



Composition and diversity of ground beetles within wooded pastures and alternative land-use systems in Swiss Jura mountains

Erwan Edgar Zimmermann ·
Yannick Chittaro · Sandrine Wider ·
Delphine Clara Zemp

Received: 17 December 2023 / Accepted: 4 July 2024 / Published online: 14 August 2024
© The Author(s) 2024

Abstract Wooded pastures combine trees and pastures in a land-use system resulting from traditional silvopastoral practices. With their sparse tree cover, wooded pastures represent an ecotone between open area pastures and forests with potentially high species diversity, although this is poorly tested for animal groups especially insects. In this study, we aimed to characterise and compare species communities in terms of species composition and diversity indices, biomass and ecological traits of ground beetles in wooded pastures, forests and non-wooded pastures. Pitfall traps were set up in 29 study sites located in the Swiss Jura mountains. Ground beetle communities in wooded pastures largely encompass those in open pastures and forests, although some species are found only in forests or open areas. Wooded pastures and open pastures have an equivalent species diversity level, which is significantly higher than the one in forests. Ground beetle diversity is positively correlated with the surfaces of Biodiversity Promotion Areas

within a 100 m radius. Areas with high tree cover (70–100%) favour brachypterous and hygrophilic species, whereas areas with reduced tree cover (0–20%) favour xerophilic and winged species. Ground beetles' size and biomass increase with tree cover. Wooded pastures are an important ecotone, ensuring a gradual change of land-use systems between open areas and forests, where a wide range of species from both land-use systems are found. These semi-natural systems are important for the conservation of ground beetles.

Keywords Pitfall traps · Silvopastoralism · Agroforestry · Land-use systems · Carabidae · Nature conservation

Introduction

Semi-open areas exist in all regions of the world where woody plant growth is possible. The origin of these environments can be the result of biotic (mainly animal grazing) or abiotic factors (Hartel and Plieninger 2014). In Europe, certain semi-open areas resulting from human activity are called wooded pastures. They are one of the oldest land-use systems on the continent, being known since the Neolithic period (Hartel et al. 2013). Wooded pastures are distributed across different biogeographical regions of Europe, but more abundantly in the Mediterranean or eastern regions and less frequently in Central Europe

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10457-024-01036-0>.

E. E. Zimmermann · S. Wider · D. C. Zemp (✉)
Laboratory of Conservation Biology, Faculty of Sciences,
Institute of Biology, University of Neuchâtel,
2000 Neuchâtel, Switzerland
e-mail: clara.zemp@unine.ch

Y. Chittaro
info fauna, 2000 Neuchâtel, Switzerland

(Plieninger et al. 2015). In the Jura mountain range, wooded pastures represent 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 biotope's type 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 from sparsely to densely wooded (Mosquera-Losada et al. 2009) and from extensive to intensive agricultural management. Consequently, there is no single type of wooded pasture, but a multitude depending on the management and abiotic factors (Gallandat et al. 1995).

Wooded pastures are characterised by the presence of scattered trees that represent keystone structures in an agricultural land, essential for a wide range of organisms (Fischer et al. 2010). For example, old and large trees with dendromicrohabitats provide the configuration and distribution of diverse ecological niches (Stein et al. 2014) for many groups of species (Larrieu and Cabanettes 2012) such as birds, bats, small terrestrial mammals (rodents such as glirids and predators such as mustelids), amphibians and invertebrates (spiders, beetles, wasps) (Bütler et al. 2012). As a consequence, these semi-open environments may host more varied floristic and faunistic communities than more homogeneous habitats such as open pastures or closed forests (Gillet and Gallandat 1996). The meta-analysis by Torralba et al. (2016) demonstrates that European agroforestry, including silvopastoralism in wooded pastures, generally enhances biodiversity compared to alternative land-use systems (e.g. forests or pastures). In southern Transylvania, Hartel et al. (2017) showed a greater specific and functional richness in bird communities in wooded pastures as opposed to forest and open lands. On the other hand, the meta-analysis by Mupepele et al. (2021) did not reveal any overall beneficial effects of wooded pastures compared with forests or pastures. Although semi-open environment is considered as an ecotone and fosters habitat heterogeneity, allowing both open and forest species to coexist (Díaz al. 2013), it might also be perceived as habitat fragmentation depending on the spatial scale of structure variability and the group of organisms (Tews et al. 2004).

In the Swiss Jura mountains, extensive studies have been conducted on plant associations (Gallandat et al. 1995). More specifically, microhabitat variability and configuration characterised by tree cover and altitude positively influence ground vegetation diversity (Dufour et al. 2006). In Switzerland, wooded pastures are mainly used to graze cattle during summer. The structure of woody vegetation on the pastures is therefore strongly influenced by livestock activity (Vandenbergh et al. 2007). There exists a complex dynamic between cattle browsing and tree regeneration (Peringer et al. 2016). A balanced grazing pressure is therefore necessary to insure sustainability of wooded pastures and to conserve their richness in terms of habitats and species diversity (Gillet 2008). Indeed, studies have raised awareness concerning the risk in losing such systems due to the separation between grazed lands and closed forests (Chételat et al. 2013). Therefore, in Switzerland subsidies exist to encourage farmers to exploit pastures in extensive ways. These are called Biodiversity Promotion Areas (RO 2013 4145 2013), which consist of portions of land that present rich botanical communities that farmers undertake to maintain through restricted grazing pressure and fertiliser use. Moreover, there exists an inventory of important dry grasslands and pastures for the whole Switzerland which are protected (Dipner et al. 2010). A noticeable portion of wooded pasture in the Jura mountains is composed of these dry pastures. The structural and abiotic conditions created by the Biodiversity Promotions Areas (BPA) and the dry grasslands and pastures provide essential resources such as food, breeding and overwintering areas and is beneficial for the conservation of several groups of organisms, such as plants, birds and butterflies (Zingg et al. 2019; Ravetto Enri et al. 2020), although the effects remain unknown for many groups of invertebrates, such as ground beetles.

There are several reasons for focusing on ground beetles. First, they play a fundamental role in ecosystems, both as an important source of food for many vertebrates, such as mammals (Thiele 1977), birds (Larochelle 1980) and herpetofauna (Holland 2002), and as predators of eggs and larvae of many other invertebrates (Holland 2002), while certain species feed on seeds of different weed. Hence, ground beetles influence multiple trophic groups through bottom-up and top-down processes. Second, ground dwelling carabids 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). Third, they exhibit a high sensitivity to environmental changes (types of exploitation or management, soil disturbance, renaturation) and their rapid response make them good indicators of the quality of their biotopes (Rainio and Niemelä 2003; Avgin and Luff 2010), at various spatial (Koi-vula 2011) and temporal scales.

Depending on their ecological preferences, some species (generalists) are able to colonise a large number of habitats, while others (specialists) are only found in very specific habitats (Rainio and Niemelä 2003). The degree of specialisation of species in relation to their habitats and their role in the ecosystem is reflected by the expression of ecological traits (Kotze et al. 2011; Tilman et al. 2014). Ecological traits are evolutionary adaptations reflecting the environmental conditions, measured at the level of the individuals and affecting their performance in an environment (Violle et al. 2007).

The composition of Carabidae communities is strongly influenced by microclimatic factors, in particular by temperature, moisture and shade (Thiele 1977) and habitat structure (Taboada et al. 2008). Forest cover therefore plays a major role in the distribution of carabid beetles (Jukes et al. 2001; Vanbergen et al. 2005; Söderström et al. 2001). Natural disturbances (storms, fires, etc. see for example Bouget and Duelli 2004) and human disturbances (logging) that modify the forest cover therefore have a major impact on ground beetle communities. For example, clear-cutting drastically alters the composition of the carabid fauna present (Thiele 1977). The large and specialised species are the most sensitive to disturbance (Lövei and Sunderland 1996; Halme and Niemelä 1993), and are often found in forest environments (Langraf et al. 2017).

Although carabid communities in forest and open environments have long been studied in Europe (see for example Thiele 1977; Butterfield et al. 1995), semi-open environments such as wooded pastures have been the subject of very few studies (Talvi 1995; Söderström et al. 2001; Vanbergen et al. 2005; Taboada et al. 2006a,b), and even fewer in Central Europe (Eggers et al. 2010; Boutaud et al. 2022).

Here, we chose ground beetles as a model group of species to explore community composition and diversity within wooded pastures in Switzerland.

We included two other land-use systems that are frequently found in the region, open pastures and forests, in order to represent the full gradient of tree cover. Our objective was to investigate (1) how ground beetle communities differ between the different land-use systems, (2) in relation to which environmental variables? And consequently, (3) what are the resulting differences in ecological traits (wing morphology, moisture preference, and average body size)? We first investigated differences in ground beetle communities between wooded pastures and the two other land-use systems. We hypothesised that:

- i. Wooded pastures harbour a large proportion of the carabid communities of neighbouring grasslands and forests, with the exception of a few specialised species.
- ii. Ground beetle species diversity indices (i.e. based on richness, Hill-Shannon and Hill-Simpson indices) and biomass are higher in wooded pastures than in forests and non-wooded pastures due to higher heterogeneity, and are influenced by environmental factors (tree cover, dry grasslands and pastures and Biodiversity Promotion Areas) hereafter referred to as “environmental variables”.

Finally, we tested the relationship between the same environmental variables and a set of important functional traits of ground beetles. The following traits were selected: (a) wing morphology as indicator of dispersal ability in relation to the degree of environmental disturbance (Gobbi et al. 2007), with species adapted to unstable conditions generally have better dispersal capacity (Niemelä 2001) than species in more stable environments; (b) moisture preference (hygrophilic, mesophilic, xerophilic, steno-hygrophilic, mesophilic-hygrophilic) as indicator of hygrometric characteristics between sites; (c) average body size (in mm) as indication of ground beetle mass. We hypothesised that (iii) species in the most open and dynamic environment (i.e. low tree cover, high BPA and dry grasslands) will have good dispersal capacities, be xerophilous and small in size, while species in more closed and stable environments (i.e. high tree cover, low BPA and dry grasslands) will be less mobile, hygrophilous and large in size.

Material and methods

Study area and sample design

This study was conducted in the Jura mountains of the canton of Neuchâtel in Switzerland (Fig. 1a). The altitude of the study sites was between 1037 and 1436 m. 29 collection sites with a minimum distance of 200 m were distributed in three different land-use systems (forests, pastures with little or no tree cover and wooded pastures) were studied (Table S1). The categorisation of these three land-use systems was done using the phytocenosis typology of Gallandat et al. (1995): 0–20% tree cover indicates “pastures with little or no trees” (NWP), 20–70% indicates “wooded pastures” (WP) and 70–100% tree cover indicates “forests and grazed

wood” (F). The percentage of tree cover was calculated within 100 m radius of the trap centroid for each study site using aerial remote sensing data (LIDAR). The choice of the 100 m radius and minimum distance between sites was chosen according to previous studies (Söderström et al. 2001; Mcadam et al. 2007, Müller and Brandl 2009; Lindberg et al. 2015). These LIDAR data were derived from the 2016 individual tree layer (30 pt/m²) and the 2018 forest cover layer (15 pt/m²) of the Canton of Neuchâtel (Données cartographiques du SITN, Service de la Géomatique et du Registre Foncier 2023). The forests of our study sites were mainly composed of beech tree and some conifers, which is related to the phytosociological classifications *Abieti-Fagenion* or *Lonicero-Fagenion* (Delarze et al. 2015). WP and NWP collections sites were at a minimum distance

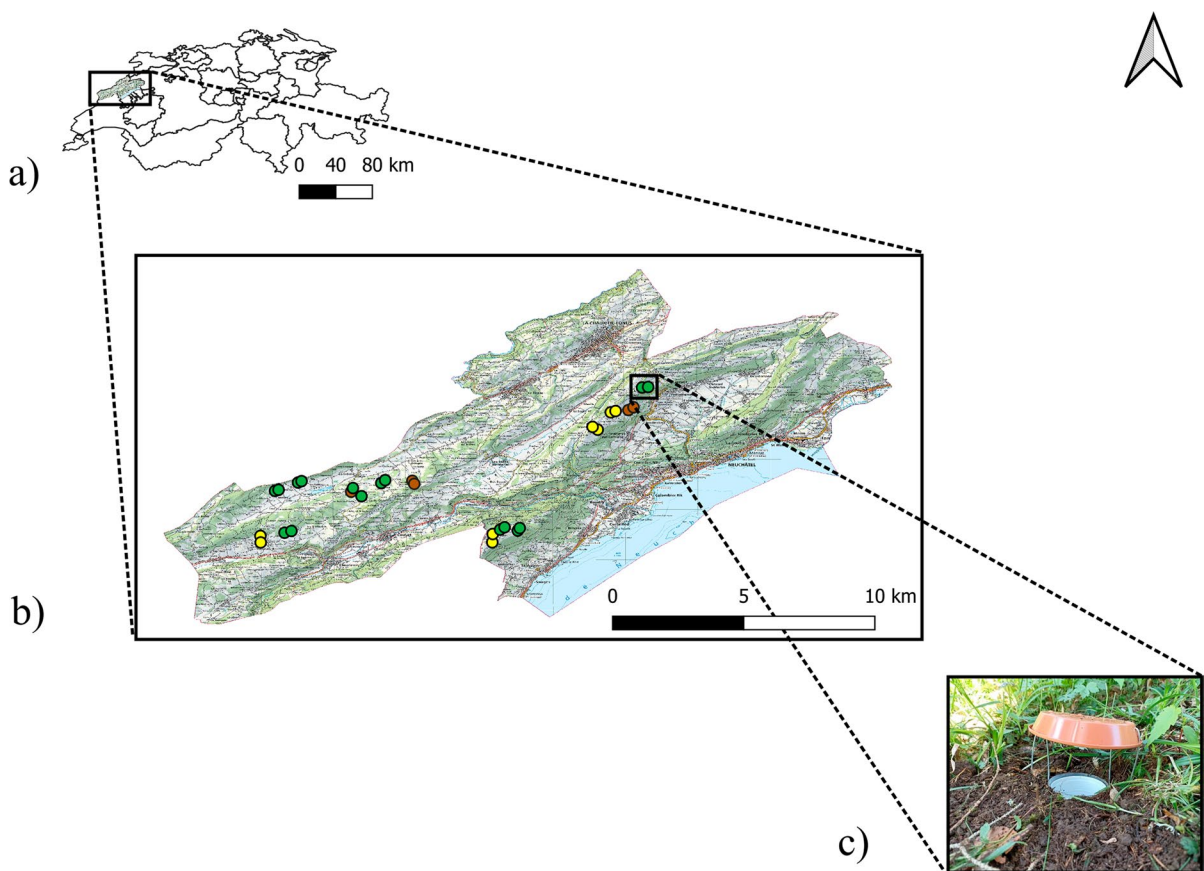


Fig. 1 Illustration of the study design. **a** location of the canton of Neuchâtel within Switzerland. **b** distribution of the 29 study sites (see Table S1 for details) across this canton (forests

and grazed wood (F) in brown, pastures with little or no trees (NWP) in yellow and wooded pastures (WP) in green). **c** pitfall trap used in this study. (Color figure online)

of 100 m from forest edges. The distances between NWP sites and WP sites were ranging between 10 and 100 m, with the majority of the distances being of 100 m and one extremely short distance being of 10 m (see Fig. S1 in the supplementary material for the histogram of the distances between WP and NWP sites). These distances were chosen according to scales used in previous studies (Söderström et al. 2001; Mcadam et al. 2007, Müller and Brandl 2009; Lindberg et al. 2015).

In each of the 29 study sites (5 F, 8 NWP, 16 WP; Fig. 1c), 3 pitfall traps were set up in a triangle. The distribution of traps by land-use system was unbalanced, because the main focus of the study was carabid's species assemblages and diversity in wooded pastures. We incorporated NWP and F sites to have representations of land-use systems to cover the full gradient of tree cover. Each trap was constituted of two cups (of diameter of 73 mm and a height of 117 mm) 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 supported by a wire to avoid overflow in case of rain and plant debris in the traps (Spence and Niemelä 1994) (Fig. 1b). 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). Each trap was spaced 1 m apart and surrounded by a fence, sometimes electrified, to prevent destruction by livestock as much as possible. 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. seven trap collections in total. The three traps at each study site were pooled into a single sample during each survey. 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 content of the traps was then preserved in a 70% alcohol solution. Trapped ground beetles (Carabidae family) were identified to species level using the identification keys of Freude et al. (2006). After identification, the insects were dried in an oven at 60 °C (Lindroth et al. 1993) for approximately 24 h (Hóðar 1996), although other methodologies use a shorter drying time (Hausmann et al. 2022). The dried insects were then weighed using a JB803-C Caratbalance. To obtain an average biomass value for each site, the dry mass of insects was then summed up and divided by

the actual number of surveys in each site (7 or less, depending on the number of missing surveys due to damaged traps).

Environmental variables and ecological traits

The variables tree cover (TC), Biodiversity Promotion Areas (BPA), dry grasslands and pastures (DGP) were calculated by percentage cover in the study sites. BPA and DGP are categories derived from the Swiss agricultural management policy. All these data were provided by the canton of Neuchâtel through spatial information layers (Données cartographiques du SITN, Service de la Géomatique et du Registre Foncier 2023). The area (in m²) of these variables was calculated within a radius of 100 m around the trap centroid for each study site using QGIS (version 3.26) (Table S1). A Pearson correlation test using the “Spearman” method was carried out and the variables considered were significantly uncorrelated. Rho of BPA and DGP is 0.3861668 and *P* value=0.039. Ground beetles' ecological traits, valid in Switzerland, were extracted from Klaiber et al. (2017). The wing morphology trait included the following levels: wingless, brachypterous, dimorphic and macropterous. For statistical analysis, brachypterous and wingless were grouped together as these two trait levels provide the same movement abilities.

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).

We first explored the differences in species composition and diversity across the different land-use systems. The representation of the species that are shared among the different land-use systems was done using the Euler diagram of the “eulerr” package (version 7.0.0). A chi-square test was performed to check for similarities in species compositions between WP and NWP plus F, as this method is well-suited for unbalanced data (Gopi et al. 2016). The chi-square matrix compared the expected species assemblage according to H_0 (no species should be common between WP and NWP plus F) and the observed species assemblage. Non-metric multidimensional scaling (NMDS) was used to display carabid beetle assemblages. The

NMDS was computed using Horn similarity index (Horn 1966), as it is sensitive to rare species in assemblages and it is suitable for differences samples densities (Jost et al. 2011). The analysis was run with the package *vegan* (version 2.6-4) (Oksanen et al. 2022).

Total species diversity (gamma diversity) indices for each land-use system were computed by combining species abundance matrix per land-use type and rarefying according to sample size. The reference value for the sample size was chosen as the land-use with the fewest ground beetles, namely NWP with 257 individuals. We used the *estimatedD* function in the *iNext* library (version 3.0.0) (Hsieh et al. 2016) to determine diversity indices by rarefaction and extrapolation for the three land use systems. We followed the methodology by Hill (1973) that provides unified diversity indicators with proportional abundance on the same scale, also called “effective number of species”. We calculated species diversity with Hill numbers $q=0, 1, 2$ that are based on species richness, Shannon and Simpson diversity, respectively (Chao et al. 2014). Species richness is more sensitive to the presence of locally rare species, whereas Simpson favours the presence of dominant species, and Shannon favours neither of both. We weighted the average biomass per study site, accounting for the number of valid surveys only. The average body size was calculated by adding the respective average body size of the individuals per site, then this sum was divided by the total number of individuals at the specific site.

Second, we focused on alpha diversity, within study sites. The response variables of our study were: species richness, Hill-Shannon, Hill-Simpson, biomass and average body size. For all 29 sites studied, the three diversity estimates (richness, Hill-Shannon, Hill-Simpson) were rarefied according to the study site with the lowest number of individuals. Each of these response variables were then entered into a linear model and related to TC, DGP and BPA as the explanatory quantitative variables. As the forest sites contained very few DGP and BPA by definition, we applied our model with and without the 5 F sites to account for potential confounding factors between the land-use type and the environmental variables. To account for the hierarchical nature of our design (collection sites being paired within study sites), we applied mixed effect models with sites as a random factor. Since the random factors were not significant,

we applied simple linear models (without the random factor). For transparency, both types of models are presented in the supplementary tables (Table S4 to S5) but only simple models are discussed in the text. We tested for outliers using the *outlierTest* function in the *car* library (version 3.1-1). Consequently, sites 12_B (WP), 20_A (WP) were found to be outliers in linear biomass model, and Hill-Simpson model respectively, and excluded from the analysis. We checked model assumptions (normality, heteroscedasticity, linearity of the residuals) using the package “performance” and *qqplots* (version 0.10.1) (Lüdtke et al. 2021). All models fulfilled the assumptions (except for the model of carabid biomass, with study site as random effect and excluding forest sites, but which is not presented in the text). Finally, we tested for correlation between explanatory variables using VIF values with the function *vif* in the *car* package (version 3.1.1) and considering a VIF value of 5 as a threshold for correlation (James et al. 2013). In all the models, no explanatory variable was correlated. A Kruskal–Wallis test with the “Bonferroni” adjustment method was performed to compare the biomass between the 3 land-use systems (F, NWP, WP). 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 variables, followed by an ANOVA. Study site 12_B was removed from the dataset because of outlier characteristics. While there is no formal and widely accepted definition of an outlier in principal component analysis, here outliers have been detected visually following previous recommendations (Jolliffe 2002).

Results

Carabid assemblage

In total, 1710 individuals of 57 species were caught, ten of which are threatened in Switzerland (Table S2). 48 species were found in WP, 34 in NWP and 22 in F (Table S2, Table S3). 88% of the NWP species and 68% of the F species were found in wooded pastures.

The number of species observed exclusively in F is 3, 6 in NWP and 11 in WP (Fig. 2).

Results from the chi-square test indicate that wooded pastures significantly include species that are present in F and NWP ($\chi^2=36.923$, $df=2$, $P<0.001$). Representations from the NMDS indicate that ground beetle communities (including species abundance) in the NWP and F were relatively similar to those in the WP as shown by the WP ellipse encompassing mostly NWP and F communities (Fig. 3). 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.

Diversity parameters and biomass

Diversity indices

Diversity indices including species richness ($q=0$), Hill-Shannon index ($q=1$) and Hill-Simpson index ($q=2$) are the lowest in the F land-use system compared to NWP and WP (Fig. 4). Because the 95%

confidence intervals do not overlap at 257 individuals (i.e., the reference level), the rarefied diversity indices are significantly different between F compared to NWP and WP. These differences remain significant regardless of the diversity index (with $q=0$, $q=1$ and $q=2$), i.e. when differentially accounting for relative abundances of species. On the other hand, diversity indices in NWP and WP are not significantly different (confidence intervals overlap at the reference level).

The linear models showed that the Biodiversity Promotion Areas (BPA) variable had a positive effect on the three diversity indices (Fig. 5). However, BPA effect was only marginal on species richness ($q=0$) ($df=3$, $F\text{-value}=1.822$, $R\text{-squared}=0.179$, $P\text{ value}=0.101$) and on the Hill-Simpson index ($q=2$) ($df=31$, $F\text{-value}=1.2653.175$, $R\text{-squared}=0.13608$, $P\text{ value}=0.109086$). The effect of BPA was close to significance on the Hill-Shannon index ($q=1$) ($df=3$, $F\text{-value}=2.283$, $R\text{-squared}=0.215$, $P\text{ value}=0.0862$), and marginally related to Hill-Simpson index. The estimates and coefficients obtained from these three linear models are presented in the supplementary material (Table S4). Linear models excluding forest land-use system showed similar

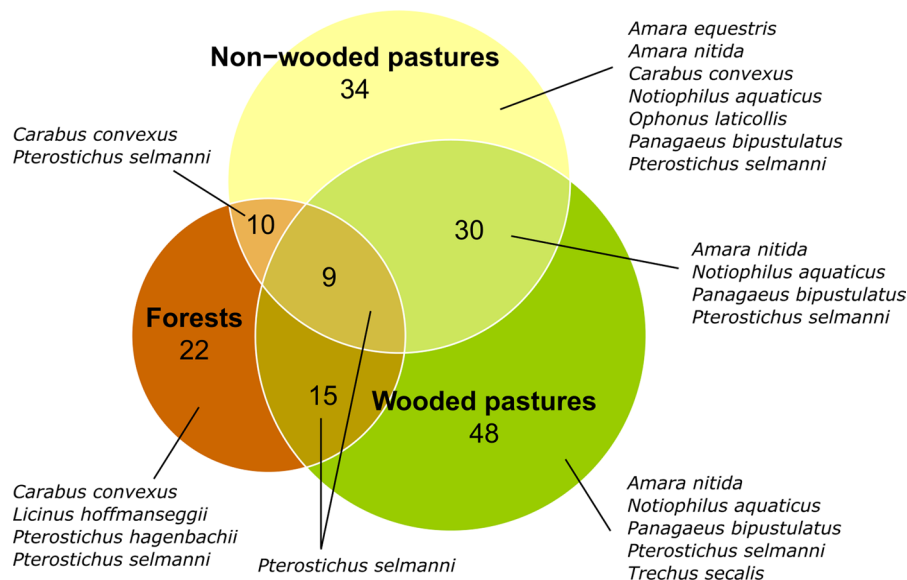


Fig. 2 Euler diagram with three coloured circles representing the three land-use systems: Wooded pastures (green), Non-wooded pastures: pastures with little or no tree (yellow) and Forests and grazed wood (brown). The numbers in the disjoint sets (non-overlapped circles) indicate the total number of species per land-use system. The intersection of the sets (overlap-

ping circles) indicate the number of species common to two or three land-use systems. The species mentioned in the land-use systems refer to threatened ground beetles according to the Swiss red list (Chittaro et al. 2024, in press). (Color figure online)

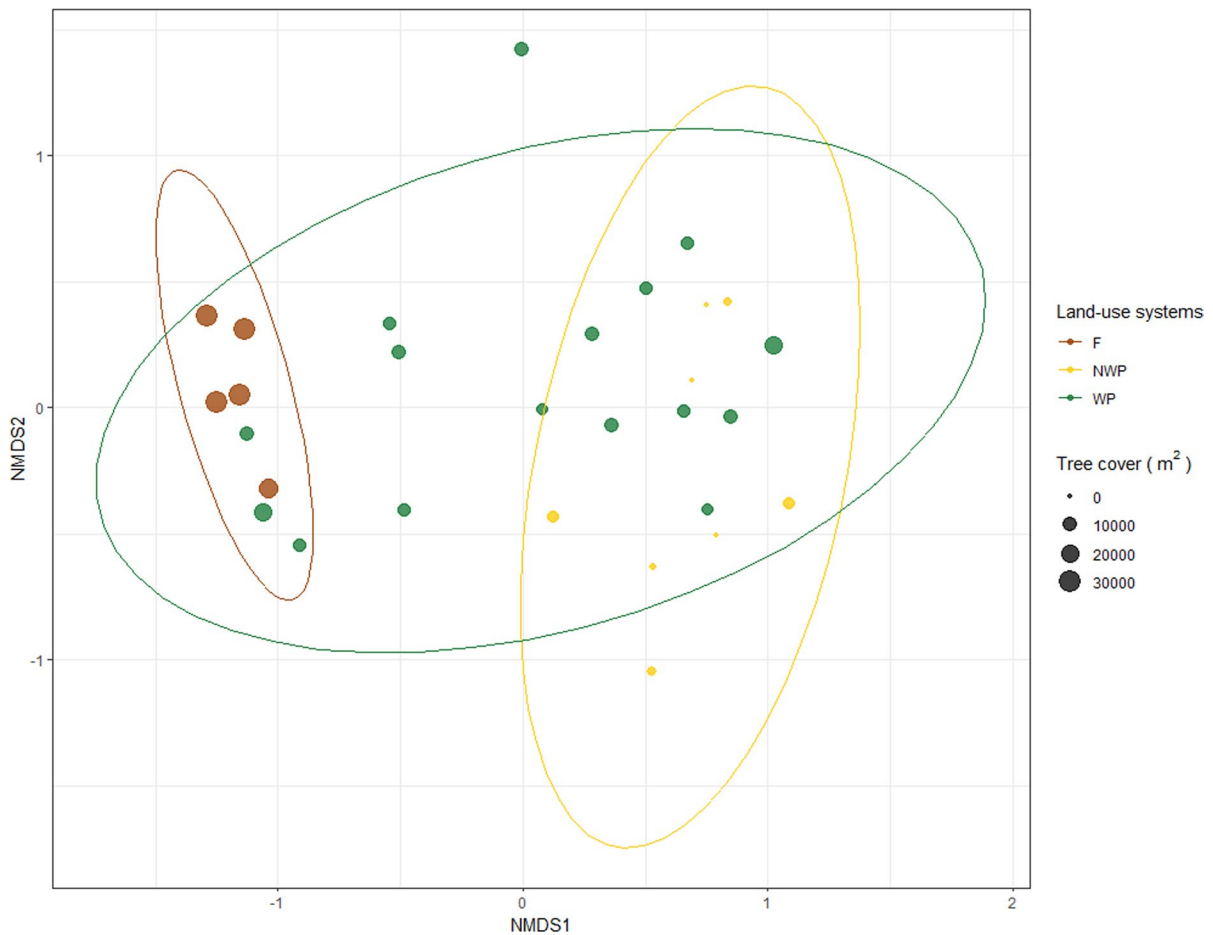


Fig. 3 Non-metric multidimensional scaling ordination of the 29 ground beetle assemblages. The colour indicates the land-use system (brown, F=forests and grazed wood; yellow, NWP=pastures with little or no trees; green, WP=wooded pastures). The size of the dots indicates the surface of tree

cover in each study site. The ellipses are the 95% confidence interval drawn around the centroid for each land-use type. Stress value for the analysis is 0.16 for the reduced dimensions of $k=2$. (Color figure online)

results, although the effects were weaker. The estimates and coefficients obtained from these supplementary models are presented in the supplementary material (Table S4 to S5).

Carabid biomass

Linear regression showed that the increase of tree cover significantly enhanced the ground beetle biomass (Fig. 6a). ($df=3$, $F\text{-value}=12.71$, $R\text{-squared}=0.613$, $P<0.001$). Forests had a significantly higher ground beetle biomass than WP and NWP (Kruskal–Wallis, $\chi^2=11.01$, $P<0.01$) (Fig. 6b). No valid model could be found for carabid

biomass when excluding forest study sites, even when excluding outliers or transforming response or explicative.

Ecological traits

Wing morphology

The measured environmental variables (TC=tree cover, BPA=Biodiversity Promotion Areas, DGP=dry grasslands and pastures) explained 30.41% of the variation in the composition of carabid wing morphologies across the study sites. Wing morphology was significantly influenced by TC ($df=1$,

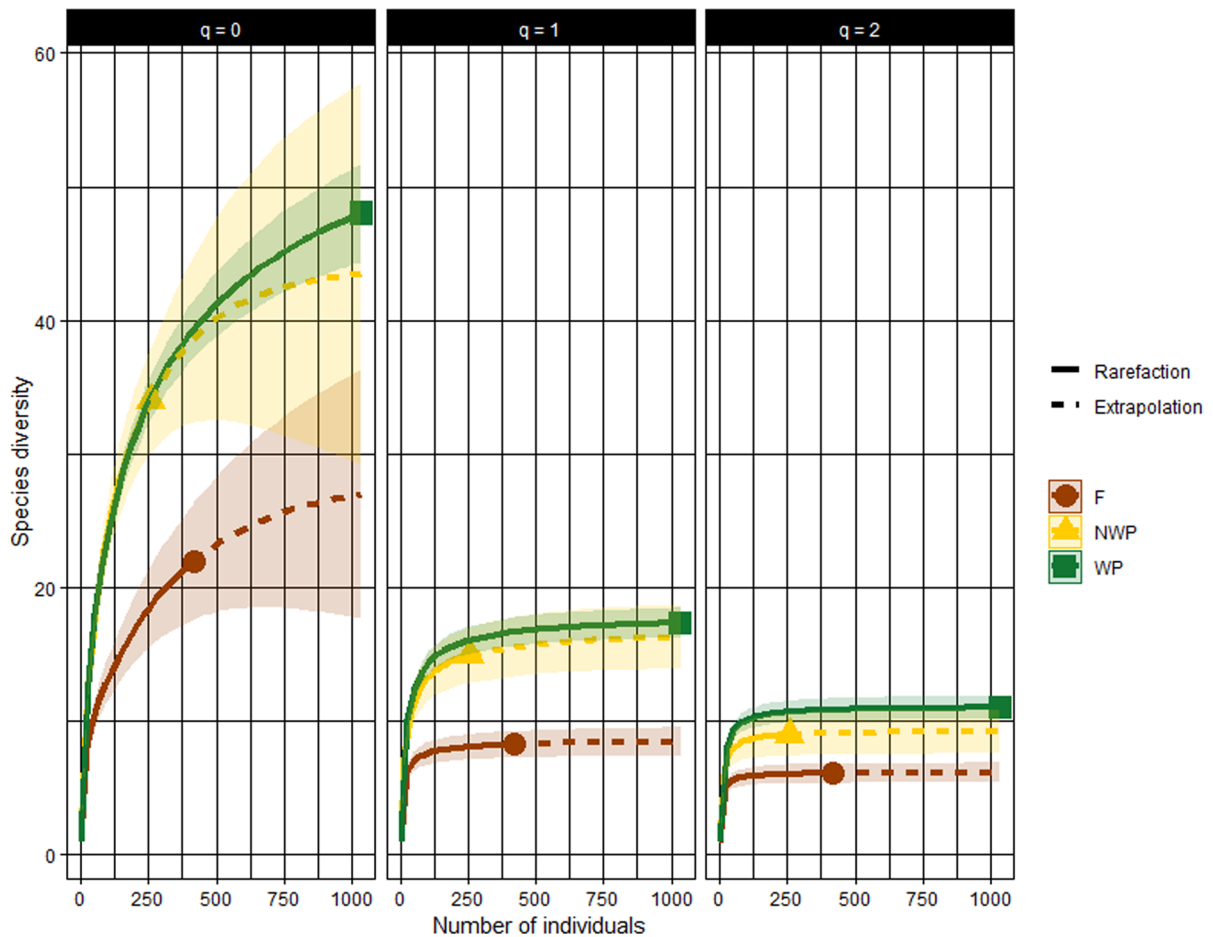


Fig. 4 Rarefaction (solid line) and extrapolation (dashed line) curves with the 95% confidence intervals for the three Hill number species diversity indices (left to right: Richness, Hill-Shannon index, Hill-Simpson index). Forests and grazed wood (F) are represented in brown, pastures with little or no trees

(NWP) are represented in yellow and wooded pastures (WP) are represented in green. The symbols represent the observed diversity indices, i.e. diversity indices at the total number of individuals sampled per land-use system. The x-axis represents the number of individuals and the y-axis the diversity index

F-value=9.776, $P < 0.001$). The variable DGP had no significant influence on this ecological trait ($df = 1$, F-value=0.241, $P > 0.05$), idem for variable BPA ($df = 1$, F-value=0.467, $P > 0.05$). Individuals with reduced wings (i.e. brachypterous and wingless species) were associated with a high tree cover, whereas individuals with developed wings (i.e. macropterous species) were associated with low tree cover. (Fig. 7a).

Moisture preference

The measured environmental variables explained 25.49% of the variation in the composition of

carabid moisture preference across the study sites. Moisture preference of ground beetles was significantly influenced by tree cover ($df = 1$, F-value=6.698, $P < 0.001$). The variable DGP did not influence this ecological trait ($df = 1$, F-value=1.074, $P > 0.05$), idem for variable BPA ($df = 1$, F-value=0.440, $P > 0.05$). The species with hygrophilic tendency was associated with increasing tree cover. In contrast, the species with xerophilic tendency were associated with a high proportion of both BPA and DGP in a 100 m radius (Fig. 7b).

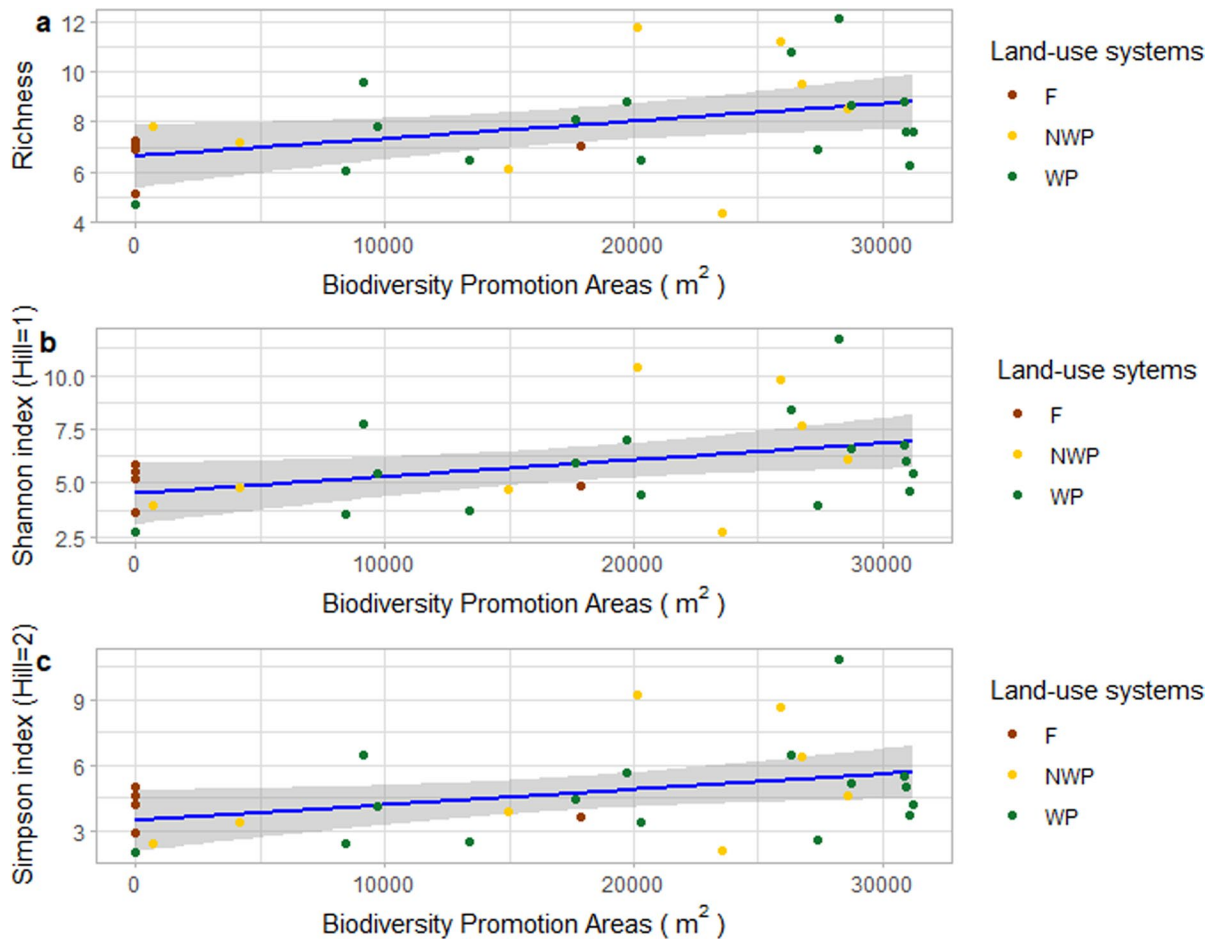


Fig. 5 Scatterplots showing the relationships between the explanatory variables, Biodiversity Promotion Areas and the three response variables, the three Hill number for species diversity indices: **a** richness ($q=0$), **b** Hill-Shannon index ($q=1$) and **c** Hill-Simpson index ($q=2$) rarefied at

257 individuals. Land-use systems are described by dots of three different colours (brown=forests and grazed wood (F), yellow=pastures with little or no trees (NWP) and green=wooded pastures (WP)). (Color figure online)

Average body size

Linear regression shows that the average body size of individuals was positively related to tree cover ($df=3$, $F\text{-value}=12.71$, $R\text{-squared}=0.613$, $P<0.001$). In general, larger ground beetles were increasingly present as tree cover increases, and conversely, smaller ground beetles were increasingly present as tree cover decreases (Fig. 8). The estimates and coefficients obtained from these supplementary models are presented in the supplementary material (Table S4 and S5). On average, the largest individuals were found in F, followed by WP and finally NWP.

Discussion

Carabid assemblage

The results show that the species assemblage of ground beetles in wooded pastures includes a large number of species common to both forests and non-wooded pastures. Hypothesis (i) is thus confirmed since ground beetle communities in wooded pastures largely encompass grassland and forest communities. Our study confirms similar results obtained by Boutaud et al. (2022) in Germany and by Talvi (1995) in Estonia. Our results also corroborate those obtained in the tropics by Ariza et al. (2021). Indeed, early

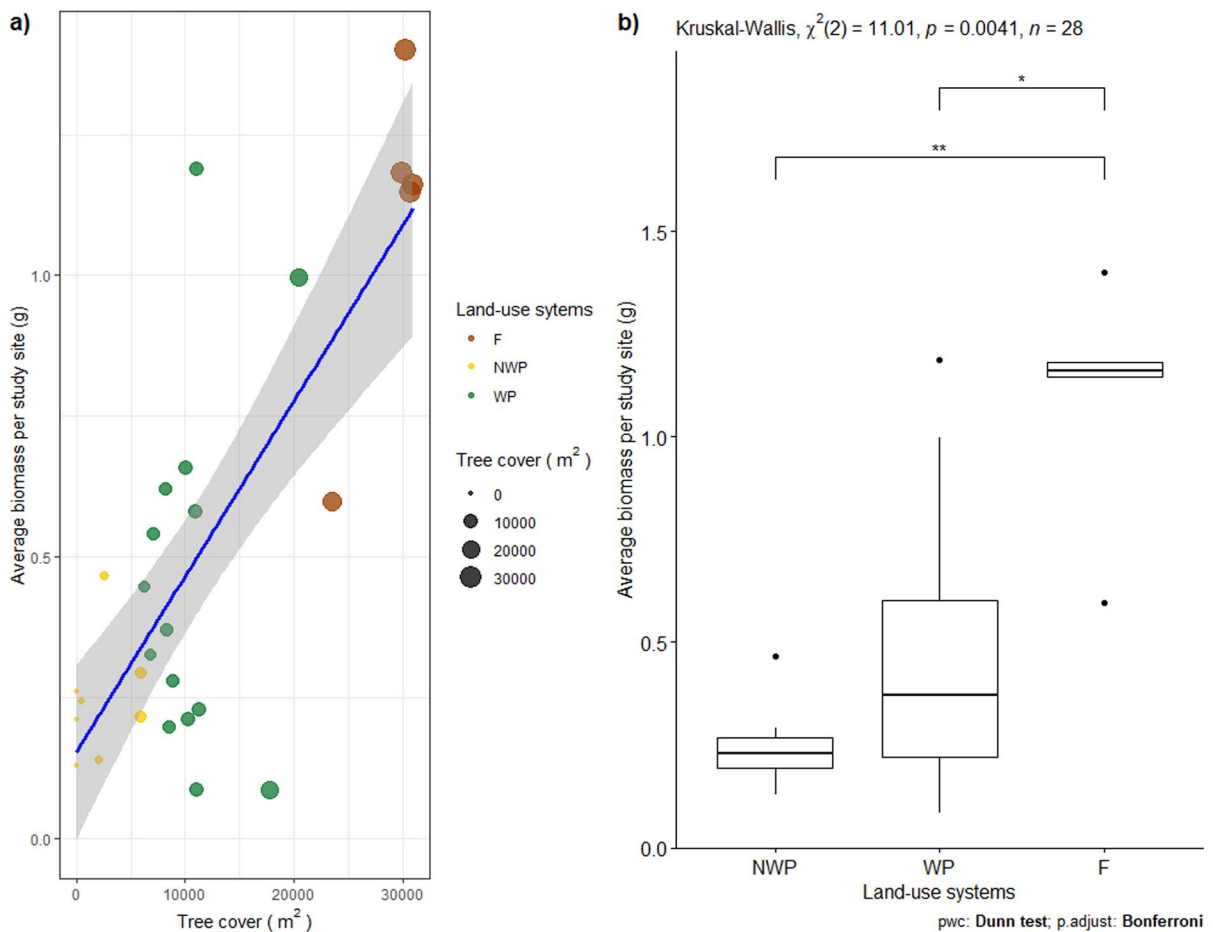


Fig. 6 **a** Scatterplot showing the relationship between carabid biomass and tree cover. The land-use systems are described by dots of three different colours: brown=forests and grazed wood (F), yellow=pastures with little or no trees (NWP) and green=wooded pastures (WP). The size of the dots indicates the surface of the tree cover of the study sites as defined in the

graph legend. **b** Boxplot representing ground beetle biomass for the three land-use systems. Interquartile range and extreme values are indicated for each land-use system. The significance level between land-use systems is indicated by asterisks (** for $P < 0.005$ and * for $P < 0.05$). (Color figure online)

successional habitats in Colombia, having undergone agricultural abandonment between 3 and 7 years, presented an assemblage of communities that overlapped with pasture and forest communities. The early successional habitat would be a mixed environment grouping together ecological elements of pastures and forests, thus a heterogeneous environment that could be exploited by a subset of ground beetle species.

According to our results, it appears that the wooded pastures of the Jura mountains act as a transition zone between forests and non-wooded pastures. Ground beetle communities in WP tend towards grassland assemblages when the semi-open area is

sparsely wooded. In contrast, WP tend towards a forest assemblage when they have a higher cover of trees (>50% of TC). The heterogeneity of the WP, therefore, results in the assemblages of certain species that are usually found in different 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).

Wooded pastures probably also allow improved connectivity between neighbouring land-use systems, resulting in easier exchange of certain individuals between habitats. The exchange of individuals would

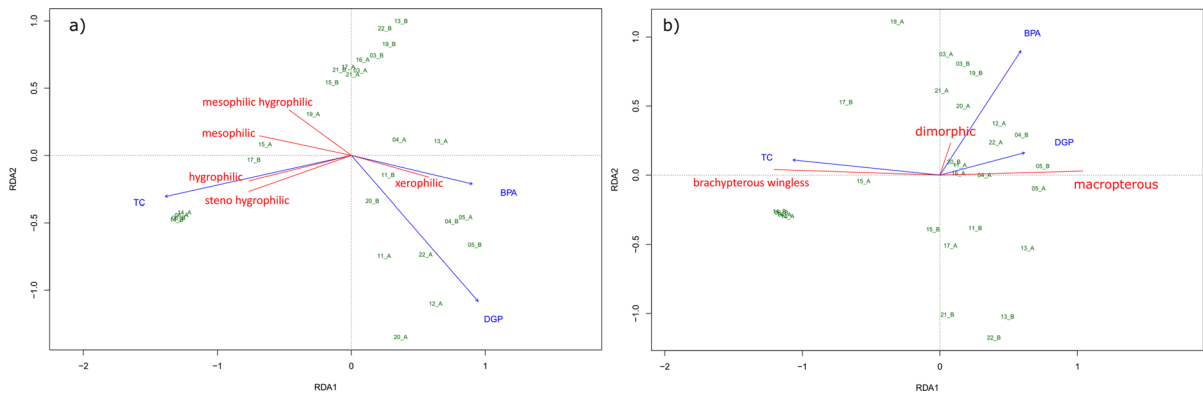


Fig. 7 Two redundancy analysis triplot plots showing the relationship between environmental variables in blue, ground beetle communities in green and ecological traits in red: moisture preference (a) and wing morphology (b). The 29 study sites in

green are abbreviated by a number and a letter (see Table S1). *TC* tree cover, *BPA* biodiversity promotion areas, *DGP* dry grasslands and pastures. (Color figure online)

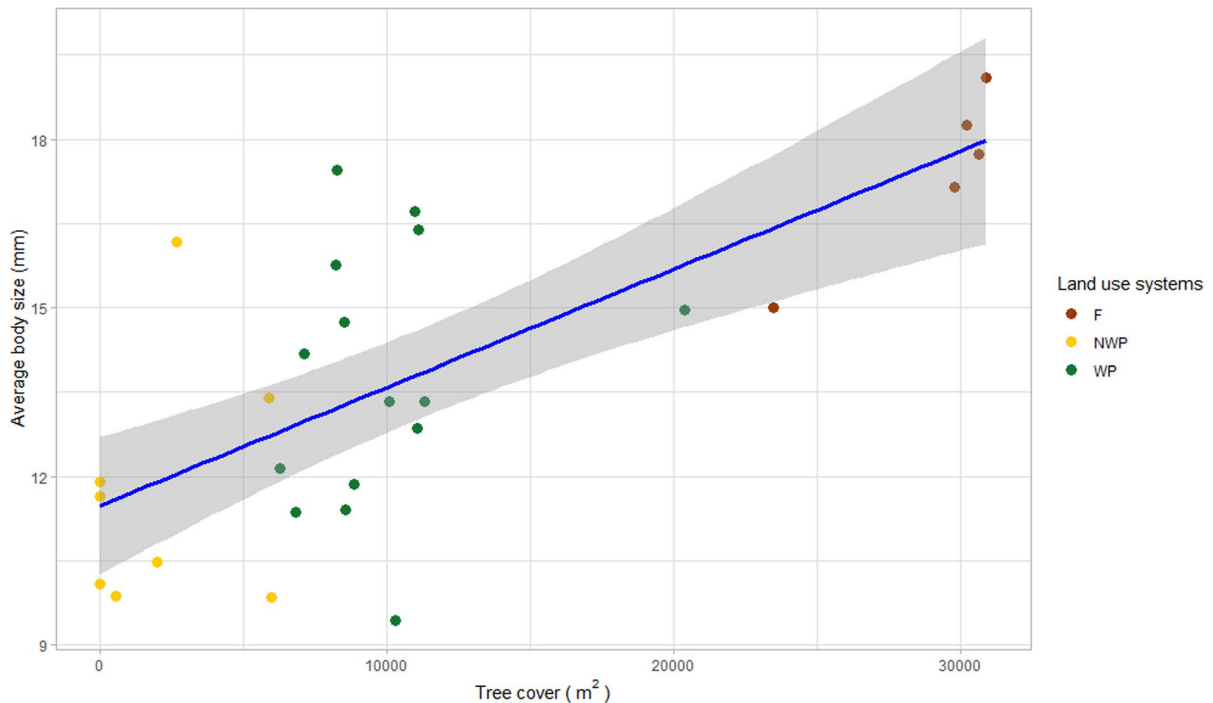


Fig. 8 Scatterplot showing the relationship between tree density and average body size of ground beetles. Land-use systems are described by points of three different colours: brown = for-

ests and grazed wood (F), yellow = pastures with little or no trees (NWP) and green = wooded pastures (WP)

be reduced in a steep interface (Eycott et al. 2012) from F to NWP, without WP ensuring the transition between land-use systems, many forest species being reluctant to cross open areas (Riecken and Raths 1996). Eggers et al. (2010) have effectively

demonstrated that semi-open corridors, resembling wooded pastures, allow certain forest carabid species to migrate and guarantee a connection across open and forested areas. This is particularly important for forest species, which are more likely to be affected by

habitat fragmentation than open-area species, which generally have better dispersal capacities (Niemelä 2001).

A substantial proportion of ground beetles were found in wooded pastures, which otherwise only exist in F or NWP. Thus, the 48 ground beetle species collected in the wooded pastures of our study represent 14% of the 342 species of native carabid beetles to the Swiss Jura Arc (info fauna 2023). If we consider all the wooded pastures in the Jura Arc, and not just those in the canton of Neuchâtel where this study was carried out, this percentage should even increase slightly, making wooded pastures an environment used by many ground beetle species. Some rare and threatened species are also concerned, as five species on the red list (Chittaro et al. 2024, in press) have been found in the WP.

Nevertheless, some species were only found in NWP and F, indicating that some stenoeconomic species cannot tolerate a semi-open environment, like wooded pastures. Structural attributes of vegetation (plant strata) 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). Fragmentation can cause disruption of key biological processes, such as dispersal and resource acquisition (Saunders et al. 1991). This habitat discontinuity favours generalist species at the expense of specialist species of adjacent land-use systems (Lövei et al. 2006), making wooded pastures not suitable for the preservation of strict open and forest specialist species.

Diversity parameters

We cannot confirm the research hypothesis (ii), but we have nevertheless shown that WP and NWP have equivalent total (gamma) diversity indices, and that both have significantly higher gamma diversity indices than F. However, the diversity indices are non-significantly different between WP and NWP. These observations are consistent regardless of whether the relative abundances of species are considered, i.e. accounting mainly for common species (as with Hill-Simpson) or also for locally rare species (as with species richness). Furthermore, the asymptotes were already tending towards horizontality when considering relative abundances of species (with Hill-Shannon and Hill-Simpson),

indicating that sampling efforts were sufficient for capturing the entire community of the common species in the three land-use systems. In general, open pastures and wooded pastures in the study area contain twice as many “effective numbers of species” than forests (based on Hill-Shannon). Because our methodology captured carabid beetles for more than 3 months, observations of several individuals in the same place indicate that they are likely in their habitat. However, we cannot rule out the possibility that a species observed only once in a place was not in its habitat, which is one of the reasons why we rely on the effective number of species instead of species richness.

The variable “Biodiversity Promotion Areas” is positively related with the local (alpha) diversity indices, in our study sites. Although significance was marginal for species richness and Hill-Simpson, and only close to significance for Hill-Shannon when considering the significance threshold at 0.05. Due to our very small sample size, we believe that marginal significance can be considered as an interesting effect as *p* values are very dependent on sampling size (Sullivan et Feinn 2012). Excluding the forest category that contained almost no BPA by definition changes slightly the strength of the results (effect of BPA on species richness is no longer significant) although the overall patterns remain unchanged. This confirms the result of Aviron et al. (2009) who showed that several taxa including ground beetles benefit from these environmental promotion measures in Switzerland, both in terms of species richness and species assemblage. These areas also improve ecosystem services such as pollination and natural pest control (Tschumi et al. 2016). Concretely, several extensive agricultural measures (Article 59 of the national direct payments ordinance) exist to promote biodiversity in agricultural lands, such as conserving indicator flora, maintaining favourable (micro-)structures (such as undergrazed areas, bushes, stones, wetlands or bare ground), preserving isolated trees, keeping mosaic of areas with staggered use over time, etc. (Stäheli et al. 2010). All these measures applied in Biodiversity Promotion Areas are therefore not detrimental for the ground beetles or might even be beneficial for them, many of whose species are often dependent on specific small structures. 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.

The change in species assemblage occurring at the boundary between different land-use systems is sometimes accompanied by increased biodiversity, although there is no consensus on this (Kark and van Rensburg 2006). Our study confirms the results obtained by Molnár et al. (2001) and Boutaud et al. (2022), which demonstrate that species diversity is higher in open and semi-open areas or forest edges than in forests. Molnár et al. (2001) did not show any significant differences between the diversity of open and forest edge areas, which resemble a semi-open ecotone between grasslands and forests where micro-sites favouring higher diversity are found.

The lower species richness and diversity in F than in open and semi-open areas is not easy to explain. This lower diversity in this land-use system is noted by Luka et al. 2009, who indicated that forests in Switzerland naturally contained fewer species of Carabidae than in other more open natural environments. Litter thickness seems to be a major factor linked to 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 strict forest species, as biotic interactions are probably more complex in this environment. In fact, litter would interfere with the movement and foraging of ubiquitous species of more open habitats, which are not adapted to such an environment (Guillemain et al. 1997).

It is an arduous task to explain why diversity indices are not different between WP and a more homogeneous habitat, the NWP. According to the study by Lacasella et al. (2015), the distance estimation 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 effect of carabids from other woodlands in the vicinity of NWP, randomly coming into NWP plots, as they might be able to move more than what we were expecting. The dispersal abilities of carabid beetles are still insufficiently known and, above all, can vary greatly from one species to another, depending in particular on their wing morphology (see paragraph below). Another hypothesis as to why NWP have such a high species diversity is that there may be a particularly

wide variety of discrete micro-structures in this environment, such as stones, rocky outcrops, puddles, bare soil patches or unevenness of the soil created by livestock trampling, which might satisfy a large number of species (Chittaro et al. 2024, in press).

Carabid biomass and average body size

We refute research hypotheses (ii) and (iii) about ground beetle biomass and average body size respectively and propose from the results that, in the context of the study, tree cover is significantly and positively correlated with ground beetle biomass and average body size. Consequently, the biomass and average body size is highest in F, followed by WP and the land-use system with the lowest values is NWP.

One explanation could be linked to the productivity of the different habitats. Fernández-Tizón et al. (2020) shows that arthropod biomass in semi-natural grasslands is directly and positively related to primary production. 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 (e.g. dry pastures dotted with lapiez with a thin layer of organic matter above the bedrock) should favour species with smaller average body sizes (Sustek 1987). On the contrary, in forest environments, ground beetles are known to have a larger body size on average than in other less forested environments based on values from Klaiber et al. (2017).

A second explanation is linked to the disturbance of the habitats. 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, in particular due to grazing and the addition of fertilisers and livestock dung. These ephemeral energy sources favour species with smaller bodies according to Schoener and Janzen (1968). A habitat with a fluctuating energy source is indeed more easily exploited by widespread, dispersive individuals capable of flight with standing large variations in population size, and such species are more likely to be characterised by small body size (Gaston and Lawton 1988). It should be noted that disturbances also occur in forests in the context of their management, but these are in principle sporadic

activities in a short period of time comparatively (even though they can be very intense).

Wing morphology

Our results show that tree cover has a significant influence on the wing morphology of ground beetles present in the three different habitats and confirm previous results.

Brandmayr (1991) showed that brachypterous species are few in number in the early stages of a habitat succession, but their numbers increase as open areas begin to be colonised by trees and shrubs. This is also confirmed by Gobbi et al. (2007), who studied the assemblage of terrestrial beetles during glacier retreat. Indeed, areas recently freed from the ice, with unstable, stony and loose soil, have low numbers of brachypterous, but a higher number of macropterous species, whereas 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 temporary environments (pioneer, ruderal, meadows, etc.), ground beetles need to disperse continuously to find favourable biotopes, and are thus mostly macropterous (Den Boer 1970). These continually disturbed open environments (by animal grazing and land clearing, in the case of our study), slows down the advance of woody plants. The macropterous species therefore have a high dispersal capacity, guaranteeing their survival thanks to the flight induced by their developed wings (Roff 1990; Shibuya et al. 2014). This flight capacity gives them a clear advantage over brachypterous species for living in open areas. On the contrary, species with low dispersal ability, such as brachypterous or wingless (being mainly medium to large in size), are more likely to be found in forest-dominated environments (Shibuya et al. 2014). Most of them hardly leave the forest canopy or only move a few tens of meters away from it, although tree rows facilitate the passage of forest species into the agricultural matrix (Della Rocca et al. 2021). It is therefore important for wingless and brachypterous ground beetles that their habitat is disturbed as little as possible, in order to guarantee the availability of the resources in the long term. Even though logging activities within a stand are typically not very frequent, timber extraction is a major threat to these species, and the lack of forest cover means

that the forest species are wiped out of the area for a while. The same applies to natural disturbances such as storms or fires, which cause major disturbances (Bouget and Duelli 2004), even if these events are sporadic.

Certain studies relate habitat structural stability or litter thickness to wing morphology (Guillemain et al. 1997; Shibuya et al. 2014). In our case, the environmental variable “tree cover” implies a certain stability of the soil, due to the rooting of the land, and guarantees a thickness of litter constantly renewed by the leaf litter fall or by the biological activity induced by the trees, that can vary according to species type (hardwood or softwood) and forest management. Although ground beetles are mainly epigeous, they are dependent on tree cover, which partially and indirectly structure the habitat and influences ecological and edaphic conditions. More research is needed to quantify the extent to which tree cover in wooded pastures allows the dispersal of forest species with specific traits (e.g. brachypterous or wingless) out of forests.

Moisture preference

Humidity and light are known to be important factors to explain ground beetle assemblage (Thiele 1977; Lövei and Sunderland 1996). In this context, tree cover plays an important role by directly influencing 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 indeed generally prefer moist soils, while intermediate and open areas species tend towards drier conditions.

In our study as well, tree cover influences the composition of ground beetles according to their preference for moisture. Hygrophilic and steno-hygrophilic species are closely linked to habitat with a high tree cover that is most likely associated with high moisture content in our study. Mesophilic and mesophilic-hygrophilic species prefer more open environments but are still linked to some presence of woody plants. In contrast, xerophilic species are only found in open areas and their presence are more correlated with the variables Biodiversity Promoting Areas and dry grasslands and pastures. These results make sense

since DGP and BPA have higher values in areas that tend to be less densely covered with trees.

Implications for the conservation and conclusion

Wooded pastures are an important transitional environment, allowing a gradual change in land-use systems between woodland and open areas. Our results don't show a significantly higher species diversity in wooded pastures than in non-wooded pastures. Still, this semi-open environment contains many ground beetle species, some of which are threatened, even though some strict forest and open area specialists are absent. The conservation of wooded pastures and the generalisation of extensive farming practices are therefore widely encouraged. This study points towards the need to favour the biodiversity promotion areas within wooded pastures as it implies an extensive way of farming and the maintaining of a variable tree cover that contributes to carabid species diversity.

Trees are the key environmental structures that influence certain environmental factors, thus defining the carabid communities present, according to their own ecological traits. Tree management and woody regeneration in wooded pastures therefore have an influence.

Wooded pastures only survive over time thanks to human action, which must therefore ensure a delicate balance between the renewal of woody species and the maintenance of grazing to ensure that the environment remains sufficiently open and heterogeneous, thus to maintain diversity of ground beetles at local and landscape scales. This land-use system is therefore a good example of how it is possible to maintain a high level of biodiversity while maintaining socio-economic activities.

Acknowledgements The authors thank the Office of Mobility and the Conservation Biology Laboratory of the University of Neuchâtel for covering the costs of transport and material. We would also like to thank the Service de la faune, des forêts et de la nature of the canton of Neuchâtel for providing us with the Lidar data and the geomatic layers. Dr. Radu Alexandru Slobodeanu is thanked for his support in the statistical processing. A particular attention is dedicated to Dr. Christophe Praz for his advice at the beginning of the project. Thanks also to Laurent Zimmermann, Vinciane Zimmermann and Sarah Rey for their help with the material logistics.

Author contributions EZ conceptualised and planned the work with the help of SW, CZ and YC; EZ and YC identified

insects; EZ analysed data with the support of CZ and SW; EZ, CZ, YC, SW wrote the paper.

Funding Open access funding provided by University of Neuchâtel. This work was supported by the Office of Mobility and the Conservation Biology Laboratory of the University of Neuchâtel. The authors did not receive any research support from other companies for this study. The authors have no relevant financial or non-financial interests to disclose.

Data availability The datasets generated during study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Ariza GM, Jácome J, Esquivel HE, Kotze DJ (2021) Early successional dynamics of ground beetles (Coleoptera, carabidae) in the tropical dry forest ecosystem in Colombia. *Zookeys* 2021:877–906. <https://doi.org/10.3897/zookeys.1044.59475>
- Avgin SS, Luff ML (2010) Ground beetles (Coleoptera: Carabidae) as bioindicators of human impact. *Munis Entomol Zool* 5(1):209–215
- Aviron S, Nitsch H, Jeanneret P et al (2009) Ecological cross compliance promotes farmland biodiversity in Switzerland. *Front Ecol Environ* 7:247–252. <https://doi.org/10.1890/070197>
- Blake S, Foster GN, Eyre MD, Luff ML (1994) Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* 38(6):502–512
- Bouget C, Duelli P (2004) The effects of windthrow on forest insect communities: a literature review. *Biol Conserv* 118:281–299. <https://doi.org/10.1016/j.biocon.2003.09.009>
- Boutaud E, Nolte D, Harry I et al (2022) Conservation value of semi-open habitats for ground beetles (Coleoptera: Carabidae, Cicindelidae) in Central Europe. *Biodivers*

- Conserv 31:1469–1489. <https://doi.org/10.1007/s10531-022-02402-z>
- Brandmayr P (1991) The reduction of metathoracic alae and dispersal power of carabid beetles along the evolutionary pathway into the mountains. In: Lanzavecchia G, Valvasori V (eds) Form and function in zoology. UZI selected symposium and monographs. 5. Mucchi Editore, Modena, pp 363–378
- Bütler R, Lachat T, Larrieu L, Paillet Y (2012) 2.1 Habitat trees: key elements for forest biodiversity
- Butterfield J, Luff ML, Baines M, Eyre MD (1995) Carabid beetle communities as indicators of conservation potential in upland forests. *For Ecol Manag* 79(1–2):63–77. [https://doi.org/10.1016/0378-1127\(95\)03620-2](https://doi.org/10.1016/0378-1127(95)03620-2)
- Buttler A, Gavazov K, Peringer A et al (2012) Conservation des pâturages boisés du Jura: défis climatiques et agropolitiques. *Rech Agron Suisse* 3:346–353
- Capellini I, Gosling LM (2007) Habitat primary production and the evolution of body size within the hartebeest clade. *Biol J Linn Soc* 92:431–440. <https://doi.org/10.1111/j.1095-8312.2007.00883.x>
- Carbonne B, Petit S, Neidel V et al (2020) The resilience of weed seedbank regulation by carabid beetles, at continental scales, to alternative prey. *Sci Rep* 10:1–14. <https://doi.org/10.1038/s41598-020-76305-w>
- Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67. <https://doi.org/10.1890/13-0133.1>
- Chételat J, Kalbermatten M, Lannas KSM, Spiegelberger T, Wettstein JB, Gillet F, Peringer A, Buttler A (2013) A contextual analysis of land-use and vegetation changes in two wooded pastures in the Swiss Jura mountains. *Ecol Soc* 18(1):art39. <https://doi.org/10.5751/ES-05287-180139>
- Chittaro Y, Hoess R, Huber C, Luka H, Marggi W, Szallies A, Gonseth Y (2024) Liste rouge des Carabidés. Espèces menacées en Suisse. Office fédéral de l'environnement (OFEV) du Département fédéral de l'environnement, des transports, de l'énergie et de la communication (DETEC) et info fauna, centre national de données et d'informations sur la faune de Suisse, Neuchâtel, in press
- Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) Guide des milieux naturels de Suisse. Rossolis, Bussigny
- Della Rocca F, Venturo A, Milanese P, Bracco F (2021) Effects of natural and seminatural elements on the composition and dispersion of carabid beetles inhabiting an agroecosystem in Northern Italy. *EcolEvol* 11:10526–10537. <https://doi.org/10.1002/ece3.7857>
- Den Boer PJ (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia* 4:1–28. <https://doi.org/10.1007/BF00390612>
- Díaz M, Tietje WD, Barrett RH (2013) Effects of management on biological diversity and endangered species. In: Campos P, Huntsinger L, Pro O, Starrs JL, Diaz PF, Standiford M, Montero RB (eds) Mediterranean oak woodland working landscapes: Dehesas of Spain and Ranchlands of California. Springer Netherlands, Dordrecht, pp 213–243. https://doi.org/10.1007/978-94-007-6707-2_8
- Dipner M, Volkart G et al (2010) Prairies et pâturages secs d'importance nationale. Aide à l'exécution de l'ordonnance sur les prairies sèches. L'environnement pratique no 1017, Office fédéral de l'environnement, Berne, p 83
- Dufourn A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography* 29(4):573–584. <https://doi.org/10.1111/j.0906-7590.2006.04605.x>
- Eggers B, Matern A, Drees C et al (2010) Value of semi-open corridors for simultaneously connecting open and wooded habitats: a case study with ground beetles. *Conserv Biol* 24:256–266. <https://doi.org/10.1111/j.1523-1739.2009.01295.x>
- Eycott AE, Stewart GB, Buyung-Ali LM et al (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc Ecol* 27:1263–1278. <https://doi.org/10.1007/s10980-012-9781-9>
- Fernández-Tizón M, Emmenegger T, Perner J, Hahn S (2020) Arthropod biomass increase in spring correlates with NDVI in grassland habitat. *Sci Nat* 107:42. <https://doi.org/10.1007/s00114-020-01698-7>
- Fischer J, Stott J, Law BS (2010) The disproportionate value of scattered trees. *Biol Conserv* 143:1564–1567. <https://doi.org/10.1016/j.biocon.2010.03.030>
- Freude H, Harde KW, Lohse GA, Klausnitzer B (2006) Die Käfer Mitteleuropas. Band 2. Adephaga. 1. Carabidae (Laufkäfer)
- Gallandat JD, Gillet F, Havlicek E, Perrenoud A (1995) PATUBOIS - typologie et systématique phytécologiques des pâturages boisés du Jura suisse. Université de Neuchâtel, Switzerland, Lab. Écol. vég.
- Gaston KJ, Lawton JH (1988) Patterns in body size, population dynamics, and regional distribution of bracken herbivores. *Am Nat* 132(5):662–680
- Gillet F (2008) Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. *Ecol Model* 217(1–2):1–18. <https://doi.org/10.1016/j.ecolmodel.2008.05.013>
- Gillet F, Gallandat JD (1996) Wooded pastures of the Jura mountains. INRA Editions, Paris, pp 37–53
- Gobbi M, Rossaro B, Vater A et al (2007) Environmental features influencing Carabid beetle (Coleoptera) assemblages along a recently deglaciated area in the Alpine region. *Ecol Entomol* 32:682–689. <https://doi.org/10.1111/j.1365-2311.2007.00912.x>
- Gopi SC, Suvarna B, Padmaja TM (2016) High dimensional unbalanced data classification vs SVM feature selection. *Indian J Sci Technol* 9(30):1–7. <https://doi.org/10.17485/ijst/2016/v9i30/98729>
- Guillemain M, Loreau M, Daufresne T (1997) Relationships between the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. *Acta Oecol* 18:465–483. [https://doi.org/10.1016/S1146-609X\(97\)80035-5](https://doi.org/10.1016/S1146-609X(97)80035-5)
- Halme E, Niemelä J (1993) Carabid beetles in fragments of coniferous forest. *Ann Zool Fenn* 30:17–30
- Hartel T, Plieninger T (2014) The social and ecological dimensions of wood-pastures. In: Hartel T, Plieninger T (eds) European wood-pastures in transition. Routledge, London, pp 3–18

- Hartel T, Dorresteyn I, Klein C et al (2013) Wood-pastures in a traditional rural region of Eastern Europe: characteristics, management and status. *Biol Conserv* 166:267–275. <https://doi.org/10.1016/j.biocon.2013.06.020>
- Hartel T, Réti KO, Craioveanu C (2017) Valuing scattered trees from wood-pastures by farmers in a traditional rural region of Eastern Europe. *Agric Ecosyst Environ* 236:304–311. <https://doi.org/10.1016/j.agee.2016.11.019>
- Hausmann A, Ulrich W, Seeger AH et al (2022) Fluctuating insect diversity, abundance and biomass across agricultural landscapes. *Sci Rep* 12:1–9. <https://doi.org/10.1038/s41598-022-20989-9>
- Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432. <https://doi.org/10.2307/1934352>
- Hódar JA (1996) The use of regression equations for estimation arthropod biomass. *Acta Oecol* 17:421–433
- Holland JM (2002) Carabid beetles: their ecology, survival and use in agroecosystems. In: Holland JM (ed) *The agroecology of carabid beetles*. Intercept, Andover, pp 1–40
- Horn HS (1966) Measurement of “overlap” in comparative ecological studies. *Am Nat* 100:419–424. <https://doi.org/10.1086/282436>
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- info fauna, Swiss fauna database (2023) <https://www.infofauna.ch>. Accessed June 2023
- James G, Witten D, Hastie T, Tibshirani R (2013) *An introduction to statistical learning: with applications in R*. Springer, 1st edn. Corr. 7th printing 2017 edition. Springer, New York
- Johnston TA, Cunjak RA (1999) Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. *Freshw Biol* 41:653–674. <https://doi.org/10.1046/j.1365-2427.1999.00400.x>
- Jolliffe IT (2002) Principal component analysis for special types of data. In: Jolliffe IT (ed) *Principal component analysis*. Springer series in statistics. Springer, New York. https://doi.org/10.1007/0-387-22440-8_13
- Jost L, Chao A, Chazdon RL (2011) Compositional similarity and β (beta) diversity. In: Magurran AE, McGill BJ (eds) *Biological diversity frontiers in measurement and assessment*. Oxford University Press, New York
- Jukes MR, Peace AJ, Ferris R (2001) Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. *For Ecol Manag* 148(1–3):271–286. [https://doi.org/10.1016/S0378-1127\(00\)00530-2](https://doi.org/10.1016/S0378-1127(00)00530-2)
- Kagawa Y, Maeto K (2014) Ground beetle (Coleoptera : Carabidae) assemblages associated with a satoyama landscape in Japan : the effects of soil moisture, weed height, and distance from woodlands. *Appl Entomol* 49:429–436. <https://doi.org/10.1007/s13355-014-0266-y>
- Kark S, van Rensburg BJ (2006) Ecotones: Marginal or central areas of transition? *Isr J Ecol Evol* 52:29–53. <https://doi.org/10.1560/IJEE.52.1.29>
- Klaiber J, Altermatt F, Birrer S et al (2017) Fauna indicativa. *WSL Berichte* 54:1–192
- Koivula MJ (2011) Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys* 100:287–317
- Komsta L (2022) outliers: tests for outliers. R package version 0.15. <https://CRAN.R-project.org/package=outliers>
- Kotze DJ, Brandmayr P, Casale A et al (2011) Forty years of carabid beetle research in Europe—from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys* 100:55–148. <https://doi.org/10.3897/zookeys.100.1523>
- Lacasella F, Gratton C, De Felici S et al (2015) Asymmetrical responses of forest and “beyond edge” arthropod communities across a forest–grassland ecotone. *Biodivers Conserv* 24:447–465. <https://doi.org/10.1007/s10531-014-0825-0>
- Langraf V, Petrovičová K, David S, Ábelová M, Schlarmanová J (2017) Body volume in ground beetles (Carabidae) reflects biotope disturbance. *Folia Oecol* 44:114–120
- Larochelle A (1980) A list of birds of Europe and Asia as predators of carabid beetles including Cicindelini (Coleoptera: Carabidae). *Cordulia* 6:1–19
- Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Can J for Res* 42:1433–1445. <https://doi.org/10.1139/X2012-077>
- Lindberg E, Roberge J-M, Johansson T, Hjältén J (2015) Can airborne laser scanning (ALS) and forest estimates derived from satellite images be used to predict abundance and species richness of birds and beetles in boreal forest? *Remote Sens* 7(4):4233–4252. <https://doi.org/10.3390/rs70404233>
- Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO₂: productivity, phytochemistry, and insect performance. *Ecology* 74:763–777. <https://doi.org/10.2307/1940804>
- Lövei GL, Sunderland KD (1996) The ecology and behavior of ground beetles. *Annu Rev Entomol* 41:231–256. <https://doi.org/10.1146/annurev.ento.41.1.231>
- Lövei GL, Magura T, Tóthmérész B, Ködöböcz V (2006) The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Glob Ecol Biogeogr* 15:283–289. <https://doi.org/10.1111/j.1466-822X.2005.00221.x>
- Lüdecke D, Ben-Shachar M, Patil I et al (2021) performance: an R package for assessment, comparison and testing of statistical models. *J Open Source Softw* 6:3139. <https://doi.org/10.21105/joss.03139>
- Luka H, Marggi W, Huber C, Gonseth Y, Nagel P (2009) *Coleoptera, Carabidae: ecology*, vol 24. Atlas. Centre suisse de cartographie de la faune
- McAdam JH, Sibbald AR, Teklehaimanot Z, Eason WR (2007) Developing silvopastoral systems and their effects on diversity of fauna. *Agrofor Syst* 70(1):81–89. <https://doi.org/10.1007/s10457-007-9047-8>
- Molnár T, Magura T, Tóthmérész B, Elek Z (2001) Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. *Eur J Soil Biol* 37:297–300. [https://doi.org/10.1016/S1164-5563\(01\)01103-7](https://doi.org/10.1016/S1164-5563(01)01103-7)

- Mosquera-Losada MR, McAdam JH, Romero-Franco R et al (2009) Definitions and components of agroforestry practices in Europe. *Agrofor Eur*. https://doi.org/10.1007/978-1-4020-8272-6_1
- Müller J, Brandl R (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *J Appl Ecol* 46(4):897–905. <https://doi.org/10.1111/j.1365-2664.2009.01677.x>
- Mupepele AC, Keller M, Dormann CF (2021) European agroforestry has no unequivocal effect on biodiversity: a time-cumulative meta-analysis. *BMC Ecol Evol* 21:1–12. <https://doi.org/10.1186/s12862-021-01911-9>
- Niemelä J (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *Eur J Entomol* 98:127–132. <https://doi.org/10.14411/eje.2001.023>
- North M, Oakley B, Fiegner R et al (2005) Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecol* 177:13–24. <https://doi.org/10.1007/s11258-005-2270-3>
- Oksanen J, Simpson GL, Blanchet FG et al (2022) Community ecology package. *Vegan Community Ecol Packag*
- Peringer A, Schulze KA, Stupariu I, Stupariu MS, Rosenthal G, Buttler A, Gillet F (2016) Multi-scale feedbacks between tree regeneration traits and herbivore behavior explain the structure of pasture-woodland mosaics. *Landscape Ecol* 31(4):913–927. <https://doi.org/10.1007/s10980-015-0308-z>
- Plieninger T, Hartel T, Martín-López B et al (2015) Wood-pastures of Europe: geographic coverage, social-ecological values, conservation management, and policy implications. *Biol Conserv* 190:70–79. <https://doi.org/10.1016/j.biocon.2015.05.014>
- Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers Conserv* 12:487–506. <https://doi.org/10.1023/A:1022412617568>
- Ravetto Enri S, Nucera E, Lonati M et al (2020) The biodiversity promotion areas: effectiveness of agricultural direct payments on plant diversity conservation in the semi-natural grasslands of the Southern Swiss Alps. *Biodivers Conserv* 29:4155–4172. <https://doi.org/10.1007/s10531-020-02069-4>
- Riecken U, Raths U (1996) Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. *Ann Zool Fennici* 33:109–116
- RO 2013 4145 (2013) Ordonnance sur les paiements directs versés dans l'agriculture (Ordonnance sur les paiements directs, OPD), Office fédéral de l'agriculture
- Roellig M, Sutcliffe LME, Sammul M et al (2016) Reviving wood-pastures for biodiversity and people: a case study from western Estonia. *Ambio* 45:185–195. <https://doi.org/10.1007/s13280-015-0719-8>
- Roff DA (1990) The evolution of flightlessness in insects. *Ecol Monogr* 60(4):389–421. <https://doi.org/10.2307/1943013>
- RStudio Team (2022) RStudio: integrated development environment for R. RStudio, PBC, Boston
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32. <https://doi.org/10.1111/j.1523-1739.1991.tb00384.x>
- Schoener TW, Janzen DH (1968) Notes on environmental determinants of tropical versus temperate insect size patterns. *Am Nat* 102(925):207–224. <https://doi.org/10.1086/282538>
- Shibuya S, Kikvidze Z, Toki W et al (2014) Ground beetle community in suburban Satoyama—a case study on wing type and body size under small scale management. *J Asia Pac Entomol* 17:775–780. <https://doi.org/10.1016/j.aspen.2014.07.013>
- Söderström B, Svensson B, Vessby K, Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodivers Conserv* 10:1839–1863. <https://doi.org/10.1023/A:1013153427422>
- Somay L, Szigeti V, Boros G et al (2020) Wood pastures: a transitional habitat between forests and pastures for dung beetle assemblages. *Forests* 12:1–16. <https://doi.org/10.3390/f12010025>
- Spence JR, Niemelä JK (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Can Entomol* 126(3):881–894. <https://doi.org/10.4039/ent126881-3>
- Stäheli B, Zurbrugg C, Benz R (2010) Les pâturages extensifs—Un milieu précieux pour la flore et la faune. *AGRIDEA*, Saint Gallen, pp 1–8
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17:866–880. <https://doi.org/10.1111/ele.12277>
- Sullivan GM, Feinn R (2012) Using effect size—or why the *P* value is not enough. *J Grad Med Educ* 4(3):279–282. <https://doi.org/10.4300/JGME-D-12-00156.1>
- Sustek Z (1987) Changes in body size structure of carabid communities (Coleoptera, Carabidae) along an urbanisation gradient. *Biologia* 42:145–156
- Taboada A, Kotze J, Salgado J, Tárrega R (2006a) The influence of habitat type on the distribution of carabid beetles in traditionally managed “dehesa” ecosystems in NW Spain. *Entomol Fenn* 17:284–295. <https://doi.org/10.33338/ef.84348>
- Taboada A, Kotze DJ, Tárrega R, Salgado JM (2006b) Traditional forest management: Do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? *For Ecol Manage* 237:436–449. <https://doi.org/10.1016/j.foreco.2006.09.077>
- Taboada A, Tárrega R, Calvo L, Marcos E, Marcos JA, Salgado JM (2008) Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. *Eur J Forest Res* 129:31–45. <https://doi.org/10.1007/s10342-008-0245-3>
- Talvi T (1995) Carabid beetle assemblages (Coleoptera) in a wooded meadow and in the adjacent land use systems on the Saaremaa Island, Estonia. *Entomol Fenn* 6:169–175. <https://doi.org/10.33338/ef.83854>
- Tews J, Brose U, Grimm V et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31:79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Thiele HU (1977) Carabid beetles in their environments: a study on habitat selection by adaptations in physiology

- and behaviour, vol 10. Springer Science & Business Media, Berlin
- Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annu Rev Ecol Evol Syst* 45:471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Torralba M, Fagerholm N, Burgess PJ et al (2016) Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. *Agric Ecosyst Environ* 230:150–161. <https://doi.org/10.1016/j.agee.2016.06.002>
- Tschumi M, Albrecht M, Bärtschi C et al (2016) Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agric Ecosyst Environ* 220:97–103. <https://doi.org/10.1016/j.agee.2016.01.001>
- Vanbergen AJ, Woodcock BA, Watt AD, Niemelä J (2005) Effect of land-use heterogeneity on carabid communities at the landscape scale. *Ecography* 28:3–16. <https://doi.org/10.1111/j.0906-7590.2005.03991.x>
- Vandenberghe C, Freléchoux F, Moravie MA et al (2007) Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. *Plant Ecol* 188:253–264. <https://doi.org/10.1007/s11258-006-9160-1>
- Violle C, Navas M, Vile D et al (2007) Let the concept of trait be functional! *Oikos* 116(5):882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York
- Zingg S, Ritschard E, Arlettaz R, Humbert J-Y (2019) Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. *Biol Cons* 231:39–48. <https://doi.org/10.1016/j.biocon.2018.12.022>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.