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„Hoverfly assemblages in the NP Gesäuse“

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1. Abstract

National parks often face the challenge of dealing with the effects of past human influence on habitats. In the NP Gesäuse (Styria, Austria) native beech-fir-spruce forests have been replaced by spruce plantations on many locations. Specific management strategies aim at the regrowth of beech trees in these artificial habitats. For planning and monitoring the success of these strategies, it is crucial to have a profound knowledge of the local flora and fauna. Therefore, hoverflies served as bioindicators for intact forest ecosystems in this study. They include several saproxylic species with good indicator qualities. To draw conclusions on habitat quality and overall species richness of the NP Gesäuse, hoverfly assemblages of the semi-natural beech-(fir)-spruce forests, former spruce plantations and avalanche corridors intersecting those forests were investigated. These habitats were sampled with the help of a butterfly net and coloured pan traps from May to August 2013.

In total 102 species with 1841 individuals including the first record of *Xanthogramma stackelbergi* in Austria were found in the NP Gesäuse.

Hoverfly assemblages exhibited distinct differences between habitats and indicator species could be identified for each of them. Avalanche corridors offering a high flower abundance exhibited the highest species richness and diversity. Most individuals, however, were recorded in the cool spruce plantations, which served as retreats from the heat on hot summer days. Differences in species richness and diversity were less pronounced between the two forest types. Generally spruce plantations exhibited a less balanced dominance structure. Nevertheless, they proved to be a suitable habitat for several species, which can partly be attributed to the favourable light conditions due to management procedures. Beech-(fir)-spruce forests exhibited the highest amount of variation in species richness and hoverfly abundance between sites, but contained most saproxylic species, which indicates an intact forest ecosystem.

Temperature and flower abundance significantly influenced hoverfly activity and served as explanations for differences in species richness and hoverfly abundance between the habitat types.

A comparison of the two catching methods revealed that the butterfly net was more efficient in terms of species and individuals caught. However, species composition differed considerably between the two methods, indicating that the net cannot fully substitute the coloured pan traps.

2. Zusammenfassung

Der Umgang mit den Auswirkungen vergangener menschlicher Einflüsse stellt eine Herausforderung für viele Nationalparks dar. Im Zuge wirtschaftlicher Waldnutzung in früheren Zeiten wurden die natürlichen Buchen-Tannen-Fichten Wälder im NP Gesäuse (Steiermark, Österreich) an vielen Orten durch Fichtenforste ersetzt. Heute wird die Verjüngung der Buche mittels gezielter Managementmaßnahmen gefördert. Für die Planung und Überwachung solcher Eingriffe ist das Wissen über die lokale Flora und Fauna von großer Bedeutung.

Im Zuge dieser Studie wurden deshalb Schwebliegen als Bioindikatoren für intakte Wald-Ökosysteme herangezogen. Sie beinhalten einige xylophage Arten mit guten Indikator-Eigenschaften. Um Rückschlüsse über die Qualität der Habitate sowie den Artenreichtum dieser Gruppe im NP Gesäuse ziehen zu können, wurden naturnahe Buchen-(Tannen)-Fichten Mischwälder, ehemalige Fichtenforste und durch diese verlaufende Lawinenrinnen untersucht. Die Schwebfliegen-Gemeinschaften wurden von Mai bis August 2013 mittels eines Schmetterlingsnetzes und Farbschalen beprobt und verglichen. Insgesamt wurden 102 Arten mit 1841 Individuen, inklusive dem Erstfund von *Xanthogramma stackelbergi* für Österreich, nachgewiesen.

Die Schwebfliegengemeinschaften der einzelnen Habitate unterschieden sich deutlich, so dass Indikatorarten für jeden Habitattyp identifiziert werden konnten. In Lawinenrinnen, mit ihrem reichhaltigen Blütenangebot, konnten die meisten Arten und die höchste Diversität nachgewiesen werden. In den kühlen Fichtenforsten, die an heißen Sommertagen als Rückzugsort vor der Hitze dienten, wurden hingegen die meisten Individuen gefangen. Unterschiede in Diversität und Artenreichtum zwischen den beiden Waldtypen waren weniger deutlich. Fichtenforste zeigten zwar die am wenigsten ausgeglichenen Dominanzverhältnisse, stellten aber, aufgrund der durch die Managementmaßnahmen günstigen Lichtverhältnisse, ein geeignetes Habitat für viele Arten dar. Buchen-(Tannen)-Fichten Mischwälder wiesen die höchste Variation in Arten- und Individuenreichtum auf und beherbergten die meisten xylophagen Arten, was auf ein intaktes Wald-Ökosystem schließen lässt.

Temperatur und Blütenangebot übten einen signifikanten Einfluss auf die Schwebfliegen-Aktivität aus und wurden zur Erklärung vorgefundener Unterschiede in Artenreichtum und Abundanz zwischen den Habitaten herangezogen.

Im Vergleich der Fangmethoden erwies sich das Schmetterlingsnetz sowohl in Bezug auf Arten- als auch Individuenzahl als effizienter. Da sich die Artenzusammensetzung zwischen den beiden Methoden aber deutlich unterschied, kann das Netz die Farbschalen nicht vollständig ersetzen.

3. Introduction

Nature reserves such as national parks often contain a country's last remnants of native ecosystems and act as refuges for rare and endangered species associated with these habitats. However, with only very few exceptions Europe's landscapes have been subject to strong human influence. Especially, forest ecosystems which originally covered large parts of Europe have been altered to varying degrees. Forest fragmentation and changes in forest structure pose a considerable threat to biodiversity conservation and have to be faced by the management of nature reserves (Wallenius et al., 2010).

Historic land use – mainly for charcoal production – has also had a strong and lasting impact on the structure and composition of the forests of the national park Gesäuse (Hasitschka, 2005), which is situated in the mountainous regions of Upper Styria, Austria. Large parts of its area are covered with forests and beech-fir-spruce habitats of montane regions once dominated the forested area. Consequently these ecosystems are of enormous significance to the national park. However, today only about 50 % of these habitats can be classified as semi-natural or moderately altered. In many areas the popularity of the Norway spruce (*Picea abies*) in forestry has led to an increase of the proportion of spruce and the disappearance of fir trees in the montane beech-fir-spruce forests. In other areas mixed forests have even been completely replaced by spruce monocultures (Carli and Kreiner, 2009).

The substitution of native deciduous or mixed forests with spruce monocultures represents a drastic intervention and entails major changes in abiotic as well as biotic conditions: The altered tree composition of the forests does not only lead to changes in soil properties like litter accumulation and nutrient cycling, but also affects local animal communities both directly and indirectly. For example, changes in soil characteristics are reflected in the structure and composition of the soil food web (Scheu et al. 2003). Especially ground dwelling insects such as carabid beetles exhibit reduced diversity in spruce plantations in comparison to native forests (Elek et al., 2001). Similarly, larger and more mobile animals like birds are affected by a change of tree composition and are represented with a lower number of species in spruce plantations (Sweeney et al., 2010). Various studies have shown that plantation forests not only support a lower biodiversity than the replaced native forests, but also differ in their species composition (e.g. Sweeney et al., 2010, Magura et al., 2002). Elek et al. (2001) identified a group of beech specific carabid species that were frequently found in beech forests, but widely absent in spruce plantations.

In addition to the change in tree composition the removal of dead wood, which often accompanies the establishment of commercially managed plantations, also contributes to the decrease in diversity, as it deprives a number of different species of an indispensable resource during their life-cycle (Jonsson et al., 2005).

Furthermore, non-native spruce monocultures are known to be prone to outbreaks of pests such as the bark beetle, which represents a considerable problem in forestry as well as in nature conservation (Janásová and Prach, 2004).

In contrast to plantation forests natural forests characterised by diverse and specified plant and animal communities have become increasingly rare in Central Europe (FAO, 2010) and thus are of high conservational value. As the protection of endangered species and habitats represents one of the major tasks of a national park, the NP Gesäuse seeks to restore the original state of its forests. To achieve this aim a forest management plan was developed in 2009. Its measures include reducing the number of spruce trees in mixed forests and thinning existing spruce plantations, so that the recolonization of native deciduous trees can take place. Furthermore, to increase the proportion of dead wood, most of the cut trees are not removed from the forest (Holzinger and Haseke, 2009).

Information on local plant and animal communities is crucial for monitoring the progress and success of existing management strategies and also provides the basis for planning new ones. However, it is not possible or at least very costly to do a complete species inventory (Lawton et al., 1998). Therefore, several taxa have been suggested as suitable bioindicators for assessing the quality of forest ecosystems, most of which include saproxylic species (e.g. Maleque et al., 2009; Smith et al., 2008, Ferris and Humphrey, 1999).

Among many other taxa hoverflies have been suggested to have good indicator qualities (e.g.: Sommagio, 1999; Smith et al., 2008). They represent a diverse insect group with about 900 European species (Speight, 2012) and 389 listed for Austria (Franz, 1989; this list is, however, incomplete and needs to be reviewed). Adult hoverflies of different species often show distinctive ecological and microclimatic preferences and can be used to characterise their habitat. A considerable amount of variation can also be found in larval lifestyles that significantly influence the distribution patterns of single species. While most generalists feed on aphids, other species show more distinctive larval habits. The semi-aquatic rat tail larvae feed on decaying organic material. Some can also be found in cow dung. Other larvae are parasites in the nests of hymenopterans and ants (Speight, 2012). When assessing the quality of woodlands, however, saproxylic species represent the most suitable indicators. Their larvae depend on senescent trees or on lying dead wood and the occurrence of these species is positively correlated with the amount of dead wood, which is usually associated with intact forest ecosystems (Smith et al., 2008).

Also, overall hoverfly diversity has been shown to depend on structural characteristics of forests: A high field layer vegetation cover was found to support diverse hoverfly assemblages, while canopy cover seems to be negatively associated with hoverfly richness (Humphrey et al., 1999).

Furthermore, some syrphid species exhibit preferences for either deciduous or coniferous forests (Speight, 2012) and can thus be expected to be good compositional indicators. Humphrey et al. (1999) reported that even southern Norway spruce and northern Sitka spruce (*Picea sitchensis*) plantations in Great Britain showed distinctive differences in the composition and diversity of hoverfly assemblages.

In the course of the present study the hoverfly assemblages of three important habitat types of the NP Gesäuse – beech-(fir)-spruce forests, former spruce plantations and avalanche corridors dissecting these forests – were sampled. The data collected on diversity, species richness and composition of local syrphid assemblages served four major aims:

1. Comparison of species richness and composition of hoverfly assemblages between the three habitat types: The present study focuses on differences between the semi-natural mixed forests and the artificial spruce plantations, using syrphids as bioindicators on a local scale to assess habitat quality.
2. Collection of first recent data on hoverfly assemblages: Data of all three habitat types are taken into account to estimate hoverfly diversity of the NP Gesäuse on a landscape level.
3. Analysis of factors influencing hoverfly activity during sampling periods
4. Comparison of the butterfly net and coloured pan traps as methods to sample hoverfly assemblages

4. Material and Methods

4.1 Sampling Sites

4.1.1 Selection of sampling sites

The study was conducted in the NP Gesäuse (Styria, Austria). Three sampling sites were selected for each habitat type (avalanche corridors, beech-(fir)-spruce forests, spruce plantations) resulting in a total of nine sites. All sites were situated in the Gesäuse valley at the northern bank of the river Enns between Gstatterboden and Hieflau.

Sites in spruce plantations were placed around existing forestry inventory points, which were arranged in a grid of 500 m x 500 m squares (Carli and Kreiner, 2009) and selected according to the following criteria: Sites should not include pastures, should not be infested with bark beetles, should not be situated on dangerously steep slopes, should be at least 500 m apart from other sites, should be easily accessible and if possible south exposed. As for beech-(fir)-spruce forests these inventory points were situated on steep slopes or in areas far away from forest roads and as for avalanche corridors such points did not exist, sites in beech-(fir)-spruce forests and avalanche corridors were not placed around inventory points but exclusively selected according to the criteria stated above.

To minimize differences in size between sampling sites a square of appr. 100 m x 100 m was marked using tape measure and flags which were placed at the corners of the squares. The GPS coordinates of these points were determined with the help of a GPS device (Geko 301, Garmin, Romsey, U.K.) to calculate the area of the plots in GIS Steiermark. Corner points of plots that were much bigger or smaller than the others were repositioned so that the calculated size of sampling plots ranged between 7000 m^2 and 8000 m^2.

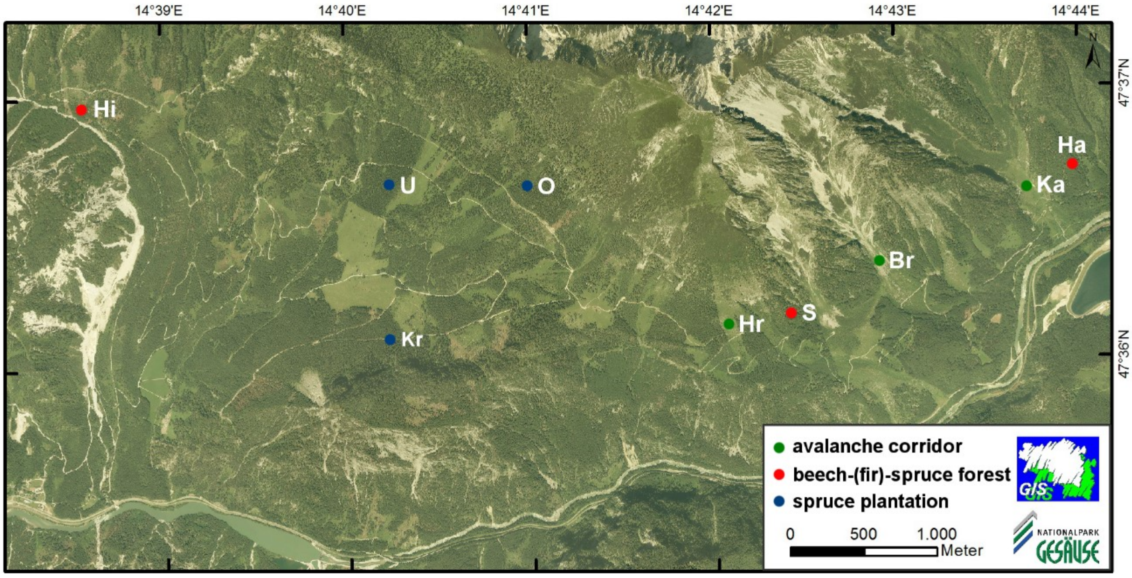

Figure 1: Overview of the location of the nine sampling sites: (Br = Brett, Ha = Hagelwald, Hi = Hinterwinkel, Hr = Hirschmauer, Ka = Kalktal, Kr = Kroisenwald, O = Oberer Steinerwald, S = Scheibenbauernschütt, U = Unterer Steinerwald).

4.1.2 Description of sampling sites

- **Avalanche corridor: Brett (N 47° 36' 21,3'' E 14° 42' 52,5'')**

The sampling site Brett lies between 880 and 950 m sea level on a south exposed slope at the foot of the Tamischbachturm. It is situated in the centre of an avalanche corridor and encompasses open grassland as well as small areas of cobble. Beech-(fir)-spruce forests extend along the western and eastern border of the sampling site, whereas dwarf pine grows in the avalanche corridor further uphill.

- **Avalanche corridor: Hirschmauer (N 47° 36' 06,9'', E 14° 42' 02,6'')**

The sampling site Hirschmauer can be found about 1 km east of the avalanche corridor Brett. It is situated in the centre of an avalanche corridor which lies on a south exposed slope at the foot of the Tamischbachturm. The sampling site extends between 1130 and 1210 m sea level. It encompasses open grassland with loosely distributed young spruce trees. Also rocks without vegetation cover can be found within the sampling site, whereas spruce plantations extend along its eastern and western border.

- **Avalanche corridor: Kalktal (N 47° 36' 35,0'', E 14° 43' 42,3'')**

The sampling site Kalktal can be found further west, close to Hieflau. It also lies in the centre of an avalanche corridor on a south exposed slope at the foot of the Tamischbachturm. Compared to the other two avalanche corridor sites it is situated at a lower sea level between 650 and 710 m and represents a suitable habitat for thermophile as well as montane to alpine species. The sampling site encompasses open grassland and small areas of cobble at the edge. Beech-(fir)-spruce forests grow to the east and the west of this avalanche corridor.

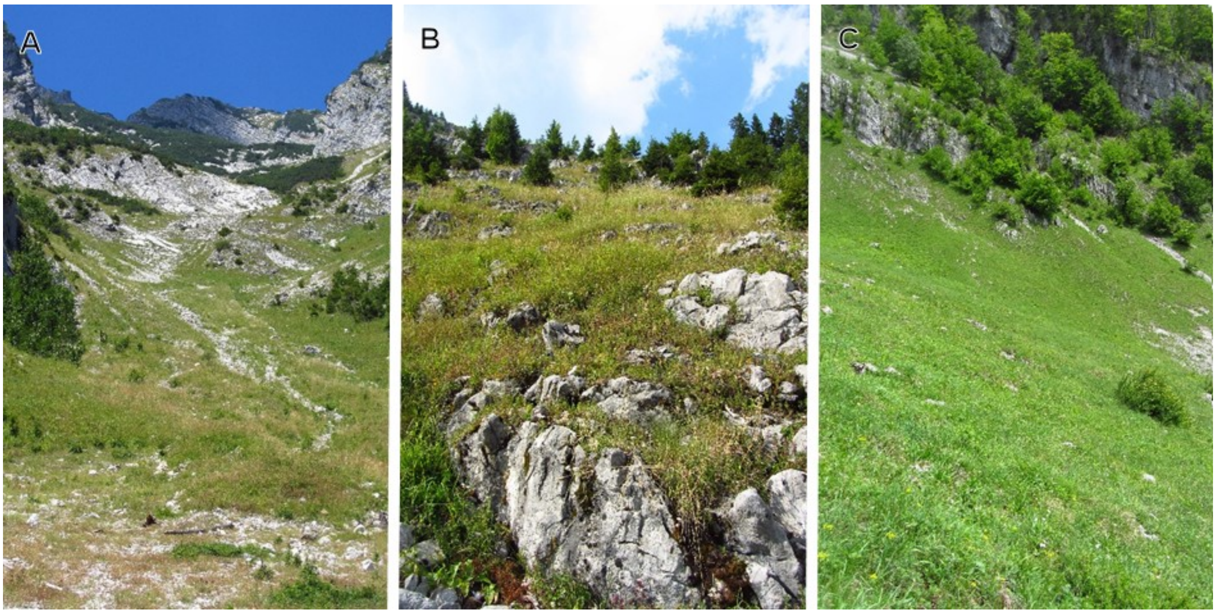

Figure 2: Brett (A), Hirschmauer (B) and Kalktal (C) represented the three sampling sites in avalanche corridors.

- **Beech-(fir)-spruce forest: Hagelwald (N 47° 36' 43,7''; E 14° 43' 55,3'')**

The beech-(fir)-spruce forest Hagelwald lies at the western end of the NP Gesäuse close to the avalanche corridor Kalktal. The sampling area can only be reached by foot on a small path and does not border a forest road. It is situated between 860 and 920 m sea level on a south exposed slope. Beech trees dominate this part of the forest and the proportion of other deciduous (maple) and coniferous (spruce) trees is relatively low. Lying and standing dead wood of both coniferous and deciduous trees can be encountered frequently. The vegetation cover of the herbal layer is low, as large areas of the forest floor are covered with fallen leaves. A few small clearings, due to fallen trees, are distributed within the sampling area.

- **Beech-(fir)-spruce forest: Hinterwinkel (N 47° 36' 56,5''; E 14° 38' 31,8'')**

The beech-(fir)-spruce forest Hinterwinkel is situated at the foot of the Große Buchstein. The sampling area lies on a south exposed slope, which is less steep than in the two other beech-(fir)-spruce forests. It extends between 870 and 920 m sea level. In comparison to the other two sites the amount of beech trees is lower and the average age of the trees is younger. Lying and standing dead wood can be found within the sampling area, but the proportion of deciduous wood is very low. Except for the forest road, which crosses the sampling site, no large clearings can be found. The floor is covered with fallen leaves and herbal vegetation is mostly restricted to the edges of the forest road.

- **Beech-(fir)-spruce forest: Scheibenbauernschütt (N 47° 36' 09,6''; E 14° 42' 21,7'')**

The Scheibenbauernschütt-site is situated within an area of beech-(fir)-spruce forest east of the avalanche corridor Scheibenbauernschütt. The sampling area does not lie far from the forest road, but is separated from it by densely growing young beech trees. It is situated on a south exposed slope at an altitude ranging between 1010 and 1080 m. Beech is the dominating tree species, although coniferous (spruce) and single other deciduous trees (maple) can be found as well. A considerable amount of lying and standing dead wood of deciduous and coniferous trees can be found within the sampling area. In the middle a large clearing, where ample vegetation grows, is situated. The forest floor is covered with fallen leaves and except for the clearing only little vegetation can be found.

Figure 3: Hagelwald (A), Hinterwinkel (B) and Scheibenbauernschütt (C) represented the three sampling sites in beech-(fir)-spruce forests.

- **Spruce plantation: Kroisenwald (N 47° 36' 04,1''; E 14° 40' 08,4'')**

The sampling site Kroisenwald lies about 1 km south of the Unterer Steinerwald-site. It is situated on a north exposed slope within a former spruce plantation. The sampling site extends between 1022 and 1076 m sea level. Except for the forest road that crosses the sampling site there is only one small clearing in the south-eastern corner. Compared to the other spruce plantations this site contains a high amount of dead wood, which mostly consists of cut spruce trees and stools with a relatively small diameter.

- **Spruce plantation: Oberer Steinerwald (N 47° 36' 37,4''; E 14° 40' 56,1'')**

About 1 km north and 1 km east of the Kroisenwald-site the sampling site Oberer Steinerwald can be found. It is situated on a south exposed slope within a former spruce plantation. The sampling site extends between 1190 and 1250 m sea level and contains one larger clearing in the north-western corner and some small forest aisles. Stools and cut trees, but only little standing dead wood can be found within the sampling area.

- **Spruce plantation: Unterer Steinerwald (N 47° 36' 39,8''; E 14° 40' 05,8'')**

The sampling site Unterer Steinerwald lies 1 km west of the Oberer Steinerwald-site. It is situated between 990 and 1020 m sea level on a south exposed slope within a former spruce plantation. Not far from the western border a small stream can be found. The sampling site contains only small forest aisles and larger clearings are missing. The vegetation of the herbal layer grows taller and is more ample than in the other two spruce plantations. Stools and cut trees, but only little standing dead wood can be found within the sampling site.

Figure 4: Kroisenwald (A), Oberer Steinerwald (B) and Unterer Steinerwald (C) represented the three sampling sites in spruce plantations.

4.2 Data collection

To capture seasonal changes of local hoverfly assemblages, data collection took place from mid-May to mid-August in 2013. As hoverfly activity is known to correlate with weather conditions (Gilbert, 1985) the following criteria had to be met for data collection to take place: No data was collected during extremely overcast conditions or rainy weather and a minimum temperature of 10°C was necessary to start data collection. Two different sampling methods were applied to compare their efficiency and potential bias in collecting data on hoverfly assemblages: a butterfly net and coloured pan traps.

- **Butterfly net**

Each site was sampled with the butterfly net on 8 days. Data collection took place between 9 am and 5 pm. Sampling units ranged from 1 to 1.5 hours and were only interrupted or stopped in case of unexpected rain. Three sites – one of each habitat type – were visited in the course of a day, when weather conditions allowed for it. The sequence in which these three sites were visited was counterbalanced to account for relations between the time of the day and hoverfly activity.

During the sampling unit I walked from one end of the site to the other in a meandering pattern. In order to catch small and inconspicuous species as well as big and conspicuous ones I walked at a slow pace and observed the ground and the air carefully. All hoverflies seen within the range of the net were caught and preserved in labelled glass tubes filled with 70 % alcohol. When I reached the other end of the site before the sampling period was over, I started to walk back in meandering patterns.

A USB data logger (Voltcraft DL-121TH, Conrad Electronic SE, Hirschau, Germany) placed at the lower end of the site recorded the air temperature every five minutes during the sampling unit. It was protected from direct sunlight and rain by a little hut made out of ply wood and put up at a height of about one metre above ground. At the end of data collection the exact duration was noted and flower abundance was estimated using the categories 1 to 5 (table 1).

Table 1: Categorization for estimating flower abundance after each sampling period.

category	criteria
1	only very few flowers can be seen
2	flowers grow loosely in some areas of the site, but there are large areas without flowers
3	flowers grow loosely across the whole sampling area
4	flowers grow densely, but there are larger areas without flowers
5	flowers grow densely with only small or no areas without flowers

- **Coloured pan traps**

Pan traps were put up on four sites in May. As only few hoverflies and many more other insects were caught, the use of coloured pan traps was paused in June. After hoverfly abundance had noticeably increased, all sites were sampled once in July and once August. Pan traps were only used on predominantly sunny days without rain. They were set up on three sites between 7 am and 10 am and collected between 4 pm and 8 pm on the same day. Data loggers recorded temperature and humidity during trap-sampling and caught specimens were stored in glass tubes filled with 70 % alcohol.

The pan traps consisted of plastic (polypropylene) bowls of three different colours (blue, white and yellow) that are known to attract syrphids more efficiently than other colours (Campbell and Hanula, 2007). As different colours have proven to attract different species of hoverflies (Haslett, 1989), all three colours were applied in this study. Blue and white bowls (Teko-plastic, Weiz, Austria) had a diameter of 20 cm and a height of 7.5 cm. Yellow pan traps consisted of similar bowls with a diameter of 19 cm and a height of 7.5 cm (Rohrmoser, Vienna, Austria). Reflectance curves between 300 and 700 nm were measured for one bowl of each colour by means of a USB 2000 spectrometer with a deuterium/halogen light source (Oceans Optics B. V., Duiven, The Netherlands). A white standard (Diffuse Reflectance Standard WS-1, Ocean Optics) was used for calibration. Data were transformed for graphical representation in R using the software Avicol_v6 (figure 5; Gomez, 2006).

Nine pan traps of each colour were arranged in a grid of approx. 20 m x 20 m squares, resulting in a total of 27 pan traps. Distances between the squares were estimated by counting steps and one bowl of each colour was placed at the points of the grid. The bowls were placed on well exposed spots on the ground, so that they were easily visible for flower visiting insects. The bowls were filled with 2-3 cm of water and two drops of unscented dishwashing detergent (Frosch Handspül-Lotion Aloe Vera, Werner-Mertz Gruppe, Mainz, Germany) was added to reduce surface tension. Additionally two drops of rose water (Tautropfen Naturkosmetik GmbH, Calw/Schwarzwald, Germany) served as a means to increase the sample size (Laubertie et al., 2006).

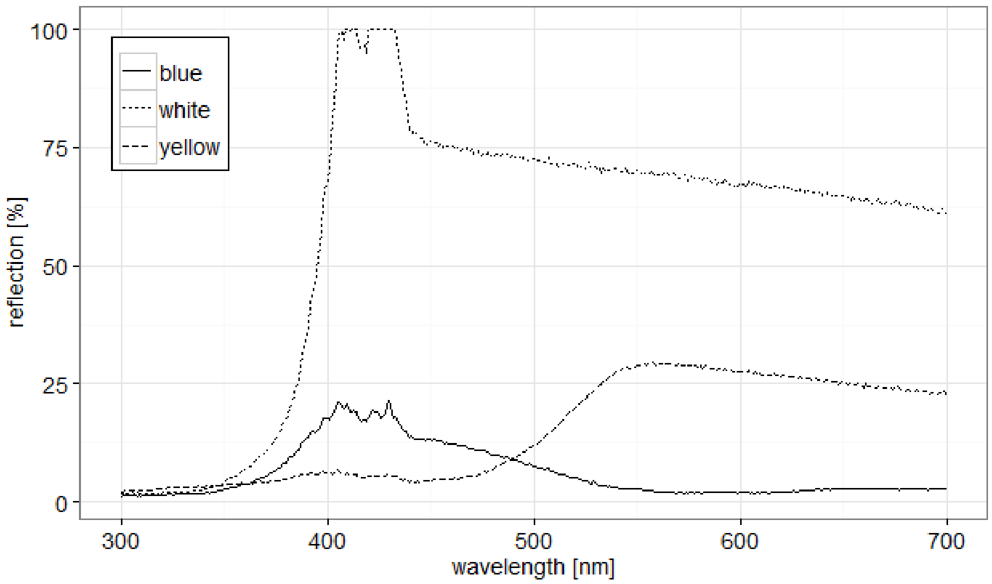

Figure 5: Reflectance curves between 300 and 700 nm for blue, white and yellow pan traps.

4.3 Determination of hoverflies

The caught specimens were determined with the help of van Veen (2010). In some cases additional literature was consulted: Hippa (1968) was used to determine individuals of the genus *Xylota* and Speight and Sarthou (2011) to determine individuals of the genus *Xanthogramma*. In addition to the determination literature hoverflies of the collection of the Museum of Natural History in Vienna served as reference material.

As literature for the determination of females of the genera *Pipizella* and *Paragus* was not available, they were only determined to genus or species complex. Individuals of genera which I could not assign to a species with certainty were classified into morphospecies (see table 8 in the appendix for a list of morphospecies and their characteristic traits).

4.4 Statistical analysis

For statistical analysis (except for the comparison of the two sampling methods) only data collected with the butterfly net was used. Females that had only been determined to genus/species complex were assigned to the most abundant species in males. All statistical tests and analyses were conducted using R 3.0.2 and R-Studio 0.98.490. Figures were created in R using the package “ggplot” and if necessary edited using GIMP 2.8.10.

4.4.1 Cluster analysis and ordination methods

To see if hoverfly assemblages differed between habitat types cluster analysis and Kruskal’s non-metric multidimensional scaling were performed using the package “vegan”. Bray-Curtis dissimilarities (d) served as dissimilarity measures.

Cluster analysis was performed three times applying single, complete and average linkage (UPGMA) strategies to see whether the results of the three methods differed. Kruskal’s non-metric multidimensional scaling was calculated using the function “isoMDS”. Environmental variables (mean temperature, mean flower abundance of the sites) were fitted onto the ordination and class centroids were calculated for the three habitat types. R^2 served as a goodness of fit statistic and p-values were based on 999 permutations.

4.4.2 Differences in species composition

In order to find indicator species for the three habitat types Dufrene-Legendre`s indicator species analysis was performed using the function “indval” of the package “labdsv”. The resulting indicator value represents a product of the relative frequency and the relative abundance of a species in a habitat type. P-values were calculated based on 1000 randomisations.

4.4.3 Species richness estimates and diversity indices

Species richness, diversity and evenness measures were all calculated using the package “vegan”. To account for potential differences in sampling completeness true species richness of all nine sites was estimated using first order jackknife (J1). The inverse Simpson’s index (D) and Pielou’s evenness (E) were calculated for all nine sites to compare diversity and evenness. To conduct comparisons between habitats the arithmetic mean of the three sites was calculated.

4.4.4 Differences in mean temperature and flower abundance

Differences in mean temperature and flower abundance during the sampling periods were analysed between the three sites of the same habitat types and between the different habitat types with the help of a Kruskal-Wallis-Anova and pairwise comparisons applying the Wilcoxon-Test for unpaired samples (also called Mann-Whitney-Test). Mean temperature during a sampling unit was calculated including all the temperature-values recorded during the time of data collection by the data logger.

4.4.5 Factors influencing hoverfly activity

A general linear model assuming a Poisson distribution was computed to model the relationship of species and individuals recorded per sampling unit. Further generalized linear models helped to explain how flower abundance and temperature affected hoverfly activity in terms of species and individuals caught per hour. Flower abundance, mean temperature and the duration of the sampling unit were included as factors and either the number of species or of individuals represented the response variable. As the effects of temperature varied among habitat types, three separate models were fitted. A polynomial and a linear model were fitted for each habitat type. A Chi^2-Test based on D^2-values was used to test for significant differences between the two models.

4.4.6 Seasonal differences in hoverfly activity

Seasonal differences in hoverfly activity were analysed for each habitat type separately: A Kruskal-Wallis-Anova was applied to test for differences in the number of species and individuals recorded per hour between the four months of data collection. Subsequently pairwise comparisons applying the Wilcoxon-Test for unpaired samples (also called Mann-Whitney-Test) were conducted.

5. Results

5.1 Species richness of the NP Gesäuse on a landscape level

In the course of this study 102 species with 1841 individuals were recorded with both the butterfly net and the coloured pan traps in the sampled areas of the NP Gesäuse (table 2). One of these species – *Xanthogramma stackelbergi* – has not yet been listed for Austria (Speight, 2012). It is represented with three specimens in the collected data. They were found at the sites Hagelwald and Scheibenbauernschütt.

The number of individuals caught per species ranges from 506 in *Episyrphus balteatus* to only one in 30 species. The majority of species (94) and individuals (1711) was collected with the butterfly net. Additionally to the species found within the selected sampling areas one individual of *Callicera aenea* was caught close to the Scheibenbauernschütt site.

Including all 102 species recorded the larvae of 18 species (17.7 %) are saproxylic and 15 species (14.7 %) can be classified as stenoecious forest species according to the classification of Waitzbauer (2001).

Table 2: List of all species recorded: stenoecious forest species are written in bold letters, unidentifiable females are listed as *Genus* sp., morphospecies as *Genus* A-G. When it was not possible to decide between two species, both are listed (ind = number of individuals, A = avalanche corridor, B = beech-(fir)-spruce forest, Sp = spruce plantation, O = outside of sampling sites).

species	ind	A	B	Sp	O
Baccha elongata (Fabricius), 1775	12		×	×	
***Blera fallax* (L.), 1758**	**3**		**×**	**×**	
***Brachyopa vittata* (Zetterstedt), 1843**	**1**			**×**	
***Brachypalpoides lentus* (Meigen), 1822**	**6**		**×**	**×**	
***Callicera aenea* (Fabricius), 1777**	**1**				**×**
***Chalcosyrphus valgus* (Gmelin), 1790**	**1**	**×**			
Cheilosia A	6	×	×	×	
Cheilosia B	14	×	×	×	
Cheilosia C	2		×	×	
Cheilosia canicularis (Panzer), 1801/*himantopus* (Panzer), 1798	14	×	×	×	
Cheilosia D	3	×			
Cheilosia E	3	×		×	
Cheilosia F	1		×		
Cheilosia G	1	×			
Cheilosia personata Loew, 1857	3	×		×	
Chrysotoxum arcuatum (L.), 1758	31	×	×	×	
Chrysotoxum bicinctum (L.), 1758	13	×	×	×	
Chrysotoxum fasciolatum (de Geer), 1776	3		×	×	
Chrysotoxum intermedium Meigen, 1822	3	×	×		
Chrysotoxum vernale Loew, 1841	2	×			
Chrysotoxum verralli (Collin), 1940	1	×			
Criorhina berberina (Fabricius), 1805	3		×		
Dasysyrphus lenensis Bagatshanova, 1980	4			×	
Dasysyrphus venustus *(Meigen), 1822*	1			×	
Didea alneti (Fallen), 1817	2	×			
Didea fasciata Macquart, 1843	5	×		×	

Epistrophe grossulariae (Meigen), 1822	1			×	
Episyrphus balteatus (de Geer), 1776	506	×	×	×	
Eristalis arbustorum (L.), 1758	14	×			
Eristalis jugorum Egger, 1858	5	×			
Eristalis nemorum (L.), 1758	2	×			
Eristalis rupium Fabricius, 1805	4	×			
Eristalis similis (Fallen), 1817	16	×	×	×	
Eristalis tenax (L.), 1758	59	×	×	×	
Eumerus flavitarsis Zetterstedt, 1843	20		×	×	
Eupeodes A	2	×	×		
Eupeodes B	6		×	×	
Eupeodes C	1	×			
Eupeodes corollae (Fabricius), 1794	7	×		×	
Eupeodes D	1	×			
***Ferdinandea cuprea* (Scopoli), 1763**	**1**		**×**		
Helophilus pendulus (L.), 1758	1	×			
Helophilus trivittatus (Fabricius), 1805	1	×			
Heringia A	1			×	
Heringia pubescens (Delucchi & Pschorn-Walcher), 1955	2	×		×	
Lapposyrphus lapponicus (Zetterstedt), 1838	189	×	×	×	
Lejota ruficornis (Zetterstedt), 1843	1	×			
Leucozona lucorum (L.), 1758	1			×	
Megasyrphus erraticus (L.), 1758	10	×	×	×	
Melangyna A	1			×	
Melanostoma scalare (Fabricius), 1794	63	×	×	×	
Meligramma cincta (Fallen), 1817	5		×	×	
Meliscaeva auricollis (Meigen), 1822	10	×	×	×	
Meliscaeva cinctella (Zetterstedt), 1843	11	×	×	×	
Merodon A	5	×			
Merodon equestris (Fabricius), 1794	1			×	
Merodon rufus Meigen, 1838	21	×			
Microdon devius (L.), 1761	29	×			
Myathropa florea (L.), 1758	7	×	×		
Paragus albifrons (Fallen), 1817	1	×			
Paragus albifrons (Fallen), 1817/*pecchiolii* Rondani, 1857	2	×	×		
Paragus haemorrhous Meigen, 1822	3	×			
Paragus sp.	12	×			
Parasyrphus lineolus (Zetterstedt), 1843	11		×	×	
Parasyrphus macularis (Zetterstedt), 1843	6	×		×	
Parasyrphus malinellus (Collin), 1952	3			×	
Parasyrphus vittiger (Zetterstedt), 1843	5	×		×	
Pipiza A	4	×		×	
Pipiza quadrimaculata (Panzer), 1802	3			×	
Pipizella annulata (Macquart), 1829	1	×			
Pipizella brevis Lucas, 1977	1	×			
Pipizella divicoi (Goeldlin), 1974	29	×	×		
Pipizella pennina (Goeldlin), 1974	5	×	×		

Pipizella sp.	55	×		×	
Pipizella viduata (L.), 1758	4	×			
Platycheirus A	1				
Platycheirus albimanus (Fabricius), 1781	21	×	×	×	
Platycheirus B	1				
Platycheirus parmatus Romani, 1857	1			×	
Platycheirus scuatus-group	2	×	×		
Rhingia borealis Ringdahl, 1928	6		×	×	
Rhingia campestris Meigen, 1822	5		×	×	
Scaeva dignota (Rondani), 1857	1			×	
Scaeva pyrastri (L.), 1758	3	×			
Scaeva selenitica (Meigen), 1822	4	×			
Sericomyia lappona (L.), 1758	3	×		×	
Sphaerophoria interrupta (Fabricius), 1805	1	×			
Sphaerophoria laurae Goeldlin, 1989/*infuscata* Goeldlin, 1974	1	×			
Sphaerophoria scripta (L.), 1758	79	×			
***Sphegina clunipes* (Fallen), 1816**	**13**			**×**	
***Sphegina montana* Becker, 1921**	**2**		**×**	**×**	
***Sphegina sibirica* Stackelberg, 1953**	**10**	**×**	**×**	**×**	
Syritta pipiens (L.), 1758	5	×			
Syrphus ribesii (L.), 1758	23	×	×	×	
Syrphus torvus Osten-Sacken, 1875	165	×	×	×	
Syrphus vitripennis Meigen, 1822	140	×	×	×	
Volucella bombylans (L.), 1758	5	×	×		
Xanthandrus comtus (Harris), 1776	1			×	
Xanthogramma dives (Rondani), 1857/*stackelbergi* Violovitsh, 1975	3		×		
Xanthogramma laetum (Fabricius), 1794	3	×	×	×	
***Xylota florum* (Fabricius), 1805**	**2**	**×**	**×**		
***Xylota ignava* (Panzer), 1798**	**4**	**×**			
***Xylota jakutorum* Bagatshanova, 1980**	**20**	**×**	**×**	**×**	
***Xylota segnis* (L.), 1758**	**27**	**×**	**×**	**×**	
Xylota sylvarum (L.), 1758	**1**		**×**		

5.2 Comparison of hoverfly assemblages on a local level

5.2.1 Different habitat types host different hoverfly assemblages

Hoverfly assemblages of the three habitat types can be clearly separated from each other. All three methods of cluster analyses to compare the hoverfly assemblages result in the same clades: An open habitat clade, containing the three avalanche corridor sites can be distinguished from a forest clade, which encompasses all spruce plantations as well as all beech-(fir)-spruce forests. Furthermore, the forest clade can be subdivided into a spruce plantation and a beech-(fir)-spruce forest clade (figure 6).

These results are supported by the NMDS ordination (stress = 5.1 %). Three separated groups corresponding to the three habitat types can be distinguished (figure 7). Avalanche corridors are clearly separated from forest habitats along the first dimension, whereas beech-(fir)-spruce forests and spruce plantations are separated along the second dimension. Class centroids for habitat types (r^2 = 0.92, $p < 0.01$) and vectors of environmental variables (flower abundance: r^2 = 0.98, $p < 0.01$, mean temperature: $r^2 = 0.77$, $p < 0.05$) are fitted. Flower abundance shows the largest differences between avalanche corridors and beech-(fir)-spruce forests. Mean temperature, in the contrary, changes most rapidly from spruce plantations to avalanche corridors.

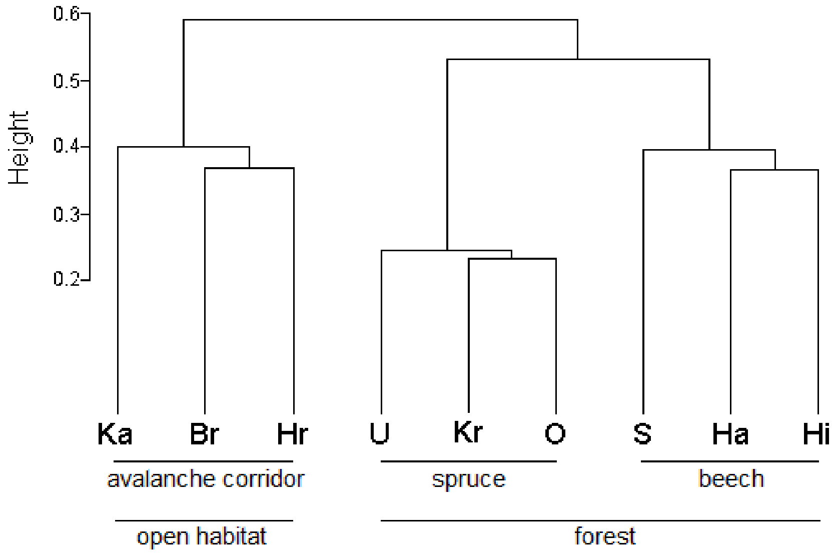

Figure 6: Average linkage tree (based on Bray-Curtis dissimilarities) representing the hoverfly assemblages of the nine sampling sites (Br = Brett, Ha = Hagelwald, Hi = Hinterwinkel, Hr = Hirschmauer, Ka = Kalktal, Kr = Kroisenwald, O = Oberer Steinerwald, S = Scheibenbauernschütt, U = Unterer Steinerwald).

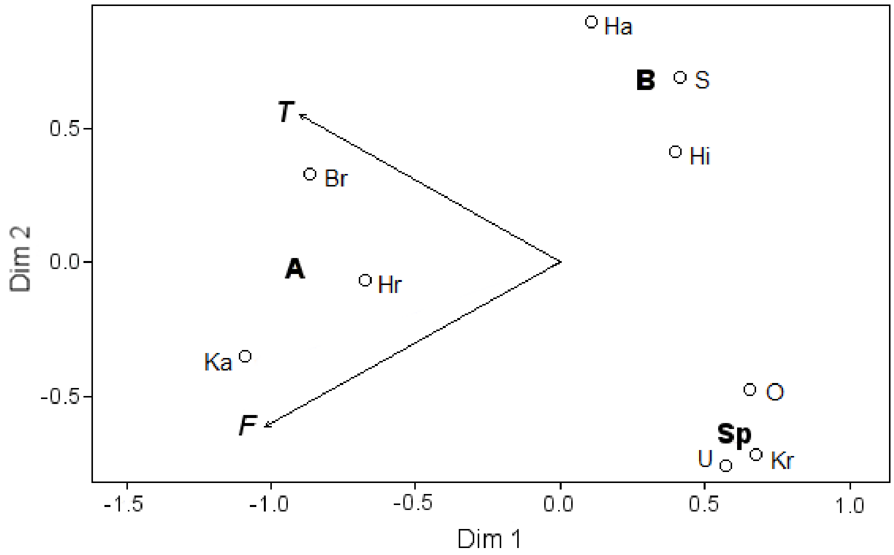

Figure 7: Results of the non-metric multidimensional scaling (stress = 5.1 %) based on Bray-Curtis dissimilarities: Hoverfly assemblages of the sampling sites are depicted as black circles (Br = Brett, Ha = Hagelwald, Hi = Hinterwinkel, Hr = Hirschmauer, Ka = Kalktal, Kr = Kroisenwald, O = Oberer Steinerwald, S = Scheibenbauernschütt, U = Unterer Steinerwald). Vectors of environmental variables are shown as arrows and labelled in italic letters (F = flower abundance, T = mean temperature) and class centroids for habitat types are depicted as bold letters (A = avalanche corridor, B = beech-(fir)-spruce forest, Sp = spruce plantation).

5.2.2 Differences in species composition between habitat types

Habitat types differ in their species composition: 19 species are shared by all three habitat types and 48 species – including 24 species represented with a single individual – are unique to one habitat type. Avalanche corridors host many more unique species (30) than the forest habitats (beech: 7, spruce: 11). Dufrene-Legendre's indicator species value shows that all three habitat types contain characteristic species (table 3). Seven indicator species were found for avalanche corridors and five for spruce plantations. For beech-(fir)-spruce forests, however, only one indicator species could be identified.

Table 3: Dufrene-Legendre's indicator species analysis resulted into seven indicator species for avalanche corridors (A), one for beech-(fir)-spruce forests (B) and five for spruce plantations (Sp) (frequency = number of sites in which the species occurs; indval = indicator value).

species	habitat type	indval	p-value	frequency
Eristalis arbustorum	A	1.000	0.048	3
Merodon rufus	A	1.000	0.041	3
Paragus haemorrhous	A	1.000	0.033	3
Pipizella viduata	A	1.000	0.036	3
Scaeva pyrastri	A	1.000	0.038	3
Sphaerophoria scripta	A	1.000	0.047	3
Pipizella divicoi	A	0.976	0.037	5
Eumerus flavitarsis	B	0.900	0.043	4
Pipiza quadrimaculata	Sp	1.000	0.048	3
Sphegina clunipes	Sp	1.000	0.034	3
Lapposyrphus lapponicus	Sp	0.694	0.033	9
Platycheirus albimanus	Sp	0.650	0.038	8
Episyrphus balteatus	Sp	0.753	0.028	9

5.2.3 Variation in species richness, abundance and diversity among habitat types

Species richness and hoverfly abundance vary among habitat types (table 4): On average, beech-(fir)-spruce forests host the lowest mean total number of both species (26.0) and individuals (115.3). The highest mean number of species and individuals, however, can be found in two different habitat types: Avalanche corridors host most species (41.0), whereas most individuals are recorded in spruce plantations (245.7).

Also hoverfly activity – the number of species and individuals caught per hour – varies among habitat types and shows significant differences (figure 8; Kruskal-Wallis-Anova; species: $\chi^2 = 23.7$, $p < 0.01$, individuals: $\chi^2 = 11.7$, $p < 0.001$). Beech-(fir)-spruce forests exhibit a significantly lower number of species and individuals caught per hour than spruce plantations (species: $W = 445.5$, $p < 0.01$, individuals: $W = 539.5$, $p < 0.001$) and avalanche corridors (species: $W = 481.5$, $p < 0.01$, individuals: $W = 486$, $p < 0.01$).

The mean estimated species richness (J1) shows the same patterns of variation among habitat types as the observed species richness (table 4): Most species are estimated to occur in avalanche corridors and fewest in beech-(fir)-spruce forests. Mean hoverfly diversity (Simpson's index), however, is not fully consistent with species richness of habitat types. On average, it is highest in avalanche corridors (11.67) and lowest in spruce plantations (5.03). Despite their low total species number beech-(fir)-spruce forests (7.32) show a slightly higher inverse Simpson's index than spruce plantations. This can be attributed to the highly unbalanced dominance structure of hoverfly assemblages in spruce plantations (mean evenness = 0.66; compared to 0.76 in beech-(fir)-spruce forests and 0.79 in avalanche corridors). Although *Episyrphus balteatus* is most abundant in all habitat types, it appears especially frequently in spruce plantations, where it constitutes 37.9 % of all individuals (for rank abundance curves see figures 15 to 17 in appendix).

Table 4: Comparison of the mean total number of caught individuals (n), species richness (S), inverse Simpson's index (D), Pielou's evenness (E) and Jack1 (J1) of the three habitat types (n=3).

	avalanche corridor	**beech-(fir)-spruce forest**	**spruce plantation**
N	209.33	115.33	245.67
S	41	26	31.67
D	11.67	7.32	5.03
E	0.79	0.76	0.66
J1	61.46	37.96	44.63

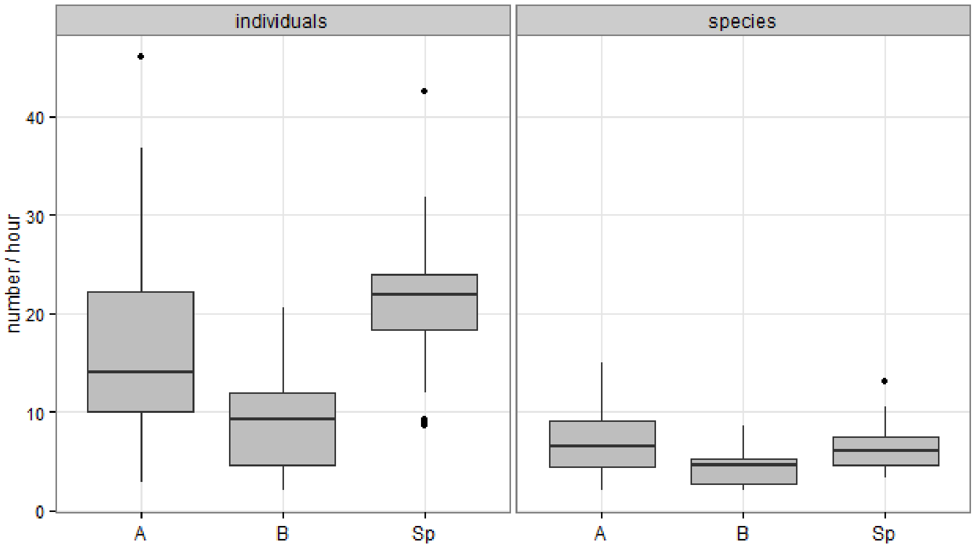

Figure 8: Boxplots of the number of individuals (left) and species (right) caught per hour in avalanche corridors (A: n=26), beech-(fir)-spruce forests (B: n=25) and spruce plantations (Sp: n=24).

5.2.4 Relative abundances of larval lifestyles of species in each habitat type

The relative abundances of larval lifestyles of the caught species show marginal differences between the habitat types. Species with 'aphidophagous and unspecific zoophagous' larvae are most common and constitute more than half of the species in all habitat types. In spruce plantations they show the highest relative abundance of all habitat types and make up more than 62.8 % of all species. The second most abundant larval lifestyle differs between habitat types: 'Phytoparasitic' species constitute 15.7 %

in spruce plantations. In avalanche corridors 'phytoparasitic' larvae and 'semi-aquatic, saprophagous' larvae are equally abundant (14.1 %), whereas 'saproxylic' larvae constitute the second most abundant category in beech-(fir)-spruce forests (19.6%). Beech-(fir)-spruce forests do not only show the highest relative amount, but also host the highest total number of saproxylic species (9). The remaining three categories ('koprophagous-saprophagous', 'myrmecophagous', 'nekro-zoophagous') are represented with only one to three species in the whole dataset.

5.2.5 Differences in hoverfly assemblages between sites of the same habitat type

Avalanche corridor sites only show marginal differences in the total numbers of species (39-44) and individuals (182-242) caught during the sampling season. Also estimated species richness (58.00-65.50), inverse Simpson's index (9.66-12.70) and evenness (0.77-0.80) of the three sites are very similar (table 5). The number of species and individuals caught per hour does not show any significant differences either (Kruskal-Wallis-Anova; species: $\chi^2 = 0.3$, $p > 0.5$, individuals: $\chi^2 = 0.4$, $p > 0.5$).

The total number of individuals caught in spruce plantation sites ranges from 213 in Oberer Steinerwald to 288 in Unterer Steinerwald, while the total number of species varies from 26 in Kroisenwald to 37 in Unterer Steinerwald (table 5). The number of species and individuals caught per hour, however, does not show significant differences (Kruskal-Wallis-Anova; species: $\chi^2 = 1.7$, $p > 0.1$, individuals: $\chi^2 = 3.2$, $p > 0.1$, n=8). Furthermore, estimated species richness (37.00-58.50), inverse Simpson's index (4.43-5.54) and evenness (0.64-0.67) vary only marginally between the spruce plantation sites.

Beech-(fir)-spruce forest sites show the highest amount of variation in the total number of species recorded (table 5). It ranges from 17 in Hagelwald to 36 in Scheibenbauernschütt and inverse Simpson's index varies according to species numbers (4.58-10.44). Estimated species richness is much higher in Scheibenbauernschütt (58.50) than in the other two sites (Hagelwald: 22.75, Hinterwinkel: 32.63) and exceeds observed species richness by 22 species. Furthermore, the Kruskal-Wallis-Anova reveals a significant difference in the number of species caught per hour between the three sites ($\chi^2 = 7.0$, $p < 0.01$). Significantly less species per hour are found in Hagelwald than in Hinterwinkel ($W = 12.5$, $p < 0.05$) and Scheibenbauernschütt ($W = 13.5$, $p < 0.05$). In comparison to the number of species the total number of individuals and the evenness exhibit less variation (species richness: 83-138, evenness: 0.72-0-79) and no significant differences in the number of individuals caught per sampling unit can be observed (Kruskal-Wallis-Anova: $\chi^2 = 5.6$, $p > 0.05$).

Table 5: Comparison of the mean total number of caught individuals (n), species richness (S), inverse Simpson's index (D), Pielou's evenness (E) and Jack1 (J1) of each sampling site (Br = Brett, Ha = Hagelwald, Hi = Hinterwinkel, Hr = Hirschmauer, Ka = Kalktal, Kr = Kroisenwald, O = Oberer Steinerwald, S = Scheibenbauernschütt, U = Unterer Steinerwald)

	avalanche corridor			**beech-(fir)-spruce forest**			**spruce plantation**		
	Br	**Hr**	**Ka**	**Ha**	**Hi**	**S**	**Kr**	**O**	**U**
n	182	204	242	83	138	125	236	213	288
S	39	44	40	17	25	36	26	32	37
D	9.67	12.70	12.65	4.58	6.95	10.44	4.43	5.12	5.54
E	0.77	0.80	0.80	0.7	0.76	0.79	0.65	0.67	0.64
J1 ± se	58.00 ± 9.00	65.50 ± 11.40	60.88 ± 8.97	22.75 ± 3.83	32.63 ± 3.93	58.50 ± 10.27	37.38 ± 7.33	45.75 ± 7.35	50.75 ± 7.92

5.3 Differences in environmental factors between habitat types

Mean temperature (Kruskal-Wallis-Anova: $\chi^2 = 15.23$, $p < 0.001$) and flower abundance (Kruskal-Wallis-Anova: $\chi^2 = 49.65$, $p < 0.001$) of sampling units differ significantly between habitat types. Mean temperature is significantly lower in spruce plantations than in avalanche corridors ($W = 505$, $p < 0.001$) and beech-(fir)-spruce forests ($W = 175$, $p < 0.05$). Flower abundance of sampling units is significantly higher in avalanche corridors than in spruce plantations ($W = 589$, $p < 0.001$) and beech-(fir)-spruce forests ($W = 630$, $p < 0.001$). Furthermore, beech-(fir)-spruce forests exhibit a significantly lower flower abundance than spruce plantations ($W = 481$, $p < 0.001$).

These factors only vary marginally between sites of the same habitat type (table 6). The Kruskal-Wallis-Anova does not show significant differences in mean temperature and flower abundance of the sampling units between the sites of any of the habitat types (avalanche corridors: $W_{temp} = 2.95$, $p_{temp} > 0.1$, $W_{flower} = 6.80$, $p > 0.05$; beech-(fir)-spruce forests: $W_{temp} = 2.02$, $p_{temp} > 0.1$, $W_{flower} = 0.96$, $p > 0.5$; spruce plantations: $W_{temp} = 0.20$, $p_{temp} > 0.5$, $W_{flower} = 0$, $p > 0.5$).

Table 6: Comparison of mean temperature and mean flower abundance between habitat types and sampling sites (A = avalanche corridor, B = beech-(fir)-spruce forest, Sp = spruce plantation).

sampling site	habitat type	mean temperature [°C]	flower abundance
Brett	A	30.54	3.75
Hirschmauer	A	25.98	4.13
Kalktal	A	29.55	4.70
mean	**A**	**28.69**	**4.19**
Hagelwald	B	24.85	1.33
Hinterwinkel	B	25.28	1.50
Scheibenbauernschütt	B	28.59	1.50
mean	**B**	**26.24**	**1.44**
Kroisenwald	Sp	22.15	2.25
Oberer Steinerwald	Sp	22.15	2.25
Unterer Steinerwald	Sp	22.74	2.25
mean	**Sp**	**22.35**	**2.25**

5.4 Factors influencing hoverfly activity

5.4.1 Relationship of species and individual number

The generalized linear model reveals a significant positive relationship between the number of species and individuals caught per sampling unit for the whole data set (figure 11; $D^2 = 0.56$, $p < 0.001$).

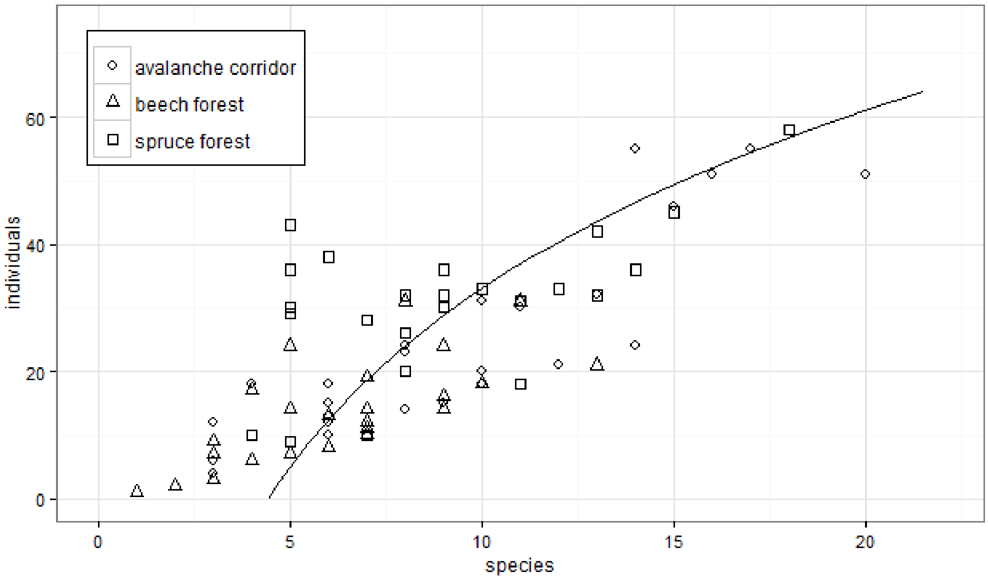

Figure 11: Relationship of the number of individuals and species caught per sampling unit for the whole data set (GLM: $D^2 = 0.56$, $p < 0.001$, $n = 75$)

5.4.2 Influence of temperature and flower abundance on hoverfly activity

As the effects of mean temperature and flower abundance during sampling units differ between habitat types, models were adjusted for each of the habitat types.

Significant effects of flower abundance and temperature on the number of species caught per sampling unit can only be observed for avalanche corridors ($p_{flower} < 0.01$ $p_{temp,linear} < 0.01$, $p_{temp,poly} < 0.05$, $D^2 = 0.52$, $n = 26$). The number of species increases with increasing flower abundance. The effect of temperature on the number of species, however, turns out to be bell shaped (figure 10). Most species are caught at an optimum temperature of 25°C and fewer species are caught at lower and higher temperatures. However, the bell-shaped effect is strongly dependent on a single data point, without which the relationship between temperature and number of species would be negatively linear.

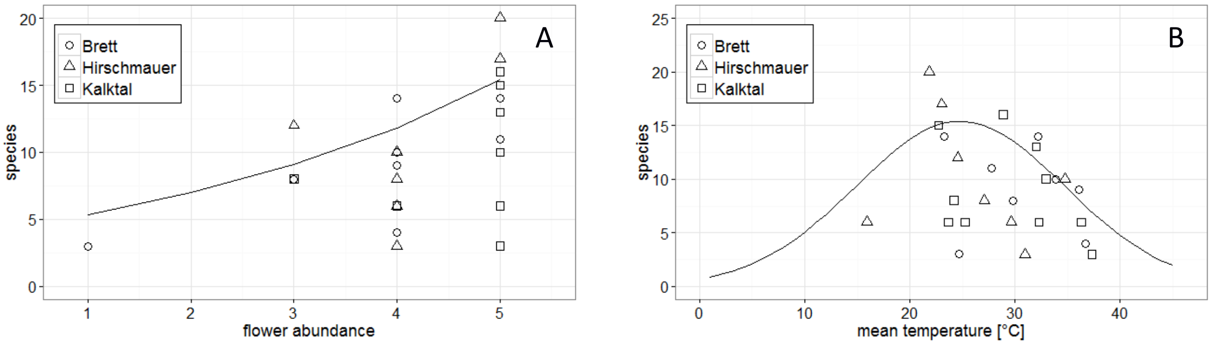

Figure 10: Effects of flower abundance and temperature on the number of species caught in avalanche corridors: **A** shows the relationship of flower abundance and the number of species caught at a constant temperature of 25 °C and sampling duration of 1.5 hours. **B** shows the influence of temperature on the number of species caught at a constant flower abundance of 5 and sampling duration of 1.5 hours (GLM: $p_{flower} < 0.01$ $p_{temp,linear} < 0.01$, $p_{temp,poly} < 0.05$, $D^2 = 0.52$, $n = 26$).

Flower abundance and mean temperature have a significant effect on the number of individuals caught per hour in all three habitat types (avalanche: $p_{flower} < 0.001$ $p_{temp,linear} < 0.001$, $p_{temp,poly} < 0.01$, $D^2 = 0.58$, $n = 26$, spruce: $p_{flower} < 0.05$ $p_{temp,linear} < 0.01$, $D^2 = 0.14$, beech: $p_{flower} < 0.05$ $p_{temp,linear} < 0.01$, $n = 24$, $D^2 = 0.10$, $n = 25$). The number of individuals increases with increasing flower abundance in all models. The effect of temperature, however, differs between the habitat types: In avalanche corridors a bell shaped relationship between temperature and hoverfly abundance (with an optimum temperature of 22°C) can be observed (figure 11). Similarly to the GLM-model explaining the relationship of species and temperature, this relationship depends on a single data point and would be negatively linear without this point. In both forest types the number of individuals and the mean temperature exhibits a linear relationship. Whereas the two variables are positively correlated in spruce plantations (figure 12), they show a negative correlation in beech-(fir)-spruce forests (figure 13). The amount of variation explained by the models for the two forest types is, however, relatively low.

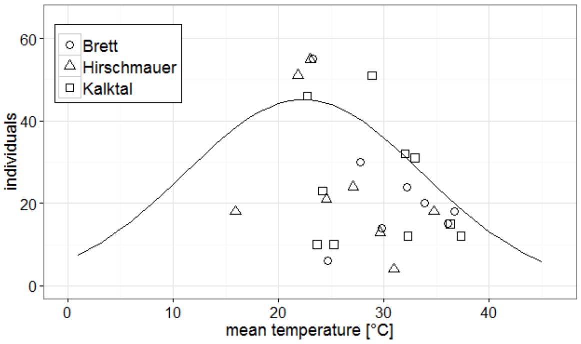

Figure 11: Relationship of temperature and individuals caught at a constant flower abundance of 5 and a sampling duration of 1.5 hours in avalanche corridors (GLM: $p_{flower} < 0.001$ $p_{temp,linear} < 0.001$, $p_{temp,poly} < 0.01$, $D^2 = 0.58$, $n = 26$)

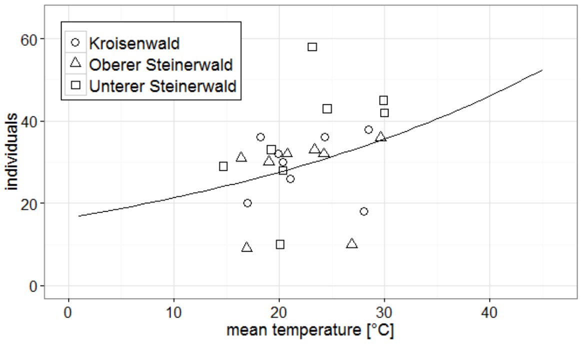

Figure 12: Relationship of temperature and individuals caught at a constant flower abundance of 3 and a sampling duration of 1.5 hours in spruce plantations (GLM: $p_{flower} < 0.05$ $p_{temp,linear} < 0.01$, , $D^2 = 0.14$)

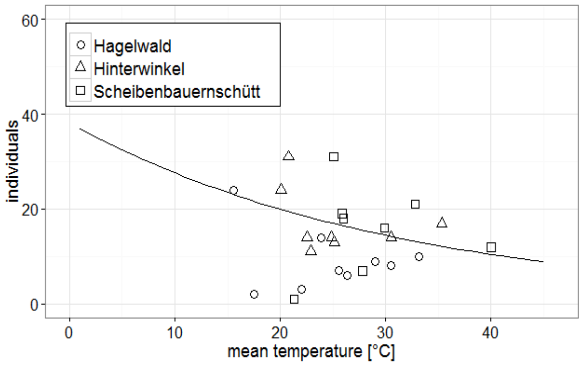

Figure 13: Relationship of temperature and individuals caught at a constant flower abundance of 2 and a sampling duration of 1.5 hours in beech-(fir)-spruce forests (GLM: $p_{flower} < 0.05$ $p_{temp,linear} < 0.01$, , $D^2 = 0.10$, n = 25)

5.5 Seasonal differences in hoverfly activity

Out of 33 species represented with at least ten individuals, seventeen were caught in all four months of data collection. Most of the other sixteen species were missing in May, with the exception of *Microdon devius* and *Sphegina clunipes* which were caught in June and July only.

Seasonal differences were analysed for each habitat type seperately (figure 14). Due to its small sample size May was excluded from statistical tests. The number of species caught per hour only shows significant differences in avalanche corridors (Kruskal-Wallis-Anova: $\chi^2 = 9.2$, $p < 0.01$): Compared to July, fewer species are caught in August (W = 53.5, $p < 0.01$). The number of individuals caught per hour differs significantly in avalanche corridors ($\chi^2 = 12.3$, $p < 0.01$) and spruce plantations ($\chi^2 = 7.5$, $p < 0.05$): In avalanche corridors the number of individuals caught per hour is higher in July than in June (W = 44.0, $p < 0.05$) and August (W = 53.0, $p < 0.01$). In spruce plantations, however, significantly less individuals per hour are caught in July than in August (W = 3.5, $p < 0.01$).

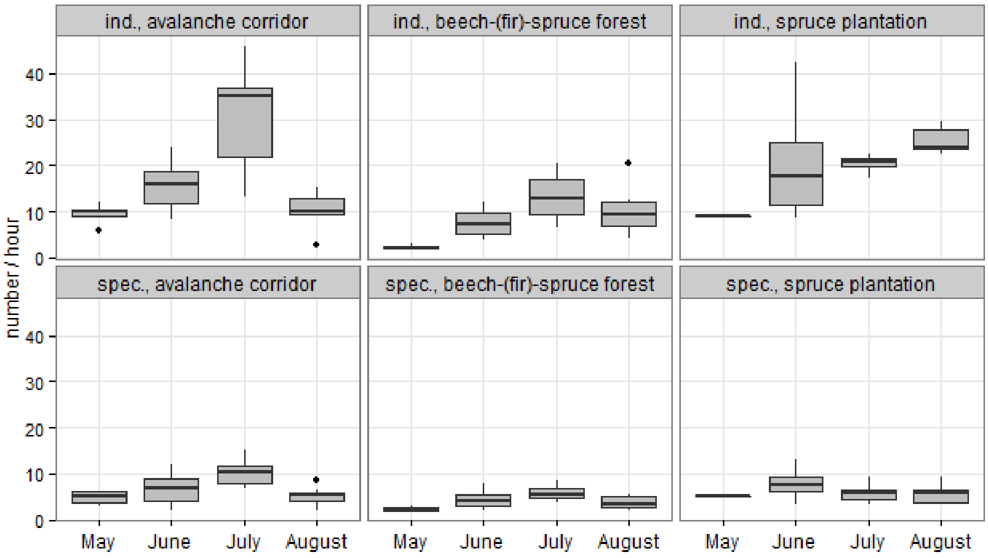

Figure 14: Boxplots of the number of individuals (ind.) and species (spec.) caught per hour in the four months of data collection for each of the habitat types.

5.6 Comparison of sampling methods: butterfly net and coloured pan traps

The two methods differ considerably in the total number of individuals and species caught: 55 species with 464 individuals were found with the help of the butterfly net, whereas only 31 species with 129 individuals could be recorded by means of coloured pan traps.

Furthermore, the species composition differs between the two catching methods (table 7): Only 18 of the caught species are represented in the data sets of both methods. 37 species were exclusively recorded with the butterfly net and 13 with the coloured pan traps. Seven of the species (*Brachyopa vittata*, *Dasysyrphus venustus*, *Heringia* sp., *Lejota ruficornis*, *Melangyna A*, *Sphaerophoria interrupta*, *Xylota ignava*) caught in pan traps were not recorded at all with the butterfly net throughout the whole sampling season from May to August. For both methods *Episyrphus balteatus* is the most abundant species. The dominance structure, however, proves to be more balanced for pan traps and especially the genera *Microdon* and *Xylota* are found more frequently in pan traps than they are recorded with the net.

Table 7: Species collected by means of the butterfly net and coloured pan traps listed from most to least abundant (n = number of recorded individuals, species caught with both methods are written in bold letters, unidentifiable females are listed as *Genus* sp., morphospecies as *Genus* A-G. When the decision between two species could not be made, both are listed).

	butterfly net		**coloured pan traps**	
Rank	**species**	**n**	**species**	**n**
1	***Episyrphus balteatus***	**183**	***Episyrphus balteatus***	**21**
2	***Syrphus vitripennis***	**47**	***Xylota segnis***	**20**
3	***Syrphus torvus***	**45**	***Microdon devius***	**17**
4	***Lapposyrphus lapponicus***	**41**	*Xylota jakutorum*	12
5	*Sphaerophoria scripta*	21	***Eumerus flavitarsis***	**10**
6	*Eristalis tenax*	17	***Merodon rufus***	**7**
7	***Melanostoma scalare***	**16**	***Syrphus torvus***	**5**
8	***Pipizella* sp.**	**15**	***Syrphus vitripennis***	**5**
9	*Chrysotoxum arcuatum*	9	*Xylota ignava*	4
10	***Merodon rufus***	**6**	***Lapposyrphus lapponicus***	**3**
11	*Paragus haemorrhous*	6	***Brachypalpoides lentus***	**2**
12	*Meliscaeva auricollis*	5	***Cheilosia* B**	2
13	*Eristalis similis*	5	***Pipizella* sp.**	**2**
14	***Microdon devius***	**5**	*Brachyopa vittata*	1
15	***Platycheirus albimanus***	**5**	***Cheilosia* A**	1
16	*Dasysyrphus lenensis*	4	***Cheilosia canicularis/himantopus***	**1**
17	*Meliscaeva cinctella*	4	*Dasysyrphus venustus*	1
18	***Cheilosia* A**	**3**	***Eristalis arbustorum***	**1**
19	*Cheilosia* D	3	***Eupeodes corollae***	**1**
20	***Eristalis arbustorum***	**3**	*Heringia pubescens*	1
21	*Eristalis rupium*	3	*Heringia* sp.	1
22	***Parasyrphus lineolus***	**3**	*Lejota ruficornis*	1
23	*Parasyrphus macularis*	3	*Melangyna* sp.	1
24	*Syrphus ribesii*	3	***Melanostoma scalare***	**1**
25	***Cheilosia canicularis/himantopus***	**2**	***Parasyrphus lineolus***	**1**
26	*Didea fasciata*	2	*Pipiza* A	1

27	*Eristalis jugorum*	2	*Pipizella pennina*	1
28	*Eupeodes* A	2	***Platycheirus albimanus***	**1**
29	***Eupeodes corollae***	**2**	*Rhingia borealis*	1
30	*Myathropa florea*	2	*Sphaerophoria interrupta*	1
31	*Rhingia campestris*	2	*Xanthogramma laetum*	1
32	***Xylota segnis***	**2**	*Xylota florum*	1
33	*Baccha elongata*	1		
34	***Brachypalpoides lentus***	**1**		
35	***Cheilosia* B**	**1**		
36	*Cheilosia* C	1		
37	*Cheilosia* E	1		
38	*Chrysotoxum bicinctum*	1		
39	*Epistrophe grossulariae*	1		
40	***Eumerus flavitarsis***	**1**		
41	*Ferdinandea cuprea*	1		
42	*Helophilus pendulus*	1		
43	*Helophilus trivittatus*	1		
44	*Melangyna cincta*	1		
45	*Paragus albifrons*	1		
46	*Pipizella viduata*	1		
47	*Platycheirus parmatus*	1		
48	*Platycheirus scuatus-group*	1		
49	*Scaeva selenitica*	1		
50	*Sericomyia lappona*	1		
51	*Sphaerophoria laurae/infuscata*	1		
52	*Sphegina clunipes*	1		
53	*Sphegina sibirica*	1		
54	*Volucella bombylans*	1		
55	*Xanthandrus comtus*	1		

6. Discussion

6.1 Species richness of the NP Gesäuse on a landscape level

A considerable number of 102 species could be recorded in the NP Gesäuse. This represents about 11.3 % of all species listed for Europe (Speight, 2012). One of these species, *Xanthogramma stackelbergi*, has been confused with a similar species (*X. pedissequum*) in the past. To my knowledge, the present study is the first record of this species in Austria. However, its occurrence is not surprising, as it has already been confirmed from neighbouring countries such as Switzerland and southern Germany (Speight, 2012). Unfortunately, a red list of endangered hoverfly species does not exist for Austria, which makes it difficult to draw conclusions on the degree of endangerment of the species recorded. However, as a substitute the red list of endangered hoverflies of Bavaria was consulted for this purpose: Among the recorded species one is listed as critically endangered, two as vulnerable and three as data deficient, but most likely endangered. Seven species were classified as near threatened and two as data deficient (Dunk et al., 2003). Two of the listed species found in the NP Gesäuse – *Lejota ruficornis* (critically endangered) and *Callicera aenea* (data deficient, but most likely endangered) – are probably closely associated with dead wood during their larval development (Speight, 2012). Furthermore, the overall number of stenoecious forest species and saproxylic species is relatively high, which suggests that the forests of the national park Gesäuse also represent a suitable habitat for other dead wood associated arthropod groups that comprise several rare and endangered species. Therefore, the maintenance of the national park's forest ecosystems has to be considered of high conservational value.

However, it proves to be difficult to compare the present results with studies in other regions, as sampling effort and methods vary considerably. Nevertheless, the comparison with similar studies can aid in the interpretation of the present results, when these factors (effort and methods) are taken into account: Austria's highest species richness of hoverflies was recorded in the Wildnisgebiet Dürrenstein (Waitzbauer, 2001), which contains the country's last primeval forest, the Rothwald. A total of 168 species, including 29 (17.3%) stenoecious forest species and 26 (15.5 %) saproxylic species could be recorded. This study was conducted over a period of two years, included data of previous studies, sampled a variety of different habitat types and applied Malaise traps as well as butterfly nets. Compared to the present study the sampling of the Wildnisgebiet Dürrenstein can be considered as far more complete. As sampling in the NP Gesäuse was restricted to predefined sites, more hoverfly species can be expected to occur in other parts and habitats, such as the floodplain forest along the Enns or alpine meadows at higher altitudes. It is also likely that some species might not have been caught in 2013 due to fluctuations in population size over the years. During one day of sampling in the course of the GEO Tag der Artenvielfalt 2014 new species could be recorded for the Hinterwinkel region. They included a conspicuous species that was observed quite frequently in 2014, but was not recorded in 2013 (personal observations). Furthermore, Waitzbauer (2001) applied Malaise traps in addition to the butterfly net, which increases the chance of finding rare species. Two other hoverfly studies in Germany, which covered two and three years respectively, resulted in a total of 99 species recorded (Messeler Forst: Hauser and Geller-Grimm, 1996; Manganfallgebirge: Löhr, 1989). Considering differences in effort between the studies, the number of recorded hoverfly species suggests that the NP Gesäuse hosts a diverse hoverfly fauna.

On the one hand, the high species richness recorded can be attributed to the national park's variety of different habitat types – including forests, avalanche corridors and mountain pastures – that occur in close proximity and on the other hand it might be due to the high quality of these habitats. Hoverfly diversity is known to benefit from a mosaic of open and closed landscapes (Sommagio, 1999): The semi-natural forests offer structural diversity and contain a high amount of dead wood, which represents an indispensable resource for saproxylic hoverflies (Jonsson, 2005). Avalanche corridors are rich in herbaceous flowering plants and offer an ample food source for adult hoverflies. Additionally, mountain pastures can contribute to hoverfly diversity as some species, such as the genera *Eristalis* and *Rhingia*, develop in cow dung (Speight, 2012).

6.2 Comparison of local hoverfly assemblages

Cluster analysis and non-metric multidimensional scaling showed that the hoverfly assemblages of the three habitat types exhibited distinctive differences: Hoverfly assemblages of sites of the same habitat type resembled each other more closely than those of sites of different habitat types. This indicates that each habitat type hosts a specific hoverfly fauna, which reflects its biotic and abiotic conditions.

Avalanche corridors differ more strongly in their microclimatic conditions from the two forest types than the two forests from each other. As open habitats they are characterised by an ample herbal vegetation and exhibited a significantly higher flower abundance than the two forest types. Thus, they are expected to host a hoverfly assemblage that is distinctively different from forests, which is confirmed by the results of cluster analysis: All three avalanche corridors form an open habitat clade which opposes the forest clade containing both beech-(fir)-spruce forests and spruce plantations. Furthermore, characteristic species for the open habitat avalanche corridor could be identified. All indicator species for avalanche corridors – with the exception of *Scaeva pyrastri* – are known to prefer open areas. *Sphaerophoria scripta* and *Eristalis arbustorum* represent two anthropophilic species that occur in many kinds of open habitats, whereas *Merodon rufus*, *Pipizella divicoi* and *Paragus haemorrhous* are characteristic for open areas in forests (Speight, 2012). It has to be noted that the abundance of *Pipizella divicoi* and *Paragus haemorrhous* has possibly been overestimated by assigning females of these genera, which cannot be determined to species level, to both species. The description of the species' ecological preferences in the literature, however, is consistent with the results of this study. All avalanche corridors are surrounded by forests and can therefore be regarded as open areas in forests. Thus the presence of these species can be regarded as a good indicator for open habitats in close vicinity of forests. *Scaeva pyrastri*, in the contrary, is described as a eurytopic species that does not exhibit preferences for specific habitats (Speight, 2012). Usually it can be encountered quite frequently and almost anywhere, even at higher altitudes (personal observations). During the sampling period, however, only three individuals could be recorded quite late in the season (August). Seeking food, they were probably attracted to the avalanche corridors by their high flower abundance and per chance one individual was caught on each avalanche corridor site. Due to the small number of caught specimens it is likely that *Scaeva pyrastri* also occurred in other habitat types, but could not be recorded there. The collected data, however, does not offer any explanations for the unusually low number of encountered individuals.

The species composition of the two forest habitats differed as well. Although they both represent closed habitats, differences in biotic and abiotic conditions relevant for hoverflies could be recorded. The mean temperature during the sampling units was significantly lower in spruce plantations than in beech-(fir)-spruce forests, whereas the mean flower abundance was significantly higher in spruce plantations. The management strategies of the national park might serve as an explanation for the somewhat surprisingly high flower abundance in spruce plantations: The former spruce plantations have been thinned to allow for the reestablishment of deciduous trees. As a consequence more light reaches the ground, which leads to a higher flower abundance. In beech-(fir)-spruce forests, in the contrary, the fallen leaves impede the growth of flowering plants in large areas, which leads to a lower flower abundance, although a lot of light reaches the ground.

For both forest types, habitat specific species could be identified. Among the five indicator species for spruce plantations two – *Pipiza quadrimaculata* and *Sphegina clunipes* – were exclusively found in this habitat type, suggesting that they prefer the cool and shady conditions of the forest, which is also supported by other records: Whereas *Pipiza quadrimaculata* also exhibited preferences for coniferous forests in previous studies, *Sphegina clunipes* was found frequently in deciduous and coniferous forests (Speight, 2012). Its absence in beech-(fir)-spruce forests in the current data could be explained by differences in flower abundance. Due to their higher flower abundance spruce plantations probably represented a more attractive habitat for these forest species in the contrary to the beech-(fir)-spruce forests, where a suitable food source was very scarce. As *Sphegina clunipes* represents a very small species and a less agile flier, it can be expected to be less mobile than other bigger species and is therefore less likely to cover long distances in search for food. Consequently, it probably stays close to its food source. In contrary to *Pipiza quadrimaculata* and *Sphegina clunipes*, the other three indicator species for spruce plantations could be found in all three habitat types. In especially high relative abundances, however, they can act as indicators for spruce plantations: *Lapposyrphus lapponicus* represents a typical species for montane conifer plantations (Speight, 2012). It is, however, a very agile flyer and can therefore be found in adjacent habitats as well. *Episyrphus balteatus* and *Platycheirus albimanus* represent two anthropophilic species which can cope with a broad variety of ecological conditions and whose larvae feed on aphids (Speight, 2012). In spruce plantations this larval food source can be expected to be available in high numbers, which could have contributed to the high abundances of these species in this habitat type.

Eumerus flavitarsis represented the only indicator species for beech-(fir)-spruce forests. It was repeatedly caught in all three sites and only once in a spruce plantation, which is consistent with Speight's (2012) findings: He also reported a preference for deciduous forests in *Eumerus flavitarsis*. The lack of other indicator species might lead to the conclusion that beech-(fir)-spruce forests host a less specific hoverfly fauna than the other habitat types and are therefore less important for hoverfly conservation. However, most species known to depend on dead wood of deciduous trees are rare and therefore less likely to be spotted and caught. Additionally, some of these species are known to spend most of their time high up in the canopy and only occasionally descend to the forest floor (Speight, 2012). Due to the considerable amount of dead wood in the mixed forests of the national park it can be expected that some of these species occur in this habitat type. Their scarcity, however, lead to a very low catch rate of only one or two individuals, which does not suffice to be identified as an indicator species. This assumption is supported by the record of *Callicera aenea*, which is associated with ancient deciduous wood and whose larvae are probably saproxylic. It was caught only once close to the beech-(fir)-spruce forest Scheibenbauernschütt, but outside of the sampling area, and was therefore not included in the analyses. As several species associated with deciduous forests have been recorded during the sampling season, the beech-(fir)-spruce forests can be expected to host a specific hoverfly fauna, despite their low number of indicator species. An additional explanation for the low number of indicator species for beech-(fir)-spruce forests could be that the hoverfly fauna of the three sites exhibited strong differences: A high amount of variation in species richness and significant differences in hoverfly activity between the sites of beech-(fir)-spruce forests were revealed. However, cluster analysis and non-metric multidimensional scaling showed that the composition of hoverfly assemblages of the three sites resembled each other.

Habitat types not only differed in their species composition, but also in abundance and species richness of hoverflies. The highest mean species richness could be observed in avalanche corridors. The number of species recorded in each of the avalanche corridors was even higher than that of all forest sites. Only marginal differences in species richness and hoverfly activity were found between the sites, indicating that all three sites resemble each other in their major structural and microclimatic parameters relevant for hoverflies. Representing an open habitat type, avalanche corridors are rich in herbaceous flowering plants, which offer food for adult hoverflies. Besides open habitat specialists, eurytopic species and also mobile species from adjacent forests are likely to be attracted to the avalanche corridors in search for food. As a result, a high variety of species could be encountered in these habitats. Furthermore, it has to be noted that avalanche corridors represent a 2D-habitat whose microhabitats could all be sampled, whereas in 3-dimensional forests only the hoverfly fauna of the ground was taken into account. The canopy, however, was not sampled at all. Although a lot of species can be found in the canopy as well as on the ground, a few species seem to be associated with the canopy (Birtele and Hardersen, 2012). Consequently, it can be expected that sampling of the canopy would lead to the discovery of additional species, which would increase species richness of spruce plantations and beech-(fir)-spruce forests in comparison to avalanche corridors.

Previous sampling in Kalktal has already indicated that the avalanche corridors of the NP Gesäuse represent a suitable habitat for flower visiting insects and host a diverse arthropod fauna: In the course of the GEO-Tag der Artenvielfalt 2010, whose sampling areas also included adjacent forests and the banks of the river Enns, 495 species of various animal taxa (Kreiner, 2011), including 180 Lepidoptera species (Habeler, 2011), could be recorded. The results of the present study confirm that not only Kalktal, but also other avalanche corridors represent important habitat types that host a considerable amount of the national park’s animal species.

Although most species could be recorded in avalanche corridors, spruce plantations exhibited the highest mean hoverfly abundance, which contradicts the GLM explaining the relationship between the number of species and individuals caught during a sampling period. It indicates that the number of individuals recorded positively correlates with the number of species. However, this model does not completely explain the variance of the data, meaning that other factors than the number of species additionally affected the number of individuals caught per hour. As the summer in 2013 was one of the hottest and driest ever recorded (ZAMG, 2013), sampling often took place on extremely warm summer days. On such days hoverfly activity seemed to be lower than usual in avalanche corridors. In spruce plantations, which exhibited the lowest mean temperature during sampling units, however, an increased hoverfly activity could be observed (personal observations). The uncomfortably high temperature in avalanche corridors could have caused habitat unspecific species to seek shelter in close and cooler spruce plantations, where extremely high temperatures were not reached: The temperatures in this habitat type were always lower than in the surrounding areas, turning them into a retreat from the heat for habitat unspecific species. Open habitat species, however, were either still active at high temperatures or hid in the vegetation. Thus the number of individuals increased in spruce plantations, whereas the number of species stayed the same. Maier and Waldbauer (1979) also observed that hoverflies switched to forests offering cooler temperatures on very hot days. Furthermore, this assumption is supported by the GLMs including the effect of temperature on the number of individuals and species caught per hour: In spruce plantations mean temperature is positively related to the number of individuals caught per hour, but the number of species caught per hour did not exhibit a significant correlation with the mean temperature. In avalanche corridors, however, the number of species and individuals recorded per hour decreased at very high temperatures.

Beech-(fir)-spruce forests exhibited the lowest mean hoverfly abundance and species richness. Furthermore, the numbers of individuals and species caught per hour were significantly lower in beech-(fir)-spruce forests than in the two other habitat types. These results might appear surprising and contradict several studies on other animal taxa, which found higher diversity in native forests (e.g.: Elek et al., 2001, Sweeney et al., 2010). However, adult hoverflies represent flower visiting animals, which depend on nectar as their primary food source. The low hoverfly activity and the resulting low overall hoverfly abundance and species richness can, therefore, probably be explained by the low flower abundance in this habitat. Furthermore, temperatures in these forests were high compared to spruce plantations and a negative relationship between temperature and individuals caught per hour could be recorded in beech-(fir)-spruce forests. Due to the relatively high temperatures adult hoverflies did not use the beech-(fir)-spruce forests as a retreat from the heat, which also contributed to the low hoverfly abundance in this habitat type. It is also important to consider that the spruce plantations of this study are no longer harvested (Holzinger and Haseke, 2009), but managed by the national park, which entails higher amounts of dead wood and better light conditions than in commercially used plantations. These management strategies might have had a positive effect on the local hoverfly fauna. An increased species richness of hoverflies and other insect groups such as hymenopterans, butterflies and beetles after thinning of conifer plantations – which was also part of the management strategies – has already been reported from other studies (e.g.: Taki et al., 2010; Maleque et al., 2007).

However, in the contrary to spruce plantations, beech-(fir)-spruce forests exhibited significant differences in the number of species and individuals caught per hour. Total species richness also varied more strongly among the sites than in the other habitat types. In Scheibenbauernschütt species richness was even higher than in two spruce plantations. This high variation makes it difficult to draw general conclusions on the species richness of beech-(fir)-spruce forests. Differences in species richness and hoverfly abundance might have been caused by differences in environmental factors between the sampling sites. Mean temperature and flower abundance exhibited some variation, but no significant differences. Another important factor, which was not recorded during this study, is canopy closure: Hagelwald, hosting fewest hoverfly species, was situated far from a forest road and only contained small clearings. The Hinterwinkel site, which exhibited intermediate species richness, was adjacent to a forest road and Scheibenbauernschütt, which contained the largest clearings, hosted most hoverfly species. Although these observations point towards a relationship between canopy closure and species richness, this assumption cannot be statistically supported as this study does not provide quantitative data on the canopy closure of the sites. However, previous studies on hoverflies (Humphrey et al., 1999) and hymenopteran flower visitors (Winfree et al. 2007; Taki et al., 2008) have shown that the number of species increases in disturbed forests, where a lot of light reaches the ground. Further research would be needed to fully explain differences in species richness and hoverfly activity in beech-(fir)-spruce forests.

Species richness, however, nearly always represents an underestimate of the true number of species, because sampling effort – especially of insect taxa in complex habitats – is rarely complete. As sampling in the course of this study was limited in time and space, further sampling effort can be expected to lead to the records of additional species for each of the habitat types. Although sampling effort was the same for all nine sites, sampling completeness might differ between them. Therefore, species richness alone does not represent an appropriate variable to compare the number of species that can be found per sampling site. To account for differences in sampling completeness Jack1 was calculated as an estimator of true species richness. Generally, the patterns of estimated species richness resemble those of observed species richness. Avalanche corridors exhibited the highest mean estimated species richness and the lowest sampling completeness (on average 20.46 additional species were estimated), whereas beech-(fir)-spruce forests showed the lowest mean estimated species richness and the highest sampling completeness (on average 11.96 additional species were estimated). However, sampling completeness varied considerably among beech-(fir)-spruce forest sites: The estimated species richness of Scheibenbauernschütt lies 22.5 species above the observed value and is much higher than the estimated species richness of all spruce plantations. Differences in observed species richness between beech-(fir)-spruce forests are therefore most likely not caused by differences in sampling completeness. On the contrary, differences in sampling completeness lead to more pronounced differences in estimated species richness, which supports the assumption that differences in environmental factors such as canopy closure between sites exerted a considerable influence on species richness and hoverfly abundance.

Inverse Simpson's index and evenness provide additional information on the structure of hoverfly assemblages in habitat types. Hoverfly assemblages in avalanche corridors exhibited the highest evenness and diversity (inverse Simpson's index). Although spruce plantations had more species than beech-(fir)-spruce forests, they were least diverse. This habitat type was highly dominated by two species (*Episyrphus balteatus*, *Lapposyrphus lapponicus*) and thus showed the lowest mean inverse Simpson's index and the lowest evenness. To some extent the spruce plantations' role as a retreat during hot summer days probably contributed to the highly unbalanced dominance structure of this habitat type. However, the two mentioned species were also extremely dominant at moderately high temperatures from July to August. The present data suggests that there might be a relationship between evenness and openness of the habitat types: Avalanche corridors representing the most open habitat type exhibited the highest evenness. Furthermore, beech-(fir)-spruce forests differed in evenness. Scheibenbauernschütt, which contained the largest clearings, exhibited the highest evenness, whereas Hagelwald, which represented the least open site, showed the lowest evenness. This, however, remains a speculation and further research is needed to clarify the relationship of openness and evenness.

Seasonal patterns of hoverfly activity also showed differences between habitat types: In all habitat types fewest individuals and species were caught in May, at the beginning of the season, because some species do not emerge before June or July (Speight, 2012). However, in avalanche corridors – in the contrary to the two forest types – significantly less species per hour were caught at the end of the season (August), when some species could not be found anymore at all or were only present in low abundances. Most species that were frequently found in the two forest types can still be found late in the season, which explains why no differences in species caught per hour were found between the months of data collection in these habitat types. Spruce forests, however, showed significant differences in individuals caught per hour. In August hoverflies were significantly more active than in July. The mean temperature during sampling units was lower in July than in August. During hot days in August hoverflies spent more time in the cool spruce plantations, leading to a higher hoverfly activity in spruce plantations during this month. The mean temperature also serves as an explanation for the significantly higher hoverfly activity in July than in June in avalanche corridors. The mean temperature was lower in July; thus more hoverflies per hour were caught in that month than in June, when the insects avoided the hot open areas.

Although the low sample size (three sites per habitat type) does not allow statistically supported statements about differences in species richness and individual abundance between habitat types, there is a clear trend that avalanche corridors host more species and a more diverse hoverfly assemblage than the two forest ecosystems. However, due to a high variation among sites of the same habitat type, especially in beech-(fir)-spruce forests, none of the two forest types can be attributed a higher species richness than the other. When using hoverflies as bioindicators for the assessment of the quality of forest ecosystems, the number of saproxylic species rather than total species richness was reported to play an important role (Smith et al., 2008). When comparing the abundances of larval lifestyles relative to the number of species, unspecific zoophagous larvae clearly represented the dominant category, whereas only few species could be assigned to the remaining categories. This is, however, the case in most hoverfly assemblages and does not have great significance in assessing habitat quality. Even in the Wildnisgebiet Dürrenstein most of the species recorded possessed zoophagous larvae (Waitzbauer, 2001). In the NP Gesäuse most of the saproxylic species were found in beech-(fir)-spruce forests, both relative to the number of species and in total number, which indicates that they represent intact ecosystems that provide a habitat for a variety of forest specific species.

To conclude, all three habitat types exhibited characteristic hoverfly assemblages that were distinctly different from each other and contained habitat specific species. No habitat type can fully replace another as a habitat for hoverflies, but all of them together contribute to the high overall species richness of the NP Gesäuse. Differences in species richness are less clear than in species composition, especially between the two sampled forest types. The former spruce plantations of the NP Gesäuse have proven to be a suitable habitat for hoverflies and host a variety of different species, which reflects the positive effects of the national park's management strategies. On the other hand the high number of saproxlic species in the semi-natural beech-(fir)-spruce forests as well as the species associated with deciduous wood that were found outside of this habitat type and that partly represent rare and endangered species emphasize the high conservational value of these semi-natural forests.

However, the data also demonstrates that adult hoverflies of most species are very mobile animals that readily move between habitat types, when they can be found in close proximity. Different habitat types must therefore not be considered as completely separated from each other. They rather complement each other in many cases. One habitat, for example, provides the food source for adult hoverflies, while the other offers suitable larval microhabitats.

6.3 Comparison of sampling methods

Sampling with the butterfly net proved to be clearly more efficient than capturing hoverflies with coloured pan traps. With the butterfly net, considerably more species and individuals were caught during a sampling day than with the pan traps. The effort of one sampling day is comparable between the two methods, as setting up and collecting the pan traps took approximately as long as a sampling unit with the butterfly net. The low capture rate of pan traps can probably be attributed to a low ability of actually capturing attracted individuals rather than a failure to attract hoverflies at all: I could observe several specimens that approached the pan traps, stopped directly above them, descended until a few centimetres above the water surface and flew away after a few seconds. Due to their excellent flight abilities syrphids are able to inspect the traps closely before landing, rendering them less likely to be caught in the traps than insects without the ability to hover. Wilson et al. (2008) offered a potential alternative explanation for the low efficiency of pan traps: A decreasing capture rate of bees could be observed at high flower abundances, as real flowers seemed to be more attractive to the insects than artificial pan traps. The data of the present study, however, shows the opposite trend: Most individuals were caught in avalanche corridors with the highest flower abundance, and less individuals were recorded in spruce plantations with a lower flower abundance, but a similar or higher hoverfly activity. The catching rate rather seemed to be influenced by hoverfly activity, because catching rates were close to zero at the beginning of the season and on hot summer days in avalanche corridors, when hoverfly activity was very low. Prolonging the time of exposure of the coloured pan traps might lead to higher efficiency, as the time needed for setting up and collecting the traps stays the same, whereas probably more individuals are caught. However, Franke and Zucchi (1996), who investigated hoverfly assemblages of meadows and exposed coloured pan traps for a week, also reported a low efficiency of pan traps compared to the butterfly net.

Apart from efficiency, bias has to be considered as well. Differences in species composition between the two methods clearly showed that they differ in their bias. Of course all catching methods are biased to some extent, first of all by hoverfly activity. Resting hoverflies will not be captured by pan traps or any other kind of trap and are less likely to be noticed when sampling with the butterfly net. Coloured pan traps are more likely to catch hungry individuals (Hickman et al., 2001) and composition and amount of caught species strongly depend on the colour of the traps, as different species exhibit different colour preferences (Haslett, 1989). Also flight abilities influence catch rates: Especially species which do usually not exhibit the typical hovering behaviour were caught in higher abundances in pan traps than with the butterfly net. To some extent, however, good fliers are also less likely to be caught with the butterfly net than poor fliers. On the other hand conspicuousness influences the chance of being detected during sampling with the butterfly net. However, this bias can be reduced by an experienced catcher, who also looks out for inconspicuous species.

The decision which method or which combination of methods should be used depends on the aim and research question of the study. Pan traps do not exclusively catch hoverflies, but also all other kinds of flower visitors (Vrdoljak and Samways, 2012). When only hoverflies are sampled, this by-catch represents a major disadvantage of pan traps. In this study, catch rates for hymenopterans in avalanche corridors and other dipterans in spruce plantations were much higher than for hoverflies. Especially in national parks by-catch should be avoided, because rare and endangered species could be negatively influenced. Therefore, the benefits and drawbacks of applying pan traps have to be weighed with care. For species inventories of hoverflies using both methods will probably yield better results than sampling with the butterfly net alone. For comparative studies of species richness and hoverfly abundance studies, where a complete list of species is not of primary importance, on the other hand, the disadvantages of pan traps outweigh the benefits.

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9. Appendix

9.1 List of morphospecies

Table 8: List of morphospecies (MS) and their characteristic traits

genus	MS	Traits
Cheilosia	A	eyes haired, sides of facial knob without hair, legs partly pale
Cheilosia	B	eyes bare, sides of facial knob without hair, legs almost completely black
Cheilosia	C	eyes bare, sides of facial knob without hair, legs partly pale
Cheilosia	D	eyes haired, sides of facial knob without hair, legs almost completely black, coxa 1 with hornlike projection
Cheilosia	E	eyes haired, sides of facial knob without hair, legs almost completely black, only middle segments of tars 1 pale
Cheilosia	F	eyes haired, sides of facial knob without hair, legs almost completely black, coxa 1 without hornlike projection
Cheilosia	G	eyes haired, sides of facial knob with long hairs, legs black
Eupeodes	A	alula partly bare, spots on tergites 3 and 4 do not reach the side margin, scutellum yellow and black haired
Eupeodes	B	alula entirely haired, lateral margin of tergite 5 yellow, front margin of spots on tergites not straight
Eupeodes	C	alula entirely haired, lateral margin of tergite 5 black
Eupeodes	D	alula entirely haired, lateral margin of tergite 5 yellow, front margin of spots on tergites nearly straight
Melangyna	A	not *Melangyna cincta*
Merodon	A	in size similar to *Merodon rufus*, but tergite 2 without yellowish markings
Pipiza	A	implantation of antennae on upper half of head, females with dust spots on frons
Platycheirus	A	spots on tergites yellow, third antennal segment partly yellow
Platycheirus	B	spots on tergites yellow, third antennal segment entirely black

9.2 Rank abundance curves

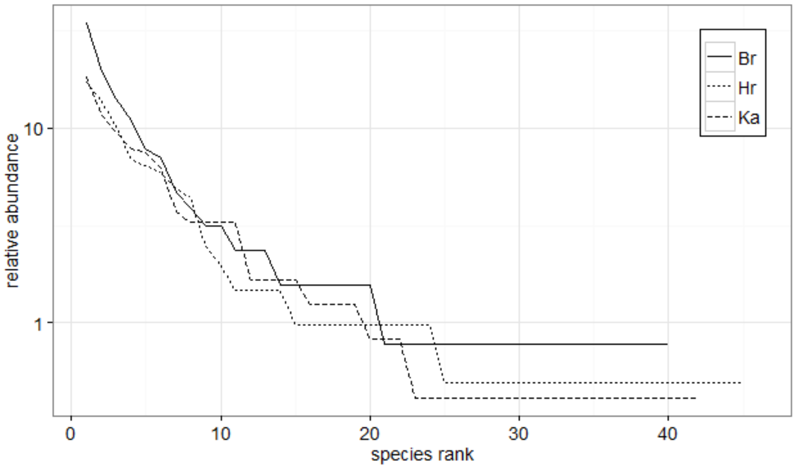

Figure 15: Rank abundance curves for the three avalanche corridor sites (Br = Brett, Hr = Hirschmauer, Ka = Kalktal).

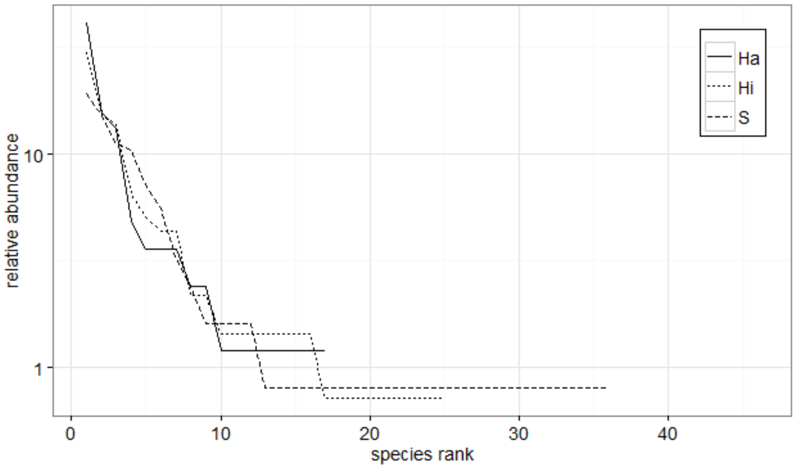

Figure 16: Rank abundance curves for the three beech-(fir)-spruce forests sites (Ha = Hagelwald, Hi = Hinterwinkel, S = Scheibenbauernschütt).

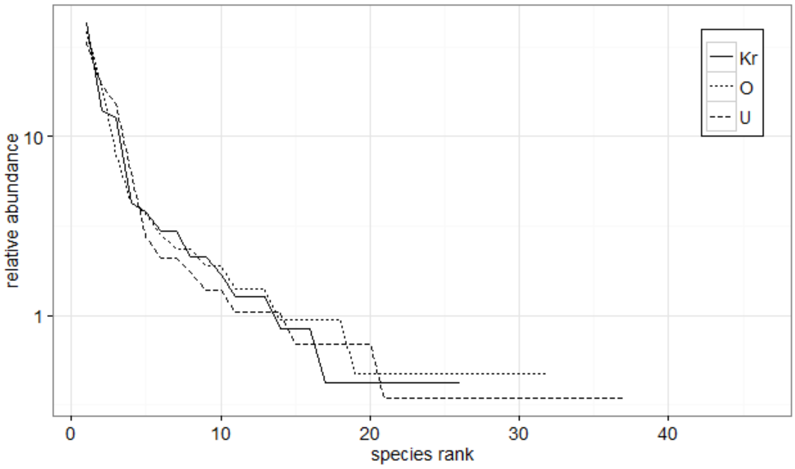

Figure 17: Rank abundance curves for the three spruce plantation sites (Kr = Kroisenwald, O = Oberer Steinerwald, U = Unterer Steinerwald).

9.3 Curriculum Vitae

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Work Experience

07/2012 – 09/2012	Internship at Nationalpark Hohe Tauern
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Training & Field Courses

2014	Field course: GIS field methods & behavioural ecology and Diversity of Neotropical amphibians, French Guyana
2013	Course: Determination of Chironomidae
	Morphology and preparation of native birds
2012	Field course: Methods in biodiversity research, NP Donauauen
	Course: Determination of native Apidae
2011	Field course: Zoological field studies in the Austrian Alps
	Field course: Flower visiting insects, NP Hohe Tauern
	Laboratory course: Morphology and evolution of Arthropoda
2010	Volunteer at Auring: bird ringing, Hohenau an der March
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