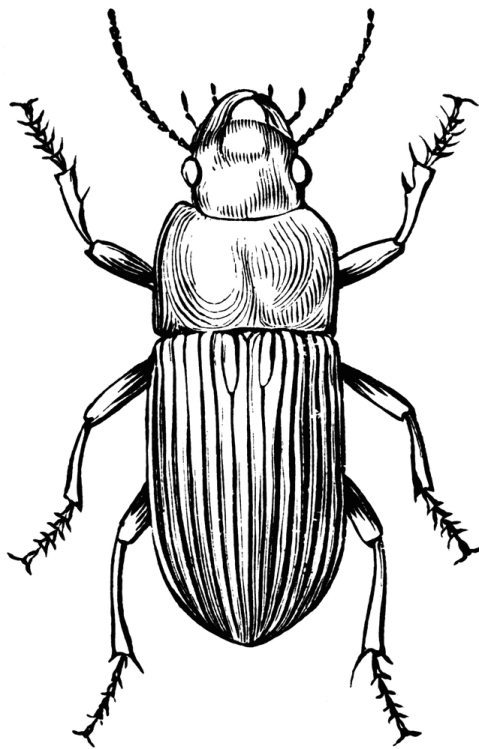


Communities, species diversity, biomass and ecological traits of carabids in the wooded pastures

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1 Abstract

Wooded pastures are greatly shaped by pastoral and silvicultural activities. Depending on abiotic factors and the intensity of human activities, the appearance and composition of wooded pastures vary considerably. There is therefore not one type of wooded pasture, but a multitude. With their sparse tree cover, semi-woodlands are an ecotone between open area pastures and forests. Transitional habitats often have a relatively high species diversity typical of the interface between two habitats. Nevertheless, wooded pastures are sometimes considered as semi-natural habitats, as these environments are mostly forged by human activities. Intensification of these activities or abandonment is a threat to wooded pastures. The aim is therefore to gain a better understanding of the ecological similarities and differences between wooded pastures and the adjacent environments: forests and non-wooded pastures. The elements tested in the three habitats are community composition, diversity indices, biomass and ecological traits in relation to environmental variable and categories to see if wooded pasture shows certain patterns compared to the other two habitats. To this end, the family *Carabidae* was collected with pitfall traps in the 29 study sites. Ground beetle communities in wooded pastures largely encompass those in open pastures and forests, although some species remain absent or found only in semi-wooded areas. The diversity indices indicate that wooded pastures and open pastures have an equivalent level of diversity and have significantly higher diversity than forests. Increasing the Biodiversity Promoting Areas leads to a greater diversity of ground beetles. Tree cover significantly influences the ecological traits of ground beetles. Areas with high tree cover favour brachyptera and wingless ground beetles, as well as hygrophilic individuals. More open areas include individuals with more developed wings and generally more xerophilic tendencies. The size and also the biomass of the carabid beetles grow with increasing tree cover and vice versa. In conclusion, wooded pastures are an important ecotone, ensuring a gradual change of habitats between open areas and forests, and where a wide range of species from both habitats are found. Diversity is higher in open and semi-wooded areas than in forests, but biomass is positively correlated with tree cover, and forests have thus a higher biomass than in more open areas. Wooded pastures are an encouraging example of human-influenced habitats that retain interesting ecological characteristics for ground beetles.

2 Keyword

Ground beetles, pitfall traps, Jura mountains, ecotone, carabidae, silvopastoralism, agroforestry, conservation nature.

3 Introduction

In the Jura mountain range, wooded pastures develop in a transition zone (*saltus*) between the cultivated areas (*ager*) around the villages and the forests (*sylva*) (Gallandat et al., 1995). These wooded pastures are also a common feature of Jura culture and serve as a place of relaxation and recreation in all seasons (Buttler et al., 2012). This type of biotope is largely shaped by pastoral and forestry activities and is sometimes referred to as a semi-natural habitat (Roellig et al., 2016). Depending on the intensity of these two activities, wooded pastures vary in appearance between two opposite habitats: sparsely wooded pasture, which

is not very productive for silviculture, and densely wooded pasture, which is more productive for silvicultural yield (Mosquera-Losada et al., 2009). The different types of management, ranging from extensive to intensive agriculture, add in addition an ecological gradient that impacts biodiversity. Consequently, the multiple use and management of wooded pastures by humans and the environmental variables, specific to each location, create defined ecological niches that modify biodiversity from one place to another. Thus, there is no single type of wooded pasture, but a multitude (Gallandat et al., 1995).

Therefore, wooded pastures generate a certain environmental heterogeneity, among others thanks to the scattered trees that can be considered as keystones, essential for a wide range of organisms (Fischer et al., 2010). These semi-wooded environments have various ecological niches that may contain more varied floristic and faunistic communities than other more homogeneous habitats (Gillet and Gallandat, 1996). A high level of biodiversity is essential for the stability and sustainability of any ecosystem (Tilman et al., 2014). The meta-analysis by Torralba et al. (2016) demonstrates that European agroforestry, including silvopastoralism in wooded pastures, enhances biodiversity. Although several studies have shown the positive effect of heterogeneity generated by silvopasture, Tews et al. (2004) highlights that the ecological effects of habitat heterogeneity would also decrease the species diversity of certain taxa. In this respect, the meta-analysis by Mupepele et al. (2021) shows that silvopasture has no benefit for biodiversity compared to forests, pastures or abandoned silvopastures. The semi-open environment is considered as an ecotone, allowing both open and forest species to coexist (Diaz et al., 2013). However, Tews et al. (2004) question at what point internal habitat heterogeneity becomes fragmentation, i.e. how to distinguish the difference between vegetation structure within the habitat and between habitats. In addition, the question arises whether the negative or positive effects of heterogeneity (or fragmentation) influence the overall species diversity in wooded pastures. Indeed, depending on the ecological habits of the species, some are specialised in purely forest or open habitats (Thiele, 2012). Other species have a greater capacity to adapt to their habitat and can be found in semi-wooded, forest or open environments. It cannot be excluded that some species are only found in ecotone environments, such as wooded pastures. Furthermore, each habitat type has a certain species composition with species that are rather generalists or specialists (Rainio and Niemelä, 2003).

For our study, it is important to include the dimension of ecological traits that allows us to understand how biodiversity is linked to the environment and how species communities are shaped by environmental constraints (Scheiner et al., 2017). A ecological trait is a morphological or physiological characteristic measured at the scale of individuals and which affects its individual performance (Violle et al., 2007). Ecological traits are evolutionary adaptations that reflect the environmental conditions of an area and are an important element in determining what influences the functioning of an ecosystem. It is therefore important to have a thorough understanding of the ecological traits of ground beetles in order to better understand the appearance or disappearance of a species whose ecological traits are characteristic of an ecological condition. Currently, the level of knowledge of ground beetle ecological traits is high (Kotze et al., 2011). In the present study, the following ecological traits were chosen: moisture preference, wing morphology and average body size. The proportionality of these traits will indicate the hygrometric tendency of the study sites and their stability, as wing morphology is widely recognised to be related to environmental stability (Gobbi et al., 2007). The average body size of ground beetle bodies gives an indication

of the biomass of the samples, as there is a correlation between mass and size. This functional diversity is ecologically important, as it is a component of diversity that influences stability, productivity and other aspects of ecosystem functioning (Tilman, 2001). Wooded pastures are no exception to this rule, especially as humans are dependent on them for forestry and forage yields. A drastic loss of biodiversity in these semi-wooded environments can undermine the proper functioning of these biotopes and reduce the quality and quantity of services provided to humans (Isbell et al., 2015). The biomass of organisms can also provide a more detailed picture of the functioning of the agroforestry ecosystem and adjacent habitats (Saint-Germain et al., 2007). Insect biomass, for example, can make an important contribution by transforming organic matter and modifying decomposition rates, which is a key component of ecosystem functioning (Yang and Gratton, 2014). Insect herbivory can have important effects on ecosystem cycling by altering the quantity, quality and timing of detrital inputs to plants (Belovsky and Slade, 2000). In addition, insect herbivory often transforms plant biomass in ways that increase the lability and mobility of nutrients (Metcalfe et al., 2014). It should be noted that predators, being numerous in ground beetles, can affect trophic cascades and create a risky environment for herbivores (Yang and Gratton, 2014). Biomass is also the cog in trophic interactions, as ground beetles are a food source for many vertebrates, such as mammals (Laroche, 1975) and birds (Laroche, 1980). The variability of ground beetle biomass directly influences the abundance of the upper links in the food chain.

In our study, we investigated the *Carabidae* communities present in three habitats: forests, unwooded pastures and wooded pastures. These organisms are good bioindicators that respond quickly to disturbances or changes in their environment and reflects the abiotic or biotic state of the environment (Avign and Luff, 2010 ; Rainio and Niemelä, 2003). Moreover, ground beetles can be easily collected using pitfall traps and in sufficient numbers to ensure statistical power. The taxonomy of this group of insects is quite stable and their morphological criteria are sufficient to identify each species (Pearce and Venier, 2006). Moreover, the *Carabidae* are among the best known insects, compiling a wealth of data and information, which makes them a good model group for biological studies (Kotze et al., 2011). In this work, the focus is on the assemblage, diversity index, biomass and ecological traits of ground beetles. Indeed, all these criteria are valuable tools to estimate natural environment's biological value and draw conclusions in a defined context.

The study question of the present work attempts to shed light on the communities, diversity, or biomass and certain ecological traits of ground beetles between wooded pastures, unwooded pastures, and forests and to what extent do the explanatory variables influence the above-mentioned parameters.

In this paper, three hypotheses are tested:

- (i) Ground beetle communities in wooded pastures largely encompass grassland and forest communities.
- (ii) Ground beetle species richness, diversity and biomass are higher in wooded pastures than in forests and unwooded pastures. In addition, some environmental variable and categories (tree cover, dry grasslands and pastures and Biodiversity Promotion Areas) are likely to influence diversity indices and biomass across study sites.

(iii) Environmental variable and categories play a role in the distribution of ecological traits (wing morphology, moisture preference, and average body size) of ground beetles across the different study sites.

4 Methods

4.1 Study area

This study was conducted in the Jura mountains of the canton of Neuchâtel in Switzerland (Fig. 1). The altitude of the study sites was between 1037 m and 1436 m. The collection sites were conducted in three different environments: forest, pasture with little or no tree cover and woody pasture. The categorisation of these 3 environments was done using the phytocenosis typology of Gallandat et al. (1995). The percentage of forest cover was calculated within a 100 m radius of the trap for each study site using LIDAR data. 0-20% tree cover indicates the category "pasture with little or no tree density" (NWP), 20-70% indicates the category "wooded pasture" (WP) and the category 70-100% tree cover indicates "forest and grazed wood" (F).

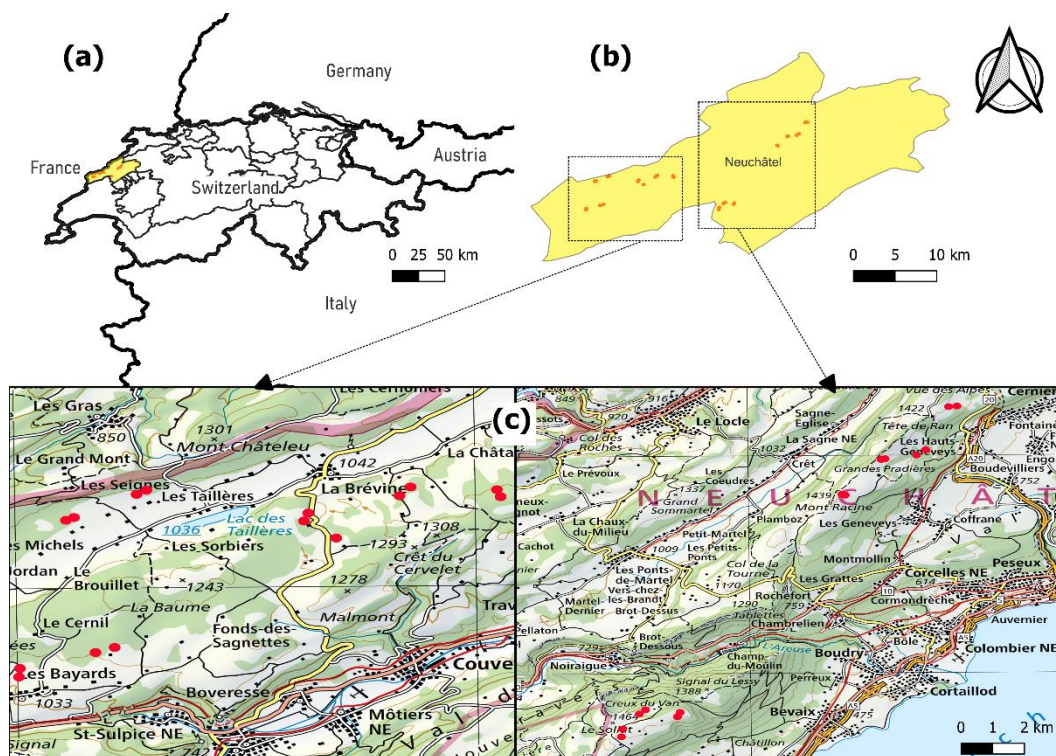


Figure 1: Maps showing the location of the sampling sites on an intra-continental and regional scale. (a) shows in yellow highlighting where the study site is located in Switzerland in relation to neighbouring countries. (b) shows more precisely the location of the sampling sites within the canton of Neuchâtel. (c) shows the 29 sample sites on two close-up maps where the localities are legible.

4.2 Experimental design

29 study sites (5 F, 8 NWP, 16 WP) (Appendix I) were set up with 3 pitfall traps per site. Each trap was spaced 1 m apart and surrounded by a fence, sometimes electrified, to prevent destruction by livestock as much as possible. The ground beetles were trapped using pitfall traps with a diameter of 73 mm and a height of 117 mm. Two cups were nested in each other, to keep the shape of the hole and to avoid partial backfilling during the surveys. A roof was created with a saucer of 120 mm diameter and wire was installed to avoid excess meteoric

water and plant debris in the traps (Spence, 1994) (Fig. 2). The trap container, filled to 2/3, was salt-saturated water, with a few drops of odourless detergent to reduce surface tension (Carbonne et al., 2020). The traps were set on 26th-27th May 2022 and removed on 1st-2nd September 2022. Traps were emptied at two-week intervals, i.e. 7 trap collections in total. 1 trap collection took two full days of work. The content of the traps was then preserved in a 70% alcohol solution. The identification of ground beetles was done in collaboration with a ground beetles specialist, Yannick Chittaro from Info Fauna. The verification of difficult-to-identify individuals was also carried out by the latter's expertise. The book "*Die Käffer Mitteleuropas*" was the main identification key to determine the individuals of the *Carabidae* family (Freude et al., 2004). Most of the specimens could be identified by their external morphology, but in some cases a dissection of the aedeagus was necessary. Moreover, the nomenclature followed the Catalogue of Palaearctic Coleoptera (Löbl & Löbl 2017). After identification, the insect biomass was dried in an oven at 60 degrees Celsius for approximately 24 hours and then weighed using a JB803-C Caratbalance.



Figure 2: Photo showing a pitfall trap in use. Two nested cups buried flush to the ground and topped with a saucer, itself erected by a rigid wire planted in the ground.

4.3 Data sets

Tree cover (TC) was selected as environmental variable, while dry grasslands and pastures (DGP) and Biodiversity Promotion Areas (BPA) were selected as the environmental categories resulting from defined agricultural practices. All these data were provided by the canton of Neuchâtel through spatial information layers (Canton of Neuchâtel, 2022). For the BPA variable, it was decided to combine the Biodiversity Promotion Areas into Utilised Agricultural Land and summer pasture. This grouping is justified by the fact that the current agricultural policy sets the same indicator plant requirements for Quality II BPA in Utilised Agricultural Land and in summer pasture areas. In addition, Article 59 (RS 910.13) on direct payments in agriculture states that only the BPA Quality II model, which is also used in Utilised Agricultural Land (UAL), can be used for the assessment of BPA in summering areas. For UAL and summer pasture wishing to acquire the Quality II BPA, their area must have > 20% vegetation characteristic of Biodiversity Promoting Areas. The many similarities in the characterisation of BPA in UAL and summer pasture led us to merge them. The area of these variables was calculated within a radius of 100 m around the traps for each study site using QGIS (version 3.26). The unit of each of these variables is m². Data on ground beetles' ecological traits were

extracted from *Fauna Indicativa* (Klaiber et al., 2017). The ecological traits selected were: wing morphology, moisture preference, hibernation stages and average body size. The selection of traits was based on dispersal ability indicating which proportion of ground beetles is more able to move far away than others. In the same way, the choice was also based on hygrometric preference, thus giving an overview of the study sites favourable to hygrophilia or xerophilia. Finally, the average body length was chosen to provide an underlying indication of ground beetle mass.

4.4 Statistical analysis

All statistical analyses were done with R (version 4.2.1) (Rstudio Team, 2022) and most graphs were performed with the ggplot2 package (version 3.4.0) (Wickham, 2016). The representation of the species across the different habitats was done using the Euler diagram of the "eulerr" package (version 7.0.0). This representation allows us to see how many species there are in common between habitats. A chi-square test was performed to check for similarities in species composition between WP and NWP plus F. The chi-square matrix compared the expected species according to H_0 (no species should be common between WP and NWP plus F) and the observed species. Non-metric multidimensional scaling (NMDS) was used to display carabid beetle assemblages. The analysis was run with the package vegan (version 2.6-4) (Oksanen et al., 2022).

Livestock damage to the traps resulted in a certain amount of missing data, i.e. 9.2 % of the surveys (22/203 surveys) could not be completed. The analysis of species richness and diversity was done using the iNext library (version 3.0.0) (Hsieh et al., 2016), which allows missing data to be taken into account, in order not to introduce bias into the results. Each study site was based on sample-size-based rarefaction/extrapolation curves with Hill numbers ($q = 0,1,2$) (Chao et al., 2014). The reference value for the sample-size was calculated using the estimatedD function of the iNext library. The output values of this function for each study site were then related to the explanatory variables in the linear models. In addition, the sampling sites were grouped into three habitats to observe differences in diversity among them, the iNext package was also used. In this case, the reference value for the sample-size was the habitat with the fewest ground beetles, namely NWP with 257 individuals. This methodology by Hill (1973) provides unified diversity indicators with proportional abundance on the same scale, called also "effective number of species".

To ensure that livestock damage does not bias the biomass statistics, an adjustment was made in the dataset. The dry biomass was divided by the number of surveys performed. This process allows the study site repeatedly impacted by livestock to have a lower denominator, resulting in a proportionally higher quotient. Thus, we opted to calculate the average biomass per study site.

Richness, species diversity, biomass and average body size were then entered into a linear model and related to TC, DGP and BPA that are the explanatory variables. All models fulfilled the assumptions (normality, heteroscedasticity, linearity), except for the linear models for Simpson index (Hill=2), biomass and average body size. The package used to check the assumptions is "performance" (version 0.10.1) (Lüdtke et al., 2021). For the linear Simpson Index model (Hill=2), TC, DGP and BPA were converted to square roots. Site 20_A was an outlier that was removed from the dataset. It was found to be significant by testing for outliers using the outlierTest function in the car library (version 3.1-1). Using the same function for the

linear biomass model this time, sample site 12_B was also found to be an outlier that should be removed. Finally, for the average body size dataset, study site 19_A also had to be removed by the same process described above, in order to fill in the assumptions.

A Kruskal-Wallis test with the "Bonferroni" adjustment method was performed to compare the biomass between the 3 habitats (F,NWP,WP). The study sites were therefore grouped into three habitat categories and thus the 29 sample sites were not treated independently in a linear model this time. Site 12_B was removed, as it showed some disparity graphically and was significant in the grubbs.test of the outliers package (version 0.15) (Komsta, 2022).

A Redundancy Analysis (RDA) was performed on ecological traits (wing morphology and moisture preferences) of ground beetles including environmental variable and categories. An ANOVA was then performed to determine the significance of the explanatory variables. Study site 12_B was removed from the dataset because of outlier characteristics. In fact, there is no formal and widely accepted definition of an outlier in principal component analysis (Jolliffe, 2002). Nevertheless, outliers have been detected by observing the increase in variance of certain variables due to their extreme value and are also detectable on a plot (Gnanadesikan and Kettenring, 1972).

5 Results

5.1 Carabid assemblage - hypothesis (i)

In total, 1710 individuals of 57 species were caught. 48 species were found in WP, 34 in NWP and 22 in F (Table 1) (Appendix II). 88% of the NWP species and 68% of the F species were also found in wooded pastures (Fig. 3).

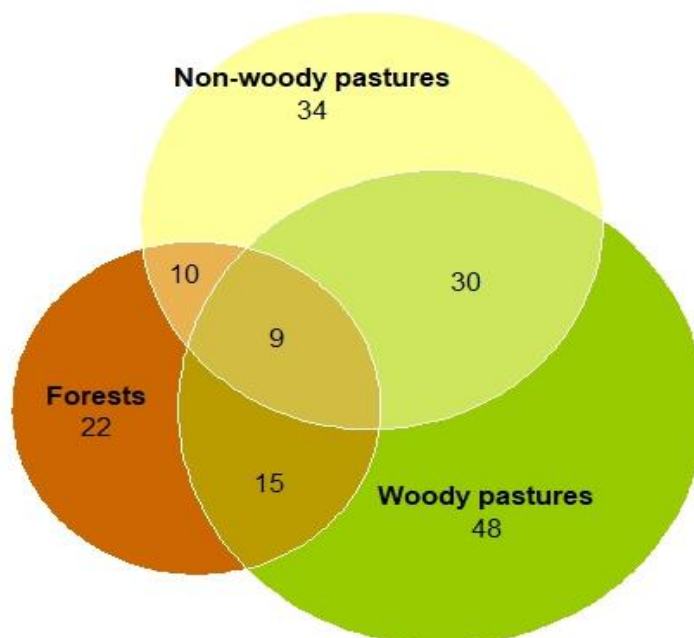


Figure 3: Euler diagram. The three coloured circles represent the three habitats: Woody pastures (green), Non-wooded pastures (yellow) and Forests (brown). The numbers in the disjoint sets (non-overlapped circles) indicate the number of species per habitat type. The intersection of the sets (overlapping circles) indicate the number of species common to two or three habitats.

Amara plebeja, *Licinus hoffmanseggii*, *Platynus assimilis* and *Pterostichus hagenbachii* were only found in F. *Amara equestris*, *Clivina fossor* and *Ophonus laticollis* were the only species found in NWP. 11 species were found only in wooded pastures: *Amara montivaga*, *Bembidion lampros*, *Harpalus signaticornis*, *Loricera pilicornis*, *Poecilus cupreus*, *Pterostichus niger*, *Pterostichus strenuus*, *Syntomus truncatellus*, *Synuchus vivalis*, *Trechus secalis* and *Trichotichnus nitens*. 9 species were found in all three habitats and 10 species were common between F and NWP (Table 1). A chi-square test was performed with the observed species and the expected species per habitat as a matrix according to H_0 . The expected species of the null hypothesis considers that there are no common species between WP and NWP plus F. Results indicate that wooded pastures significantly include a large proportion of species present in F and NWP ($\chi^2 = 36.923$, $df = 2$, $P\text{-value} = 9.6e-09$). Including species abundance, ground beetle communities in the NWP and F were relatively similar to those in the WP. Indeed, ordination showed that the WP ellipse encompassed mostly NWP and F communities. Note that ground beetle NWP communities tend to be closer in the NMDS to sparsely wooded pastures (20-30 % of TC) than to pastures with high tree cover (> 50 % of TC), and vice versa for forest communities. (Fig. 4).

Table 1: Compilation of caught abundance carabid species (1710 individuals for 57 species) in 29 study sites grouped by habitat and some ecological traits extracted from “Fauna Indicativa” (Klaiber et al., 2017). The content of the brackets indicate the number of sites occupied per habitat for each species.

Species	Habitat type			Wing morphology	Moisture preferences	Average body size (mm)
	F	NWP	WP			
<i>Abax ovalis</i> (Duftschmid, 1812)	45 (5)	0 (0)	10 (3)	brachypterous	hygrophilic	13
<i>Abax parallelepipedus</i> (Piller & Mitterpacher, 1783)	118 (5)	4 (3)	60 (10)	brachypterous	mesophilic	19
<i>Abax parallelus</i> (Duftschmid, 1812)	0 (0)	1 (1)	7 (2)	brachypterous	hygrophilic	15,5
<i>Amara aenea</i> (De Geer, 1774)	0 (0)	9 (2)	4 (3)	macropterous	mesophilic	7
<i>Amara communis</i> (Panzer, 1797)	0 (0)	1 (1)	10 (3)	macropterous	mesophilic	6
<i>Amara convexior</i> Stephens, 1828	0 (0)	5 (1)	2 (1)	macropterous	mesophilic	8
<i>Amara equestris</i> (Duftschmid, 1812)	0 (0)	1 (1)	0 (0)	macropterous	xerophilic	10,5
<i>Amara familiaris</i> (Duftschmid, 1812)	0 (0)	4 (2)	1 (1)	macropterous	mesophilic	7
<i>Amara lunicollis</i> Schiødte, 1837	0 (0)	31 (6)	35 (7)	macropterous	mesophilic	7,5
<i>Amara montivaga</i> Sturm, 1828	0 (0)	0 (0)	1 (1)	macropterous	xerophilic	8
<i>Amara nitida</i> Sturm, 1828	0 (0)	10 (6)	13 (7)	macropterous	mesophilic	8
<i>Amara ovata</i> (Fabricius, 1792)	0 (0)	5 (2)	4 (3)	macropterous	mesophilic	8,5
<i>Amara plebeja</i> (Gyllenhal, 1810)	1 (1)	0 (0)	0 (0)	macropterous	mesophilic	7
<i>Badister bullatus</i> (Schränk, 1798)	0 (0)	2 (2)	2 (2)	macropterous	mesophilic	5
<i>Bembidion lampros</i> (Herbst, 1784)	0 (0)	0 (0)	13 (3)	dimorphic	mesophilic	3

<i>Bembidion properans</i> (Stephens, 1828)	0 (0)	1 (1)	7 (4)	dimorphic	mesophilic	3,5
<i>Calathus fuscipes</i> (Goeze, 1777)	0 (0)	34 (8)	82 (7)	dimorphic	mesophilic	12
<i>Calathus melanocephalus</i> (Linné, 1758)	0 (0)	2 (2)	6 (5)	dimorphic	xerophilic	7,5
<i>Carabus auronitens</i> Fabricius, 1792	24 (5)	0 (0)	10 (5)	brachypterous	hygrophilic	25,5
<i>Carabus convexus</i> Fabricius, 1775	1 (1)	5 (1)	0 (0)	brachypterous	xerophilic	17
<i>Carabus coriaceus</i> Linné, 1758	1 (1)	2 (2)	2 (2)	brachypterous	hygrophilic	37
<i>Carabus monilis</i> Fabricius, 1792	0 (0)	1 (1)	9 (4)	brachypterous	mesophilic	24
<i>Carabus nemoralis</i> O. F. Müller, 1764	6 (3)	3 (3)	4 (4)	brachypterous	hygrophilic	23
<i>Carabus problematicus</i> Herbst, 1786	3 (2)	10 (4)	13 (9)	brachypterous	hygrophilic	25
<i>Carabus violaceus</i> Fabricius, 1787	17 (3)	4 (3)	24 (8)	brachypterous	mesophilic- hygrophilic	30
<i>Clivina fossor</i> (Linné, 1758)	0 (0)	1 (1)	0 (0)	dimorphic	mesophilic	6
<i>Cychrus attenuatus</i> (Fabricius, 1792)	3 (2)	0 (0)	2 (1)	brachypterous	hygrophilic	15,5
<i>Cychrus caraboides</i> (Linné, 1758)	2 (2)	0 (0)	1 (1)	brachypterous	steno-hygro- philic	17
<i>Dyschirius globosus</i> (Herbst, 1784)	0 (0)	6 (1)	34 (5)	dimorphic	hygrophilic	2,5
<i>Harpalus latus</i> (Linné, 1758)	0 (0)	2 (2)	12 (4)	macropterous	mesophilic	9,5
<i>Harpalus rufipes</i> (De Geer, 1774)	0 (0)	1 (1)	2 (2)	macropterous	mesophilic	13,5
<i>Harpalus signaticornis</i> (Duftschmid, 1812)	0 (0)	0 (0)	1 (1)	macropterous	xerophilic	6,5
<i>Licinus hoffmanseggii</i> (Panzer, 1803)	1 (1)	0 (0)	0 (0)	wingless	mesophilic	12
<i>Loricera pilicornis</i> Fabricius, 1775	0 (0)	0 (0)	9 (2)	macropterous	hygrophilic	7
<i>Microlestes minutulus</i> (Goeze, 1777)	0 (0)	2 (1)	9 (2)	macropterous	xerophilic	2,5
<i>Molops piceus</i> (Panzer, 1793)	7 (4)	3 (1)	18 (8)	brachypterous	hygrophilic	11,5
<i>Nebria brevicollis</i> (Fabricius, 1792)	2 (1)	0 (0)	5 (5)	macropterous	hygrophilic	11,5
<i>Notiophilus aquaticus</i> (Linné, 1758)	0 (0)	5 (2)	5 (2)	dimorphic	mesophilic	5
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	1 (1)	0 (0)	0 (0)	dimorphic	hygrophilic	4,5
<i>Ophonus laticollis</i> Mannerheim, 1825	0 (0)	1 (1)	0 (0)	macropterous	xerophilic	9,5
<i>Panagaeus bipustulatus</i> (Fabricius, 1775)	0 (0)	3 (2)	1 (1)	macropterous	xerophilic	7
<i>Platynus assimilis</i> (Paykull, 1790)	1 (1)	0 (0)	0 (0)	macropterous	hygrophilic	11,5
<i>Poecilus cupreus</i> (Linné, 1758)	0 (0)	0 (0)	7 (4)	macropterous	mesophilic	11
<i>Poecilus versicolor</i> (Sturm, 1824)	0 (0)	61 (7)	138 (13)	macropterous	mesophilic	10
<i>Pterostichus burmeisteri</i> Heer, 1838	37 (5)	4 (3)	77 (6)	brachypterous	mesophilic	13,5
<i>Pterostichus hagenbachii</i> Sturm, 1824	2 (1)	0 (0)	0 (0)	brachypterous	mesophilic	15

<i>Pterostichus madidus</i> (Fabricius, 1775)	63 (5)	0 (0)	142 (12)	dimorphic	mesophilic	16,5
<i>Pterostichus melanarius</i> (Illiger, 1798)	2 (1)	31 (6)	185 (13)	dimorphic	hygrophilic	15
<i>Pterostichus niger</i> (Schaller, 1783)	0 (0)	0 (0)	1 (1)	dimorphic	hygrophilic	18,5
<i>Pterostichus selmanni</i> (Dejean, 1828)	81 (5)	1 (1)	51 (9)	brachypterous	hygrophilic	16
<i>Pterostichus strenuus</i> (Panzer, 1796)	0 (0)	0 (0)	1 (1)	dimorphic	hygrophilic	6
<i>Pterostichus vernalis</i> (Panzer, 1796)	0 (0)	1 (1)	2 (2)	dimorphic	mesophilic	6,5
<i>Syntomus truncatellus</i> (Linné, 1761)	0 (0)	0 (0)	4 (2)	dimorphic	mesophilic	2,5
<i>Synuchus vivalis</i> (Illiger, 1798)	0 (0)	0 (0)	2 (1)	dimorphic	mesophilic	7
<i>Trechus secalis</i> (Paykull, 1790)	0 (0)	0 (0)	3 (3)	brachypterous	hygrophilic	3,5
<i>Trichotichnus laevicollis</i> (Duftschmid, 1812)	1 (1)	0 (0)	2 (2)	dimorphic	hygrophilic	7
<i>Trichotichnus nitens</i> (Heer, 1837)	0 (0)	0 (0)	1 (1)	dimorphic	hygrophilic	8

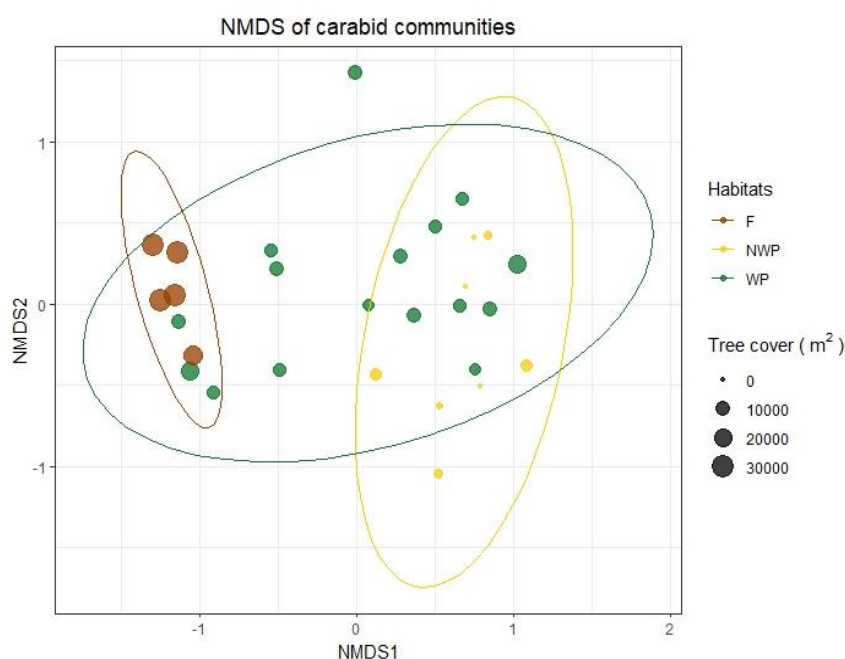


Figure 4: Non-metric multidimensional scaling ordination of carabid beetle assemblages. Each colour defines a habitat-specific carabid community, which is abbreviated in the graph legend. In brown, F = forest and grazed wood; in yellow, NWP = pasture with little or no tree density; in green, WP = wooded pastures. The size of the dots indicates the amplitude of tree cover in the sample site. The ellipses are delineated with a 95% confidence interval.

5.2 Diversity parameters and biomass - hypothesis (ii)

5.2.1 Diversity indices

Taking into account that the numbers of Hill are equal to 0, 1 and 2 and rarefying the data of F and WP, from the number of individuals observed in NWP, it can be seen that F is the habitat

with the lowest species richness ($q = 0$), Hill-Shannon index ($q = 1$) and Hill-Simpson index ($q = 2$) of the three habitats. Nevertheless, this gap in diversity index narrows more and more when the Hill index increases from 0 to 2. On the other hand, NWP and WP have each diversity index almost equivalent. As the confidence intervals of the curves overlap for each Hill number between NWP and WP, it seems that the three types of diversity indices of WP are not significantly higher than that of NWP. (Fig. 5). With the available data, it seems impossible to determine which of these two habitats is more likely to support the highest ground beetle richness ($q = 0$) and diversity ($q = 1,2$). Therefore, we cannot confirm the research hypothesis (i), but we have nevertheless shown that WP have higher diversity indices than F and that NWP are a good habitat for reaching diversity indices of ground beetles that are as high as in WP.

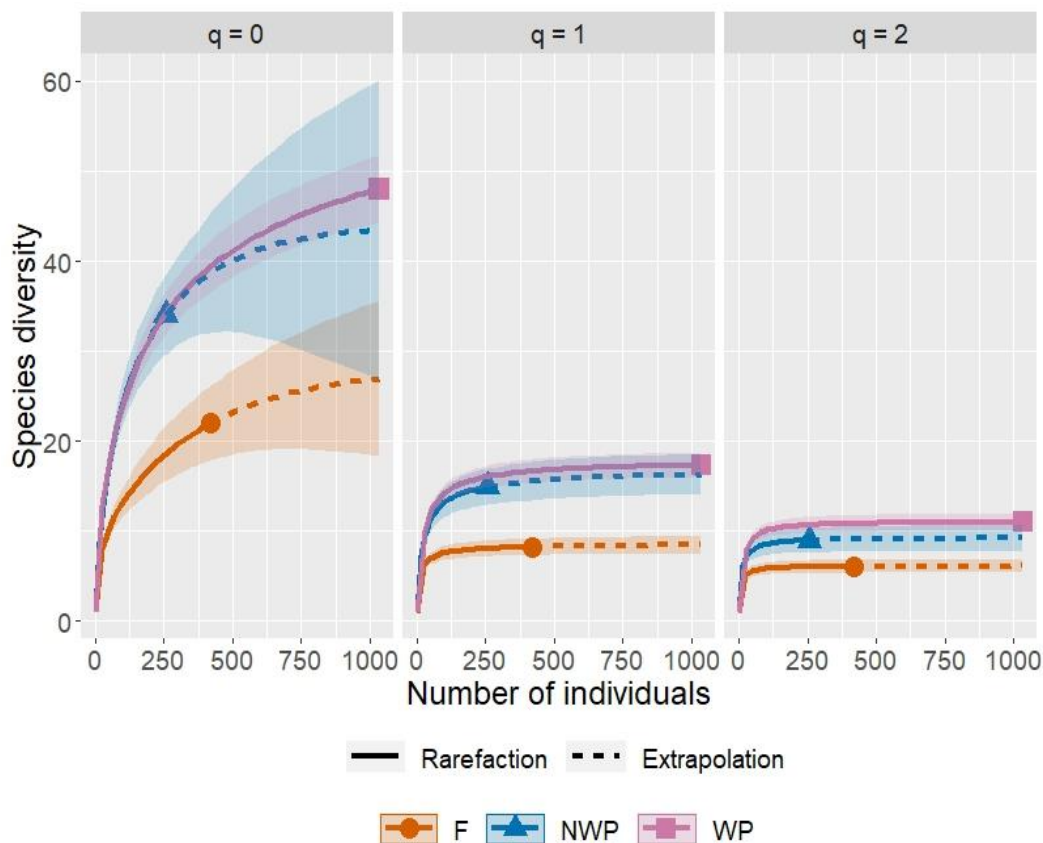


Figure 5: Rarefaction (solid line) and extrapolation (dashed line) curves for the three Hill number diversity indices represented in the shaded columns (l-r: Richness, Hill-Shannon index, Hill-Simpson index). Forest (F) is represented in orange, pasture with little or no tree density (NWP) is represented in pink and woody pastures are represented in blue. These asymptotes with a 95% confidence interval have a characteristic symbol, representing the total number of individuals caught per habitat. These asymptotes with a 95% confidence interval have a characteristic symbol, representing the total number of individuals caught per habitat in relation to the x-axis and the amount of diversity in relation to the y-axis.

Each diversity index of rarefied Hill number ($q = 0,1,2$) introduced in a separate linear model and compared to the explanatory variables showed that the Biodiversity Promotion Areas (BPA) variable had a role to play in relation to the diversity indices. Indeed, BPA was significant in relation to species richness ($q=0$) ($df = 1$, F-value = 5.4242, Multiple R-squared = 0.1673, P-value = 0.02759), as was the Hill-Shannon index ($q=1$) ($df = 1$, F-value = 5.2734, Multiple R-squared = 0.1634, P-value = 0.02982). The BPA variable, on the other hand, was substantially significant in relation to the Hill-Simpson index ($df = 1$, F-value = 3.1757, Multiple R-squared =

0.1088, P -value = 0.08674). The graph effectively shows that Biodiversity Promoting Areas are positively correlated with the three diversity indices (Fig. 6).

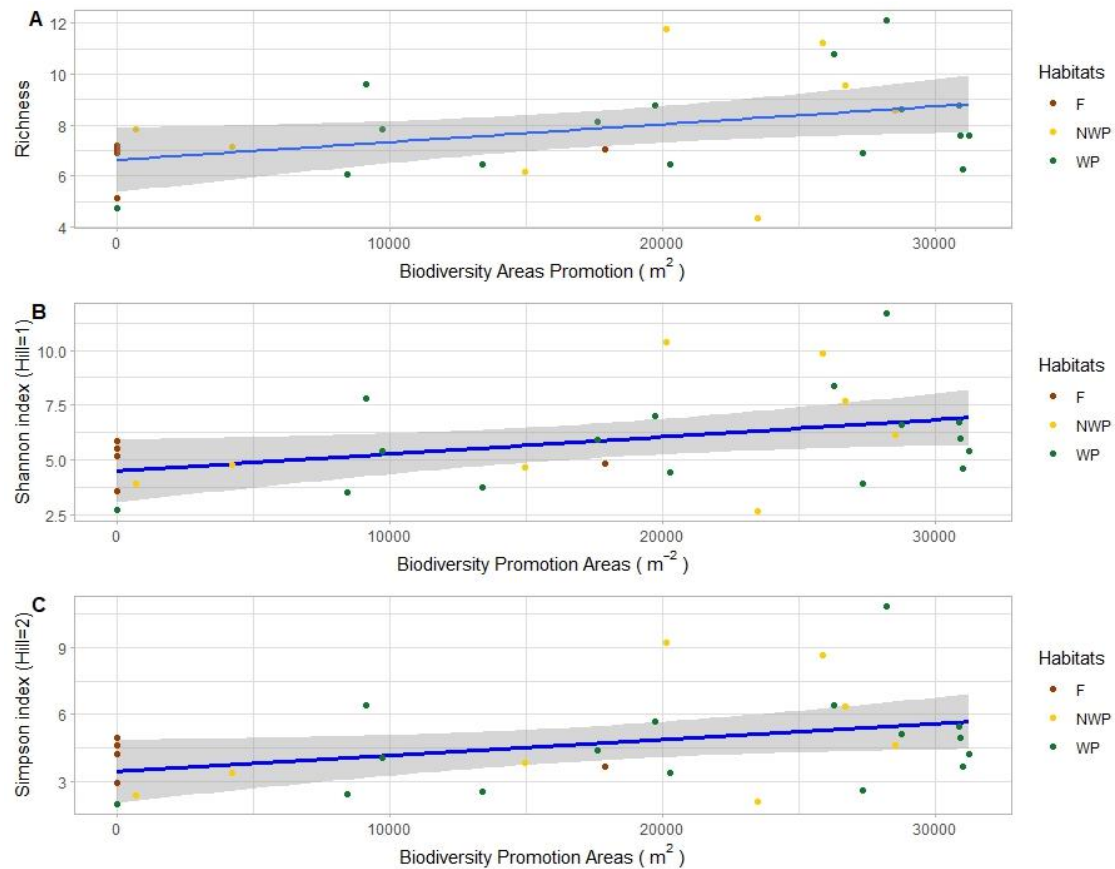


Figure 6: Scatterplots showing the relationships between Biodiversity Promotion Areas and the three Hill number diversity indices: (A) richness ($q = 0$), (B) Hill-Shannon index ($q = 1$) and (C) Hill-Simpson index ($q = 2$). Missing data were taken into account for the calculation of diversity indices. The regression lines with confidence intervals describe a positive slope in each case. Habitats are described by dots of three different colours: brown = forest and wooded pasture (F), yellow = pasture with little or no tree density (NWP) and green = wooded pasture (WP)

5.2.2 Carabid biomass

WP is not the habitat with the highest ground beetle biomass. Linear regression showed that tree density significantly influences the biomass value found in the sample sites (Fig. 7). Ground beetle biomass is positively correlated with tree cover ($df=1$, F -value = 24.241, Multiple R-squared = 0.4825, P -value=4.113e-05). Furthermore, F have the highest biomass, followed by WP and finally NWP.

By grouping the study sites by habitat, the trend that emerges is the same as with linear regression. The WP is not the habitat with the highest biomass. F has significantly more ground beetle biomass than WP and NWP (Kruskal-Wallis, $\chi^2= 11.01$, $p=0.0041$) (Fig. 8). We can therefore refute this part of the research hypothesis (ii) and propose from the results that, in the context of the study, tree cover is significantly and positively correlated with carabid biomass.

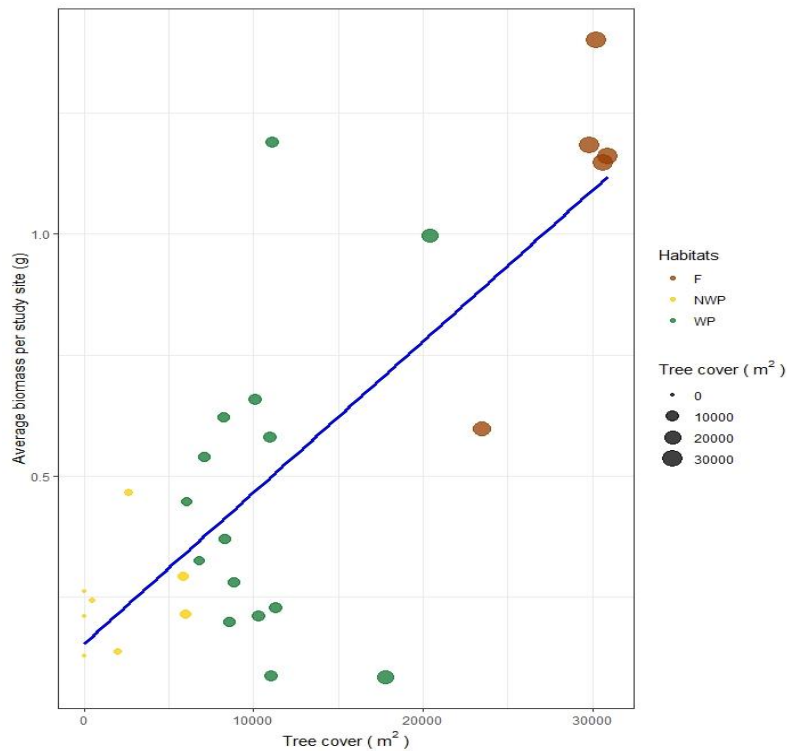


Figure 7: Scatterplot showing the relationship between carabid biomass and tree cover. The regression line describes a positive slope. The habitats are described by dots of three different colours: brown = forests and grazed wood (F), yellow = pasture with little or no tree density (NWP) and green = woody pastures (WP). The size of the dots indicates the amplitude of the tree cover of the sample site as defined in the graph legend.

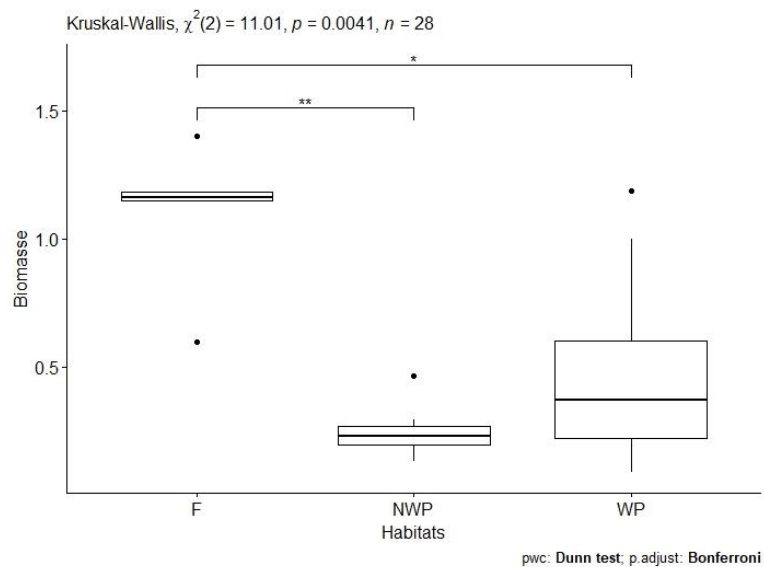


Figure 8: Boxplot representing ground beetle biomass in relation to the three habitats. Standard error and extreme values are indicated for each habitat. The level of significance between habitats is indicated by asterisks.

5.3 Ecological traits - hypothesis (iii)

5.3.1 Wing morphology

Tree cover was the only environmental variable that significantly influenced wing morphology ($df = 1$, F -value = 9.7769, P -value = 0.001). The variable DGP did not influence this ecological trait ($df = 1$, F -value = 0.2413, P -value = 0.910), *idem* for variable PBA ($df = 1$, F -value = 0.4677, P -value = 0.733). The measured environmental variables explained 30.41% of the variation in the composition of carabid wing morphologies across the study sites. Reduced wings and wingless individuals are typical of densely wooded areas such as F or WP with a high density of trees. Macropterous individuals are more common in open areas such as NWP and WP with low tree density. Dimorphic wings are found halfway between the spatial distribution of brachypterous and macropterous ones (Fig. 9).

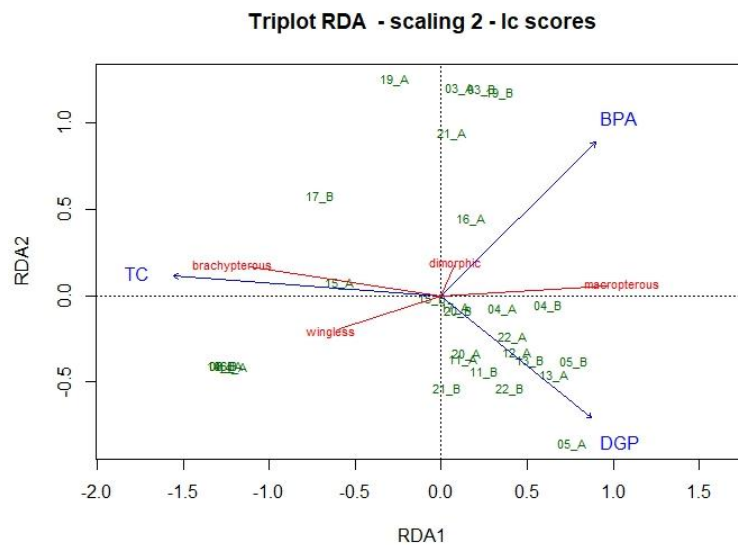


Figure 9: Redundancy analysis triplot showing the relationship between environmental variable and categories in blue, wing morphology in red and ground beetle communities in green. The 29 study sites in green are abbreviated by a number and a letter. The species score had to be omitted, in order to keep the ordering clear. Abbreviations : TC = tree cover, BPA = Biodiversity Promotion Areas, DGP = dry grasslands and pastures.

5.3.2 Moisture preference

Tree cover significantly influences the preference for moisture of ground beetles ($df = 1$, F -value = 6.6983, P -value = 0.001). The variable DGA did not influence this ecological trait ($df = 1$, F -value = 1.0741, P -value = 0.373), *idem* for variable BPA ($df = 1$, F -value = 0.4402, P -value = 0.811). The number of hygrophilic individuals increases in positive correlation with tree cover. Xerophilic individuals tend to have a negative correlation with tree cover. The measured environmental variables explained 25.49 % of the variation in the composition of carabid moisture preference across the study sites. Sites with a decrease in trees result in an increase of mesophilic individuals. Xerophilic individuals are therefore typical of treeless areas and therefore present in the PBA and DGA areas characteristic of more open areas (Fig. 10). Following this logic, the categories "mesophilic" and "mesophilic/hygrophilic" should be reversed, which is not the case in the result of this RDA.

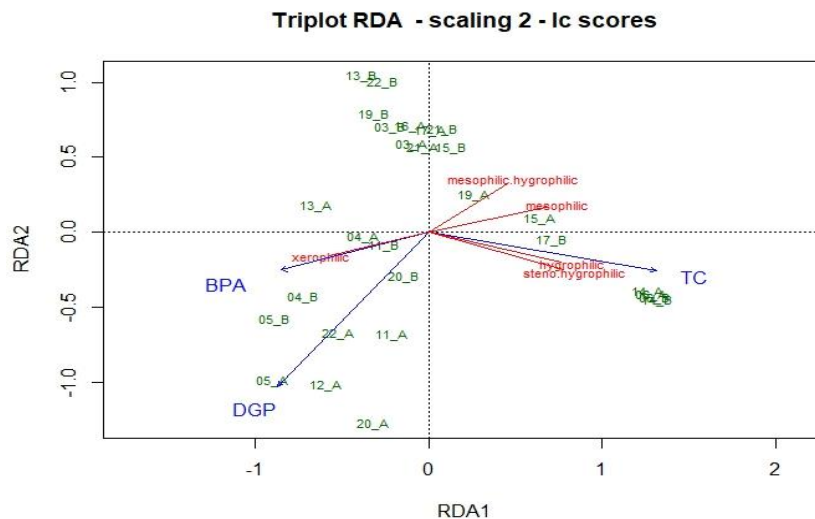


Figure 10: Redundancy analysis triplot showing the relationship between environmental variable and categories in blue, moisture preference in red and carabid communities in green. The 29 study sites in green are abbreviated by a number and a letter. The species score had to be omitted, so that the ordering remains clear. Abbreviations: TC = tree cover, BPA = Biodiversity Promotion Areas, DGP = dry grasslands and pastures.

5.3.3 Average body size

Linear regression showed that the mean size of individuals is significantly higher in wooded areas than in open areas ($df=1$, F -value=26.664, Multiple R-squared = 0.5063, P -value=2.18e-05). In general, ground beetle size increases with increasing tree cover and vice versa. In the same way as with biomass, the size of individuals increases significantly as a function of the tree cover variable (Fig. 11). On average, the largest individuals are found in F, followed by WP and finally NWP.

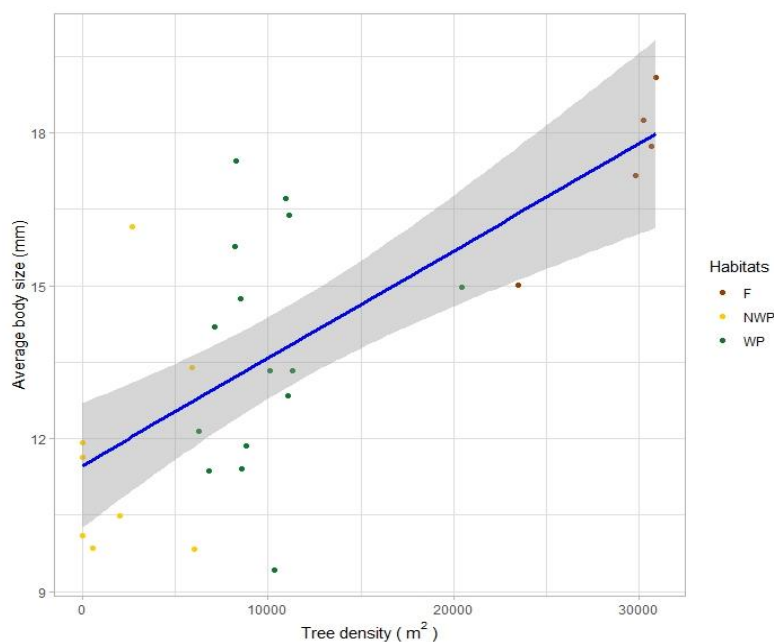


Figure 11: Scatterplot showing the relationship between tree cover and average ground beetle size. The regression line describes a positive slope. Habitats are described by points of three different colours: brown = forests and grazed wood (F), yellow = pasture with little or no tree density (NWP) and green = wooded pastures (WP).

6 Discussion

6.1 Carabid assemblage - hypothesis (i)

The results show that the species composition of wooded pasture ground beetles includes a large number of species common to both forests and non-wooded pastures. Thus, ground beetle communities in wooded pastures largely encompass grassland and forest communities.

Our study confirms the results obtained by [Boutaud et al. \(2022\)](#) who also showed that ground beetle community assemblages in semi-open areas combined species present in open and forest habitats. Semi-open areas are a fortiori influenced by these two adjacent environments. In the same vein, similar results were demonstrated in the tropics by [Ariza et al. \(2021\)](#). Indeed, early successional habitats, having undergone an agricultural abandonment between 3 and 7 years, presented an assemblage of communities that overlapped with pasture and forest communities. The early succession habitat would be a mixed environment with ecological elements of pasture and forest, thus a heterogeneous environment that could be exploited by a subset of ground beetle species. Another study on an Estonian island again showed that the ground beetle assemblage in wooded meadows mainly encompasses the composition of the two "extreme" habitat types, i.e. grassland and forest ([Talvi, 1995](#)).

According to the results, it would appear that the wooded pastures of the Jura mountains act as a transition zone between forests and unwooded pastures. Indeed, some ground beetle communities may find similar ecological niches in the WP as in the F and NWP. Ground beetle communities in WP tend towards grassland assemblages when the semi-open area is sparsely wooded and conversely. In contrast, WP tend towards a forest assemblage when these semi-wooded areas have a higher density of trees (>50% of TC). The ecological niches of wooded pastures are quite varied and can constitute a substitute habitat for certain species with a certainly generalist tendency. However, it should also be noted that several ground beetle species were only found in WP, which indicates that some species are more restricted to semi-wooded areas. The heterogeneity of the WP, therefore, results in the assemblages of certain species that usually live in contrasting environments. Similar results for the family Geotrupidae have shown that wooded pastures support a dung beetle assemblage that is transitional between F and NWP assemblages ([Somay et al., 2020](#)). Thus, it seems that several families of beetles are fond of these semi-open environments. The edge effect is a change in species composition occurring at the boundary between different habitats and often accompanied by increased biodiversity. This effect may explain why the community assemblage of the WP resembles a large extent the communities of adjacent habitats ([Magura et al., 2001](#)).

As several species were only found in wooded pastures, this shows that this habitat also supports species that are more specialised in semi-wooded environments and do not necessarily find suitable ecological niches in F and NWP. In contrast, some species were only found in NWP and F, indicating that some species cannot tolerate a semi-open environment, like wooded pastures. These specialised NWP and F species therefore need an environment with lots of light and lots of shade respectively. Structural attributes of vegetation that create environmental heterogeneity, valued by a wide range of species, may be perceived by other species as fragmentation of their habitat ([Tews et al., 2004](#)). Environmental heterogeneity can be defined as the degree of non-uniformity of the land-cover, whereby structural, biotic and climatic factors determine the configuration and distribution of ecological niches ([Stein et al., 2014](#)). Fragmentation can cause disruption of key biological processes, such as dispersal

and resource acquisition (Saunders et al., 1991). This habitat discontinuity creates an abundance of adaptive generalist species at the expense of specialist species (Lövei et al., 2006) of adjacent habitats, making wooded pastures less suitable for the preservation of open and forest specialist species, but suitable for the preservation of semi-wooded specialist species.

Radio-tracking has shown that forest ground beetle species are reluctant to cross open areas (Riecken and Raths, 1996). This suggests that the forest-only species in our study are highly dependent on the size of their forest patch to maintain themselves and have a viable effective population size in the long term. De Vries (1994) has shown that the number of species with reduced dispersal ability increases with patch size. Furthermore, the survival of forest specialists also depends on short distances and connections to other alternative patches (Niemelä, 2001). Species adapted to unstable conditions in open areas have good dispersal capacity (Niemelä 2001) and this suggests that they are less affected by habitat fragmentation than forest species with reduced dispersal capacity. Indeed, open area species in general are more able to move to alternative, less fragmented habitats.

Wooded pastures probably allow improved connectivity between neighbouring habitats, resulting in easier exchange of forest individuals between forests. The exchange of forest individuals would probably be reduced in a steep interface from F to NWP, without WP ensuring the transition between habitats. In addition, WP provide additional available habitat for a substantial proportion of ground beetles, which otherwise only survive in F or NWP, and thus provide them with additional habitat surface. Moreover, the 48 ground beetle species collected in wooded pastures represent 9% of the 525 species of carabid beetles native to Switzerland (Chittaro 2023, pers. comm.). If this result is extrapolated to all wooded pastures in the Jura Arc, this percentage can increase considerably, making wooded pastures an important habitat for the conservation of a large number of ground beetle species.

In view of the cited studies praising semi-open habitats as transitional habitats for carabid communities, this study also supports this view with its results. Specifically, wooded pastures of the Jura, although greatly influenced by humans, constitute a transitional habitat, an ecotone between mountain forests and open pastures. However, these semi-woodland environments do not have the ecological niches required to host certain forest and grassland specialist species.

6.2 Hypothesis (ii)

6.2.1 Diversity parameters

The results indicate that species richness and diversity are higher in WP than in F. However, the diversity parameters are equal between WP and NWP, it is impossible to distinguish which is superior. The variable "Biodiversity Promotion Areas" significantly influences the diversity parameters among the study sites.

Extensive agriculture and biodiversity areas have a positive effect on biodiversity in general. Biodiversity Promoting Areas is positively correlated with ground beetle species diversity. Aviron et al. (2009) show that several taxa including ground beetles benefit from these environmental protection measures in Switzerland, both in terms of species richness and species composition. These areas have been designed to optimally promote the diversity of birds, arthropods or flowering plants or ecosystem services such as pollination and natural pest control

(Tschumi et al., 2016). Indeed, several extensive agricultural measures have been introduced to take biodiversity into account as much as possible, such as: conserving indicator flora, maintaining structures such as undergrazed areas (grass left standing), bushes, stones, wetlands or bare ground, enriching the pasture and favouring small fauna, mosaic of areas with staggered use over time, etc.) (Stäheli et al., 2010 ; art. 59, OPD).

Studies on ground beetle diversity parameters are sometimes counter-intuitive concerning homogeneous and heterogeneous habitats. Indeed, ground beetles show a higher species richness and diversity in open areas, such as pastures with high disturbance, than in more heterogeneous habitats in terms of ecological niches, such as mosaic units (da Silva et al., 2008). Furthermore, research by Boutaud et al. (2022), quite similar to the present study, showed that α diversity, i.e. the species richness at a given location, was equal between open and semi-open habitats and richer than in forests. However, γ diversity, the sum of α diversity of communities in different habitats at the landscape scale, showed a slightly higher value in semi-open areas than in open areas and forests. In the study of Molnár et al. (2001), species diversity was compared between forest, grassland and forest edge. The results showed that species diversity was higher in forest edge and grassland than in forest. In contrast, there was no significant difference in species diversity between grassland and forest edge. The forest edge is, in some respects, a transition zone between open and forested areas, similar to wooded pastures. This same author also considered that an ecotone between two environments contributes to habitat heterogeneity and generates a variety of microsites, which is favourable to higher diversity.

The lower species richness and diversity in F than in open and semi-open areas is not easy to explain. Some of the answers may lie in the lower quality of the forests or in the fact that the size of the forests is too small to support a higher species diversity. Nevertheless, litter thickness seems to be a major factor in ground beetle composition and abundance. A forest floor with a high litter thickness decreases the abundance and species richness of ground beetles and increases the presence of forest species. Consequently, litter would interfere with the movement and foraging of ubiquitous and more open species, which are not adapted to live in such an environment (Guillemain et al., 1997). A habitat that tends towards a forest environment restricts the size of the ecological niche for many ground beetle species, thus reducing the number of species adapted to live there. Molnár et al. (2001) emphasise that the structure of the vegetation and its derived variations creating microclimates is one of the most important factors to determine the distribution of ground beetles. It is argued that a fairly high diversity of vegetation led to a higher diversity of ground beetles.

The high species diversity of ground beetles in wooded pastures could be the result of the edge effect from the dispersal of individuals present in adjacent habitats (Magura et al., 2001). It is not easy to explain why diversity indices are equal between WP and a more homogeneous habitat, the NWP. According to the study by Lacasella et al. (2015), the estimation of a distance of 600 m in the heart of open pastures from the trap site to the first trees is necessary to avoid the appearance of forest species during surveys. In the case of our study, this buffer zone for NWP was not always respected, so there may have been an edge effect with other woodlands in the vicinity of NWP. Another hypothesis as to why NWP have such a high species diversity is perhaps because there are many discrete micro-structures such as stones, rocky outcrops, puddles, bare soil patches or unevenness of the soil created by livestock trampling, which satisfy a large number of species (Chittaro et al. 2023, submitted).

6.2.2 Features of diversity indices

Regarding the influence of relative abundance on the diversity indices, we note that for the three diversity indices, the asymptotes of WP and NWP overlap and are always higher than that of F. This distance between WP plus NWP and F is well marked for species richness, then decreases for the Hill-Shannon index and decreases again for the Hill-Simpson index. It should also be noted that the specific diversity of WP and NWP in the Hill-Shannon index is slightly higher than the specific diversity with the Hill-Simpson index. This can be explained by the fact that there are several species found with a low abundance and considered as rare which gives more weight to the calculation with the Hill-Shannon index. Indeed, the Hill-Shannon index uses the geometric mean to calculate the diversity index, whereas the Hill-Simpson index uses the harmonic mean. Differences may appear in the way they scale these values (Roswell et al., 2021). It should be noted that the distribution of individuals within each species influences diversity for both the Hill-Shannon and Hill-Simpson indices. An unbalanced distribution of individuals per species implies a reduction in diversity. In our case, we see that this lack of balance in relative abundance lowers each of our asymptotes in comparison to species richness. This also shows us how important it is not to focus only on species richness to assess biodiversity, and that relative abundance allows us to refine our knowledge of this topic. Furthermore, habitat diversity rankings vary according to the completeness of sampling and this almost always affects diversity estimates.

By taking into account the influence of the total number of individuals without rarefaction from the habitat with the lowest sample, we note that the interpretation in terms of species richness would be biased. Indeed, the richness of NWP would be underestimated compared to that of WP. The same observation can be made for the species richness of F. The extrapolation shows us that other species could still have been observed. However, this habitat remains well below the observable species richness compared to the other two habitats. The Hill-Shannon index for the NWP habitat shows that there would be a slight increase in diversity by extrapolating the curve from the minimum number of individuals observed. In contrast, the Hill-Shannon index for the other two habitats and the Hill-Simpson index for each habitat would not show large differences in diversity results, either by rarefying the number of individuals from the smallest sample or by extrapolating from the largest sample. Indeed, all of these asymptotes were already tending towards horizontality from their total number of individuals per habitat, indicating a sufficient amount of sampling sizes per habitat in these cases.

6.2.3 Carabid biomass and average body size

(As size directly influences carabid biomass, it was decided to merge these two related topics, to avoid redundancy in the discussion)

The results indicate that ground beetle size and biomass increased linearly with the increase of the tree cover variable. Consequently, the biomass is highest in F, followed by WP and the habitat with the lowest biomass is NWP.

The study by Fernández-Tizón et al. (2020) shows that primary production is directly and positively related to arthropod biomass in semi-natural grasslands. Primary production could be positively correlated with the body size of some individuals, suggesting that the primary production of a habitat could lead to morphological evolution between taxa (Capellini and Gosling, 2007). In this logic, habitats with low primary productivity should favour species with

smaller average body sizes (Sustek, 1987). In forest environments, ground beetles seem to have a larger body size on average than in other less forested environments. Therefore, a change in body size automatically affects the total mass of the insect. The capacity of woodlands to mobilise mineral matter to create plant organic matter is high. Therefore, there is a bottom-up effect on the entire food chain, which must therefore adapt to this high primary productivity. In our study, we are not able to test this hypothesis and there is no evidence to support it.

Disturbed agricultural ecosystems, such as pastures, experience large fluctuations in their total energy value (Blake et al., 1994), i.e. the nutrient resources exploitable by organisms. Disturbances also occur in forests in the context of their management, but these are in principle sporadic activities in a short period of time compared to the management of agricultural areas. It should be noted that energy resources in the herbaceous layer can be rapidly converted into livestock biomass through grazing. Possible fertiliser additions and livestock dung also add rapid and substantial changes in available energy resources. Moreover, these ephemeral energy sources favour species with smaller bodies (Schoener and Janzen, 1968). A habitat with a fluctuating energy source is more easily exploited by widespread, dispersive individuals capable of withstanding large variations in population size, and such species are more likely to be small (Gaston and Lawton, 1988).

The present study shows that, on average, the ground beetles most able to live in a heavily wooded environment are larger and therefore have a higher mass. More open environments with lower primary production contain smaller ground beetles on average and therefore lower mass. Wooded pastures have a ground beetle biomass intermediate between forest and non-wooded environments.

6.3 Hypothesis (iii)

6.3.1 Wing morphology

The results show that tree cover is a variable playing a significant role in the distribution of wing morphology and moisture preference of ground beetles.

Research by Gobbi et al. (2007), studying the assemblage of terrestrial beetles during glacier retreat, yields results quite similar to ours. Areas recently freed from the ice, with unstable, stony and loose soil, have low numbers of brachyptera. This is because in such temporary environments (pioneer, ruderal, meadows, etc.), which can be quickly reforested, many ground beetles, which logically have a higher (re-)colonisation capacity (Den Boer, 1970), need to disperse continuously to find favourable biotopes. Areas that have been ice-free for a longer period of time, with a higher vegetation cover and more mature soils, have more brachypterous species. In principle, these wooded areas tend to be occupied by brachyptera ground beetles, which no longer need to disperse, as the resources are available in the long term.

Other research, such as that of Brandmayr (1991), shows that brachyptera are few in number in the early stages of a habitat succession and that brachyptera numbers increase as open areas begin to be colonised by trees and shrubs. Individuals with low dispersal ability, such as brachyptera or wingless being mainly medium to large in size, are more likely to be found in forest-dominated environments (Shibuya et al., 2014). Moreover, most of them hardly leave the forest canopy or only move a few tens of meters away from it (Della Rocca et al. 2021).

Macropterous species, which are highly dispersive, are common in grasslands ([Shibuya et al., 2014](#)).

Many studies relate soil stability or litter thickness to wing morphology. In the case of our paper, the environmental variable, "tree cover" ensures soil stability and induces soil litter thickness. It seems therefore that tree cover determines the composition of ground beetle wing morphology. It should be noted that soil stability and litter thickness are probably factors resulting from and correlated with tree cover. Although it should be said that litter thickness and soil stability can vary according to species type and forest management. Woody plants have an environmental structuring role from which several ecological parameters are derived that define the size of ecological niches. Ground beetles, although mostly epigeous, are dependent on the tree surface to survive in a given environment. Their small wings do not allow them to flee quickly in case of disturbance. It is therefore important for wingless and brachypterous ground beetles that their environment is disturbed as little as possible, which is the case of a forest compared to a meadow. Although the timber extraction causes a lot of disturbance, it is not very frequent because of the long time lapse from one cut to another in the same place. The same applies to natural disturbances such as storms or fires that cause major disruptions ([Bouget and Duelli, 2004](#)), but these events remain sporadic and in principle rare. Open environments are more disturbed, particularly through animal grazing, agricultural and forestry work which slows down the progress of woody plants. In this case, developed wings allow an efficient dispersal capacity which is crucial for the survival of ground beetles ([Roff, 1990](#)). The flight ability of macroptera gives them a clear advantage over brachyptera in living in more open areas.

6.3.2 Moisture preference

Humidity and light are known to be limiting factors for ground beetle assemblage ([Lövei and Sunderland, 1996](#)). Tree cover directly influences temperature and light at the site scale, their interaction varies moisture level ([North et al., 2005](#)). According to the study by [Kagawa and Maeto \(2014\)](#), soil moisture had a marked effect on the abundance and distribution of ground beetle species. Forest species prefer moist soils, while intermediate and open area species tend towards drier conditions.

It seems that tree cover influences again the composition of ground beetles due to their preference for moisture. Hygrophilic and stenohygrophilic species are closely linked to the environment with a high tree cover. Wooded environments, therefore, guarantee soils with high moisture content. Mesophilic and mesophilic-hygrophilic individuals tend towards slightly more open environments but are still linked to some presence of woody plants. Xerophilic individuals are more correlated with the variables Biodiversity Promoting Areas and dry grasslands and pastures and the opposite of wooded areas. This is logical since DPA and PBA have higher values in areas that tend towards reduced afforestation. Xerophiles are therefore in open non-forested areas and lightly wooded pastures. Soil moisture is an ecological factor influencing the distribution of ground beetles. According to our results, the tree cover, and thus the shading induced by it, apparently conserves moisture and produces a set of ground beetles with hygrophilic habits. Although it should be mentioned that many other abiotic factors contribute to the variation in humidity of an environment. Trees constitute apparently environmental keystones that considerably define ecological niches and induce certain environmental factors.

6.4 Future research

With regard to the issue of species distribution across habitats, it would be interesting to investigate in more detail the composition and botanical diversity of the habitats: F, NWP and WP. Separating these environments into three arbitrary habitats does not necessarily reflect the ecological differences within the same habitat between several study sites. These ecological differences between study sites of the same habitat would mark a change in the ground beetle assemblage. By defining the botanical composition of the study sites, it could be possible to see variations in community composition within habitats. This would result in further explanations for ground beetle species composition influenced by insect-plant interaction across study sites. Although most ground beetles are carnivorous, floral diversity may play a role in the availability of prey for ground beetles depending on the floral composition.

It would also be useful to measure in the field the microclimatic parameters (temperature, sunshine, precipitation, relief, pH, soil compaction) and the structure of the terrain (height of vegetation, bare ground area, hiding places, etc.) that may influence the presence of ground beetles.

For further research on the topic of *Carabidae* biomass, it would be interesting to refine the bottom-up approach on several levels of the food web and to define the possibilities of a concrete top-down approach. Indeed, ground beetle biomass may also be regulated by higher links in the food chain. It should be possible to count and identify potential ground beetle predators at different study sites. The type and pressure of predators would not necessarily be the same depending on the habitat.

6.5 Limitations

In order to improve the methodology of the study, the study sites should have been more evenly distributed between the three habitats studied. Pitfall traps are activity traps, which means that this method of trapping depends on the movements and activity period of ground beetles, so it is possible that we have missed some species present in early spring, as the traps were set in late May. In addition, small species may be under-represented as the trap edge may be an impassable ledge for them. Traps that are vulnerable to cattle should be protected from the moment the study sites are set up using electric batteries and/or barbed wire. This would avoid several consecutive destructions at the same locations during the peak of ground beetle activity. For future site selection, it would be wise to select study sites with as even a staggering of tree cover as possible between 0 and 100% tree cover. As this variable is a main element of the study, an overrepresentation of sites between 20-30% and an underrepresentation of sites between 50-80% afforestation should be avoided. It should also be possible to define the coarse composition of tree cover, such as the proportion of broadleaved and softwood trees. If possible, more environmental variables should also be tested to get a better overview of the parameters defining ground beetle composition, as for example: granulometry, hygrometry, type and quantity of soil pollutants, livestock units, type of livestock, etc.

6.6 Conclusion

In conclusion, wooded pastures are an important transitional habitat, allowing a gradual change of habitats between forests and open areas. This semi-woodland environment is an ecotone with a multitude of ecological niches where most ground beetle communities of the F and NWP can be found, but some forest and open-areas species cannot be found in WP. Indeed, these species are more specialised in purely forest and grassland environments and these individuals may perceive semi-forested habitats as a fragmentation of their habitat and/or the necessary climatic parameters are not adequate for their survival. The diversity is higher in open and semi-open areas than in forests, but the forest environment still contains a higher biomass than in more open areas. Conserving wooded pastures and generalising extensive agricultural policy by means of Biodiversity Promotion Areas would be beneficial to a wide range of ground beetles. It should be noted that wooded pastures persist over time due to human actions. This habitat is an encouraging example of where consistent human activities can be reconciled with diverse ground beetle communities. In addition, we recommend preserving wooded pastures by ensuring a balance between renewal of woody species, and the maintenance of grazing to ensure that the environment remains sufficiently open, thus to conserve α diversity. However, in order to achieve high γ diversity at the landscape scale, in parallel to wooded pastures, some areas of completely open pastures and large forests with good connections between them are needed to allow open and forest dependent species to persist.

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9 Appendix

Appendix I: Table showing the abbreviations of the sample sites associated with their Swiss geographical coordinates, their habitats and the numerical values of the environmental variable and the two categories of environments.

Sampling sites	TC (m ²)	DGP (m ²)	BPA (m ²)	Habitats	X Coordinates	Y Coordinates
03_A	11102.4363696991	0	30955.2044765054	WP	556337	212219
03_B	8839.23626718057	0	31049.9071281053	WP	556601	212249
04_A	5887.99241018161	10618.2932222346	20155.2367797732	NWP	554319	209837
04_B	2646.84248452999	22384.6145067203	28572.1765291055	NWP	554194	209807
05_A	0	23519.1136187428	23520.0799723306	NWP	553052	208173
05_B	0	26734.1720051985	26735.1383587862	NWP	552955	208220
06_A	30214.0112746986	0	0	F	555600	210242
06_B	30639.206942135	0	0	F	555309	210007
11_A	10079.0679202682	20274.0982710668	20275.0646246545	WP	547684	198024
11_B	6803.12925778411	13386.8962511482	13387.8626047359	WP	547768	198222
12_A	6284.623846	28769.3126610072	28769.3126610072	WP	546676	198348
12_B	8510.67607201737	19915.5810900103	27353.6046549484	WP	546478	198154
13_A	0	14685.6754730888	14937.8937594924	NWP	545953	197472
13_B	523.763644562356	496.70574410526	4201.70539955189	NWP	545905	197113
14_A	29815.8735965442	0	0	F	540552	202809
14_B	30910.7523010809	0	0	F	540474	203032
15_A	20407.4550661768	0	9734.07968944024	WP	538358	202861

15_B	10968.1132210014	0	9116.5797468658	WP	538601	203137
16_A	8274.88577193257	0	17634.0202693245	WP	536969	201536
17_A	8551.26292282068	0	8452.6948320792	WP	536369	202334
17_B	23490.1230111102	0	17875.6086662628	F	536275	202082
19_A	17755.7808213814	0	31241.2451384805	WP	532863	203099
19_B	7097.8671020489	0	30882.7279574239	WP	532649	202966
20_A	11077.3112085313	28926.828295811	28242.6499556816	WP	531105	202163
20_B	10306.1610133903	14097.166138147	19746.4692121535	WP	531282	202246
21_A	11293.7743800743	0	26290.6157084197	WP	532118	198119
21_B	8220.76997101838	0	0	WP	531700	197962
22_A	5986.56049348786	23432.141795845	25866.3864833959	NWP	530029	197206
22_B	2000.35192664959	0	667.750329137616	NWP	530052	197478

Appendix II: Table showing the abundance of the 57 species recorded for each of the 29 study sites.

Study sites	03_A	03_B	04_A	04_B	05_A	05_B	06_A	06_B	11_A	11_B	12_A	12_B	13_A	13_B	14_A	14_B	15_A	15_B	16_A	17_A	17_B	19_A	19_B	20_A	20_B	21_A	21_B	22_A	22_B	
<i>Abax ovalis</i>		7	0	0	0	0	0	6	3	0	0	0	0	0	0	12	17	2	1	0	0	7	0	0	0	0	0	0	0	
<i>Abax parallelepipedus</i>		21	4	2	1	0	0	43	26	3	0	7	8	1	0	28	15	2	10	3	0	6	0	0	0	0	1	1	0	0
<i>Abax parallelus</i>		4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	
<i>Amara aenea</i>		0	0	0	0	0	0	0	0	0	2	0	0	0	8	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
<i>Amara communis</i>		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	7	0	0	0	1
<i>Amara convexior</i>		0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
<i>Amara equestris</i>		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amara familiaris</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0
<i>Amara lunicollis</i>		0	0	3	0	1	0	0	0	2	0	0	15	1	23	0	0	0	9	1	0	0	3	0	1	4	0	0	2	1
<i>Amara montivaga</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Amara nitida</i>		0	2	1	1	0	2	0	0	1	0	2	2	0	1	0	0	0	0	0	0	0	1	0	0	3	2	0	4	1
<i>Amara ovata</i>		0	0	4	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amara plebeja</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Badister bullatus</i>		0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>Bembidion lampros</i>		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	11	0	0	0	0	0	0	0
<i>Bembidion properans</i>		0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	1	0	2	0	0	0	0
<i>Calathus fuscipes</i>		0	10	1	11	1	6	0	0	14	30	5	0	7	4	0	0	0	1	0	0	0	0	0	0	21	1	0	2	2
<i>Calathus melanocephalus</i>		0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1
<i>Carabus auronitens</i>		5	0	0	0	0	0	9	6	0	0	0	1	0	0	1	7	2	1	0	0	1	0	0	0	0	0	1	0	0
<i>Carabus convexus</i>		0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carabus coriaceus</i>		1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carabus monilis</i>		0	0	0	0	0	0	0	0	0	0	0	5	1	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0
<i>Carabus nemoralis</i>		0	0	1	1	0	1	1	4	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
<i>Carabus problematicus</i>		3	0	1	5	0	0	0	0	1	1	0	2	0	2	2	0	2	0	0	0	1	1	1	0	0	1	1	2	0
<i>Carabus violaceus</i>		1	0	0	0	1	0	2	0	0	0	0	1	0	2	3	12	0	6	5	2	0	0	5	2	0	2	0	0	1
<i>Clivina fossor</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Cychrus attenuatus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cychrus caraboides</i>		0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dyschirius globosus</i>		0	0	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	0	1	0	22	2	0	8	0	0	0	0
<i>Harpalus latus</i>		0	4	0	1	0	1	0	0	0	0	6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Harpalus rufipes</i>		0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Harpalus signaticornis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Licinus hoffmanseggii</i>		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Loricera pilicornis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	2	0	0	0	0	0	0	0	0	0
<i>Microlestes minutulus</i>		0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4	0	0	0
<i>Molops piceus</i>		2	0	3	0	0	0	1	2	1	0	2	4	0	0	1	0	2	3	0	0	3	0	0	0	1	0	3	0	0
<i>Nebria brevicollis</i>		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	1	1	0	0	1	0	0	0
<i>Notiophilus aquaticus</i>		0	0	0	0	0	4	0	0	1	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Notiophilus biguttatus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Ophonus laticollis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Panagaeus bipustulatus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1
<i>Platynus assimilis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Poecilus cupreus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	0	1	0	0	0	0	1	0	0
<i>Poecilus versicolor</i>		0	15	3	0	21	3	0	0	18	3	23	3	11	5	0	0	0	2	2	27	0	14	7	1	15	8	0	3	15
<i>Pterostichus burmeisteri</i>		33	0	2	0	0	1	2	5	0	0	1	6	0	1	9	5	22	0	1	0	16	0	0	0	0	0	14	0	0
<i>Pterostichus hagenbachii</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pterostichus madidus</i>		17	0	0	0	0	0	2	14	2	1	9	5	0	0	12	5	27	4	13	1	30	0	0	1	0	3	59	0	0
<i>Pterostichus melanarius</i>		3	0	1	1	9																								