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

2 **diversity**

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13 **Abstract**

14 Calcareous grasslands and orchard meadows are among the most species-rich semi-natural

15 habitats in Europe, but they are severely threatened by intensified land use and abandonment.

16 Here, we focus on the effects of management vs. abandonment of these grasslands in

17 agricultural vs. forest-dominated landscapes of Germany. We recorded butterflies and birds

18 and classified them in farmland and woodland species according to their habitat preferences.

19 Species richness and abundance of farmland butterflies were higher on calcareous grasslands

20 than orchard meadows and benefited from forested landscapes in case of orchard meadows.

21 Species richness of woodland butterflies was higher on abandoned than managed grasslands,

22 independent of habitat type and landscape context. Richness and abundance of farmland birds

23 benefited from managed orchard meadows, and were more abundant in agricultural

24 landscapes. On calcareous grasslands, however, the abandonment led to higher richness and

25 abundance of farmland birds. Woodland birds exhibited higher species richness in abandoned

26 than managed grasslands, especially in orchard meadows. Woodland birds and butterflies

27 appeared to be less affected by habitat type, management or landscape context than farmland

28 species. Calcareous grasslands were much more important for butterfly diversity than orchard

29 meadows, but suitability of orchards for butterflies was improved when embedded in forested

30 landscapes. In contrast to butterflies, bird diversity benefited more from orchard meadows

31 than calcareous grasslands, which had higher diversity when management was abandoned. In

32 conclusion, landscape context can shape communities in these two grassland habitat types, so

33 conservation management should consider reserves in both agricultural and forested

34 landscapes and thereby, diversify regional biota.

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36 **Keywords:** biodiversity; extensive management; farmland species; habitat abandonment;

37 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

64   island biogeography, species diversity of fragmented semi-natural habitats such as calcareous

65   grasslands and orchard meadows is influenced by movement between habitat fragments

66   through the surrounding landscape matrix (McArthur and Wilson, 1967). Landscape structure

67   and land use surrounding the habitat fragments may therefore improve or hinder dispersal

68   through the landscape matrix or even provide additional resources to some species, depending

69   on the quality of the matrix and the species' environmental needs (Eycott et al., 2012;

70   Öckinger et al., 2012). Thus, landscape context measures might reflect the quality of the

71   landscape matrix for population movement between the remaining habitat fragments and

72   availability of additional resources.

73   Both butterflies and birds are representatives of the most studied and ecologically best

74   known invertebrates and vertebrates (Schlegel and Rupf, 2010). In particular, butterflies

75   which have been categorized as grassland specialists have been found to decline in

76   distribution across Europe (van Swaay et al., 2006). Birds, on the other hand, often rely on the

77   presence of scattered trees such as fruit trees in orchard meadows, which act as local and

78   landscape keystone structures in intensively managed landscapes that are otherwise poor in

79   landscape elements (Manning et al., 2006). Overall, population declines of birds over the last

80   decades have been widely reported, especially of farmland birds, but of woodland birds as

81   well (Gregory et al., 2005, 2007).

82   This is the first study investigating the potentially complex effects of changing

83   environments and their interactions at three spatial scales: management practices

84   (mowing/grazing or abandonment), habitat type (calcareous grassland or orchard meadow)

85   and landscape context (agricultural or forested landscape) on two flagship taxa of nature

86   conservation. We focused on butterflies and birds, which were classified as farmland or

87   woodland species according to their known principal habitat occurrence. We hypothesise that

88   (i) farmland butterflies and birds prefer calcareous grasslands, whereas woodland species

89   prefer orchard meadows, (ii) regular local management of calcareous grasslands and orchard

90 meadows positively affects farmland species, whereas abandonment benefits woodland

91 species, and (iii) there are more farmland species in agricultural landscapes, whereas there are

92 more woodland species in forest-dominated landscapes (Fig. 1).

93

94 **2. Material and methods**

95 *2.1. Study area*

96 The study area was situated in southern Lower Saxony (Germany) in the districts of Göttingen

97 and Northeim (about 1000 km²; see Appendix A1 in Supplementary online material). The

98 main land use types are arable fields, intensively used meadows and semi-natural deciduous

99 forests. The surveys were conducted in calcareous grasslands (*Mesobrometum erecti* Koch

100 1926) covering only 0.26 % and in orchard meadows (*Arrhenatheretum elatioris* Braun 1915)

101 covering 0.39 % of the study area. Both semi-natural grassland habitats are patchily

102 distributed across the landscape, and managed either by mowing or grazing with sheep, goats,

103 cattle or horses. Many smaller fragments and party also the larger ones are in a process of

104 abandonment with shrub encroachment and/or dye off of old fruit trees.

105

106 *2.2. Study design*

107 We surveyed butterfly and bird species in 20 orchard meadows and 20 calcareous grasslands

108 in a full factorial design (mean ± SEM distance between sites: 17.9 ± 0.3 km; range of

109 distance between sites: 0.5 – 52.0 km; fruit tree density on abandoned orchard meadows: 38.6

110 ± 4.4 (23.9 – 67.9) and on managed orchard meadows: 36.4 ± 5.5 (16.4 – 70.5)). The habitat

111 fragments were selected according to differences in landscape context (forested vs. agriculture

112 dominated landscapes) and management status (managed vs. abandoned), resulting in five

113 replicates per treatment (Fig. 1). Within a 500 m buffer area around each habitat fragment,

114 forest-dominated landscapes had 44 ± 2% (mean ± SEM) forest cover ranging from 28 to

115 63%, whereas agricultural landscapes had 14 ± 2% forest cover ranging from 0 to 28% (forest

116   cover was measured in ArcGIS 10.4). As many semi-natural habitats are neither fully

117   managed nor completely abandoned, we selected managed habitat fragments to be managed

118   each year by grazing or mowing, whereas abandoned fragments to be irregularly or not

119   managed characterised by high degree of succession to woody shrubs or dead wood. In

120   summary, majority of the managed grasslands were grazed extensively (< 1 LUI/ha) between

121   May and September with different livestock including cattle, sheep, goat, horse or donkey

122   (calcareous grasslands: eight fragments grazed, one mown and one both grazed and mown;

123   orchard meadows: eight fragments grazed and two mown). In order to minimize the effect of

124   habitat size on species richness and abundance, fragments with a similar size were chosen,

125   and species were surveyed on a 0.8 ha patch in each study site. The area of the selected

126   habitat fragments was 2.64 ± 0.27 ha (mean ± SEM) for calcareous grassland (ranging from

127   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).

128

129   *2.3. Sampling methods*

130   Butterflies (Lepidoptera: Hesperidae and Papilionidea) and burnet moths (Lepidoptera:

131   Zygaenidae) were sampled from 24th of May until 19th of August 2015 with three survey

132   rounds (roughly one survey/month) by a 20 minute zig-zag transect-walk (split into 5 four-

133   minute sections) once on each habitat fragment (following Krauss et al., 2003; Brückmann et

134   al., 2010). Butterflies were surveyed visually or using a butterfly net between 10.45 am and

135   5.30 pm, and were identified and released immediately. Surveys were conducted on a 5 m

136   wide corridor under suitable weather conditions for butterfly activity (dry conditions, wind

137   speed less than Beaufort scale 5, and temperature 13 °C or higher if there was at least 60 %

138   sunshine, or more than 17 °C if overcast (Pollard, 1977)). To characterise the availability of

139   nectar resources, the percent cover of flowering plants inside the transect corridor was

140   estimated at the end of each transect walk. We classified butterfly species to farmland or

141   woodland species based on literature (van Swaay et al., 2006; Plattner et al., 2010).

142   We recorded birds between 8th and 22nd of May and between 8th and 28th of June 2015

143   in two survey rounds by a 12 minute point-count on 0.8 ha patches half an hour after sunrise

144   until 4 hours after sunrise under calm and dry weather conditions (Bibby et al., 1992). There

145   were 22 habitat fragments with two 0.8 ha survey patches as they were larger than 1.6 ha. In

146   the 18 remaining, smaller habitat fragments there was one 0.8 ha survey patch in each habitat

147   fragment. Due to the high degree of heterogeneous structures and the different shape of the

148   habitat fragments, each point-count was split into three 4-minute sections placed at points

149   suitable to represent the study design (managed or abandoned). This guaranteed to perceive

150   all acoustic signals of the birds and to detect them visually. To characterise the availability of

151   nesting and foraging sites, the percent bush cover in each 0.8 ha study patch was estimated in

152   the end of each survey. We classified bird species to farmland or woodland species based on

153   literature (Gregory et al., 2005, 2007; Südbeck et al., 2005; Batáry et al., 2012). Species

154   habitat affinity and specialism might change with different European regions suggesting that

155   our classification approach may lead to different results there (see e.g. Koleček et al., 2010).

156

157   *2.4. Statistical analysis*

158   Abundance of butterflies was summed over transects and sampling occasions. For each bird

159   species we pooled the data using the maximum abundance of the two survey rounds per patch.

160   Species richness of birds was calculated as the number of species that were present in the

161   particular sampling patch at least in one survey round.

162   For both taxa we applied linear regression models for analysing the species richness and

163   abundance of farmland and woodland species. Habitat type (calcareous grassland vs. orchard

164   meadow), management status (managed vs. abandoned), landscape context (forested vs.

165   agriculture dominated landscapes) and their two-way interactions were used as explanatory

166   design variables. In case of bird models, the survey patch within habitat fragment was used as

167   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,

193   2001). To assess for statistical significance, a permutation test based on 999 permutations was

194   calculated using the package vegan (Oksanen et al., 2017).

195

196   **3. Results**

197   On the 20 calcareous grassland and 20 orchard meadow fragments we recorded 5182

198   individual butterflies belonging to 55 butterfly species (seven of them burnet moths, hereafter

199   also called butterflies) and 1075 individuals of 55 bird species. Classification based on

200   environmental preferences resulted in 35 farmland butterfly species with 3973 individuals and

201   20 woodland butterfly species with 1209 individuals (Table A2) as well as 22 farmland bird

202   species with 272 individuals and 33 woodland bird species with 803 individuals (Table A3).

203   The most abundant farmland butterflies were *Maniola jurtina*, *Polyommatus coridon* and

204   *Melanargia galathea*, whereas the most abundant woodland butterflies were *Aphantopus*

205   *hyperantus*, *Pieris napi* and *Coenonympha arcania* (Table A2). For birds, the most abundant

206   farmland species were *Emberiza citrinella*, *Sylvia communis* and *Columba palumbus*, whereas

207   the most abundant woodland birds were *Parus major*, *Turdus merula* and *Cyanistes caeruleus*

208   (Table A3).

209

210   *3.1. Effects on butterflies*

211   We found habitat type to be the most important factor determining farmland butterfly species

212   richness and abundance with higher values in calcareous grasslands than in orchard meadows

213   (Table 1; Fig. 2a,c). Farmland species richness and abundance depended on an interaction

214   between landscape context and habitat type; high species richness and abundance were found

215   in both agricultural and forest-dominated landscapes of calcareous grasslands, but lower

216   values in orchard meadows with a decrease from forested to agricultural landscapes.

217   Additionally, farmland butterfly abundance was influenced by management in interaction

218   with habitat type. Management increased butterfly abundances in calcareous grasslands, but

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219   decreased them in orchard meadows. In contrast, abandonment increased the abundance of

220   woodland butterflies, but not their species richness (Fig. 2c,d).

221   The RDA of butterfly community composition revealed significant associations with

222   habitat type and landscape context (Table 3; Fig. 3a). In the ordination biplot, the first axis

223   separated calcareous grasslands from orchard meadows with e.g. chalkhill blue (*Polyommatus*

224   *coridon*) as characteristic species in calcareous grasslands and ringlet (*Aphantopus*

225   *hyperantus*) as characteristic species in orchard meadows. The second axis separated

226   agricultural from forest-dominated landscapes with small white (*Pieris rapae*) being a

227   characteristic agricultural species and small skipper (*Thymelicus sylvestris*) being a species

228   associated with forest.

229

230   *3.2. Effects on birds*

231   Performing generalized linear mixed effects models on birds, we found that management type

232   was the variable that most strongly explained both farmland and woodland species richness

233   and abundance (Table 2). This was, however, in an interaction with habitat type in case of

234   farmland species (Fig. 4a,c). Farmland birds preferred managed over abandoned fragments in

235   orchard meadows, and abandoned over managed fragments in calcareous grassland.

236   Additionally, they were more abundant in agricultural than forest-dominated landscapes. In

237   contrast, woodland birds (both richness and abundance) were more common in abandoned

238   than in managed fragments (Fig. 4b,d). Finally, woodland bird abundance was higher in

239   orchard meadows than in calcareous grasslands.

240   In the RDA of bird communities all three variables explained a significant part of the

241   variation in community composition (Table 3). Landscape context explained the smallest part,

242   followed by management and habitat type, explaining the largest part of the variation. The

243   first axis separated in particular abandonment and management, but also orchard meadows

244   and calcareous grasslands (Fig. 3b). For example, chiffchaff (*Phylloscopus collybita*) showed

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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

270   often been reported (e.g. Krämer et al., 2012), and highlights the disproportionate high value

271   of calcareous grassland for butterfly conservation (van Swaay, 2002).

272   As hypothesised, management had a negative effect on woodland butterfly abundance,

273   but not on species richness. Woodland butterflies were more common in abandoned semi-

274   natural grasslands, which can be explained by increasing microhabitat heterogeneity and the

275   availability of plant communities typical for different successional stages (WallisDeVries et

276   al., 2002). On the contrary, farmland butterfly abundance increased with management, but

277   only in calcareous grassland, where abundances were generally higher than in orchard

278   meadows. Abandonment appeared to provide less life-sustaining resources for farmland

279   butterflies such as flowering plants and warm micro-climate (van Swaay, 2002). Surprisingly,

280   in orchard meadows farmland butterfly abundance increased with abandonment. This might

281   have been caused by the fact that management was characterised by high stocking rates,

282   fertilisation and frequent mowing, degrading the diversity of herbs and flowers (Uchida et al.,

283   2016). Abandoned orchard meadows were characterised by additional resources such as

284   flowering forbs or shrubs, for example blackberries, but in the long run, late successional

285   stages may decrease butterfly species richness and abundance (Balmer and Erhardt, 2000;

286   Kesting et al., 2015). There is a lack of target-oriented management in orchard meadows,

287   which should be regularly restored by clearance of shrubs and trees, opening of the canopy for

288   light and warm micro-climate as well as reducing grazing density or intensified hay-making to

289   facilitate larval hosts and nectar-providing plants.

290   In contrast to our hypothesis, farmland butterfly species richness was higher in orchard

291   meadows when embedded in forest-dominated landscapes but not agricultural landscapes.

292   Forest-dominated landscapes are more heterogeneous providing more resources than simple

293   landscapes dominated by agriculture (Öckinger et al., 2012). Compared to calcareous

294   grassland, local habitat conditions in orchard meadows were worse (less food resources) and

295   farmland butterflies appeared to use additional resources in the surroundings (Krämer et al.,

296 2012; Villemey et al., 2015). In this study we found more flowering plants in orchard

297 meadows of forest-dominated than agricultural landscapes, which suggests that non-arable

298 patches may act as buffer against intensive agricultural practices such as chemical weed

299 control (Gonthier et al., 2014; Villemey et al., 2015).

300   As shown in the redundancy analysis, the greatest variability in community composition

301 was explained by habitat type with most butterfly species showing a strong preference for

302 calcareous grasslands especially by farmland species. For example, chalkhill blue is regarded

303 as threatened in the red list of the study region (Lower Saxony, (Lobenstein, 2004)), and was

304 the most characteristic farmland species on calcareous grasslands. The high population

305 density of chalkhill blue is determined by the presence of the larva's food plant *Hippocrepis*

306 *comosa* (Krauss et al., 2005), which is dispersed by the hooves of livestock (Brereton et al.,

307 2008). Hence, this result reflects the need for appropriate habitat management for specialised

308 butterflies in the study region. Contrastingly, the community composition for orchard

309 meadows showed that management can be important habitat for species that are associated

310 with open woodland. For example, ringlet (*Aphantopus hyperatus*) occurred in relatively high

311 abundances in orchard meadows. This species was often shown to be present in grasslands

312 and mixed woodlands, but also in tree lines (van Swaay et al., 2006). Thus, orchard meadows

313 potentially provide habitat for species that are associated with woodland edges and can be

314 assumed to provide habitat to an even wider range of open-woodland butterfly species

315 profiting from improved management practices. Hay-making or low-intensity grazing with

316 reduced fertiliser use and allowance of seed maturation could restore the degraded orchard

317 meadows in the study region.

318

319 *4.2. Effects on birds*

320 Regarding farmland bird species richness and abundance, our first and second hypotheses

321 were only party confirmed, because we found an interaction of habitat type and management.

322   Abandonment caused an increase in farmland bird species richness and abundance in

323   calcareous grasslands, but a decrease in orchard meadows. Partly abandoned calcareous

324   grasslands were characterised by less disturbance and provided a wide range of niches,

325   because of their heterogeneous habitat characteristics caused by higher amounts of woody

326   vegetation and heterogeneous sward structures (Hartel et al., 2014). This supported nesting

327   sites and foraging opportunities, e.g. for insects on the ground (Vickery et al., 2001).

328   However, abandonment can benefit farmland birds only on a short term and further

329   succession will exclude farmland birds (Gregory et al., 2007). Contrastingly to calcareous

330   grasslands, farmland bird species richness and abundance were higher in managed compared

331   to abandoned orchard meadows. Scattered trees act as keystone habitat for farmland birds and

332   provide nesting and foraging opportunities as well as song posts (Fischer et al., 2010;

333   Jakobsson and Lindborg, 2017). Since orchard meadows were mostly grazed by livestock,

334   they were suitable for foraging, e.g. of insects on animal dung, or as ground-nesting sites in

335   patches avoided by livestock. Nevertheless, some orchard meadows were frequently used and

336   there might be a higher potential for farmland birds as the positive effect of management on

337   biodiversity may be restricted to low levels of interference. Intensified grassland management

338   decreases the suitability as habitat for feeding and nesting because of higher disturbance

339   levels and a fast growing, homogeneous grassland structure as a consequence (Vickery et al.,

340   2001). Management activities should provide feeding and nesting sites, such as breeding

341   burrows of old trees, shelter of bushes for ground breeding birds and heterogeneous, open

342   sward structures.

343   Corresponding to our hypotheses, woodland bird species richness and abundance were

344   higher in abandoned compared to managed grassland fragments and abundance was also

345   higher in orchard meadows than in calcareous grassland. Abandoned habitat fragments are

346   structurally more similar to forest as they contain a high bush and tree cover. Orchard

347   meadows were characterised by high, old fruit trees representing structurally rich stands

348   important for birds nesting in treetops and hollows (Tworek, 2002), which can be compared

349   with forest structures as well, but being more open. Thus, habitat structural diversity might be

350   reasonable for some parts of the habitat, but probably favours primarily forest species and not

351   characteristic semi-open woodland species. Long-term abandonment should be avoided as

352   orchard meadows would develop into forest.

353   In accordance with the third hypothesis, farmland bird abundance increased in semi-

354   natural grassland located in agricultural landscapes. Similar results were found by Wretenberg

355   et al., (2010) with a positive effect of low-intensity land use on farmland birds in open

356   landscapes with low forest cover. This indicates that farmland birds are using resources from

357   different semi-natural grasslands, but also the surrounding agricultural landscape. Birds

358   experience the landscape at a large scale, which also enables them to react fast to local habitat

359   changes (Tscharntke et al., 2012). Hence, semi-natural grassland can be regarded as a

360   valuable landscape element for landscape-wide conservation management.

361   Analysing the bird community composition, habitat type and management explained the

362   greatest part of its variation. For abandoned orchard meadows, for example, chiffchaff

363   (*Phylloscopus collybita*) was a characteristic woodland species nesting on the ground or in

364   herbaceous woody vegetation structures (Südbeck et al., 2005; Gregory et al., 2007).

365   However, for orchard meadows there are also some semi-open woodland bird species

366   regarded as characteristic due to their ecological requirements (Herzog et al., 2005), but only

367   two of them were found in this study (*Phoenicurus phoenicurus; Picus viridis)* and one of

368   them, namely *P. phoenicurus,* only with one individual. This indicates that the ecological

369   requirements of many characteristic species for orchard meadows cannot be fulfilled by the

370   current habitat status, e.g. for ortolan (*Emeriza hortulana*) and hoopoe (*Upupa epops*), which

371   are regarded as threatened in the red list of the study region (Lower Saxony, (Krüger and

372   Nipkow, 2015)). This shows the importance of orchard meadows for a wide range of bird

373   species, but emphasises the urgent need for conservation management to work more target-

374 oriented with land owners. Thus, abandoned orchard meadows should be taken into low-

375 intensity management again, while nest-holes and heterogeneous structures must be preserved

376 at the same time. Another rare open woodland species is tree pipit (*Anthus trivialis*), which is

377 specialised on open semi-natural grassland with single trees and characteristically occurred in

378 managed calcareous grassland of forest-dominated landscapes. High solitary trees are used as

379 perches, and an increasing shrub cover was shown to negatively affect the occurrence

380 (Kumstátová et al., 2004). This suggests that the tree pipit, being in a sharp decline across

381 Europe (Gregory et al., 2007), was favoured by open semi-natural grassland with single

382 perches and would be disadvantaged by abandonment.

383

384 **5. Conclusions**

385 Our results show that the classification of species into farmland and woodland traits can help

386 to disentangle the complex local and landscape effects on butterflies and birds in semi-natural

387 grasslands. Results of this study detail the relative importance of local and landscape

388 management and their complex interaction for understanding and applying best conservation

389 measures. Woodland birds and butterflies appeared to be less affected by habitat type,

390 management or landscape context than farmland species. Calcareous grasslands were much

391 more important for butterfly diversity than orchard meadows, but suitability of orchards for

392 butterflies was improved when embedded in forested landscapes. In contrast to butterflies,

393 bird diversity benefited more from orchard meadows than calcareous grasslands, which had

394 higher diversity when management was abandoned. Hence, short-term abandonment can

395 improve habitats for birds and butterflies, but of course, long-term abandonment would

396 destroy the identity of these openland habitats and their associated community. Landscape

397 context can shape communities in these two grassland habitat types, so conservation

398 management should consider reserves in both agricultural and forest landscapes and thereby,

399 diversify regional biota.

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544 **Table 1.** Summary table for generalized linear regression model results on farmland and

545 woodland butterfly species richness and abundance testing the effects of habitat type (H:

546 calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and

547 landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best

548 candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-

549 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

550

551 [a] Farmland species richness and abundance and woodland abundance butterfly models were

552 fitted with negative binomial distribution, whereas woodland species richness with Poisson

553 distribution

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

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

556

557   **Table 2.** Summary table for generalized linear mixed-effects model results on farmland and

558   woodland bird species richness and abundance testing the effects of habitat type (H:

559   calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and

560   landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best

561   candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-

562   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

563

564   [a] All models were fitted with Poisson distribution

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

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

567   **Table 3.** Results of redundancy analyses to test the effect of habitat type (H: calcareous

568   grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape

569   context (L: agricultural vs. forest-dominated) on the community composition of all butterfly

570   and bird species. % var.: percentage variation explained. *P* values < 0.05 are in bold

571   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**

572
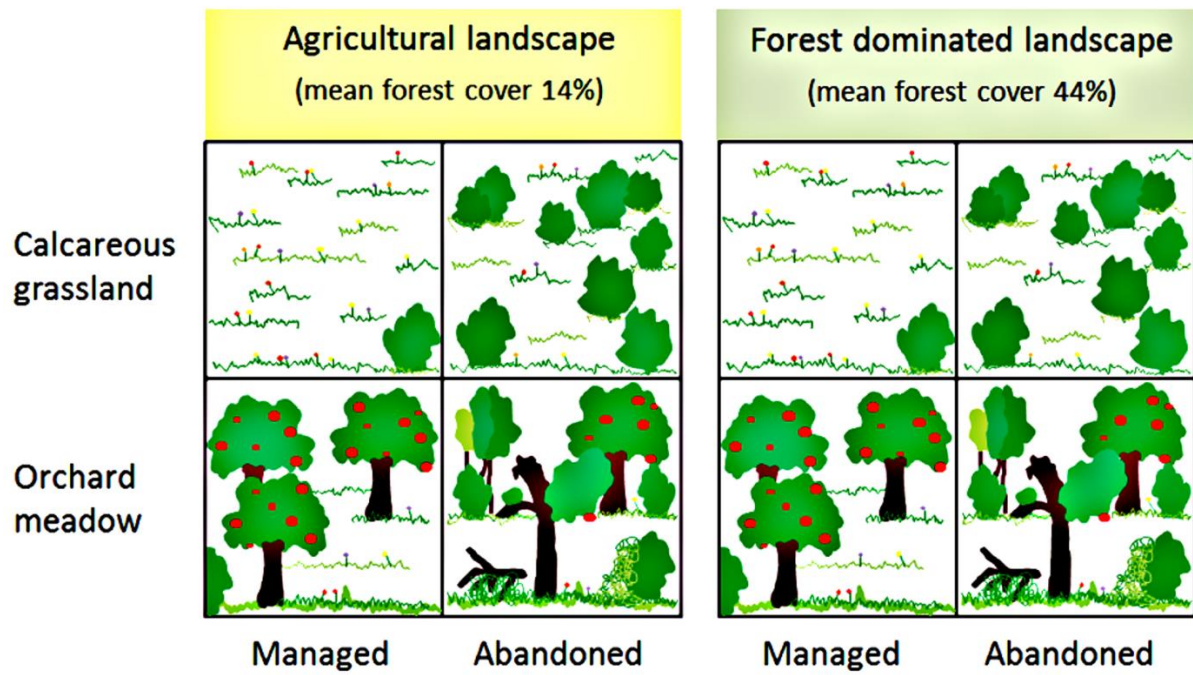
573   **Figure 1.** Schematic figure of the study design representing the study sites. There were five

574   replicates per treatment resulting in 20 calcareous grasslands and 20 orchard meadows located

575   in contrasting landscape context (agricultural or forest-dominated) differing in management

576   (regularly managed or abandoned management).
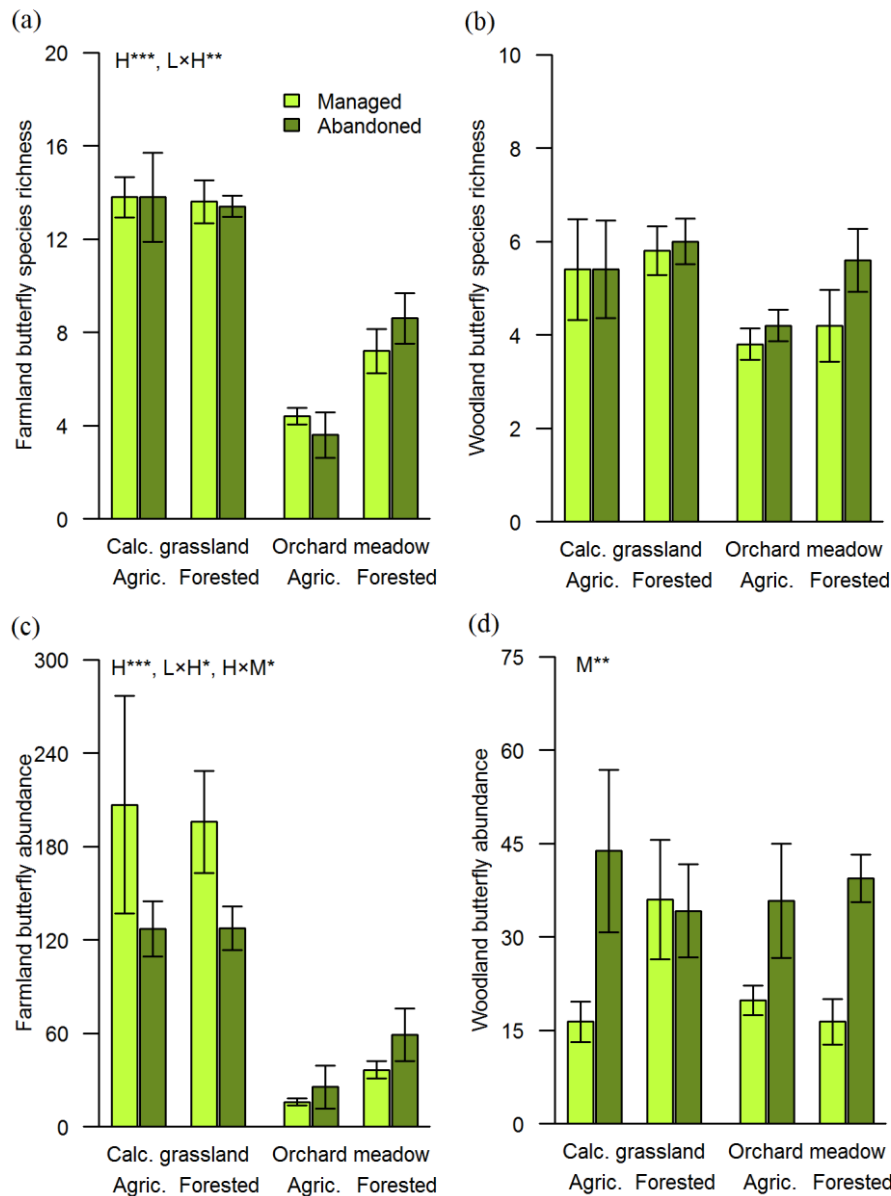
Figure 2. Mean (± SEM) farmland (a) and woodland (b) butterfly species richness and farmland (c) and woodland (d) butterfly abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear regression 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).
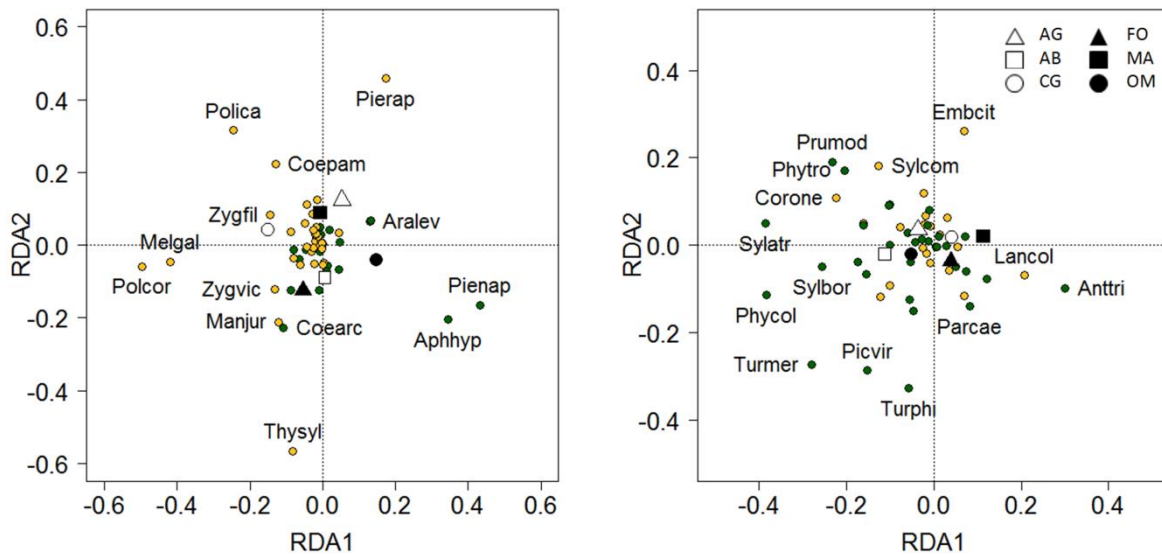
Figure 3. Redundancy analysis biplots for all species of (a) butterfly and (b) bird communities (yellow circles: farmland species, green circles: woodland species) showing the effect of habitat type (CG: calcareous grassland, OM: orchard meadow), presence of management (AB: abandoned, MA: managed) and 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).
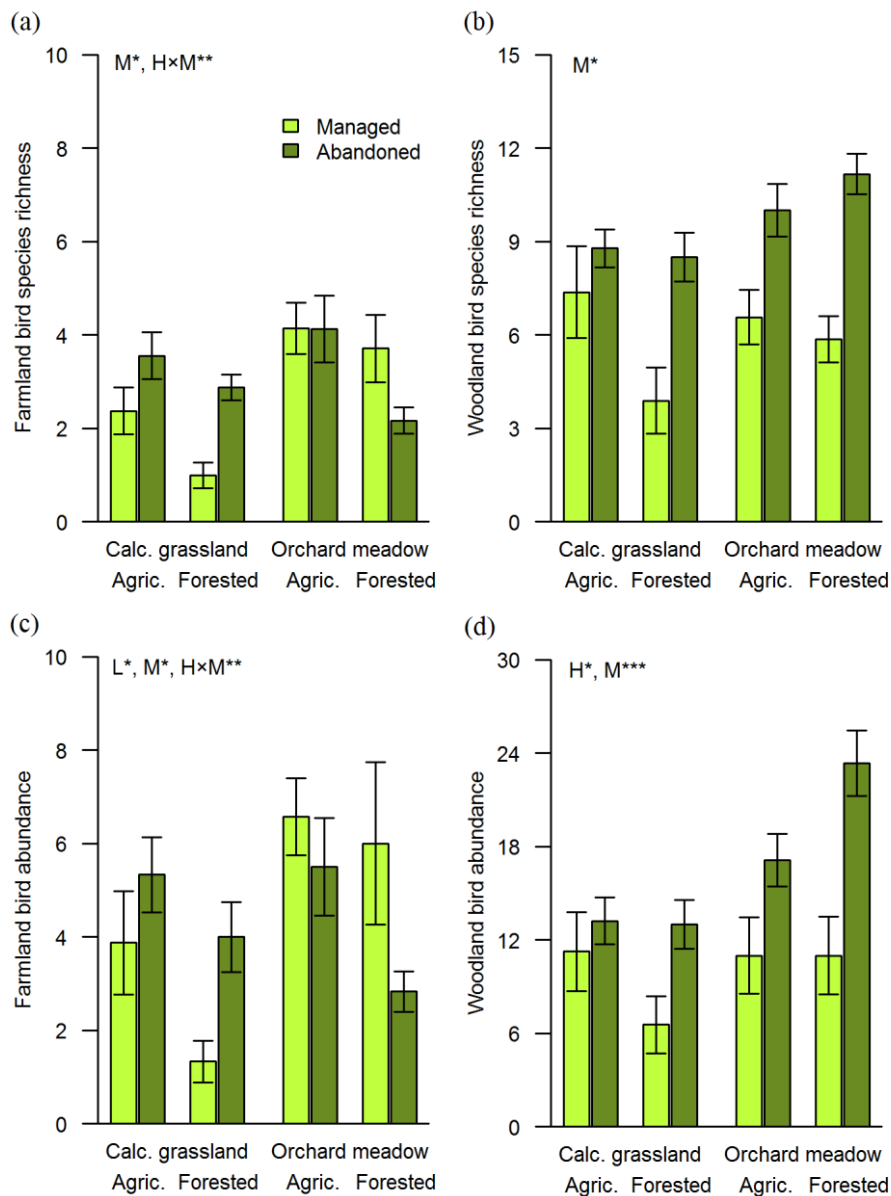
Figure 4. Mean (± SEM) farmland (a) and woodland (b) bird species richness and farmland (c) and woodland (d) bird abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear mixed-effects 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).