



Bird and hoverfly communities are impacted by vegetation heterogeneity in wood-pastures in the Swiss Jura

Sandrine Wider¹ · Delphine Clara Zemp¹

Received: 20 September 2024 / Revised: 29 January 2025 / Accepted: 21 March 2025 /
Published online: 10 April 2025
© The Author(s) 2025

Abstract

Wood-pastures are a type of agroforestry system consisting of assemblages of cattle-grazed pastures and scattered trees. They maintain biodiversity because of their environmental heterogeneity due to irregular tree cover that promotes diversity of resources and habitats. Agricultural intensification threatens the fragile balance of these traditional systems. Thus, we aimed to assess which factors associated with trees, shrubs and pasture heterogeneity within wood-pastures influence the community composition and diversity of different groups of animal species. We selected 45 wood-pasture sites of 20 ha along a gradient of tree density in the Swiss Jura mountains. In each site, we used remote sensing data and agricultural inventories to characterize the tree, shrub and herb layers' structural and compositional heterogeneity. In study sites we also conducted survey of birds and hoverflies (Syrphidae) and evaluated the relationships between species composition and diversity with environmental variables. Tree density and tree spatial distribution were the main drivers of differences in community specific composition for the two groups of species. For hoverflies, botanically rich pastures and elevation were also driving differences in species composition between communities. Increased tree density showed a generally positive effect on birds and Syrphidae diversity indices. Moreover, for birds, scattered trees' spatial distribution and a high percentage of deciduous trees also promoted species diversity. In this study, we highlight the importance of trees in pastures for bird and hoverfly diversity, as well as the necessity for trees to be heterogeneously distributed across the pastures and composed of a mix of deciduous and coniferous species.

Keywords Agroforestry · Agroecology · Biodiversity · Community ecology · Environmental heterogeneity · Structural heterogeneity

Communicated by Stephen Garnett.

✉ Sandrine Wider
sandrine.wider@unine.ch

¹ Laboratory of Conservation Biology, Faculty of Sciences, Institute of Biology, University of Neuchâtel, CH-2000 Neuchâtel, Switzerland

Introduction

Wood-pasture is a specific type of agroforestry system consisting of cattle grazed pastures and scattered trees or shrubs (Bergmeier et al. 2010). It is a traditional agricultural system based on a multiple use of natural resources (Buttler et al. 2009). This human-influenced landscape is the result of a fragile equilibrium due to the dynamic of cattle grazing and natural reforestation (Gillet et al. 2002). Wood-pastures are strongly influenced by management policies and resulting land use practices (Plieninger et al. 2015). In the Swiss Jura, a trend toward the separation of grazed lands and closed forests has gone on alert (Chételet et al. 2013), threatening the persistence of this traditionally heterogeneous agricultural landscape.

The loss of ecological heterogeneity in agricultural landscapes is a major driver of biodiversity decline (Benton et al. 2003; Fahrig et al. 2011), with several studies demonstrating that the presence of trees within agricultural systems promotes the diversity of many organisms, such as birds, bats and insects (Fischer et al. 2010; Fischer & Lindenmayer 2002; Ramírez-Hernández et al. 2014; Söderström et al. 2001). Wood-pastures are thus agroforestry systems that may be promoted for their potential to reconcile agriculture and biodiversity (Jakobsson et al. 2020; Plieninger et al. 2015).

Environmental heterogeneity is linked to species diversity through enhanced structural complexity and diversity in habitat types and resources promoting species coexistence (Guariento et al. 2024; Stein et al. 2014). The effect of vegetation structural characteristics on biodiversity has been highlighted, with species living in forested environments that are highly sensitive to structural complexity, cover and density of woods and shrub assemblages (Delabye et al. 2021; Gittings et al. 2006; Uhl et al. 2024). The density and structural properties of shrubby and woody vegetation also play a crucial role for biodiversity in a more open environment, in which structurally rich wood-pastures presented higher species of butterflies (Ouin et al. 2021), mammals (Gonçalves et al. 2012) and birds (Anderle et al. 2023; Oksuz et al. 2021) than closed forest or open lands.

In Switzerland, previous studies have focused on the relationship between wood-pastures environmental heterogeneity and botanical diversity. Gallandat et al. (1995) made a very precise typological and systemic study of the vegetation in the Swiss Jura mountains, showing a great variety of associations within trees and herb layers at varying scales and environmental conditions. They highlighted that one sixth of the Swiss flora occurs in the Jura wood-pastures. Along this line, Gillet et al. (1999) showed that the complex spatial mosaic of trees, shrubs and open grassland creates a wide variety of microhabitats, promoting plant diversity in Swiss sub-alpine wood-pastures. And, at the local scale, Dufour et al. (2006) showed the positive effect of environmental heterogeneity characterized by microhabitat variability and configuration linked to tree cover and microtopography on ground vegetation diversity in wood-pastures of the Swiss Jura mountains. However, such information on animal diversity is still missing. That's why, in this study, we investigate the effect of environmental parameters reflecting heterogeneity on animal diversity, across a range of wood-pastures in the Swiss Jura mountains.

We focus on two different groups of species: birds and hoverflies. Birds are good ecological indicators (Browder et al. 2002; Canterbury et al. 2000). They react quickly to environmental changes, such as landscape homogenization (Donald et al. 2006) and they encompass various groups of species with very different ecological needs (Lovette & Fitzpatrick 2016). Moreover, birds could also be used as a good proxy for other taxa (Anderle et al. 2024). Similarly, hoverflies represent a very wide group of Dipteran characterized by a

wide variety of larvae ecological needs (Speight 2020) related to precise micro-habitats properties. Thus communities of hoverflies have been proved to be strongly influenced by landscape and vegetation structures (Haenke et al. 2014; Inclán et al. 2016; Schirmel et al. 2018) and they are increasingly used as ecological indicators, especially in agricultural systems. (Burgio & Sommaggio 2007; Gabriel et al. 2010; Power et al. 2016; Schweiger et al. 2007). To reflect wood-pastures environmental heterogeneity, we selected variables representing first structural heterogeneity, such as number of trees and shrubs per hectare and a measure of trees' spatial distribution, describing if trees are occurring in patches or if they are heterogeneously scattered on the pastures. Second, two other variables were selected to describe compositional heterogeneity in trees and herb layers, which were percentage of deciduous trees and the percentage cover of extensively managed pastures. Therefore, we assessed how environmental variables, representing different characteristics of vegetational heterogeneity, were associated with bird and hoverfly species composition and diversity. We discuss the way birds and hoverflies differ in their response to environmental heterogeneity, and the implication of our results for the management of wood-pastures in the Swiss Jura mountains.

We selected wood-pasture sites along a gradient of tree cover, so we expect the two extreme situations of either densely wooded pastures or very open ones to be associated with forest or open land specialist species of birds and hoverflies. Higher degrees of heterogeneity represented by semi-open pastures are expected to be associated with a mixture of forest and open land specialist species but also specialists from semi-open habitats and more generalist species. We hypothesize that species diversity of birds and hoverflies will be positively related to environmental heterogeneity, such as intermediate value of trees and shrub cover and scattered tree spatial distribution, as well as a high percentage of deciduous trees, and a high percentage cover of extensively managed pasture stages.

Methods

Study sites and environmental data

The study was led in the Jura mountains in the canton of Neuchâtel, Switzerland (Fig. 1a). The study area encompassed the Jura crests from the far western part of the canton of Neuchâtel to the far eastern part. Study sites were situated at elevations ranging between 1000 and 1450 m above sea level (asl). The landscape of the Jura mountains varies between temperate forests, open pastures and wood-pastures. Generally, dominant trees in wood-pastures are spruce (*Picea abies*), and few sites are dominated by beeches (*Fagus sylvatica*). Isolated silver fir (*Abies alba*), sycamores (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*) are also found, such as groups of rowans (*Sorbus aucuparia*) and other smaller trees and bushes, such as blackthorn (*Prunus spinosa*), common hawthorn (*Crataegus monogyna*) or dog rose (*Rosa canina*). Cows are the main type of grazing livestock on wood-pastures and open pastures in the studied region.

The study was led at 45 study sites of 20 ± 3 ha (Supplementary Information Table S1 and Fig. 1b), evenly distributed over the entire study area. Sites were separated by a minimum distance of 500 m, except in two situations where sites were separated by 200 and 300 m, respectively. The sizes of study sites and distances between them were chosen according to documented passerine birds' territories, generally ranging between 2 and 40 ha (Lovette & Fitzpatrick 2016) and based on the results of a previous study which, using

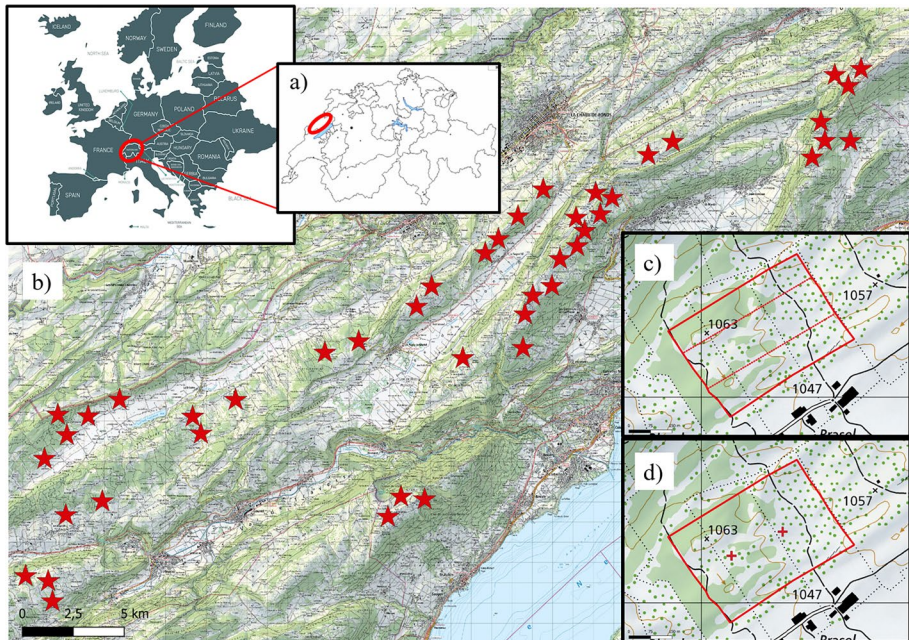


Fig. 1 **a** Map of Switzerland within Europe, and the canton of Neuchâtel within the red circle **b** Red stars represent the 45 study sites distributed over the Jura mountains in the canton of Neuchâtel **c** One example of a study site delimited with the red line, and bird transects inside, red dashed line **d** Same study site as (c) with hoverflies sampling sites inside represented by the two red cross

a multi-spatial scale approach, showed that the optimal scale to predict bird richness consisted of 19.6 ha (Morelli et al. 2013). In addition, the home range of hoverflies has been documented to be not greater than 500 m (Gens et al. 2017; Gittings et al. 2006), which supports the independence of our study sites. We selected study sites along a gradient of tree cover in order to include extremes, we selected three sites that were open pastures, while the rest of the 42 sites were wood-pastures, with a gradient of tree cover ranging from 1 to 75%. We selected study sites according to agriculture parcels so that pasture management could be assumed to be homogenous within every study site.

Bird communities were monitored at each study sites. Environmental variables were assessed at the scale of the study sites of 20 ha. Because of time constraints and permission to access sites, hoverfly communities were sampled in 29 of the 45 study sites. We chose the study sites for hoverfly sampling so that they would represent as much as possible the same gradient of tree cover as for birds, including three open-pasture sites and 26 wood-pastures with a tree cover between 4 and 75%. In addition, we chose hoverfly-sampling sites so that they would be distributed over the entire study area. There were two hoverfly-sampling locations per study site (Fig. 1d). The two sampling locations were separated by a minimum distance of 200 m, except in one study site where the distance between the two samplings was 150 m. Environmental variables were measured within plots of 100 m' radius around each sampling location.

Environmental variables were grouped into two categories describing structural and compositional heterogeneity. The variables reflecting structural heterogeneity were: density

of trees per hectare, density of shrubs smaller than three meters per hectare and a measure of tree spatial distribution, computed as the length of tree patches edges (LTPE). Heterogeneity is considered maximal at the intermediate value of trees and shrubs density. A high value of LTPE represent a scattered distribution of trees which reflects heterogeneity as opposed to segregated patches of trees and open pastures. Variables describing compositional heterogeneity were: percentage of deciduous trees and percentage cover of extensively managed pastures (Biodiversity Promotion Area, BPA). The higher the percentage of deciduous trees and BPA, the higher the compositional heterogeneity. To measure the percentage cover of deciduous trees, we used a model based on data from the Swiss national forest inventory, with a resolution of 25 m² (Waser et al. 2017). Lidar data sets provided by the canton of Neuchâtel (Supplementary Information Table S2) were used to compute the rest of the tree-stands' variables. Percentage cover of extensively managed pastures, BPA, was identified using agriculture data provided by the canton of Neuchâtel. They correspond to agriculture surfaces where at least six indicators of plant species are recorded and for which farmers undertake to respect extensive management constraints (Office fédéral de l'agriculture OFAG, 2023). The BPA areas represent, hence, a higher level of botanical diversity in pasture composition than intensively managed ones. Finally, two abiotic variables, elevation and exposure, extracted from the Swiss national topographic map at a scale of 1:25,000, were also recorded for the 45 study sites.

A PCA of the 45 study sites (Supplementary Information Fig. S1) showed that shrub density was closely related to tree density. The gradient of percentage cover of deciduous trees was opposed to the gradient of elevation. LTPE was slightly positively related to percentage cover of deciduous trees and BPA was another independent gradient. Therefore, study sites were distributed among these gradients, with some sites higher in elevation having less trees and more BPA, some sites having intermediate values of tree density and displaying either highly scattered trees and high percentage of deciduous trees or more clustered trees and more homogenous coniferous tree-stands and finally sites with high tree and shrub density.

Birds and hoverflies data

Bird and hoverfly monitoring was done over 2 years (2022 and 2023) with 20 and 13 study sites covered in 2022 for birds and hoverflies, respectively, and another 25 and 16 sites in 2023. The same observer systematically monitored birds during the two years, whereas hoverfly data collection was done by two observers in 2023.

Birds were monitored during the breeding season (from mid-April until the end of June) and identified acoustically or visually (using binoculars) (Bibby 1992). Sites were visited twice, with an average of 5 weeks between the two visits. Monitoring was conducted from sunrise to 11 pm at the latest and during dry and windless days. Linear transects separated with a distance of 150 m were used (Fig. 1c). As the shape of study sites varied (according to management parcels), the length of the transects was not always the same. But transects were always positioned parallel to the longer side of the sites (except in five cases where topography would not allow it), with an average distance of 100 m to the site limit. Two to three transects were on average fully covering the sites. The observer would walk along the transect and record birds on both sides. Based on previous studies, we estimated the bird detection distance to vary between 100 m in open pastures and 50 m in densely forested pastures (Gottschalk & Huettmann 2011). We therefore chose a maximum detection distance of 75 m. For each observation of the species detected, its precise position was

registered. For each species, the highest number of individuals across two visits was kept as a measure of density.

Samples of hoverflies were taken using two methods: pan traps and sweep net (Spafford & Lortie 2013). Pan traps were made of three colored plates (yellow, white and blue), triangularly positioned on a wooden stick planted in the ground, with the plates at vegetation height (Supplementary Information Fig. S2). The plates were half filled with water, containing a drop of liquid odorless soap. Pan traps were positioned at the two sampling locations within each study site. At each sampling location, two pan traps were set, one meter away from each other, as replicates. The pan traps were activated simultaneously for a sampling session lasting three to four days and during dry weather conditions. For each year, there were two sampling sessions: one in early-summer, end of May, (four days) and one in mid-summer, beginning of July, (3 days in 2022, 4 days in 2023). For each sampling session, transects with a sweep net were also realized at each sampling location. Two transects of 30 m' length each were carried out. The transects began at the pan traps' location and moved away from one another at an angle between 90° and 180°. The positions of the transects were defined to avoid the most heavily grazed areas. All hoverfly individuals collected with pan traps and sweep net were pinned and dried for identification. Identification to species level was done using three keys of European hoverflies (Speight et al. 2016; Speight & Sarthou 2017; van Veen 2010).

Statistical analysis

All analyses were performed using R (version 4.2.2) (Rstudio Team 2020), with separate analyses systematically conducted for the bird and hoverfly communities. We first inspected the relations between the species composition of communities of birds and hoverflies and environmental gradients using canonical correspondence analysis (CCA, Braak 1986) from the 'vegan' package (V2.6–4; Oksanen J. et al. 2022), with Hellinger transformation to standardize community data (using 'Decostand' in 'vegan'). We chose this constrained method because we were interested in a unimodal model of species response to our selected environmental variables (McCune et al. 2002). We tested which environmental gradients had significant impacts on community compositions in the CCA, using permutation tests and the Chis-square statistic. We highlighted species conservation status based on the swiss red list (Knaus et al. 2021) for birds and a European dataset (Speight 2020) for hoverflies.

We then computed diversity indices of the bird and hoverfly communities. Diversity indices and related graphs were computed using the 'iNext' package (v2.0.12; T. C. Hsieh 2016). We followed the methodology proposed by Hill (1973) to compute the "effective number of species" (also called Hill-numbers), that provide diversity indices with proportional abundances on the same scale. We used the three diversity indices: Hill-Richness, Hill-Shannon and Hill-Simpson, corresponding to the Hill numbers $q = [0, 1, 2]$. We calculated diversity estimates, using the method suggested by Chao and Jost (2012) which computes the diversity estimates at equal sample coverage corresponding to the minimum sample coverage value for samples extrapolated to double the sample sizes. In Supplementary Information Fig. S3 and S4, we show rarefaction and extrapolation of species accumulation curves for the three Hill numbers.

Finally, we tested the relationships between diversity indices and environmental variables using estimated Richness, Hill-Shannon and Hill-Simpson, as response variables.

Explanatory variables were number of trees per hectare, number of shrubs per hectare, Length of Tree Patches Edges (LTPE), percentage of deciduous trees, and percentage cover of BPA. We added elevation and exposition to control for potential abiotic effects of study site locations. As we suspected year to have an effect on the population of birds and hoverflies as was the case in previous studies (Barnagaud et al. 2017; Petanidou et al. 2011), we decided to control for the effect of sampling year by incorporating it as an interaction term with all other explanatory variables. We tested for variables collinearity using variance inflation factors (VIF) values, with the function ‘vif’ in the ‘car’ package (v3.1.1; Fox and Weisberg 2019) and considering a VIF value of five as a threshold for correlation (James et al. 2013). In both models of birds and hoverflies, we excluded “exposure” that had a VIF value higher than five. We visualized residual plots (Supplementary Information Fig. S5 and S6) to validate linear model assumptions of residuals’ normal distribution, homogeneity of variance, linearity and cook distances. For hoverflies, it was necessary to log transform the response variable in order to respect linearity assumption. To account for the nested design in hoverfly sampling (sampling locations grouped by two within larger study sites), we included study site as a random factor in the models, function ‘lme’ in the ‘nlme’ package (v3.1–160; Pinheiro et al. 2021) and compared them with simple linear models based on AIC corrected for small sample sizes, AICc (Rencher 2002). As mixed models were not performing better, we decided to use simple linear models with Gaussian distribution. In addition, in both bird and hoverfly analysis we tested generalized least squared models (GLS) with spatial correlation structure with the function ‘gls’, ‘nlme’ R package (v3.1–160; Pinheiro et al. 2021), using geographical coordinates of sampling sites in a correlation function within the model. We compared them with simple linear models using AICc. As a result, including spatial correlation structures did not improve the models. Finally, we proceeded to a multi model selection on the AICc (Sakamoto et al. 1986) using the ‘dredge’ function in the ‘MuMIn’ package (Barton 2018), and we averaged the best models within $\Delta AICc < 2$ (Burnham and Anderson 2003) using the ‘model.avg’ function, R package MuMIn (Barton 2018). We show the model conditional averaged parameters and the ranked best models. Lastly, we plotted significant explanatory variables with response variables extracted from the best models including all significant averaged predictors.

Results

Birds and hoverflies community composition in relation to environmental variables

We recorded 46 bird species and 90 hoverfly species. In the canonical correspondence analysis (CCA) for birds (Fig. 2), environmental gradients explain 35.7% of the total variance in bird communities. Number of trees per hectare had a significant effect on bird communities ($\chi^2=0.21$, $df=1$, $P=0.001$), as well as LTPE ($\chi^2=0.18$, $df=1$, $P<0.001$). Percentage of deciduous trees explained a marginal part of total variation ($\chi^2=0.04$, $df=1$, $P=0.06$), as well as elevation ($\chi^2=0.05$, $df=1$, $P=0.05$). The CCA graph displays two strong environmental gradients; one is related to tree (score CCA1=0.67, score CCA2=−0.70) and shrub density (score CCA1=0.30, score CCA2=−0.17) and the other gradient mostly represents LTPE (score CCA1=0.61, score CCA2=0.62) and percentage of deciduous trees (score CCA1=0.27, score CCA2=0.70). A third gradient would be elevation (score CCA1=−0.57, score CCA2=0.26); it seems that cover of BPA (score

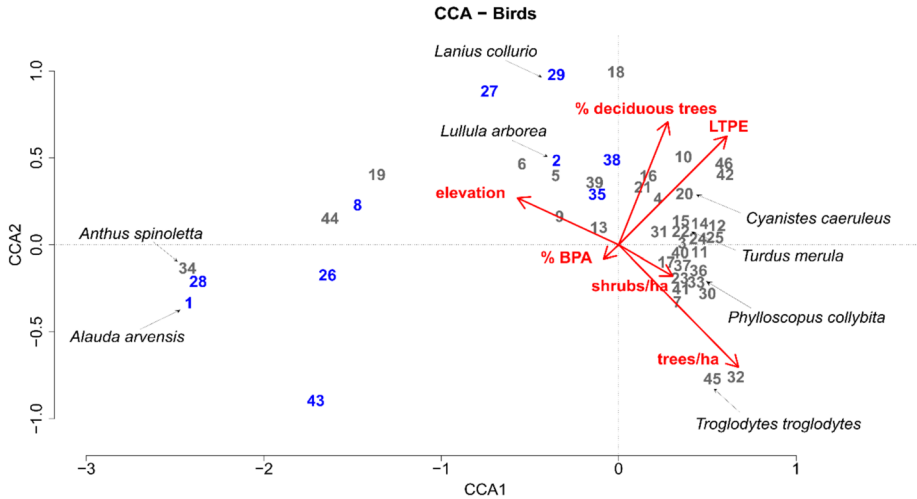


Fig. 2 Canonical correspondence analysis (CCA) of environmental gradients (red arrows) and bird species (numbers, with list of species corresponding to numbers in Supplementary information Table S3, with species names for some examples), 71% of the CCA variance explained by CCA1 and 11.2% explained by CCA2. Numbers in bold blue, bird species with vulnerable or nearly threatened status on swiss red list

CCA1 = -0.08, score CCA2 = -0.08) has a minor contribution to the CCA graph. On the extreme left of the graph, we observe specialist bird species of open lands that are highly differentiated from the other species in the CCA, being associated with very low values of tree cover and higher altitudes: *Anthus pratensis* (no 28), *Alauda arvensis* (no 1), *Coturnix coturnix* (no 8), *Saxicola torquatus* (no 44), *Anthus spinoletta* (no 34), *Oenanthe Oenanthe* (no 43), and *Linaria cannabina* (no 19). For medium values of tree cover, species are distributed along a gradient of tree spatial distribution, from clustered in patches (low values of LTPE) to scattered (high values of LTPE), and a gradient of tree mixture. We first find a group of species relying on low tree density and associated with high values of structural and compositional tree-stand heterogeneity (i.e., a high percentage of deciduous trees and a scattered distribution of trees), such as *Phylloscopus bonelli* (no 27), *Lanius collurio* (no 29, NT), and *Ficedula hypoleuca* (no 18). A second group of species are specialists to semi-open habitat, such as *Lullula arborea* (no 2, VU), *Anthus trivialis* (no 35, NT), and *Phoenicurus phoenicurus* (no 38, NT) (Knaus et al. 2018). They are linked to a slightly higher tree density and also to high values of structural and compositional tree-stand heterogeneity. In increasing tree density, we find more generalist species, such as *Cyanistes caeruleus* (no 20), *Sylvia atricapilla* (no 11), *Turdus merula* (no 22), and *Serinus serinus* (no 41). Finally, on the bottom right of the graph, the CCA clearly displays typical forest species, such as *Periparus ater* (no 24), *Phylloscopus collybita* (no 33) and *Troglodytes troglodytes* (no 45), associated with high tree density, a low value of LTPE, reflecting sites with clusters of trees, and a low percentage of deciduous trees.

In the canonical correspondence analysis for hoverflies (Fig. 3), environmental gradients explain 15.3% of the total variation in hoverflies communities. Number of trees per hectare had a significant effect on community structure ($\chi^2=0.18$, $df=1$, $P=0.001$), such as cover of BPA ($\chi^2=0.12$, $df=1$, $P=0.01$), LTPE ($\chi^2=0.10$, $df=1$, $P=0.039$) and elevation ($\chi^2=0.12$, $df=1$, $P=0.009$). The CCA plot displays two main environmental gradients; the first is number of trees per hectare (score CCA1 = -0.96, score CCA2 = -0.07);

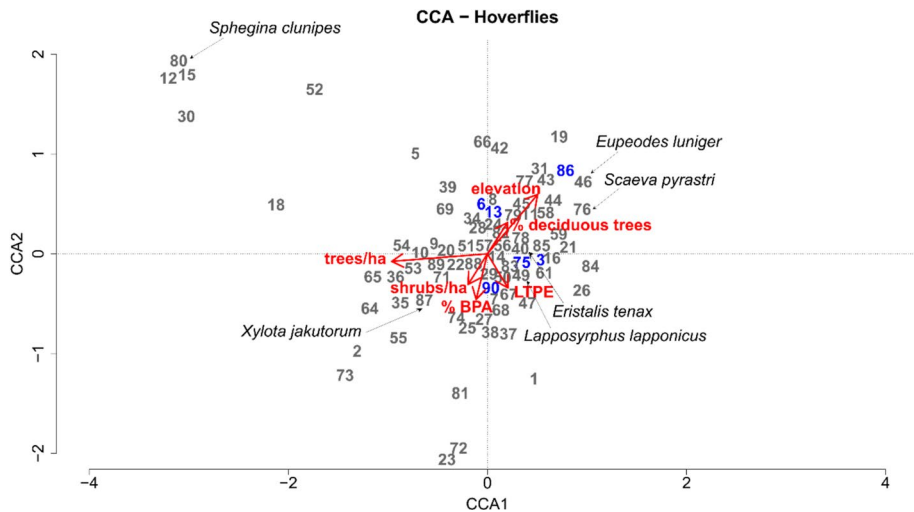


Fig. 3 Canonical correspondence analysis (CCA) of environmental gradients (red arrows) and hoverflies species (numbers, with list of species corresponding to numbers in Supplementary information Table S4, with species names for some examples), 26.3% of CCA explained by CCA1 and 21.5% explained by CCA2. Numbers in bold blue, hoverflies species considered as threatened by Speight et al. (2020)

the second is percentage of deciduous trees (score CCA1=0.20, score CCA2=0.31) and elevation (score CCA1=0.50, score CCA2=0.59) which is opposed to shrub density (score CCA1=− 0.19, score CCA2=− 0.30); and BPA cover (score CCA1=− 0.11, score CCA2=− 0.45), partially correlated to LTPE (score CCA1=0.20, score CCA2=− 0.34). There is no clear structure for the species distribution in relation to environmental gradients. However, we can see open land species on the far right of the CCA graph, such as *Scaeva pyrastris* (no 76), *Syrphus vitripennis* (no 84), *Eupeodes luniger* (no 46) and forest species on the far left, such as *Xylota* (no 87, 88, 89), *Meliscaeva* (no 54, 55) and *Meligramma* genera (no 52, 53), *Sphegina clunipes* (no 80) and *Baccha elongate* (no 2). In between, there is a mix between forest and open land species as well as species known to be generalists, such as species from the genera *Sphaerophoria* (no 78, 79) and other genera suspected to be generalists or specialists of semi-open land, such as *Eristalis* (no 37–40), *Lapposyrphus* (no 49), *Episyrphus* (no 34), *Myathropa* (no 59), *Volucella* (no 85) and *Orhtonevra* (no 63). Finally, six species are considered as threatened in Switzerland (Speight 2020): *Cheilosia faucis* (no 13), *Eumerus tricolor* (no 6), *Brachyopa pilosa* (no 3), *Scaeva dignota* (no 75), *Xanthogramma citrofasciatum* (no 86) and *Xylota xanthocnema* (no 90). In the CCA, they all are situated in mid-tree density sites to open sites and with high to mid percentages of deciduous trees and altitude.

Diversity metrics

Accumulation curves have been calculated for each community and for the three hill numbers (Supplementary Information Fig. S3 and S4). In both groups of species, the highest diversity index is always Richness, corresponding to Hill number $q=0$, as all species are considered with this index regardless of their abundance. Species accumulation curves for birds often tend to reach a plateau for higher hill numbers, indicating

that our sampling effort is sufficient to capture communities of the abundant species. In hoverflies, several curves keep a steep slope even for the higher hill numbers (Supplementary Information Fig. S4), indicating that more sampling efforts would be needed to capture the whole community.

Linear models of species diversity in relation to environmental variables

In linear models for both groups of species, year of sampling had an impact on diversity indices. Year is systematically included as a significant parameter in the best models, either independently (for bird Shannon and Simpson diversity indices, diversity being higher in year 2023), or as an interaction with other parameters (for all the models in both groups of species) (Tables 1 and 2). The only best model for which year was not selected was for bird Richness.

In the best models for both groups of species, tree density is also always included (Tables 1 and 2), except in models with Hill-Simpson indices for hoverflies (Table 2). In birds, the effect of tree density differs depending on the indices (Table 3, Fig. 4), it has a positive but marginal effect on bird species Richness and a strong positive effect on Hill-Shannon and Hill-Simpson bird diversity in 2022, which is lighter on Hill-Shannon diversity and almost neutral on Hill-Simpson diversity in 2023 (Fig. 4). In hoverflies, for models with Richness and Hill-Shannon diversity, tree density had a stronger positive effect on diversity in year 2023 than in year 2022 (Table 4 and Fig. 5).

Percentages of deciduous trees and length of tree patches edges (LTPE) are included in the best models for all diversity indices in birds (Table 1) and have a positive effect on diversity (Table 3, Fig. 4).

Shrub density is included in the best model for hoverfly species richness, and had a positive effect on the index in 2022 and a negative effect in 2023 (Table 4, Fig. 5).

Table 1 For bird diversity ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLik, AICc, Δ AICc and model weights, for species Richness, Hill Shannon and Hill Simpson diversity indicators

Model	df	logLik	AICc	delta	weight
Richness					
LTPE + trees/ha + % deciduous trees	5	− 114.99	241.52	0.0	0.59
LTPE + trees/ha + % deciduous trees + year + trees/ha	7	− 112.60	242.22	0.7	0.41
Hill_Shannon					
LTPE + trees/ha + % deciduous trees + year + trees/ha:year	7	− 100.56	218.16	0.00	0.73
Hill_Simpson					
LTPE + trees/ha + % deciduous trees + year + trees/ha:year	7	− 93.03	203.09	0.00	0.68
LTPE + trees/ha + % deciduous trees + year + trees/ha:year + % deciduous trees:year	8	− 92.28	204.56	1.47	0.32

Table 2 For hoverflies diversity, ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLik, AICc, Δ AICc and model weights, for species richness, hill Shannon and hill Simpson diversity indicators

Models	df	logLik	AICc	delta	weight
Richness					
elevation	3	− 43,5069	93,4667	0	0,1103
elevation + shrubs/ha + trees/ha + year + elevation:ear + shrubs/ha:year + trees/ha:year	9	− 36,0865	94,0028	0,5361	0,0844
trees/ha + % BPA	4	− 42,635	94,0393	0,5726	0,0828
trees/ha	3	− 43,8215	94,0958	0,6291	0,0805
elevation + trees/ha + year + elevation:year	6	− 40,2685	94,217	0,7502	0,0758
trees/ha + % BPA + year	5	− 41,5774	94,3313	0,8645	0,0716
elevation + trees/ha + % BPA + year + elevation:year	7	− 39,0365	94,3587	0,892	0,0706
elevation + % BPA	4	− 42,9006	94,5704	1,1037	0,0635
(Null)	2	− 45,1957	94,6137	1,147	0,0622
elevation + year + elevation:year	5	− 41,7681	94,7127	1,246	0,0591
elevation + year	4	− 43,0494	94,868	1,4013	0,0547
elevation + % BPA + year	5	− 41,9569	95,0903	1,6235	0,049
elevation + trees/ha	4	− 43,1875	95,1443	1,6776	0,0477
elevation + LTPE	4	− 43,229	95,2272	1,7605	0,0457
elevation + % deciduous trees	4	− 43,3106	95,3905	1,9238	0,0421
Shannon					
elevation	3	− 42,7077	91,8683	0	0,1149
trees/ha + % BPA	4	− 41,8274	92,424	0,5557	0,087
trees/ha	3	− 43,0005	92,4538	0,5855	0,0857
elevation + trees/ha + year + elevation:year	6	− 39,5197	92,7194	0,8511	0,0751
trees/ha + % BPA + year	5	− 40,7993	92,775	0,9067	0,073
(Null)	2	− 44,2785	92,7792	0,911	0,0729
elevation + trees/ha + % BPA + year + elevation:year	7	− 38,3069	92,8995	1,0313	0,0686
elevation + % BPA	4	− 42,0957	92,9606	1,0923	0,0666
elevation + year + elevation:year	5	− 40,9696	93,1157	1,2475	0,0616
elevation + year	4	− 42,2682	93,3056	1,4374	0,056
elevation + % BPA + year	5	− 41,1774	93,5313	1,663	0,05
elevation + LTPE	4	− 42,4084	93,5861	1,7178	0,0487
elevation + trees/ha	4	− 42,4118	93,5928	1,7245	0,0485
elevation + shrubs/ha + trees/ha + year + elevation:year + shrubs/ha:year + trees/ha:year	9	− 35,9273	93,6844	1,8161	0,0463
elevation + % deciduous trees	4	− 42,4865	93,7422	1,8739	0,045
Simpson					
elevation	3	− 41,9723	90,3974	0	0,1168
tree.ha	3	− 42,2004	90,8537	0,4564	0,093
trees/ha + %BPA	4	− 41,0563	90,8819	0,4845	0,0917
(Null)	2	− 43,3696	90,9614	0,564	0,0881
elevation + trees/ha + year + elevation:year	6	− 38,8784	91,4368	1,0394	0,0695
trees/ha + % BPA + year	5	− 40,1528	91,482	1,0846	0,0679
elevation + % BPA	4	− 41,3654	91,5001	1,1027	0,0673
elevation + trees/ha + % BPA + year + elevation:year	7	− 37,7331	91,752	1,3546	0,0594
elevation + year + elevation:year	5	− 40,2976	91,7717	1,3743	0,0588

Table 2 (continued)

Models	df	logLik	AICc	delta	weight
elevation + year	4	− 41,6055	91,9802	1,5829	0,0529
elevation + LTPE	4	− 41,6569	92,0831	1,6857	0,0503
elevation + trees/ha	4	− 41,6916	92,1525	1,7551	0,0486
% BPA	3	− 42,9114	92,2756	1,8782	0,0457
elevation + % BPA + year	5	− 40,5634	92,3034	1,906	0,045
elevation + % deciduous trees	4	− 41,7694	92,308	1,9106	0,0449

Table 3 For bird diversity, model-averaged conditional estimates, standard errors (SE), z values and p-values for species Richness, Hill Shannon and Hill Simpson diversity indicators

Models	Estimate	Std. Error	z. value	Pr(> z)
Richness				
(Intercept)	6.6067261	1.8082470	3.565	0.0003
LTPE	0.0007715	0.0001793	4.174	0.0003
trees/ha	0.0553265	0.0322083	1.692	0.0906
% deciduous trees	0.0866431	0.0229116	3.668	0.0002
year23	2.1382257	1.8236912	1.136	0.2559
trees/ha:year23	− 0.0671	0.0345	1.883	0.0596
Hill-Shannon (only 1 model)				
(Intercept)	3.6883741	1.4692899	2.510	0.01632
LTPE	0.0005669	0.0001392	4.073	0.00022
trees/ha	0.0751239	0.0220242	3.411	0.00152
% deciduous trees	0.0541920	0.0174637	3.103	0.00355
year23	3.3752704	1.3958242	2.418	0.02037
trees/ha:year23	− 0.0693497	0.0264276	− 2.624	0.01234
Hill-Simpson				
(Intercept)	3.0897981	1.3020958	2.302	0.0213
LTPE	0.0003688	0.0001176	3.037	0.0023
trees/ha	0.0606970	0.0186657	3.150	0.0016
% deciduous trees	0.0343577	0.0191677	1.746	0.0807
year23	3.1502049	1.3910814	2.202	0.0276
trees/ha:year23	− 0.0605831	0.0224339	2.616	0.0088
% deciduous trees:year23	0.0305463	0.0268669	1.101	0.2710

Discussion

Influence of environmental heterogeneity on bird and hoverfly communities' composition

Our results clearly show that, for both groups, species are distributed along a gradient of tree cover, with a maximum number of species at intermediate values of tree cover.

For birds, few species are strictly associated with open lands and four of these species have a priority status in Switzerland ranging from nearly threatened (NT), for *Saxicola*

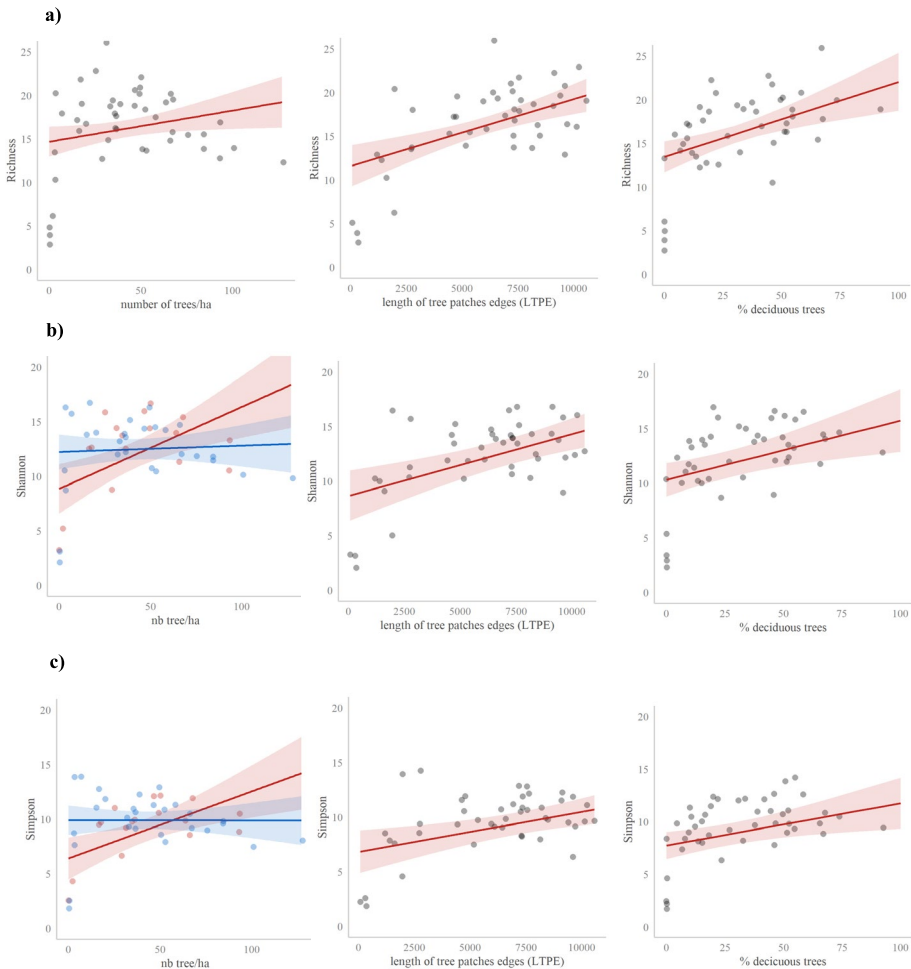


Fig. 4 Best linear model predictions for bird, **a** Richness, **b** Hill-Shannon and **c** Hill Simpson estimated diversity indicators according to significant (p .value<0.05) and marginally significant (p .value<0.1) variables in the averaged model: tree density, Length of Tree Patches Edges (LTPE) and percentage of deciduous trees. In graphs with two curves of different colors, red line is the relationship for 2022 and blue line is the relationship for 2023

torquatus to vulnerable (VU) for *Anthus pratensis*, *Alauda arvensis* and *Coturnix coturnix*. Because the main threat for these birds is agricultural intensification (Donald et al. 2001), open pastures in the Jura mountains might represent refuges for these species, as for other agroforestry systems (Guariento et al. 2024). Similarly, the two groups of species found at intermediate tree cover are also generally declining in Europe, as they rely on extensive land use and a high degree of landscape heterogeneity with the presence of scattered trees and shrubs (Freeman & Crick 2003; Goodenough et al. 2009; Maggini et al. 2014). Some of these have threat levels ranging from nearly threatened (NT) for *Lanius collurio*, *Anthus trivialis* and *Phoenicurus phoenicurus*, to vulnerable (VU) for *Anthus pratensis* *Lullula arborea*. As tree density increases, more generalist species and some forest specialists are observed, increasing community diversity. Such species can be found in small

Table 4 For hoverflies diversity, model-averaged conditional estimates, standard errors (SE), z values and p-values for species Richness, Hill Shannon and Hill Simpson diversity indicators

Models	Estimate	Std. error	Adjusted SE	z value	Pr(> z)
Richness					
(Intercept)	1,7981	1,0677	1,0799	1,6651	0,0959
elevation	– 0,0013	0,0007	0,0007	1,6874	0,0915
Shrubs/ha	0,0079	0,0109	0,0112	0,7029	0,4821
trees/ha	0,004	0,0031	0,0031	1,2574	0,2086
year23	– 3,0161	3,0232	3,0462	0,9901	0,3221
elevation:year23	0,0037	0,0021	0,0021	1,7566	0,079
shrubs/ha:year23	– 0,0545	0,0217	0,0222	2,4536	0,0141
trees/ha:year23	0,0149	0,0066	0,0067	2,2116	0,027
% BPA	– 0,0029	0,002	0,0021	1,4129	0,1577
LTPE	– 0,0001	0,0001	0,0001	0,7112	0,477
% deciduous trees	– 0,0017	0,0028	0,0029	0,5972	0,5503
Hill Shannon					
(Intercept)	1,6682	1,0247	1,0363	1,6097	0,1075
elevation	– 0,0012	0,0007	0,0007	1,6311	0,1029
trees/ha	0,004	0,0029	0,003	1,3411	0,1799
% BPA	– 0,0029	0,002	0,0021	1,4061	0,1597
year23	– 2,5878	2,7451	2,7665	0,9354	0,3496
elevation:year23	0,0034	0,0019	0,002	1,7272	0,0841
LTPE	– 0,0001	0,0001	0,0001	0,7381	0,4604
shrubs/ha	0,0075	0,0109	0,0112	0,67	0,5029
shrubs/ha:year23	– 0,0497	0,0216	0,0222	2,244	0,0248
trees/ha:year23	0,0139	0,0065	0,0067	2,0768	0,0378
% deciduous trees	– 0,0018	0,0028	0,0028	0,6342	0,526
Hill Simpson					
(Intercept)	1,4484	0,9549	0,9654	1,5004	0,1335
elevation	– 0,0011	0,0007	0,0007	1,5395	0,1237
trees/ha	0,004	0,0026	0,0027	1,4913	0,1359
% BPA	– 0,0027	0,002	0,002	1,3071	0,1912
year23	– 2,0246	2,2533	2,2727	0,8908	0,373
elevation:year23	0,0029	0,0016	0,0016	1,7906	0,0734
LTPE	– 0,0001	0,0001	0,0001	0,7578	0,4486
% deciduous trees	– 0,0017	0,0027	0,0028	0,6072	0,5437

forest patches within agricultural areas, close to forest edges as well as in gardens and villages (Cody 1985; Hatchwell et al. 1996; Heldbjerg et al. 2017, Knaus et al. 2018). For this reason, our results support the hypothesis that varying tree density within agricultural landscapes favors the diversity of birds, in line with previous studies (Berg 2002; Fischer et al. 2010; Godinho & Rabaça, 2011). However, our results also point towards a trade-off between trees on pasture promoting bird diversity, and specific habitat needs of rare species represented by extensively managed open land. A similar trend has been shown in birds in coastal saline habitats (Godet et al. 2016). Where a landscape favoring taxonomic diversity

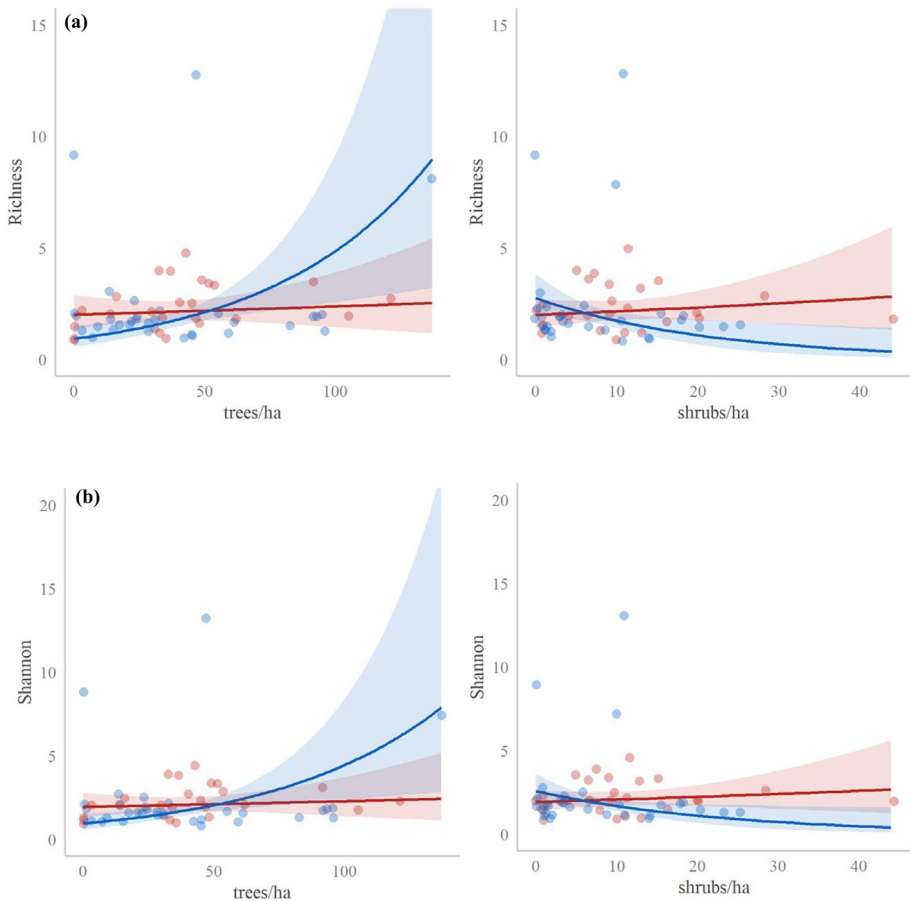


Fig. 5 Best linear model predictions for hoverflies, **a** Richness, **b** Hill-Shannon estimated diversity indicators according to significant variables (p -value < 0.05) in the averaged model: tree density in interaction with year, shrub density in interaction with year, red curve for year 2022 and blue curve for year 2023

does not necessarily promote rare species, which are rather associated to extreme habitats. Along this line, functional diversity could bring additional information on the effect of environmental heterogeneity on bird communities. For example, in forested landscapes, forest fragmentation leads to a functional homogenization in bird communities which could be underestimated by an apparent increase in taxonomic diversity (Santillán et al. 2019).

Our results indicate that forest-dwelling hoverfly species are well differentiated in the community and are associated with high tree density. We also showed that species from the genera *Eristalis*, *Lapposyrphus*, *Episyrphus*, *Myathropa*, *Volucella* and *Orhtonevra* are mainly found in semi-open pastures, in line with previous studies indicating that they are either generalist species or specialists of semi-open lands (Speight 2020, Pétremand et al. 2022). It seems that a high number of species are clustered in medium tree density together with high shrub density, high BPA cover and highly scattered spatial distribution of trees. This could reflect the fact that BPA offers flower resources that promote hoverfly diversity, as shown in previous studies (Haenke et al. 2009; Meyer et al. 2009; Moquet et al. 2018). It

also aligns with findings highlighting the importance of spatial structures for several hoverfly species on agricultural lands (Pfister et al. 2017; Schirmel et al. 2018) as well as forested habitats (Gittings et al. 2006). Finally, although our results show that the percentage of deciduous trees does not explain a significant part of the total variation in community compositions of hoverflies, four rare species in Switzerland are associated with sites with a high percentage of deciduous trees, corresponding to their ecology described in Speight et al. (2020) (*Brachyopa pilosa*, *Cheilosia albipila*, *Scaeva dignota* and *Xanthogramma citrofasciatum*). This highlights the potential conservation role of particular tree species on agricultural land for threatened hoverfly species.

Diversity metrics show different community structures between birds and hoverflies

The 45 sampled bird communities seemed to be well-described for Hill-Shannon and Hill-Simpson indicators, while for hoverflies there is a lot of variation between species accumulation curves. Among the 29 sampled communities, some display curves that never reach a plateau, even when extrapolated for Hill-Simpson diversity indicators. This highlights the difference between hoverfly communities in term of species compositions, with some communities composed in majority of a few common and abundant species (*Eristalis Tenax*, *Merodon cinnereus*, *Merodon aureus*, *Sphaerophoria scripta*), while other communities consist of a few individuals from many different species that are present in few sites. Such community structure in hoverflies has already been documented in previous studies (Janković et al. 2019; Ricarte et al. 2011). Our results are in line with (Ricarte et al. 2011), indicating high beta diversity in hoverflies related to the very great species turnover between communities in a landscape. This important turnover of locally rare species between sites might be due to the dependence of some species on very localized resources (Meyer et al. 2009).

Species diversity is impacted by environmental heterogeneity

The year of survey always has an impact, but it is slightly different for both groups of species. Diversity is higher for birds in 2023. For hoverflies, the year mainly impacts relationships with environmental variables such as trees and shrub densities. While we can't exclude an effect of the environmental characteristics of the sites sampled in the different years that we might have missed (e.g., related to pasture management regimes), it is important to note the very different weather conditions in Switzerland between winter and spring 2022 and 2023. Both winter and spring were warmer than the norm, but winter 2021–2022 registered a higher amount of precipitation in the Jura mountains, with 120–125% of the norm (MétéoSuisse 2021/22), whereas winter 2022–2023 had 70% of the normal precipitation (MétéoSuisse 2022/23). Hard winter conditions can affect overwintering bird populations, especially in high-elevation habitats, the amount of precipitation being one of the detrimental factors (Canonne et al. 2023). This might have had an effect on our sampled bird populations in 2022. Spring 2022 was particularly dry and sunny, being among the 10 driest springs in Switzerland and the fourth sunniest since 1961, when measurements began (MétéoSuisse 2022). In contrast, spring 2023 was particularly cloudy and precipitation were higher than the norm (MétéoSuisse 2023). This might have had an impact on the hoverfly populations we sampled, as spring and summer weather have been shown to

highly impact insect biomass (Müller et al. 2024), and the diversity of hoverfly communities has been shown to increase with temperature (Janković et al. 2019).

Contrary to our expectations, the relationships between species richness and tree density were positive and linear in both groups of species, and not hump shaped. Further research is needed to investigate species diversity at higher tree cover (> 75%) which was lacking in our study. In both groups of species diversity measured with Hill-Shannon (and also Hill-Simpson for birds) show a positive and significant relationship with tree density, meaning that it is not a few locally rare species that are driving differences among study sites, but communities differing in species that are abundant in each site.

A large number of hoverfly species have larvae with specific microhabitat needs: they can be aphidophagous, saprotrophic, herbivorous, and/or microorganism-fed (Speight 2020). It is still not well understood whether the observed adult hoverfly diversity is related to the proximity of a larval microhabitat or adult feeding resources (Power et al. 2016). It is also not clear how far hoverflies can disperse. Some species do not move further than 50 m, whereas others can fly up to distances of 400 m (Wratten et al. 2003). It is probable that the more trees there are in the pastures, the more diversity of potential hoverfly larvae microhabitats there will be. Therefore, along with our results, this could be an explanation for the positive relationship between tree density and species richness, which supports previous findings (Ricarte et al. 2011). In addition, wood-pastures with varying tree densities could also be used by many species as connectivity corridors in the landscape, as has been shown in semi-open habitats for carabid species (Boutaud et al. 2022), or within hedgerows in an agricultural matrix for different pollinator species (Holzschuh et al. 2010) and for birds (Hinsley & Bellamy 2000).

Shrub density had no impact on bird diversity and a nuanced impact on species richness in hoverflies, promoting richness in 2022 and strongly decreasing it in 2023, which makes it difficult to interpret. Nevertheless, previous studies have shown that hedgerows (defined as assemblages of shrubs and trees in agricultural landscapes) promote hoverfly (Power et al. 2016; Schirmel et al. 2018) and bird richness (Hinsley & Bellamy 2000). For birds, hedgerows offer nesting and food resources and shelter against predators. But they are also connectivity elements in the landscape (Hinsley & Bellamy 2000). For hoverflies, hedgerows could also serve as movement corridors (Haenke et al. 2014), and/ or as refuges during extreme weather conditions or from predators (Sutherland et al. 2001). More research would be needed to disentangle the effect of shrubs from other elements (e.g. trees) on hoverflies and bird communities in pasture lands.

Our results show the important positive effect of structural and compositional tree-stand heterogeneity on bird species diversity, as the level of tree mixture and length of tree patches edges both increased diversity regardless of the indicators. The importance of heterogeneous assemblages of trees or bushes for bird diversity has been also shown in previous studies focusing on semi-open environments (Berg 1997; Godinho & Rabaça, 2011), ecotones areas (Jähnig et al. 2018) as well as on forests (Camprodon & Brotons 2006; Gil-Tena et al. 2007; Rigo et al. 2024). The presence of deciduous trees might improve nesting resources as well as feeding resources (Gil-Tena et al. 2007), while scattered trees' spatial distribution favors a variety of environmental conditions (Dufour et al. 2006) that may support a diversity of food and nesting resources.

The percentage of deciduous trees had no effect on the hoverfly diversity in our study, although importance of broadleaf trees has been shown by Gittings et al. (2006) to promote the diversity of hoverflies in coniferous forests. Neither did LTPE. More research would be needed to investigate the effects of such environmental parameters on hoverflies at various scales, for example, larger than 100 m as conducted in our study.

BPA had no effect on diversity in both groups. Although herbaceous diversity has been shown to have significant positive effect on many groups of species such as bees and hoverflies (Haenke et al. 2009; Meyer et al. 2009; Pardo et al. 2023; Tschumi et al. 2016). In our study, BPA percentage cover might have been a category too broad to represent pasture botanical composition. These surfaces are mapped based on a list of 57 indicator plants, but only 6 of them need to be present, reducing considerably the information on the plant community. However, we chose this variable as it also represents an extensive type of pasture management. Farmers need to respect a set of particular rules to be able to receive subsidies, such as no fertilizer, no pesticides, no external supply of forage, and limited cattle load. Such extensive agricultural management is usually linked with higher species diversity of different groups of species such as butterflies, bugs, orthopterans, spiders, and birds (Balmer & Erhardt 2000; Dennis et al. 2001; Di Giulio et al. 2001; Klein et al. 2020; Vickery et al. 2001). While most previous studies were conducted in open pastures, our results suggest that grassland compositions might be less important for bird and hoverfly diversity compared to the presence of trees and shrubs providing keystone structures in agricultural landscapes (Manning et al. 2006).

Conclusion

Birds and hoverflies diversity reacted very similarly to tree density, although birds' diversity indicators were more sensitive to changes in the structural and compositional heterogeneity of tree-stands. In terms of diversity, none of the studied species groups were influenced by our indicators of herb-layer compositional heterogeneity, even if this variable influenced the composition of hoverfly communities in ordination analyses. Our results show the importance of trees in agricultural landscapes to promote species richness in these two groups of species. This aligns with previous findings that put forward a trend for agroforestry to sustain biodiversity (Guariento et al. 2024; Jakobsson et al. 2020; Marsden et al. 2020; Mcadam et al. 2007), or more generally that the presence of trees in agricultural landscapes notably improves biodiversity (Fischer et al. 2010; Söderström et al. 2001). According to our results, not only the presence of trees is important, but wood-pastures in the Swiss Jura mountains should be managed in order to promote scattered distribution of trees on pastures as well as a high degree of mixture between deciduous and coniferous trees to support diversity, especially in birds and for some locally rare hoverfly species. This confirms the importance of environmental heterogeneity for species diversity (Hekkala et al. 2023; Priyadarshana et al. 2024; Stein et al. 2014). However, our analysis also highlights the crucial role of mid-altitude, open pastures to maintain communities of vulnerable farmland bird species associated with extensive agricultural management, almost disappearing in the lowland in Switzerland (Donald et al. 2006; Gregory et al. 2004; Knaus et al. 2021). This is in line with the results of Katayama et al. (2014) supporting the necessity of patches of more homogenous environments, such as forest or open habitats for species with reduced habitat generalization capacities, versus species with wide environmental niches that are favored by environment heterogeneity. We suggest that varying tree density across space, including pastures without trees, would promote birds and hoverflies diversity at a landscape scale, while maintaining farmland bird species of conservation concerns.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-025-03066-1>.

Acknowledgements We would like to thank the cantonal offices from Neuchâtel for the availability of Lidar data and agriculture inventories: Service de la faune des forêts et de la nature (SFFN), Service de la géomatique et du registre foncier and Service de l'agriculture. We also thank the Office fédéral de topographie swisstopo for the online topographic maps of Switzerland (<https://map.geo.admin.ch>). We specially thank Frédéric Wyss and Philippe Jacot from the SFFN for their input of knowledge about the wood-pastures management in the canton of Neuchâtel. We thank Lisa Fisler (Centre Suisse de Cartographie de la Faune) and Daniel Ston (consultancy office of ecology) for their valuable help in hoverflies identification as well as Dr. Claudio Quilodran (University of Geneva) for his precious support in data analysis. Finally, we are very grateful to Dr. Jean-Yves Humbert (University of Bern) and Dr. Christophe Praz (University of Neuchâtel) for their advice at the beginning of the study and their feedbacks all along the project.

Author contributions SW: conceptualized and designed the study with the help of CZ. SW: collected the data. SW: identified the hoverflies with the help of experts. SW: analyzed and interpreted the results with the help of CZ. SW: wrote the draft of the manuscript and reviewed it with the help of CZ. All authors reviewed the results and approved the final version of the manuscript.

Funding Open access funding provided by University of Neuchâtel. This work was financed by the University of Neuchâtel through the Conservation Biology research group under the direction of Clara Zemp.

Data availability The dataset analyzed in this study is available from the corresponding author upon request.

Declarations

Conflict of interest The authors have not disclosed any 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

- Anderle M, Brambilla M, Hilpold A, Matabishi JG, Paniccia C, Rocchini D, Rossin J, Tasser E, Torresani M, Tappeiner U, Seeber J (2023) Habitat heterogeneity promotes bird diversity in agricultural landscapes : insights from remote sensing data. *Basic Appl Ecol* 70:38–49. <https://doi.org/10.1016/j.baec.2023.04.006>
- Anderle M, Brambilla M, Angelini L, Guariento E, Paniccia C, Plunger J, Seeber J, Stifter S, Tappeiner U, Tasser E, Hilpold A (2024) Efficiency of birds as bioindicators for other taxa in mountain farmlands. *Ecol Ind* 158:111569. <https://doi.org/10.1016/j.ecolind.2024.111569>
- Balmer O, Erhardt A (2000) Consequences of succession on extensively grazed grasslands for central European butterfly communities : rethinking conservation practices. *Conserv Biol* 14(3):746–757. <https://doi.org/10.1046/j.1523-1739.2000.98612.x>
- Barnagaud J-Y, Gaüzère P, Zuckerberg B, Princé K, Svenning J-C (2017) Temporal changes in bird functional diversity across the United States. *Oecologia* 185(4):737–748. <https://doi.org/10.1007/s00442-017-3967-4>
- Bartoń, K., 2018. MuMin: multi-model inference, R Package Version 1.42.1
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity : is habitat heterogeneity the key? *Trends Ecol Evol* 18(4):182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)
- Berg Å (1997) Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. *Bird Study* 44(3):355–366. <https://doi.org/10.1080/00063659709461071>
- Berg Å (2002) Composition and diversity of bird communities in Swedish farmland–forest mosaic landscapes. *Bird Study* 49(2):153–165. <https://doi.org/10.1080/00063650209461260>

- Bergmeier E, Petermann J, Schröder E (2010) Geobotanical survey of wood-pasture habitats in Europe : diversity, threats and conservation. *Biodivers Conserv* 19(11):2995–3014. <https://doi.org/10.1007/s10531-010-9872-3>
- Bibby CJ, Burgess ND, Hill DA (1992) Bird census techniques, 2nd edn. Academic Press, London
- Boutaud E, Nolte D, Harry I, Assmann T, Drees C (2022) Conservation value of semi-open habitats for ground beetles (Coleoptera : Carabidae, Cicindelidae) in Central Europe. *Biodivers Conserv* 31(5–6):1469–1489. <https://doi.org/10.1007/s10531-022-02402-z>
- Browder SF, Johnson DH, Ball IJ (2002) Assemblages of breeding birds as indicators of grassland condition. *Ecol Ind* 2(3):257–270. [https://doi.org/10.1016/S1470-160X\(02\)00060-2](https://doi.org/10.1016/S1470-160X(02)00060-2)
- Burgio G, Sommaggio D (2007) Syrphids as landscape bioindicators in Italian agroecosystems. *Agr Ecosyst Environ* 120(2):416–422. <https://doi.org/10.1016/j.agee.2006.10.021>
- Burnham KP, Anderson DR (2003) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, Berlin
- Buttler A, Kohler F, Gillet F (2009) The swiss mountain wooded pastures : patterns and processes. In: Rigueiro-Rodríguez A, McAdam J, Mosquera-Losada MR (eds) Agroforestry in Europe : current status and future prospects. Springer, Netherlands, pp 377–396
- Camprodon J, Brotons L (2006) Effects of undergrowth clearing on the bird communities of the North-western Mediterranean Coppice Holm oak forests. *For Ecol Manage* 221(1):72–82. <https://doi.org/10.1016/j.foreco.2005.10.044>
- Canonne C, Bernard-Laurent A, Souchay G, Perrot C, Besnard A (2023) Contrasted impacts of weather conditions in species sensitive to both survival and fecundity : a montane bird case study. *Ecology* 104(2):e3932. <https://doi.org/10.1002/ecy.3932>
- Canterbury GE, Martin TE, Petit DR, Bradford DF (2000) Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conserv Biol* 14(2):544–558. <https://doi.org/10.1046/j.1523-1739.2000.98235.x>
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation : standardizing samples by completeness rather than size. *Ecology* 93(12):2533–2547. <https://doi.org/10.1890/11-1952.1>
- Chételat J, Kalbermatten M, Lannas KSM, Spiegelberger T, Wettstein J-B, 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):39. <https://doi.org/10.5751/ES-05287-180139>
- Cody ML (1985) Habitat Selection in Birds. Academic Press, Cambridge
- Delabie S, Maicher V, Sáfián S, Doležal J, Altman J, Janeček Š, Kobe IN, Murkwe M, Šebek P, Tropek R (2021) Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon. *Biotropica* 53(2):567–580. <https://doi.org/10.1111/btp.12900>
- Dennis P, Young MR, Bentley C (2001) The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agr Ecosyst Environ* 86(1):39–57. [https://doi.org/10.1016/S0167-8809\(00\)00263-2](https://doi.org/10.1016/S0167-8809(00)00263-2)
- Di Giulio M, Edwards PJ, Meister E (2001) Enhancing insect diversity in agricultural grasslands : the roles of management and landscape structure. *J Appl Ecol* 38(2):310–319
- Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceed Royal Soc Lond Series b: Biol Sci* 268(1462):25–29. <https://doi.org/10.1098/rspb.2000.1325>
- Donald PF, Sanderson FJ, Burfield IJ, van Bommel FJP (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agr Ecosyst Environ* 116(3):189–196. <https://doi.org/10.1016/j.agee.2006.02.007>
- Dufour 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>
- Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin J-L (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes : heterogeneity and biodiversity. *Ecol Lett* 14(2):101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Fischer J, Lindenmayer DB (2002) The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 1. Species composition and site occupancy patterns. *Biodivers Conserv* 11(5):807–832. <https://doi.org/10.1023/A:1015371511169>
- Fischer J, Stott J, Law BS (2010) The disproportionate value of scattered trees. *Biol Cons* 143(6):1564–1567. <https://doi.org/10.1016/j.biocon.2010.03.030>
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Freeman SN, Crick HQP (2003) The decline of the spotted flycatcher *Muscicapa striata* in the UK : an integrated population model. *Ibis* 145(3):400–412. <https://doi.org/10.1046/j.1474-919X.2003.00177.x>

- Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG (2010) Scale matters : the impact of organic farming on biodiversity at different spatial scales. *Ecol Lett* 13(7):858–869. <https://doi.org/10.1111/j.1461-0248.2010.01481.x>
- Gallandat J-D, Gillet F, Havlicek E, Perrenoud A (1995) *PATUBOIS - Typologie et systématique phytocécologiques des pâturages boisés du Jura suisse*.
- Wider S and Zemp DC (2024) Composition and diversity of birds and hoverflies communities are impacted by vegetation heterogeneity in wood-pastures in the Swiss Jura => This reference is wrong as it is the name of the paper.
- Gillet F, Murisier B, Buttler A, Gallandat J-D, Gobat J-M (1999) Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Appl Veg Sci* 2(1):47–54. <https://doi.org/10.2307/1478880>
- Gillet F, Besson O, Gobat J-M (2002) PATUMOD : a compartment model of vegetation dynamics in wooded pastures. *Ecol Model* 147:267–290. [https://doi.org/10.1016/S0304-3800\(01\)00427-6](https://doi.org/10.1016/S0304-3800(01)00427-6)
- Gil-Tena A, Saura S, Brotons L (2007) Effects of forest composition and structure on bird species richness in a mediterranean context : implications for forest ecosystem management. *For Ecol Manage* 242(2):470–476. <https://doi.org/10.1016/j.foreco.2007.01.080>
- Gittings T, O'Halloran J, Kelly T, Giller PS (2006) The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. *For Ecol Manage* 237(1–3):290–300. <https://doi.org/10.1016/j.foreco.2006.09.052>
- Godet L, Devictor V, Burel F, Robin J-G, Ménanteau L, Fournier J (2016) Extreme landscapes decrease taxonomic and functional bird diversity but promote the presence of rare species. *Acta Ornithologica* 51(1):23–38. <https://doi.org/10.3161/00016454AO2016.51.1.003>
- Godinho C, Rabaça JE (2011) Birds like it Corky : the influence of habitat features and management of 'montados' in breeding bird communities. *Agrofor Syst* 82(2):183–195. <https://doi.org/10.1007/s10457-010-9345-4>
- Gonçalves P, Alcobia S, Simões L, Santos-Reis M (2012) Effects of management options on mammal richness in a mediterranean agro-silvo-pastoral system. *Agrofor Syst* 85(3):383–395. <https://doi.org/10.1007/s10457-011-9439-7>
- Goodenough AE, Elliot SL, Hart AG (2009) The challenges of conservation for declining migrants : are reserve-based initiatives during the breeding season appropriate for the Pied Flycatcher *Ficedula hypoleuca*? *Ibis* 151(3):429–439. <https://doi.org/10.1111/j.1474-919X.2009.00917.x>
- Gottschalk TK, Huettmann F (2011) Comparison of distance sampling and territory mapping methods for birds in four different habitats. *J Ornithol* 152(2):421–429. <https://doi.org/10.1007/s10336-010-0601-1>
- Gregory RD, Noble DG, Custance J (2004) The state of play of farmland birds : population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146(s2):1–13. <https://doi.org/10.1111/j.1474-919X.2004.00358.x>
- Guariento E, Obwegs L, Anderle M, Bellè A, Fontana P, Paniccia C, Plunger J, Rüdisser J, Stifter S, Giombini V, Egarter Vigl L, Tappeiner U, Hilpold A (2024) Meadow orchards as a good practice example for improving biodiversity in intensive apple orchards. *Biol Cons* 299:110815. <https://doi.org/10.1016/j.biocon.2024.110815>
- Haenke S, Scheid B, Schaefer M, Tscharnkte T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *J Appl Ecol* 46(5):1106–1114. <https://doi.org/10.1111/j.1365-2664.2009.01685.x>
- Haenke S, Kovács-Hostyánszki A, Fründ J, Batáry P, Jauker B, Tscharnkte T, Holzschuh A (2014) Landscape configuration of crops and hedgerows drives local syrphid fly abundance. *J Appl Ecol* 51(2):505–513. <https://doi.org/10.1111/1365-2664.12221>
- Hatchwell BJ, Chamberlain DE, Perrins CM (1996) The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. *Ibis* 138(2):256–262. <https://doi.org/10.1111/j.1474-919X.1996.tb04337.x>
- Hekkala A-M, Jönsson M, Kärvelo S, Strengbom J, Sjögren J (2023) Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecol Ind* 148:110069. <https://doi.org/10.1016/j.ecolind.2023.110069>
- Heldbjerg H, Fox AD, Thellessen PV, Dalby L, Sunde P (2017) Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. *PLoS ONE* 12(8):e0182504. <https://doi.org/10.1371/journal.pone.0182504>
- Hill MO (1973) Diversity and Evenness : A Unifying Notation and Its Consequences. *Ecology* 54(2):427–432. <https://doi.org/10.2307/1934352>

- Hinsley SA, Bellamy PE (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds : a review. *J Environ Manage* 60(1):33–49. <https://doi.org/10.1006/jema.2000.0360>
- Holzschuh A, Steffan-Dewenter I, Tscharnkte T (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J Anim Ecol* 79(2):491–500. <https://doi.org/10.1111/j.1365-2656.2009.01642.x>
- Hsieh T. C., Ma K. H. and Chao Anne. 2016 iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12 URL: <http://chao.stat.nthu.edu.tw/blog/software-download/>.
- Inclán DJ, Dainese M, Cerretti P, Paniccio D, Marini L (2016) Spillover of tachinids and hoverflies from different field margins. *Basic Appl Ecol* 17(1):33–42. <https://doi.org/10.1016/j.baae.2015.08.005>
- Jähnig S, Alba R, Vallino C, Rosselli D, Pittarello M, Rolando A, Chamberlain D (2018) The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. *J Ornithol* 159(3):747–759. <https://doi.org/10.1007/s10336-018-1549-9>
- Jakobsson S, Wood H, Ekroos J, Lindborg R (2020) Contrasting multi-taxa functional diversity patterns along vegetation structure gradients of woody pastures. *Biodivers Conserv* 29(13):3551–3572. <https://doi.org/10.1007/s10531-020-02037-y>
- James G, Witten D, Hastie T, Tibshirani R (2013) An introduction to statistical learning. Springer, New York
- Janković M, Nedeljković Z, Milovac Ž, Vujić A (2019) Diversity and structure of hoverfly (Diptera: Syrphidae) communities in agricultural areas in Vojvodina Province (Serbia) a case study on *Brassica napus* L. *J. Entomol Res Soc* 21(2):129–144
- Katayama N, Amano T, Naoe S, Yamakita T, Komatsu I, Takagawa S, Sato N, Ueta M, Miyashita T (2014) Landscape Heterogeneity-biodiversity relationship : effect of range size. *PLoS ONE* 9(3):e93359. <https://doi.org/10.1371/journal.pone.0093359>
- Klein N, Theux C, Arlettaz R, Jacot A, Pradervand J-N (2020) Modeling the effects of grassland management intensity on biodiversity. *Ecol Evol* 10(23):13518–13529. <https://doi.org/10.1002/ece3.6957>
- Knaus P, Antoniazza S, Wechsler S, Guélat J, Kéry M, Strebel N, Sattler T (2018). Atlas des oiseaux nicheurs de Suisse. Vogelwarte.ch, p 648
- Knaus P, Antoniazza S, Keller V, Sattler T, Schmid H, Strebel N 2021 Liste rouge des oiseaux nicheurs. Espèces menacées en Suisse. Office fédéral de l'environnement (OFEV). Station ornithologique suisse. *L'environnement pratique* 2124, p 54
- Lovette IJ, Fitzpatrick JW (2016) Handbook of bird biology. Wiley, Hoboken
- Maggini R, Lehmann A, Zbinden N, Zimmermann NE, Bolliger J, Schröder B, Foppen R, Schmid H, Beniston M, Jenni L (2014) Assessing species vulnerability to climate and land use change : the case of the Swiss breeding birds. *Divers Distrib* 20(6):708–719. <https://doi.org/10.1111/ddi.12207>
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures – implications for conservation. *Biol Cons* 132(3):311–321. <https://doi.org/10.1016/j.biocon.2006.04.023>
- Marsden C, Martin-Chave A, Cortet J, Hedde M, Capowiez Y (2020) How agroforestry systems influence soil fauna and their functions—a review. *Plant Soil* 453(1):29–44. <https://doi.org/10.1007/s11104-019-04322-4>
- McCune B, Grace JB (2002) Analysis of ecological communities.
- 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>
- Météo Suisse. Bulletin climatologique hiver 2021/22. Genève. <https://www.meteosuisse.admin.ch/services-etpublications/publications/rapports-et-bulletins/2022/bulletin-climatologique-hiver-2021-22.html>
- Météo Suisse. Bulletin climatologique printemps 2022. Genève. <https://www.meteosuisse.admin.ch/services-etpublications/publications/rapports-et-bulletins/2022/bulletin-climatologique-printemps-2022.html>
- Météo Suisse. Bulletin climatologique hiver 2022/23. Genève. <https://www.meteosuisse.admin.ch/services-etpublications/publications/rapports-et-bulletins/2023/bulletin-climatologique-hiver-2022-23.html>
- Météo Suisse. Bulletin climatologique printemps 2023. Genève. <https://www.meteosuisse.admin.ch/services-etpublications/publications/rapports-et-bulletins/2023/bulletin-climatologique-printemps-2023.html>
- Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl Ecol* 10(2):178–186. <https://doi.org/10.1016/j.baae.2008.01.001>
- Moquet L, Laurent E, Bacchetta R, Jacquemart A-L (2018) Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. *Insect Conserv Divers* 11(1):72–87. <https://doi.org/10.1111/icad.12245>

- Morelli F, Pruscini F, Santolini R, Perna P, Benedetti Y, Sisti D (2013) Landscape heterogeneity metrics as indicators of bird diversity : determining the optimal spatial scales in different landscapes. *Ecol Ind* 34:372–379. <https://doi.org/10.1016/j.ecolind.2013.05.021>
- Müller J, Hothorn T, Yuan Y, Seibold S, Mitesser O, Rothacher J, Freund J, Wild C, Wolz M, Menzel A (2024) Weather explains the decline and rise of insect biomass over 34 years. *Nature* 628(8007):349–354. <https://doi.org/10.1038/s41586-023-06402-z>
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). *_vegan: Community Ecology Package_*. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>
- Oksuz DP, Palmeirim JM, Correia RA (2021) Bird taxonomic and functional responses to land abandonment in wood-pastures. *Agrofor Syst*. <https://doi.org/10.1007/s10457-021-00649-z>
- Ouin A, Holland GJ, Tessier M, Clarke RH, Bennett AF (2021) Do butterfly communities benefit from woodland restoration in rural environments? A landscape perspective from south-eastern Australia. *Restor Ecol* 30(1):e13478. <https://doi.org/10.1111/rec.13478>
- Pardo A, Rolo V, Carrascosa A, Gonzalez-Bornay G, Moreno G (2023) Management linked to ecological intensification supports insect pollinators in Iberian wood-pastures. *Landscape Ecol*. <https://doi.org/10.1007/s10980-023-01637-7>
- Petanidou T, Vujić A, Ellis WN (2011) Hoverfly diversity (Diptera : Syrphidae) in a Mediterranean scrub community near Athens, Greece. *Annales De La Société Entomologique De France (n.s.)* 47(1–2):168–175. <https://doi.org/10.1080/00379271.2011.10697709>
- Pétrement G., bessat M., Castella E., Speight M. (2022). *Genève sous la loupe: les syrphes du canton (Diptera, Syrphidae)*. Editions Faune Genève, Genève.
- Pfister SC, Sutter L, Albrecht M, Marini S, Schirmel J, Entling MH (2017) Positive effects of local and landscape features on predatory flies in European agricultural landscapes. *Agr Ecosyst Environ* 239:283–292. <https://doi.org/10.1016/j.agee.2017.01.032>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2021). *nlme: Linear and Nonlinear Mixed Effects Models*. <https://CRAN.R-project.org/package=nlme>
- Plieninger T, Hartel T, Martín-López B, Beaufoy G, Bergmeier E, Kirby K, Montero MJ, Moreno G, Oteros-Rozas E, Van Uytvanck J (2015) Wood-pastures of Europe : Geographic coverage, social–ecological values, conservation management, and policy implications. *Biol Cons* 190:70–79. <https://doi.org/10.1016/j.biocon.2015.05.014>
- Power EF, Jackson Z, Stout JC (2016) Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. *Insect Conserv Divers* 9(3):244–253. <https://doi.org/10.1111/icad.12163>
- Priyadarshana TS, Martin EA, Sirami C, Woodcock BA, Goodale E, Martínez-Núñez C, Lee M-B, Pagani-Núñez E, Raderschall CA, Brotons L, Rege A, Ouin A, Tschantke T, Slade EM (2024) Crop and landscape heterogeneity increase biodiversity in agricultural landscapes : a global review and meta-analysis. *Ecol Lett* 27(3):e14412. <https://doi.org/10.1111/ele.14412>
- Ramírez-Hernández A, Micó E, Marcos-García MDLÁ, Brustel H, Galante E (2014) The “dehesa”, a key ecosystem in maintaining the diversity of mediterranean saproxylic insects (coleoptera and diptera : syrphidae). *Biodivers Conserv* 23(8):2069–2086. <https://doi.org/10.1007/s10531-014-0705-7>
- Rencher AC (2002) *Methods of multivariate analysis*, 2nd edn. Wiley, Hoboken
- Ricarte A, Ángeles Marcos-García M, Moreno CE (2011) Assessing the effects of vegetation type on hoverfly (Diptera : Syrphidae) diversity in a Mediterranean landscape: implications for conservation. *J Insect Conserv* 15(6):865–877. <https://doi.org/10.1007/s10841-011-9384-9>
- Rigo F, Paniccia C, Anderle M, Chianucci F, Obojes N, Tappeiner U, Hilpold A, Mina M (2024) Relating forest structural characteristics to bat and bird diversity in the Italian Alps. *For Ecol Manage* 554:121673. <https://doi.org/10.1016/j.foreco.2023.121673>
- RStudio Team (2020). *RStudio: Integrated Development for R*. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.
- Sakamoto Y, Ishiguro M, Kitagawa G (1986) *Akaike Information Criterion Statistics*. The Netherlands, Dordrecht
- Santillán V, Quitián M, Tinoco BA, Zárate E, Schleuning M, Böhning-Gaese K, Neuschulz EL (2019) Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient. *Oecologia* 189(4):863–873. <https://doi.org/10.1007/s00442-018-4309-x>
- Schirmel J, Albrecht M, Bauer P-M, Sutter L, Pfister SC, Entling MH (2018) Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. *J Appl Ecol* 55(4):1747–1758. <https://doi.org/10.1111/1365-2664.13095>

- Schweiger O, Musche M, Bailey D, Billeter R, Diekötter T, Hendrickx F, Herzog F, Liira J, Maelfait J-P, Speelmans M, Dziock F (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos* 116(3):461–472. <https://doi.org/10.1111/j.2007.0030-1299.15372.x>
- 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(11):1839–1863. <https://doi.org/10.1023/A:1013153427422>
- Spafford RD, Lortie CJ (2013) Sweeping beauty: is grassland arthropod community composition effectively estimated by sweep netting? *Ecol Evol* 3(10):3347–3358. <https://doi.org/10.1002/ece3.688>
- Speight MCD, Sarthou J-P (2017). StN keys for the identification of the European species of various genera of Syrphidae 2017/Clés StN pour la détermination des espèces Européennes de plusieurs genres des Syrphidae 2017. Syrph the Net, the database of European Syrphidae (Diptera), Syrph the Net publications, Dublin. 99, pp 139
- Speight MCD, Withers P, Dussaix C (2016). Clé StN pour la détermination des genres de Syrphidae Européens 2016 Syrph the Net, the database of European Syrphidae (Diptera). Syrph the Net publications, Dublin. 91, pp 40
- Speight MCD, Castella E, Sarthou J-P (2020) StN 2020. In: Syrph the Net on CD, Issue 12. Speight M.C.D., Castella E., Sarthou J.-P. & Vanappelghem C. (Eds.) ISSN 1649–1917. Syrph the Net Publications, Dublin.
- Speight MCD (2020) Species accounts of European Syrphidae, 2020. Syrph the Net, the database of European Syrphidae (Diptera), Syrph the Net publications, Dublin. 104, p 314
- 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(7):866–880. <https://doi.org/10.1111/ele.12277>
- Sutherland JP, Sullivan MS, Poppy GM (2001) Distribution and abundance of aphidophagous hoverflies (Diptera : Syrphidae) in wildflower patches and field margin habitats. *Agric for Entomol* 3(1):57–64. <https://doi.org/10.1046/j.1461-9563.2001.00090.x>
- Tschumi M, Albrecht M, Collatz J, Dubsky V, Entling MH, Najar-Rodriguez AJ, Jacot K (2016) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *J Appl Ecol* 53(4):1169–1176. <https://doi.org/10.1111/1365-2664.12653>
- Uhl B, Schall P, Bässler C (2024) Achieving structural heterogeneity and high multi-taxon biodiversity in managed forest ecosystems: a European review. *Biodivers Conserv*. <https://doi.org/10.1007/s10531-024-02878-x>
- Van Veen, M.P. (2010). Hoverflies of Northwest Europe: identification keys to the Syrphidae. KNNV Uitgeverij. ISBN: 9789050111997.
- Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J Appl Ecol* 38(3):647–664. <https://doi.org/10.1046/j.1365-2664.2001.00626.x>
- Waser L, Ginzler C, Rehush N (2017) Wall-to-wall tree type mapping from countrywide airborne remote sensing surveys. *Remote Sens* 9(8):766. <https://doi.org/10.3390/rs9080766>
- Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM (2003) Field boundaries as barriers to movement of hover flies (Diptera : Syrphidae) in cultivated land. *Oecologia* 134(4):605–611. <https://doi.org/10.1007/s00442-002-1128-9>

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