



# Importance of habitat area, quality and landscape context for heteropteran diversity in shrub ecotones

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## Abstract

**Context** Habitat loss and degradation impose serious threats on biodiversity. However, not all habitats receive the attention commensurate with their ecological importance. Shrub ecotones (successional stages between grasslands and forests) can be highly species-diverse but are often restricted to small areas as prevalent management practices either promote open

grassland or forest habitats, threatening the effective conservation of ecotone species.

**Objectives** In this study, we assessed the importance of habitat and landscape features of shrub ecotones for the rarely studied true bugs (Heteroptera), a functionally diverse taxon that comprises highly specialized species and broad generalists.

**Methods** True bugs were sampled with a beating tray in 118 spatially independent shrub ecotones in a region of 45,000 square kilometers in Germany. In addition to habitat area and landscape context, we used a hedge index to evaluate habitat quality.

**Results** Shrub ecotones in open habitats harbored a greater species richness and abundance compared to shaded ones in later seral stages, and species composition differed. Richness and abundance were positively affected by increasing habitat area and quality, whereas an increase in the proportion of semi-natural habitats within 1 km only enhanced richness. While feeding and habitat specialists were more sensitive to habitat area reduction than generalists, this was not the case for weak dispersers and carnivores.

**Conclusions** Our findings emphasize the importance of large and high-quality ecotones that form a patchy mosaic of shrubs and herbaceous plants. Such ecotones can benefit both grassland species and species depending on woody plants. Conservation authorities should balance between promoting shrubs and keeping such habitats open to maximize species diversity.

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## Introduction

Habitat area, habitat quality and the landscape context are key drivers of species diversity in terrestrial ecosystems (Tschardt et al. 2005; Poniatowski et al. 2018, 2020; Cardoso et al. 2020). However, many habitats are increasingly under threat by human activities, such as the conversion of semi-natural habitats to cropland (Newbold et al. 2015; Cardoso et al. 2020), but also by long-term land abandonment (Strijker 2005). The remaining habitat patches are often small and vulnerable to disturbances such as nutrient input and pesticide drift from adjoining arable land (Botías et al. 2016). Furthermore, expanding field sizes and removing semi-natural structures like hedgerows have led to greater homogeneity in agricultural landscapes (Robinson and Sutherland 2002). This has resulted in increasingly isolated habitat patches, impeding the persistence of species as well as the recolonization of the remaining habitat. The cumulative effects of habitat loss, habitat degradation, and homogenization of the landscape result in sharp declines in arthropod biomass and species richness (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019; Seibold et al. 2019), and shifts in species composition towards a higher dominance of generalist species (Gámez-Virueés et al. 2015; Habel et al. 2016; Thorn et al. 2022; Gossner et al. 2023), leading to a reduction of ecosystem functions and services (Balvanera et al. 2006).

The positive relationship between habitat area and species richness has long been recognized by ecologists. The *area-per-se hypothesis*, derived from the theory of island biogeography, postulates that the number of species in a patch is determined by colonization and extinction rates, whereby the colonization rate is higher and extinction risk is lower in large and connected compared to small and isolated sites (MacArthur and Wilson 2001). The view that habitat size and isolation have distinct effects on species numbers is challenged by the *habitat amount hypothesis*, where species numbers are driven by a single process, the sample-area effect (Fahrig 2013). The *habitat heterogeneity hypothesis* posits that larger patches are more

likely to contain more microhabitats and resources (MacArthur and MacArthur 1961). Unequal sampling intensity (*sampling hypothesis*) might additionally explain higher species numbers in larger study sites (Rosenzweig 1995).

Habitat quality has rarely been studied due to its complexity and its subjective nature, as indices of habitat quality are prone to circular reasoning, e.g. when habitat quality is defined as the known habitat requirements of certain species, or when the criteria for habitat quality are developed after the sampling (Mortelliti et al. 2010). An index based on the habitat preferences of certain species will inevitably find that these species occur in high-quality habitats (Thomas et al. 2001). Some authors have applied very simple indices, dividing habitats into “good” and “poor”, losing information and imposing a discrete threshold on what should be a continuum (Garratt et al. 2017). Here, we applied an index a priori to assess the quality of shrub ecotones, comprising four important characteristics: species richness of woody plants and their value for biodiversity, the age structure of the woody plants and the edge density in the surroundings. This index provides a continuous value and is targeted to assess habitats containing shrubs in Central Europe from a conservation perspective (Zwölfer 1982).

Species richness is not only determined by habitat area and quality but also by the surrounding landscape composition. The *landscape species pool hypothesis* suggests that species richness in a habitat patch is moderated by the landscape-wide species pool (Tschardt et al. 2012). Landscapes rich in semi-natural habitats (SNH) provide more potential habitat and are more heterogeneous than simplified agricultural landscapes (Dufflot et al. 2015), leading to greater landscape species pools and thus to more species in habitat patches (Schirmel et al. 2018). Species richness is furthermore influenced by matrix properties, with benign matrices allowing for higher colonization rates (Fahrig 2020), mitigating the negative impact of habitat fragmentation.

Habitat loss is the strongest driver of species declines, but not all species are affected equally. Species assemblages are filtered via species traits (Brousseau et al. 2018). Specialized species, whether in their habitat affinity (Mortelliti et al. 2010; Matthews et al. 2014; Habel et al. 2019a) or diet (Öckinger et al. 2010), are more severely affected than generalists.

Similarly, higher trophic levels should be at higher risk as they rely on the stability of lower trophic ranks and have smaller population sizes (Staab et al. 2023). Weak dispersers, which depend on the stability of their habitat, should be more sensitive than good dispersers as they may not be able to move to new areas and recolonize a habitat after local extinction (van Noordwijk et al. 2015).

While forests (Gossner et al. 2013; Thorn et al. 2015; Kozák et al. 2021) and grasslands (Öckinger et al. 2012; Rösch et al. 2013; Woodcock et al. 2021) have been extensively studied, the successional stages between them, i.e., shrub ecotones have received little attention (Swanson et al. 2011), apart from studies from South and Eastern Central Europe (Chytrý et al. 2022; Penado et al. 2022), where shrub ecotones can be the climax stage (Acácio et al. 2007). In Western Central Europe, shrub ecotones develop from grasslands and abandoned agricultural fields and at the edges between different habitats. These shrub ecotones have unique species assemblages, especially when they are favored by a warm microclimate in early seral stages when they still maintain an open character (Habel et al. 2019b; Helbing et al. 2021). Shrubs can be vital refuges for insects from intensively managed grasslands, where management practices lead to a homogenization of grassland communities (Gossner et al. 2016), and to a significant decline in the number of insects (Hemmann et al. 1987; Steidle et al. 2022). Additionally, insects suffer from increased sward temperature in mown grassland (Gardiner and Hassall 2009), whereas their thermoregulation is facilitated in shrub ecotones, where the shrubs provide shade. In the course of succession, however, a few competitive, tall-growing shrubs such as *Prunus spinosa* or *Crataegus monogyna* become dominant in Central European shrub ecotones (Korrmann et al. 2015; Schüle et al. 2023), which eventually leads to a loss of thermophilic species (Butaye et al. 2005) and the development of deciduous forest as the climax stage (Milberg 1995; Poschlod and WallisDeVries 2002).

True bugs (Heteroptera) are a highly abundant and species-rich taxon in shrub ecotones. Many species rely on both, the xerothermic conditions of open habitats and the presence of shrubs (Hilmers et al. 2018; Niedringhaus et al. 2020). They are often highly specific to particular plant species (Gossner et al. 2015) and habitats (Zurbrügg and Frank 2006). In shrub

ecotones, true bugs occupy various niches, are found at different trophic levels, and occur in all vegetation layers and on the ground. These characteristics make them sensitive to habitat loss and reduced habitat quality. There is a rich body of literature on the decline of Hymenoptera (Jauker et al. 2013), Lepidoptera (Warren et al. 2021), and Coleoptera (Hallmann et al. 2020). Heteropterans, however, despite their high species richness of ~45,000 species worldwide (Henry 2017) and >1,100 in Central Europe (Günther and Schuster 2000) have rarely been studied (but see Schuch et al. 2012). Some true bugs are economically relevant as serious pest species (Haye et al. 2015) or effective biocontrol agents (Gödel et al. 2020).

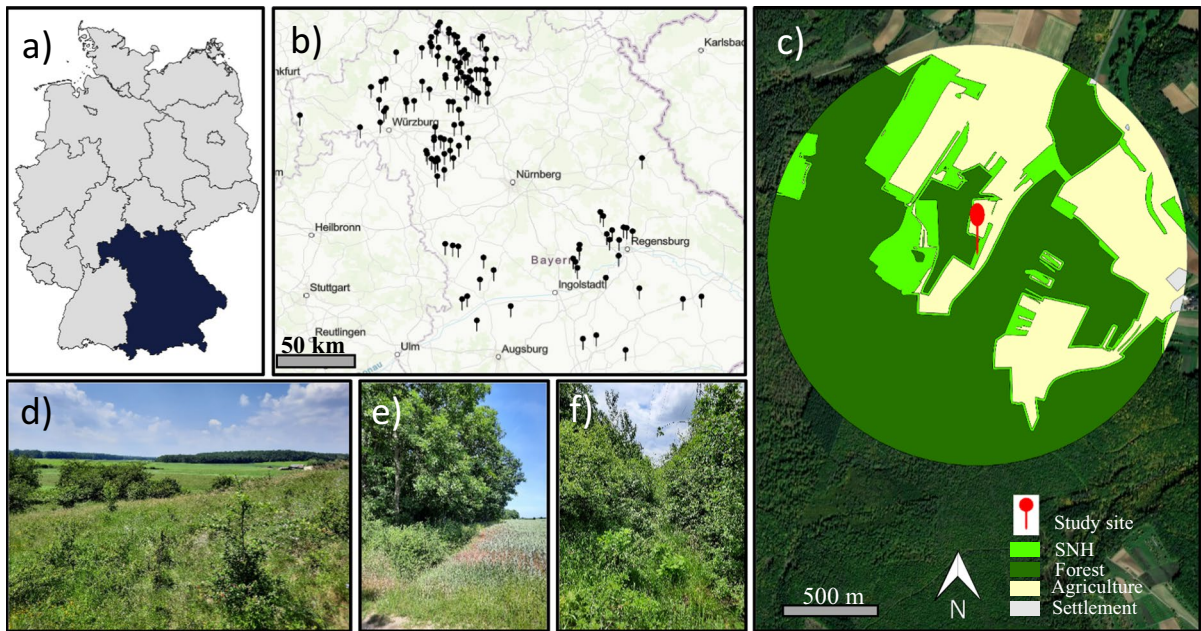
In this study, we sampled true bugs in shrub ecotones differing in foliage cover of shrubs, habitat area, habitat quality, and landscape context. We developed the following predictions:

- I) Open shrub ecotones support higher species richness and abundance and differ in their assemblage compared to shaded shrub ecotones.
- II) Species richness and abundance increase with increasing habitat area, habitat quality and a higher proportion of semi-natural habitat in the surrounding landscape.
- III) Species richness of habitat and feeding specialists, higher trophic levels, and weak dispersers declines more sharply with decreasing habitat area than that of habitat and feeding generalists, herbivores, and good dispersers.

## Materials and methods

### Study region and sites

The study was conducted in a region of approximately 45,000 km<sup>2</sup> in Bavaria (Southern Germany; Fig. 1a–c). Most sites were on Keuper formation. We selected 118 shrub ecotones that were at least 2 km apart from each other to ensure spatial independence. A shrub is a perennial woody plant that is less than 10 m tall and that has no clear trunk (Allaby 2019). To increase the comparability of the shrub ecotones, all study sites had to contain at least the plant species French rose (*Rosa gallica*). The French rose is typically found in shrub ecotones of the phytosociological



**Fig. 1** **a** Location of the study region (Bavaria) in Germany, **b** location of the 118 study sites in Bavaria, **c** example of the landscape analysis of the study site Grossbardorf, **d** open shrub

ecotone in grassland, **e** half-open shrub ecotone along a forest margin, **f** shaded ecotone through increased shrub encroachment

orders *Origanitelia vulgaris* and *Rhamno-Prunetea* (Oberdorfer et al. 2021) in the study region and is listed as endangered in Bavaria (Scheuerer and Ahlmer 2003). Thus, we ensure similarity in habitat conditions according to the requirements of the rose. These are, e.g., alternating wet and dry conditions on predominantly loamy soils, warm microclimate, low to moderate nutrient availability, and extensive management (Hegi 2000), conditions that are commonly met in the study region. Multi-annual mean temperatures within the reference period 1991–2020 vary from 7.9 to 10.3 °C and precipitation ranges from 563 to 932 mm within the study region (Data: ‘Deutscher Wetterdienst’).

#### True bug sampling

True bugs (Heteroptera) were sampled using a 72 cm diameter funnel-shaped beating tray with a hole tunnel in the center to attach a collection can (Suppl. S1). Sampling was conducted at each site during five rounds between May 13th and August 6th, 2021. Beating was performed for three minutes each on French rose and accompanying shrubs using a 1.20 m bamboo stick with the tip wrapped in armor tape.

The beating rate was 20 beats per minute, resulting in approximately 120 beats per study site and sampling round. Sampling was conducted at three randomly selected locations within each study site for one minute each, with locations spaced further apart in larger sites. All study sites were visited at regular intervals during the sampling period, following a random sequence. Sampling was carried out on dry days and in the absence of strong winds (Bft. < 4). The temperature was at least 15 °C. True bugs were determined to species level in the laboratory with the help of entomological literature (Wagner 1952, 1966, 1967; Niedringhaus et al. 2020) and the software Corisa ([www.corisa.de](http://www.corisa.de)). Nomenclature follows Deckert and Wachmann (2020). If possible, late instars (L4 and L5) were also identified to species level, while early instars were counted and used for abundance data. All data were pooled to obtain one value per site.

#### Ecotone type and area

We divided the shrub ecotones into three groups (open, half-open, shaded; hereafter called ecotone type) depending on the foliage cover of at least 1 m high shrubs in the ecotones (Fig. 1d–f). Shrub

ecotones were classified as open when the proportion of foliage cover of shrubs was <30%, half-open when the cover was between 30 and 70%, and shaded when the cover was >70% (Costermans 1981). This procedure resulted in 33 of the ecotones being classified as open, 70 as half-open, and 15 as shaded. The area of the shrub ecotones ranged from 5 to 3,672 m<sup>2</sup>. We recorded the temperature at all sites using Thermochron iButtons (Maxim Integrated Systems, temperature accuracy <±0.5 °C), which were placed into the vegetation at approx. 30 cm height to protect them from direct solar radiation. The sensors were set to record instantaneous values of temperature every hour over the sampling period (Suppl. S2).

Habitat quality

To evaluate the quality of the shrub ecotones, we applied a hedge quality index (Zwölfer 1982). The index takes into account (i) the woody plant species richness of a shrub ecotone as well as their value for biodiversity, (ii) the age structure, and (iii) the edge density in the surroundings, defined as the length of hedgerows and forest edges per hectare within a 1 km radius. Plant species that are considered of higher value for animal biodiversity, such as roses (*Rosa spp.*), hawthorn (*Crataegus spp.*) or blackthorn (*Prunus spinosa*), are assigned a higher score. These plants are especially valuable in terms of berry provision and floral resources (Jacobs et al. 2009). They complement each other in terms of the flowering period. In the case of true bugs, these

shrubs support a higher number of species than plants with a lower score (Deckert and Wachmann 2020). Roses, hawthorn and blackthorn are widespread species, characteristic for shrub ecotones in Central Europe. Furthermore, through their complementing growth forms, their co-occurrence maximizes the structural diversity of woody elements (Zwölfer 1982). They offer shelter and protection from predators through their density and spination. As the value of additional species saturates with increasing species richness, non-dominant woody plants are assigned lower values in species-rich than in species-poor shrub ecotones. The scores of the individual plant species are summed up to a species factor (Table 1a). Thus, the species score provides information that goes beyond the mere counting of species. The age class depends on the age span of the woody plants, with a high diversity of age classes resulting in a higher value (Table 1b). The mixture of different age classes enhances the structural complexity, which is an important driver for true bug species richness and abundance (Jacobs et al. 2009). Edge density describes the length of woody edges in the surroundings per hectare, resulting in a density factor, which can take three values (Table 1c). We adjusted the factor in a way that all three values were roughly as frequent. The product of the three factors gives the hedge quality index. As an additional indicator of habitat quality, we estimated flowering herbaceous plant species richness once in June within three plots of 1 m<sup>2</sup> size at the locations where the true bugs were sampled.

**Table 1** The components of the hedge index after Zwölfer (1982) to assess habitat quality. **a** Woody plant species are assigned a score according to their ecological value. The sum of the scores gives the species factor. **b** The age class factor, depending on the age span of the shrubs in the ecotone. **c** the density factor, derived from the mean edge density per hectare in a 1 km radius. The product of the three factors gives the hedge index

a) Species factor		b) Age class factor	
Woody plant species	Species score	Age span (years)	Age factor
<i>Prunus spinosa</i>	3	<6 to >20	2
<i>Crataegus spp.</i>	3	<6 to >10	1
<i>Rosa spp.</i>	3	>10 to >20	1
<i>Salix caprea</i>	2	<6 to <10	0.5
<i>Corylus avellana</i>	2	<6	0.25
<i>Rubus spp.</i>	1		
<i>Acer campestre</i>	1		
<i>Sorbus aucuparia</i>	1		
One to five further woody species	0.5		
Every further woody species	0.2		
	Σ = Species factor		
		c) Density Factor	
		Edge density (m/ha)	Density factor
		>80	2
		25–80	1.5
		<25	1

## Landscape context

The landscape context, defined as the proportion of SNH in the surroundings of the study sites was calculated with ArcGIS pro 2.7.2 (ESRI) with modified digital thematic maps (ATKIS-DLM 25/1, Landesamt für Digitalisierung, Breitband und Vermessung, 2021; BIOTOP, Bayerisches Landesamt für Umwelt, 2023, [www.lfu-bayern.de](http://www.lfu-bayern.de)). We defined SNH as (1) extensive grassland, (2) forest edge: 10 m inner buffer ring of deciduous and coniferous forest, and (3) woody structure in the open landscape. We then calculated the proportion of SNH in perimeters of 500 m, 1 and 2 km around the study sites (Grab et al. 2018). Additionally, we calculated the proportion of shrub ecotones (habitat amount) within a radius of 1 km around the study sites and the isolation of the study sites by calculating nearest-neighbor distances.

## Life-history traits

Species traits were obtained from Gossner et al. (2015) and the field guides of Wachmann et al. (2004; 2006; 2007; 2008). We selected habitat and feeding specialization, the feeding guild (trophic level) and dispersal ability as responsive traits (Suppl. S3). We defined species as habitat specialists that are associated with shrubs or with the characteristic accompanying herbaceous flora (units *Origanitelia vulgaris* and *Rhamno-Prunetea*; (Sturm et al. 2018), and are xero- and/or thermophilic. We classified 111 species as generalists and 59 as specialists. The feeding specialization was classified into two categories: oligophagous (species that consume only plants from one plant family), and polyphagous (species that feed indifferently on a diverse set of plants). We did not include predominately carnivorous species for this trait. Thus, we had 77 oligophagous species and 58 polyphagous species. The feeding guild was based on the main food source during both the larval and the adult stage. The true bugs were classified into herbivores (both stages feed predominately on plants), omnivores (both stages consume both plants and arthropods or there is a switch in feeding guild from the larval to the adult stage), and carnivores (both stages feed predominately on other arthropods). This resulted in 109 herbivorous species, 26 omnivorous and 35 carnivorous species. We used community-weighted mean (CWM) body size (distance from the

tip of the head to the end of the abdomen) as dispersal-related trait. Body size has been shown to be an appropriate proxy for dispersal abilities in a range of taxa (Stevens et al. 2014).

## Statistical analysis

Data were analyzed with R 4.2.2 (R Core Team 2022). To visualize the difference of true bug assemblages between the three ecotone types, we performed non-metric multidimensional scaling (NMDS) within the ‘vegan’ package (Oksanen et al. 2022) with 9999 permutations and three dimensions (stress=0.182). We selected Bray-Curtis-distance as distance metric and used the relative abundances of the true bug species. We checked for compositional differences in the true bug assemblages between the ecotone types with a permutational multivariate analysis of variances (‘adonis’ test with 999 permutations). A test for multivariate homogeneity of group dispersions confirmed the homogeneity of variances between the groups (‘betadisper’ test,  $p=0.372$ ).

The impact of habitat area, quality and proportion of SNH on the species richness of heteropteran assemblages was analyzed with linear models. For abundance, we ran a generalized linear model with negative binomial error distribution and log-link function within the package ‘MASS’ (Venables and Ripley 2002). Explanatory variables were fitted in the following order: Ecotone type, habitat area, proportion of SNH, habitat quality, flowering herbaceous plant species richness. We calculated Pearson correlations with the package ‘corrplot’ (Wei and Simko 2021) to ensure that all variables used were not strongly correlated with each other ( $r < 0.5$ ; Suppl. S4). Variables were also tested for interactions with the ecotone type, and the models were simplified by sequentially removing non-significant interactions. We also ran models that included the proportion of shrub ecotones and the isolation of the study sites, respectively, instead of SNH at the 1 km scale. These alternative models performed equally well ( $\Delta$  AICc < 2). To determine which variables were significant, we performed sequential ANOVAs with Type I sums of squares. For models containing interactions, the ‘emmeans’ package (Lenth 2022) was used to test whether the slopes were significantly different from zero. We additionally show single factor models to illustrate the direct effects of the variables.

To assess the effect of SNH on the true bug assemblages at different landscape scales, we ran the full models with 500 m, 1000 and 2000 m radii around the study sites and compared them using AICc values. The model that included the 1 km landscape scale resulted in the lowest AICc value ( $\Delta \text{AICc} > 2$ ), indicating a better model fit. A scale of 1 km has been widely used across many insect taxa, such as carabids (Barber et al. 2022), butterflies (Denning and Foster 2018) and grasshoppers (König and Krauss 2019).

To evaluate whether species with different traits (habitat and feeding specialization, trophic level) responded differently to habitat area, we ran linear mixed effects models using the ‘lme4’ package (Bates et al. 2014) with the number of species within each group as the dependent variable and the interaction between habitat area (log10-transformed) and the life-history trait as explanatory variable. We added the site identity as random term to correct for pseudoreplication (Pinheiro and Bates 2006). To account for the discrepancy in species numbers between habitat generalists and habitat specialists, we applied a log10+1-transformation to the species richness ( $z$ -values), allowing for a more meaningful comparison between the two groups (Krauss et al. 2009). For dispersal ability, we ran a linear model with the CWM of body size as dependent variable.

To find the best fitting error distribution for our data we used the package *fitdistrplus* (Delignette-Muller and Dutang 2015) with AICc as goodness-of-fit criterion. Normal and negative binomial distribution resulted in the lowest AICc for the species richness and the abundance model, respectively. For all models, we used the ‘DHARMA’ package (Hartig 2022) to check the model assumptions (linear relationship, homoscedasticity, normality of the residuals, independent  $x$ ). To detect possible spatial autocorrelation, we calculated the degree of correlation of the model residuals with geographic coordinates by use of spline correlograms from the ‘ncf’ package (Bjornstad 2022) for each model. We did not find any spatial autocorrelation in our model residuals (Suppl. S5).

## Results

We sampled 13,700 individuals from 170 heteropteran species, representing 25% of the terrestrial

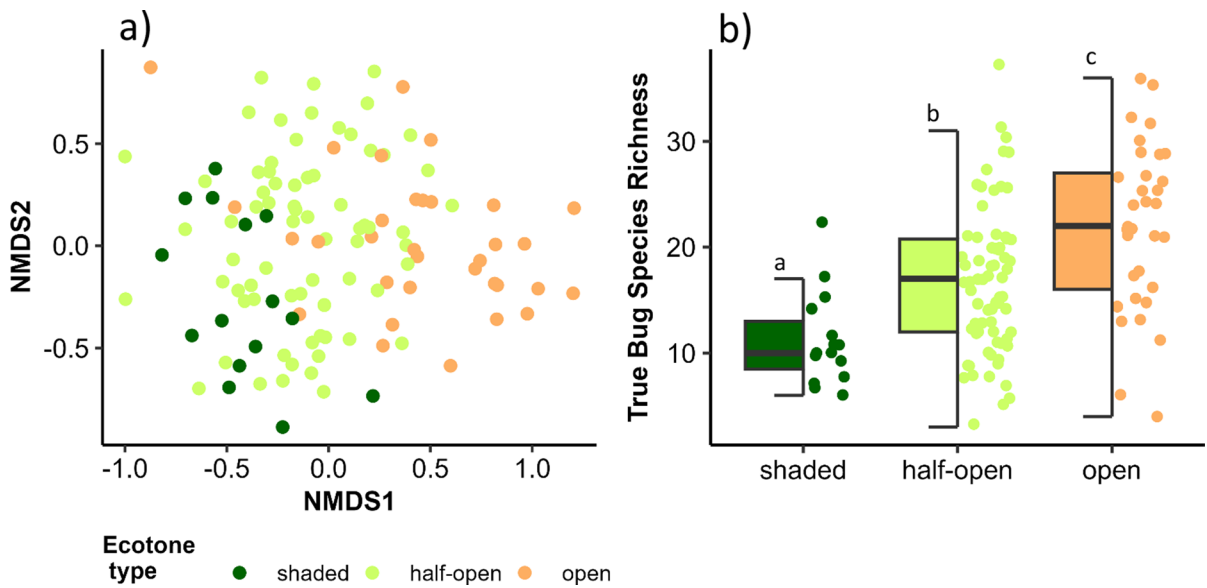
true bug species known for Bavaria (Achtziger et al. 2003). The plant bugs (Miridae) were the most abundant (7,718 individuals) and species-rich (86 species) family, with *Stenodema laevigata* being the prominent species with 1,734 individuals (Suppl. S3). The mean number of species per site was  $17.5 \pm 7.6$  (mean  $\pm$  SD), with an average of  $117.9 \pm 97.6$  individuals.

### The influence of ecotone type on true bug assemblages

We found a gradual shift in the true bug assemblage composition from open shrub ecotones to shaded shrub ecotones (Fig. 2a). Ecotone type explained 10.3% of the observed variation ( $p < 0.001$ ). Moreover, we found that the ecotone type had a significant effect on both the species richness and abundance of true bugs. Specifically, open shrub ecotones had the highest species richness ( $22.0 \pm 7.9$ ), followed by half-open shrub ecotones ( $16.7 \pm 6.9$ ) and shaded shrub ecotones ( $11.3 \pm 4.3$ ). Similarly, most true bug individuals were sampled in open shrub ecotones ( $177.1 \pm 135.2$ ), whereas there were fewer individuals in half-open ( $97.9 \pm 64.8$ ) and shaded ( $65.6 \pm 62.5$ ) shrub ecotones (Fig. 2b).

### Assemblage-level patterns

The simplified linear model explained a significant proportion of the variance of species richness (Adjusted  $R^2 = 51.0\%$ ,  $F_{8,111} = 21.32$ ,  $p < 0.001$ ; Table 2). Based on single factor models, species richness nearly quadrupled with increasing habitat area, with an increment from 8 to 31 species from the smallest ( $5 \text{ m}^2$ ) to the largest ( $3672 \text{ m}^2$ ) shrub ecotones (Fig. 3a). Species richness increased with increasing habitat quality from 15 in the habitats of the lowest quality to 24 in the habitats of the highest quality (Fig. 3b). The proportion of SNH, which ranged from 1.05 to 35.90%, did also impose a significant effect on species richness (Fig. 3c), but only when analyzed in a single factor model. Flowering herbaceous plant species richness was positively associated with true bug species richness, leading to a doubling of true bug species richness from 13 to 28 species along the gradient (Fig. 3d). The proportion of shrub ecotones, ranging from 0 to 20.32%



**Fig. 2** The effect of the ecotone type on **a** true bug assemblage composition as calculated by non-metric multidimensional scaling (NMDS) and **b** true bug species richness. Different letters indicate significant differences

(median 0.91%) was also positively related to species richness, while isolation had a negative impact (Suppl. S6).

The simplified negative binomial model explained a substantial portion of the variance observed in true bug abundance (pseudo- $R^2 = 46.8\%$ ,  $X^2_{8,109} = 108.60$ ,  $p < 0.001$ ; Table 2). In a single factor model, abundance increased almost fourfold from 45 to 186 individuals over the habitat area gradient (Fig. 4a). An increase in habitat quality had no significant effect on true bug abundance (Fig. 4b). However, habitat quality was significant in the full model after controlling for ecotone type and habitat area. The total effect of the proportion of SNH was also insignificant, however, there was a significant interaction with ecotone type: while there was an insignificant positive trend of true bug abundance with increasing SNH in open shrub ecotones, there was a sharp decline in abundance in shaded ones, where abundance fell from 118 to 13 in shrub ecotones with more SNH in the surrounding landscape (Fig. 4c). However, true bug abundance increased fivefold (64 vs. 335) from habitats with few flowering herbaceous plants to habitats with numerous herbs in flower (Fig. 4d). The proportion of shrub ecotones did not have a significant effect, while increasing isolation reduced true bug abundance (S6).

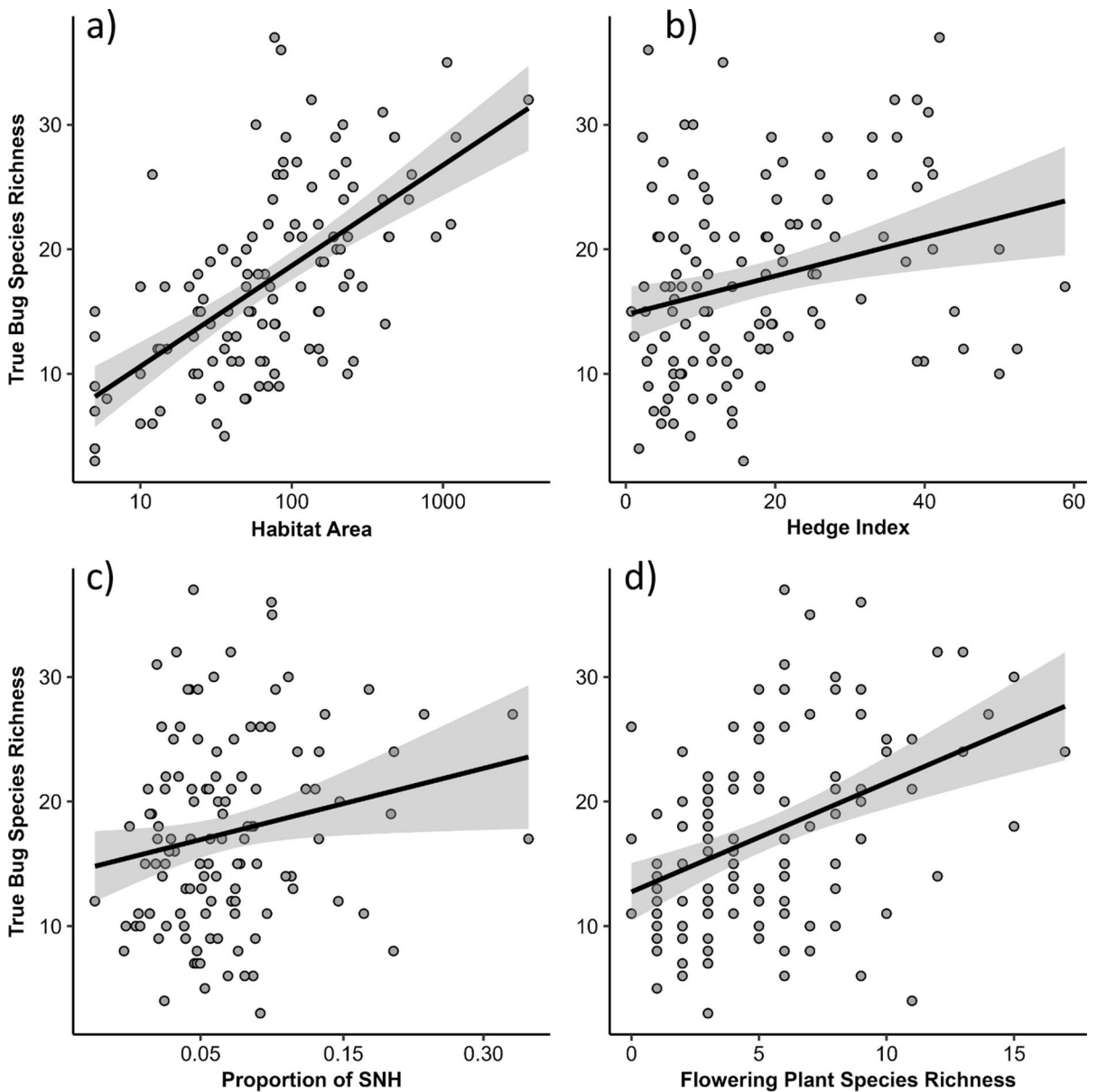
#### Life-history traits

Species richness of habitat specialists ( $z$ -value=0.27) decreased more steeply with decreasing habitat area than generalists ( $z$ -value=0.18,  $F_{1,116} = 5.39$ ,  $p = 0.022$ ; Fig. 5a). Species richness of feeding specialists decreased more steeply than species richness of feeding generalists ( $F_{1,116} = 9.17$ ,  $p = 0.003$ ; Fig. 5b). Herbivores increased more steeply than carnivores and omnivores ( $F_{2,232} = 18.91$ ,  $p < 0.001$ ; Fig. 5c). CWM body size decreased over the habitat area gradient, but the effect was only marginally significant ( $F_{1,116} = 3.38$ ,  $p = 0.069$ ; Fig. 5d; Suppl. S7).

#### Discussion

Our results show compelling evidence for the ecological significance of shrub ecotones as important habitats for true bugs. In accordance with our expectations, open shrub ecotones supported the most species and the highest abundance, while the shaded ones were poor in individuals and species. Furthermore, the ecotone type not only affected species richness and abundance but also shaped the true bug assemblages. We also found significant positive effects of habitat area, habitat quality,





**Fig. 3** Effects of habitat area **a**, habitat quality (hedge index) **b**, landscape context (proportion of semi-natural habitat) **c**, and flowering herbaceous plant species richness **d** on true bug spe-

cies richness in the single factor models. Dashed lines indicate non-significant effects. Grey areas correspond to the 95% confidence interval around the mean species richness

proportion of SNH and flowering herbaceous plant species richness on true bug species richness. Habitat area and flowering herbaceous plant species richness had also a positive impact on true bug abundance. While habitat and feeding specialists were more sensitive to habitat loss than habitat

generalists and species with a broad diet, higher trophic levels did not show a steeper decline with decreasing habitat area contrary to our expectations. Body size did not decrease significantly along the habitat area gradient.

**Table 2** Results of the simplified linear and negative binomial model (Type I sums of squares) analyzing drivers of true bug species richness and abundance

Response	Predictor	df	Test statistic	Value	p
Species richness	Ecotone type	2,111	F	22.68	<0.001***
	Habitat area <sup>1</sup>	1,111	F	68.30	<0.001***
	Hedge index	1,111	F	9.69	0.002**
	SNH <sup>2</sup>	1,111	F	0.52	0.472 n.s
	Flowering plant SR	1,111	F	4.03	0.047*
Abundance	Ecotone type	2,109	chisq	41.26	<0.001***
	Habitat area <sup>1</sup>	1,109	chisq	43.00	<0.001***
	Hedge index	1,109	chisq	5.15	0.023*
	SNH <sup>2</sup>	1,109	chisq	0.60	0.438 n.s
	Ecotone type*SNH	2,109	chisq	6.00	0.049*
	Flowering plant SR	1,109	chisq	12.60	<0.001***

<sup>1</sup>: log10-transformed

<sup>2</sup>: arcsine square root transformed

### Ecotone type

The combination of habitat with characteristic grassland herbaceous species and areas covered with shrubs offers a diverse range of microhabitats with varying degrees of light, temperature, and moisture, enabling the co-occurrence of species of different environmental requirements. Species highly reliant on open shrub ecotones are, e.g., the rare mirid *Excetriscus planicornis* recorded only once in Germany in the last 75 years (Mandery 2012), the red-listed stenocephalid *Dicranocephalus agilis*, and the coreid *Gonocerus acuteangulatus*. These species, like many other true bug species in Central Europe (Achtziger et al. 2007), are thermophilic, probably the main reason for their absence in ecotones with high shrub foliage cover in this study.

### Habitat area

Our results support the close relationship between habitat area and species richness (MacArthur and Wilson 2001) and corroborate the assumption that habitat loss is one of the most important drivers of species declines (Caro et al. 2022). This adds to the existing empirical studies on the species-area relationship across different species groups (Lomolino 2000). We used an equal sampling approach despite the large differences in sites between the shrub ecotones. This might lead to an underestimation of true bug species richness in large habitats compared to small ones. However, this approach enabled us directly to compare the species numbers along the habitat area gradient, while this effect would have

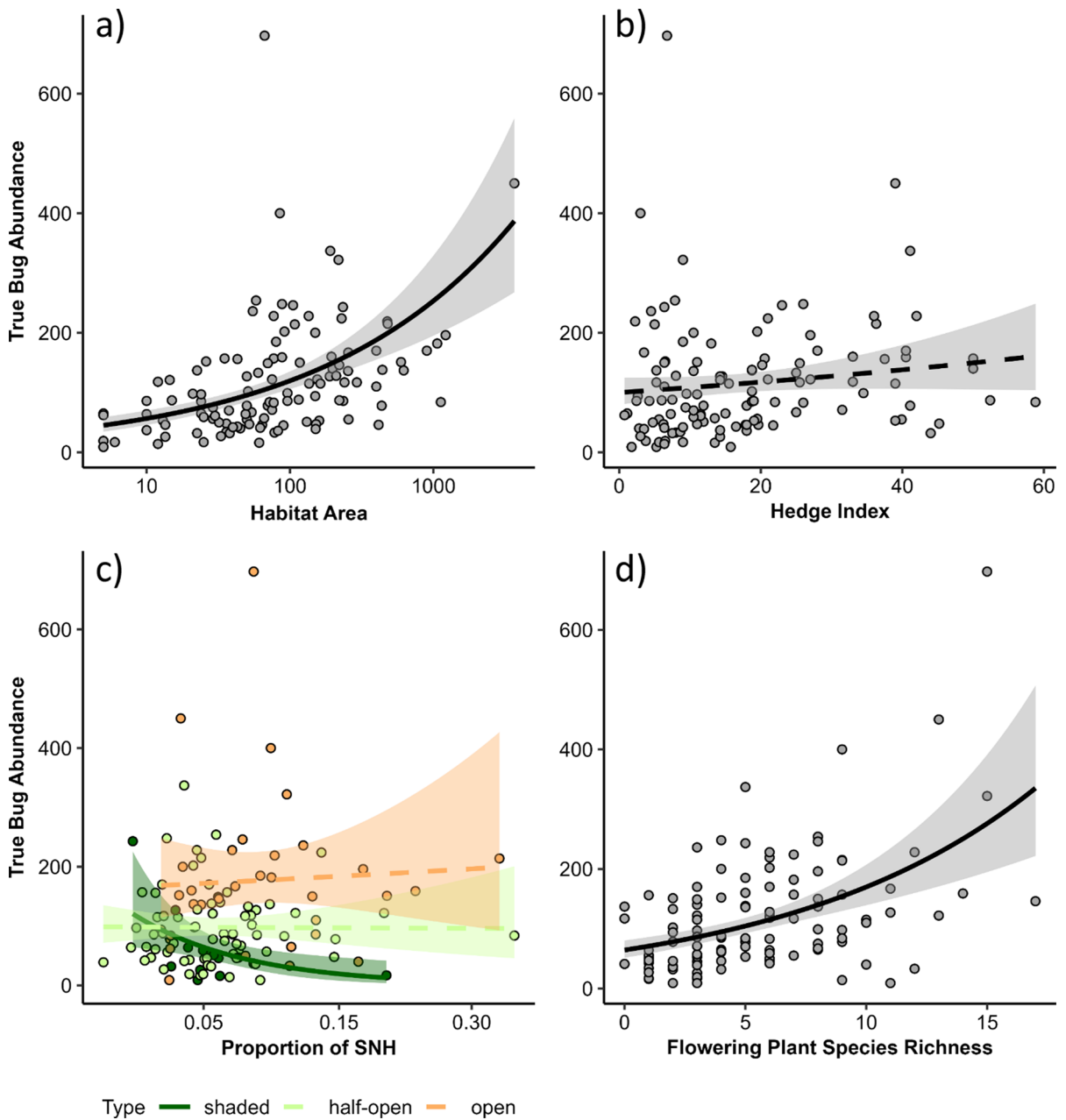
been obscured by differences in sampling intensity with area-adjusted sampling. True bug abundance was higher in large ecotones compared to small ones despite the equal sampling intensity in small and large sites, implying that true bug density was higher in the larger ecotones.

### Habitat quality

Habitat quality had a positive effect on true bug species richness but to a lesser degree than habitat area. Other studies describe habitat quality with individual variables such as plant species richness (Schubert et al. 2022), resource availability (Münsch et al. 2019) and vegetation structure (Čelik et al. 2015; Poniatowski et al. 2018), or use it to describe distribution patterns of a few selected species (Thomas et al. 2001; Krauss et al. 2005; Münsch et al. 2019), which might be of limited value for promoting overall diversity. Here, we used an index of habitat quality comprising species richness, age structure and edge density of woody plants to describe diversity patterns of the diverse group of true bugs. The index could also be applied to other groups reliant on woody structures, such as spiders (Rosas-Ramos et al. 2018) and wasps (Holzschuh et al. 2010). Besides the hedge index, the species richness of herbaceous flowering plants was also a good predictor of true bug species richness in our and other studies (Rösch et al. 2015).

### Landscape context

According to our expectations, a higher proportion of SNH did result in a higher species richness, although

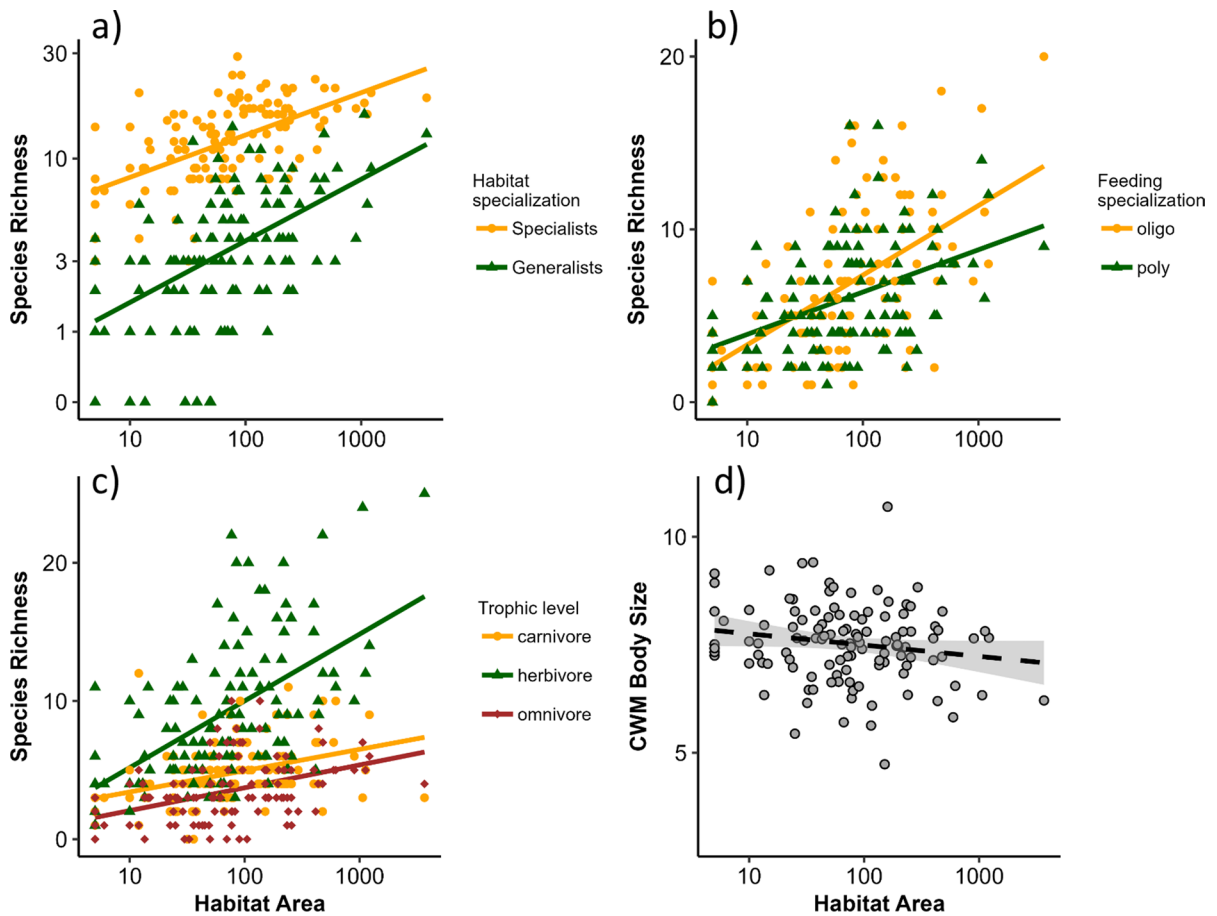


**Fig. 4** Effects of habitat area **a**, habitat quality (hedge index) **b**, landscape context (proportion of semi-natural habitat) **c**, and flowering herbaceous plant species richness **d** on true bug

abundance in the single factor models. Dashed lines indicate non-significant effects. Grey areas correspond to the 95% confidence interval around the mean abundance

this effect was weaker than for the parameters acting at the habitat scale. The effect was significant only when analyzed individually in a single factor model and vanished in the full model when corrected for other, weakly correlated variables. The *landscape*

*species pool hypothesis* (Tscharrntke et al. 2012) predicts that in complex landscapes the landscape species pool is richer, leading to higher species numbers at the habitat scale. SNH provides overwintering sites, food resources, refuges and source populations



**Fig. 5** Linear mixed effect models showing the effect of habitat area (log<sub>10</sub>-transformed) on the species richness of different functional guilds: **a** habitat specialists vs. generalists, **b**

oligophagous vs. polyphagous species, **c** carnivores vs. omnivores vs. herbivores, **d** good vs. poor dispersers. Species richness of (a) was log<sub>10</sub> + 1-transformed before the analysis

for disturbed habitats, thus promoting species persistence at the landscape level (Billeter et al. 2008). The relation is underpinned by empirical studies for true bugs (Kőrösi et al. 2012) and other groups (Steffan-Dewenter 2002; Mestre et al. 2018; Daelemans et al. 2023). The effect of the landscape context on species abundance is less obvious, but in general inherent habitat properties, such as area or resource availability are considered more important drivers (Curtis et al. 2015).

#### Life-history traits

In line with our predictions, habitat specialists decreased more steeply with decreasing habitat area than habitat generalists when comparing log-log

regression slopes. Feeding specialists were more affected by decreasing habitat area than feeding generalists, presumably due to the loss of habitat heterogeneity (Ewers and Didham 2006). The responses of carnivores and weak dispersers were inconsistent with our predictions. Herbivore species richness increased more strongly with increasing habitat area than carnivores. Higher trophic levels are more sensitive to habitat loss than herbivores due to a decline of population size with trophic rank and through dependence on species of a lower trophic level (Holt et al. 1999; Roslin et al. 2014). However, the pattern can be blurred or even reversed when the higher trophic levels are generalist and opportunistic at the same time (Holt et al. 1999), for example the damselfly *Nabis pseudoferus* (Garay et al. 2018), a common

species in our study. Contrary to our expectations, CWM body size did not increase significantly with decreasing habitat area. Larger species are considered to be superior colonizers as they can cover longer distances during flight (Stevens et al. 2014), increasing the chance to find also small habitat patches. While body size can be a useful but rough indicator of dispersal ability, the employment of morphometric traits like relative wing length would be a more powerful predictor of the dispersal ability of true bug species (Simons et al. 2016).

## Conclusions

Shrub ecotones support a high share of the terrestrial true bug species of the study region, in particular when these ecotones are open, large, of high quality, and situated in landscapes rich in semi-natural habitats (SNH). While ongoing succession jeopardizes the persistence of thermophilic species, a decrease in ecotone size disproportionately affects habitat and feeding specialists compared to generalists. Therefore, it is crucial to recognize shrub ecotones as valuable habitats alongside grasslands and forests in the cultural landscape. Management schemes that aim to remove all shrubs should be avoided. Instead, a mosaic of open areas and shrubs should be maintained to conserve the unique and species-rich assemblages of these habitats.

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**Author contributions** FSK, JK, KM and CS designed the study, FSK and MB identified the true bugs, JZ performed the landscape analyses, FSK collected the data, FSK led the statistical analysis of the data with substantial input from JK and SK, FSK led the writing of the manuscript, with substantial input from all co-authors. All co-authors gave their final approval for the publication of the manuscript.

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## Declarations

**Competing interests** The authors declare no competing interests.

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