Grassland management in agricultural vs. forested landscapes drives butterfly and bird diversity

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Abstract

Calcareous grasslands and orchard meadows are among the most species-rich semi-natural habitats in Europe, but they are severely threatened by intensified land use and abandonment. Here, we focus on the effects of management vs. abandonment of these grasslands in agricultural vs. forest-dominated landscapes of Germany. We recorded butterflies and birds and classified them in farmland and woodland species according to their habitat preferences. Species richness and abundance of farmland butterflies were higher on calcareous grasslands than orchard meadows and benefited from forested landscapes in case of orchard meadows. Species richness of woodland butterflies was higher on abandoned than managed grasslands, independent of habitat type and landscape context. Richness and abundance of farmland birds benefited from managed orchard meadows, and were more abundant in agricultural landscapes. On calcareous grasslands, however, the abandonment led to higher richness and abundance of farmland birds. Woodland birds exhibited higher species richness in abandoned than managed grasslands, especially in orchard meadows. Woodland birds and butterflies appeared to be less affected by habitat type, management or landscape context than farmland species. Calcareous grasslands were much more important for butterfly diversity than orchard meadows, but suitability of orchards for butterflies was improved when embedded in forested landscapes. In contrast to butterflies, bird diversity benefited more from orchard meadows than calcareous grasslands, which had higher diversity when management was abandoned. In conclusion, landscape context can shape communities in these two grassland habitat types, so conservation management should consider reserves in both agricultural and forested landscapes and thereby, diversify regional biota.

Keywords: biodiversity; extensive management; farmland species; habitat abandonment; species richness; woodland species

1. Introduction

Land use change by agricultural intensification has led to a widespread biodiversity loss in human-dominated landscapes causing reduced habitat area and increased habitat degradation of natural and semi-natural habitats (Fischer and Lindenmayer, 2007). At small spatial scales, vegetation heterogeneity originates from different management practices and the habitat type, whereas at larger scales, landscape heterogeneity contributes to the local community structure (Stein et al., 2014).

Due to their extensive management and high structural diversity, semi-natural habitats such as orchard meadows and calcareous grasslands are among the most species rich habitats in Western Europe and important for butterfly and bird conservation (van Swaay, 2002; Herzog et al., 2005). Orchard meadows are characterised by sparse, old, tall fruit trees, species-rich herbaceous vegetation and greatly differ from intensively managed fruit plantations as trees have a heterogeneous spatial pattern (Mycko et al., 2013). However, extensively managed semi-natural grassland often faces two contrasting trajectories. On the one hand, traditional low-intensity management such as extensive grazing, hay making and fruit harvesting is often abandoned, resulting in massive regeneration of shrubs and ultimately the loss of these habitats (Poschlod and WallisDeVries, 2002; Plieninger et al., 2015). On the other hand, management intensification and land conversion also threatens them (Stoate et al., 2009; Plieninger et al., 2015). Species respond differently to changing environmental variables. For example van Swaay et al. (2006) identified agricultural intensification, such as conversion of grassland into arable land, the fertilisation of grassland as well as abandonment as main threats to butterflies. However, in early succession stages after abandonment insect species richness might increase, but overall habitat quality is changing over time, leading to the decline of specialist species (Balmer and Erhardt, 2000; Kormann et al., 2015).

In order to understand the effects of management practices on biodiversity, it is important to consider the landscape-scale (Tscharntke et al., 2012). According to the theory of island biogeography, species diversity of fragmented semi-natural habitats such as calcareous grasslands and orchard meadows is influenced by movement between habitat fragments through the surrounding landscape matrix (McArthur and Wilson, 1967). Landscape structure and land use surrounding the habitat fragments may therefore improve or hinder dispersal through the landscape matrix or even provide additional resources to some species, depending on the quality of the matrix and the species' environmental needs (Eycott et al., 2012; Öckinger et al., 2012). Thus, landscape context measures might reflect the quality of the landscape matrix for population movement between the remaining habitat fragments and availability of additional resources.

Both butterflies and birds are representatives of the most studied and ecologically best known invertebrates and vertebrates (Schlegel and Rupf, 2010). In particular, butterflies which have been categorized as grassland specialists have been found to decline in distribution across Europe (van Swaay et al., 2006). Birds, on the other hand, often rely on the presence of scattered trees such as fruit trees in orchard meadows, which act as local and landscape keystone structures in intensively managed landscapes that are otherwise poor in landscape elements (Manning et al., 2006). Overall, population declines of birds over the last decades have been widely reported, especially of farmland birds, but of woodland birds as well (Gregory et al., 2005, 2007).

This is the first study investigating the potentially complex effects of changing environments and their interactions at three spatial scales: management practices (mowing/grazing or abandonment), habitat type (calcareous grassland or orchard meadow) and landscape context (agricultural or forested landscape) on two flagship taxa of nature conservation. We focused on butterflies and birds, which were classified as farmland or woodland species according to their known principal habitat occurrence. We hypothesise that (i) farmland butterflies and birds prefer calcareous grasslands, whereas woodland species prefer orchard meadows, (ii) regular local management of calcareous grasslands and orchard meadows positively affects farmland species, whereas abandonment benefits woodland species, and (iii) there are more farmland species in agricultural landscapes, whereas there are more woodland species in forest-dominated landscapes (Fig. 1).

2. Material and methods

2.1. Study area

The study area was situated in southern Lower Saxony (Germany) in the districts of Göttingen and Northeim (about 1000 km²; see Appendix A1 in Supplementary online material). The main land use types are arable fields, intensively used meadows and semi-natural deciduous forests. The surveys were conducted in calcareous grasslands (*Mesobrometum erecti* Koch 1926) covering only 0.26 % and in orchard meadows (*Arrhenatheretum elatioris* Braun 1915) covering 0.39 % of the study area. Both semi-natural grassland habitats are patchily distributed across the landscape, and managed either by mowing or grazing with sheep, goats, cattle or horses. Many smaller fragments and party also the larger ones are in a process of abandonment with shrub encroachment and/or dye off of old fruit trees.

2.2. Study design

We surveyed butterfly and bird species in 20 orchard meadows and 20 calcareous grasslands in a full factorial design (mean ± SEM distance between sites: 17.9 ± 0.3 km; range of distance between sites: 0.5 – 52.0 km; fruit tree density on abandoned orchard meadows: 38.6 ± 4.4 (23.9 – 67.9) and on managed orchard meadows: 36.4 ± 5.5 (16.4 – 70.5)). The habitat fragments were selected according to differences in landscape context (forested vs. agriculture dominated landscapes) and management status (managed vs. abandoned), resulting in five replicates per treatment (Fig. 1). Within a 500 m buffer area around each habitat fragment, forest-dominated landscapes had 44 ± 2% (mean ± SEM) forest cover ranging from 28 to 63%, whereas agricultural landscapes had 14 ± 2% forest cover ranging from 0 to 28% (forest cover was measured in ArcGIS 10.4). As many semi-natural habitats are neither fully managed nor completely abandoned, we selected managed habitat fragments to be managed each year by grazing or mowing, whereas abandoned fragments to be irregularly or not managed characterised by high degree of succession to woody shrubs or dead wood. In summary, majority of the managed grasslands were grazed extensively (< 1 LUI/ha) between May and September with different livestock including cattle, sheep, goat, horse or donkey (calcareous grasslands: eight fragments grazed, one mown and one both grazed and mown; orchard meadows: eight fragments grazed and two mown). In order to minimize the effect of habitat size on species richness and abundance, fragments with a similar size were chosen, and species were surveyed on a 0.8 ha patch in each study site. The area of the selected habitat fragments was 2.64 ± 0.27 ha (mean ± SEM) for calcareous grassland (ranging from 0.90 ha to 5.38 ha) and 1.45 ± 0.15 ha for orchard meadows (ranging from 0.85 ha to 3.34 ha).

2.3. Sampling methods

Butterflies (Lepidoptera: Hesperidae and Papilionidea) and burnet moths (Lepidoptera: Zygaenidae) were sampled from 24th of May until 19th of August 2015 with three survey rounds (roughly one survey/month) by a 20 minute zig-zag transect-walk (split into 5 four-minute sections) once on each habitat fragment (following Krauss et al., 2003; Brückmann et al., 2010). Butterflies were surveyed visually or using a butterfly net between 10.45 am and 5.30 pm, and were identified and released immediately. Surveys were conducted on a 5 m wide corridor under suitable weather conditions for butterfly activity (dry conditions, wind speed less than Beaufort scale 5, and temperature 13 °C or higher if there was at least 60 % sunshine, or more than 17 °C if overcast (Pollard, 1977)). To characterise the availability of nectar resources, the percent cover of flowering plants inside the transect corridor was estimated at the end of each transect walk. We classified butterfly species to farmland or woodland species based on literature (van Swaay et al., 2006; Plattner et al., 2010).

We recorded birds between 8th and 22nd of May and between 8th and 28th of June 2015 in two survey rounds by a 12 minute point-count on 0.8 ha patches half an hour after sunrise until 4 hours after sunrise under calm and dry weather conditions (Bibby et al., 1992). There were 22 habitat fragments with two 0.8 ha survey patches as they were larger than 1.6 ha. In the 18 remaining, smaller habitat fragments there was one 0.8 ha survey patch in each habitat fragment. Due to the high degree of heterogeneous structures and the different shape of the habitat fragments, each point-count was split into three 4-minute sections placed at points suitable to represent the study design (managed or abandoned). This guaranteed to perceive all acoustic signals of the birds and to detect them visually. To characterise the availability of nesting and foraging sites, the percent bush cover in each 0.8 ha study patch was estimated in the end of each survey. We classified bird species to farmland or woodland species based on literature (Gregory et al., 2005, 2007; Südbeck et al., 2005; Batáry et al., 2012). Species habitat affinity and specialism might change with different European regions suggesting that our classification approach may lead to different results there (see e.g. Koleček et al., 2010).

2.4. Statistical analysis

Abundance of butterflies was summed over transects and sampling occasions. For each bird species we pooled the data using the maximum abundance of the two survey rounds per patch. Species richness of birds was calculated as the number of species that were present in the particular sampling patch at least in one survey round.

For both taxa we applied linear regression models for analysing the species richness and abundance of farmland and woodland species. Habitat type (calcareous grassland vs. orchard meadow), management status (managed vs. abandoned), landscape context (forested vs. agriculture dominated landscapes) and their two-way interactions were used as explanatory design variables. In case of bird models, the survey patch within habitat fragment was used as random factor. Models were fitted with Poisson distribution or in case of overdispersion with negative binomial distribution using the MASS (for butterflies, Venables and Ripley, 2002) and lme4 packages (for birds, Bates et al., 2015) of R software (R Development Core Team, 2017). We calculated all models nested in the global model by the command ‘dredge’ in the package MuMIn (Barton, 2016), and compared them based on Akaike Information Criterion corrected for small sample size (AICc). We performed model averaging (Burnham and Anderson, 2002), if the top model and subsequent models differed less than two units in AICc. Model-averaged parameter estimates were calculated over the subset of models including the parameter (conditional average) to avoid shrinkage towards zero (Grueber et al., 2011). We present the 95% confidence intervals (CI) of parameter estimates and the relative importance of each parameter. Relative importance is 100%, when the parameter is present in all top models.

We also performed further linear regression models to test for effects of explanatory design variables on percent flowering plants and percent bush cover (both normal distribution), potentially important for butterflies and birds, respectively. The percent flowering plants was significantly higher in calcareous grasslands than in orchard meadows (Table A1; Fig. A1a). The percent bush cover was mainly determined by the management with about three times higher cover of bushes in abandoned than in managed sites (Fig. A1b). Nevertheless bush cover was also significantly higher in calcareous grasslands than in orchard meadows and in agricultural than in forested landscapes.

Furthermore, we applied redundancy analyses (RDA) to assess the variability in species composition of butterfly and bird communities explained by the environmental variables habitat type, management status and landscape context. For the bird analysis we included habitat patch as conditional variable as the study design was nested. The results were presented in ordination biplots to visualise the variability in species composition. Prior to analyses, community data matrices were Hellinger-transformed (Legendre and Gallagher, 2001). To assess for statistical significance, a permutation test based on 999 permutations was calculated using the package vegan (Oksanen et al., 2017).

3. Results

On the 20 calcareous grassland and 20 orchard meadow fragments we recorded 5182 individual butterflies belonging to 55 butterfly species (seven of them burnet moths, hereafter also called butterflies) and 1075 individuals of 55 bird species. Classification based on environmental preferences resulted in 35 farmland butterfly species with 3973 individuals and 20 woodland butterfly species with 1209 individuals (Table A2) as well as 22 farmland bird species with 272 individuals and 33 woodland bird species with 803 individuals (Table A3). The most abundant farmland butterflies were *Maniola jurtina*, *Polyommatus coridon* and *Melanargia galathea*, whereas the most abundant woodland butterflies were *Aphantopus hyperantus*, *Pieris napi* and *Coenonympha arcania* (Table A2). For birds, the most abundant farmland species were *Emberiza citrinella*, *Sylvia communis* and *Columba palumbus*, whereas the most abundant woodland birds were *Parus major*, *Turdus merula* and *Cyanistes caeruleus* (Table A3).

3.1. Effects on butterflies

We found habitat type to be the most important factor determining farmland butterfly species richness and abundance with higher values in calcareous grasslands than in orchard meadows (Table 1; Fig. 2a,c). Farmland species richness and abundance depended on an interaction between landscape context and habitat type; high species richness and abundance were found in both agricultural and forest-dominated landscapes of calcareous grasslands, but lower values in orchard meadows with a decrease from forested to agricultural landscapes. Additionally, farmland butterfly abundance was influenced by management in interaction with habitat type. Management increased butterfly abundances in calcareous grasslands, but decreased them in orchard meadows. In contrast, abandonment increased the abundance of woodland butterflies, but not their species richness (Fig. 2c,d).

The RDA of butterfly community composition revealed significant associations with habitat type and landscape context (Table 3; Fig. 3a). In the ordination biplot, the first axis separated calcareous grasslands from orchard meadows with e.g. chalkhill blue (*Polyommatus coridon*) as characteristic species in calcareous grasslands and ringlet (*Aphantopus hyperantus*) as characteristic species in orchard meadows. The second axis separated agricultural from forest-dominated landscapes with small white (*Pieris rapae*) being a characteristic agricultural species and small skipper (*Thymelicus sylvestris*) being a species associated with forest.

3.2. Effects on birds

Performing generalized linear mixed effects models on birds, we found that management type was the variable that most strongly explained both farmland and woodland species richness and abundance (Table 2). This was, however, in an interaction with habitat type in case of farmland species (Fig. 4a,c). Farmland birds preferred managed over abandoned fragments in orchard meadows, and abandoned over managed fragments in calcareous grassland. Additionally, they were more abundant in agricultural than forest-dominated landscapes. In contrast, woodland birds (both richness and abundance) were more common in abandoned than in managed fragments (Fig. 4b,d). Finally, woodland bird abundance was higher in orchard meadows than in calcareous grasslands.

In the RDA of bird communities all three variables explained a significant part of the variation in community composition (Table 3). Landscape context explained the smallest part, followed by management and habitat type, explaining the largest part of the variation. The first axis separated in particular abandonment and management, but also orchard meadows and calcareous grasslands (Fig. 3b). For example, chiffchaff (*Phylloscopus collybita*) showed a preference for abandoned orchard meadows, whereas tree pipit (*Anthus trivialis*) was a characteristic species of managed calcareous grassland. The second axis separated agricultural from forest-dominated landscapes with green woodpecker (*Picus viridis*) as characteristic woodland species in grassland fragments of forest-dominated landscapes and yellowhammer (*Emberiza citrinella*) being a characteristic farmland species in grasslands of agricultural landscapes.

4. Discussion

We studied the effects of habitat type (calcareous grassland vs. orchard meadow), management (managed vs. abandoned) and landscape context (forested vs. agricultural landscape) in a full factorial design and found that the classification into farmland and woodland traits helps to identify key factors of diversity and abundance patterns for conservation management strategies. Farmland butterflies were more diverse in calcareous grasslands than farmland birds, which exhibited higher species richness in orchard meadows. Woodland butterfly and bird abundance increased with abandonment, whereas regular management affected farmland butterflies in calcareous grassland positively. Surprisingly, landscapes dominated by forest had a positive effect on farmland butterfly richness and abundance, but not on woodland butterflies. Farmland bird abundance was higher in agricultural landscapes, while woodland bird diversity and abundance benefited from abandonment.

4.1. Effects on butterflies

Supporting our first hypothesis, species richness and abundance of farmland butterflies was highest in calcareous grasslands. Management such as mowing and grazing leads to high cover of flowering plants as feeding and reproduction resources. This positive relationship has often been reported (e.g. Krämer et al., 2012), and highlights the disproportionate high value of calcareous grassland for butterfly conservation (van Swaay, 2002).

As hypothesised, management had a negative effect on woodland butterfly abundance, but not on species richness. Woodland butterflies were more common in abandoned semi-natural grasslands, which can be explained by increasing microhabitat heterogeneity and the availability of plant communities typical for different successional stages (WallisDeVries et al., 2002). On the contrary, farmland butterfly abundance increased with management, but only in calcareous grassland, where abundances were generally higher than in orchard meadows. Abandonment appeared to provide less life-sustaining resources for farmland butterflies such as flowering plants and warm micro-climate (van Swaay, 2002). Surprisingly, in orchard meadows farmland butterfly abundance increased with abandonment. This might have been caused by the fact that management was characterised by high stocking rates, fertilisation and frequent mowing, degrading the diversity of herbs and flowers (Uchida et al., 2016). Abandoned orchard meadows were characterised by additional resources such as flowering forbs or shrubs, for example blackberries, but in the long run, late successional stages may decrease butterfly species richness and abundance (Balmer and Erhardt, 2000; Kesting et al., 2015). There is a lack of target-oriented management in orchard meadows, which should be regularly restored by clearance of shrubs and trees, opening of the canopy for light and warm micro-climate as well as reducing grazing density or intensified hay-making to facilitate larval hosts and nectar-providing plants.

In contrast to our hypothesis, farmland butterfly species richness was higher in orchard meadows when embedded in forest-dominated landscapes but not agricultural landscapes. Forest-dominated landscapes are more heterogeneous providing more resources than simple landscapes dominated by agriculture (Öckinger et al., 2012). Compared to calcareous grassland, local habitat conditions in orchard meadows were worse (less food resources) and farmland butterflies appeared to use additional resources in the surroundings (Krämer et al., 2012; Villemey et al., 2015). In this study we found more flowering plants in orchard meadows of forest-dominated than agricultural landscapes, which suggests that non-arable patches may act as buffer against intensive agricultural practices such as chemical weed control (Gonthier et al., 2014; Villemey et al., 2015).

As shown in the redundancy analysis, the greatest variability in community composition was explained by habitat type with most butterfly species showing a strong preference for calcareous grasslands especially by farmland species. For example, chalkhill blue is regarded as threatened in the red list of the study region (Lower Saxony, (Lobenstein, 2004)), and was the most characteristic farmland species on calcareous grasslands. The high population density of chalkhill blue is determined by the presence of the larva's food plant *Hippocrepis comosa* (Krauss et al., 2005), which is dispersed by the hooves of livestock (Brereton et al., 2008). Hence, this result reflects the need for appropriate habitat management for specialised butterflies in the study region. Contrastingly, the community composition for orchard meadows showed that management can be important habitat for species that are associated with open woodland. For example, ringlet (*Aphantopus hyperatus*) occurred in relatively high abundances in orchard meadows. This species was often shown to be present in grasslands and mixed woodlands, but also in tree lines (van Swaay et al., 2006). Thus, orchard meadows potentially provide habitat for species that are associated with woodland edges and can be assumed to provide habitat to an even wider range of open-woodland butterfly species profiting from improved management practices. Hay-making or low-intensity grazing with reduced fertiliser use and allowance of seed maturation could restore the degraded orchard meadows in the study region.

4.2. Effects on birds

Regarding farmland bird species richness and abundance, our first and second hypotheses were only party confirmed, because we found an interaction of habitat type and management.

Abandonment caused an increase in farmland bird species richness and abundance in calcareous grasslands, but a decrease in orchard meadows. Partly abandoned calcareous grasslands were characterised by less disturbance and provided a wide range of niches, because of their heterogeneous habitat characteristics caused by higher amounts of woody vegetation and heterogeneous sward structures (Hartel et al., 2014). This supported nesting sites and foraging opportunities, e.g. for insects on the ground (Vickery et al., 2001). However, abandonment can benefit farmland birds only on a short term and further succession will exclude farmland birds (Gregory et al., 2007). Contrastingly to calcareous grasslands, farmland bird species richness and abundance were higher in managed compared to abandoned orchard meadows. Scattered trees act as keystone habitat for farmland birds and provide nesting and foraging opportunities as well as song posts (Fischer et al., 2010; Jakobsson and Lindborg, 2017). Since orchard meadows were mostly grazed by livestock, they were suitable for foraging, e.g. of insects on animal dung, or as ground-nesting sites in patches avoided by livestock. Nevertheless, some orchard meadows were frequently used and there might be a higher potential for farmland birds as the positive effect of management on biodiversity may be restricted to low levels of interference. Intensified grassland management decreases the suitability as habitat for feeding and nesting because of higher disturbance levels and a fast growing, homogeneous grassland structure as a consequence (Vickery et al., 2001). Management activities should provide feeding and nesting sites, such as breeding burrows of old trees, shelter of bushes for ground breeding birds and heterogeneous, open sward structures.

Corresponding to our hypotheses, woodland bird species richness and abundance were higher in abandoned compared to managed grassland fragments and abundance was also higher in orchard meadows than in calcareous grassland. Abandoned habitat fragments are structurally more similar to forest as they contain a high bush and tree cover. Orchard meadows were characterised by high, old fruit trees representing structurally rich stands important for birds nesting in treetops and hollows (Tworek, 2002), which can be compared with forest structures as well, but being more open. Thus, habitat structural diversity might be reasonable for some parts of the habitat, but probably favours primarily forest species and not characteristic semi-open woodland species. Long-term abandonment should be avoided as orchard meadows would develop into forest.

In accordance with the third hypothesis, farmland bird abundance increased in semi-natural grassland located in agricultural landscapes. Similar results were found by Wretenberg et al., (2010) with a positive effect of low-intensity land use on farmland birds in open landscapes with low forest cover. This indicates that farmland birds are using resources from different semi-natural grasslands, but also the surrounding agricultural landscape. Birds experience the landscape at a large scale, which also enables them to react fast to local habitat changes (Tscharntke et al., 2012). Hence, semi-natural grassland can be regarded as a valuable landscape element for landscape-wide conservation management.

Analysing the bird community composition, habitat type and management explained the greatest part of its variation. For abandoned orchard meadows, for example, chiffchaff (*Phylloscopus collybita*) was a characteristic woodland species nesting on the ground or in herbaceous woody vegetation structures (Südbeck et al., 2005; Gregory et al., 2007). However, for orchard meadows there are also some semi-open woodland bird species regarded as characteristic due to their ecological requirements (Herzog et al., 2005), but only two of them were found in this study (*Phoenicurus phoenicurus; Picus viridis)* and one of them, namely *P. phoenicurus*, only with one individual. This indicates that the ecological requirements of many characteristic species for orchard meadows cannot be fulfilled by the current habitat status, e.g. for ortolan (*Emeriza hortulana*) and hoopoe (*Upupa epops*), which are regarded as threatened in the red list of the study region (Lower Saxony, (Krüger and Nipkow, 2015)). This shows the importance of orchard meadows for a wide range of bird species, but emphasises the urgent need for conservation management to work more target-oriented with land owners. Thus, abandoned orchard meadows should be taken into low-intensity management again, while nest-holes and heterogeneous structures must be preserved at the same time. Another rare open woodland species is tree pipit (*Anthus trivialis*), which is specialised on open semi-natural grassland with single trees and characteristically occurred in managed calcareous grassland of forest-dominated landscapes. High solitary trees are used as perches, and an increasing shrub cover was shown to negatively affect the occurrence (Kumstátová et al., 2004). This suggests that the tree pipit, being in a sharp decline across Europe (Gregory et al., 2007), was favoured by open semi-natural grassland with single perches and would be disadvantaged by abandonment.

5. Conclusions

Our results show that the classification of species into farmland and woodland traits can help to disentangle the complex local and landscape effects on butterflies and birds in semi-natural grasslands. Results of this study detail the relative importance of local and landscape management and their complex interaction for understanding and applying best conservation measures. Woodland birds and butterflies appeared to be less affected by habitat type, management or landscape context than farmland species. Calcareous grasslands were much more important for butterfly diversity than orchard meadows, but suitability of orchards for butterflies was improved when embedded in forested landscapes. In contrast to butterflies, bird diversity benefited more from orchard meadows than calcareous grasslands, which had higher diversity when management was abandoned. Hence, short-term abandonment can improve habitats for birds and butterflies, but of course, long-term abandonment would destroy the identity of these openland habitats and their associated community. Landscape context can shape communities in these two grassland habitat types, so conservation management should consider reserves in both agricultural and forest landscapes and thereby, diversify regional biota.

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Table 1. Summary table for generalized linear regression model results on farmland and woodland butterfly species richness and abundance testing the effects of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-dominated, MA: managed, OM: orchard meadow. Significant estimates are in bold characters.

Model[a]	Variable	Relative importance (%)[b]	Multimodel estimate ± 95 % CI[c]	Direction
Species richness				
Farmland	Landscape (L)	100	0.026 ± 0.312	
	Habitat (H)	100	**-1.217 ± 0.415**	CG>OM
	Management (M)	100	0.054 ± 0.31	
	L × H	100	**0.702 ± 0.448**	
	L × M	100	-0.095 ± 0.403	
	H × M	100	-0.042 ± 0.436	
Woodland	Landscape (L)	30	0.139 ± 0.276	
	Habitat (H)	63	-0.239 ± 0.278	
	Management (M)	13	0.099 ± 0.276	
Abundace				
Farmland	Landscape (L)	100	0.029 ± 0.481	
	Habitat (H)	100	**-1.792 ± 0.718**	CG>OM
	Management (M)	100	0.458 ± 0.465	
	L × H	62	**0.863 ± 0.697**	
	H × M	62	**0.934 ± 0.675**	
Woodland	Landscape (L)	20	0.138 ± 0.344	
	Habitat (H)	28	-0.198 ± 0.341	
	Management (M)	100	**-0.554 ± 0.345**	CG>OM

[a] Farmland species richness and abundance and woodland abundance butterfly models were fitted with negative binomial distribution, whereas woodland species richness with Poisson distribution

[b] Each variable's importance within the best candidate models (ΔAIC < 2)

[c] Estimates with 95 % CI values after multimodel averaging of the top-model set (ΔAIC < 2)

Table 2. Summary table for generalized linear mixed-effects model results on farmland and woodland bird species richness and abundance testing the effects of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-dominated, MA: managed, OM: orchard meadow. Significant estimates are in bold characters.

Model[a]	Variable	Relative importance (%)[b]	Multimodel estimate ± 95 % CI[c]	Direction
Species richness				
Farmland	Landscape (L)	100	-0.437 ± 0.492	
	Habitat (H)	100	-0.032 ± 0.448	
	Management (M)	100	**-0.659 ± 0.518**	AB>MA
	L × H	100	0.09 ± 0.612	
	L × M	100	0.022 ± 0.61	
	H × M	100	**0.853 ± 0.602**	
Woodland	Landscape (L)	70	-0.043 ± 0.329	
	Habitat (H)	52	0.133 ± 0.261	
	Management (M)	100	**-0.381 ± 0.335**	CG<OM
	L × H	12	0.286 ± 0.418	
	L × M	49	-0.439 ± 0.443	
Abundace				
Farmland	Landscape (L)	100	**-0.518 ± 0.408**	AG>FO
	Habitat (H)	100	-0.145 ± 0.495	
	Management (M)	100	**-0.629 ± 0.49**	AB>MA
	L × H	28	0.283 ± 0.666	
	H × M	100	**1.086 ± 0.671**	
Woodland	Landscape (L)	27	-0.097 ± 0.305	
	Habitat (H)	100	**0.338 ± 0.305**	CG<OM
	Management (M)	100	**-0.545 ± 0.307**	AB>MA

[a] All models were fitted with Poisson distribution

[b] Each variable's importance within the best candidate models ($\Delta AIC < 2$)

[c] Estimates with 95 % CI values after multimodel averaging of the top-model set ($\Delta AIC < 2$)

Table 3. Results of redundancy analyses to test the effect of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) on the community composition of all butterfly and bird species. % var.: percentage variation explained. *P* values < 0.05 are in bold characters.

	% var.	*F*	*P*
Butterfly			
Landscape	5.61	2.86	**0.012**
Habitat	21.33	10.88	**0.001**
Management (M)	2.49	1.27	0.229
Total constrained	29.43	5.00	**0.001**
Bird			
Landscape	2.30	1.52	**0.023**
Habitat	3.56	2.35	**0.001**
Management (M)	3.50	2.30	**0.001**
Total constrained	9.37	2.06	**0.001**

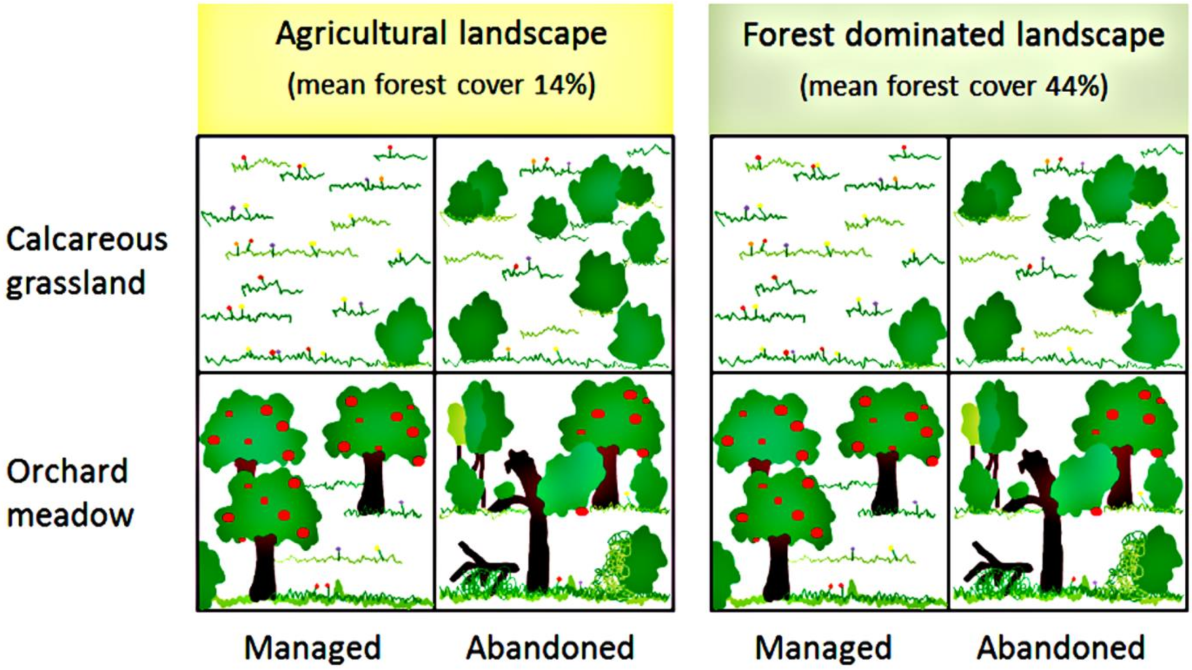

Figure 1. Schematic figure of the study design representing the study sites. There were five replicates per treatment resulting in 20 calcareous grasslands and 20 orchard meadows located in contrasting landscape context (agricultural or forest-dominated) differing in management (regularly managed or abandoned management).

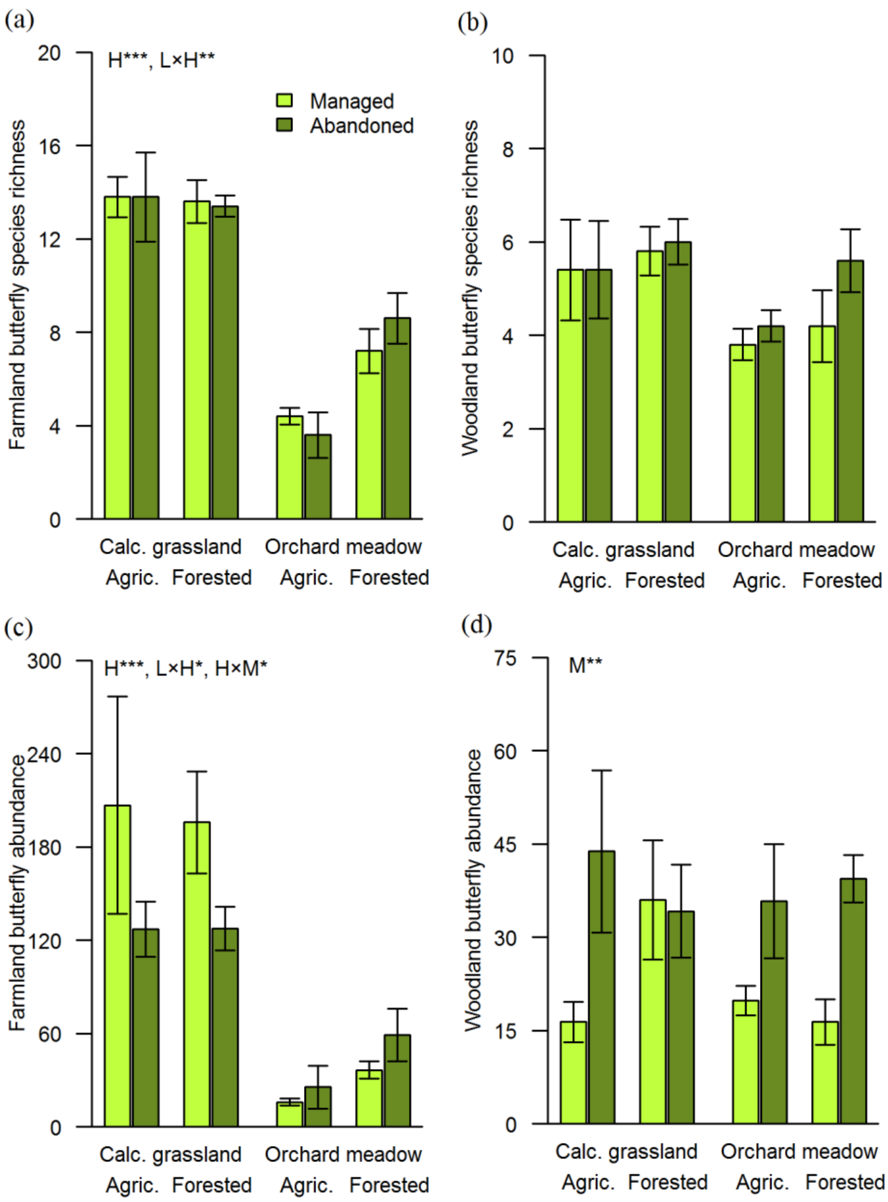

Figure 2. Mean (± SEM) farmland (a) and woodland (b) butterfly species richness and farmland (c) and woodland (d) butterfly abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear regression models (see Table 1) with $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ (H: Habitat type, L: Landscape context, M: Management type).

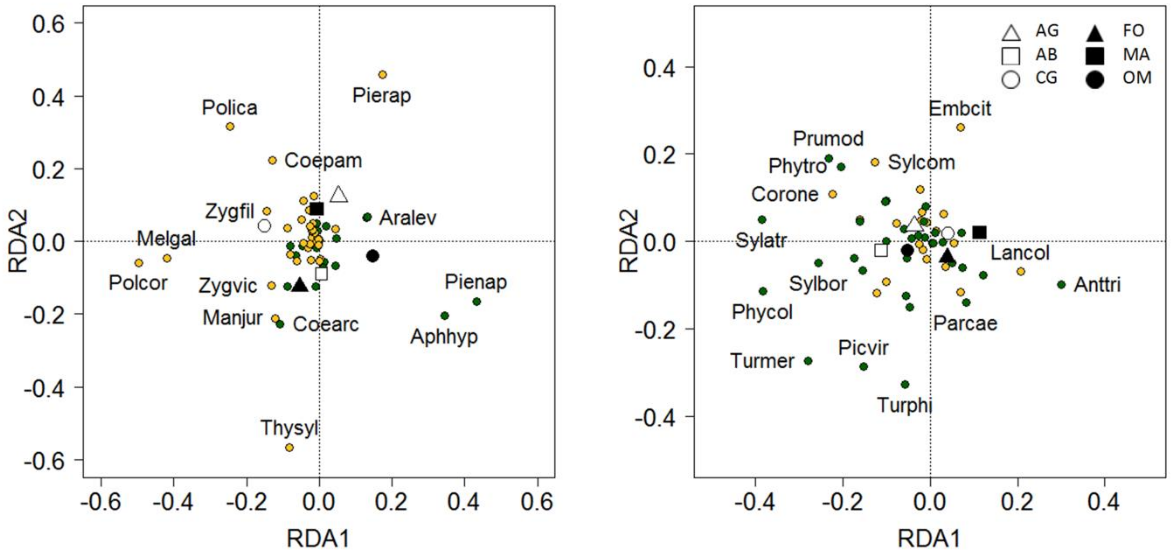

Figure 3. Redundancy analysis biplots for all species of (a) butterfly and (b) bird communities (yellow circles: farmland species, green circles: woodland species) showing the effect of habitat type (CG: calcareous grassland, OM: orchard meadow), presence of management (AB: abandoned, MA: managed) and landscape context (AG: agricultural, FO: forest-dominated landscape). For visibility, only species with the highest fraction of variance fitted by the two first RDA axes are indicated. Species code consists of the first three letters of genus plus the first three letters of species names (Table A2, A3).

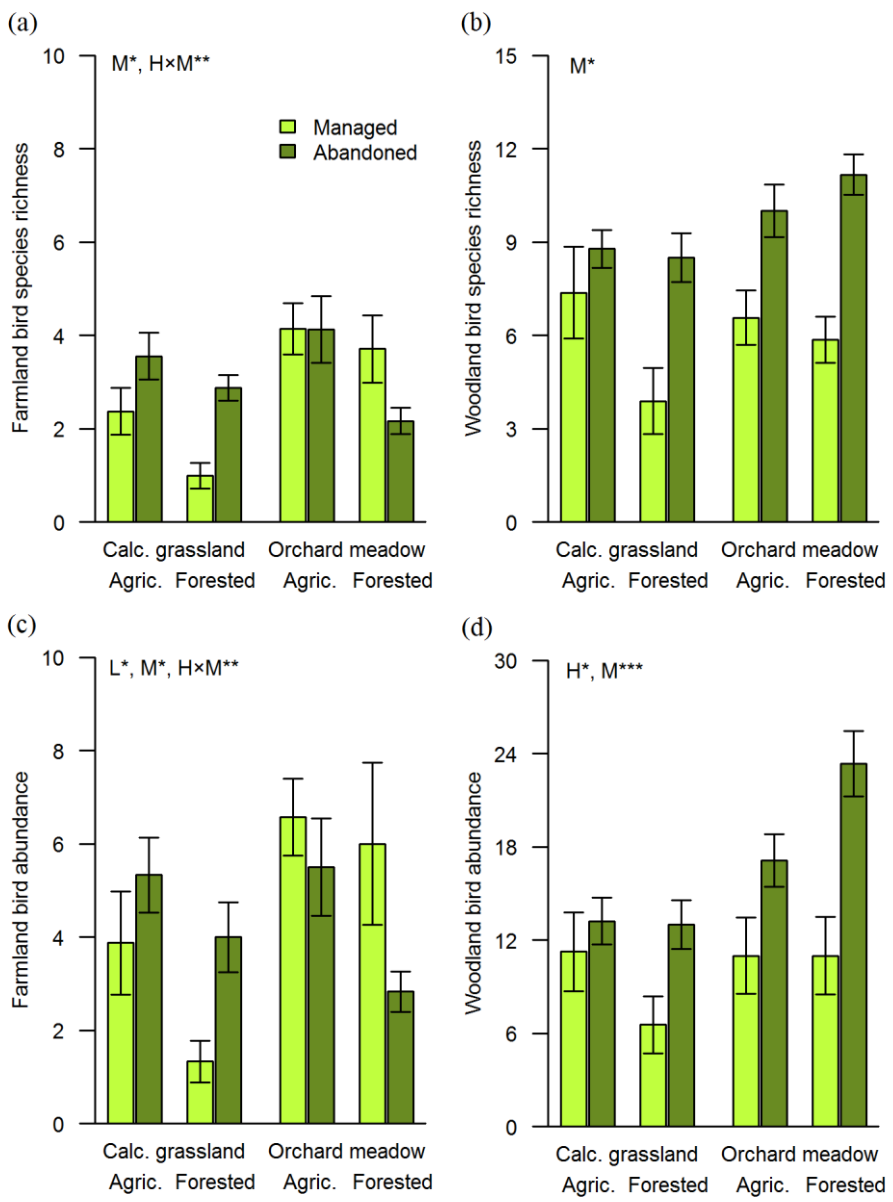

Figure 4. Mean (± SEM) farmland (a) and woodland (b) bird species richness and farmland (c) and woodland (d) bird abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear mixed-effects models (see Table 2) with $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ (H: Habitat type, L: Landscape context, M: Management type).