loss (Memmott *et al.*, 2004; Bascompte and Scheffer, 2023). Such species loss is often the result of the unique functional characteristics of individual species may make them particularly sensitive to net environmental change (Vandewalle *et al.*, 2010; Oliver *et al.*, 2015). It is also likely that species associated with natural system's, such as those within the Park National de la Vanoise, may be more susceptible to species loss and collapse of key trophic interactions (Redhead *et al.*, 2018; Powney *et al.*, 2019). There is a need an evidence base to contribute to strategic management strategies within the park to support insect pollinator assemblages. This will maintain not only their value within the reserve, but their role in supporting and maintain the diversity of this key group at a national and international scale.

OBJECTIVES

The key objectives of this research program was to quantify the impact of a range of environmental risks associated with land use change within the Park National de la Vanoise that may impact on the diversity and robustness of insect pollinator systems. The Vanoise National Park represents an Alpine biome that has a history of both human habitation as well as agricultural and recreational use that pre-dates its establishment in 1963. The park is characterised by large areas of agricultural pasture management focusing on cattle, with this extending into lower levels of stocking within more semi-natural pasture areas. In fully protected areas of the park direct livestock pasture management is prohibited in what can be considered as natural areas, although the historical basis of some of these areas will reflect their altitude and ease of access by farmers. Adjoining the main park are urban centres, which while comparatively small, may act as an intensification driver resulting from civil and amenity management decision in green areas impacting on pollinator community within their boundaries. In this study we assess the consequences of land use on insect pollinator communities with a focus on the structure of foraging relationships that characterise their interaction with plant communities. This study is intended to provide an evidence base to support longer term management decisions in relation to land use within the national park.

METHODS

Summary of the study locations

This study focuses on the impact of human activity on pollinators in the Vanoise National Park. Sites were selected to be representative of a gradient of land use intensification from urban systems on the park edge, though to unmanaged natural systems located far more centrally within its boundaries. To do this we selected three urban sites (with more than 50% urban infrastructure on a diameter of 500m from the sampling location), three agricultural pasture systems, and three semi-natural sites with low intensity livestock utilisation. These land uses were also compared to a natural site, in the heart of the reserve, where human activity was largely absent with the except of recreational hikers. All the sites were located between 1400m and 1800m above sea level so as to make communities as comparable as possible. In addition, each study site was chosen to be at least 2 km away from adjacent samples areas to minimise spatial autocorrelation.

The below fig. 1 shows the location of these sample points, with a summary of the 10 sites following this.

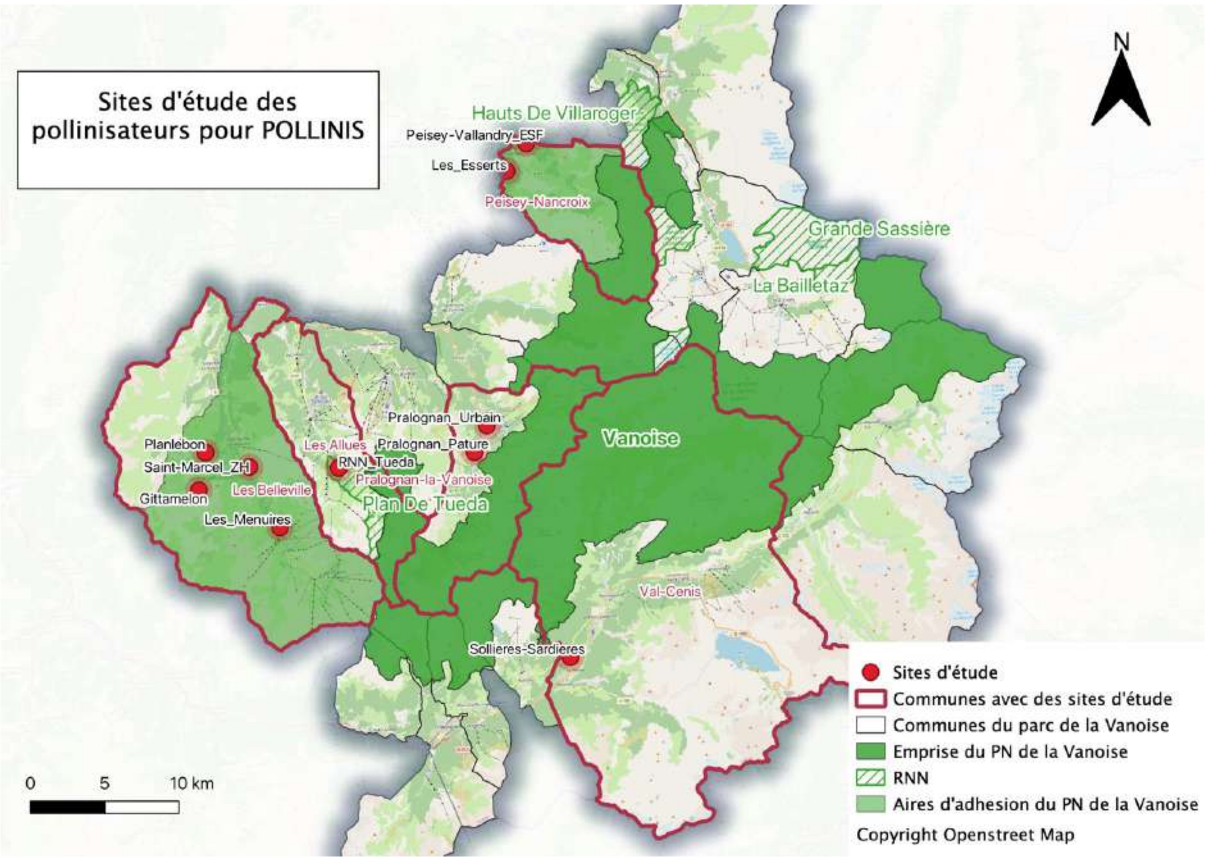


Fig. 1. Location of study sites in the Vanoise National Park region.

Urban land use sites: As a living landscape there are areas of urbanisation in close proximity to the National park. Three of these areas were sampled for pollinators, although in all cases the sampling location was still focused green spaces of semi-natural habitat that would contain flowering resources for insect pollinators. The samples sites were: Les Ménuires - Saint-Martin-de-Belleville - 73440 Les Belleville (lat. 45.325123, long. 6.537299). The Ménuires site was located in the heart of the city, close to the sports facilities. The plot was managed in a patchwork with some locations regularly mowed while others having a delayed mowing schedule with the first cut in September. In the sample year at least some of this area was mowed in August to make way for horses as part of a city attraction. ESF peisey-Vallandry - Peisey-Nancroix 73210 (lat. 45.551063, long. 6.763868). The ESF Peisey-Vallandry site was located in the ski resort's romper where skiers arrive. The plot is located in the heart of the town of Peisey-Nancroix, close to the main road and shops. This area is often under construction, which was the case for the year 2021. However, as the work is limited to the periphery of the site, floral resources remain available in the study area. Most of the space is mowed in July. Pralognan-la-Vanoise Urban site - Pralognan-la-Vanoise 73710 (lat. 45.382794, long. 6.719728). The urban site of Pralognan is located in the heart of the city, close to the cemetery. Due to its steep slope, it is an area that is only partially mowed and therefore remains flowery for most of the year. The abundance and diversity of flowers found at this site is likely promoted by the low fertility of the soil.

Agricultural pasture land use: Land use within the Vanoise National Park includes significant areas of pasture and livestock management, although these are typically managed at a relatively low intensity relative more productive lowland systems. Sampling of insect pollinator populations was undertaken at three of these sites. These were: Les Esserts, Peisey-Nancroix 73210 (lat: 45.536416, long: 6.746462). The Esserts site was grazed twice in the sample year (2021) with the second sample round occurring after a grazing event. Normal grazing management for the site varies in response to seasonal sward productivity. Although the stocking density visual observation of the plants suggested they were heavily grazed and characterised by a short sward height. Plateau pralognan - Pralognan-la-Vanoise 73710 (lat. 45.365924, long. 6.706954). The Pralognan Pâture site was grazed by cattle and goats historically, although in the sample year (2021) was only grazed by cattle. Stocking density was relatively high so that by the third survey many of the flowers had disappeared from the plot. Gittamelon - Les Belleville, Vallon des Encombres, (lat. 45.351060, long. 6.468415). In contrast to the other agricultural sites Gittamelon is managed with a late sward cut combined with areas of aftermath cattle grazing. Mowing was delayed to the end of August/beginning of September to facilitate sampling. Even so the third sample round occurred was carried out after the mowing of the meadow.

Semi-Natural pasture land use sites. These locations are still managed by grazing but at a much lower level of exploitation than the agricultural pasture land use above. These areas are still predominantly managed pasture systems, but may also contain other types of habitat. The three study sites were: Planlebon - Parking des Frachettes (lat. 45.373916, long. 6.475410). The Planlebon site was located towards the heart of the park within an area that was extensively grazed by cattle as summer pasture. The area is popular with hikers. Part of the site is made up of a compacted sandy area at the foot of an electricity pylon which diversifies the flora of the site. ZH-Saint-Marcel - Saint-Martin-de-Belleville - 73440 Les Belleville (lat. 45.364236, long. 6.512805). The Saint-Marcel Wetland is a site close to an urbanized area. The site is divided into 2 sectors, a meadow with abundant flowers and mowed at the end of the year and a drier area unmanaged during the sample period but covered in flowers. These two sectors are separated by a small waterway. As the meadow was mowed in July-August, the transect sampled in the third period had to be moved. Honeybee hives are located near the site all year round. Sollières-Sardières Bis - Route forestière du Crêt, au sud-est de Sardières. Sollières-Sardières - 73500 Val-Cenis (lat. 45.240480, long. 6.778950). The Sollieres-Sardière site is a dry limestone meadow notable for the presence of several species of orchids and containing a high level of floral diversity. The area contains the fodder legume sainfoin which has been actively cultivated. It is likely that honeybee hives may be close to this site as many were observed during sampling.

Natural land use site. This area was fully protected and so was not available for agriculture, no matter how extensive. Only a single natural area was sampled during the study, and as such this represents a comparison site acting as a reference for the other land uses. The sites chosen was RNN Tuéda - Les Allues 73550 (lat. 45.356243, long. 6.599609). This is a protected area subject to regulations prohibiting the taking of plants or animals from the reserve. The survey area was located on a south-facing hillside. As this area was a nature reserve capture permits were applied for and the reserve manager was contacted to request permission to access the site by vehicle.

Insect pollinator sampling

Pan trapping: Pan trapping uses bowls coloured blue, yellow and white (i.e. 3 bowls per site) to simulate flowering plants (Fig. 1). Insect alighting onto the bowls believing them to be flowers are then trapped in the liquid they contain where they can be subsequently collected and identified. The solution within the traps was water with a small quantity of unscented detergent to decrease surface tension. Sampling using pan traps occurred during three 24-hour periods at each of the 10 sites in June, July and August/September. Each pan trap was 20 cm in diameter. Traps were placed on poles so that they were just under the level of the flowers (Tuell and Isaacs, 2009). Pan traps contents was preserved in 70% alcohol and returned to the lab for counting and identification to morphospecies. Sample were identified to the board morphotypes of: 1) bumblebee, 2) Wasps; 3) honeybees; 4) solitary bees below 10mm in length; 5) solitary bees above 10mm in length; 6) ants; 7) other Hymenoptera, including parasitical and sawflies; 8) hoverflies (Syrphidae); 9) bee flies (Bombyliidae); 10) other flies; 11) butterflies; 12) macro-moths; 13) micro-moths; 14) Meloidae beetles; 15) Cleridae beetles; 16) other beetles below 8 mm in length; 17) other beetles above 8 mm in length; 18) True bugs (Hemiptera); 19) spiders; 20) grasshoppers and crickets (orthoptera); 21) earwigs (Dermaptera); 22) Ephemoptera; 23) Neuroptera;) woodlouse (Isopoda); and 24) Thipidae. All data analysed was based on averages across the pan traps (blue, yellow and white) and across the three trapping periods.

Fig. 1. Example pan trap deployment.

Transect walks to describe pollinator-plant feeding relationships: Transect walks represent a standardised sampling method that quantifies the density of insect pollinators per unit area using a combination of identification in the field and collection for subsequent identification using conventional taxonomic or eDNA barcoding approaches. As transect walks observe insects in the field they can also be used for identifying what individuals of each pollinator species are feeding on in terms of flowering plants. Each transect at a site is composed of a single 50 x 2m transect located though an area representative of site in terms of overall habitat. Transects were walked by fieldworkers in dry and calm weather conditions from 10:00 and 16:00h and when the temperature was above 15^{o}C and the Beaufort scale wind speed was below 6. These conditions broadly follow those laid out by Pollard and Yates (1993). Each transect is walked three times in June, July and August/September. Pollinating insects observed are (1) identified to species (or similar taxonomic resolution) and (2) the host plant they are foraging on is recorded. Insect pollinators not foraging on a flower can be recorded with this information used to contribute to overall site measures of pollinator abundance and species richness – although this will not be used in the derivation of plant-pollinator bipartite food webs. Overall, bees and wasps, hoverflies, beetles and butterflies and moths were identified to species, although some were only identified to genera, while unidentifiable individual were allocated to an order level classification (e.g. Diptera sp., Hymenoptera sp., Lepidoptera sp., and Coleoptera sp.). All data for an individual site was summed over the three trapping periods.

Floral abundance: To provide a measure floral resource abundance, and hence attractiveness to pollinators, each transect walk was repeated and the number of floral units (defined as a single flower or an umbel, spike or capitulum on multi-flowered stems) was counted for each flowering species. Abundance were scored as 1-10 or 10-50 or 50-100 or 100-500 or 500-1000 or >1000 floral units. These abundance values of flowering units were summed for each site across three sampling periods.

Plant Quadrats: Within each of the transects five 0.5x0.5m quadrats were used to quantify plant species percentage cover as assessed via vertical projection. Vertical projection refers to looking down onto the canopy and estimating the total area covered by each species. Note as plants can overlap vertically, the summation of percentage covers across all species may exceed 100%. Quadrats were placed at random throughout the length of the 50 m pollinator transect. Percentage cover of all plants (excluding mosses and bryophytes) was assessed, including plant that are not of direct value to pollinators either because they are not in flower or do not rely on insect-based pollination systems such as grasses. Average percentage cover was determined for each of the ten sites.

Statistical analysis

Pollinator abundance and species richness. Total abundance and species richness for each site was determined across all beetles, flies, bees and wasps, and butterflies and moths collected using the transect method. Similarly average abundance and morphospecies richness was calculated for the pan trap data. General linear models were implemented in the R statistical environment (R_Core_Development_Team, 2023) testing for the response of these variables to the explanatory metrics of: 1) land use type, defined as urban, agricultural pasture, and semi-natural pasture; 2) altitude; 3) number of flowers as a measure of floral resources (ln N+1transformed). Response covariates were log natural transformed to normalise the data. No interaction terms were considered, and model simplification was by deletion of least significant terms assessed using Fisher's test statistic. Due to the ack of replication of natural sites this was excluded from the analysis.

Plant total flower number and plant quadrat species richness. The same approach as described above using general linear models was used to assess the response of total flower number and plant quadrat species richness to: 1) habitat type, defined as urban, agricultural pasture, and semi-natural pasture; and 2) altitude. No interaction terms were considered, and model simplification was again by deletion of lease significant terms assessed using Fisher's test statistic. Due to the lack of replication of the natural sites these were again excluded from the analysis. Response covariates were log natural transformed.

Plant and pollinator community structure changes: Canonical Correspondence Analysis (CCA) is a multivariate statistical technique used to explore relationships between species abundance data and environmental variables. It is an extension of correspondence analysis, commonly used in ecology and community ecology, and so aims to elucidate patterns of species distribution and their association with environmental factors. We apply this approach using the vegan package in R (Oksanen *et al.*, 2019). For both the pollinator and plant communities we focus on that subset of species that are present in at least three of the 10 sites. Environmental variables considered to constrain the ordination and predict the response of the pollinator communities were nominally coded for using the land use classes of urban, agricultural pasture, semi-natural pasture and natural system. In addition, altitude and total flower number (for the pollinators only) were included as explanatory variables. The significance of these environmental variables on constraining the CCA ordination were assessed though permutation tests and stepwise deletion from a saturated model. No interaction terms were considered.

Measures of plant-pollinator mutualistic interactions: Bipartite pollinator feeding webs describing the quantitative frequency of mutualistic feeding relationships between insects and flowering plants. We derived bipartite webs at the scale of each land use type, so that the interactions were summed across the three replicate sites for urban, agricultural pasture and semi-natural pasture. For this reason, these webs are considerably more complete that those derived from the single natural site. However, as described below we do attempt to account for differences in web size and structure by applying a z-value correction. For each of the four bipartite webs we derived the following web metrics using the Bipartite package in R version 4.3.1 (Dormann *et al.*, 2008; Dormann *et al.*, 2009; R_Core_Development_Team, 2023):

1) Weighted connectance representing the marginal totals-weighted diversity of interactions per species divided by the number of species in the network. This is a fundamental metric of overall mutualistic web structure shown to be linked to community robustness (Dunne *et al.*, 2002; Thébault and Fontaine, 2010).
2) Nested structure (NODF) describes the extent to which specialists (pollinators foraging on a restricted number of plant species) interact with subsets of plant species that the generalist pollinators forage upon. Nestedness has been shown to contribute to the stability of the overall network (Bascompte *et al.*, 2003; Bastolla *et al.*, 2009; Thébault and Fontaine, 2010).
3) Generality defines the breath of foraging relationships between pollinators and plants. This weighted index is the effective number of plant species per pollinator weighted by the marginal totals (Tylianakis *et al.*, 2007). We also derived in the companion metric vulnerability which describes the effective number of pollinator species per plant.
4) Robustness of the pollinators to extinctions of plants was defined as the area below a secondary extinction curve resulting from the sequential random deletion of plant species (Memmott *et al.*, 2004; Burgos *et al.*, 2007). This metric provides a measure of system robustness to plant species loss which may occur due to a switch in management or stochastic environmental events like drought. We derive robustness under the assumption of random deletion of plant species to consider the impact this has on pollinators dependent on these plants.

5) Robustness of the plants to extinctions of pollinators. The equivalent of the above metrics but testing for the effect of random deletion of pollinators on the survival of plants which depend on them.

It is common for measures of network structure, such as connectance, nestedness, generality and robustness, to be sensitive to the size of the network (e.g. number of plant and pollinator species) (e.g. Dormann *et al.*, 2009; Vanbergen *et al.*, 2017; Larkin and Stanley, 2023). To account for this each of these metrics was standardised by comparing its value relative to a distribution of the same metric derived form 10,000 permutations of a null model that keeps key aspects of network structure constant while otherwise randomising potential plant-pollinator interactions (Almeida-Neto *et al.*, 2008). In each case this comparison was done using z-scores (z = [metric value - mean metric value from 10000 random null model permutation]/ standard deviation of 10000 random null model permutation). The choice of null model chosen depended on the metric. In the case of nestedness and generality/vulnerability we used the Vaznul model which randomizes the overall number of observed unique interactions found in the original web while keeping the overall web connectance and marginal web matric totals the same (Vázquez *et al.*, 2007). In the case of connectance and robustness (which can respond to connectance) this null model would have been inappropriate, and so we applied the Patefield's algorithm which maintains the marginal totals of the web matrix rows and columns while changing the cell values allowing connectance to vary (Dormann *et al.*, 2009; Larkin and Stanley, 2023).

RESULTS

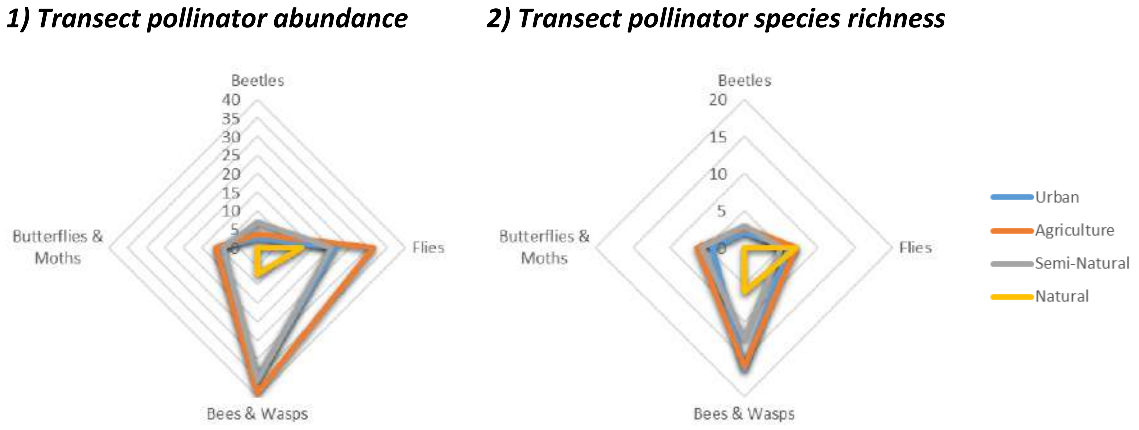
Overall trends in insect pollinators

Overall, 698 insect pollinators were recorded from the transect based observations and a further 3398 from the pan traps. From the transect based walks 165 distinct taxonomic units from species to order level were recorded, with the majority of these at the level of species. Table 1 shows summary site level values for abundance and species richness from the transect walks and the pan traps. Figures 2 show the distribution of transect observed abundance and species richness between the urban, agricultural pasture, semi-natural pasture and natural unmanaged sites. The general pattern strongly suggests that the natural unmanaged community was characterised by low abundance and species richness, although as only one natural site was sampled and as such may not be representative of natural unmanaged sites in the wider Vanoise area. Across all land use types the abundance and species richness of bees and wasps was higher than that of the other considered insect orders, although flies were similar (Fig. 2). The abundance of flies was relatively higher in the agricultural pasture relative to those of the other land uses. Abundance of butterflies and moths was typically highest in semi-natural pasture and lowest in urban environments.

			Transect		**Pan traps**	
Site	***Land use habitat***	***Altitude***	***Abundance***	***Species Richness***	***Abundance***	***Morpho-species richness***
Gittamelon	Agric	1676	19	14	41.6	4.4
Les Esserts	Agric	1697	103	40	43.4	4.4
Plateau de Pralognan	Agric	1559	133	42	36.7	4.1
Planlebon	SemiNat	1453	23	18	29.4	4.5
Saint-Marcel ZH	SemiNat	1478	182	51	25.6	3.1
Sollieres-Sardieres	SemiNat	1501	10	9	24.2	5.2

Les Menuires	Urban	1787	42	26	62.7	3.5
Peisey-Vallandry ESF	Urban	1603	151	47	52.5	4.7
Pralognan Urbain	Urban	1408	16	13	41.7	5.8
RNN Tueda	Natural	1784	19	13	19.2	3.5

Table 1. Summary of pollinator abundance and species richness from the transect walks and pan traps. Land use: Agric. = managed agricultural pasture; SemiNat= semi-natural low intensity management pasture system; Natural = unmanaged natural system.



1) Transect pollinator abundance

2) Transect pollinator species richness

Fig. 2. Spider graph showing the average abundance and species per site of flies, beetles, bees and wasps, and butterflies and moths derived from the transect based observations. This includes all pollinator species observed, including those not seen directly foraging on a flowering plant.

Responses of pollinator abundance and species richness

General linear models were used to assess the response of pollinator abundance and (morpho-) species richness to land use type (urban, agricultural pasture and semi-natural pasture), altitude and the availability of flower resources across the sampled period. Note, that as the natural site was not replicated it was excluded from this analysis. In the case of the transect based walks there was no evidence that any of these three explanatory covariates predicted either abundance or species richness of pollinators (Table 2). While this was also true for pan trap morpho-species richness, in the case of pan-trap total abundance both habitat type and altitude had a significant predictive effect (Table 2). Unexpectedly, pan trap abundance decreased along the proposed extensification gradient from urban to agricultural pasture to semi-natural pasture, with the unreplicated natural site having the lowest reported abundance (Fig. 3). In the case of altitude there was a significant positive correlation with pan trap abundance (Fig. 4). The pan trap counts included all arthropods, not just the species identified in the transects (i.e. Hymenoptera, Diptera, Coleoptera and Lepidoptera). This therefore provides a more comprehensive assessment of the communities. However, model fit (likely due to sample size) was relatively poor and so the robustness of the significance values is questionable.

	Habitat type	Altitude	Abundance of flowering resources
Transect based walks			
Pollinator abundance	F(2,4)=0.05, p>0.05	F(1,6)=0.31, p>0.05	F(1,7)=2.48, p>0.05
Pollinator species richness	F(2,4)=0.14, p>0.05	F(1,6)=0.51, p>0.05	F(1,7)=3.25, p>0.05
Pan trap morph-species sampling			
Pollinator abundance	**F(2,5)=29.77, p>0.01**	**F(1,5)=13.6, p=0.02**	F(1,4)=3.68, p>0.05
Pollinator species richness	F(2,5)=0.98, p>0.05	F(1,7)=1.53, p>0.05	F(1,6)=1.02, p>0.05

Table 2. Significance values for the effect of habitat type (urban, agricultural pasture and semi-natural), site altitude and abundance of flowers (log N+1) on measures of pollinator abundance and species richness. Sampling using focused transect based walks and continuous pan trap sampling are compared. The transect based walks has higher resolution in terms of identification of beetles, flies, bees and wasps and butterflies and moths. The pan trap focuses on a morpho-species approach that allows quantification of a wider range of insect and non-insect arthropod taxa. Degrees of freedom for F-test statistics are given in parenthesis. Significance values at p<0.05 are highlighted in bold.

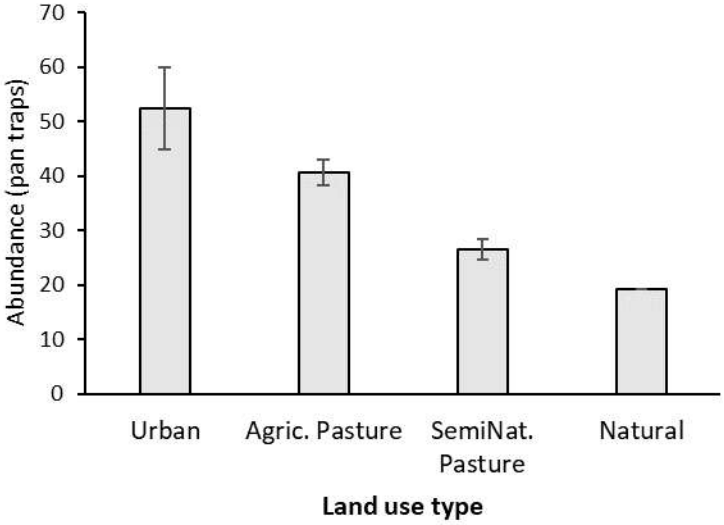


Fig. 3. Effect of land use on pan trap recorded abundance (±SE). Note the un-replicated natural community was not used in the analysis and is only included for reference.

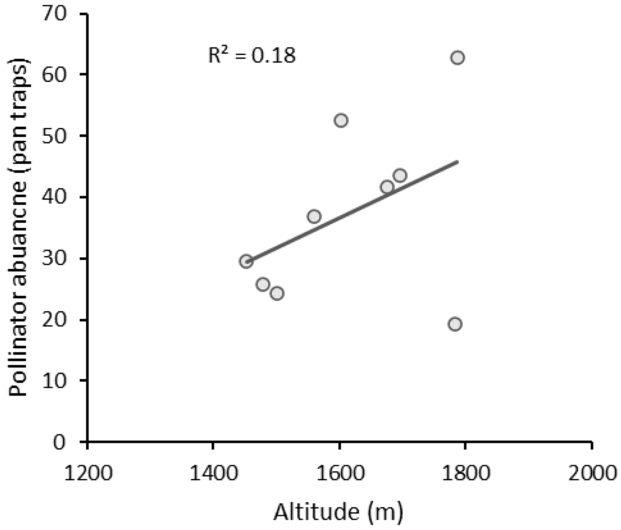


Fig.4. The correlation between pollinator abundance in pan traps and site altitude.

Impacts of land use on overall community structure

We also considering the effect of environmental variables on the overall structure of the pollinator community using canonical correspondence analysis, specifically looking at the effects of land use type (urban, agricultural pasture, semi-natural pasture and natural unmanaged), altitude and floral abundance. This analysis focused on change in community structure (i.e., the relative abundance responses covarying between individual species) based on the highly taxonomically resolved transect data. Table 3. Shows the significance of the explanatory covariates in constraining the canonical ordination axis and identifies that only the land use type of semi-natural pasture had a significant impact on the structure of insect pollinator community. Again, the low replication of the natural managed sites mean that this was unlikely to be statistically distinct. There were no other significant environmental drivers of pollinator community structure. The CCA had a total inertia of 1.86, and canonical unconstrained axis scores of CA1=0.56 and CA2=0.36.

	Df	**AIC**	**F**	**p**
Semi-Natural pasture	1	45.817	1.62	0.02
Altitude	1	46.021	1.43	0.14
Agricultural pasture	1	46.855	0.67	0.73
Flower abundance	1	46.941	0.60	0.82
Urban	1	47.057	0.50	0.91
Natural	1	47.559	0.08	1.00

Table 3. This table shows the significance of the explanatory covariates in constraining the canonical ordination axis for the Canonical Correspondence Analysis of the insect pollinator communities as recorded from the transect walks. Significance values are based on permutation tests. Degrees freedom (dF), Akaike information criterion (AIC), F-test static (F) and the probability (p, where $p<0.05$ is significant) are provided.

Overall trends in the plant communities.

Overall, there was considerable heterogeneity within the data in terms of the plant communities (Table 4). As a result, there were no significant effects of land use type on the total abundance of flower counts, the species richness of plants in flower, or the total quadrat-based species richness of the overall plant community (Table 5). There was also no significant effect of altitude on any of these variables (Table 5). When using canonical correspondence analysis to test for differences in community structure in response to land use and altitude there was similarly no significant effect of any of these explanatory covariates (Table 6). Total inertia for the CCA was 2.39, with the unconstrained axis scores of CA1=0.41 and CA2=0.38.

Site	*Land use habitat*	*Flower abundance*	*Species richness of plants in flower*	*Overall plant community species richness*
Gittamelon	Agric	10095	62	49
Les Esserts	Agric	4605	61	52
Plateau de Pralognan	Agric	4265	77	45
Planlebon	SemiNat	4570	63	44
Saint-Marcel ZH	SemiNat	8080	62	53
Sollieres-Sardieres	SemiNat	15850	63	50
Les Menuires	Urban	8655	67	53
Peisey-Vallandry ESF	Urban	8920	53	50
Pralognan Urbain	Urban	9400	69	43
RNN Tueda	Natural	9680	61	41

Table 4. Summary of pollinator community flowering resources and overall community species richness from the 10 sites. Land use: Agric. = managed agricultural pasture; SemiNat= semi-natural low intensity management pasture system; Natural = unmanaged natural system.

	Land use type	**Altitude**
Flower counts only		
Abundance	F(2,6)=0.78, p>0.05	F(1,5)=0.10, p>0.05
Species richness	F(2,5)=0.47, p>0.05	F(1,6)=0.25, p>0.05
Quadrat based estimation		
Species richness	F(2,6)=2.50, p>0.05	F(1,5)=1.22, p>0.05

Table 5. Significance values for the effect of land use type (urban, agricultural pasture and semi-natural pasture) and site altitude on measures of plant community structure. Flower counts only refers to direct counts of flowers in the sample areas and represent a measure of floral foraging resources for pollinators. Quadrat based estimates refer to assessment of plant community percentage cover by vertical projection and includes all plants, including those with flower attractive to bees (both in flower and not in flower) and not attractive to bees, such as grasses.

	Df	**AIC**	**F**	**p**
Natural	1	27.642	1.1844	0.185
Agricultural pasture	1	27.796	1.0441	0.325
Urban	1	27.837	1.0071	0.41
Altitude	1	27.853	0.9923	0.575
Semi-Natural pasture	1	27.994	0.8665	0.805

Table 6. Shows the significance of the explanatory covariates in constraining the canonical ordination axis for the Canonical Correspondence Analysis of the plant communities. Significance values are based on permutation tests. Degrees freedom (dF), Akaike information criterion (AIC), F-test static (F) and the probability (p, where p<0.05 is significant) are provided.

Plant pollinator feeding relationships.

Transect based walks were used to quantify the foraging relationships of individual pollinators with different flowering plants found within the urban, agricultural pasture, semi-natural pasture and natural systems. In each case these were assessed these by combining all sites within a land use, although in the case of the natural sites this means that this was based on a single replicate only. The bipartite graphs showing the structure of these feeding relationships can be seen in figure 5 below.

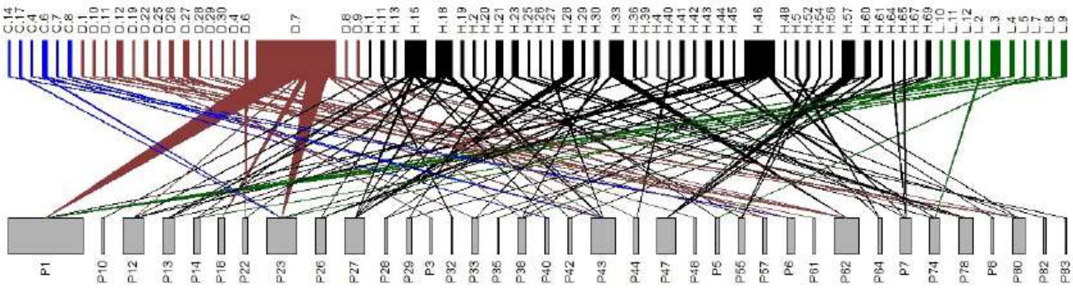
While these bipartite graphs provide a visual tool for understanding differences in the mutualistic insect pollinator-plant feeding relationships their interpretation is best done though specific metrics describing this structure (Table 7, Fig. 6). We derived the following metrics for each of these webs and report on these below. Note that we use a z-metric standardisation. This approach creates a random null model which describes plant-pollinator interactions, albeit interactions constrained by certain rules, to which the observed web metric can be compared. This controls for aspects like differences in web size and allows for a more robust comparisons between land use types. As such comparisons of the relatively under sampled natural unmanaged land use (one site) are comparable to the other webs, but should still be treated with caution. It is also important to note that not all species are resolved to species level. As such these aggregates of trophic relationships likely hide considerable additional complexity in terms of the web structure that is not currently revealed. These are likely to alter the web metrics, however, for the well sampled urban, agricultural pasture and semi-natural pasture this effect may be minimal. For the under sampled natural land use with only one replicate site this problem is likely more significant.

Weighted connectance: This represents a fundamental metric of overall mutualistic web structure (Dunne *et al.*, 2002; Thébault and Fontaine, 2010). Overall levels of connectance are similar between the urban, agricultural pasture and semi-natural pasture, with the under sampled Natural sight have very high levels of connectance relatively (Fig. 6).

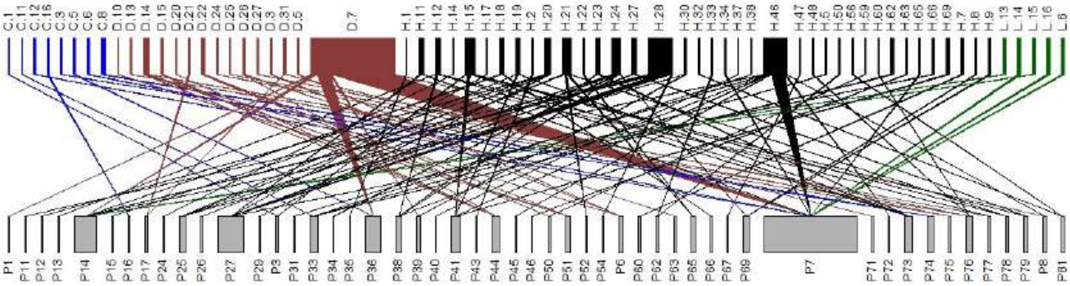
Nested structure (NODF): This describes the extent to which specialist pollinators foraging on a restricted number of plant species are a subset of those generalist pollinators interact with. As for connectance levels of nestedness are similar between the urban, agricultural pasture and semi-natural pasture, with the under sampled natural site being characterised by high levels of this metric (Fig. 6).

Generality of pollinators: This metric defines the breath of foraging relationships between pollinators and plants and is a measure of the effective number of plant species per pollinator (Tylianakis *et al.*, 2007). Pollinators associated with the urban land use tend to show the highest levels of generality utilising the widest range of host plants on average. The natural unmanaged site and semi-natural pasture systems were comparable, while the agricultural pasture had the lowest levels of generality for it pollinator species.

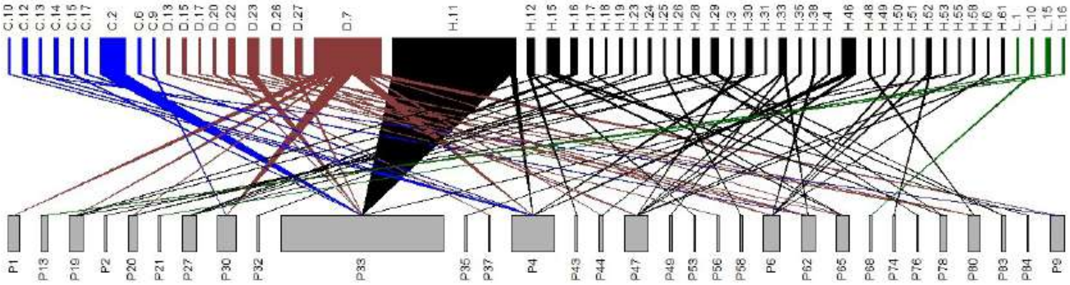
Urban



Agricultural pasture



Semi-Natural pasture systems



Natural unmanaged upland system *(based on a single site only)*

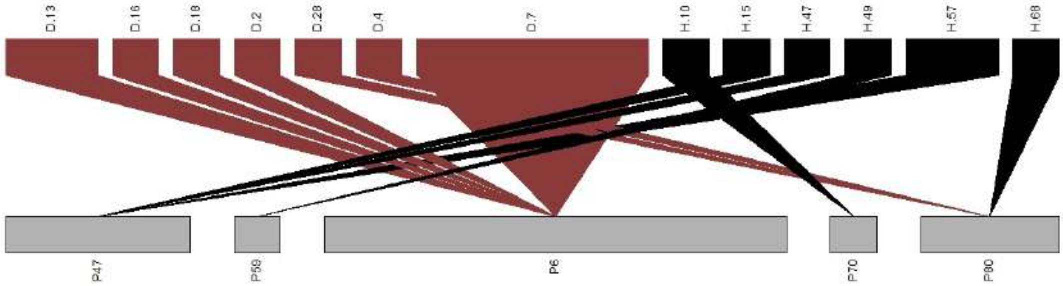


Fig. 5. Bipartite interaction networks for insect pollinator communities found in urban, agricultural pasture, semi-natural pasture and urban land uses within the Vanoise park. With the exception of the 'natural system' category all webs are a composite of the three sampled locations. Insect pollinators are shown as bars running across the top of a bipartite web, the width of these proportional to the abundance of that pollinator species. Where: blue= beetle (Coleoptera), red = flies (Diptera), black = bees and wasps (Hymenoptera) and green= butterflies and moths (Lepidoptera). The Plants are shown as grey bars on the bottom row. The width of the bar is proportional to the number of pollinator species utilising that plant as a foraging resource. Full codes for all plants and pollinators are given in Appendix 1, however, for convenience we list the abbreviations for the commoner species here. **BEETLES (Coleoptera):** *C.2=Brachyta interrogationis; C.6=Coleoptera; C.7=Cryptocephalus aureolus; C.8=Cryptocephalus sp.; C.12=Oxythyrea funesta; C.14=Phyllopertha horticola.* **FLIES (Diptera):** *D.2=Cheilosia gigantea; D.4=Cheilosia spp.; D.7=Diptera spp.; D.12=Melanogaster nuda; D.13=Melanostoma*

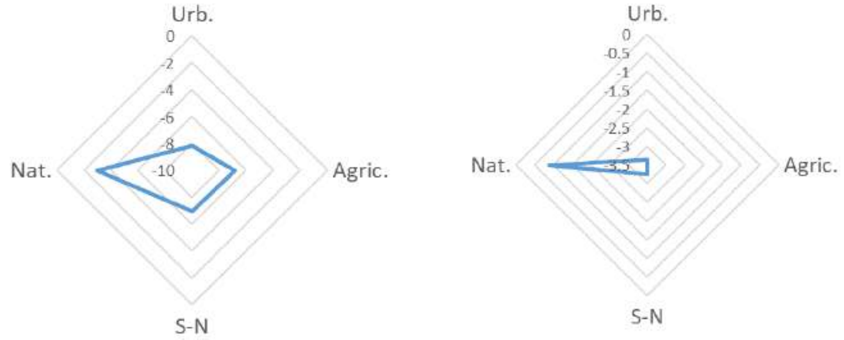
mellinum; D.14=Merodon aeneus; D.16=Neoascia meticulosa; D.18=Parasyrphus lineolus; D.22=Platycheirus albimanus; D.22=Platycheirus manicatus; D.26=Sphaerophoria spp.; D.27=Sphaerophoria scripta; D.28=Syrphidae spp.; **Wasps and bees (Hymenoptera):** *H.10=Anthophora atroalba; H.11=Apis mellifera - Honeybee; H.15=Bombus humilis; H.16=Bombus hypnorum; H.18=Bombus lapidarius; H.21=Bombus mesomelas; H.24=Bombus pratorum; H.28=Bombus soroeensis; H.29=Bombus sylvarum; H.30=Bombus terrestris; H.33=Chelostoma florisomne; H.46=Hymenoptera; H.47=Lasioglossum albipes; H.49=Lasioglossum spp.; H.57=Megachile parietina; H.60=Nomada succincta; H.68=Seladonia tumulorum.* **Butterflies and Moths:** *L.3=Coenonympha pamphilus; L.4=Colias alfacariensis; L.6=Erebia sudetica; L.15=Speyeria aglaja*. **Flowering Plants:** *P1=Achillea millefolium; P4=Angelica sylvestris; P6=Apiaceae; P7=Asteraceae; P14=Centaurea sp.; P23=Daucus carota; P27=Epilobium angustifolium; P33=Geranium sylvaticum; P36=Heracleum sphondylium; P43=Leontodon hispidus; P47=Lotus corniculatus; P59=Potentilla aurea; P62=Ranunculus acris; P65=Rhinanthus alectorolophus; P70=Sempervivum montanum; P80=Veronica chamaedrys.*

Vulnerability of plants: This is the companion metric to generality above, but seen from the perspective of the plants as it describes the effective number of pollinator species per plant. The agricultural pasture systems had the lowest levels of vulnerability for the plants as on average they have more pollinators foraging on them relative to the urban and semi-natural land uses communities. However, the plant communities of the natural system had the highest vulnerability.

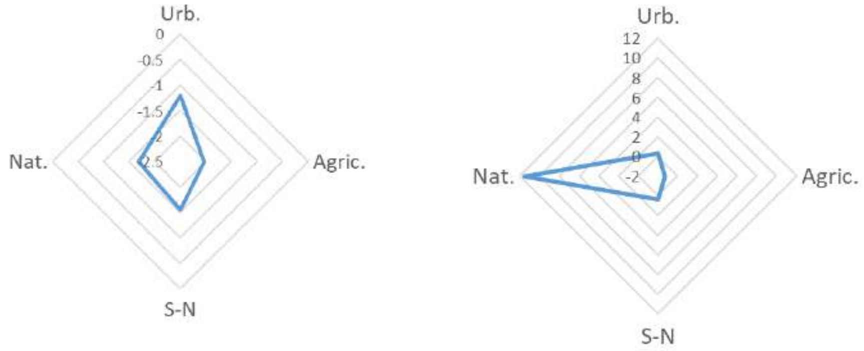
Robustness of the pollinators to extinctions of plants: This is defined as the area below a secondary extinction curve resulting from the sequential random deletion of plant species (Memmott *et al.*, 2004; Burgos *et al.*, 2007). That if all the plant species go locally extinct that a particular insect pollinator feeds on as seen in the bipartite webs (Fig. 5) then that pollinator species must also go extinct. Where plant species go randomly extinct the likely consequences for secondary extinctions of the pollinator community are highest for natural, and then the urban and agricultural pasture land uses. The chance of secondary pollinator extinctions is lowest for the semi-natural extensively managed pasture systems. As already talked about the under sampled nature of the natural community pollinator-plant web means that this measure of robustness should be treated with caution.

Robustness of the pollinators to extinctions of plants: This is defined as the area below a secondary extinction curve resulting from the sequential random deletion of pollinator species, and so is the companion for the previous robustness metric (Memmott *et al.*, 2004; Burgos *et al.*, 2007). Where pollinators go randomly extinct the chances of secondary extinctions in the plant community are broadly equivalent for the agricultural pasture, semi-natural pasture and natural unmanaged land uses. However, they are considerably higher in the semi-natural pasture systems, suggesting that loss of pollinators in this habitat may have a far greater consequence for the plant communities.

1) Connectance ***2) Nestedness***



3) Generality of pollinators ***4) Vulnerability of plants***



5) Robustness of pollinators to the loss of plants ***6) Robustness of plants to loss of pollinators***

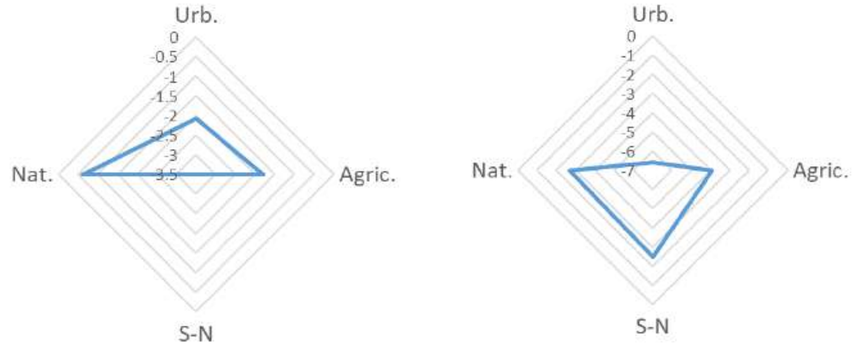


Fig. 6. Spider graphs showing the differences in key metrics of pollinator interaction web structure between the four different land uses of urban (Urb: three sites combined), agricultural pasture (three sites combined), semi-natural extensive pasture (S-N: three sites combined) and unmanaged natural systems within the park (Nat.: one site only). Web metrics are: 1) Weighted connectance as a measure of the number of interactions between plants and pollinators divided by the total number of species in the network; 2) NODF metric of nested structure which describes the extent to which specialists (pollinators foraging on a restricted number of plant species) interact with plant species that generalist pollinators also interact with; 3) Generality is the effective number of plant species per pollinator; 4) Vulnerability which is the effective number of pollinators species per plant; 5) Robustness of the pollinators to extinctions of plants as a measure of system tolerance to plant species loss; 6) Robustness of the plants to extinctions of pollinators as a second measure of system tolerance. Each of these metrics has been corrected using z-scores relative to null model webs.

	Connectance	Nestedness (NODF)	Generality	Vulnerability	Robustness to loss of pollinators	Robustness to loss of plants
Urban	-8.16	-3.35	-1.21	0.259	-2.09	-6.59
Agricultural	-6.82	-3.5	-2.03	-1.3	-1.79	-3.93
Semi Natural	-6.96	-3.26	-1.56	0.354	-3.49	-2.48
Natural	-2.98	-0.89	-1.68	11.5	-0.61	-2.69

Table 7. key metrics of pollinator interaction web structure between the four different land uses of urban (Urb: three sites combined), agricultural pasture (three sites combined), semi-natural pasture (S-N: three sites combined) and unmanaged natural systems within the park (Nat.: one site only). See above figure caption for the description of the metrics.

DISCUSSION

Land use within the Park Nationals de la Vanoise represents an important potential environmental driver of biodiversity trends, affecting aspects of management intensity such as grazing presence and frequency, as well as the diversity of habitats likely to be found within a particular area. In this study we have used a natural experimental design classifying major land use practices as management treatments implemented along an intensification gradient to understand impact on pollinator communities. We consider the land use types urban, agricultural pasture, extensively managed semi-natural pasture and unmanaged natural communities, although of these the latter was included only as an unreplicated reference community. While insect pollinators represent a fraction of the invertebrates likely to be found within the park they have been suggested to serve as indicators for wider trends in native wildlife as well as directly providing an indication of pollination as a fundamental ecosystem process (Scherber *et al.*, 2019; Naeem *et al.*, 2020; Albertazzi *et al.*, 2021; Larkin and Stanley, 2021; Benvenuti, 2022). As such, while we consider the reported pollinator trends to provide important information on wider biodiversity, more detailed assessments of other non-pollinator taxa would be valuable. In the following discussion we will consider each land use by type and make inferences about the value of these habitats for supporting insect pollinators.

Urban land use

The urban land use was largely comparable to the other land uses in terms of the pollinator communities, specifically when compared to the agricultural pasture and semi-natural pasture systems. For example, all three land uses had similar levels of species richness, while in the case of the urban land use higher abundance as detected by the pan traps relative to these other habitats was found. This suggested that at least within the context of the sampled location amenity management of grassland habitats within or near urban centres could have value for insect pollinators. This agrees with previous studies that have shown how urban environments can have important habitats for insect pollinators due to both the prevalence of floral resources in domestic and amenity garden settings as well as the heterogeneity in habitat types encountered within their boundaries (Baldock *et al.*, 2015). Even so the positive effects of urban environments are diverse and where urban localities replace critical of more natural habitats they will have negative net effects, at the very least on specific sub-sets of the pollinator communities (Ahrné *et al.*, 2009; Rader *et al.*, 2014; Dylewski *et al.*, 2019). Relatively the urban spaces considered in this study are comparatively small compared to major cities and are of a far more open in structure. The grassland green areas within their boundaries were managed in a variety of ways, including arguably non-typical management for urban spaces, such as grazing by horses at the Les Ménuires site. As smaller cities there is also a greater potential for the species of pollinator found within these locations to have population centres in surrounding agricultural or semi-natural pasture (Fischer *et al.*, 2016; Dylewski *et al.*, 2019). As such, while they may be utilising these areas for foraging resources, they may not necessarily be able to persist within the urban boundary alone. This reflects the wider nature of highly mobile pollinator communities persisting on resources at landscape scales (Steffan-Dewenter and Kuhn, 2003; Potts *et al.*, 2006; Öckinger and Smith, 2007; Rader *et al.*, 2014; Fischer *et al.*, 2016; Dylewski *et al.*, 2019; Redhead *et al.*, 2020). The likelihood of the pollinator communities observed in the urban landscapes being at least in part composed of foraging populations from surrounding land uses is reflected by the absence of a significant difference in their community structure from surrounding agricultural pastures as determined by the CCA analysis.

Visualization of the overall insect pollinator feeding relationships with flowering plants using bipartite webs (Fig 5) emphasises the very large range of species when summed across all three urban sites that can be found relative to the other land use types of agricultural pasture, semi-natural pasture or natural systems. To a large part this is likely to be driven by the high habitat heterogeneity within the boundaries of cities compared to larger homogenous management systems applied in larger agricultural fields (Baldock *et al.*, 2015; Dylewski *et al.*, 2019). This heterogeneity both within urban spaces, and between them in terms of what habitats are present, provides a large niche space for pollinators supporting higher beta diversity (Benton *et al.*, 2003; Tews *et al.*, 2004). It is likely however that in the context of urban environments some species would be more likely to benefit than others, although more specialist species associated with semi-natural or natural environments being less likely to be able to utilise this anthropogenic habitat (Rader *et al.*, 2014). When considering metrics of pollinator – plant feeding relationships there is little difference between the urban sites when compared to the agricultural and semi-natural pasture land uses in terms of either web connectance and nestedness. However, pollinators associated with the urban land use tended to show the highest levels of generality (excluding the under-replicated natural land use), i.e. on average they utilised the widest range of host plants on average. In general generalist species tend to be more common as they are able to make use of more diverse resources, for example short tongues bumblebees with a more restricted foraging diet are less common that generalist longer tongued species (Goulson and Darvill, 2004; Goulson *et al.*, 2005). Generalisation in pollinator-plant food web structure has been previously shown to be a function of land use intensification (Goulson and Darvill, 2004; Redhead *et al.*, 2018).

The robustness of the pollinator communities to secondary extinctions resulting from the loss of plant species within the urban land use was relatively high, and comparable to that of the agricultural pasture systems described below. This robustness to the loss of plants is likely a product of the generality seen in the pollinators, whereby they can make use of a wide range of alternative foraging resources should any individual species go locally extinct. It is worth noting that these modelled effects are a simplification as pollinators are likely to show plasticity in their feeding relationships (Brosi and Briggs, 2013). Even so, this metric does suggest that in the case of the pollinators changing management of amenity areas that negatively impacts on the floral community structure may have less of an impact on the pollinator communities than is seen in agricultural or semi-natural pasture areas. In contrast, the robustness of the plant communities to secondary extinctions resulting from the loss of pollinators was the lowest for any of the considered land uses. That means that the loss of pollinators resulting from local extinctions is predicted to impact very negatively on the pool of pollinator in urban (Memmott *et al.*, 2004; Vanbergen *et al.*, 2017). As for the previous measure of robustness this is a model assumes that when all the pollinator species identified as foraging on a particular plant disappear the plant loses insect pollination and so suffers a reduction in fitness. This again is a simplification, both because the food webs may be only partially resolved (Vanbergen *et al.*, 2014), pollinators can show plasticity in their feeding relationships (Brosi and Briggs, 2013) and as plant breeding systems rarely rely solely on insect pollinators (Bernardello *et al.*, 2001; Culley *et al.*, 2002; Rosas-Guerrero *et al.*, 2014).

Agricultural and semi-natural pasture land-uses

In Winfree *et al.* (2009) meta-analysis of bee responses to anthropogenic disturbance they showed that while habitat loss was a consistent predictor of declines in abundance and species richness, grazing in general did not have a consistent effect either positive or negative. Even so, extensively managed grassland systems characterised by a high diversity of floral resources provide crucial foraging and breeding habitat for a wide range of bees and other insect pollinators (Steffan-Dewenter and Tscharntke, 1999; Öckinger and Smith, 2007; Woodcock *et al.*, 2013; Rotches-Ribalta *et al.*, 2018; Woodcock *et al.*, 2021; Larkin and Stanley, 2023). Indeed restoration or recreation of species rich grasslands is a critical management practice in pollinator ecology, particularly in intensively managed landscapes where there is limited availability of other foraging resources (Woodcock *et al.*, 2012; Harmon-Threatt and Hendrix, 2015; Winsa *et al.*, 2017; Luong *et al.*, 2019; Redhead *et al.*, 2020; Woodcock *et al.*, 2021). Here we have considered two pasture systems, albeit ones that are relative to high input lowland grassland systems likely to be on the more extensive side of management. The agricultural pasture is actively managed for livestock grazing, principally cattle, or for harvest of stored grass projects like hay. The semi-natural pasture systems are a more extensively managed version of this, although typically grazed far less frequently and at lower stocking densities. There is a considerable degree of consistency between the two communities, with there being no difference between them in terms of their species richness, either assessed via transect walks or pan traps.

This consistency in species richness hides more fundamental shifts in pollinator community structure including a lower pollinator abundance as observed via the pan-traps. This reduction in pollinator abundance from the pan traps seems to be negatively correlated with the gradient of intensity from urban to natural land uses, with the lowest abundances of pollinators found at the natural site (Fig. 3). This suggests lower productivity of these land uses, but one that does not necessarily impact on the species richness of insects within the locations. It is worth noting that pan traps are a continuous sampling technique that likely attracts insect pollinators from large areas, and indeed for this reason may introduce some bias in sites where limited floral diversity mean that there is a concentration of pollinators into pan traps that appear to be the only available flowering resources (Westphal *et al.*, 2008; O'Connor *et al.*, 2019). In contrast, transect walks are instantaneous (or relatively) assessments of pollinators taken within a fixed areas and so provide a comparable measure of density between sites (Westphal *et al.*, 2008). It is important therefore that for this more site targeted estimate of density there was no difference in abundance. Further, the absence of significant differences between agricultural and semi-natural pasture in terms of summed numbers of floral resources (i.e. flowers on which pollinators feed) is consistent with the absence of a difference in pollinator abundance as determined from the density measuring transect walks.

Outside of the simple measures of pollinator community structure there is evidence that the intensity of pasture management does have an impact on the underlying structure of the pollinator communities. This is seen initially in the form of the CCA analysis which shows that the semi-natural pasture was the only one of our four land uses to have a significant impact on the relative composition of pollinator species within communities. While the overall species richness may be consistent between the agricultural and semi-natural pasture, there is a shift in what species are present. Looking at the summary bipartite interaction networks which describe the structure of transect based insect pollinator - plant feeding relationships (Fig. 5) there are strong visual differences between the two communities. Notably, in the semi-natural pastures *Gernium sylvaticum* L. (Geraniaceae) is a key plant visited by many insect pollinators, including the very large relative numbers of honeybees (H11 in Fig. 5). While the aggregate taxonomic category of other flies (those not identified to species) is particularly common in the semi-natural and agricultural pastures (D7 in Fig. 5), it is plants of the Asteraceae family (P7 in Fig. 5) that are most frequently visited in the latter. Although not significantly different between sites within a land use, when summed across the sites the agricultural pastures have a higher transect species richness of both plants and pollinators. This is effectively beta diversity, i.e. the ratio between regional and local species pools. This strongly suggests that the relatively higher level of variability between sites, although it is worth noting that this was not identified in the CCA of the plant communities (but see notes below under limitations), may be driving greater overall levels of pollinator diversity.

Looking at detailed bipartite web metrics which act to quantitatively describe the structure of feeding relationships there are also further differences between the two pasture land uses. Overall measures of bipartite web connectance, nestedness and generality are similar between the agricultural and semi-natural pasture, however, the agricultural pasture systems have the lowest levels of vulnerability. This means that for the plants on average they have more pollinators foraging on them relative to the semi-natural pasture. This has translated into our assessment of robustness of the pollinators to the loss of plant species from these communities. Here we found that the agricultural pasture had far higher robustness scores than those of the semi-natural pasture, as defined by the area below a secondary extinction curve resulting from the sequential random deletion of plant species (Memmott *et al.*, 2004; Burgos *et al.*, 2007). This suggests that the agricultural systems are less likely to undergo a collapse in pollinator species resulting from the loss of plant species relative to those of the semi-natural pastures. Such plant species loss may be the result of several factors, including changes in the intensity of local management, such as grazing or cutting (Duffey *et al.*, 1974; Woodcock *et al.*, 2021), as well as longer term larger scale effects of atmospheric nitrogen deposition (Stevens *et al.*, 2010; Feest *et al.*, 2014; Nijssen *et al.*, 2017) and climate change (Olesen and Bindi, 2002; Voight *et al.*, 2003; Winslow *et al.*, 2003; Morecroft *et al.*, 2004). In contrast, the semi-natural pastures have plant assemblages that are slightly more robust to the extinction of pollinator species than those of the intensive agricultural pastures, suggesting that these plant communities are less likely to suffer a net reduction in pollination services when pollinator species go locally extinct.

Naturally managed land uses

This natural alpine protected area was not available for livestock, and so differs from both the agricultural pasture and semi-natural pasture systems. As only a single area was sampled within this land use (RNN Tuéda) inferences possible from this site are limited, with formal statistical comparisons to the other land uses not possible. However, its inclusion in the study provides a useful benchmark for comparison, albeit one that may not be representative of natural sites at a wider scale across the Park Nationals de la Vanoise. Perhaps the most noticeable aspect of this natural site was its far lower levels of abundance and species richness (Fig 2 and 3). Indeed, when considering pollinator abundance as determined from the pan traps there does seem to be a trend as already mentioned for a reduction in overall abundance along the extensificaiton gradient from urban to natural. In the case of the transect walks flies were the only identified group for which the species richness in the natural sites was comparable to that of the urban, agricultural and semi-natural pastures. In all other cases (beetles, bees, wasps, butterflies and moths), the abundance and species richness was considerably lower.

The single site bipartite plant-pollinator feeding interaction networks emphasise the importance of Apiaceae flowering plants as critical for many pollinating species in the natural site (Fig. 5). Importantly, neither beetles nor butterflies and moths were seen to pollinate the plants present at the natural sites. While simple visual comparisons of the bipartite pollinator-plant feeding interactions with the other land uses are hard to make (other webs are composites of multiple sites), the use of z-score standardisations against null models improve our ability to make direct comparison using the web metrics. Even so they should still be treated with caution as this site is likely under sampled as a result of the lower abundance of pollinators. However, we see high levels of weighted connectance which represents a fundamental metric of overall mutualistic web structure and has been shown to be linked to some aspects of community robustness (Dunne *et al.*, 2002; Thébault and Fontaine, 2010). In addition, the degree to which specialist pollinators foraging on a restricted number of plant species within those subsets of plants that generalist pollinators forage on (Nestedness) is relatively high. This metric describes non-random structure in the plant-pollinator network (Bascompte *et al.*, 2003) and has been shown to contribute to the stability of the overall network (Bascompte *et al.*, 2003; Bastolla *et al.*, 2009; Thébault and Fontaine, 2010). While the generality of the networks in terms of the average number of plants that pollinator species feed on is comparable to other and uses, this is not the case for vulnerability. The vulnerability metric describes the effective number of pollinator species per plant and was high for the natural site. Interestingly the levels of robustness of the pollinators to the random extinction of plants, as well as the reverse metric looking at the robustness of plants to random extinctions of pollinators, were broadly comparable to the higher values seen for the other land use classes.

Limitations of sampling

Even within the context of the targeted sampling program employed in this report which attempts to restrict sampling to specific land use types there exists considerable within category variation in current and historic management. These factors introduce heterogeneity in the habitats that will affect individual species community composition and so responses to environmental drivers. As is the case for many ecological studies sampling intensities has been limited due to available resources such that replication within the land use categories of urban, agricultural pasture and semi-natural pasture was limited to three sites. This limited replication reduces the ability of analyses to detect more subtle effect size changes in considered metrics of pollinator community structure. It is reasonable to infer therefore that the absence of an effect of a land use class on pollinator community structure does not preclude the possibility that differences may have been detected under a more extensive sampling strategy. As already mentioned above the natural managed land use is unreplicated, and so while acting as a reference community it its wider representativeness of natural pollinator systems in the Vanoise region is unclear.

Conclusions

In contrast to expectations there was relatively little difference in key metrics of insect pollinator community structure, specifically species richness between the land use classes of urban, agricultural pasture and semi-natural pasture. This was unexpected and may in part be an artifact of the considered intensity gradient being biased considerably towards the extensive end of the spectrum (Potts *et al.*, 2010; Vanbergen *et al.*, 2013). For example, green spaces sampled within the context of urban land uses were located in relatively low-density human habitation compared to more major cities. Even so, there is a strong suggestion that the urban environments may have potential to support diverse pollinator communities, albeit ones that may be significantly different in their community structure when compared to semi-natural pastures. At least in the context of the urban systems the highly mobile nature of insect pollinator means that they are likely operating across landscapes, making use of complex resources available in diffuse habitat patches both within and outside the urban environment (Greenleaf and Kremen, 2006; Morandin *et al.*, 2007; Goulson *et al.*, 2010; Holzschuh *et al.*, 2010; Carvell *et al.*, 2011; Alejandre *et al.*, 2023). As such, the high general quality of the Park Nationals de la Vanoise landscape may help buffer local low quality areas by providing a diverse species pool that may be unable to persist within purely urban environments but are able to make use of these locations within a wider network of foraging habitats (Harrison and Winfree, 2015; Jauker *et al.*, 2019; Olsson *et al.*, 2021).

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Appendices

Appendix 1. Plant and pollinator species codes for the bipartite webs.

Plant species codes for bipartite webs

Plant	**lb nom plante**
P1	*Achillea millefolium*
P2	*Ajuga genevensis*
P3	*Ajuga reptans*
P4	*Angelica sylvestris*
P5	*Anthyllis vulneraria*
P6	*Apiaceae*
P7	*Asteraceae*

P8	*Astrantia major*
P9	*Bistorta sp.*
P10	*Campanula rhomboidalis*
P11	*Campanule sp.*
P12	*Carduus sp.*
P13	*Centaurea jacea*
P14	*Centaurea sp.*
P15	*Centaurea uniflora*
P16	*Centauree photos*
P17	*Cerastium fontanum*
P18	*Chamomille sp.*
P19	*Cirsium palustre*
P20	*Cirsium sp*
P20	*Cirsium sp.*
P21	*Cirsium vulgare*
P22	*Crepis sp.*
P23	*Daucus carota*
P24	*Digitalis ambigua*
P25	*Digitalis grandiflora*
P26	*Echium vulgare*
P27	*Epilobium angustifolium*
P28	*Eryngium alpinum*
P29	*Euphrasia sp.*
P30	*Filipendula ulmaria*
P31	*Geraium pyrenaicum*
P32	*Geranium sp.*
P33	*Geranium sylvaticum*
P34	*Geum rivale*
P35	*Helianthemum nummularium*
P36	*Heracleum sphondylium*
P37	*Hippocrepis sp.*
P38	*Knautia arvensis*
P39	*Knautia dipsacifolia*
P40	*Knautia sp.*
P41	*Lathyrus odoratus*
P42	*Lathyrus pratensis*
P43	*Leontodon hispidus*
P44	*Leucanthemum vulgare*
P45	*Liguliflore capitule*
P46	*Liguliflore sp.*
P47	*Lotus corniculatus*
P48	*Lotus major*
P49	*Medicago lupulina*
P50	*Myosotis sp.*
P51	*Myosotis sylvatica*

P52	*Onobrychis viciifolia*
P53	*Phyteuma orbiculare*
P54	*Phyteuma spicatum*
P55	*Pilosella officinarum*
P56	*Plantago lanceolata*
P57	*Plantago media*
P58	*Polygala sp.*
P59	*Potentilla aurea*
P60	*Potentilla reptans*
P61	*Poterium sanguisorba*
P62	*Ranunculus acris*
P63	*Ranunculus bulbosus*
P64	*Reseda lutea*
P65	*Rhinanthus alectorolophus*
P66	*Salvia pratensis*
P67	*Satureja montana*
P68	*Scabiosa sp.*
P69	*Sedum ochroleucum*
P70	*Sempervivum montanum*
P71	*Silene dioica*
P72	*Silene vulgaris*
P73	*Stachys recta*
P74	*Taraxacum sp.*
P75	*Taraxacum udum*
P76	*Thymus serpyllum*
P77	*Trifolium montanum*
P78	*Trifolium pratense*
P79	*Trifolium repens*
P80	*Veronica chamaedrys*
P81	*Vicia argentea*
P82	*Vicia cracca*
P83	*Vicia sepium*
P84	*Ziziphora granatensis*

Pollinator species codes used in bipartite webs

Insect code	**Pollinator speceis**
C.1	Anastrangalia dubia (Scopoli, 1763)
C.2	Brachyta interrogationis (Linnaeus, 1758)
C.3	Bromius obscurus (Linnaeus, 1758)
C.4	Cantharis nigricans (O.F. Müller, 1776)
C.5	Carilia virginea (Linnaeus, 1758)
C.6	Coleoptera Linnaeus, 1758
C.7	Cryptocephalus aureolus Suffrian, 1847
C.8	Cryptocephalus Geoffroy, 1762

C.9	Gnorimus nobilis (Linnaeus, 1758)
C.10	Leptura quadrifasciata Linnaeus, 1758
C.11	Oedemera Olivier, 1789
C.12	Oxythyrea funesta (Poda, 1761)
C.13	Pachytodes cerambyciformis (Schrank, 1781)
C.14	Phyllopertha horticola (Linnaeus, 1758)
C.15	Phytoecia affinis (Harrer, 1784)
C.16	Potosia fieberi (Kraatz, 1880)
C.17	Rhagonycha fulva (Scopoli, 1763)
D.1	Cheilosia albitarsis (Meigen, 1822)
D.2	Cheilosia gigantea (Zetterstedt, 1838)
D.3	Cheilosia impressa Loew, 1840
D.4	Cheilosia Meigen, 1822
D.5	Cheilosia proxima (Zetterstedt, 1843)
D.6	Chrysotoxum festivum (Linnaeus, 1758)
D.7	Diptera Linnaeus, 1758
D.8	Eristalis jugorum Egger, 1858
D.9	Eristalis tenax (Linnaeus, 1758)
D.10	Eupeodes corollae (Fabricius, 1794)
D.11	Eupeodes luniger (Meigen, 1822)
D.12	Melanogaster nuda (Macquart, 1829)
D.13	Melanostoma mellarium (Meigen, 1822)
D.13	Melanostoma mellinum (Linnaeus, 1758)
D.14	Merodon aeneus Meigen, 1822
D.15	Merodon Meigen, 1803
D.16	Neoascia meticulosa (Scopoli, 1763)
D.17	Paragus Latreille, 1804
D.18	Parasyrphus lineolus (Zetterstedt, 1843)
D.19	Pipiza austriaca Meigen, 1822
D.20	Pipizella Rondani, 1856
D.21	Pipizella viduata (Linnaeus, 1758)
D.22	Platycheirus albimanus (Fabricius, 1781)
D.22	Platycheirus manicatus (Meigen, 1822)
D.23	Rhingia campestris Meigen, 1822
D.24	Scaeva Fabricius, 1805
D.25	Scaeva pyrastri (Linnaeus, 1758)
D.26	Sphaerophoria Lepeletier Audinet-Serville in Latreille, 1828
D.27	Sphaerophoria scripta (Linnaeus, 1758)
D.28	Syrphidae Latreille, 1802
D.29	Syrphus ribesii (Linnaeus, 1758)
D.30	Trichopsomyia lucida (Meigen, 1822)
D.31	Volucella bombylans (Linnaeus, 1758)
H.1	Andrena curvungula Thomson, 1870
H.1	Andrena haemorrhoa (Fabricius, 1781)
H.2	Andrena humilis Imhoff, 1832
H.3	Andrena intermedia Thomson, 1870

H.4	Andrena labiata Fabricius, 1781
H.5	Andrena nigroaenea (Kirby, 1802)
H.6	Andrena simontornyella Noskiewicz, 1939
H.7	Andrena subopaca Nylander, 1848
H.8	Anthidiellum strigatum (Panzer, 1805)
H.9	Anthidium oblongatum (Illiger, 1806)
H.10	Anthophora atroalba Lepeletier, 1841
H.11	Apis mellifera Linnaeus, 1758
H.12	Bombus bohemicus Seidl, 1838
H.13	Bombus campestris (Panzer, 1801)
H.14	Bombus hortorum (Linnaeus, 1760)
H.15	Bombus humilis Illiger, 1806
H.16	Bombus hypnorum (Linnaeus, 1758)
H.17	Bombus jonellus (Kirby, 1802)
H.18	Bombus lapidarius (Linnaeus, 1758)
H.19	Bombus Latreille, 1802
H.20	Bombus lucorum (Linnaeus, 1760)
H.21	Bombus mesomelas Gerstäcker, 1869
H.22	Bombus monticola Smith, 1849
H.23	Bombus pascuorum (Scopoli, 1763)
H.24	Bombus pratorum (Linnaeus, 1760)
H.25	Bombus ruderarius (Müller, 1776)
H.26	Bombus rupestris (Fabricius, 1793)
H.27	Bombus sichelii Radoszkowski, 1859
H.28	Bombus soroeensis (Fabricius, 1777)
H.29	Bombus sylvarum (Linnaeus, 1760)
H.30	Bombus terrestris (Linnaeus, 1758)
H.31	Bombus vestalis (Geoffroy in Fourcroy, 1785)
H.32	Bombus wurflenii Radoszkowski, 1859
H.33	Chelostoma florisomne (Linnaeus, 1758)
H.34	Dufourea minuta Lepeletier, 1841
H.35	Eucera longicornis (Linnaeus, 1758)
H.36	Halictus Latreille, 1804
H.37	Halictus quadricinctus (Fabricius, 1776)
H.38	Halictus rubicundus (Christ, 1791)
H.39	Halictus simplex Blüthgen, 1923
H.40	Heriades truncorum (Linnaeus, 1758)
H.41	Hoplitis adunca (Panzer, 1798)
H.42	Hoplitis anthocopoides (Schenck, 1853)
H.43	Hoplitis lepeletieri (Pérez, 1879)
H.44	Hoplitis tuberculata (Nylander, 1848)
H.45	Hylaeus signatus (Panzer, 1798)
H.46	Hymenoptera Linnaeus, 1758
H.47	Lasioglossum albipes (Fabricius, 1781)
H.48	Lasioglossum calceatum (Scopoli, 1763)
H.49	Lasioglossum Curtis, 1833

H.50	Lasioglossum fulvicorne (Kirby, 1802)
H.51	Lasioglossum laevigatum (Kirby, 1802)
H.52	Lasioglossum leucozonium (Schrank, 1781)
H.53	Lasioglossum rufitarse (Zetterstedt, 1838)
H.54	Lasioglossum villosulum (Kirby, 1802)
H.55	Megachile ligniseca (Kirby, 1802)
H.56	Megachile nigriventris Schenck, 1870
H.57	Megachile parietina (Geoffroy in Fourcroy, 1785)
H.57	Megachile pyrenaica Lepeletier, 1841
H.58	Megachile willughbiella (Kirby, 1802)
H.59	Nomada ruficornis (Linnaeus, 1758)
H.60	Nomada succincta Panzer, 1798
H.60	Osmia aurulenta (Panzer, 1799)
H.60	Osmia labialis Pérez, 1879
H.61	Osmia mustelina Gerstäcker, 1869
H.62	Panurginus sericatus (Warncke, 1972)
H.63	Panurgus banksianus (Kirby, 1802)
H.64	Panurgus calcaratus (Scopoli, 1763)
H.65	Panurgus dentipes Latreille, 1811
H.66	Polistes biglumis (Linnaeus, 1758)
H.67	Seladonia Robertson, 1918
H.68	Seladonia tumulorum (Linnaeus, 1758)
H.69	Trachusa byssina (Panzer, 1798)
L.1	Aglais io (Linnaeus, 1758)
L.2	Aglais urticae (Linnaeus, 1758)
L.3	Coenonympha pamphilus (Linnaeus, 1758)
L.4	Colias alfacariensis Ribbe, 1905
L.5	Cupido minimus (Fuessly, 1775)
L.6	Erebia sudetica Staudinger, 1861
L.7	Fabriciana adippe (Denis & Schiffermüller, 1775)
L.8	Hipparchia semele (Linnaeus, 1758)
L.9	Issoria lathonia (Linnaeus, 1758)
L.10	Lepidoptera Linnaeus, 1758
L.11	Leptidea Billberg, 1820
L.12	Maniola jurtina (Linnaeus, 1758)
L.13	Muschampia floccifera (Zeller, 1847)
L.14	Pyrgus carlinae (Rambur, 1839)
L.15	Speyeria aglaja (Linnaeus, 1758)
L.16	Thymelicus lineola (Ochsenheimer, 1808)