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Effects of Ground Cover Management, Landscape Elements and Local Conditions on Carabid (Coleoptera: Carabidae) Diversity and Vine Vitality in Temperate Vineyards

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Abstract: Sustainable vineyard management in inter-rows may improve biodiversity and ecosystem service provision in landscapes with a high density of vineyards. The current work investigates the effect of three inter-row ground cover treatments (bare soil by tillage, alternating and complete vegetation cover) on carabid beetle communities and vine vitality, in relation to climatic, soil and landscape parameters. Pitfall traps were used to collect carabids in the spring and autumn of 2016 from nine Austrian vineyards, with all three ground cover treatments established in each vineyard. Additionally, grape berry samples were collected before harvest in order to determine juice quality parameters. Generalized linear mixed models revealed that complete vegetation cover, the most extensive vineyard inter-row management, decreased both carabid density and species richness. The variables hours of sunshine, vineyard cover at the landscape scale and mesofauna abundance had negative impacts on species richness. The largest differentiator of carabid communities was the sampling timepoint, and we observed clustering associated to vineyard manager, whereas ground cover treatment played no significant role. The importance of treatment on vine vitality parameters was low; however, complete vegetation cover was detrimental to vine vegetative growth and berry weight. On the basis of our results, we conclude that although community composition may be influenced by pedo-climatic conditions and landscape components, alternating vegetation cover is an option for maintaining both carabid diversity and high-quality berries in vineyards.

Keywords: ground beetles; biodiversity; viticulture; grapevine; extensive inter-row management

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1. Introduction

Besides overexploitation, the current intensity and expansion of modern agriculture is one of the major drivers for the worldwide biodiversity loss [1–3] and diminishing ecosystem services, such as pest control, soil fertility and carbon sequestration [4]. This situation has been pronounced as particularly dire for the world's entomofauna [2,5] and their related ecosystem services, such as pollination and pest control [2,6]. Grapevines, the world's most valuable horticultural crop, represent an important farming system which shapes viticultural landscapes and, consequently, the aesthetic quality and recreational value of several wine-growing regions. Although vineyards are intensively managed agro-ecosystems, they may offer habitats for a range of organisms [7]. The perennial nature of vineyards in combination with inter-row vegetation further lends to their offering of ecosystem services [8,9]. In the last decade, an integration of farming practices that balance provisioning services and the promotion of ecological benefits has taken center stage in agricultural research [10,11]. One example of such a practice in viticulture is the replacement of high-intensity inter-row management, such as herbicide use and soil tillage, with more extensive ground cover management by sowing cover crops, or allowing local vegetation to flourish [9,12].

Although the benefits of nutrient mixing and soil aeration have known importance to the provisioning service of a grape harvest in regards to biodiversity, soil tillage has a negative impact, destroying vegetation, below- and above-ground fauna through mechanical processes, both directly and by damaging preferred habitats and food sources [13,14]. Meanwhile, the benefits of more extensively managing inter-row vegetation are multifaceted. Cover crops contribute to better soil trafficability, thus reducing soil erosion and nutrient losses [15–17]. Additionally, cover crops in inter-rows have been shown to support soil fertility via nutrient mineralization and degradation of organic matter through plant-supported microbiomes [18].

Moreover, extensive inter-row management with vegetation cover also impacts biodiversity in vineyards, which benefits a range of trophic levels, from microbes [19] to small mammals and birds [15,20]. Attributes of vegetation physical architecture, above and below ground, also provide alternative food and shelter for arthropods and mesofauna [21–23]. More specifically, ground cover vegetation in perennial systems is seen to increase the abundance of natural enemies [24] as well as influence herbivorous pest species, natural enemies and their interactions in vineyards, depending also on the landscape context [25,26]. Flower-rich cover-crop mixtures in vineyards are expected to increase the abundance of a range of natural enemies, including carabids [27–29]. Effective biological control offers the potential to reduce the use of pesticides contributing to the EU policy goal of halving pesticide use by 2030 [30]. However, different taxonomic groups show divergent responses to inter-row ground cover management: a recent study found that cavity-nesting, predatory wasp populations benefitted from an increase in vegetation cover, while the activity density and richness of carabid beetles declined [23].

Carabid beetles (Coleoptera: Carabidae) are ground beetles which are considered valuable contributors to integrated pest management, in addition to being indicators of agricultural disturbance [31–33]. As omnivorous generalist predators, most carabids feed on a variety of crop pests (e.g., damage by the light brown apple moth *Epiphyas postvittana* (Walker, Lepidoptera: Torticide) [34]), and contribute to weed seed predation [35], as some carabid genera, such as *Harpalus* and *Amara*, are granivorous [32,36]. Furthermore, carabids may be used as bioindicators, e.g., for soil disturbance, as some species develop only reduced wings (brachypterous species) and are therefore supported in higher numbers in more stable environments [32,37,38], such as in untilled inter-rows of perennial vineyards. However, some species are better adapted for dispersal, or are even dependent on bare, disturbed soils [32,39].

The benefits of cover crops depend on many factors (e.g., selection of seeded species, climate, soil quality or yield expectation), and results related to the effects on vine growth and grape quality are mixed [15,20,40,41]. A central concern for winegrowers is the competition of cover crops for water and nutrients, potentially negatively impacting vine vegetative growth and fruit composition [16,42,43]. On the other hand, in humid climates, vegetation cover in inter-rows could reduce vine vigor, leading to less dense canopies that allow for more bunch aeration and more hours of sunlight exposure, hence impacting berry composition and reducing the incidence of mildew diseases [44–46].

Viticultural practices varying in intensity and frequency can influence habitats of macro- to microfauna, and may also impact grapevine growth and fruit quality [10,43,47,48]. Most studies focus either on biodiversity in vineyards or neglect this aspect by only addressing the agronomic relevance of applied measures. Herein, we report on a study that investigates the effects of different inter-row ground cover managements on carabid beetle activity density, species richness and community composition, in addition to the effects of implementing these treatments on grapevine growth and grape berry quality. Thereby, we aim to evaluate the potential synergies or trade-offs of ground cover management practices on carabid diversity and grape production. In order to investigate the relative importance of this factor in comparison to other local, landscape and biological factors, we conducted generalized linear mixed regression models (on activity density and species richness). We hypothesize that the carabid diversity will increase with more extensive management of the vegetation cover in vineyard inter-rows. Additionally, we hypothesize that complete vegetation cover in vineyard inter-rows may only marginally decrease vine vigor, and that only minor effects on most grape juice quality parameters, if any, would be observed.

2. Materials and Methods

2.1. Study Sites

The study was conducted in nine vineyards, five located in the federal state of Lower Austria (AT01, AT02, AT07–AT09), and four in Burgenland (AT03–AT06) (Figure 1, Table S1). The climate classification of all vineyards according to Köppen-Geiger is a warm-summer humid continental climate; more specifically, the mean precipitation ranged from 487–567 mm per year during the study period from 2015 to 2017, with an annual mean temperature of 11.2–12.0 °C (Table S1). All vineyards were rainfed without further irrigation. The training system in all vineyards is a Vertical Shoot Positioned Trellis (VSP) system, and vines are pruned with one or two-sided canes, according to farm preferences. Management strategies for plant protection and vine nutrition were applied according to local practices of the respective winegrowers; among the study vineyards, three (AT07–AT09) were managed according to organic management regulations.

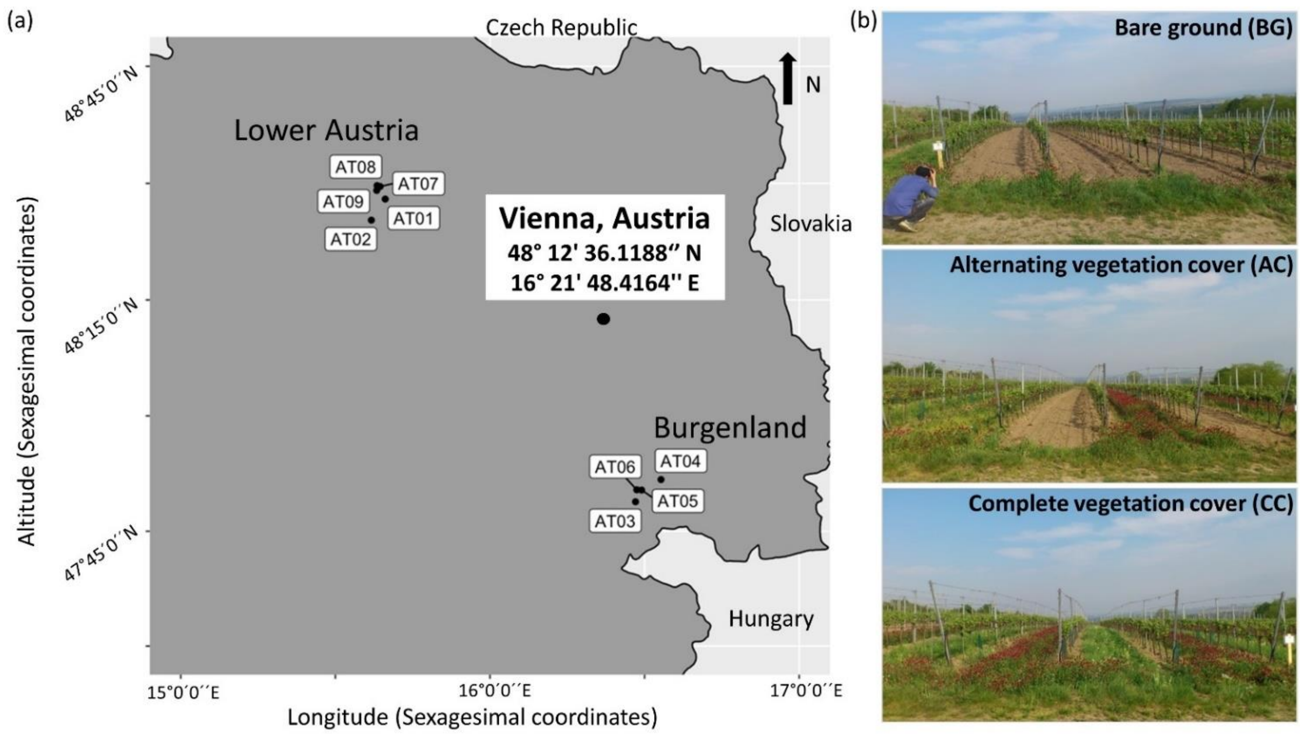

Figure 1. Location of the nine commercial vineyards in two viticulture regions in Austria, Lower Austria vineyards AT01, AT02, AT07–AT09 and Burgenland vineyards AT03–AT06 (**a**) and representative pictures of the different ground cover treatments established in each of the vineyard sites (**b**). Treatments: bare ground by tillage (BG), alternating vegetation coverage (AC) and complete vegetation coverage (CC).

2.2. Experimental Design

Three inter-row ground cover treatments were established in 2015 in all study vineyards, each in four inter-rows: bare ground (BG) by soil tillage three times per season carried out in April, at the end of May and mid-July; complete vegetation cover (CC) established through sowing seed mixtures in April 2015 in all inter-rows; and alternating vegetation cover (AC) with soil tillage in every second inter-row, while a continuous vegetation cover was kept in every other inter-row (Figure 1). Used seed mixtures were the following: Rebenfit (*Camelina sativa* ((L.) Crantz, Brassicales), *Plantago lanceolate* (L., Lamiales), *Centaurea cyanus* (L., Asterales), *Eruca sativa* ((L.) Cav., Brassicales), *Trifolium incarnatum* (L., Fabales), *Trifolium repens* (L., Fabales), *Medicago lupulina* (L., Fabales)) in vineyards AT07, AT08, AT09; Wolff mixture (main components-*Trifolium alexandrinum* (L., Fabales), *Melilotus albus* (Medik., Fabales), *Onobrychis viciifolia* (Scop., Fabales), *Medicago lupulina* (L., Fabales), *Trifolium incarnatum* (L., Fabales), *Medicago sativa* (L., Fabales), *Trifolium resupinatum* (L., Fabales), *Phacelia tanacetifolia* (Benth., Boraginales), *Trifolium hybridum* (L., Fabales), *Vicia villosa* (Roth., Fabales)) in AT01, AT02, AT06, AT06; and an individual seed mixture (*Avena fatua* (L., Poales), *Hordeum vulgare* (L., Poales), *Vicia villosa* (Roth., Fabales), *Lathyrus sativus* (L., Fabales), *Sorghum bicolor* ((L.) Moench, Poales), *Pisum sativum* (L., Fabales), *Triticum aestivum* (L., Fabales)) in AT03, AT04. Inter-rows with vegetation cover were frequently mulched throughout the season: at the end of May, June, July and August. The area below the vines was kept free of vegetation using soil tillage in all vineyards, and no herbicides were applied. Measurements were conducted and samples were collected in the second and third inter-row of each treatment block within each vineyard (total of 54 inter-rows).

2.3. Carabid Sampling

Carabid pitfall traps were set up in all experimental vineyards within each of the three ground cover management treatments in two of the four inter-rows that were differentially managed. Additionally, one trap was placed under the vine row between the sampled inter-rows, equating to 3 traps per treatment per vineyard. Pitfall traps are the most universally used traps in ecological studies, and reflect not only the density but also the activity of carabids in an area [38,49]. Plastic beakers with a volume of 250 mL (diameter 8 cm) were used as pitfall traps, and 100 mL of 25% propylene glycol was used as collection solution. Pitfall traps were placed at distances of 8–10 m to each other, and were covered with hoods made from a drip plate (20 cm diameter), in order to prevent flooding due to rainfall. Carabid collection occurred over a period of five days in June and September of 2016 (starting on 2 June 2016 and 9 September 2016). Collected insects were separated according to different taxa, stored in 70% alcohol and carabid beetle adults were identified by using binocular microscope and taxonomic keys and species descriptions provided by Mike Hackston [50] on the basis of Lindroth (1974) [51] and Hůrka (1996) [52].

2.4. Environmental and Landscape Variables

Climate data were acquired from the Austrian Central Institution for Meteorology and Geodynamics at the Krems, Langenlois and Eisenstadt weather station locations that were located at a distance of 10 to 15 km from the individual vineyards. Average, minimum and maximum temperatures (°C), as well as precipitation (mm) and number of sunshine hours (h) were averaged across the month of sampling in combination with the previous month, in order to account for the conditions previous to the sampling events.

Landscape elements were digitized using QGIS 2.18.9 [53]. Utilizing ortho-images, percent cover of vineyards (%), woody habitats (woods and tree alleys) (%), herbaceous habitats (semi-natural pastures and meadows) (%), as well as annual and other perennial crops (orchards) (%) were calculated within a radius of 1 km around the nine vineyard centroids (Figure S1, Table S2). Woody and herbaceous habitats were combined for further analyses with semi-natural habitats. Furthermore, as a measure of connectivity, the minimum distances in meters from vineyard centroid to the next herbaceous or woody habitat were determined.

Soil physical and chemical parameters of all vineyards were determined from 250-gram samples of dry soil by the soil laboratory of the Hochschule Geisenheim University according to standardized procedures [54]. Measured parameters included soil particle size distribution (% clay, % silt, % sand), total elemental carbon and nitrogen (%), soil pH ($CaCl_2$), as well as plant available phosphorous (mg 100 g^{-1} dry soil), potassium (mg 100 g^{-1} dry soil), magnesium content (mg 100 g^{-1} dry soil) and the calcium-carbonate fraction (%) of the soils; in addition, the bioavailable copper (mg kg^{-1} dry soil) content after diethylenetriaminepentaacetic acid extraction was measured. The calcium-carbonate fraction was subtracted as a representation of inorganic carbon (%) from the total carbon in order to derive organic carbon content (%), while the percentage of soil organic matter (SOM, %) was derived by multiplying the organic carbon content by a factor of 1.72 (Table S3).

2.5. Soil Mesofauna Sampling

Sampling of soil mesofauna took place twice during the year 2016: at flowering (6 June 2016) and before harvest (5 September 2016). Samples were taken from each inter-row with a soil core borer (2.5 cm × 10 cm), in order to obtain a pooled sample from 8 individual collection sites within each inter-row. Berlese funnels were built with a 2-millimeter mesh size, and mesofauna collection was performed for 5 days under continuous light exposure. *Acari*, *Collembola* and total mesofauna abundance (including Acari, Collembola, Centipedes, Coeloptera, Diplura, Diptera, Enchitraede, Hemiptera, Hymenoptera, Isopoda, Milipedes, Nematodes, Pauropoda, Phylloxera, Protura, Pseudoscorpion, Symphyla, Thysanoptera) were counted and recorded [55].

2.6. Vine Vitality and Grape Quality Parameters

Grape berries (300–400) were randomly sampled in all vineyards and treatments, in order to determine grape juice quality parameters at harvest in 2016 as well as in 2017. Two pooled samples per vineyard, treatment and year were analyzed, and both years were used for statistical analyses. The berry weight of 100 berries (g) was used as an estimation of treatment effects on grape berry growth. Grape juice, obtained by squeezing the berries manually in a plastic bag, was filtered (Whatman filter 520 A 1/2) and centrifuged for 5 min at 3500 rpm in a 50-milliliter Falcon tube. The clarified juice was analyzed via Fourier-Transformation-IR-Spectroscopy (FTIR, OneoFOSS, FOSS GmbH, Hamburg, Germany). Obtained parameters were as follows: total soluble solids (TSS, °Brix), total titratable acidity (TA, g L^{-1}) and yeast assimilable nitrogen (YAN, mg L^{-1}). The shoot pruning weight (PW, kg per vine) was determined after the season 2016 and was used to analyze the impact of the different inter-row ground cover treatments on vine vigor for the year 2016; 20 vines per vineyard and treatment were evaluated.

2.7. Data Analysis

The majority of statistical analyses was performed in R Version 4.0.5 [56] using the packages tidyverse [57], readxl [58] and writxl [59] for data handling operations, and then imported. Entries with missing values were removed from the data set. The carabids collected below the vines were evenly distributed to the two neighboring inter-rows. We calculated the inventory reliability using the coverage estimator ($\hat{C}n$) as previously described for each vineyard and for the complete data set [60,61]. The complete obtained carabid count data resulted in a coverage of 96%, while individual vineyards ranged between 82% and 98%. In detail, AT01 = 82%; AT02 = 93%; AT03 = 98%; AT04 = 98%; AT05 = 87%; AT06 = 94%; AT07 = 95%; AT08 = 95%; and AT09 = 98%.

Carabid community composition was explored using the program Canoco 5 [62]. Carabid species collected in June and September were first analyzed with canonical correspondence analysis (CCA) of the count data, in order to evaluate the influence of the sampling time on carabid species composition and the Shannon–Wiener Index. Adjacent analyses, namely forward selection redundancy analysis (RDA), were performed to evaluate the influencing factors (environment, climate, landscape) on carabid species composition using the additive data per inter-row from both June and September 2016. Count data were log10 (x + 1) transformed, and species with ≤3 individuals found (in total across all treatments and vineyards) were deleted from the data set to reduce the influence of rare species on the analyses (23 species from 35 remaining).

Generalized linear mixed effects models (GLMMs) were used to assess the effect of inter-row ground cover treatments (factor with three levels "CC", "AC" and "BG"), with additional climatic, landscape, soil and mesofauna variables (summary of metadata affiliations Table S4) on carabid ground beetle activity density and carabid species richness, using the package lme4 [63]. Linear mixed models were conducted for the vine vitality parameters of pruning weight, total soluble solids, 100-berry weight, titratable acid and yeast assimilated nitrogen, focusing solely on the treatments' impacts. In order to account for the locational non-independent observations within the same vineyard, vineyard site was used as a random intercept factor in both carabid and vine vitality models (1 | vineyard), while year was also used in vine vitality parameters that had data from both 2016 and 2017 (1 | vineyard/year). A Gaussian distribution was used for the continuous dependent variables of vine vitality, while a Poisson distribution was fitted for the carabid activity density and species richness data. However, as dispersion was calculated and overdispersion encountered during model confirmation assessment (package DHARMa) [64], the carabid activity density models were refit with a negative binomial distribution [65]. Data exploration followed common recommendations [66].

Available continuous and categorical explanatory variables (Table S4) were individually selected for both GLMMs of carabid activity density and species richness using a three-step process: (1) Selection of variables of interest and biological relevance to the response variable was performed through graphical interpretations, and only those with the highest Spearman correlation ($r > 0.15$) with the dependent variable were considered. (2) As these statistical analyses are sensitive to collinearity between predictor variables, we used the Spearman correlation coefficient with values of 0.55 or greater [67] to exclude correlated variables. For each set of significantly correlated variables, we retained only one that was considered to be the most intuitive and interpretable [60,65]. (3) In a final step, VIF (variable inflation factor) values for the remaining explanatory variables were tested and verified to be under 4, in order to be included in GLMM [65]. As a result, the variables presented in Tables 1 and 2 were used in the analysis of carabid activity density and species richness, respectively. All selected continuous explanatory data were centered and scaled by standard deviation before modeling, in order to allow for a relative comparison of effect sizes. Complete cover cropped inter-row (CC) management was used as the baseline for parameter estimation in the models.

Table 1. Candidate models for carabid activity density used for model averaging, where df represents the degrees of freedom used, AICc the second order Akaike Information Criterion, Δ AICc the difference between AICc to the most parsimonious model, ωi the Akaike's weight within the candidate models, R^2m as the marginal R^2 value and R^2c as the conditional R^2 value. Vineyard sites are used as random factors in all models (1 | vineyard).

Fixed Factors	df	AICc	ΔAICc	ω_i	R^2m	R^2c
TRT [1], Cu [2], % Sand [3], P_2O_5 [4], % Vine [5]	9	682.38	0	0.26	0.401	0.449
TRT, Cu, % Sand, P_2O_5	8	682.79	0.41	0.21	0.304	0.433
TRT, Cu, % Sand, P_2O_5, % Vine, Acari [6]	10	683.92	1.54	0.12	0.418	0.453
TRT, Cu	6	684.05	1.67	0.11	0.131	0.476
TRT, Cu, % Sand, P_2O_5, % Vine, SOM [7]	10	684.14	1.76	0.11	0.431	0.453
TRT, % Sand, P_2O_5	7	684.25	1.87	0.10	0.183	0.469
TRT, Cu, % Vine	7	684.30	1.92	0.10	0.209	0.445

[1] TRT: inter-row ground cover treatment, [2] Cu: soil copper concentration (mg kg^{-1} dry soil), [3] % sand: percentage of sand of the soil texture, [4] P_2O_5: soil phosphate concentration (mg 100 g^{-1} dry soil), [5] % vine: percentage of vineyard area covered in a 1 km radius around the study vineyard, [6] Acari: Acari abundance, [7] SOM: percentage of soil organic matter in the soil.

Table 2. Candidate models for carabid species richness used for model averaging, where df represents the degrees of freedom used, AICc the second order Akaike Information Criterion, Δ AICc the difference between AICc to the most parsimonious model, ωi the Akaike's weight within the candidate models, R^2m as the marginal R^2 value and R^2c as the conditional R^2 value. Vineyard sites are used as random factors in all models (1 | vineyard).

Fixed Factors	df	AICc	ΔAICc	ω_i	R^2m	R^2c
TRT [1], Sun [2], Meso.abun [3], Cu [4], SOM [5], % Vine [6]	9	448.22	0	0.17	0.361	0.476
TRT, Sun, Meso.abun, SOM [7], % Vine	8	448.28	0.06	0.17	0.342	0.537
TRT, Sun, Meso.abun, Cu, % Vine	7	448.5	0.28	0.15	0.315	0.535
TRT, Sun, Meso.abun, Cu, % Vine	8	448.97	0.75	0.12	0.339	0.492
Sun, Meso.abun, Cu, SOM, % Vine	7	449.17	0.95	0.11	0.363	0.47
TRT, Sun, Meso.abun	6	449.74	1.52	0.08	0.319	0.573
TRT, Dis.Herb [8], Sun, Meso.abun, % Vine	8	450.06	1.84	0.07	0.304	0.524
TRT:Dis.Herb [9], Sun, Meso.abun, % Vine	10	450.19	1.97	0.06	0.315	0.531
TRT, Dis.Herb, Sun, Meso.abun, SOM, % Vine	9	450.2	1.98	0.06	0.335	0.533

[1] TRT: inter-row ground cover treatment, [2] Sun: hours of sunshine, [3] Meso.abund: abundance of mesofauna, [4] Cu: soil copper concentration (mg kg^{-1} dry soil), [5] SOM: percentage of soil organic matter in the soil, [6] % vine: percentage of vineyard area covered in a 1-kilometer radius around the study vineyard, [7] SOM: percentage of soil organic matter in the soil, [8] Dis.Herb: minimal distance to herbaceous area, [9] TRT:Dis.Herb: interaction between treatment and minimal distance to herbaceous area.

All possible combinations of the selected explanatory variables from Tables 1 and 2 were manually arranged, modelled and ran through model selection using the MuMIn package [68], with Akaike information criterion corrected for small sample sizes (AICc) as a determinant of model quality. Any models within a Δ AICc < 2 of the highest quality model, i.e., that with the lowest AICc, was considered an identically good fit, resulting in a set of seven equally correct models for activity density (Table 1), and nine for species richness (Table 2). For each dependent variable, the highest quality model was used in graphing the modeled effects of the explanatory variables. The zero method [69] was then used in estimating the averaged explanatory parameter coefficients, using the function "model.avg" [68]. The parameter estimates were left untransformed, in order to emphasize the strongest effect on and relative importance to carabid activity density and species richness [70,71], and were therefore also used as representations of effect sizes [72]. These models were further verified through visual inspection of diagnostic plots including the following: QQ-plots, residuals vs. predicted values, and residuals vs. explanatory variable values via the package DHARMa [73,74]. Effect plots were created with ggplot2 [75], GGally [76], gridExtra [77], ggeffects [78] and jtools [79]. In contrast, vine vitality and grape quality dependent variables were run only against inter-row cover treatments while considering the random effect of different vineyard sites, with REML set to false. Likelihood ratio tests were conducted relating the models with treatment to a null model. Confidence intervals provided additional evidence supporting significant *p*-values.

3. Results

3.1. Drivers of Carabid Species Community Composition

In total, across the nine vineyard sites, 1150 individual carabids were captured, belonging to 35 carabid species (Table S5). In June, 514 individuals of 30 species, whereas in September, 636 individuals across 20 species were captured. In June, approximately 55% of the individuals belonged to the top five carabid species determined, which were *Brachinus crepitans*, *Amara aenea*, *Harpalus distinguendus*, *Ophonus azureus* and *Nebria brevicollis.* In September, the three most dominant species—*Harpalus rufipes, Calathus fuscipes* and *Harpalus griseus*—accounted for over 85% of the individuals collected at this time point (Figure 2a). In the canonical correspondence analysis (CCA), the explanatory factor sampling timepoint clearly showed a strong association with the first ordination axis, separating June and September. A forward selection CCA with additional variables confirmed the sampling timepoint as the strongest influence, with June and September together accounting for 33%

of the species composition variation. Hours of sunshine and percentage of semi-natural habitats also contributed to the explained variability, although only marginally at 6.6% and 3.5%, respectively. The Shannon–Wiener-Index ranged from 0.1 to 2.1, with higher values determined in samples collected in June as compared to September (Figure 2b).

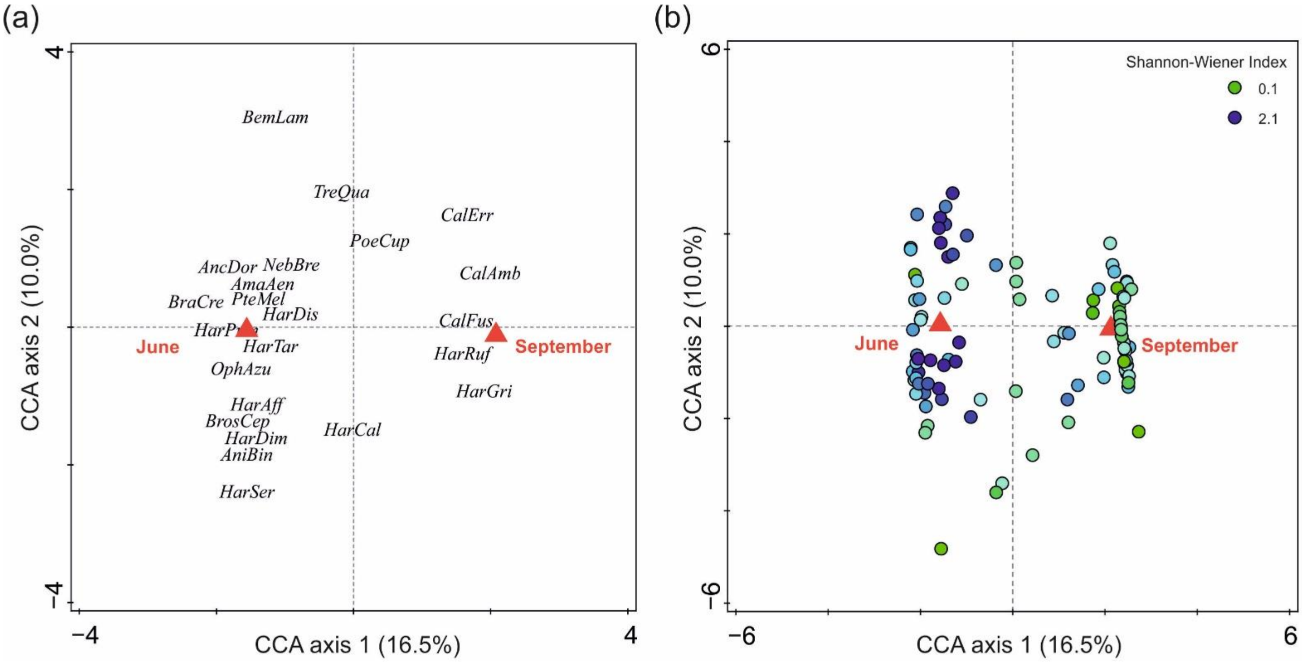

Figure 2. Canonical correspondence analysis (CCA) ordination of ground beetle communities collected at two sampling times (June, September 2016). (**a**) CCA species (abbreviated by the genus and species names) separated according to the sampling timepoint. (**b**) Shannon–Wiener-Index calculated from the samples obtained in June (n = 54) and September (n = 54) across the nine vineyard sites and three inter-row management treatments in each vineyard.

A redundancy analysis (RDA) was run on the session combined data (Figure 3), showing that the explanatory variables account for 61.9% of the explained variation across all axes. The first two axes of RDA ordination accounted for 38.4% of the total variance within the species data. Ground cover treatments led to minimal differentiation of community composition (5.7% of total variability). Meanwhile, soil factors such as potassium oxide concentration, bioavailable soil copper concentration, sand and clay texture percentages, SOM percent, CN ratio, mesofauna abundance and soil pH, as well as a combination of landscape and weather parameters (e.g., distance to the next herbaceous habitat, percentage of semi-natural habitat or percentage of vineyards, as well as hours of sunshine) had greater influences. Clustering of samples by vineyard manager was evident (Figure 3b). The largest cluster of species richness was formed by the vineyards AT07, AT08 and AT09, which were managed organically. This cluster included species such as *Amara aenea*, *Nebria brevicollis*, *Brachinus crepitans* and the genus *Calathus* (Figure 3a,b), with the latter three representing the most abundant predacious carabid species. Higher percentages of sand and concentrations of soil potassium, as well as percentage of SNHs, were the main factors that were associated to the carabid community composition of these vineyards. The genus *Harpalus*, the species *Ophonus azureus* and *Anisodactylus binotatus*, all granivorous species, formed a cluster associated with two other vineyards managed by the same winegrower (AT03, AT04). This cluster was associated with more hours of sunshine and lower soil potassium content. Vineyards AT01, AT02 and AT05 formed a less clearly distinguishable group, with AT01 forming towards an edge of the RDA, and was associated with low sand contents in the soil, higher amounts of SOM and mesofauna abundance, with larger counts of *Bembidion lampros.*

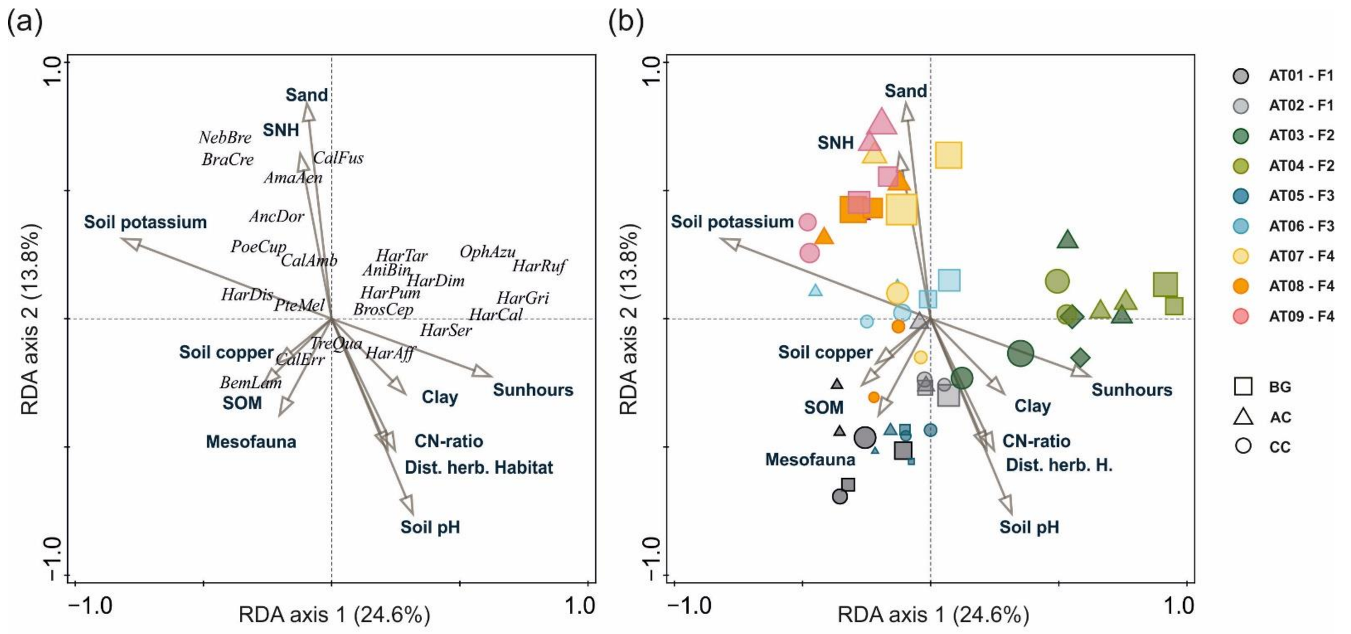

Figure 3. Redundancy analysis (RDA) ordination of carabid communities across both sampling dates. (**a**) Carabid species composition of the forward selection RDA analysis in relation to the continuous variables of soil texture (percentage sand, percentage clay), soil variables (potassium content, copper content, pH, CN-ratio and soil organic matter (SOM)), mesofauna abundance, climate (sun hours) and landscape variables (percentage of semi-natural habitats (SNH) and minimal distance to herbaceous habitats). $n = 54$ pitfall traps. (**b**) Species richness shown from the same RDA analysis indicating the different treatments by different symbols (square: bare ground (BG); triangle: alternating vegetation cover (AC); and circle: complete vegetation cover (CC)). Size of the symbols represents the species richness ranging from 4 to 14. Similar colors for vineyards represent the same farmer (F1: AT01, AT02 in grey; F2: AT03, AT04 in green; F3: AT05, AT06 in blue; F4: AT07-AT09 in red/orange/yellow).

3.2. Drivers of Carabid Activity Density and Species Richness

In relation to the inter-row ground cover management, across all nine vineyards 426, 459 and 247 individuals were respectively collected from bare ground (BG), alternating vegetation cover (AC) and complete vegetation cover (CC) treatment plots, with a maximum number of 59 individuals found in a sample within the bare ground treatment (Tables S6 and S7 for vineyards). The seven most parsimonious models used for averaging carabid activity density (Table 1) showed a moderate influence of the random factor, vineyard site; marginal R^2 values, representing only the fixed variables, ranged from 0.131 to 0.431 in comparison to the conditional R^2 values, including random and fixed variables, which ranged from 0.433 to 0.476. Similarly, the nine species richness models (Table 2) resulted in marginal R^2 values of 0.304 to 0.363 in relation to conditional R^2 values from 0.470 to 0.573. Factors impacting both carabid activity density and carabid species richness were inter-row treatments, soil parameters, weather and landscape elements, as well as mesofauna abundance.

The effect sizes (estimate values ± SE) of the averaged models for carabid activity density and carabid species richness are summarized in Figure 4. Carabid activity density (Figure 4a), as well as carabid species richness (Figure 4b) to a lesser extent, were strongly influenced by the inter-row ground cover treatments, with increases in both parameters related to bare ground (BG) and alternating vegetation cover (AC) management. The most parsimonious fitted model means and interval bars plotted over the observed data in Figure 5a,b affirmed AC as the most beneficial treatment regarding both carabid activity density and carabid species richness, while complete vegetation cover was detrimental in comparison.

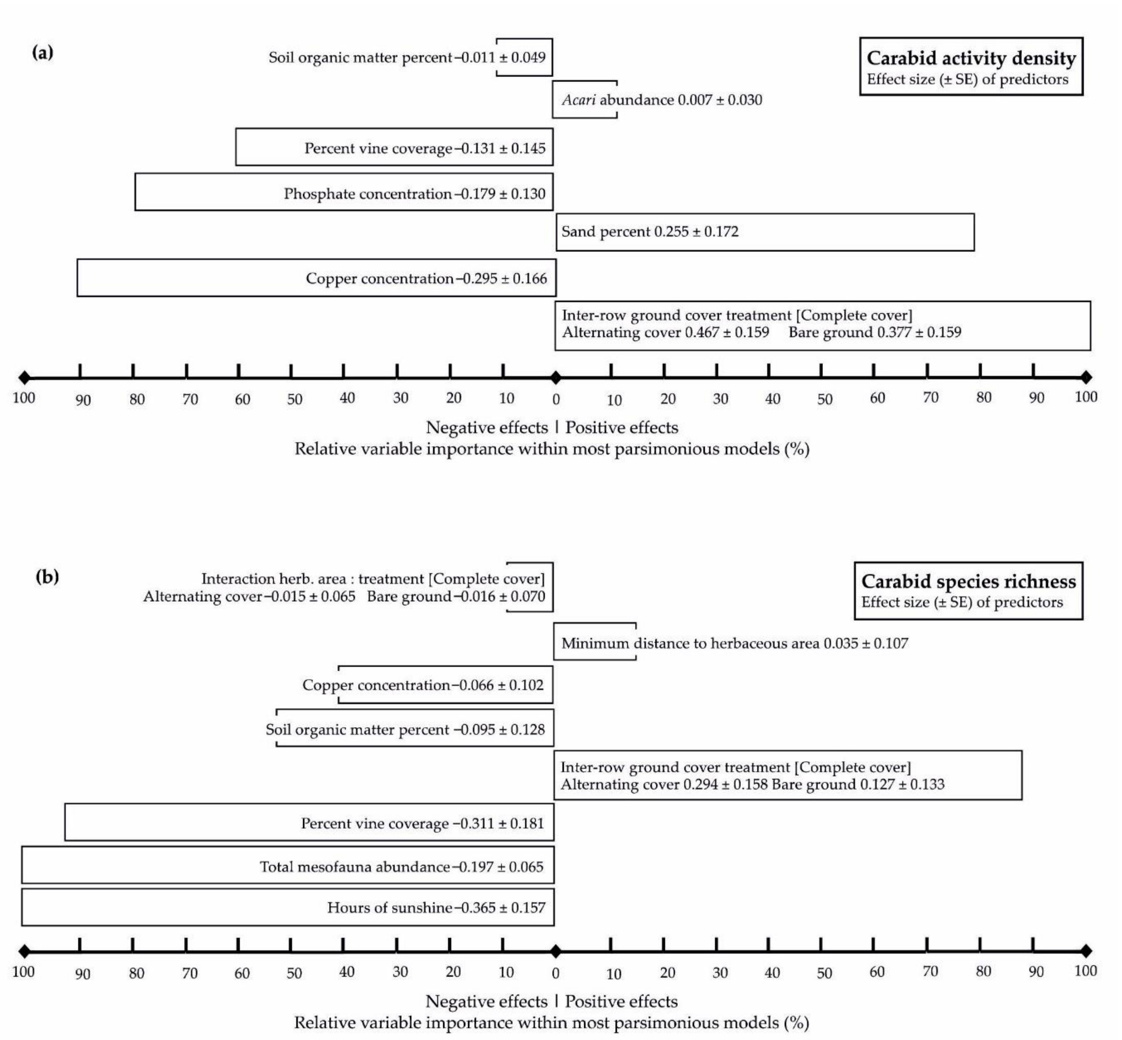

Figure 4. The relative variable importance within the most parsimonious models for (**a**) carabid activity density and (**b**) species richness. Percent relative importance for each explanatory variable was calculated accordingly [69], with negative effects indicated to the left and positive effects indicated to the right. Effect sizes (estimate values ± SE) are derived from model averaging results.

Several soil parameters contributed negatively to both activity density and species richness. Copper concentration levels showed particularly negative effects for carabids (Figure 5b), whereas the sand content increased the activity density of carabids. Surprisingly, hours of sunshine decreased carabid species richness (Figures 4b and 5e). Furthermore, an increasing percentage of vineyard cover within the surrounding landscape decreased both carabid activity density and even more strongly species richness (Figure 4a,b). Species richness was also negatively related to decreasing distance to the next herbaceous habitat in the surrounding area. Furthermore, a higher total abundance of mesofauna correlated negatively with carabid species richness (Figures 4b and 5d), whereas carabid activity density slightly increased with higher abundance of Acari in the soil (Figure 4a).

3.3. Effects of Inter-Row Ground Cover Treatments on Vine Vitality and Grape Quality

Our study revealed an influence of different inter-row ground cover treatments on grapevine pruning weight and most grape quality parameters when vineyard sites as well as the year of sampling were used as random factors to account for their variability (Table 3). Although significant differences between treatments were found, marginal R^2 values were very low, with ground cover management treatments explaining less than 5% of the variability.

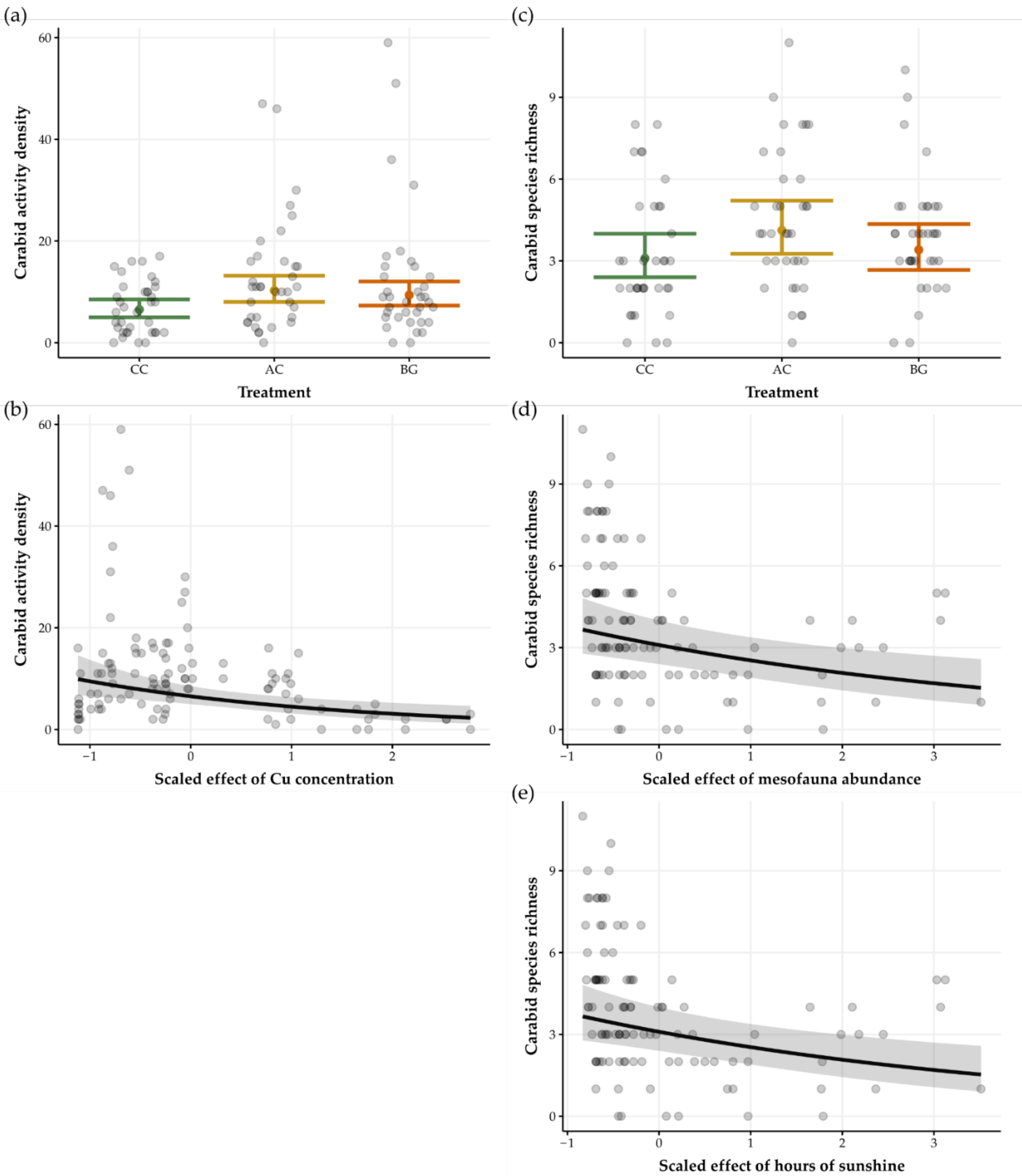

Figure 5. The observed and predicted carabid activity density and species richness in relation to (**a**,**b**) treatment, (**c**) carabid activity density to scaled copper concentration and carabid species richness to (**d**) scaled mesofauna abundance and (**e**) scaled hours of sunshine. As a categorical variable, the mean value of each treatment is represented by the center point with the 95% confidence interval bars, with complete vegetation cover (CC) as the baseline model intercept, and alternating vegetation cover (AC) and bare ground by tillage (BG) as additions thereafter. The solid lines of the continuous variables represent the predicted model with all other variables held constant, with 95% confidence intervals in grey.

Nevertheless, all measured parameters with the exception of total soluble solids were impacted by the different inter-row cover management treatments (Figure 6). The shoot pruning weight was higher in inter-rows with bare ground management (Figure 6a), an effect which was also observed for berry weight (Figure 6b). Additionally, the growth promotion in inter-rows with bare ground led to higher amounts of yeast assimilable nitrogen in grape juice, a parameter important for fermentation (Figure 6c). Differences in total titratable acidity were marginal, with a minor trend of higher values in inter-rows for alternating vegetation coverage (Figure 6d).

Table 3. Summary of the coefficients obtained by GLMM with the fixed factors inter-row ground cover treatment for the response variables of shoot pruning weight (PW), 100-berry weight (BW), total soluble solids (TSS), total titratable acidity (TA) and yeast assimilable nitrogen (YAN). Mixed models included the nested random factor (1 | vineyard), and where data from more than one year existed, (1 | vineyard/year). Significances were obtained using the likelihood ratio test. Marginal R^2 gives explained variation without, and conditional R^2 with the random factor. Gaussian distributions were utilized for all data sets. The *p*-values of significant predictors ($p < 0.05$) are printed in bold. Treatments: AC (alternating vegetation cover), BG (bare ground), with CC (complete vegetation cover) as the baseline intercept.

Fixed Effect Variable	PW		BW		TSS		TA		YAN	
	Estimate	*p*-Value	Estimate	*p*-Value	Estimate	*p*-Value	Estimate	*p*-Value	Estimate	*p*-Value
Intercept	0.66	<0.001	180.31	<0.001	19.9	<0.001	10.34	<0.001	108.87	<0.001
AC	0.03	0.247	6.95	**0.044**	−0.22	0.327	0.57	**0.006**	12.03	0.112
BG	0.14	**<0.001**	9.92	**0.004**	0.22	0.314	0.16	0.433	23.97	**0.002**
Observations	600		65		61		66		36	
R^2m/R^2c	0.035/0.540		0.025/0.819		0.014/0.781		0.014/0.884		0.053/0.814	

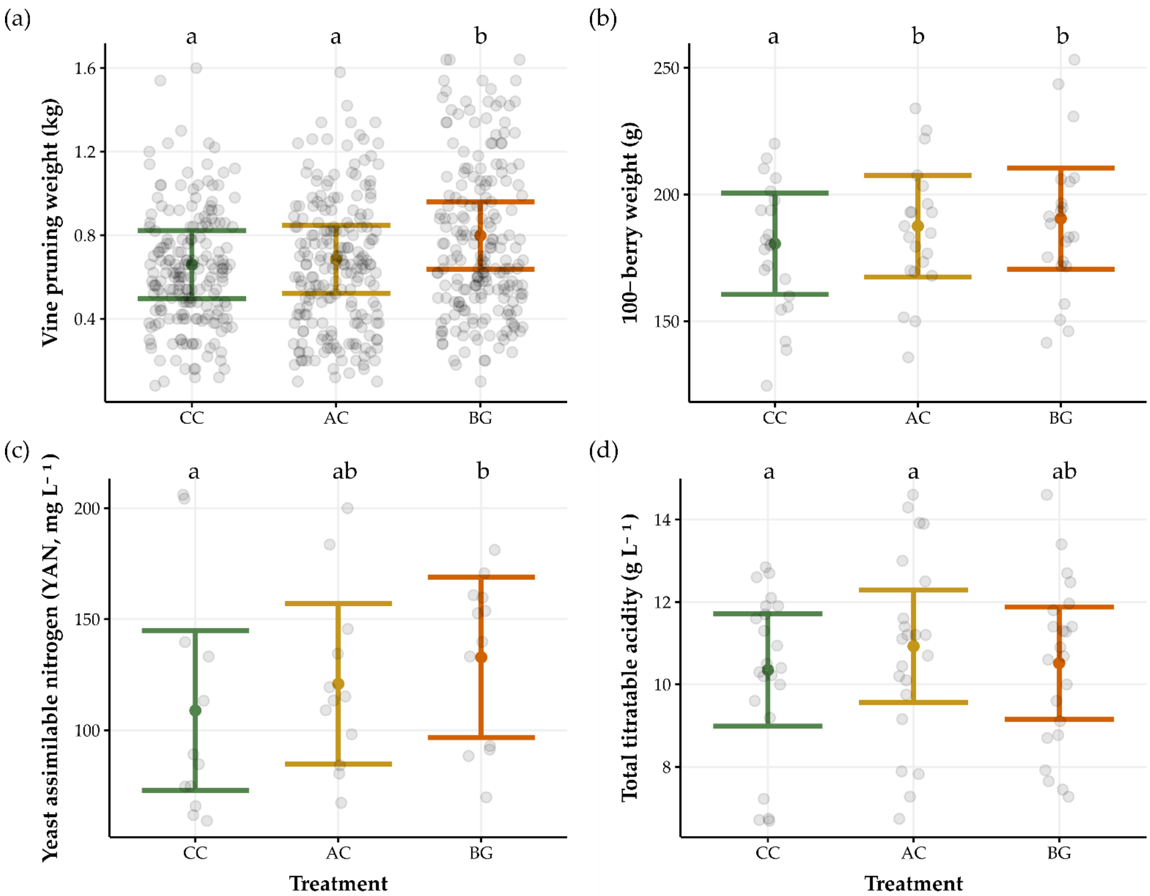

Figure 6. The observed and model-predicted values of each vine vitality parameter: (**a**) vine pruning weight, (**b**) 100-berry weight, (**c**) yeast assimilated nitrogen and (**d**) total titratable acidity. The mean values of each treatment are represented by a center point with the 95% confidence interval bars, with complete cover (CC) as the baseline model intercept, and alternating cover (AC) and bare ground (BG) as additions thereafter. Significant differences in treatments' impact, affirmed by likelihood ratio tests, are represented by different lettering.

4. Discussion

The present study showed that carabid activity density and species richness were both driven by inter-row ground cover management. Surprisingly, vineyards with complete vegetation cover decreased both carabid activity density and species richness in comparison to vineyards with bare soil and alternating vegetation cover. In addition, variables such as bioactive copper content in the soil, mesofauna abundance, hours of sunshine and higher vineyard cover at the landscape scale decreased both activity density and species richness. In contrast, carabid communities did not differentiate according to the ground cover treatments, but according to the winegrowers responsible for all aspects of vineyard management.

The high number of variables within the top models for carabid activity density and species richness indicates a variation in strong influencing factors between sites, with few influencing variables preserved across all vineyards sampled. Furthermore, the lower marginal R^2 value in both analyses shows additional, unidentified site-specific variables that further impacted carabid diversity.

4.1. Effects of Vineyard Management on Carabid Beetle Diversity and Community Composition

The maintenance of complete cover vegetation across all inter-rows had a negative influence on the number of species and individual carabids collected, with alternating vegetation cover harboring the greatest number of carabids in both measured parameters. This conforms to established literature which indicates that few species prefer dense vegetation, with more carabids favoring crop environments that combine open spaces (often having higher temperatures for greater activity) with neighboring, more heavily vegetated areas (with higher humidity) [39,80].

A recent study in Germany also found a negative effect of increasing vegetation cover in vineyard inter-rows for carabid activity density, both in absolute numbers and the movement of carabids [23]. The authors of this study similarly suggested that minimal vegetation cover might provide favorable microclimatic conditions, including higher irradiation at ground level, for carabids [32,39]. Furthermore, another comprehensive study conducted in vineyards of northern Italy found a comparable negative effect of increasing grass cover on carabid activity density and richness; however, this only pertained to macropterous species (e.g., *Harpalus rufipes* or *Amara aenea*), while brachypterous species (e.g., *Calathus fuscipes*) showed no correlation [81].

On the other hand, a large amount of recent literature found a positive association of beetle diversity parameters with increasing vegetation cover in agricultural landscapes [7,21,82]. These findings are supported by the assumption that feeding opportunities increase in denser vegetation, either through the direct provision of seeds or by attracting a more diverse assortment of prey above- and below-ground [36,83]. Our results indicate that an intermediate amount of vegetation cover, provided by the alternating inter-rows, promotes the greatest activity density and highest species richness in comparison to complete vegetation cover or bare ground [84]; this could be related to both the positive effects of greater food availability in the vegetated inter-row, and of more open space for unimpeded movement in the alternate inter-row of the vineyard.

However, it should be noted that the observed activity density of carabids per inter-row in our study could have been influenced by the selected method of sampling. Pitfall traps do not measure absolute population density [38,85]. This issue was made evident in a study that assessed plots of increasing vegetation coverage; it was found that although the absolute population densities estimates from mark-and-release methodology did not differ across plots, the activity density of carabids acquired via pitfall traps significantly decreased in areas with denser vegetation [85]. Furthermore, a more comprehensive investigation into different parameters of vegetation cover (e.g., association with plant species or vegetation height) could further elucidate the drivers behind carabid preference for alternating inter-row cover.

Carabid diversity's link to viticultural management practices was further suggested by the species composition clustering according to the same winegrower, made particularly apparent by the geographical variation between vineyards operated by the same winegrower (Figure 3b). Other elements that impacted carabid diversity within the present study, such as soil potassium, phosphate and carbon content, in addition to SOM and CN ratio, could be related to further management decisions, particularly in regards to fertilizer and pest management.

Although the literature reviewing the impact of fertilizers on natural predators is limited [86], carabid activity density has been positively linked to soil organic carbon content [87,88], as well as potassium and phosphate content [89–91], in both agricultural and forested systems. Increasing levels of organic carbon, often through addition of SOM and therefore leading to higher CN ratios, may be associated with increasing amounts in soil microorganisms and mesofauna, indirectly promoting the carabid food chain. However, the results of our study showed the opposite trend, with carabid species activity density and richness decreasing with the chemical and biological aspects of soil fertility, i.e., SOM, phosphate content and mesofauna abundance. The prevalence of mesofauna as a strong negative influence could be explained as mesofauna being a limiting food source that, once abundant, allows certain species to thrive and dominate the community composition, hence reducing richness.

Bioactive soil copper levels, most likely residues of copper fungicides, showed negative correlations with activity density and species richness of carabids in our study. This negative effect on carabids was also found in annual cropping systems under transition to organic management [92]. Copper may directly or indirectly affect carabids by affecting their food chain, as copper fungicides that damage the soil fauna, particularly in light sandy soils [93].

4.2. Effects of Site and Landscape Properties on Carabid Diversity and Community Composition

Although inter-row vegetation management showed the largest influence on activity density, in addition to a relatively strong effect on species richness, some environmental factors comparably affected the variance of carabid diversity.

In our study, the soil sand content had a relatively large positive influence on carabid activity density, which was, however, mostly characteristic of the three organic vineyards (Figure 3b) that contained the largest number of omnivorous and predacious species [94]. This positive relationship is in line with studies conducted in arable sites and other land uses [32,95,96]. However, this is surprising as soils rich in clay are hypothesized to promote diversity due to both better environmental conditions and higher food abundance [39].

Furthermore, in our investigation, hours of sunshine positively impacted a community of carabids dominated by the genus *Harpalus*, with general species richness being negatively influenced. A number of species within the genus *Harpalus* are pale or metallic [94], benefitting from higher activity on warm dry days [39]. *H. rufipes* in particular is known to be thermophilic [39], perhaps explaining the predominance of the species during September in vineyards with more hours of sunshine. On the contrary, black colored beetles, such as *B. lampros*, *N. brevicollis* and *C. fuscipes*, have been noted to be more active on cooler, darker days [39]. These species did clearly separate in the RDA from members of the *Harpalus* genus.

Aside from vineyard management and local site factors, the surrounding landscape composition influences carabid diversity in vineyards [23,35,82,97,98]. The proximity of the carabid communities of the vineyards AT07, AT08 and AT09, with shorter distances to the next herbaceous habitat in addition to higher percentages of semi-natural habitat, suggests that these species' preference for a more complex, heterogenous landscape [23,98]. Furthermore, the higher species richness observed in several of those vineyards could be linked to a potential migration from those non-crop habitats [99].

The overall decline in carabid activity density and species richness in relation to the increasing vineyard cover could be related to landscape simplification [23] and the intensive use of pesticides in vineyards; for example, in France, 15% of the total amount of pesticides were applied in vineyards covering only 3% of the total agricultural area [100]. On the other hand, the present study's weak correlation of carabid species richness with increasing distance to the next herbaceous habitat could be related to a theory of semi-natural habitats' role as a potential higher quality habitat for carabid beetles at the landscape scale [35,101,102], or acting as a barrier to dispersion [35,101,102]. Non-crop landscape elements, such as woody or herbaceous habitats, have been observed to play an important role in some carabid life cycles; for example, the spring-breeding species *Amara aenea* or *Bembidion lampros* depend on semi-natural habitats to overwinter, whereas autumn-breeding species, such as *Harpalus rufipes* and *Nebria brevicollis*, overwinter in the soil [18].

4.3. Inter-Row Ground Cover Treatment Effects on Vine Vitality Measures

We found a significant increase in the relative amount of vine vegetative growth measured as shoot pruning weight in bare ground treatments in comparison to alternating and complete vegetation cover. Our results match the majority of literature, as this trend has been seen across vineyards of various climate zones [47,103–105]. These results have been attributed to the competition for water between cover crops and vines for below-ground resources, namely water, as well as through the uptake, the physical and chemical retention and the stabilization of nitrogen and other nutrients; this results in a further downstream impact on shoot fertility, fruit set, berry development and finally yield [16,43,106–108]. Furthermore, a slight reduction in vegetative growth may be seen as a provisioning service in vineyards, especially in moderate to humid climates, as the growth reduction may replace or supplement the expensive and time-consuming canopy thinning management [44,45,109,110].

Although it is often assumed that secondary metabolites in grapes build up as a result of greater amounts of stress, current studies are inconsistent and inconclusive in their findings, with often limited to no difference in total soluble solids (TSS), total titratable acidity, macronutrients or phenolic compounds [41,110]. With respect to the berry chemical composition metrics in our study, TSS showed no relation to ground cover management, whereas total titratable acidity and yeast assimilated nitrogen in berries increased with tillage compared to fully or partly vegetated inter-rows. The nutrient cycling created by tillage could explain the increase in yeast assimilable nitrogen (YAN) from the bare ground treatment, as a correlation has been observed in bioavailable soil nitrogen and subsequently, though delayed, increases in YAN [109,110]. However, an overwhelming portion of variability in all three parameters (TSS, acidity and YAN) is explained by vineyard site rather than by treatment, and is likely due to management and varietal differences between vineyards.

5. Conclusions

Carabid beetles are anthropods of particular interest, partially due to their role as omnivorous natural enemies. Despite extensive research invested in harnessing carabids as pest predators, results that demonstrate the advantage of carabids as biocontrol agents have been inconsistent across trophic levels. This, however, does not diminish their potential as bioindicators, nor their utility in exemplifying the challenge of biodiversity preservation in agricultural management; the difficulty is in identifying one umbrella practice for universal (species) benefit.

Our study did show that alternative vegetation cover resulted in the best management option for supporting both ground beetle biodiversity and provisioning ecosystem services in vineyards, although attention should be paid to grape berry acidity. This result was also shown for some other functional groups, such as pollinators, which could be related to the larger heterogeneity in microclimatic and biotic conditions of vineyards that have both vegetated and bare soil inter-rows. Furthermore, although various environmental parameters showed influence on carabids in different vineyard sites, large differentiations by seasonality and clustering associated to vineyard managers were apparent in carabid species composition. Future studies that investigate the seasonal impacts of ground cover management on carabid diversity and community composition could help to identify recommendations for the timing of management operations and their potential trade-offs or synergies for wine production. This study suggests that sustainable management practices, such as alternating inter-row cover cropping, do not hamper winegrowers' main objective of producing high quality berries for wine production, while supporting carabid activity density and diversity.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12061328/s1, (a) Supplementary tables: Table S1: Site and soil details of the vineyard sites; Table S2: Summary of landscape elements; Table S3: Summarized chemical and physical soil parameters; Table S4: Metadata information and their selection for GLMM; Table S5: Counts of carabid beetle species according to sampling time-points; Table S6: Counts of carabid beetle species according to inter-row cover management treatment; Table S7: Counts of carabid beetle species within each vineyard. (b) Supplementary figures: Figure S1: Visualization of the landscape elements within a 1-kilometer radius of the vineyard.

Author Contributions: A.F. and M.G. conceived the study design in cooperation with the PromESSinG project group; M.G. and co-workers collected the insects with pitfall traps and collected samples for vine analyses; S.K. assisted in data collection and determined all carabid individuals to species level; L.P. and M.G. performed all data analyses, prepared the figures and interpreted the results with assistance from S.W.; L.P., with the assistance of M.G., drafted the manuscript. All authors have read and agreed to the published version of the manuscript.

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