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Author(s): Elo, Merja; Ketola, Tarmo; Komonen, Atte

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Species co-occurrence networks of ground beetles in managed grasslands

Merja Elo¹ · Tarmo Ketola¹ · Atte Komonen¹

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Abstract

Grassland biodiversity, including traditional rural biotopes maintained by traditional agricultural practices, has become threatened worldwide. Road verges have been suggested to be complementary or compensatory habitats for species inhabiting grasslands. Species co-occurrence patterns linked with species traits can be used to separate between the different mechanisms (stochasticity, environmental filtering, biotic interactions) behind community structure. Here, we study species co-occurrence networks and underlying mechanisms of ground beetle species (Carabidae) in three different managed grassland types (meadows, pastures, road verges, $n = 12$ in each type) in Central Finland. We aimed to find out whether road verges can be considered as compensatory to traditional rural biotopes (meadows and pastures). We found that stochasticity explained over 90% of the pairwise co-occurrences, and the non-random co-occurrences were best explained by environmental filtering, regardless of the grassland type. However, the identities and traits of the species showing non-random co-occurrences differed among the habitat types. Thus, environmental factors behind environmental filtering differ among the habitat types and are related to the site-specific characteristics and variation therein. This poses challenges to habitat management since the species' response to management action may depend on the site-specific characteristics. Although road verges are not fully compensatory to meadows and pastures, the high similarity of species richness and the high level of shared species suggest that for carabids road verges may be corridors connecting the sparse network of the remaining traditional rural biotopes.

Keywords Biodiversity · Carabidae · Environmental filtering · Joint species distribution models · Species traits

Background

Understanding processes structuring communities has been a longstanding core topic in ecology, and it is crucial to applied research such as conservation biology and habitat management. At ecological time scales, communities may be structured by drift, dispersal and selection resulting from environmental or biotic factors (Vellend 2010). While it is increasingly accepted that all these processes affect community structure (Ricklefs 1987; Cottenie 2005; Chase and Myers 2011), relative contributions of the processes may

vary across habitat types and spatial scales (Cottenie 2005). This has resulted in a wide interest in separating the effects of drift, dispersal as well as the two sources of selection, environmental filtering and biotic interactions on community structure (Ovaskainen et al. 2010; Boulangeat et al. 2012; Blois et al. 2014; D'Amen et al. 2018).

Traditionally, species co-occurrence patterns have been used to resolve whether biotic interactions, and interspecific competition in particular, affect species' occurrences (Connor and Simberloff 1983; Diamond 1975). The key idea in the classical studies was that interspecific competition should lead to disjunct occurrence of the competing species living in similar habitats (Diamond 1975), when compared to a prediction by a null model (Connor et al. 2013; Connor and Simberloff 1983). Currently, many statistical techniques have been developed to study whether species are found together less often (negative co-occurrence; segregation) or more often (positive co-occurrence; aggregation) than predicted by random chance (see Dormann et al. 2018 for an overview). However, interpreting the causes of positive and

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✉ Merja Elo
merja.t.elo@jyu.fi

¹ Department of Biological and Environmental Science, School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, Jyväskylä 40014, Finland

negative co-occurrences is not straightforward, as environmental filtering and biotic interactions may yield similar co-occurrence patterns. Positive co-occurrence between species can result from mutualistic interactions or similar habitat requirements. Similarly, negative co-occurrence among species may result from antagonistic interactions or dissimilar habitat requirements. One way to separate between the effect of environmental filtering and biotic interactions is to link the observed co-occurrences to species functional traits (Mönkkönen et al. 2017). For example, Kohli et al. (2018) proposed a coherent analytical framework as a form of a logic tree. There pairwise species co-occurrences are calculated at two hierarchical scales resulting in nine possible combinations of co-occurrences, and for each, a trait-based test is used to separate between the two possible mechanisms, environmental filtering or biotic interactions (Fig. 1).

The whole network of species co-occurrences has proven to be a useful way to visualize the community and offer interesting insights as any pairwise co-occurrences may be more readily understood in the context of all other co-occurrences (Araújo et al. 2011; Barberán et al. 2012; Morueta-holme et al. 2016). The co-occurrence network and changes in its structure may indicate changes in environmental conditions, such as in climate (Araújo et al. 2011). Particularly, a loss of overall co-occurrence (i.e., reduced number of links) have been found in sites with high anthropogenic disturbance

compared to less disturbed sites (Kay et al. 2018; Tulloch et al. 2018). In terms of ecosystem functions, reduced number of positive co-occurrences is a severe phenomenon when occurring in species interaction networks constructed across trophic levels (e.g., plant–pollinator relationships; Burkle et al. 2013). However, changes in networks constructed also within trophic levels (e.g., competitive relationships; Steen et al. 2014) may result in important insights. For example, Tulloch et al. (2018) showed that species co-occurrences can be used to predict the responses of species to different management practices. Hence, changes in co-occurrence networks and their interpretation from conservation and management perspective deserve more attention, also when the networks are constructed within trophic level.

We studied species co-occurrence networks and underlying processes in grasslands. Grasslands host high species diversity and have become globally threatened habitats (Hoekstra et al. 2005). Especially traditional rural biotopes, such as meadows and pastures maintained by traditional agricultural practices, have become rare (Tschardt et al. 2005). At the same time, expanding road network has created “modern” grasslands, i.e., road verges. Road verges have been suggested to be complementary or compensatory habitats for grassland species (Munguira and Thomas 1992; Cousins 2006). Thus, species communities in road verges should be compositionally and structurally similar to other

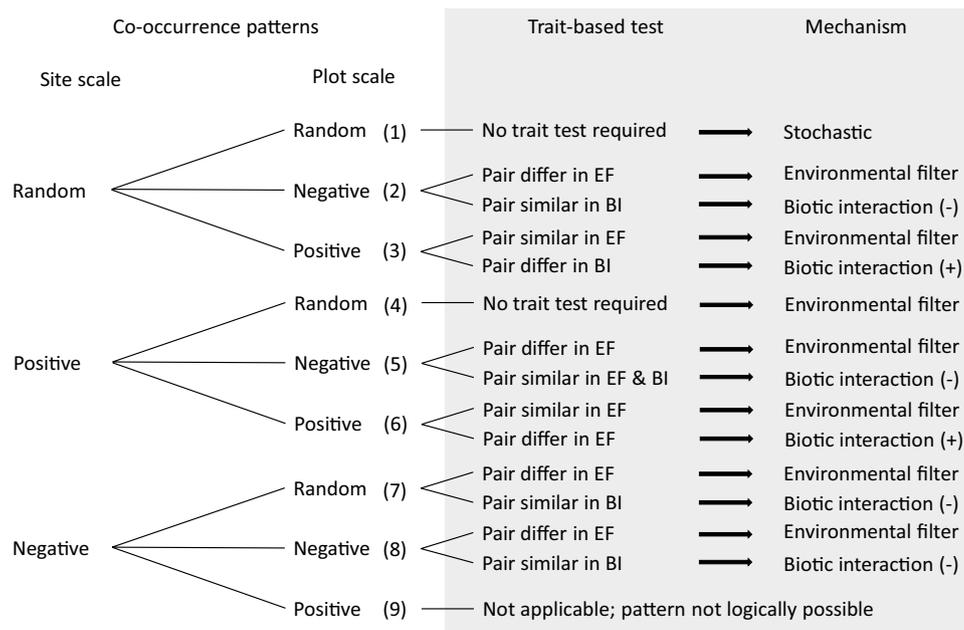


Fig. 1 Analytical framework for incorporating trait similarity to identify the mechanisms affecting pairwise co-occurrence patterns. The framework includes nine possible combinations of co-occurrence patterns across two scales (site, plot) as well as the test based on species trait similarity to separate between the two mechanisms. The negative and positive co-occurrence patterns indicate whether the two species

occur less or more often than predicted by chance only, according to joint species distribution model (see Statistical Analyses). The traits associated with Environmental Filtering (‘EF’) used here are sun exposure and soil moisture, and traits associated with Biotic Interactions (‘BI’) are trophic level and body size. Redrawn after Kohli et al. (2018) with small terminological modifications

grasslands. However, traditional rural biotopes, i.e., meadows and pastures, have some important differences in relation to road verges. Historically in Finland, meadows and pastures were situated in relatively nutrient poor or remote areas as the most productive areas were reserved for agriculture (Kontula and Raunio 2018). Thus, it can be assumed that the biotas in meadows and pastures were originally similar and have remained so, at least in comparison with the constructed road verges. However, current management practices among the three grassland types would suggest that the meadows would be somewhat more similar to road verges than pastures. In Finland, road verges are mowed to increase the safety on the road: without trees and bushes, cervids can be observed more easily which reduces the probability of accidents. Finnish meadows and road verges are mowed a few times annually but with different methodologies: meadows are hand-mowed, and road verges machine-mowed. In pastures, livestock grazing is more continuous and selective than mowing and removes vegetation closer to the ground (Rook et al. 2004). Moreover, the three habitat types can be assumed to differ in the level of disturbances, not directly related to mowing intensity. In pastures, animal activities, such as trampling and feces, have a significant effect on the environment (Kohler et al. 2006; Bilotta et al. 2007), whereas in road verges disturbances are more variable. Roads are structural dispersal barriers, traffic causes direct mortality, and pollution and road maintenance affect insects directly and indirectly via vegetation (Trombulak and Frissell 2000; Truscott et al. 2005; Muñoz et al. 2015). Taken together, meadows and pastures have similar historical origin but different management currently, whereas road verges have different origin than meadows and pastures but somewhat similar management to meadows. These differences in origin, management and disturbances may be reflected in the community structure of plants and animals.

We focused on species co-occurrences of ground beetles (Carabidae) in three types of managed grasslands: meadows and pastures (i.e., traditional rural biotopes) and road verges. Carabids are frequently used in studies concerning grassland management (Lengyel et al. 2016; Massaloux et al. 2020; Tsafack et al. 2020), as their ecology is well-known and they are caught in numbers that allow quantitative analyses. We studied whether (1) the co-occurrence networks and (2) the mechanisms behind the co-occurrences are similar in the three habitat types. In addition, we studied (3) if the species showing non-random (negative/positive) co-occurrences have common traits. In Finland, carabids are mainly predators and have species which prefer different microclimate, soil and vegetation (Lindroth 1986). Thus, we hypothesized that rather than mutualistic or antagonistic interactions, positive and negative co-occurrence of carabids reflect similarities and differences in their habitat preferences. Moreover, we hypothesized that this applies to all of the habitat types.

Although the same mechanism behind co-occurrence pattern would operate *within* each habitat type, it may result in different network structures *among* the habitats type if, for example, the factor behind the mechanism is different. Considering our study taxon, road verges can have positive or negative effects on carabids, depending on their habitat, microclimate and diet preferences (Vermeulen 1993; Eversham and Telfer 1994; Melis et al. 2010). Previously, the level of anthropogenic disturbance has been shown to reduce the proportion of positive co-occurrences within the species co-occurrence network (Kay et al. 2018), and road verges clearly have more anthropogenic disturbance compared to pastures and meadows. Moreover, in very homogenous environment, the level of positive and negative co-occurrences should be smaller, and road verges are relatively homogenous. Thus, we hypothesized road verges represent reduced proportion of positive co-occurrences in comparison to meadows and pastures. If the co-occurrence networks differ among the habitat types, this suggests that species respond differently to management in these habitat types due to differences in habitat characteristics and their spatial distribution either within or among sites. Particularly, if the road verges differ from meadows, this would suggest that similarities in management practices do not guarantee similar community structures.

Methods

Study sites

The study sites are in southern and middle boreal vegetation zone in Central Finland. The region is mostly forest, and meadows and pastures together cover only 0.04% (742 ha) of the total land area. We selected all the traditional rural biotopes which were (1) classified as locally, regionally or nationally valuable sites in the Finnish inventory of traditional rural biotopes in the 1990s (Vainio et al. 2001), (2) ≥ 0.2 hectares according to Vainio et al. (2001), (3) mesic or dry meadows and (4) managed by grazing or mowing for some decades and still under management. This resulted in 12 meadows and 12 pastures, which were distributed rather evenly throughout Central Finland. In one case the meadow and the pasture were almost adjacent to each other (0.05 km), in one case 64 km from each other, but generally some to tens of kilometers from each other. The area of meadows and pastures, re-measured in 2014, ranged from 0.1 to 8.6 ha, the exceptions being the two largest farms for which the combined area of meadows and pastures was 11.9 and 32.5 ha. It is not meaningful to use area for road verges, which are continuous habitats.

We selected a priori the road verges from maps such that they were distributed as evenly as possible among the

pastures and meadows. The criteria for the selection of the road were as follows: (1) local tarmacked road or bigger according to the Finnish road classification to ensure at least 3-m-wide verges, (2) built > 20 years ago to allow grassland vegetation time to develop and (3) no visible renovation actions. After a priori selection, we drove from the predetermined starting point and selected the first suitable site. We did this in mid-May so there was no green vegetation to influence site selection. The map showing the locations of the study sites are shown as Online Resource 1. The immediate surrounding of pastures and meadows often included varying types of human influence because they were situated near settlements or farmhouses. None of the studied habitat types were surrounded by wetlands or lakes, i.e., the matrix was mainly varying types of forest and was relatively similar for all of the habitat types. Details of the study site selection and detailed information of the study sites can be found from Komonen and Elo (2017).

We surveyed vascular plants and vegetation height (cm) from sample plots (see below) during the peak flowering season (between 16-Jun-2014 and 8-Jul-2014) and before the sites were mowed. Bryophytes were surveyed after the vascular plant survey. All species were recorded, and their cover percentage was estimated visually using quadrats (for all species having < 1% cover, we used 0.5%).

Species sampling

In each study site, we placed five 2 m × 2 m sample plots in 10-m intervals along a randomly placed 50-m transect; in meadows and pastures the plots were at least 5 m from the forest edge (a figure showing the sampling design can be found as Online Resource 2). In small sites, we divided transect in two, such that the second transect run perpendicularly to the first one. At the road verges, plot edge was at least one meter from the tarmac. We used the 2 m × 2 m sample plots because they fit in the road verges and were of suitable size to record all vascular plants and estimate bryophyte cover.

We used pitfall traps (200 ml, 6.5 cm diameter) to catch insects. Traps were filled with saltwater to preserve the material and with soap to reduce surface tension. We covered all pitfall traps with a plywood roof (2 cm above ground) to exclude rainwater. Two pitfall traps were placed in the opposite corners of each plot, i.e., there were 10 pitfall traps in each site. Traps were set up 26–30 May 2014 and emptied twice (18–22 June and 7–11 July 2014) such that they all were catching equal time periods. Cattle partly destroyed 7.9% of traps in pastures, and road maintenance 1.7% of traps in road verges. However, as the traps were only partly destroyed, some of them had specimens and could be used in analyses. Because we only included species with > 10 individuals and species occupancy (instead of abundance) in the analyses, a small number of missing individuals do not

add considerable bias in the analyses. Adult specimens were identified using Lindroth (1985, 1986) and the nomenclature follows Rassi et al. (2015).

Statistical analyses

Original data included 66 carabid species. We focused on relatively common species and selected the species represented by > 10 individuals. This resulted in 30 carabid species. For estimating species co-occurrences, we applied Bayesian joint species distribution models, namely Hierarchical Modelling of Species Communities (HMSC, Ovaskainen et al. 2017). HMSC uses latent variable approach where residual variation (i.e., variation not explained by the fixed factors) in species occurrences is captured by latent variables. These latent variables can be estimated at any level of the hierarchical sampling scheme. Species-to-species residual association matrices, (Ω) unique for each level of the hierarchical sampling scheme, are then estimated as variance–covariance matrices of the loadings of the latent variables. Further, species-to-species association networks are represented by the correlation matrix \mathbf{R} , defined as $R_{j_1 j_2} = \Omega_{j_1 j_2} / \sqrt{(\Omega_{j_1 j_1} \Omega_{j_2 j_2})}$, where $\Omega_{j_1 j_2}$ describes the amount of covariation among the species j_1 and j_2 . The element $R_{j_1 j_2}$ measures to what extent species j_1 and j_2 are found together more or less often than expected by chance.

We modeled the $n_y \times n_s$ response matrix \mathbf{Y} consisting of presence–absences of the n_s = number of species in n_y = 60 plots with a generalized linear model (probit distribution), separately for each habitat type. We excluded the species not occurring in the habitat type in question, resulting in 28, 27 and 26 species for meadows, pastures and road verges, respectively. We did not include any environmental variables and modeled the response matrix with only an intercept and the two random factors, site and plot (nested within the site) representing the hierarchical structure of the study. At the plot scale, positive co-occurrence means that the two species are found together more than expected by chance in the same plots, and at the site scale, positive co-occurrence means that the two species are found together more than expected by chance in the same sites. Thus, all the variation in species occupancies is considered “residual variation” and captured by the latent variables. Thus, our species-to-species association networks are in essence co-occurrence networks.

All statistical analyses were done with R version 3.4.4 (R Development Core Team 2017). We fitted the model to the data using the package ‘HMSC-R’ (Tikhonov et al. 2019). We assumed the default prior distributions and sampled the posterior distribution for 1000 samples (1 000,000 iterations with thinning of 1000), using transient phase of 500 000. We assessed the converge of the Markov chain Monte Carlo chain for Ω :s for 100 randomly selected species pairs by ensuring that effective sample sizes are close to actual

sample sizes and the potential scale reduction factors are close to one. We estimated the explanatory power of the model with Tjur's R^2 .

We selected the species pairs for which the posterior probability of having positive or negative co-occurrence was 0.95 for further analyses. We quantified the total number of positive and negative co-occurrences within a network. As these numbers are sensitive to the total number of species in each network we divided them by the total number of possible pairs and achieved the proportion of positive and negative co-occurrences. The interpretation of the proportion of positive co-occurrences equals the widely used network connectance.

Individual species may have different numbers of co-occurrences in different habitat types if the species' occurrence differs. To interpret whether changes in species' co-occurrences were related to changes in species occurrences, we calculated a general linear mixed model using package 'nlme' for those 13 species having positive co-occurrences at least one of the habitats (Pinheiro et al. 2017). We used species' link density (the proportion of positive co-occurrences from all possible co-occurrences) as a response variable, species' occurrence as a fixed variable and species identity as a random factor. Because it is well documented that microclimate, vegetation and soil affect insect abundance, and community composition and diversity in meadows and pastures (e.g., Brose 2003; Schaffers et al. 2008), we analyzed whether mean and variation in vegetation height and bryophyte cover differ between habitat types at the plot scale. We used linear mixed model with mean vegetation height (cm) and bryophyte cover (%) of a plot as a response variable, site as a random factor and habitat type (meadows used as a baseline) as a fixed factor. We fitted a general linear model with coefficient of variation of vegetation height (cm) and bryophyte cover (%) of plots within a site as a response variable and habitat type (meadows used as a baseline) as an explanatory factor. The results are shown as Online Resource 3.

To separate stochasticity, environmental filtering and biotic interactions behind the observed co-occurrences we used the analytical framework by Kohli et al. (2018). Dispersal has been sometimes included into similar frameworks (e.g., D'Amen et al. 2018). We did not consider it here because the extent of our study area is rather limited. All the 30 species are widespread in Finland, and our study area in Central Finland is not near to the edge of their distributions (Rassi et al. 2015). Thus, it is reasonable to assume that all the sites have the same regional species pool. In addition, it must be noted that it is difficult to determine dispersal ability unambiguously for carabids because they show polymorphism in wing and wing muscle development from population to population (Venn 2016). Following Kohli et al. (2018), we included four traits in our framework: traits

associated with environmental filtering were species' preferences for sun exposure (forest, open land, generalist) and soil moisture (moist, dry, generalist), and traits associated with biotic interactions were species' trophic level (predator, herbivore, omnivore) and body size range (in mm). Traits were obtained from Lindroth (1985, 1986). In addition, trophic level was updated from a more recent database (Holmburg et al. 2013). If in discrepancy with Lindroth (1985, 1986), the more recent data were used. In few cases, we could not find information on traits, and in these cases, we assumed that all species in a given genus share traits. These exceptions as well as all traits are presented in Online Resource 4. The test to discern between the environmental filtering and biotic interactions is based on whether the species show similarity in the traits associated with a given mechanism. The match for traits associated with environmental filtering thus means that the species belong to the same trait group for sun exposure and soil moisture. The match for traits associated with biotic interactions means that the species belong to the same trophic group and their body size range overlap (body size shows a substantial range within each species). This similarity of traits represents competition. In addition, we checked whether predation–prey interaction would be a meaningful interpretation, i.e., at least the other species a predator and larger in size.

To analyze whether species showing non-random occurrences are associated with particular traits we used a randomization procedure. Separately for each habitat type and for positive and negative co-occurrences, we randomly selected the number of species observed to have positive/negative co-occurrences and recorded their traits. We repeated the procedure 1000 times and calculated the mean number (and 95% confidence intervals) of species showing a specific level for each trait as well as the mean body size. In addition, we checked whether certain trait groups occurred more often in certain habitat types than in the other. We fitted a general linear model with a proportion of a certain trait group relative to all occurrences in a site as a response variable and habitat type (meadows used as a baseline) as an explanatory factor. As the observations of trait groups are not independent since they are proportions, we base our inference on 95% confidence intervals, rather than p-values.

Results

At the plot scale, none of the species pairs showed co-occurrences in any of the habitat types with posterior probability of 0.95 (Table 1). Thus, there was only tentative support (posterior probability of 0.85) for positive co-occurrences and no negative co-occurrences at the plot scale. At the site scale, the highest proportion of positive and negative co-occurrences was in pastures (Table 1). In relation to the

Table 1 Species co-occurrences of carabids at two spatial scales (plot, site) in three different grassland types

	Meadow	Pasture	Road verge
Total no. of species	28	27	26
Site species richness (mean \pm SD)	13.6 (\pm 4.1)	11.8 (\pm 3.8)	10.1 (\pm 2.7)
Plot occupancy (mean \pm SD)	13.7 (\pm 4.1)	11.7 (\pm 4.1)	10.4 (\pm 4.1)
No. of pairs	378	351	325
Site scale			
Positive	6	17	6
Negative	4	11	6
Non-random (%)	2.6	8	3.7
Positive (%)	1.6	4.8	1.8
Plot scale			
Non-random (%)	0	0	0

Number of species occurring in the habitat types, number of pairs, number of significant positive (i.e., posterior probability at least 0.95), negative and random co-occurrences, and percent of non-random and positive co-occurrences from total number of co-occurrences are shown. At the plot scale, all occurrences were random with posterior probability at least 0.95

number of positive co-occurrences, the number of negative co-occurrences was smaller (meadows and pastures) or equal (road verges) (Table 1). The explanatory power of the model was 11.4% in meadows, 12.4% in pastures and 9.9% in road verges.

In general, the co-occurrences in all habitat types were sparse and among limited number of species. At the plot scale, the tentative positive co-occurrences (posterior probability 0.85) in meadows were among three (*Ophonus rufibarbis*, *Amara nitida*, *A. aulica*) and in pastures among five species (*Harpalus rufipes*, *H. latus*, *A. communis*, *A. montivaga*, *A. nitida*). In road verges, the highest posterior probability for co-occurrences was as low as 0.65 at the plot scale.

At the site scale, co-occurrences in meadows were among five species, four of which (*Poecilus cupreus*, *Pterostichus melanarius*, *Poecilus versicolor*, *Syntomus truncatellus*) had positive co-occurrence with each other and negative co-occurrence with *Pterostichus oblongopunctatus* (Fig. 2a). In pastures, the positive and negative co-occurrences were distributed among nine species (Fig. 2b) and in road verges among eight species (Fig. 2c).

Changes in individual species' link density (i.e., the proportion of positive co-occurrences from all possible co-occurrences) can merely result from changes in species' occurrence. At the site scale, individual species' link density was not associated positively with their occurrence (mean parameter estimate from the linear model for occupancy = -0.00002, SE = 0.00098; Fig. 3). For instance, *Poecilus versicolor* showed almost equal occupancy in all of the habitat types but had link density above zero only in meadows (Fig. 3k). One exception to the general pattern was *Pterostichus melanarius* which showed a clear pattern of decrease in link density associated with decrease in occurrence (Fig. 3h).

As all species pairs showed random co-occurrences at the plot scale, we had to consider only three of the nine possible pathways in the analytical logic tree (Fig. 1). For species pairs with random co-occurrence at both scales, there was no need for a trait-based test, as stochasticity best explained the co-occurrences (path 1 in Fig. 1). This applied to over 90% of the species pairs, regardless of the habitat type (Table 1). The species pairs with positive co-occurrences at the site scale and random co-occurrences at the plot scale showed a pattern predicted by environmental filtering, and no trait-based test was required (path 4 in Fig. 1). By contrast, for species pairs showing negative co-occurrences at the site scale, and random co-occurrences at the plot scale, a trait-based test was required (path 7 in Fig. 1). In meadows and in road verges, all of the species pairs differed in their traits associated with environmental filtering (i.e., preferences for sun exposure and/or soil moisture). Hence, environmental filtering was interpreted to be the mechanism structuring the co-occurrence patterns for these species pairs. In pastures, two of the 11 pairs (*Poecilus cupreus* and *Amara aulica*, *P. cupreus* and *Bembidion guttula*) did not differ in their traits associated with environmental filtering. However, these species did not show similar traits related to biotic interactions (i.e., trophic level, body size range): *P. cupreus* is a medium-sized omnivore, whereas *A. aulica* is a similar-sized herbivore and *B. guttula* a small predator.

Overall, the species showing positive or negative co-occurrences were not random samples from the species pool (Table 2). Particularly in pastures, the species showing positive co-occurrences were more often related to dry soil types, and species showing negative co-occurrences were more often related to moist soil types than predicted by random sampling of species. In meadows, it was notable that none of the species showing co-occurrences was

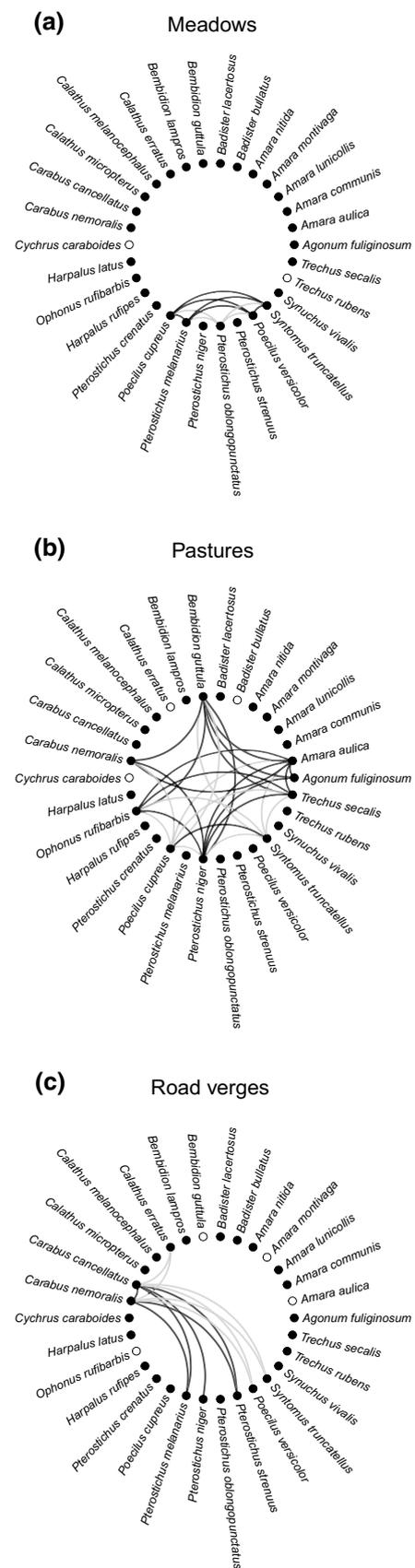
Fig. 2 Species co-occurrence networks of carabids in a) meadows, b) pastures and c) road verges at the site scale. Positive co-occurrences are shown in black and negative co-occurrences in gray. Species that are absent in the given habitat type are shown with open circles

herbivorous. In road verges, the mean body size of species showing non-random co-occurrences was larger than predicted by random sampling (Table 2). The relative occurrences of specific traits were quite similar among the three habitat types (Fig. 4). The only difference was that herbivores had larger proportion of all occurrences in meadows than in road verges whereas predators had larger proportion in road verges than in meadows (Fig. 4c).

Discussion

Carabid species co-occurrence networks in the managed grassland types, meadows, pastures and road verges, were sparse and among few species. Also, the mechanisms behind the community structure within each grassland type were similar. Over 90% of the pairwise co-occurrences were stochastic, regardless of the grassland type, and the non-random co-occurrences were best explained by environmental filtering rather than biotic interactions. Despite these similarities, there were also important differences: the identities as well as the traits of the species showing non-random co-occurrences differed among the habitat types. This suggests that the specific environmental factors behind environmental filtering differ among the three habitat types and are related to the site-specific environmental characteristics and variation therein. As species co-occurrences can be used to predict the effect of management on specific species (Tulloch et al. 2018), the different co-occurrence network structure on road verges compared to meadows and pastures suggests that mowing per se is not enough to make road verges compensatory habitats for grassland species.

The major mechanism behind co-occurrence patterns was stochasticity: in all habitat types over 90% of the species pairs showed random co-occurrences at both the site and plot scale. This is not an unusual result since several studies of pairwise co-occurrences have reported random co-occurrence patterns to prevail across different taxa (Pitta et al. 2012; Lyons et al. 2016; Kohli et al. 2018). Particularly, a low number of positive co-occurrences has been thought to be characteristic for disturbed sites (Kay et al. 2018). Although all the studied grassland types are disturbed at various extent through management and other disturbances, the reasons for the random co-occurrences may be numerous. At the plot scale, all the species pairs, regardless of the grassland type, showed random co-occurrence. In part, this likely results from a true random distribution of carabids at small scales: they are mobile and generalist predators, which



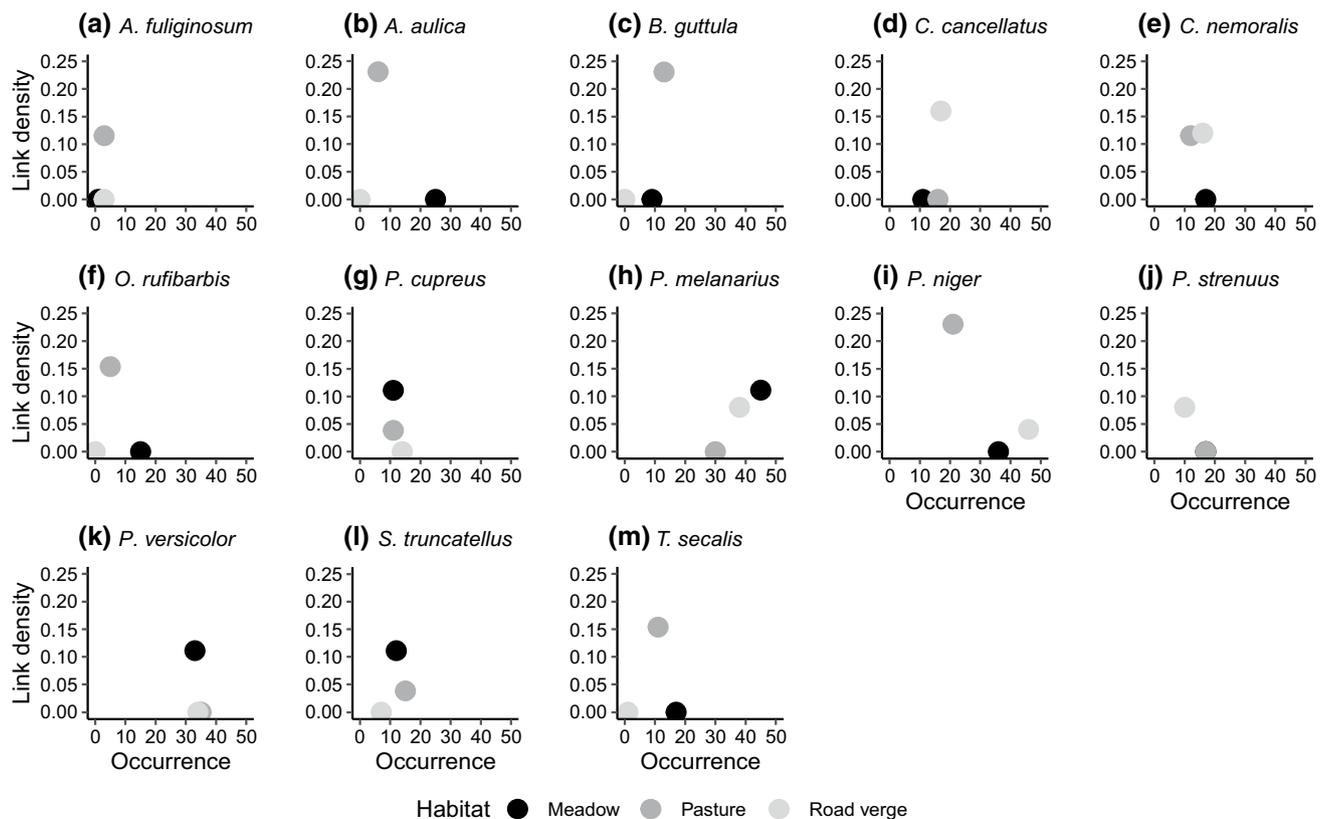


Fig. 3 Carabid species' link density (number of positive co-occurrences of all possible co-occurrences) and occurrence in different habitat types. Only the 13 species having positive co-occurrences are shown

actively search for prey. Also, the random co-occurrence is to some extent likely resulting from sampling error at the plot scale, as capturing these highly mobile animals is challenging. At the site scale, the random co-occurrences may result from the fact that the sites did not show strong environmental gradients. Environmental filtering is expected to be high when environmental conditions show a wide variation. When the sites are relatively similar, the stochasticity is expected. Finally, random co-occurrences may result from surrounding matrix. All the studied habitat types are small and may contain species from the surrounding forest and other habitats as a result of an edge effect (Magura et al. 2017). This was reflected in our data as a relatively high proportion of species preferring forests rather than open lands (Fig. 4a). It is, however, important to note that for small organism like insects, the studied sites are likely to maintain permanent populations.

The non-random co-occurrences in all grassland types were best explained by environmental filtering. Although also biotic interactions have been shown to affect species communities at relatively small spatial scales (Wisz et al. 2013), environmental filtering override biotic interactions in recent studies (D'Amen et al. 2018; Kohli et al. 2018). It is notable that only two relatively rough categorizing

variables (i.e., species preferences for sun exposure and soil moisture) were enough to explain the negative co-occurrences for almost all species pairs. Only two pairs showing negative co-occurrences had matching preferences for traits associated with environmental filtering. However, for these species the traits associated with biotic interactions did not match. Thus, biotic interaction as a form of competition is not a reason, and also intraguild predation is an unlikely reason for the negative co-occurrence between the species pair. Most likely, these species show differences in their preferences other habitat characteristics not covered by sun exposure or soil moisture.

The identities of the species showing non-random co-occurrences differed among the three grassland types. Generally, this was not explained by different levels of occurrence in each grassland type. Only one species (*Pterostichus melanarius*) showed high proportion of positive co-occurrences (i.e., link density) and also relatively high occurrence in both meadows and road verges. The species is a predator and has benefitted from agriculture (Lindroth 1986). Interestingly, the species showing non-random co-occurrences were not random samples from the species pool in terms of their traits. There were three notable differences.

Table 2 Observed and expected (mean and 95% confidence intervals) number of species showing a non-random co-occurrence (positive/negative) and specific level of each trait, as well as the mean body size, in three different grassland types (meadows, pastures, road verges)

Co-occurrence	Trait		Meadows			Pastures			Road verges					
			Observed	Expected		Observed	Expected		Observed	Expected				
				mean	95% CIs		mean	95% CIs		mean	95% CIs			
Positive	Sun exposure	Forest	<i>0</i>	<i>1</i>	<i>1</i>	<i>1</i>	2	2	2	2	2	<i>1</i>	<i>1</i>	<i>1</i>
		Open	3	2	2	2	4	5	5	5	1	2	2	3
		Generalist	1	1	1	1	3	2	2	2	2	<i>1</i>	<i>1</i>	<i>1</i>
	Soil moisture	Dry	2	2	2	2	2	4	4	4	<i>1</i>	2	2	2
		Moist	<i>1</i>	2	2	2	7	4	4	4	3	2	2	2
		Generalist	1	1	1	1	0	<i>1</i>	<i>1</i>	<i>1</i>	1	1	1	1
	Trophic level	Herbivore	<i>0</i>	<i>1</i>	<i>1</i>	<i>1</i>	2	3	3	3	0	<i>1</i>	<i>1</i>	<i>1</i>
		Predator	3	3	3	3	6	6	6	6	5	4	4	4
		Omnivore	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	1	0	0	0	0	0	0	0
		Mean body size	<i>10.2</i>	9.7	9.8	9.5	<i>10.1</i>	9.5	9.5	9.6	17.6	10.0	9.8	10.1
Negative	Sun exposure	Forest	1	1	1	1	1	2	2	2	0	<i>1</i>	<i>1</i>	<i>1</i>
		Open	3	3	3	3	4	4	4	5	4	2	2	3
		Generalist	1	1	1	1	3	2	2	2	1	1	1	1
	Soil moisture	Dry	3	2	2	2	6	3	3	3	4	2	2	2
		Moist	<i>1</i>	2	2	2	2	4	3	4	1	2	2	2
		All	1	1	1	1	0	<i>1</i>	<i>1</i>	<i>1</i>	0	<i>1</i>	<i>1</i>	<i>1</i>
	Trophic level	Herbivore	0	2	2	2	2	3	3	3	0	<i>1</i>	<i>1</i>	<i>1</i>
		Predator	4	3	3	3	6	5	5	5	5	4	4	4
		Omnivore	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	1	0	0	0	0	0	0	0
		Mean body size	<i>10.4</i>	9.6	9.7	9.4	<i>10.5</i>	9.6	9.5	9.7	14.4	10.0	9.8	10.1

The observed values which do not fall within the 95% CIs are in italics, and the observed values which fall significantly (i.e., ≥ 2) outside the 95% CIs are in italics and in bold

First, no herbivore species was among the species showing non-random co-occurrences in meadows. This is intriguing since meadows had a higher proportion of herbivore occurrences in comparison to the other habitat types. The high proportion of herbivores is most likely related to the fact that meadows had also higher vegetation than the other two habitat types. It may be that for herbivores, the resources were evenly distributed among the sites, resulting in random occurrences between species pairs. The non-random co-occurrences in meadows were among just a five species: a forest species *Pterostichus oblongopunctatus* had a negative association with four species preferring open habitats which all had positive associations with each other. This may reflect the site-specific preferences for these species.

Second, non-random co-occurrences in pastures were related to the species preference for soil moisture: species preferring moist soil showed positive co-occurrences, whereas species preferring dry soil showed negative co-occurrences. Moreover, pastures showed more non-random co-occurrences than meadows or road verges. The pastures showed differences in the grazing pressure and trampling, making the sites quite heterogeneous in terms of vegetation height and composition, as well as top soil moisture

and structure. As carabid species prefer different soil types (Lindroth 1985, 1986), this may explain the relatively high number of non-random co-occurrences among pastures.

Third, species showing non-random co-occurrences were considerably larger than predicted by random chance. This was because some very large species (*Carabus cancellatus*, *C. nemoralis*, *Pterostichus niger* and *P. melanarius*) had positive co-occurrences with each other and negative co-occurrences with other species. It is not easy to explain positive co-occurrences for such eurytopic (generalist) species. They are generalist predators, but feed also on carrion (Lindroth 1985, 1986). The two *Carabus* species and *P. melanarius* feed also on slugs, which, if more common in road verges than in meadows and pastures, could explain positive co-occurrences. All these species are all particularly favored by human activities and are common in parks and gardens. Although the varying traffic load could increase heterogeneity among sites, and thus the number of positive co-occurrences at the site scale co-occurrence networks, the studied road verges were relatively similar in size and traffic load, so this effect should not be overwhelmingly great.

Network metrics and their conservation implications have been largely derived from biotic interaction networks

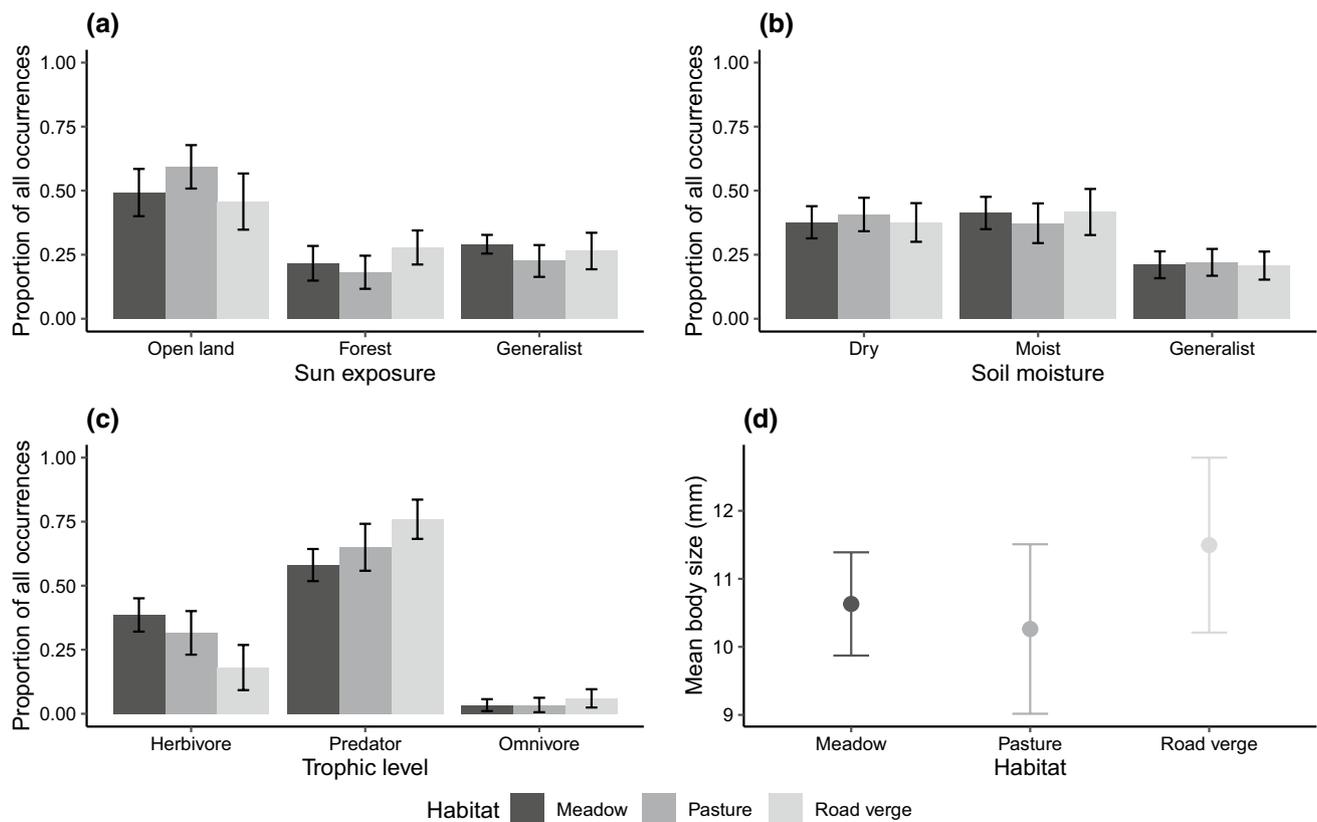


Fig. 4 Relative proportion of occurrence of carabid species representing the specific level of each trait from all occurrences at the site scale ($n=12$). Traits are sun exposure (open land, forest, generalist),

soil moisture (dry, moist, generalist), trophic level (herbivore, predator, omnivore) and mean body size (mm). The error bars represent 95% confidence intervals

(Tylianakis et al. 2010). In such systems, the loss of positive co-occurrences can cause decline in ecological functions of the ecosystems, although the interpretation is not straightforward and caution is needed (Tylianakis et al. 2010). From the conservation perspective, it can matter if certain species co-occur in certain environments and species co-occurrences can be used to predict management effects (Tulloch et al. 2018). In our study, different grassland types showed different co-occurrence structures stemming most likely from the site-specific characteristics. This suggests that species in different habitat types may respond differently to management practices, depending on the prevailing environmental conditions.

Conclusions

We showed that different managed grassland types, albeit very similar in species richness (Komonen and Elo 2017) and sharing most species, have different species co-occurrence networks. This underscores the fact that neither species richness nor composition can be solely used to assess the compensatory role of different habitats. Moreover, as

the identities and traits of the species showing non-random co-occurrences differed among the grassland types, also their response to habitat management may differ. This poses challenges to habitat management of different grasslands since the species' response to management action may depend on the site-specific characteristics. On the other hand, although road verges may not be fully compensatory to meadows and pastures, the high similarity of species richness and the high level of shared species shows that grassland carabids utilize road verges. It is also possible that road verges may be used as corridors (Haddad and Baum 1999; Collinge 2000) in the sparse network of the remaining traditional rural biotopes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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Availability of data and materials The dataset supporting the conclusions of this article is included as Online Resource 5.

Code availability The codes applied were derived from the executory material from the package ‘HMSC-R’ (Tikhonov et al. 2019). The exact scripts are available on request from the corresponding author.

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