



Effects of coppicing on butterfly communities of woodlands



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ABSTRACT

During the past 150 years traditional forest management practices have been neglected in most parts of Central Europe with severe consequences for biodiversity. Coppicing has in the past been one of the most important forms of management for broadleaved woodlands. To investigate the effects of coppicing, we analyzed species richness and density of butterfly communities in coppiced woodlands with standards in the French Alsace. We sampled butterflies and environmental parameters through standardized transect walks ($n = 37$ plots) in five different successional stages (first-year, second-year, fringe, shrub and wood stage). With 36 butterfly species in total, among them 13 threatened species, coppice woodlands had a comparatively high species richness. Butterflies showed a clear response to coppicing, with each successional stage harboring a unique assemblage. However, species richness and densities of resident and threatened species were highest in early and mid-successional stages (second year and fringe stage) and lowest in the latest successional stage (wood). The pattern was slightly different for migratory species. Species richness and densities decreased along the successional gradient from the first-year to the wood stage. Warm microclimatic conditions (all groups), the availability of nectar resources (migratory species) and sufficient host-plants growing under suitable conditions (resident and threatened species) were associated with higher densities and greater diversity of butterflies. Based on our results, maintenance and expansion of coppice management should be a suitable tool to counteract the general decline of woodland butterflies and the loss of early-successional species in woodlands.

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1. Introduction

Woodlands are, on the basis of area occupied, one of the most important land-use types in Central Europe, covering about 30% of the total land surface (Steinecke and Venzke, 2003). However, despite a continuous increase in forest cover, species richness in woodlands is decreasing (Vodka et al., 2009). As shown for many other habitats (Foley et al., 2005; Sala et al., 2000; Vitousek, 1994) land-use change has been identified as the major threat to forest biodiversity (Peterken, 1996; Simberloff, 1999; Warren and Key, 1991).

In the past, temperate woodlands had to satisfy a variety of different human requirements (Vera, 2000). They were used as coppice, wood-pasture or wood-meadow; pollarding, litter raking and wood sampling were widespread (Ellenberg and Leuschner, 2010; Horák et al., 2012; Peterken, 1996). Traditionally managed woodlands were sunny and heterogeneous, comprising mosaics of different stages of forest succession, and had a high biodiversity (Benes et al., 2006; Vodka et al., 2009; Warren and Thomas, 1992). Over the past 150 years, traditional management practices have

become neglected in most parts of Central Europe (Bergmeier et al., 2010; Güthler et al., 2005). Consequently, these formerly open woodlands have developed into shady high forests with a low species richness.

Coppicing was in the past one of the most important traditional forms of management for broadleaved woodlands. Coppices are woods that are repeatedly cut down and which regenerate by sprouting from stumps of felled trees (Buckley, 1992; Peterken, 1996). In the 17th and 18th centuries, coppice woodlands were the dominant forest type in many parts of Central Europe (Güthler et al., 2005), but at the present time, in most countries, occupy a share of clearly below 1% of all woodlands (Germany: BMELF, 1998; Czech Republic: Settele et al., 2009). However, in Northern and North-eastern France coppiced woodlands are still traditionally managed and common (Treiber, 2003). Our study region, the Upper Rhine Rift Valley in the French Alsace, contains approximately 3000 ha of managed coppice with standards.

Butterflies are excellent indicators for the effects of forest management. They have very specific habitat requirements, such as needing specific host plants (Munguira et al., 2009) and microhabitats for their immature stages (García-Barros and Fartmann, 2009). Moreover, woodlands are among the most species-rich habitats for butterflies throughout Europe (Van Swaay et al., 2006). Many butterflies reach their northern range limit in central Europe,

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and this is the reason why many of them occur in sunny open habitats (Warren and Key, 1991). Open patches created by coppicing favor the growth of host plants and nectar resources, and provide a warm microclimate for larval development (Smallidge and Leopold, 1997; Warren, 1985).

In general, there have only been a few studies on butterflies of coppice woodlands and these mostly involve a small number of species or single species (Warren and Thomas, 1992). Many aut-ecological studies concerning coppice management and its influence on butterflies have been carried out in Britain (Clarke and Robertson, 1993; Fuller and Warren, 1993; Hodgson et al., 2009; Warren, 1987a,b,c, 1991; Warren et al., 1984). Recently, the effects of coppicing on butterflies have attracted considerable interest in Central Europe. However, these studies have also focussed on the analysis of a single species (Freese et al., 2006; Konvička and Kuras, 1999; Konvička et al., 2008). Exceptions include a study on the effects of intensive game keeping and coppicing on butterflies in a woodland in the Czech Republic (Benes et al., 2006) and a descriptive study on the butterflies of the coppice woodlands of the French Alsace (Treiber, 2003). Accordingly, despite the high conservation value of coppice woodlands (BLF, 2008; Buckley, 1992; Gütthler et al., 2005; Peterken, 1996), a large gap exists in knowledge about the effects of coppicing on butterfly communities in general and particularly in Central Europe.

By considering butterfly communities for certain stages of woodland succession, we expected to provide distinctly deeper insights into the response of butterflies to coppicing. We studied resident, migratory and threatened species separately in order to develop conservation recommendations for butterflies in woodlands.

The main hypotheses are:

- (i) Coppice woodlands are refuges for many, in some cases threatened, butterfly species.
- (ii) Early successional stages are of special relevance to butterfly conservation, as species richness and density decrease with increasing shade and decreasing host-plant and nectar-resource availability.
- (iii) Resident, migratory and threatened species have different requirements concerning host-plant and nectar-resource availability.

2. Materials and methods

2.1. Study region and study areas

The study region, the Alsacian Hardt in the Upper Rhine Rift Valley, is located in North-eastern France near the border to Germany (48°06'N, 7°30'E and 47°52'N, 7°25'E) at an elevation of ~200 m a.s.l., and has a north–south extension of about 22.5 km (Fig. 1). Due to the location in the rain shadow of the Vosges, the climate is generally very dry and warm with an annual precipitation of 550–640 mm and a mean annual temperature of ~10 °C (stations Colmar, Neuf-Brisach, Meyenheim; Treiber and Remmert, 1998).

The study was carried out in coppice woodlands with standards within five larger woodlands: Bois de Biesheim, Kastenwald, Bois de Dessenheim, Niederwald and Bois de Rothleible (hereafter called study areas) (Fig. 1). The size of the woodlands ranged from 140 to 1303 ha (mean \pm SE = 697 \pm 180 ha). Coppicing is the traditional management form of these oak-hornbeam woodlands (*Galio-Carpinetum*; Treiber, 2003) that are protected by the EU Habitats Directive (Ssymank et al., 1998). Usually the size of the 'coupes' (areas of woodland subject to felling) is between 1 and 3 ha and the coppice cycle is 31 and 41 years, respectively (Treiber, 2003).

2.2. Study plots

Due to their vegetation structure the study plots were differentiated into five successional stages: first year (1ST YEAR), second year (2ND YEAR) and several years after felling with a dense herb layer (FRINGE; 3–7 years after felling), shrub layer (SHRUB; 8–15 years) or tree layer (WOOD; more than 15 years) (Fig. 2). In total we sampled 37 plots (4–15 per study area) with 7 and 8 plots for each successional stage, respectively. Each plot had a size of 500 m² (20 m \times 25 m) and was established in the center of the patch to avoid edge effects. Each first-year and second-year plot was adjacent to the next following stage to avoid the potential effects of a colonization lag due to isolation (cf. Thomas, 1991; Warren and Thomas, 1992).

2.3. Butterflies

We sampled butterflies in 2010 using standardized transect counts (Pollard and Yates, 1993). Butterflies and their flower visits were recorded along a sinusoidal transect of 5 m width covering the whole study plot. Each transect walk took exactly 15 min, excluding time taken to identify butterfly or flower species. We visited all plots seven times every two weeks (May–August), between 10:00 and 17:00 h (GTM +2) and only during suitable weather conditions (cf. Pollard, 1977). Species numbers were pooled for each study plot over the sampling period. To counteract the influence of voltinism, we used the maximum number of individuals seen during one of the seven transect walks per plot for further analysis of butterfly density. According to Eitschberger et al. (1991) butterfly species are differentiated into resident and migratory species. Butterfly threat status was classified using the red data book for the Alsacian Hardt (Treiber, 2003). Butterfly nomenclature follows Karsholt and Razowski (1996).

2.4. Habitat quality

We sampled habitat quality parameters (Table 1) in the study plot once between the end of June and the beginning of July 2010. Only nectar abundance was recorded for each transect walk. We quantified nectar abundance after each transect walk by counting all inflorescences in an area of 9 m² (3 m \times 3 m) inside the study plot (Fartmann, 2004). In order to take account of butterfly mobility, we moved the sampling area to the location where most of the flowers were found during the transect walk (Krämer et al., 2012). We weighted nectar abundance according to its use by butterflies derived both from data in the literature (Ebert and Rennwald, 1991a) and field observations. Flowers which were visited frequently received a higher Preference Class (PC) than unpopular flowers (Krämer et al., 2012). To calculate the weighted nectar abundance (NA_i) of the nectar plant species i , we used the following formula (Krämer et al., 2012):

$$NA_i = na_i \times \sum_{j=1}^k \frac{PC_{ij}}{NP_j}$$

where na_i is the absolute nectar abundance of the nectar plant species i , k is the number of butterfly species using plant species i as a nectar plant, PC_{ij} is the Preference Class of the butterfly species j for the nectar plant species i , and NP_j is the number of nectar plants of the butterfly species j . For further explanations see Krämer et al. (2012). We calculated the sum of all weighted nectar abundances for each plot at each transect walk, herein called 'nectar resources'. Nectar resources from the different transect walks were pooled by calculating means for each plot.

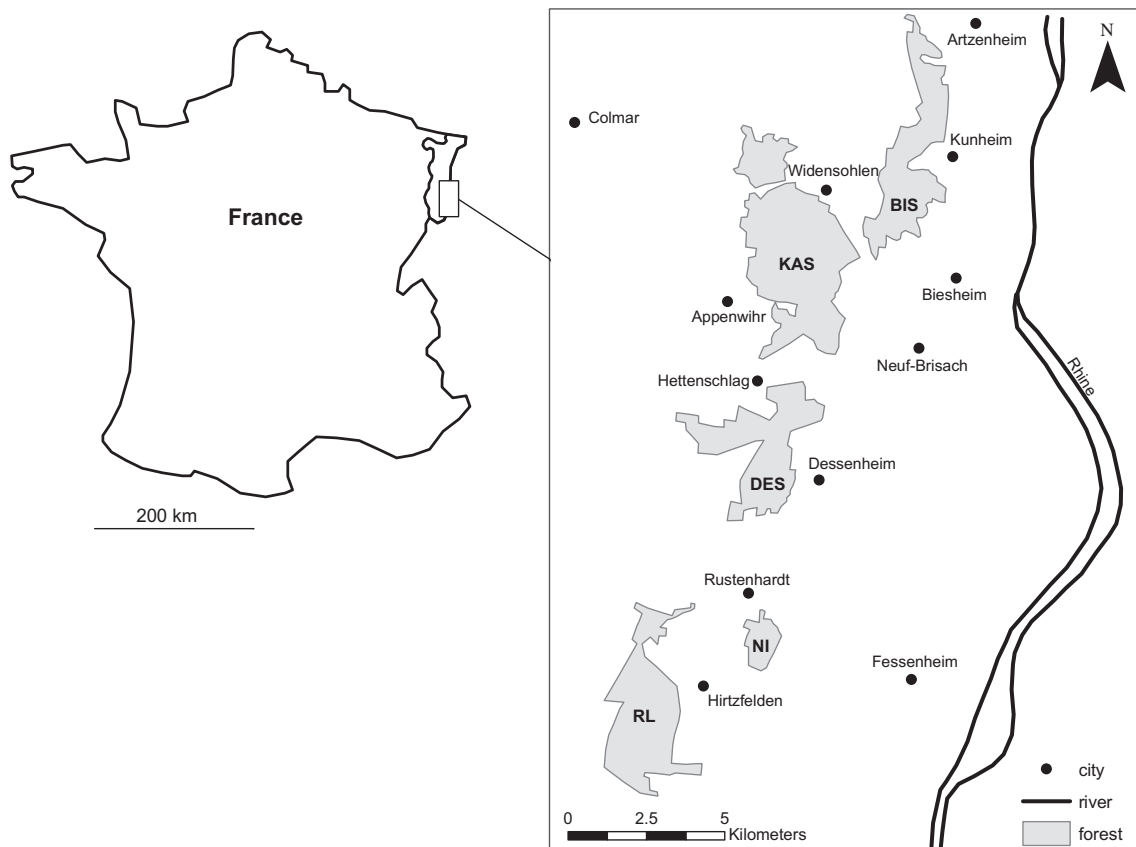


Fig. 1. Location of the study area, the Alsacian Hardt in North-eastern France. BIS = Bois de Biesheim, KAS = Kastenwald, DES = Bois de Dessenheim, NI = Niederwald, RL = Bois de Rothleible.

2.5. Statistical analysis

We conducted Generalized Linear Mixed-effects Models (GLMM: Imer, Bates et al., 2010) with Poisson error structure using R 2.10.1 (R Development Core Team, 2010) to analyze if environmental variables (Table 1) as well as species richness and density of resident, migratory and threatened butterfly species differed between the five successional stages. If overdispersion was detected then standard errors were corrected using quasi-Poisson GLMM (Crawley, 2007; Zuur et al., 2009). For all GLMMs, the variable *study area* was setup as a random factor. The significance of the predictor variables was assessed using likelihood ratio tests (Type III test). Differences between the successional stages were analyzed using post hoc tests. In the case of normal distribution and variance homogeneity, we applied a Tukey test; in all other cases a Dunn's test was used (using Sigma Plot 11).

In order to analyze which habitat quality parameters explained species richness and density of resident, migratory and threatened butterfly species we used the aforementioned GLMM procedures. To deal with multicollinearity, we summarized some variables prior to analysis (Table 1; for further information see Schröder et al., 2009). The effects of habitat quality on species composition were analyzed by Detrended Correspondence Analysis (DCA) in Canoco 4.5. Rare species, occurring in less than four of the 37 plots (frequency < 10%), were excluded from the analysis.

3. Results

3.1. Environmental conditions

All environmental parameters differed substantially among the five woodland stages (Table 2). Duration of sunshine during the

growing season decreased along the successional gradient from the very sunny first-year stage to the very shady wood stage. Tree-layer cover peaked in the wood stage, shrub-layer cover in the shrub stage and host-plant cover in the fringe stage. High bare ground coverage was characteristic of the first-year and wood stage. Availability of nectar resources was highest in the first three successional stages. The second-year and the fringe stage had the best-developed herb layer.

3.2. Butterflies

In total, we recorded 36 butterfly species, of which 13 were threatened (Appendix A), comprising a total of 1066 individuals on the 37 plots. The most frequent and abundant species were *Argynnis paphia* and *Pyronia tithonus*, both occurring in more than 80% of the plots and each comprising more than 10% of all individuals.

3.2.1. Species richness and densities

Both butterfly species richness and density differed for all three groups (resident species, migratory species and threatened species) among the five woodland stages (Fig. 3). Resident and threatened species showed similar patterns. Species richness and densities were highest in early and mid-successional stages (2ND YEAR, FRINGE) and lowest in late successional stages (WOOD and, partially, SHRUB). The pattern was slightly different for migratory species. Species richness and densities decreased along the successional gradient from the first-year to the wood stage.

Sunshine/nectar (all three groups) and herb layer (resident and threatened species) were the most important predictors of butterfly species richness and density (Table 3). Host-plant cover was a further predictor for the density of resident species. Moreover,

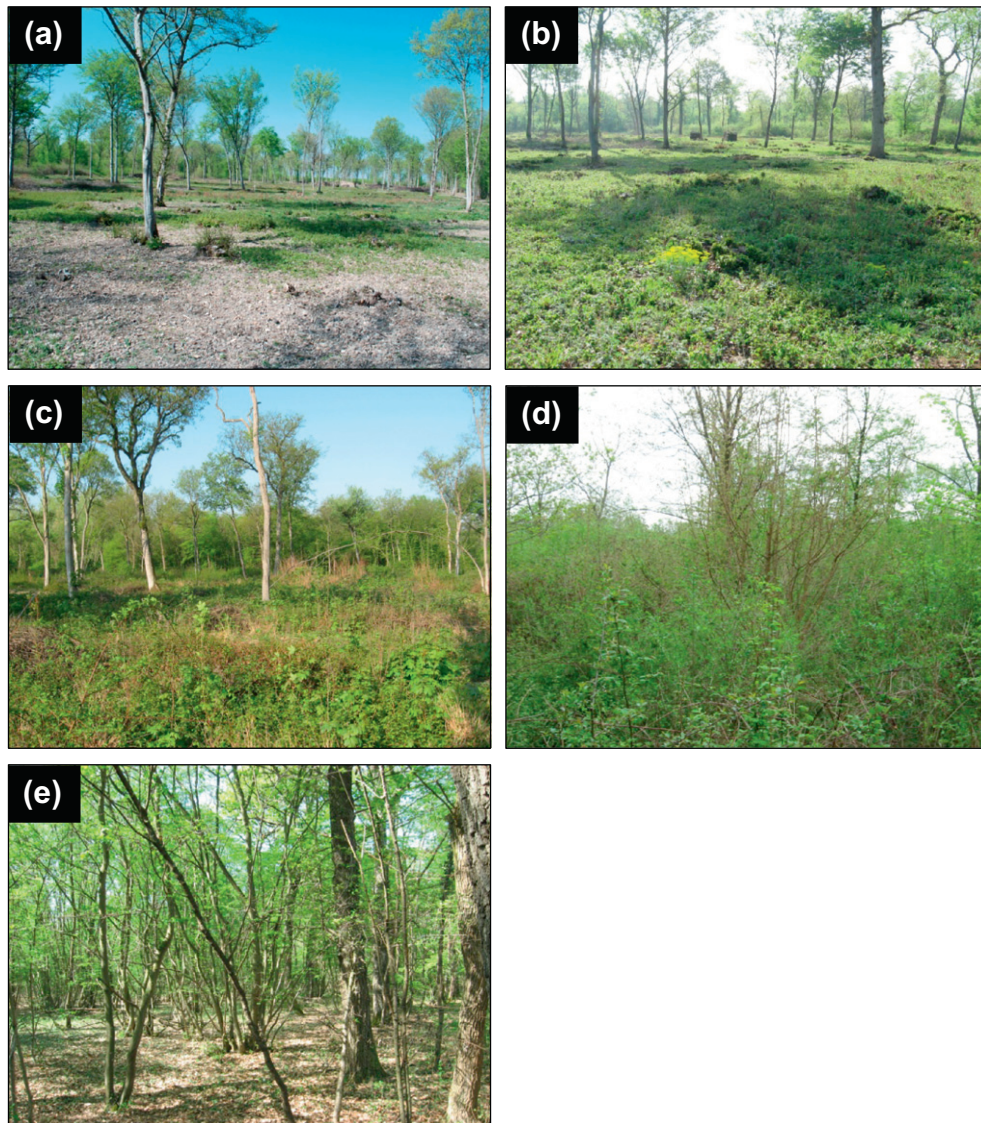


Fig. 2. Typical stands of the five woodland stages 1ST YEAR (a), 2ND YEAR (b), FRINGE (c), SHRUB (d) and WOOD (e) in the Alsacian Hardt, France.

the density of threatened species decreased with shrub-layer cover. The explanatory power of the models was generally high, with Pseudo R^2 [McFadden] values of 0.26–0.79 (Table 3).

3.2.2. Species response to environmental variables

DCA ordination showed a clear separation of butterfly species along the first two axes (Fig. 4). The variation in species composition was mainly determined by two environmental gradients. Sunshine/nectar and, to a lesser extent, herb layer were negatively correlated with the first axis (Fig. 4 and Table 4). Hence, sunshine duration, nectar resources and the cover, height and density of the herb layer decreased along the first axis. In contrast, the cover of trees and bare ground increased. The second axis was positively correlated with host-plant cover (Fig. 4 and Table 4).

Five groups of species were clustered, representing the different woodland stages and showing a similar response to the environmental variables (Fig. 4). The number of characteristic species for a certain stage was high in the first three successional stages, with six to eight species, of which one to three were threatened. The shrub stage had four and the wood stage only one typical species.

Species of the first-year stage (e.g. *Argynnis adippe* and *Boloria dia*) were associated with high bare ground cover, high sunshine

duration and a good availability of nectar resources. Sunny conditions and a well-developed herb layer with a high cover of host plants and nectar resources favored species of the second year stage (e.g. *Melitaea athalia* and *M. diamina*). Species of the fringe stage (e.g. *Brenthis daphne* and *P. tithonus*) preferred sites with a well-established herb and shrub layer including a high cover of host plants and moderately sunny conditions. Species occurring in the shrub stage (e.g. *Limenitis camilla*) were found under relatively shady conditions with a high cover of shrubs. The only species thriving in the wood stage with a dense tree canopy was *Pararge aegeria*.

4. Discussion

Butterflies showed a clear response to coppicing, with each successional stage harboring a unique assemblage. Both richness and density of butterfly species differed for all three groups (resident, migratory and threatened species) between the five woodland stages. Resident and threatened species showed similar patterns; species richness and densities were highest in early and mid-successional stages (2ND YEAR, FRINGE) and lowest in late successional stages (WOOD and, partially, SHRUB). The pattern was

Table 1

Overview of sampled parameters and their analysis in Generalized Linear Mixed-effects Models (GLMM) and Detrended Correspondence Analysis (DCA). Spearman's rank correlation coefficients (r_s) were calculated for all pairs of predictor variables. Strongly correlated variables ($r_s > |0.7|$) were summarized by applying Principle Component Analysis (PCA: Legendre and Legendre, 1998) into a single principal component, which was used in the subsequent analysis (cf. Poniatowski and Fartmann, 2011).

Parameter	Correlation		Factor levels	Statistics
	r_s	Used variable		
<i>Response variables</i>				
Species number ^a	.	.	Metric	GLMM
Density (individuals/100 m ²) ^a	.	.	Metric	GLMM, DCA
<i>Predictor variables</i>				
Successional stage ^b	.	.	5	GLMM
Herb-layer cover (%) ^c	0.91	Principal component: 'Herb layer'	Metric	DCA, GLMM
Herb-layer height (cm) ^c	0.83		Metric	
Herb-layer density (%) ^d	0.92		Metric	
Bare ground (%) ^c	−0.82		Metric	
Host plants (%) ^e	.	.	Metric	DCA, GLMM
Shrub layer cover (%) ^c	.	.	Metric	DCA, GLMM
Sunshine (h) ^f	0.88	Principal component: 'Sunshine/nectar'	Metric	DCA, GLMM
Nectar resources ^g	0.87		Metric	
Tree-layer cover (%) ^c	−0.82		Metric	
<i>Random effects</i>				
Study area ^h	.	.	5	GLMM

^a Values for 'resident', 'migratory' and 'threatened' species were tested separately in GLMM analysis.

^b See 'Study plots' (Section 2.2).

^c Measured three times at a randomly chosen location of 9 m² (3 m × 3 m) inside the study plot. For the tree layer the area size was 100 m² (10 m × 10 m). Means were calculated afterwards.

^d Measured within a frame of 30 cm depth and 50 cm width for different layers in 0–5, 5–10, ..., 25–30 cm height above ground (Poniatowski and Fartmann, 2008), here: summation of the mean values of all layers.

^e Cover of host plants (Ebert and Rennwald, 1991a,b) of monophagous and oligophagous butterflies.

^f Sum of potential daily sunshine duration for of all months (May–September) during the growing season; measured in the center of the plot with a horizontoscope after Tonne (1954), accuracy: ½ h.

^g See 'Habitat quality' (Section 2.4).

^h See 'Study region and study areas' (Section 2.1).

Table 2

Mean values (±SE) of environmental parameters in the five woodland stages. Differences between successional stages were tested using Generalized Linear Mixed-effects Models with Poisson or quasi-Poisson error structure and *study area* as a random factor. Different letters indicate significant differences (Tukey's test for herb-layer cover, otherwise Dunn's test; $P < 0.05$).

Parameter	1ST YEAR	2ND YEAR	FRINGE	SHRUB	Wood	P
<i>Cover (%)</i>						
Tree layer	12.1 ± 1.8 ^a	22.1 ± 5.1 ^a	24.3 ± 7.1 ^a	23.1 ± 4.5 ^a	78.8 ± 2.3 ^b	***
Shrub layer	3.0 ± 1.6 ^a	24.2 ± 8.0 ^{ab}	53.6 ± 8.4 ^{bc}	76.3 ± 2.5 ^c	16.0 ± 2.5 ^{ab}	***
Herb layer	44.6 ± 8.1 ^{ab}	74.3 ± 2.3 ^c	67.9 ± 4.4 ^{bc}	40.1 ± 10.4 ^{ab}	26.5 ± 7.4 ^a	***
Bare ground	35.7 ± 9.6 ^b	8.9 ± 1.9 ^{ab}	3.0 ± 0.8 ^a	17.1 ± 6.4 ^{ab}	50.6 ± 9.3 ^b	***
Host plants	21.1 ± 4.7 ^a	35.2 ± 5.4 ^{ab}	79.3 ± 15.0 ^b	56.2 ± 15.1 ^{ab}	40.7 ± 10.6 ^{ab}	***
Herb-layer height (cm)	30.0 ± 6.6 ^a	100.0 ± 8.7 ^c	88.6 ± 10.3 ^{bc}	42.5 ± 10.4 ^{ab}	33.6 ± 4.3 ^a	***
Herb-layer density (%)	113.1 ± 19.2 ^{ab}	309.7 ± 27.7 ^b	308.9 ± 27.4 ^b	140.9 ± 37.9 ^{ab}	28.6 ± 8.7 ^a	***
Nectar resources	918.3 ± 325.4 ^b	1125.1 ± 331.1 ^b	709.0 ± 142.9 ^b	349.0 ± 153.4 ^{ab}	9.4 ± 5.8 ^a	***
Sunshine (h)	32.9 ± 1.6 ^c	28.3 ± 1.8 ^{bc}	25.6 ± 4.3 ^{bc}	12.4 ± 4.4 ^{ab}	1.2 ± 0.2 ^a	***

*** $P < 0.001$.

slightly different for migratory species. Species richness and densities decreased along the successional gradient from the first-year to the wood stage.

In our study the summarized variable sunshine/nectar was the most important factor determining butterfly species richness and density. These results are in line with studies from the UK that identified shading in woodlands as the main driver of butterfly diversity and abundance (Greateorex-Davies et al., 1993; Sparks et al., 1996; Warren, 1985). Shading affects butterflies indirectly by altering the microclimatic conditions and the quantity of host plants and nectar resources (Sparks et al., 1996; Warren, 1985). The early successional stages in our study having high sunshine durations were characterized by a warm microclimate (cf. Greateorex-Davies and Marrs, 1992), and therefore by conditions that should generally favor butterflies (Thomas, 1993; Warren and Thomas, 1992; Wickman, 2009). In contrast, dense and shady forests (WOOD) provided relatively poor conditions for butterflies.

P. aegeria was often the only species occurring in these woodland stands (cf. Benes et al., 2006; Greateorex-Davies et al., 1993; Warren, 1985; Warren and Key, 1991).

Migratory species are by definition characterized by a high mobility and are often rather opportunistic concerning the habitats in which they occur. Diversity and density of migratory species is usually more strongly affected by adult food resources than by their larval host plants (Fartmann, 2004; Warren, 1985; Warren et al., 2001). Because sunshine duration, as a measure for microclimatic conditions, and nectar abundance were inter-correlated in our study, we are not able to disentangle the effects of each of the two parameters on butterflies. However, for migratory species we assume that nectar-resource abundance also promoted species richness and density.

Migratory species were the only group where diversity and density peaked in the first-year stage, although nectar resource abundance was higher in the second-year stage. A possible explanation

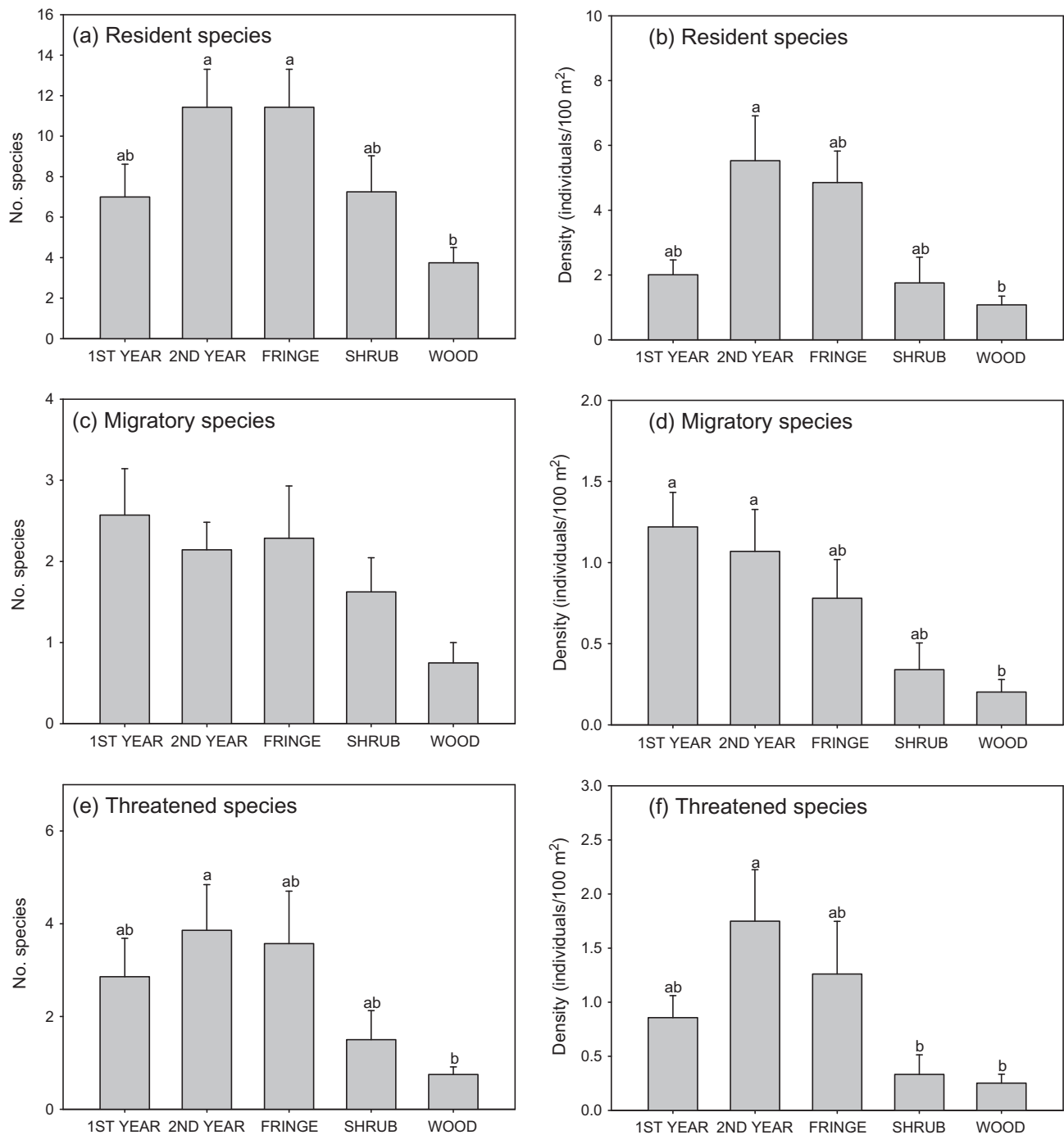


Fig. 3. Mean values (\pm SE) of species number and maximum density (individuals/100 m²) of resident (a and b), migratory (c and d) and threatened species (e and f) in the five woodland stages. Differences between the successional stages were tested for all three response variables using a GLMM with Poisson error structure and study area as random factor. Statistics of GLMM: (a) $\chi^2 = 44.244$, $df = 4$, $P < 0.001$; (b) $\chi^2 = 15.105$, $df = 5$, $P < 0.01$; (c) $\chi^2 = 10.059$, $df = 4$, $P < 0.05$; (d) $\chi^2 = 51.568$, $df = 5$, $P < 0.001$; (e) $\chi^2 = 37.298$, $df = 4$, $P < 0.001$; (f) $\chi^2 = 15.422$, $df = 5$, $P < 0.01$. Different letters indicate differences between the stages (Dunn's test; $P < 0.05$).

for this pattern might be that the first-year stage allows: (i) ease of searching for nectar resources due to the open structure; and (ii) the adults to spend more time foraging and possibly maximizing the intake of floral nectar due to the very warm microclimatic conditions (cf. [Greateorex-Davies and Marrs, 1992](#)). However, these assumptions need further testing.

In contrast to the case for migratory species, host-plant quantity is more important to more sedentary species (resident or threatened species) ([Fartmann, 2004](#); [Krämer et al., 2012](#)). However, to our surprise the influence of host-plant cover on species richness and density of resident or threatened butterflies was rela-

tively low. It was solely the density of resident species which increased with host-plant cover. However, it should be taken into account that host-plant cover was generally high in all successional stages, except the first-year stage. Accordingly, we assume that host-plant quantity might only become a limiting factor for resident or threatened species in the first-year stage, therefore possibly explaining why species number and density peaked in the second-year stage and not in the first-year stage.

Many butterfly species occurring in coppice woodlands are known to be sedentary ([Thomas, 1993](#); [Warren and Thomas, 1992](#)). Hence, one might assume that the time period for coloniza-

Table 3

Statistics of GLMM: Relationship between species number or maximum density (individuals/100 m²) of resident, migratory and threatened species number (Poisson error structure) and several environmental parameters (predictor variables) (Table 1). Non-significant predictors were excluded from the final model by stepwise backward-selection ($P > 0.05$). Study area was set up as random factor. Estimates (\pm SE) are given for significant environmental parameters. The goodness of fit of each model is shown by McFadden pseudo R^2 values.

Parameter	Resident species		Migratory species		Threatened species	
	No.	Density	No.	Density	No.	Density
Herb layer	$0.274 \pm 0.085^{**}$	$0.545 \pm 0.074^{***}$	n.s.	n.s.	$0.286 \pm 0.144^*$	$0.548 \pm 0.125^{***}$
Sunshine/nectar	$0.215 \pm 0.088^*$	$0.299 \pm 0.076^{***}$	$0.427 \pm 0.142^{**}$	$0.723 \pm 0.121^{***}$	$0.554 \pm 0.159^{***}$	$0.541 \pm 0.134^{***}$
Host plants	n.s.	$0.003 \pm 0.002^*$	n.s.	n.s.	n.s.	n.s.
Shrub layer cover	n.s.	n.s.	n.s.	n.s.	n.s.	$-0.006 \pm 0.003^*$
Pseudo R^2	0.57	0.73	0.26	0.44	0.79	0.62

n.s. Not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

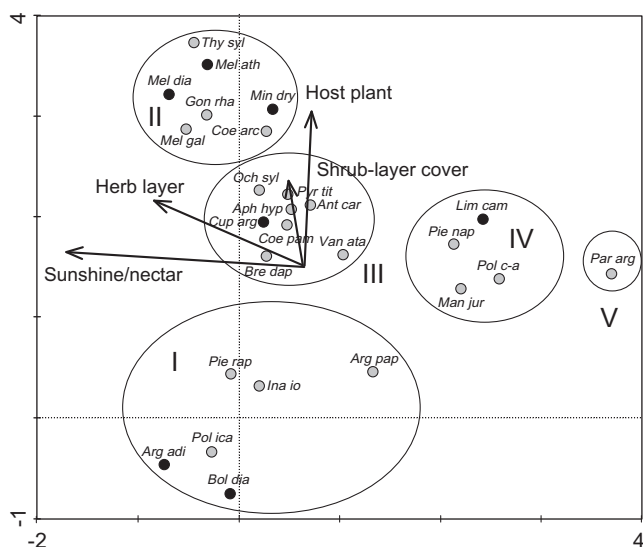


Fig. 4. Detrended Correspondence Analysis (DCA) of the most frequent butterfly species in coppice woodlands with standards. The length of the gradient on the 1st axis is 3.7; the 1st axis explains 23.1% and the 1st and 2nd axes 39.8% of total variance; the sum of all eigenvalues is 1.55. Species occurring in less than four of the 37 plots (frequency <10%) were excluded from the analysis. Arrows denote major environmental gradients (overlay). Species are indicated by dots (black = threatened species). Complete species names are given in Appendix A. Ellipses enclose groups of butterflies associated with one of the five woodland stages: Group I = 1ST YEAR, group II = 2ND YEAR, group III = FRINGE, group IV = SHRUB, group V = WOOD. Data basis: maximum number of individuals per 500 m² out of seven transect walks and environmental parameters of 37 plots.

Table 4

Eigenvalues of the first two axes of the Detrended Correspondence Analysis (DCA) and the intraset correlations between DCA axes and the environmental variables.

Axes	1	2
Eigenvalues	0.36	0.26
Herb layer	-0.53	0.28
Sunshine/nectar	-0.79	0.06
Host plants	0.03	0.59
Shrub layer	-0.05	0.34

tion of the first-year stage was too short for some of the species. However, as all first-year plots were situated adjacent to patches of the second-year stage this is rather unlikely.

In this study, host-plant quality seems to be more important than host-plant quantity. Butterflies have usually very specific requirements concerning vegetation structure and microclimate around their host plants (Fartmann and Hermann, 2006; García-

Barros and Fartmann, 2009). The number and density of both resident and threatened species was positively correlated with the summarized variable herb layer. As even the successional stage with the highest herb-layer cover (second-year stage) had at least some amount of bare ground (Table 2), we interpret high values of the summarized variable as a measure for structural and microclimatic heterogeneity representing plots that, although dominated by high and dense vegetation, included mosaics of open soil, and both low- and high-growing ground vegetation (own observation). Habitat heterogeneity is well-known to be beneficial for animal diversity (Tews et al., 2004).

Moreover, density of threatened species was negatively affected by shrub cover. Increasing shrub cover in coppiced woodlands leads to cooler microclimatic conditions (Gretorex-Davies et al., 1993). In particular among threatened species (e.g. *A. adippe* or *M. athalia*) there are found many that have high temperature requirements for breeding sites and which depend on the earliest successional stages of woodlands (this study; Warren and Key, 1991).

To conclude, warm microclimatic conditions promoted diversity and density of all three butterfly groups in coppiced woodlands. In addition, the availability of nectar resources (migratory species) and sufficient host-plants growing under suitable conditions (resident and threatened species) were also important.

5. Implications for conservation

Our study clearly showed that coppice woodlands are hotspots for butterfly diversity in general and refuges for many threatened species. This also applies for other insect taxa such as moths (Broome et al., 2011; Dolek et al., 2008) or xylophagous beetles (Dolek et al., 2008). All successional stages of coppice woodlands are relevant to maintenance of butterfly biodiversity as each of the stages has characteristic species. However, early and mid-successional stages have the highest priority (Benes et al., 2006; Warren and Thomas, 1992). They exhibited the highest density, overall species richness and number of threatened and characteristic species.

Woodland butterflies are among the most rapidly declining butterfly groups throughout Europe (Van Swaay et al., 2006). The loss of open woodland habitats has been identified as the main reason for this decline (e.g. Anthes et al., 2008; Benes et al., 2006; Fartmann, 2006; Freese et al., 2006; Streiterberger et al., 2012). Based on our results, maintenance and expansion of coppice management should be a suitable tool to counteract the general decline of woodland butterflies and the loss of early-successional species in woodlands. Ride widening and management of the rides as coppice will also promote species associated with coppice rotation (Clarke et al., 2011). Although the area size of these rides on its

own is usually too small to maintain very specialist early-successional species, they can function as important corridors between the coupes.

However, even in areas where coppice forest management is still in practice, such as in the Alsatian Hardt, there is, for economic reasons, a tendency to transform coppice woodlands into modern high forests (Treiber, 2003). The increasing demand for fire and fuel wood, however, might offer new opportunities, with coppice woodlands possibly becoming an economic alternative to high forests (Benes et al., 2006; Freese et al., 2006).

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Appendix A

See Table A1.

Table A1

Frequency (%) of butterfly species in each of the five woodland stages as well as mobility and threat status of each species. R = resident species, M = migratory species, x = threatened species. For further information see 'Butterflies' (Section 2.3).

Species	Mobility	Threat status	Frequency					Total
			1ST YEAR	2ND YEAR	FRINGE	SHRUB	WOOD	
<i>Anthocharis cardamines</i>	R	.	29	29	14	.	.	14
<i>Aphantopus hyperantus</i>	R	.	43	71	100	100	.	62
<i>Argynnis adippe</i>	R	x	71	86	71	.	.	43
<i>Argynnis paphia</i>	R	.	100	100	100	75	50	84
<i>Aricia agestis</i>	R	.	.	29	.	.	.	5
<i>Boloria dia</i>	R	x	57	86	57	25	13	46
<i>Brenthis daphne</i>	R	.	43	57	71	38	.	41
<i>Celastrina argiolus</i>	R	.	14	29	.	.	.	8
<i>Coenonympha arcania</i>	R	.	.	43	43	25	.	22
<i>Coenonympha pamphilus</i>	R	.	14	29	14	13	13	16
<i>Cupido argiades</i>	M	x	43	14	29	.	.	16
<i>Gonepteryx rhamni</i>	M	.	29	29	14	13	.	16
<i>Hamearis lucina</i>	R	x	.	.	.	13	.	3
<i>Inachis io</i>	M	.	29	.	29	.	.	11
<i>Limenitis camilla</i>	R	x	43	43	57	63	50	51
<i>Maniola jurtina</i>	R	.	57	100	100	75	63	78
<i>Melanargia galathea</i>	R	.	29	43	57	38	13	35
<i>Melitaea athalia</i>	R	x	14	29	29	13	.	16
<i>Melitaea diamina</i>	R	x	14	29	29	.	.	14
<i>Minois dryas</i>	R	x	29	57	43	38	13	35
<i>Neozephyrus quercus</i>	R	.	.	.	14	13	.	5
<i>Nymphalis polychloros</i>	R	x	.	.	14	.	.	3
<i>Ochlodes sylvanus</i>	R	.	14	71	71	38	13	41
<i>Papilio machaon</i>	R	x	.	.	14	.	.	3
<i>Pararge aegeria</i>	R	.	.	.	43	13	100	32
<i>Pieris napi</i>	M	.	57	57	57	63	63	59
<i>Pieris rapae</i>	M	.	100	100	86	63	13	70
<i>Polygonia c-album</i>	R	.	14	.	29	25	13	16
<i>Polyommatus bellargus</i>	R	x	14	14	.	.	.	5
<i>Polyommatus coridon</i>	R	x	.	29	.	.	.	5
<i>Polyommatus icarus</i>	R	.	14	57	14	.	.	16
<i>Pyrgus malvae</i>	R	x	.	.	14	.	.	3
<i>Pyronia tithonus</i>	R	.	86	100	100	100	38	84
<i>Thecla betulae</i>	R	13	.	3
<i>Thymelicus sylvestris</i>	R	.	.	14	43	13	.	14
<i>Vanessa atalanta</i>	M	.	.	14	14	25	.	11
N plots			7	7	7	8	8	

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