Received: 15 October 2024 | Accepted: 17 March 2025

DOI: 10.1111/1365-2664.70061

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

RESEARCH ARTICLE

Life at the (h)edge—Multidiversity in shrub ecotones is driven by habitat quality and shrub foliage cover

Fabian S. Klimm[1] | Fabian A. Boetzl[2] | Sebastian König[3,4] | Markus Bräu[5] | Lara Burtchen[1] | Klaus Mandery[6] | Jean-Léonard Stör[1] | Jochen Krauss[1]

[1]Department of Animal Ecology and Tropical Ecology, Biocenter, University of Würzburg, Würzburg, Germany; [2]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; [3]Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Freising, Germany; [4]Berchtesgaden National Park, Berchtesgaden, Germany; [5]Amperstraße 13, Munich, Germany and [6]Institut für Biodiversitätsinformation (IfBI) Ebern, Ebern, Germany

Correspondence
Fabian S. Klimm
Email: fabian.klimm@uni-wuerzburg.de

Funding information
Bundesamt für Naturschutz

Handling Editor: Lan Qie

Abstract

1. Shrub ecotones, the species-rich transitional zones between grasslands and forests, serve as important refuges for biodiversity but are often confined to small and degraded areas due to prevailing management practices that prioritise either grasslands or forests. This loss of habitat area and quality threatens and impoverishes biodiversity reliant on shrub ecotones. Despite their importance for biodiversity, shrub ecotones were rarely considered in ecological studies, and the drivers affecting their biodiversity across taxa remain unknown.
2. We assessed the effects of multiple shrub ecotone habitat and landscape characteristics for five taxa and their combined multidiversity in 45 sites in Germany. These taxa vary in habitat requirements and dispersal capacities, inhabit different strata and represent multiple trophic levels: herbaceous plants, orthopterans, true bugs, carabids and spiders. The shrub ecotones differed in (i) type (open vs. half-open), (ii) ecotone area, (iii) habitat quality and (iv) surrounding semi-natural habitat cover as potential drivers of diversity (species richness, Hill–Shannon diversity and Hill–Simpson diversity) and multidiversity.
3. Shrub ecotone type and habitat quality were the most important drivers of multidiversity, which peaked in open shrub ecotones of high habitat quality. Open ecotones of high quality contained the highest species richness of herbaceous plants, orthopterans and true bugs, while ecotone area and semi-natural habitat cover were less important. Spiders had the highest Hill–Shannon and Hill–Simpson diversity in open ecotones, while carabids were most speciose in half-open ecotones of lower quality.
4. *Synthesis and applications*. Our multi-taxa assessment is the first comprehensive study of diversity across taxa and multidiversity in shrub ecotones. By combining multiple diversity metrics, our findings provide a more nuanced understanding

of biodiversity patterns, which can better inform conservation strategies. To maximise biodiversity benefits across taxa, we recommend managing shrub ecotones at the landscape scale, maintaining a mosaic of open and half-open shrub ecotones. Designated shrub transition zones with reduced management should be established around suitable habitats to promote the formation of new shrub ecotones.

KEYWORDS

carabid beetles (Carabidae), grasshoppers and crickets (Orthoptera), habitat quality, hedgerows, semi-natural habitat, spiders (Araneae), true bugs (Heteroptera)

1 | INTRODUCTION

Before the advent of *Homo sapiens*, the browsing and trampling by megaherbivores created dynamic tessellated landscapes comprising open habitats, light woodlands and closed forests in Central Europe (Pearce et al., 2023). These landscapes were thus rich in shrub-dominated ecotones forming transition zones between open habitats and forests. The extant Central European flora and fauna were shaped under these conditions and contain a high share of species adapted to open habitats and ecotones (Feurdean et al., 2018). The arrival of *Homo sapiens* is correlated with the extinction of megaherbivores that had maintained these open landscapes (Pearce et al., 2023). But only the abandonment of traditional wood pastures and the dawn of modern forestry in the 19th century led to the development of denser and structurally homogeneous forests (Rösch et al., 2019).

In current Central European landscapes, shrub ecotones are typically restricted to narrow hedgerows or forest fringes, exposing the species that depend on these structures to edge effects (Vanneste et al., 2020). Shrub ecotones host both thermophilic and shade-tolerant species through a mosaic of different microclimatic conditions and a heterogeneous vegetation structure (Fartmann et al., 2012). They play a critical role as refugia for arthropods in agricultural landscapes, for foraging, breeding and overwintering, moderate temperature extremes, and offer shelter from management activities, adverse weather and predators (Graham et al., 2018; Lecq et al., 2017; Staley et al., 2016). Without management actions, a few competitive tall shrub species, such as blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus monogyna*), dominate shrub ecotones, ultimately leading to the development of deciduous forests (Poschlod & WallisDeVries, 2002). Despite their significance for biodiversity conservation, shrub ecotones have received limited research attention. While some studies have focussed on hedgerows (Ferrante et al., 2024; Graham et al., 2018; Holzschuh et al., 2010), shrub ecotones along forest margins or fallows were not considered.

The disappearance of extensive shrub ecotones in Central European landscapes is particularly alarming as the loss of suitable habitats is suspected as a main driver of insect declines (Bergmeier et al., 2010; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019; van Klink et al., 2024). Habitat area has been extensively demonstrated as a driver of species richness in empirical studies, known as the 'species–area relationship' (Dembicz et al., 2021; Gallé et al., 2022; Krauss et al., 2009). Larger habitats can sustain larger populations, reduce extinction rates and facilitate the colonisation of new species, especially when habitats are close to one another (MacArthur & Wilson, 2001). In addition, larger habitats tend to be more heterogeneous than smaller ones, providing niches for a wider array of species (Stein et al., 2014).

Yet not only the quantity but also the quality of shrub ecotones is decreasing. Intensive management (Klaus et al., 2018), excessive nutrient input (Staley et al., 2013) and the abandonment of traditional land-use practices (Strijker, 2005) jointly contribute to ongoing habitat deterioration. As the shrub ecotones are currently typically restricted to narrow edges, they lack their characteristic structure, comprised of shrub species with various growth forms and shrubs of different age classes (Zwölfer, 1982). This degradation of shrub ecotones especially threatens the persistence of specialised species (Simons et al., 2016), leading to more homogenous assemblages dominated by few generalist species (Thorn et al., 2022). Habitat quality of shrub ecotones has so far received little attention due to its subjectivity and the difficulties in quantification.

The loss of semi-natural habitats (SNH) such as shrub ecotones depauperates the landscape species pool even if isolated suitable habitats remain (Rösch et al., 2013; Tscharntke et al., 2012). Due to the impoverished landscape species pools, local extinctions in isolated SNH can hardly be compensated by colonisations from the surrounding landscape (Tscharntke et al., 2012). Diversity in shrub ecotones should thus depend on landscape SNH cover.

When assessing the effects of the habitat conditions on biodiversity, it is beneficial to include multiple taxa, as diversity patterns often vary considerably across taxa (Boetzl et al., 2021; Manning et al., 2015; Venturo et al., 2024), and management actions that aim to support the diversity of one taxonomic group might be ineffective or even detrimental to others. Here, we used a combination of complementary sampling methods to capture species from five different taxa: herbaceous plants, orthopterans, true bugs (Heteroptera), carabids and spiders (Araneae). These groups are abundant in shrub ecotones, have distinct habitat requirements, differ in their dispersal capacities, live in different habitat strata and belong to different trophic levels. In particular, true bugs and herbaceous plants contain a high share of shrub ecotone specialists (Deckert & Wachmann, 2020; Sturm et al., 2018).

This study examines the influence of four key habitat and landscape parameters: shrub foliage cover (ecotone type), ecotone area, habitat quality and the cover of SNH in the surrounding landscape on complementary aspects of diversity: species richness, Hill–Shannon, and Hill–Simpson diversity of five taxa, as well as the multidiversity. We predicted that

(i) all taxa are more diverse in ecotones with lower shrub foliage cover (open ecotones) compared to ecotones with higher shrub foliage cover (half-open ecotones);
(ii) there is a positive relationship between diversity and ecotone area, that is a species–area relationship;
(iii) an increase in habitat quality is associated with an increase in diversity; and
(iv) an increase in landscape-level SNH is associated with an increase in species richness.

2 | MATERIALS AND METHODS

2.1 | Study region and sites

Our study was performed in an area of approximately 45,000 km^2 in Bavaria (Southern Germany) predominantly situated on the Keuper formation. We selected 45 shrub ecotones with a minimum distance of 2 km to each other as study sites (Supporting Information S1). As 'shrub', we regarded a perennial woody plant that is less than 10 m tall and without a clear trunk (Allaby, 2019). To ensure comparable habitat conditions, we selected shrub ecotones that contained the French rose (*Rosa gallica*) (Klimm et al., 2024). The French rose requires alternating wet and dry conditions on predominantly loamy soils, a warm microclimate, low-to-moderate nutrient availability and extensive management (Conert et al., 2000), as occurring in the phytosociological orders *Origanetalia vulgaris* and *Rhamno-Prunetea* (Oberdorfer et al., 2021). These conditions are common in the study region. We included shrub ecotones along forest margins ($n = 19$) as well as hedgerows and woody islands embedded in the agricultural landscape ($n = 26$). Multi-annual mean temperatures in the study region varied from 7.9°C to 10.4°C and precipitation ranged from 593 mm to 932 mm between 1991 and 2020 (Data: 'Deutscher Wetterdienst').

2.2 | Data collection

Permits for arthropod collection were issued by the nature conservation authorities of the Bavarian administrative districts (Swabia; permit number 55.3-8646-2/660, Upper Bavaria; ROB-55.1-8646.NAT_02-2-11-7, Lower Bavaria; 55.1-8646.202-1-5-5, Upper Palatinate; 55.1-8622-1-5-8, Middle Franconia; RMF-SG55.1-8646-6-42-2, Lower Franconia; RUF-55.1-2-8646.11-1-16-6, Upper Franconia; 55.1-8622). The sampling did not require ethics approval. Arthropods were sampled in 2021 and 2022 from May to September. Different methods were employed to capture both arboricol and epigeal species in the shrub ecotone. Arboricol species (orthopterans, true bugs, spiders) were collected with a funnel-shaped beating tray with a collection jar during five intervals between 13 May 2021 and 6 August 2021. The French rose and accompanying shrubs were beaten for 3 min each with a beating rate of 20 beats per minute. Within each study site, sampling was carried out at three randomly chosen locations that were sampled for 1 min each. Beating tray sampling for arboricol taxa was carried out during dry weather, absence of strong winds (Bft. <4) and temperatures of at least 15°C (Klimm et al., 2024).

In addition, we recorded orthopteran individuals found within 10 standard box quadrats (Bioform, 141 × 141 × 80 cm) per site in August and September 2022. The quadrats were placed to cover the heterogeneity of the specific ecotone. Surveys were performed between 10 AM and 6 PM on sunny and dry days with temperatures above 25°C and wind below Bft. 4.

For epigeal species (true bugs, carabids and spiders), we deployed five pitfall traps per site. As pitfalls, we used glass jars (7.5 cm diameter, 400 mL volume) and filled them with a 1:3 mixture of Propylene glycol and water. The distance between traps was 5 m unless the size of the ecotones required narrower inter-trap spacing. This was the case for six small ecotones, where the distance between traps had to be reduced, with the smallest ecotone having trap distances of 1.5 m. The spatial arrangement of the traps depended on the shape of the individual shrub ecotone. Traps were active within three periods in May, June and July 2022 for 2 weeks each. The number of herbaceous plant species was counted within three 1 m^2 squares in June 2021 (Figure 1), obtaining presence–absence data.

Flowering herbaceous plant species were identified in the field. Adult orthopterans were identified based on morphological characters and their species-specific stridulation. We identified true bugs using entomological literature sources (Niedringhaus et al., 2020; Wagner, 1952) and the Corisa software (www.corisa.de). Spiders were determined with online resources provided at www.araneae.nmbe.ch. Carabids were identified in the laboratory, their nomenclature following Müller-Motzfeld (2006). Abundances of the arthropod groups were pooled per species and site.

2.3 | Habitat parameters

Shrub ecotones were classified as open or as half-open depending on the foliage cover of at least 1-m-tall shrubs in the ecotones, with open ecotones having <30% shrub foliage cover, half-open ecotones having between 30% and 70% shrub foliage cover (Costermans, 1981). Of the selected ecotones, 25 were open, and 20 were half-open. The area of the shrub ecotones varied between 10 and 3672 m^2.

Journal of Applied Ecology

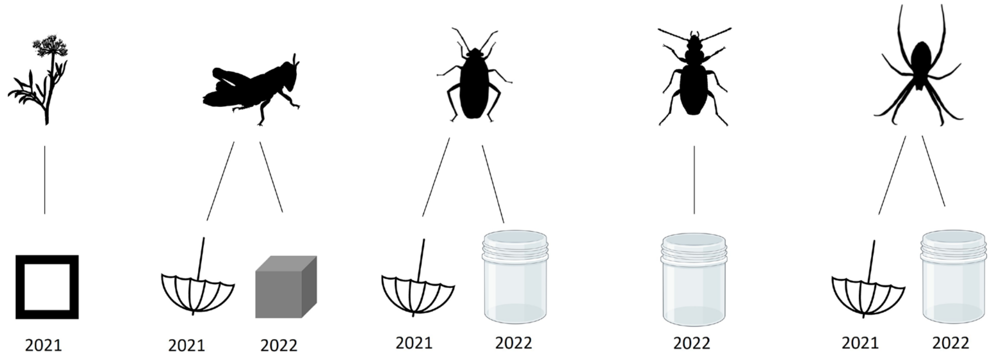

FIGURE 1 Illustration of the sampling scheme. Herbaceous plants were recorded within three squares of 1 m^2 in 2021. Orthopterans were sampled with a beating tray and box quadrats in 2021 and 2022. True bugs and spiders were sampled with a beating tray and pitfalls in 2021 and 2022. Carabids were sampled with pitfalls in 2021.

To assess the quality of the shrub ecotones, we utilised the 'hedge index' (Zwölfer, 1982), a product of three factors: (i) the richness of woody plant species within a shrub ecotone and their value for biodiversity, (ii) the age distribution of these species and (iii) the edge density in the surrounding area, defined as the length of hedgerows and forest edges per hectare within a radius of 1000 m (Supporting Information S2). Species with greater value for animal biodiversity, such as roses (*Rosa* spp.), hawthorn (*Crataegus* spp.) or blackthorn (*Prunus spinosa*), are assigned higher scores in this assessment. We assessed these parameters across the whole ecotone area. For a more detailed description, see Klimm et al. (2024).

2.4 | SNH cover

SNH cover, defined as the proportion of SNH in the surroundings at 500, 1000, 1500 and 2000 m scale 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). We defined SNH as (1) extensive grassland, (2) forest edge: 10 m inner buffer zone of deciduous and coniferous forest and (3) woody elements (hedgerows, woody strips) in the open landscape.

2.5 | Statistical analysis

Data were analysed with R 4.2.2 (R Core Team, 2022). We compared species diversity with Hill numbers (Hill, 1973): (i) the species richness ($q=0$) of each taxon, as well as (ii) the Hill–Shannon diversity ($q=1$) and (iii) the Hill–Simpson diversity ($q=2$) of all taxa except herbaceous plants. We additionally calculated sampling coverage for arthropod taxa to assess the completeness of diversity estimates at each site (Supporting Information S3). Calculations were performed with the 'iNEXT' package version 4.2.3 (Chao et al., 2014). With increasing Hill number, the impact of rare species on the diversity estimates diminishes (Roswell et al., 2021). In addition, we calculated the multidiversity at each site. This index combines the standardised diversity of the taxa studied (Allan et al., 2014), allowing for comparisons between taxa that vary in species richness. Multidiversity is regarded as a more reliable reflection of ecosystem processes (Boetzl et al., 2021; Manning et al., 2015) than diversity measures considering only single taxa.

To elucidate the drivers of multidiversity in shrub ecotones, we fitted a beta regression with the 'betareg' package version 3.1.4 (Cribari-Neto & Zeileis, 2010) with ecotone type (factor, 2 levels), ecotone area (continuous), habitat quality (continuous) and the SNH cover (continuous) as independent variables (Supporting Information S4). We also tested for interactions between ecotone type and all continuous variables but subsequently simplified models as no interaction was significant. For the Hill numbers of the different taxa, we fitted generalised linear mixed models (command 'glmmTMB', 'glmmTMB' package version 1.1.8 (Brooks et al., 2017)) with the same independent variables and a gamma distribution with log link (McCullagh & Nelder, 2019). As some pitfall traps were lost due to farming, we used an offset (the log10 of the number of traps) to account for the differences in sampling intensity in models for true bugs, carabids and spiders. Compliance with model assumptions was confirmed graphically using the 'DHARMa' package version 0.4.6 (Hartig, 2022). Models were tested with type II χ^2 tests using the command 'Anova' from the 'car' package version 3.1.2 (Fox & Weisberg, 2018). In addition, we performed analyses for multidiversity and single taxa only including species of conservation concern (Supporting Information S5).

We tested for differences in assemblage compositions using a PERMANOVA with 999 permutations (command 'adonis2') including ecotone type, ecotone area, hedge index and SNH cover as explanatory variables and visualised assemblage differences between ecotone types with a non-metric multidimensional scaling (NMDS; command 'metaMDS', two dimensions). Both were based on Bray–Curtis distances of relative abundances for the arthropod groups and the Jaccard-distances for herbaceous plants and computed using the 'vegan' package version 2.6-4 (Oksanen et al., 2022; Supporting Information S6).

To evaluate the spatial scale on which SNH affects the assemblages of the studied taxa most, we fitted separate models for the radii of 500, 1000, 1500 and 2000 m around the study sites, and compared their respective AICc values (Vogel et al., 2023). Models including the 1 km scale had the lowest AICc values, indicating the best model fit. The 1 km scale was similarly found to be a suitable scale of effect in previous landscape scale studies in the region (Barber et al., 2022; Klimm et al., 2024; König & Krauss, 2019).

We checked for correlations between the independent variables using Pearson's correlations and detected no strong correlations between them (|r| < 0.3; Supporting Information S7). In addition, we calculated Pearson correlations between all response variables and the three factors comprising the hedge index (Supporting Information S8). We tested for spatial autocorrelation of the model residuals with the 'testSpatialAutocorrelation' from the 'DHARMa' package and found no spatial autocorrelation.

3 | RESULTS

In total, we collected 33,787 individuals from 551 arthropod species, including 14,384 true bugs (185 species, ~52% unidentified nymphs), 3349 orthopterans (33 species, ~8% nymphs but all identifiable to species level), 2917 carabids (88 species, only imagines recorded) and 13,137 spiders (245 species, ~22% unidentified spiderlings). In addition, 85 herbaceous plant species were recorded in the shrub ecotones. A total of 142 species were classified in the regional red lists for the respective taxa (Achtziger et al., 2003; Blick & Scheidler, 2003; Lorenz & Fritze, 2020; Klotz et al., 2024; Poniatowski et al., 2024). The most abundant species for each group were *Chorthippus biguttulus* (orthopterans, 605 individuals), *Megaloceroea recticornis* (true bugs, 1046 individuals), *Brachinus crepitans* (carabids, 1026 individuals) and *Pardosa palustris* (spiders, 2433 individuals). *Galium mollugo agg.* was the most frequent herbaceous plant, occurring in 15 shrub ecotones (Supporting Information S9).

3.1 | Multidiversity in shrub ecotones

Open ecotones had a higher multidiversity than half-open ecotones (Figure 2a). Multidiversity was independent of ecotone area (Figure 2b) but positively related to habitat quality (Figure 2c) and

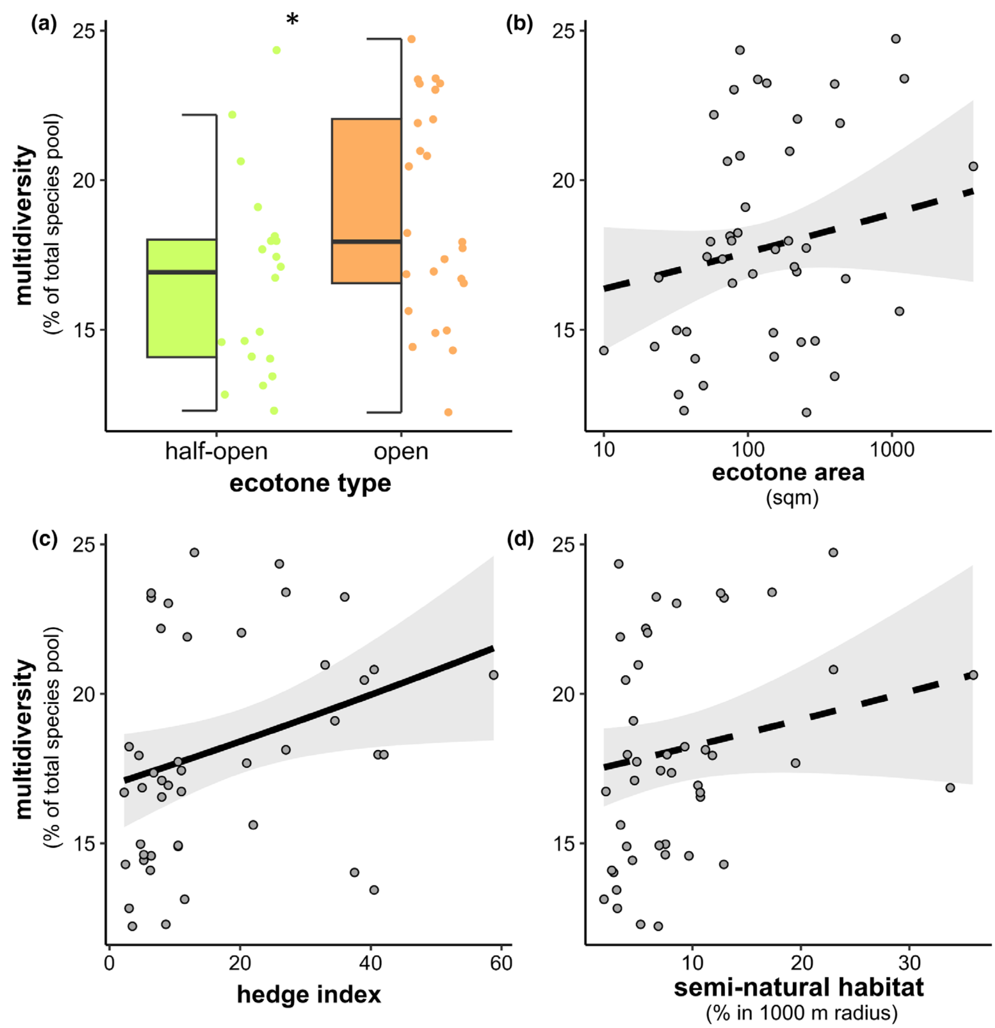

FIGURE 2 Effects of ecotone type (a), ecotone area (b), habitat quality (hedge index) (c), and landscape semi-natural habitat cover (d) on multidiversity. Dashed lines indicate non-significant effects ($p > 0.05$). Grey areas correspond to the 95% confidence interval around the regression line. (*) indicates $p < 0.05$. For statistics, see Supporting Information S4.

unrelated to the proportion of SNH at the 1000-m scale (Figure 2d). We obtained similar results when we focussed on species of conservation concern only (Supporting Information S10).

3.2 | Assemblage-level responses of single taxa

The studied taxa showed distinct patterns to the ecotone type. Herbaceous plants, orthopterans and true bugs were more species-rich in open ecotones, while carabids had more species in half-open ecotones. Spider species richness was not related to the ecotone types. We found 36 species to be unique in open and four species to be unique in half-open shrub ecotones (Supporting Information S11). The Hill–Shannon and Hill–Simpson diversities did not differ between ecotone types for orthopterans, true bugs and carabids, but spiders were more diverse in open shrub ecotones (Figure 3; Supporting Information S12). Ecotone type significantly shaped orthopteran, true bug and spider assemblages, while herbaceous plants and carabids were unaffected (Supporting Information S13). The other predictors did not affect any of the taxa.

Ecotone area was positively related to true bug species richness, with richness increasing by 9.15% per 100 m^2 increase in ecotone area. We found no significant relations between ecotone area and the species richness of the remaining taxa or the Hill–Shannon or Hill–Simpson diversities of all taxa (Figure 3; Supporting Information S14a–c), except for a marginally positive relationship between Hill–Shannon diversity and ecotone area in true bugs.

Habitat quality was positively related to herbaceous plant, orthopteran and true bug richness. Herbaceous plant richness increased by 10.0% per 10 units increase in the hedge index, while orthopteran and true bug richness increased by 9.6% and 7.2%, respectively. In contrast, habitat quality was negatively related to carabid richness, with a sharp decline of 14.5% per 10 units increase in the hedge index, while it was unrelated to spider species richness.

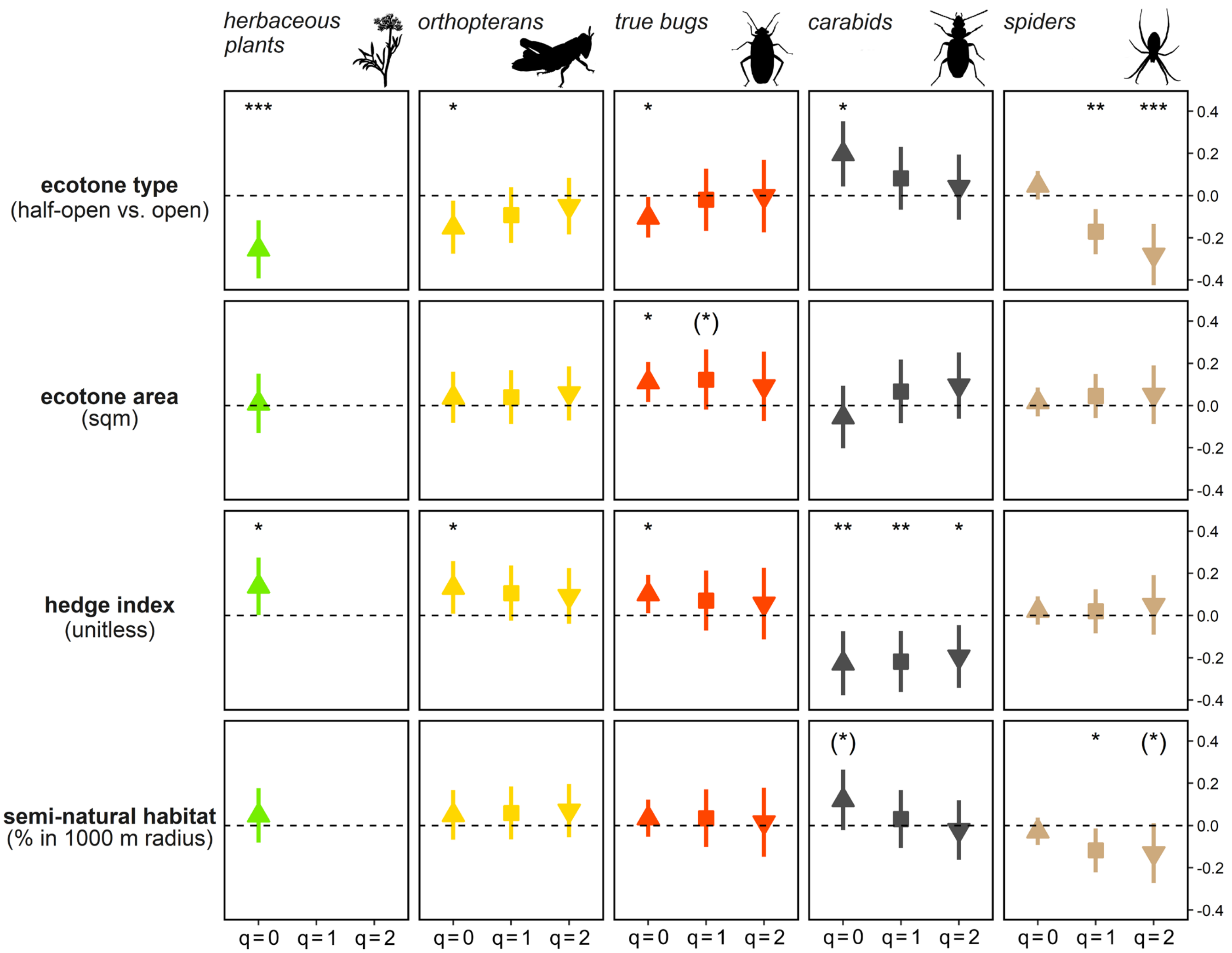

FIGURE 3 Model coefficients for ecotone type, ecotone area, hedge index and semi-natural habitat cover for the Hill numbers $q=0$ (species richness), $q=1$ (Hill–Shannon diversity) and $q=2$ (Hill–Simpson diversity) for herbaceous plants, orthopterans, true bugs, carabids and spiders with 95% confidence intervals. Fixed effects were scaled to magnitudes of the standard deviation (z-scaling), thus coefficients can be interpreted as changes in the response on the log scale per 1 standard deviation of the fixed effect. (*) indicates $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$. For statistics, see Supporting Information S4.

Habitat quality was also negatively related to Hill–Shannon and Hill–Simpson diversity of carabids, while there were no significant relations in the other taxa (Figure 3; Supporting Information S14d–f).

We found no significant relation to SNH in any of the taxa. In spiders, the SNH in the surrounding landscape was negatively related to Hill–Shannon diversity and marginally negatively related to Hill–Simpson diversity (Figure 3; Supporting Information S14g–i).

4 | DISCUSSION

In the light of the widespread loss of the species-rich shrub ecotones in Central European landscapes, it is crucial to protect and manage the remaining ecotones effectively. Here, we showed that multidiversity in open shrub ecotones was higher than in half-open shrub ecotones and was positively linked to habitat quality, while ecotone area and SNH landscape cover were less important. Consequently, even small shrub ecotones embedded in homogeneous agricultural landscapes can be of conservation value if these ecotones have a shrub foliage cover below 30% and are of high quality, that is contain a species-rich assemblage of shrubs of different ages, ranging from less than 6 years to more than 20 years. This finding was supported by the responses of taxa on lower trophic levels (herbaceous plants, orthopterans, true bugs). In contrast, the predominantly predatory groups, especially carabids, deviated from the overall diversity pattern. Carabids were more species-rich in half-open ecotones of low quality. Spider species richness was unrelated to ecotone type and habitat quality, but the assemblages were more diverse in open ecotones in terms of Hill–Shannon and Hill–Simpson indices. Both carabids and some groups of spiders often differ in their responses from other taxa, benefitting from conditions most other taxa suffer from (Birkhofer et al., 2014). Our results suggest that there is no one-size-fits-all management scheme to benefit all taxa. Instead, conservation efforts must be tailored to maximise their value for the targeted taxon.

4.1 | Ecotone type

Increased shrub foliage cover alters microclimatic conditions, with lower temperatures and higher moisture levels in half-open compared to open shrub ecotones. Accordingly, the ecotone type affected the studied taxa, with higher multidiversity in open compared to half-open ecotones. For individual taxa, we found contrasting patterns. In line with our expectations, herbaceous plants, orthopterans and true bugs had on average more species in open than in half-open shrub ecotones. While many herbaceous plant species are able to persist in open shrub ecotones, their species richness declines when shrubs become increasingly dominant by overgrowing and shading the herbaceous plants (Wieczorkowski & Lehmann, 2022). A habitat with moderate shrub encroachment also enables both herbicol and arboricol orthopteran and true bug species to co-exist. True bugs benefit from a moderate degree of shrub encroachment, as many species are reliant on fruiting shrubs and trees for protein uptake (Niedringhaus et al., 2020). In contrast to the general pattern, we found more carabid species in the half-open habitats. In these habitats with higher foliage cover, carabids may find protection from avian predators. Alternatively, the observed difference in species richness may be abundance-mediated, as the average number of captured individuals was lower in open than in half-open ecotones. The differences in species richness between the ecotone types were largely driven by species represented by single or few individuals for orthopterans, true bugs and carabids, whereas spider assemblages had a more even abundance distribution of common species in open ecotones. Therefore, spiders were more diverse in open than in half-open ecotones in terms of Hill–Shannon and Hill–Simpson indices.

4.2 | Ecotone area

The positive relationship between habitat area and species richness is well-evidenced (Dembicz et al., 2021; Gallé et al., 2022). In contrast to our expectations, ecotone area did not affect the multidiversity of the studied taxa and was a significant driver for true bug richness only. True bugs include a high share of species adapted to shrub ecotones (Klimm et al., 2024; Niedringhaus et al., 2020). Consequently, their response to an increase in area is expected to be more pronounced than for taxa that do not include a significant share of ecotone specialists, such as orthopterans, carabids or spiders. Though herbaceous plants also include a substantial share of specialised ecotone species, we found no effects of ecotone area, likely as plants are able to persist in small and isolated habitats as long as habitat quality remains constant (Eriksson, 1996; Zulka et al., 2014). Due to the constant sampling effort across the ecotone area gradient, it is also possible that small ecotones were sampled more completely compared to large ecotones.

4.3 | Habitat quality

In line with our expectations, habitat quality was positively related to multidiversity, being a better predictor for diversity than ecotone area. Habitat quality in shrub ecotones is driven by an increased habitat heterogeneity regarding food plants, structural complexity and the developmental stages of the shrubs in the ecotone. The higher heterogeneity translates into higher diversity, with more species finding habitats that meet their requirements (Stein et al., 2014). At the single taxon level, the richness of herbaceous plants, orthopterans and true bugs was positively related to habitat quality, while carabids were negatively related, and spiders were not affected. Herbaceous plants, orthopterans and true bugs may benefit from small fringes along woody edges, as they shelter against frequent management activities, buffering of temperature and drought extremes and increased landscape connectivity. Carabids were negatively correlated with an increase in age classes of the shrubs but also to an increase in the species score. Both quality parameters contribute to an increased structural complexity in the shrub ecotone, making it less permeable for epigeal species (Thomas et al., 2006). Accordingly, carabids preferred half-open shrub ecotones with less dense vegetation. Pitfall traps in habitats with less complex vegetation structure can capture higher densities of epigeal species, which might have affected our observed species richness (Woodcock, 2005). The positive effects of habitat quality on true bugs and orthopterans were not detected in Hill–Shannon and Hill–Simpson diversities, indicating that additional rare species in high-quality ecotones largely drove the observed patterns, whereas the negative relation between habitat quality and carabids remained.

4.4 | SNH cover

Semi-natural habitats (SNH) can be vital for the survival of certain species in agricultural landscapes (Lecq et al., 2017; Rösch et al., 2013). We did, however, not detect any significant positive response to an increase in landscape SNH cover in any of the diversity metrics analysed. The Hill–Shannon diversity of spiders even decreased with increasing SNH cover in the landscape. While we detected positive trends in other taxa (true bugs, orthopterans and carabids), the variance was considerably high. This finding suggests that the drivers acting on the local scale were more important for diversity than SNH on the landscape scale. For herbaceous plants, for example local habitat quality is more important than the connection to other habitat patches in the surroundings (Zulka et al., 2014). Studies that found positive effects of SNH were often focussed on specialists that may find nesting sites or food plants exclusively in SNH (Brückmann et al., 2010). In contrast, many generalists also persist in the surrounding landscape matrix (König & Krauss, 2019), which might explain why we did not observe significant positive effects of SNH cover.

5 | CONCLUSIONS

By combining complementary diversity metrics, we gained nuanced insights into the drivers of diversity in the species-rich but understudied Central European shrub ecotones. Prioritising the preservation of open ecotones with shrub foliage cover below 30%, and supporting a mosaic of shrubs at varying growth stages is overall most beneficial for the diversity of herbaceous plants, true bugs, orthopterans and spiders. To further support these taxa, shrub species that offer abundant resources and complement each other through different growth forms, such as hawthorn or wild roses, should be promoted. Given the deviating response of carabids, however, a one-size-fits-all approach to management is ineffective. To balance habitat requirements of different taxa and maximise biodiversity benefits, conservation efforts should operate at the landscape level, maintaining a mix of open and half-open ecotones. This could be achieved by implementing gradual transitions from grasslands to forests, with a belt of perennial forbs and small shrubs blending into a layer with taller shrubs. Given the scarcity of shrub ecotones, it is imperative to maintain the remaining ones and foster the development of new shrub ecotones by reducing mowing or grazing along grassland edges and allowing shrubs to grow along forest margins, for example by assigning dedicated shrub transition zones in suitable habitats. Such measures require collaboration between landowners, landscape conservation associations, and nature conservation authorities. By promoting these intermediate succession stages between grassland and dense forests, historic species-rich habitats that were once widespread can be restored in managed landscapes with a minimal sacrifice of area.

AUTHOR CONTRIBUTIONS

Jochen Krauss, Klaus Mandery and Fabian S. Klimm conceived the ideas and elaborated the methods; Jochen Krauss and Klaus Mandery were involved in project administration; Fabian S. Klimm, Fabian A. Boetzl, Sebastian König, Markus Bräu, Lara Burtchen and Jean-Léonard Stör collected the data; Fabian S. Klimm curated the data; Fabian S. Klimm, Fabian A. Boetzl and Sebastian König analysed the data; Fabian S. Klimm, Fabian A. Boetzl, Sebastian König and Jochen Krauss interpreted the results; Fabian S. Klimm wrote the original draft; all authors contributed to the reviewing and editing of the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Franziska Engelhardt, Konrad Güntner, Alina Koeters, Michael Polzer, Louis Pouille, Selina Schramm and Matthias Weid for assistance in the field and in the laboratory, the Nature Conservation authorities for collection permits and the Botanische Staatssammlung München for the provision of floristic records from survey studies. Funding for the project 'Rettet Rosi' was provided by the Federal Office for Nature Conservation with resources from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection within the Federal Biological Diversity Program. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests and there was no financial support for this work that could have influenced the outcome of this paper. Fabian A. Boetzl is an Associate Editor of the *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

The data used for the analysis are available at https://doi.org/10.6084/m9.figshare.28638929 (Klimm et al., 2025).

ORCID

Fabian S. Klimm https://orcid.org/0000-0002-8074-4143
Fabian A. Boetzl https://orcid.org/0000-0001-5121-3370
Sebastian König https://orcid.org/0000-0003-3253-8457
Jean-Léonard Stör https://orcid.org/0009-0009-4241-8425

Jochen Krauss https://orcid.org/0000-0003-2304-9117

REFERENCES

Achtziger, R., Bräu, M., & Schuster, G. (2003). *Rote Liste gefährdeter Landwanzen (Heteroptera: Geocorisae) Bayerns*. Bayerisches Landesamt für Umwelt (LfU).

Allaby, M. (2019). *A dictionary of plant sciences*. Oxford University Press.

Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tscharntke, T., Blüthgen, N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., … Fischer, M. (2014). Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 308–313. https://doi.org/10.1073/pnas.1312213111

Barber, N. A., Sauer, N., Krauss, J., & Boetzl, F. A. (2022). Grazing conserves threatened carabid beetles in semi-natural calcareous grasslands better than mowing, especially at low intensities. *Biodiversity and Conservation*, *31*, 2857–2873. https://doi.org/10.1007/s10531-022-02463-0

Bergmeier, E., Petermann, J., & Schröder, E. (2010). Geobotanical survey of wood-pasture habitats in Europe: Diversity, threats and conservation. *Biodiversity and Conservation*, *19*, 2995–3014. https://doi.org/10.1007/s10531-010-9872-3

Birkhofer, K., Ekroos, J., Corlett, E. B., & Smith, H. G. (2014). Winners and losers of organic cereal farming in animal communities across central and northern Europe. *Biological Conservation*, *175*, 25–33.

Blick, T., & Scheidler, M. (2003). *Rote Liste gefährdeter Spinnen (Arachnida: Araneae) Bayerns*. Bayerisches Landesamt für Umwelt.

Boetzl, F. A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., Krimmer, E., Prante, M., Martin, E. A., Holzschuh, A., & Steffan-Dewenter, I. (2021). A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2016038118. https://doi.org/10.1073/pnas.2016038118

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400. https://doi.org/10.32614/RJ-2017-066

Brückmann, S. V., Krauss, J., & Steffan-Dewenter, I. (2010). Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, *47*, 799–809. https://doi.org/10.1111/j.1365-2664.2010.01828.x

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*, 45–67. https://doi.org/10.1890/13-0133.1

Conert, H. J., Jäger, E. J., Kadereit, J. W., Schultze-Motel, W., Wagenitz, G., & Weber, H. E. (2000). *Illustrierte Flora von Mitteleuropa*. Blackwell.

Costermans, L. F. (1981). *Native trees and shrubs of south-eastern Australia*. Nokomis Publications.

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, *34*, 1–24. https://doi.org/10.18637/jss.v034.i02

Deckert, J., & Wachmann, E. (2020). *Die Wanzen Deutschlands. Entdecken–Beobachten–Bestimmen*. Quelle & Meyer.

Dembicz, I., Moysiyenko, I. I., Kozub, Ł., Dengler, J., Zakharova, M., & Sudnik-Wójcikowska, B. (2021). Steppe islands in a sea of fields: Where Island biogeography meets the reality of a severely transformed landscape. *Journal of Vegetation Science*, *32*, e12930. https://doi.org/10.1111/jvs.12930

Eriksson, O. (1996). Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos*, *77*, 248–258. https://doi.org/10.2307/3546063

Fartmann, T., Krämer, B., Stelzner, F., & Poniatowski, D. (2012). Orthoptera as ecological indicators for succession in steppe grassland. *Ecological Indicators*, *20*, 337–344. https://doi.org/10.1016/j.ecolind.2012.03.002

Ferrante, M., Schulze, M., & Westphal, C. (2024). Hedgerows can increase predation rates in wheat fields in homogeneous agricultural landscapes. *Journal of Environmental Management*, *349*, 119498. https://doi.org/10.1016/j.jenvman.2023.119498

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biological Conservation*, *228*, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. SAGE Publications.

Gallé, R., Korányi, D., Tölgyesi, C., Lakatos, T., Marcolin, F., Török, E., Révész, K., Szabó, Á. R., Torma, A., Gallé-Szpisjak, N., Marja, R., Szitár, K., Deák, B., & Batáry, P. (2022). Landscape-scale connectivity and fragment size determine species composition of grassland fragments. *Basic and Applied Ecology*, *65*, 39–49. https://doi.org/10.1016/j.baae.2022.10.001

Graham, L., Gaulton, R., Gerard, F., & Staley, J. T. (2018). The influence of hedgerow structural condition on wildlife habitat provision in farmed landscapes. *Biological Conservation*, *220*, 122–131. https://doi.org/10.1016/j.biocon.2018.02.017

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*, 427–432. https://doi.org/10.2307/1934352

Holzschuh, A., Steffan-Dewenter, I., & Tscharntke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, *79*, 491–500. https://doi.org/10.1111/j.1365-2656.2009.01642.x

Klaus, V. H., Schäfer, D., Prati, D., Busch, V., Hamer, U., Hoever, C. J., Kleinebecker, T., Mertens, D., Fischer, M., & Hölzel, N. (2018). Effects of mowing, grazing and fertilization on soil seed banks in temperate grasslands in Central Europe. *Agriculture, Ecosystems & Environment*, *256*, 211–217. https://doi.org/10.1016/j.agee.2017.11.008

Klimm, F. S., Boetzl, F. A., König, S., Bräu, M., Burtchen, L., Mandery, K., Stör, J.-L., & Krauss, J. (2025). Data from: Life at the (h)edge—Multidiversity in shrub ecotones is driven by habitat quality and shrub foliage cover. *Figshare Data Repository*. https://doi.org/10.6084/m9.figshare.28638929

Klimm, F. S., Bräu, M., König, S., Mandery, K., Sommer, C., Zhang, J., & Krauss, J. (2024). Importance of habitat area, quality and landscape context for heteropteran diversity in shrub ecotones. *Landscape Ecology*, *39*, 3. https://doi.org/10.1007/s10980-024-01798-z

Klotz, J., Wagner, A., Fleischmann, A., Ruff, M., Niederbichler, C., Scheuerer, M., Wagner, I., Woschée, R., Gilck, F., & Zehm, A. (2024). *Rote Liste der Farn- und Blütenpflanzen (Gefäßpflanzen—Tracheophyta) Bayerns*. Bayerisches Landesamt für Umwelt (LfU).

König, S., & Krauss, J. (2019). Get larger or grow longer wings? Impacts of habitat area and habitat amount on orthopteran assemblages and populations in semi-natural grasslands. *Landscape Ecology*, *34*, 175–186. https://doi.org/10.1007/s10980-018-0762-5

Krauss, J., Alfert, T., & Steffan-Dewenter, I. (2009). Habitat area but not habitat age determines wild bee richness in limestone quarries. *Journal of Applied Ecology*, *46*, 194–202. https://doi.org/10.1111/j.1365-2664.2008.01582.x

Lecq, S., Loisel, A., Brischoux, F., Mullin, S. J., & Bonnet, X. (2017). Importance of ground refuges for the biodiversity in agricultural hedgerows. *Ecological Indicators*, *72*, 615–626. https://doi.org/10.1016/j.ecolind.2016.08.032

Lorenz, W. M. T., & Fritze, M.-A. (2020). *Rote Liste und Gesamtartenliste Bayern—Laufkäfer und Sandlaufkäfer—Coleoptera: Carabidae*. Bayerisches Landesamt für Umwelt.

MacArthur, R. H., & Wilson, E. O. (2001). *The theory of Island biogeography*. Princeton University Press.

Manning, P., Gossner, M. M., Bossdorf, O., Allan, E., Zhang, Y.-Y., Prati, D., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Hölzel, N., Jung, K., Klaus, V. H., Klein, A. M., Kleinebecker, T., Krauss, J., Lange, M., Müller, J., Pašalić, E., … Fischer, M. (2015). Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa. *Ecology*, *96*, 1492–1501. https://doi.org/10.1890/14-1307.1

McCullagh, P., & Nelder, J. A. (2019). *Generalized linear models* (2nd ed.). Routledge. https://doi.org/10.1201/9780203753736

Müller-Motzfeld, G. (2006). Band 2, Adephaga 1: Carabidae (Laufkaefer). In H. Freude, K. W. Harde, G. A. Lohse, & B. Klausnitzer (Eds.), *Die Käfer Mitteleuropas* (p. 521). Spektrum.

Niedringhaus, R., Stöckmann, M., & Wachmann, E. (2020). *Die Wanzen Deutschlands: Bestimmungsschlüssel für alle Familien und Gattungen*. Wissenschaftlich Akademischer Buchvertrieb—Fründ.

Oberdorfer, E., Schwabe, A., & Müller, T. (2021). *Pflanzensoziologische Exkursionsflora: Für Deutschland und angrenzende Gebiete*. Ulmer.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community ecology package*. R package version 2.6–4. https://CRAN.R-project.org/package=vegan

Pearce, E. A., Mazier, F., Normand, S., Fyfe, R., Andrieu, V., Bakels, C., Balwierz, Z., Bińka, K., Boreham, S., Borisova, O. K., Brostrom, A., de Beaulieu, J.-L., Gao, C., González-Sampériz, P., Granoszewski, W., Hrynowiecka, A., Kołaczek, P., Kuneš, P., Magri, D., … Svenning, J.-C. (2023). Substantial light woodland and open vegetation characterized the temperate forest biome before Homo sapiens. *Science Advances*, *9*, eadi9135. https://doi.org/10.1126/sciadv.adi9135

Poniatowski, D., Detzel, P., Drews, A., Hochkirch, A., Hundertmark, I., Husemann, M., Klatt, R., Klugkist, H., Köhler, G., Kronshage, A., Maas, S., Moritz, R., Pfeifer, M. A., Stübing, S., Voith, J., Winkler, C., Wranik, W., Helbing, F., & Fartmann, T. (2024). Rote Liste und Gesamtartenliste der Heuschrecken und Fangschrecken (Orthoptera et Mantodea) Deutschlands. *Naturschutz und Biologische Vielfalt*, *170*(7), 88 S.

Poschlod, P., & WallisDeVries, M. F. (2002). The historical and socioeconomic perspective of calcareous grasslands—Lessons from the distant and recent past. *Biological Conservation*, *104*, 361–376. https://doi.org/10.1016/S0006-3207(01)00201-4

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rösch, V., Hoffmann, M., Diehl, U., & Entling, M. H. (2019). The value of newly created wood pastures for bird and grasshopper conservation. *Biological Conservation*, *237*, 493–503. https://doi.org/10.1016/j.biocon.2019.07.036

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2013). Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, *50*, 387–394. https://doi.org/10.1111/1365-2664.12056

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*, 321–338. https://doi.org/10.1111/oik.07202

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*, 671–674. https://doi.org/10.1038/s41586-019-1684-3

Simons, N. K., Weisser, W. W., & Gossner, M. M. (2016). Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. *Ecology*, *97*, 754–764. https://doi.org/10.1890/15-0616.1

Staley, J. T., Botham, M. S., Chapman, R. E., Amy, S. R., Heard, M. S., Hulmes, L., Savage, J., & Pywell, R. F. (2016). Little and late: How reduced hedgerow cutting can benefit Lepidoptera. *Agriculture, Ecosystems & Environment*, *224*, 22–28. https://doi.org/10.1016/j.agee.2016.03.018

Staley, J. T., Bullock, J. M., Baldock, K. C. R., Redhead, J. W., Hooftman, D. A. P., Button, N., & Pywell, R. F. (2013). Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management. *Biological Conservation*, *167*, 97–105. https://doi.org/10.1016/j.biocon.2013.07.033

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*, 866–880. https://doi.org/10.1111/ele.12277

Strijker, D. (2005). Marginal lands in Europe—Causes of decline. *Basic and Applied Ecology*, *6*, 99–106. https://doi.org/10.1016/j.baae.2005.01.001

Sturm, P., Zehm, A., Baumbach, H., von Vrackel, W., Verbücheln, G., Stock, M., & Zimmermann, F. (2018). *Grünlandtypen. Erkennen—Nutzen—Schützen*. Quelle & Meyer.

Thomas, C. F. G., Brown, N. J., & Kendall, D. A. (2006). Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. *Agriculture, Ecosystems & Environment*, *113*, 51–61. https://doi.org/10.1016/j.agee.2005.08.033

Thorn, S., König, S., Fischer-Leipold, O., Gombert, J., Griese, J., & Thein, J. (2022). Temperature preferences drive additive biotic homogenization of Orthoptera assemblages. *Biology Letters*, *18*, 20220055. https://doi.org/10.1098/rsbl.2022.0055

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biological Reviews*, *87*, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

van Klink, R., Bowler, D. E., Gongalsky, K. B., Shen, M., Swengel, S. R., & Chase, J. M. (2024). Disproportionate declines of formerly abundant species underlie insect loss. *Nature*, *628*, 359–364. https://doi.org/10.1038/s41586-023-06861-4

Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C., Brunet, J., Cousins, S. A. O., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Heinken, T., Helsen, K., Kapás, R. E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., … De Frenne, P. (2020). Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology*, *57*, 1244–1257. https://doi.org/10.1111/1365-2664.13620

Venturo, A., González, E., Štrobl, M., Tajovský, K., Skuhrovec, J., Benda, D., Seidl, M., Dvořák, T., Kadlec, T., & Knapp, M. (2024). A multi-taxa approach reveals contrasting responses of arthropod communities and related ecosystem services to field margin proximity and crop type. *Agriculture, Ecosystems & Environment*, *368*, 109010. https://doi.org/10.1016/j.agee.2024.109010

Vogel, C., Poveda, K., Iverson, A., Boetzl, F. A., Mkandawire, T., Chunga, T. L., Küstner, G., Keller, A., Bezner Kerr, R., & Steffan-Dewenter, I. (2023). The effects of crop type, landscape composition and agroecological practices on biodiversity and ecosystem services in tropical smallholder farms. *Journal of Applied Ecology*, *60*, 859–874. https://doi.org/10.1111/1365-2664.14380

Wagner, E. (1952). Blindwanzen oder Miriden. In M. Dahl & H. Bischoff (Eds.), *Die Tierwelt Deutschlands und der angrenzenden Meeresteile*. Gustav Fischer Verlag.

Wieczorkowski, J. D., & Lehmann, C. E. R. (2022). Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. *Global Change Biology*, *28*, 5532–5546. https://doi.org/10.1111/gcb.16300

Woodcock, B. A. (2005). Pitfall trapping in ecological studies. In S. Leather (Ed.), *Insect sampling in forest ecosystems* (pp. 37–57). Blackwell Science.

Zulka, K. P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T., & Zechmeister, H. (2014). Species richness in dry grassland patches of eastern Austria: A multi-taxon study on the role of local, landscape and habitat quality variables. *Agriculture, Ecosystems & Environment*, *182*, 25–36. https://doi.org/10.1016/j.agee.2013.11.016

Zwölfer, H. (1982). *Die Bewertung von Hecken aus tierökologischer Sicht*. Laufener Seminarbeiträge.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1: Location of the study region in Germany with the location of the 45 study sites and an example of the landscape analysis for an individual study site.

Supporting Information S2: The components of the hedge index after Zwölfer (1982) to assess habitat quality.

Supporting Information S3: Abundance, observed and estimated species richness, and sampling coverage of the 45 sites for each arthropod taxon.

Supporting Information S4: Model results for multidiversity, species richness, Hill–Shannon diversity and Hill–Simpson diversity for each arthropod taxon.

Supporting Information S5: Model results for multidiversity and species richness of species of conservation concern.

Supporting Information S6: Differences in assemblage composition for each arthropod taxon according to a PERMANOVA.

Supporting Information S7: Correlation plot showing the correlations between the explanatory variables used in the models.

Supporting Information S8: Pearson correlations between species richness ($q=0$), Hill–Shannon diversity ($q=1$) and Hill–Simpson diversity ($q=2$) and the individual components of the hedge index and each taxon.

Supporting Information S9: Species list of the sampled taxa including abundances, number of occurrences and red list status.

Supporting Information S10: Effects of ecotone type, ecotone area, habitat quality, and landscape SNH cover on multidiversity of species of conservation concern.

Supporting Information S11: Unique species for each ecotone type.

Supporting Information S12: Differences in species richness, Hill–Shannon diversity and Hill–Simpson diversity of herbaceous plants, orthopterans, true bugs, carabids and spiders between half-open and open shrub ecotones.

Supporting Information S13: Differences in species composition between open and half-open shrub ecotones for herbaceous plants, orthopterans, true bugs, carabids, and spiders.

Supporting Information S14: Differences in species richness, Hill–Shannon diversity and Hill–Simpson diversity of spiders, true bugs, orthopterans, herbaceous plants and carabids for ecotone area, habitat quality and SNH cover.

How to cite this article: Klimm, F. S., Boetzl, F. A., König, S., Bräu, M., Burtchen, L., Mandery, K., Stör, J.-L., & Krauss, J. (2025). Life at the (h)edge—Multidiversity in shrub ecotones is driven by habitat quality and shrub foliage cover. *Journal of Applied Ecology*, *62*, 1520–1530. https://doi.org/10.1111/1365-2664.70061