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Butterflies benefit from forest edge improvements in Western European lowland forests, irrespective of adjacent meadows' use intensity

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ABSTRACT

The joint effect of forest edge (FE) heterogeneity and management intensity of the adjacent farmland on FE insect communities is still poorly understood. In this study, a pairwise design was established, consisting of 36 Western European lowland FEs, with each of the 18 FE pairs containing one improved and one nearby non-improved FE. Half of the FE pairs were situated along extensively used and half along intensively used meadows, leading to gradual contrast patterns. Butterflies were selected as the survey group because they contain widely recognized flagship species and are meaningful indicators of landscape quality and resource availability. The main outcomes were as follows: (i) FE improvements led to higher overall FE heterogeneity scores, calculated on the basis of 16 floristic and structural indicator values. (ii) Overall butterfly species richness and butterfly abundance both benefited from higher FE heterogeneity. (iii) Butterfly species richness was higher on improved FEs, irrespective of adjacent meadows' use intensity. (iv) Butterfly abundance was higher on improved FEs, mainly due to high contrast situations between improved FEs and adjacent intensively used meadows. (v) FE improvements resulted in higher butterfly indicator species richness and abundance. The strategy of the canton of Aargau in Switzerland, where this study was conducted, to ecologically improve around 200 km of additional FEs in the longer term is believed to further promote butterfly diversity in the transition zone between closed forest and open landscape.

1. Introduction

In many European regions, forest edges (hereafter referred to FEs) are widespread and characteristic features of the cultural landscape, due to a long history of forest fragmentation driven by agricultural and urbanization dynamics (Hofmeister et al., 2019; Terraube et al., 2016). The interface between forest and adjacent landscape is gaining research relevance as it represents a substantial area (Meeussen et al., 2020): nearly 20 % of the world's remaining forest is within 100 m of an edge, in close proximity to agricultural, urban, or other modified environments (Haddad et al., 2015). In the European Union this proportion is even as high as around 40 % (Estreguil et al., 2013). In Switzerland, woody areas cover 31.9 % of the national territory, and FE extend over 115,000 km (Brändli et al., 2020). Overall, 44 % of the FEs in Switzerland are well structured, 13 % poorly structured and 43 % show intermediate structural quality (Abegg et al., 2020).

FEs are transition zones ("ecotones") with gradual abiotic and biotic changes from the forest to the non-forested open landscape. In comparison with forest interiors, FEs are characterized by different microclimate, higher levels of atmospheric nitrogen deposition, and higher influx of herbicides and fertilizers from adjacent arable lands (Meeussen et al., 2020). Forest microclimate effects on species communities have been documented at tens of meters from the physical FE (Harper et al., 2005). Many FEs in the agricultural landscape show an abrupt change with only marginal or even complete absence of transition zones, which may lead to a loss of their ecotone function, resulting in negative impacts on species communities (Non & Vries, 2013). Complex and broad edges with structurally diverse vertical layers often provide shelter and, due to complementary resources (Van Halder, 2017), suitable habitat conditions for a variety of species from both adjoining habitats (Duelli et al., 2002; Matlack & Litvaitis, 1999; Meeussen et al., 2020; Tóthmérész et al., 2014). Additionally, FEs can harbour distinct edge-associated species communities which are not, or only marginally, present in either of the adjacent habitats (Magura, 2002) or which explicitly depend on transition zones between closed forest and open landscape for their development (Habel et al., 2022). The predominantly positive edge effects of well-structured FEs on multi-taxa biodiversity is widely acknowledged, e.g. for birds (Terraube et al., 2016), spiders (Downie et al. 1996), ground beetles (Magura, 2002) and butterflies (Ries & Sisk, 2008).

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Understanding how the edge type may alter the dispersal behaviour and the composition of the species diversity is of high importance not only for identifying response patterns to edge effects but also for predicting species community composition in human-dominated fragmented landscapes (Alignier et al., 2014; Van Halder et al., 2011). Currently, the underlying mechanisms of FE effects are poorly understood (Czaja et al., 2021). In particular, we lack consistent approaches to quantify the impacts of edge effects in a rigorous manner across species and key functional groups, leading to potentially distorted projections of overall changes in biodiversity in fragmented landscapes (Pfeifer et al., 2017). When studying FEs, most authors have provided a relatively limited description of the structure only, which makes it hard to compare edge influences. As agricultural land use strongly impacts species composition and abundance (Liivamägi et al., 2014), multi-site comparative studies of the surrounding landscape should be always implemented in ecological FE investigations (Terraube et al., 2016).

Butterflies are perceived as an important model group in ecology (Krämer et al., 2012). Their flagship quality makes them excellent promoters of nature conservation projects (Schlegel et al., 2015). Butterflies have often been used as surrogates for the diversity of other taxa (Viljur et al., 2020). Most butterfly species need complementary resources like host plants for larvae, nectar plants for adults and sites for resting or overwintering (Rossi & Van Halder, 2010). Due to their environmental sensitivity, they respond rapidly to environmental changes, being widely considered as key indicators for tracking changes in habitats and landscapes (Fartmann et al., 2013; van Swaay et al., 2006). Most butterfly species avoid large open areas and seek shelter in wind-protected structures, such as FEs (Dover et al., 1997). As outlined in an overview by Ries & Sisk (2008), several studies have shown that certain butterfly species either avoid or are attracted to edges, and grasslands with a high nutrient level often contain only few butterfly individuals (Schneider & Fry, 2001). However, to the best of my knowledge, no major studies to date have cross-checked the joint impact of structural FE diversity and the use intensity of the adjacent farmland on local butterfly communities.

The Swiss Federal Office for the Environment (BAFU) has defined a set of focal species, as representatives of extensively managed grasslands and well-structured agricultural landscapes, in collaboration with the Swiss Federal Office for Agriculture (BLW) as part of the *Swiss Federal Environmental Objectives for the Agricultural Sector* (EOAS) (BAFU/BLW, 2008). The list contains, among other taxonomic groups, 140 "EOAS Butterfly species" of conservation concern and includes selected species that have been evaluated separately in this study.

In this study, a pairwise design was established, consisting of 36 lowland FEs, with each of the 18 FE pairs containing one improved and one nearby non-improved FE. Half of the FE pairs were situated along extensively used and half along intensively used meadows, leading to gradual contrast patterns. Within this setting, the study focused on the following research questions:

(i) How does the structural diversity of FEs interact with their butterfly diversity and abundance?
(ii) To what extent are butterfly diversity and abundance of FEs with differing structural diversity affected by land use intensity of adjacent meadows?
(iii) From a nature conservation point of view and as a follow-up of question (ii): Can FE improvements further promote butterfly diversity and abundance even when adjacent extensively used and unfertilized meadows already harbour a diverse butterfly fauna? And, on the other hand, can FE improvements promote butterfly diversity even then, when carried out along intensively used and fertilized meadows with a more uniform butterfly fauna?
(iv) How can above questions be answered from the perspective of target butterfly species, which are considered focal species for intact agricultural landscapes in Switzerland ("EOAS Butterfly species")?

2. Methods

2.1. Study area and sampling design

The study was conducted in the canton of Aargau on the Swiss Central Plateau (midpoint canton of Aargau: 47° 24′ 35″ N, 8° 9′ 25″ E). Before, aerial photographs and GIS data were consulted to obtain an overview of the distribution and location of ecological compensation areas (ECAs) and improved FEs within the study area (Kanton Aargau, 2016). ECAs are conditional cross-compliance requirements in Switzerland. In order to qualify for direct payments, farmers must manage 7 % or more of their land as ECAs, e.g. extensively used meadows (Schweizer Bundesrat, 2013). On this basis, a pairwise design with 18 FE pairs was implemented, each pair consisting of an improved and a non-improved FE (denoted as "FE status" in Table A1 of the Appendix), resulting in n = 36 FEs. Ecological upgrading of all improved FEs took place between 2006 and 2013.

To avoid within-pair butterfly species interference, only FEs that were at least 200 m apart were selected. Each of the 18 FE pairs was situated along a mixed deciduous forest, adjoining agricultural grassland, and had a length of 100 m. The main tree species were *Fagus sylvatica, Carpinus betulus, Quercus robur, Picea abies,* and *Acer pseudoplatanus*. Along certain FEs, *Fraxinus excelsior, Prunus avium, Acer campestre,* and *Quercus petrea* were frequent as well. Nine FE pairs were situated next to extensively used meadows, nine next to intensively used meadows with higher nutrient input (denoted as "Use intensity of adjacent meadow" in Table A1 of the Appendix). The exposition (i.e. sun exposure) of improved and non-improved FEs was not significantly different, neither for FEs along intensively, nor for those along extensively used meadows (Fisher's exact-tests, ps > 0.05).

All of the 18 adjacent extensive meadows were ECAs. From a plant sociological view they could be predominantly assigned to the group of Arrhenatherion or Mesobromion meadows (Delarze et al. 2015). The management regulations for Swiss ECA meadows include postponed mowing with a first cut not before 15 June at lower elevations, and prohibition of fertilizers and pesticides, single plant herbicide application excepted (Schweizer Bundesrat, 2013). All of the 18 adjacent intensively used meadows were monotonous rich meadows with regular fertilization and multiple cuts mostly between April and September.

2.2. Forest edge heterogeneity

Based on 16 floristic and structural indicators, Krüsi and Schütz (1994) developed a point score classification for the scientific assessment of FE heterogeneity. Their method is valid for lower to medium altitudes in Switzerland below mountainous regions (personal note: and presumably for neighboring regions abroad as well) and has been regularly applied in scientific studies and for evaluation assessments (Fuhrer et al., 2017). The heterogeneity score is measured along a FE of 100 m length and mainly depends (i) on the average depth of FE, shrub layer and herbaceous margin between the closed forest and the open landscape, (ii) on the species diversity of trees, shrubs and herbaceous layer (bonus points for ecologically valuable thorny shrubs), (iii) on the quantity and characteristics of small structures such as deadwood, branch piles or stony heaps, (iv) on the presence and share of neophytes (negative points) and (v) on the occurrence and spatial configuration of FE protrusions (wavy lines with small pockets protected from the wind). A detailed guideline is given by Krüsi et al. (1997), an updated online version can be found online (ZHAW, 2020). The FE heterogeneity classification is derived as follows: "extremely low" (≤19 points), "very low" (19–28 points), "low" (29–38 points), "medium" (39–48 points), "high" (49–58 points) and "very high" (≥58 points).

2.3. Butterfly sampling and nomenclature

Directly next to each of the 36 FEs described above, all butterfly species (Lepidoptera: Rhopalocera, including Hesperiidae) and burnet moths (Lepidoptera: Heterocera, Zygaenidae), hereafter referred to as butterflies, were recorded along transects of 100 m length, slightly adapted to the transect count method employed by Pollard & Yates (1993).

To facilitate comparisons, additional reference transects of 100 m length were established in each of the adjacent meadows at a distance of at least 30 m from the corresponding FE. Accordingly, 18 reference transects were placed in extensively and 18 in intensively used meadows. Subsequently, two transects of the latter had to be omitted as the grassland had been converted to cropland, finally leading to a total of n = 34 meadow transects. Butterflies of the reference transects were recorded on the same survey dates as butterflies of the corresponding FEs.

The sampling order was randomized. All individuals seen in a ca. 3 m wide strip along the transect and no more than 5 m in front of the recording person were counted at a slow walking pace. Care was taken to avoid multiple counts of the same individuals as far as possible. The survey of the first 10 FE pairs and corresponding reference transects took place in 2016, with four recordings of each transect between 20 May and 25 August 2016. The second survey was in 2017, with eight FE pairs and corresponding reference transects being recorded three times each between 15 May and 15 August 2017.

All recordings were carried out between 10:00 and 17:00 CEST under mostly sunny weather conditions with cloud cover < 20 %, at wind strengths < 3 on the Beaufort scale and temperatures > 17° C. The butterflies were visually identified with close-focus binoculars or caught with a sweep net (diameter 50 cm), identified and then released. *Melitaea athalia aggr.* and *Melitaea parthenoides* were both present at selected study sites; certain individuals with distinct wing patterns could be identified without doubt. For statistical analysis, however, their numbers were pooled, because many individuals exhibited intermediate wing patterns and thus could not be identified beyond doubt during field surveys. The species pairs *Colias hyale / C. alfacariensis* and *Leptidea sinapis / L. juvernica*, which cannot be clearly distinguished on the basis of external characteristics, were combined and counted as single species. The nomenclature follows the Swiss Centre for the Cartography of Fauna (CSCF, 2022).

2.4. Data analysis and statistics

First, butterfly species count data from all surveys were pooled for each of the 36 FE transects and 34 meadow reference transects. In accordance with the pairwise study design, subsequent paired t-tests were performed to evaluate differences in “Butterfly species richness” and “Butterfly abundance” between improved and non-improved FEs. Similar tests were applied for the response variables “EOAS Butterfly species richness” and “EOAS Butterfly abundance”. All these analyses were performed separately for FE pairs adjacent to both extensively used and intensively used meadows. For paired t-tests, the only requirement is that the difference of each pair is normally distributed (McDonald, 2014). Corresponding tests proved approximate normal distribution for paired “Butterfly species richness” data and a well fitted normal distribution for paired “Butterfly abundance” data (Shapiro-Wilks tests, P = 0.11, and P = 0.94). For paired “EOAS Butterfly species richness” and paired “EOAS Butterfly abundance” data, (log + 1)-transformation was applied to achieve well fitted normal distribution (Shapiro-Wilks tests on (log + 1)-transformed data, P = 0.76, and P = 0.94).

To evaluate the joint impact of the two predictors “FE status” (improved vs. non-improved) and “Use intensity of adjacent meadow” (extensive vs. intensive) on the response variables “Butterfly species richness”, “EOAS Butterfly species richness”, “Butterfly abundance”, and “EOAS Butterfly abundance”, separate linear mixed effects models were built, using the “lme4” and «lmerTest» R packages (Bates et al., 2014; Kuznetsova et al., 2017). Beforehand, the most appropriate maximum likelihood fitted distribution was selected for each model, performing the *fitdist* command of the «fitdistrplus» R package (Delignette-Muller & Dutang, 2015). Q-Q plots were applied for visual checks of theoretical and empirical quartiles. As a consequence, no data transformation was required for the response variable “Butterfly species richness”, whereas (log + 1)-transformation was selected for the response variables “Butterfly abundance” and “EOAS Butterfly species richness”, leading to linear mixed effects models with restricted maximum likelihood fit (REML). Generalized linear effects models with negative binomial distribution, fitted with maximum likelihood approach (Laplace approximation), were applied to the response variable “EOAS Butterfly abundance”. “FE pair ID” and “FE exposition” were both defined as random variables in all mixed effects models. To decide whether interaction terms of the predictors “FE status” and “Use intensity of adjacent meadow” should be included in the models, AIC values were calculated using the *aictab* command of the «AICcmodavg R» package (Mazerolle, 2020), implementing maximum likelihood fit instead of REML fit. The comparisons revealed that all models without interaction terms had a better fit with lower AIC values than respective models containing interaction terms. Collinearity between the fixed predictors was checked with the variance inflation factor (VIF), provided by the «car» R package (Fox & Weisberg, 2018). All VIF values were 1, thus indicating low collinearity (Zuur et al., 2009). Finally, joint and partial regressions were run for improved and non-improved FEs to assess the effect of “FE heterogeneity” on “Butterfly species richness”, “Butterfly abundance”, “EOAS Butterfly species richness” and “EOAS Butterfly abundance”. Adjusted R^2-values were used as goodness-of-fit measures to evaluate model accuracy (Welham et al., 2014).

3. Results

3.1. Overview of butterfly species richness and abundance

In total, 50 butterfly species with 2853 individuals along the 36 FE transects and 34 meadow reference transects were recorded (Table A2 in the Supplementary material). FE transects contained 44 species with 1172 individuals, including 18 EOAS species with 217 individuals. Meadow reference transects contained 37 species with 1681 individuals, including 16 EOAS species with 504 individuals.

According to the Swiss Red List for Butterflies (Wermeille et al., 2014), *Melitaea didyma* (Esper, 1778), *Melitaea parthenoides* Keferstein, 1851, *Polyommatus thersites* (Cantener, 1835) and *Satyrium pruni* (L., 1758) are considered to be vulnerable (VU). *Boloria dia* (L., 1767), *Brintesia circe* (Fabricius, 1775), *Cupido argiades* (Pallas, 1771), *Pieris mannii* (Mayer, 1851), *Pyrgus armoricanus* (Oberthür, 1910) and *Spialia sertorius* (Hoffmannsegg, 1804) are listed as near threatened (NT).

3.2. Butterflies’ response to forest edge improvements and forest edge heterogeneity

Improved FEs had significantly more butterfly species (mean 8.72 ± S.D. 3.91) and butterfly individuals (mean 40.22 ± S.D. 25.47) than non-improved FEs (mean 5.39 ± S.D. 2.97 and 24.89 ± S.D. 27.35) (paired t-tests, $P < 0.001$ and $P = 0.016$) (Fig. 1). EOAS species also manifested a strong preference for improved FEs, resulting in higher “EOAS Butterfly species richness” and “EOAS Butterfly abundance” values compared to non-improved FEs (paired t-tests on (log + 1)-transformed data, ps < 0.001) (not shown).

In total, FEs with higher heterogeneity scores had significantly more butterfly species than FEs with lower heterogeneity scores (overall linear regression, multiple $R^2 = 0.184$, $P = 0.009$) (Fig. 2). No significant results emerged, however, when heterogeneity scores were separately fitted to «Butterfly species richness» of improved and non-improved FEs (partial regressions, multiple $R^2 = 0.108$, $P = 0.18$ and multiple $R^2 =$

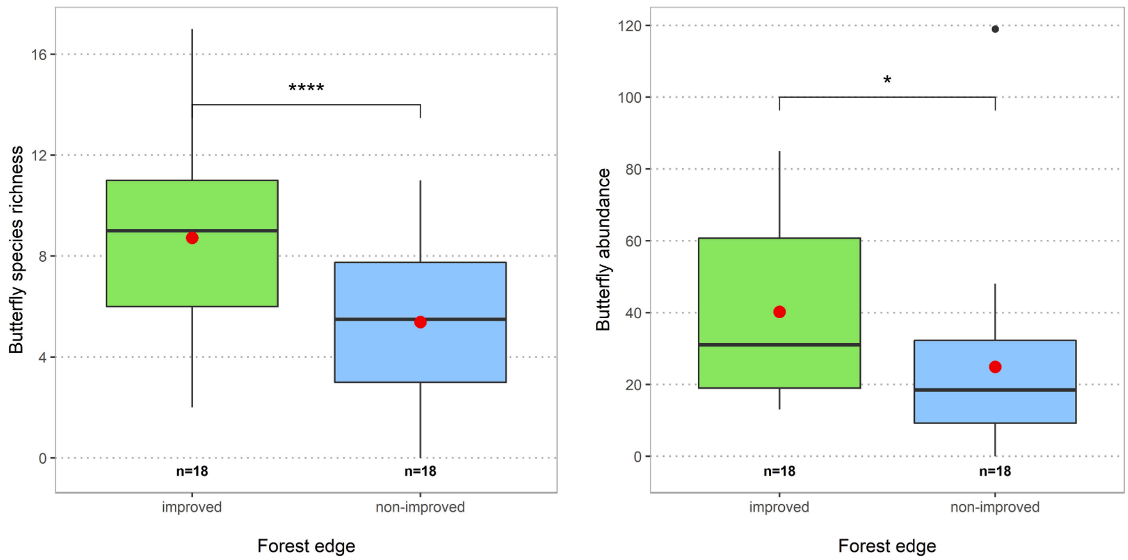

Fig. 1. "Butterfly species richness" (left) and "Butterfly abundance" (right) along improved FEs (green) and non-improved FEs (blue). Median (bold line), mean (point), interquartile range (box), min–max values (whisker), and outlier (small point) are shown. The significance levels represent outcomes of paired t-tests. n = sample size. **** $P < 0.0001$; * $P < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

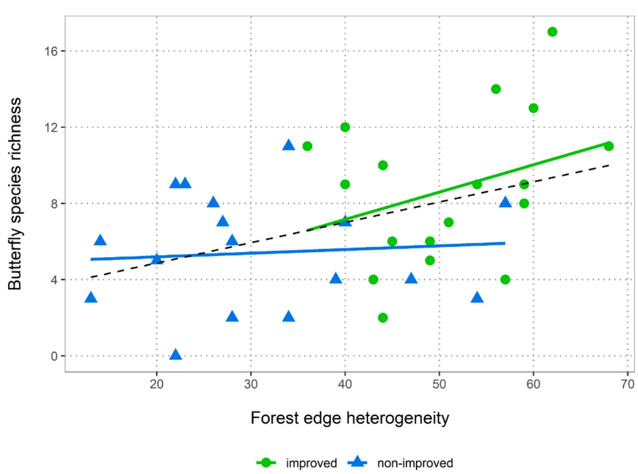

Fig. 2. Effect of "FE heterogeneity" on "Butterfly species richness" along improved FEs (green) and non-improved FEs (blue). "FE heterogeneity" scores relied on 16 floristic and structural indicators (for details see ZHAW, 2020). The dotted black line represents overall regression ($F_{1,34}$, multiple $R^2 = 0.184$, $P = 0.009$), the green line partial regression on improved FEs ($F_{1,16}$, multiple $R^2 = 0.108$, $P = 0.18$), and the blue line partial regression on non-improved FEs ($F_{1,16}$, multiple $R^2 = 0.007$, $P = 0.74$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

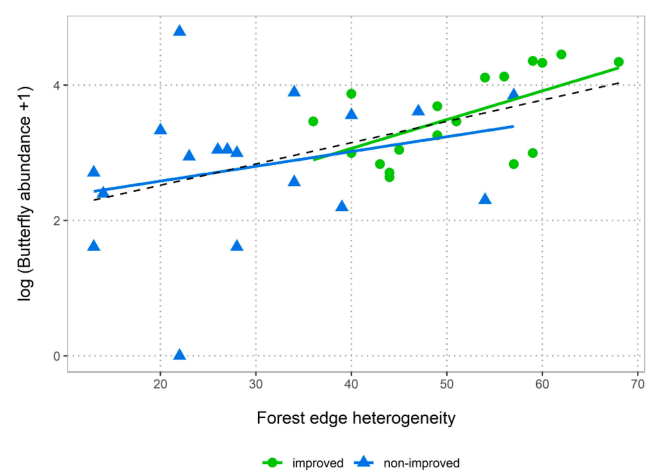

Fig. 3. Effect of "FE heterogeneity" on "Butterfly abundance" along improved FEs (green) and non-improved FEs (blue). "Butterfly abundance" data presented as (log + 1)-transformed values. "FE heterogeneity" scores relied on 16 floristic and structural indicators (for details see ZHAW, 2020). The dotted black line represents overall regression ($F_{1,34}$, multiple $R^2 = 0.261$, $P = 0.002$), the green line partial regression on improved FEs (partial linear regression, $F_{1,16}$, multiple $R^2 = 0.351$, $P = 0.001$) and the blue line partial regression on non-improved FEs ($F_{1,16}$, multiple $R^2 = 0.072$, $P = 0.28$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.007, $P = 0.74$).

In total, FEs with higher heterogeneity scores contained significantly more butterfly individuals than FEs with lower heterogeneity scores (overall linear regression, multiple $R^2 = 0.261$, $P = 0.002$) (Fig. 3). When fitting the heterogeneity scores to "Butterfly abundance" of improved and non-improved FE separately, the respective partial regressions yielded a significant effect for improved FEs (partial linear regression on (log + 1)-transformed data, multiple $R^2 = 0.351$, $P = 0.001$), but no significant effect for non-improved FE (partial linear regression on (log + 1)-transformed data, multiple $R^2 = 0.072$, $P = 0.28$).

"EOAS Butterfly species richness" of improved and non-improved FEs were both positively influenced by higher heterogeneity scores (partial linear regressions, multiple $R^2 = 0.281$, $P = 0.024$ and multiple $R^2 = 0.252$, $P = 0.034$). Along improved FEs, "EOAS Butterfly abundance" increased markedly with higher "FE heterogeneity" (partial linear regression on (log + 1)-transformed data, multiple $R^2 = 0.367$, $P = 0.008$), but no significant effect was found along non-improved FEs (partial linear regression on (log + 1)-transformed data, multiple $R^2 = 0.126$, $P = 0.15$) (not shown).

3.3. *Effect of adjacent meadows' use intensity on forest edge butterflies*

"Butterfly species richness" was significantly higher on improved FEs compared to non-improved FEs, regardless of adjacent meadows' use intensity (paired t-tests for FEs adjacent to extensively used and FEs adjacent to intensively used meadows, $P = 0.004$ and $P < 0.001$) (Fig. 4).

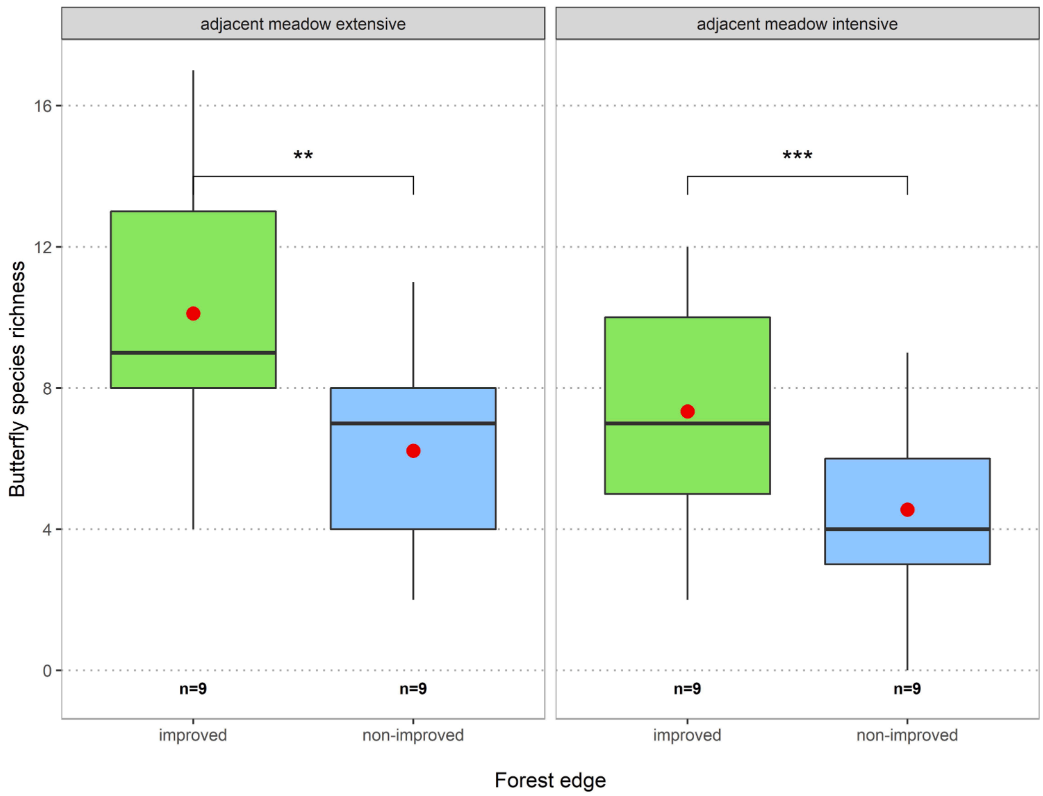

Fig. 4. "Butterfly species richness" along improved FEs (green) and non-improved FEs (blue) adjacent to extensively (left) and intensively (right) used meadows. Median (bold line), mean (point), interquartile range (box), min–max values (whisker) are shown. The significance levels represent outcomes of paired t-tests. n = sample size. *** P < 0.001; ** P < 0.01. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

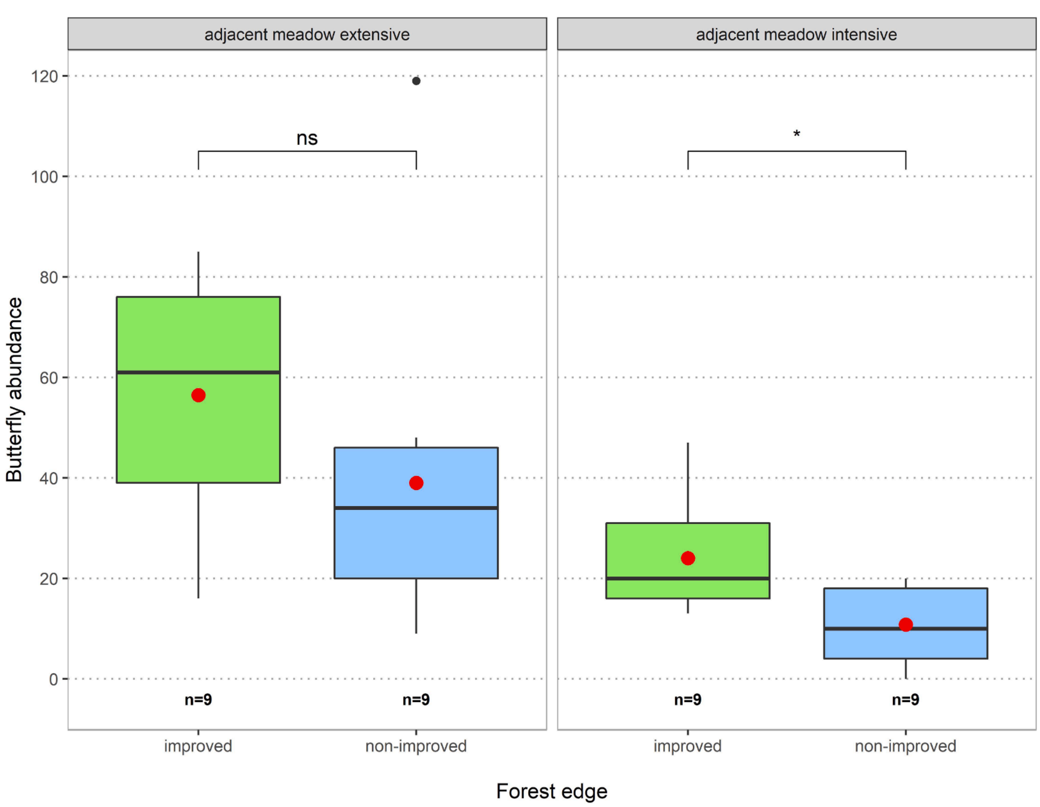

Fig. 5. "Butterfly abundance" along improved FEs (green) and non-improved FEs (blue) adjacent to extensively (left) and intensively (right) used meadows. Median (bold line), mean (point), interquartile range (box), min–max values (whisker) and outlier (small point) are shown. The significance levels represent outcomes of paired t-tests. n = sample size. * P < 0.05; ns = not significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

There was no significant difference in “Butterfly abundance” between improved and non-improved FEs adjacent to extensively used meadows (paired *t*-test, P = 0.10), but a significantly higher “Butterfly abundance” along FE transects adjacent to intensively used meadows (paired *t*-test, P = 0.018) (Fig. 5).

“Butterfly species richness” of reference transects on extensively used meadows was marginally significantly higher when these meadows were situated along improved instead of non-improved FEs (paired *t*-test, P = 0.077). “Butterfly abundance” of reference transects, however, did not significantly depend on “FE status” (paired *t*-test, P = 0.30). Corresponding analyses for “Butterfly species richness” and “Butterfly abundance” of reference transects on intensively used meadows yielded no significant effect of “FE status” either (paired t-tests, P = 0.81 and P = 0.68) (not shown).

3.4. Combined effect of forest edge quality and adjacent meadows' use intensity on butterflies

When exploring the combined effect of the two predictors “FE status” and “Use intensity of adjacent meadow” in a mixed effects model, with “FE pair ID” and “FE exposition” as random variables, the essentials of the paired t-tests, as illustrated in Figs. 4 and 5, could be confirmed. As preliminary calculations revealed that “FE heterogeneity” scores were consistently higher on improved FE than on non-improved ones (50.89 points ± S.D. 8.95 versus 30.06 points ± S.D. 13.18; Welch two sample *t*-test, P < 0.001), “FE heterogeneity” was considered to be adequately represented by the predictor “FE status” and therefore excluded from all mixed effects models.

The final model output shows a significant positive effect of “FE status” on “Butterfly species richness” (linear mixed effects model, P < 0.001), while the effect “Use intensity of adjacent meadow” was less evident and not significant (Table 1). With respect to “Butterfly abundance”, both predictors yielded significant positive effects (linear mixed effects models, P = 0.003 and P < 0.001). “EOAS Butterfly species richness” benefited significantly from improved FEs and extensively used adjacent meadows (linear mixed effects models, P < 0.001 and P = 0.007). Comparable results were obtained for “EOAS Butterfly abundance” (generalized linear mixed effects models, ps < 0.001).

Table 1
Results of (generalized) mixed effects models, testing for the impact of the predictors “FE status” and “Use intensity of adjacent meadow” on “Butterfly species richness” and “Butterfly abundance”, with separate calculations for EOAS species. “FE pair ID” and “FE exposition” are defined as random variables. Estimates represent t-values for normal and lognormal distributions, and z-values for negative binomial distributions.

Response variable	Predictor variable	Estimate	S.E.	P	Distribution
Butterfly species richness	FE status [level improved]	3.33	0.52	<0.001	normal
	Adjacent meadow [level extensive]	2.22	1.50	0.158	
EOAS Butterfly species richness	FE status [level improved]	0.57	0.12	<0.001	lognormal
	Adjacent meadow [level extensive]	0.63	0.20	0.007	
Butterfly abundance	FE status [level improved]	0.73	0.21	0.003	lognormal
	Adjacent meadow [level extensive]	1.02	0.25	<0.001	
EOAS Butterfly abundance	FE status [level improved]	1.39	0.34	<0.001	negative binomial
	Adjacent meadow [level extensive]	2.27	0.50	<0.001	

4. Discussion

4.1. Butterflies' response to forest edge improvements and forest edge heterogeneity

In the longer term, the canton of Aargau, where this study took place, aims to ecologically improve a total of 400 km of FEs, of which more than 200 km have already been completed (Kanton Aargau, 2019). The higher botanical and structural “FE heterogeneity” of improved FEs compared to non-improved FEs support this ongoing cantonal promotion scheme. “Butterfly species richness” and “Butterfly abundance” were themselves positively associated with higher “FE heterogeneity”, suggesting a direct link between the structural and botanical diversity of FEs and their butterfly fauna. Comparable results were obtained when the data set was restricted to a subsample of stenotopic EOAS butterfly species as indicators for extensively managed farmland.

In a previous pilot research project on the contribution of forest ecotone structures to regional biodiversity in Switzerland, about one third more arthropod species were found in structurally heterogeneous FEs compared to steep and uniform FEs (Flückiger & Duelli, 1997). Although butterflies were not assessed in that study, the results support the assumption whereas the contribution of managed forests to regional biodiversity in Western Europe is largely determined by the structure of their marginal areas. Such ecotones have proven to be crucial for the development of specialized butterfly species (Habel et al., 2022).

The vast majority of European butterfly species is heliophilous and avoids shady conditions (Settele et al., 2009). However, at high temperatures above 30 °C approximately, the body temperature of butterflies can rise beyond a lethal maximum (Settele et al., 2009). In such conditions, butterflies restrict their activities to shaded FEs and higher vegetation structures (Wickman, 1988). The strength of this microclimatic effect is related to latitude, orientation and density of the vegetation (Herlin, 2001). Therefore, it is assumed that in diverse and highly structured FEs, a broad range of microclimatic niches allows for selective thermal regulation during the day and between seasons. For this reason, and with special regard to possible negative effects on grassland butterflies which are fully exposed to solar radiation, butterfly conservation schemes should incorporate measures to promote the maintenance of undisturbed woody vegetation in the immediate vicinity of grasslands. Or, at least, they should prevent the complete mowing of large areas (Marini et al., 2009). Such measures seem to be even more relevant with respect to climate warming (Stuhldreher & Fartmann, 2018).

Woodland margins can provide important habitats for edge-associated butterfly species with shrub-feeding caterpillars (Pullin, 2012). Such species found in this study include *Gonepteryx rhamni* (L., 1758) (mainly on *Frangula alnus* and *Rhamnus cathartica*), *Limenitis camilla* (L., 1764) (mainly on *Lonicera xylosteum*), *Satyrium w-album* (Knoch, 1782) (on *Ulmus* spp.), the Red List species *Satyrium pruni* (L., 1758), and *Thecla betulae* (L., 1758) (both mainly on *Prunus spinosa*). *G. rhamni* and *S. w-album* (singleton) were only present on improved FEs, whereas the only individual of *S. pruni* was found on a non-improved FE. *L. camilla* was more frequent on non-improved FEs, and *T. betulae* was present on both FE types with one specimen each. All in all, these species distributions do not provide a clear-cut picture of the effect of FE improvements on shrub-feeding butterfly species.

4.2. Combined effect of forest edge heterogeneity and landscape management on butterflies

The conservation of biodiversity in complex landscapes depends on the ability to preserve both forest and open habitats within the landscape (Lacasella et al., 2015). In early spring, FEs and hedgerows offer the main nectar resources (Langlois et al., 2020), and only later in the year, butterflies primarily depend on nearby flower-rich open grasslands. The availability of shelter and food resources has been regarded as one of the main elements which determine habitat quality for butterflies (Dennis & Sparks, 2006; Schlegel & Hofstetter, 2021). The richest sites in butterfly species are those containing a mosaic of grassland, shrub and woodland, which enhances the heterogeneity around the meadows (Marini et al., 2009). An increase in available niche space, provision of refuges and opportunities for isolation and divergent adaptation are thought to enhance species coexistence, persistence and diversification (Stein et al., 2014). A fine grained and dynamic landscape pattern with a high density of semi-natural grassland and many FEs increases such heterogeneity (Schneider & Fry, 2001). Extensively used semi-natural ECA meadows are crucial in this context, as plant species richness and abundance benefit from a higher share of ECAs (Stoeckli et al., 2017).

Positive edge responses on butterflies have been found to be due to increased access to resources near the edge of a preferred habitat or to particular complementary resources that are confined to the adjacent patch (Ries & Sisk, 2008). Forests might mitigate the negative effects of habitat loss caused by agricultural intensification, which may be particularly important for those butterfly species that respond differently to land cover in their neighborhood (Bergman et al., 2018). In the present study, the landscape context has been taken into account by placing half of the improved and half of the non-improved FEs along extensively and intensively used meadows. This leads to a gradual contrast pattern with high contrast situations between improved FEs with high heterogeneity scores and adjoining intensively used meadows and, on the other hand, low contrast situations between non-improved FEs with low heterogeneity scores and adjoining intensively used meadows. This methodological approach is in line with the recommendations of Alignier et al. (2014), who emphasize the need for careful consideration of edge types, e.g. their contrast with adjoining non-forested habitats, to identify the relevant factors and mechanisms behind edge-related biodiversity response patterns.

Since most semi-natural meadows in ecological compensation areas (ECAs) of the lower Swiss Central Plateau are mown shortly after the first legally permitted cutting date of June 15 (Schweizer Bundesrat, 2013), nectar resources for adult butterflies and caterpillar food plants often disappear in one fell swoop over larger areas. Certain butterfly species, such as *Melanargia galathea* (L., 1758), which are also common in the present study, are known to prefer taller sward-conditions for oviposition (Schweizerischer Bund für Naturschutz, 1987). Thus, *M. galathea* and similar species depend on late cuts or asynchronous management. A study conducted in the Swiss lowlands showed higher butterfly abundance on uncut refuges after mowing, by a factor of about three, than on control meadows (Kühne et al., 2015). However, according to current legislation, it is not obligatory for farmers in Switzerland to leave uncut refuges after cutting (Schweizer Bundesrat, 2013). Thus, uncut or later-cut margins along edges may not only provide corridors for butterflies to move across the landscape (Dover, 1994), but potentially also offer additional nectar resources and egg-deposition sites in a resource-poor matrix. Keeping unmown or later-mown grass refuges along herbaceous FEs can therefore be considered as a simple and easy measure to promote butterfly populations in semi-natural grasslands, particularly when FEs provide supplementary or complementary food resources (Ouin et al., 2004; Van Halder et al., 2011).

Wermeille et al. (2014) emphasize, that fresher and west to east facing FEs should not be neglected, since several butterfly species are known to find suitable humid conditions for the development of pre-imaginal stages there. Higher humidity favors woody species like the European aspen (*Populus tremula*), the main caterpillar food plant of the vulnerable Swiss Red List species *Limenitis populi* (L., 1758) or the common willow (*Salix caprea*), the main caterpillar food plant of the potentially threatened species *Apatura iris* (L., 1758) (Schweizerischer Bund für Naturschutz, 1987).

For conservation reasons, and as is the case in the study area (Kanton Aargau, 2020), it is more likely that FE improvements will be carried out along extensively used meadows with already higher ecological quality rather than along monotonous extensively used meadows. Furthermore, sun-exposed and nutrient-poor FEs often enjoy priority for FE improvements, also in the study area, as they generally exhibit a higher potential for improving ecological quality (Babbi et al., 2016). For this reason, the higher butterfly diversity found on improved FEs could also be due to the fact that (i) their surroundings or (ii) their sun exposure both offer better conditions for butterflies. The methodological approach of this study addressed these potential biases as follows:

(i) Reference meadow transects were implemented to compare the adjacent meadows' specific butterfly fauna. It turned out that extensively used meadows along improved FEs tended to be slightly more species-rich than those along non-improved FEs, without being statistically significant though. With respect to "Butterfly abundance", no obvious difference was found. Additionally, no considerable variation in "Butterfly species richness" and "Butterfly abundance" was observed between intensively used meadows along improved and non-improved FEs. Consequently, the significant positive effect of FE improvements on butterflies, as found in this study, is consistent and has only to be put somewhat into perspective in the case of the improved FEs adjoining extensively used meadows.

(ii) Improved and non-improved FEs adjacent to extensively used meadows did not differ significantly, but marginally significantly, in their exposition. Therefore, possible biases of "FE exposition" on "Butterfly species richness" and "Butterfly abundance" were accounted for by defining "FE exposition" as a random factor in all mixed effects models.

5. Conclusions and conservation implications

In summary, this study revealed (i) that FE improvements in the study area had positive impacts on structural and botanical "FE heterogeneity", (ii) that overall "Butterfly species richness" and overall "Butterfly abundance" benefited from higher "FE heterogeneity", (iii) that "Butterfly species richness" and "EOAS Butterfly species richness" were higher on improved FEs, irrespective of adjacent meadows' use intensity, and (iv) that "Butterfly abundance" and "EOAS Butterfly abundance" were both higher on improved FEs, for the former mainly due to high contrast situations between improved FEs and adjacent intensively used meadows. Therefore, FE improvement activities don't necessarily need to focus on south-facing FEs adjacent to extensively used farmland, such as proposed by the canton of Aargau (Kanton Aargau, 2020). Additionally, it seems advisable to improve selected FEs next to intensively used meadows and to include more humid and sun-protected FEs as shady butterfly retreat sites during the increasingly hot summer days and as potential reproduction sites for specialized hygrophilous butterfly species.

CRediT authorship contribution statement

Jürg Schlegel: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix Table A1

FE pair ID	FE status	FE latest improvement	FE exposition	FE m a.s.l.	FE heterogeneity [points]		Use intensitiy of adjacent meadow	Butterfly recording year
1	improved	2006	SW	417	high	56	extensive	2017
1	non-improved	–	SW	345	very low	27	extensive	2017
2	improved	2007	S	622	very high	59	extensive	2016
2	non-improved	–	S	742	low	34	extensive	2016
3	improved	2007	S	578	very high	59	extensive	2017
3	non-improved	–	S	552	high	57	extensive	2017
4	improved	2008	S	677	high	57	extensive	2016
4	non-improved	–	S	712	high	54	extensive	2016
5	improved	2008	SE	508	very high	62	extensive	2016
5	non-improved	–	S	551	very low	22	extensive	2016
6	improved	2010	SW	476	very high	68	extensive	2016
6	non-improved	–	SW	543	medium	40	extensive	2016
7	improved	2012	SW	711	high	54	extensive	2017
7	non-improved	–	NE	658	very low	20	extensive	2017
8	improved	2011	S	485	very high	60	extensive	2016
8	non-improved	–	S	510	medium	34	extensive	2016
9	improved	2013	W	514	high	49	extensive	2017
9	non-improved	–	N	598	medium	47	extensive	2017
10	improved	2006	SE	417	high	49	intensive	2016
10	non-improved	–	E	392	very low	28	intensive	2016
11	improved	2009	E	349	medium	43	intensive	2016
11	non-improved	–	E	459	extremely low	13	intensive	2016
12	improved	2008	W	677	low	36	intensive	2017
12	non-improved	–	NW	659	extremely low	14	intensive	2017
13	improved	2009	SW	524	medium	40	NA	2017
13	non-improved	–	NW	521	very low	28	NA	2017
14	improved	2009	SE	508	medium	40	intensive	2017
14	non-improved	–	SW	461	very low	23	intensive	2017
15	improved	2012	SW	424	high	51	intensive	2016
15	non-improved	–	NW	427	extremely low	13	intensive	2016
16	improved	2012	SE	414	medium	45	intensive	2016
16	non-improved	–	SE	445	medium	39	intensive	2016
17	improved	2011	E	490	medium	44	intensive	2017
17	non-improved	–	NW	505	very low	26	intensive	2017
18	improved	2013	SW	338	medium	44	intensive	2016
18	non-improved	–	NW	340	very low	22	intensive	2016

Supplementary material Table A2

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120413.

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