



Modern forest management and the decline of the Woodland Brown (*Lopinga achine*) in Central Europe

Merle Streitberger^a, Gabriel Hermann^b, Wolfgang Kraus^c, Thomas Fartmann^{a,*}

^a Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Robert-Koch-Str. 26–28, 48149 Münster, Germany

^b Working Group for Animal Ecology and Planning, Johann-Strauß-Str. 22, 70794 Filderstadt, Germany

^c Landratsamt Garmisch-Partenkirchen, Bahnhofstr. 30, 82467 Garmisch-Partenkirchen, Germany

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ABSTRACT

The Woodland Brown (*Lopinga achine*) is a characteristic flagship species for forests. Although it has experienced a dramatic decline, our knowledge concerning the reasons for the population loss is scarce. In this paper: (i) we analyze its habitat preferences on a regional scale in the Bavarian Alps; and (ii) we attempt to determine potential drivers of the decline on a national scale across Germany.

Vegetation structure, microclimate and host-plant availability were the most crucial factors explaining habitat selection. Forests with a light canopy on south-facing slopes were the preferred woodland type in the study area. They had a medium-high and dense herbaceous layer rich in low-competitive sedges. *Carex alba* appeared to be the main host plant. Dense stands of *C. alba* are necessary to fulfill the eggs' humidity requirements and to enable ease of access by the larvae. The preference for extraordinarily light forests on warm south-facing slopes most likely reflects a compensation for the cold mountain climate near the altitudinal range limit.

Within Germany, *L. achine* populations have become extinct in regions with a mild climate, while most of the remaining colonies are restricted to areas with cold winters. However, the explanatory power of the model was very low. As the disappearance of the species coincides temporally with the abandonment of coppicing and wood pasture, we assume that the cessation of this management technique was the major driver of the range retraction. In most of the Central European habitats, long-term survival of *L. achine* strongly depends on suitable forest management.

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1. Introduction

Global biodiversity loss has now reached a hitherto unknown extent. Consequently, it has been hypothesized that we are approaching the sixth major extinction event (Chapin et al., 2000; Thomas et al., 2004). In contrast to all previous such events, the current extinction crisis is not driven by natural change, but is man-made. Land-use change, climate change and nitrogen deposition have been identified as the major drivers of this dramatic species loss (Sala et al., 2000).

Woodlands are among the dominant habitat types of Central Europe, covering approximately 30% of the land surface (Steinecke and Venzke, 2003). Although forest cover is continuously increasing, woodland biodiversity is decreasing (Vodka et al., 2009). During the past 150 years, woodlands have been considerably altered by modern forestry. In ancient times, forests had to satisfy different human requirements (Vera, 2000). Forests were used as grazing sites for cattle, and wood pasture was therefore widespread. More-

over, wood sampling, litter raking and coppicing were common. Hence, the structure of woodlands differed notably from today's modern high forests, which function solely as plantations for wood supply (Benes et al., 2006). Ancient woodlands were open and diverse, comprising clearings and other different early successional stages. Because of their high structural diversity these woodlands exhibited a higher species richness compared to our modern forests.

Besides the deterioration in habitats caused by altered land-use, other indirect human impacts also contributed to the decrease of biodiversity. Global warming has become another important threat to wild biota. Although climate change is a relatively recent phenomenon, its impacts are already pronounced and manifold (Parmesan, 2006; Parmesan et al., 1999; Walther et al., 2002). Range shifts are among the best documented ecological responses to climate change. For many species, polewards and uphill range shifts have been observed (Hickling et al., 2006; Hill et al., 1999; Parmesan et al., 1999; Perry et al., 2005; Walther et al., 2002; Wilson et al., 2005). In contrast, there has so far been only rare documented evidence of a retreat of species at their low latitudinal or elevational distribution limits. Most of the retracting taxa are

* Corresponding author. Tel.: +49 251 8331967; fax: +49 251 8338338.

E-mail address: fartmann@uni-muenster.de (T. Fartmann).

northern and mountain species, because habitats at lower latitudinal or elevational range margins have become unsuitable, limiting the extent of available habitats (Franco et al., 2006; Wilson et al., 2005).

During the last decades, atmospheric nitrogen deposition has been detected as a further important trigger of species loss in industrialized countries (Bobbink et al., 1998; Maskell et al., 2010; Stevens et al., 2004). The herbaceous layer of temperate forest ecosystems responds to the increased nitrogen availability by increasing the dominance of a few competitive high-growing plants at the expense of many low-competitive species (Gilliam, 2006). The consequence is a decrease in the number of species and a biotic homogenization of the ground flora.

Butterflies are characterized by a high host plant specificity (Munguira et al., 2009) and a metapopulation structure that depends on a network of suitable habitats (Anthes et al., 2003; Eichel and Fartmann, 2008; Thomas et al., 2001). Due to these complex requirements, the decline of butterflies exceeds those of many other animal groups or vascular plants (Thomas, 2005; Thomas et al., 2004). Accordingly, butterflies are a well established model group in ecology and conservation (Ehrlich and Hanski, 2004), and function as sensitive indicators for environmental change (Thomas, 2005; Thomas and Clarke, 2004; Thomas et al., 2004).

Woodlands are among the most species-rich butterfly habitats throughout Europe (van Swaay et al., 2006). Many woodland butterflies depend upon semi-open or light structures, and are strongly declining (Settele et al., 2009; van Swaay et al., 2006; Warren and Key, 1991). A characteristic representative of this guild, and a flagship species for woodlands, is the Woodland Brown (*Lopinga achine*). In Europe, *L. achine* is vulnerable (van Swaay et al.,

2010) and in Germany, is threatened with extinction (BfN, 1998). It is included, with a few other butterfly species, in Annex IV of the EU Habitats Directive (Ssymank et al., 1998). Studies from Sweden showed that, in particular, the cessation of historical forest management promoted the decline of *L. achine* (Bergman, 1999, 2000, 2001). However, studies concerning the habitat requirements and the reasons for the colony loss in Central Europe are largely absent. Konvička et al. (2008) identified the abandonment of ancient land-use that created open forest structures, and eutrophication leading to a displacement of the host plants, as the drivers of the decline in the Czech Republic. Moreover, Settele et al. (2008) showed through modelling on a European scale that *L. achine* is sensitive to climate warming.

In this paper: (i) we analyze the habitat preferences of adult *L. achine* and oviposition site selection in one of the last two strongholds in Germany, the Bavarian Alps (Fig. 1); (ii) we attempt to disentangle the impacts of climate change, forest management and nitrogen deposition on the decline of *L. achine* on a national scale across Germany. Finally, we use this data to derive management recommendations for the conservation of *L. achine*.

2. Material and methods

2.1. Study species

L. achine is a Palaearctic species (Ebert and Rennwald, 1991; Kudrna, 2002). In Europe, it has a scattered distribution with a southern range margin along a line from southern France to Hungary, and reaches its northern distribution border in southern Sweden and Finland. Within Germany, *L. achine* occurs from the level of the plain up to approximately 1300 m a.s.l. (own observation) (Fig. 1).

L. achine is univoltine and hibernates in the larval stage (Ebert and Rennwald, 1991). In Central Europe, its flight period lasts for approximately four or five weeks between mid-June and mid-July. The females do not attach their eggs to the host plant, but rather drop them on the ground (Wiklund, 1984). Different grass species are considered to be possible host plants: in particular, the genus *Carex* is regarded as important. In southern Sweden, *Carex montana* serves as the main host plant: however, larvae were also found on Poaceae and Juncaceae (Bergman, 2000). In contrast, for Central Europe the host plants are poorly known. From southern Germany, there are larvae observations on *Carex alba* and *C. montana*, but also on *Brachypodium pinnatum* (Ebert and Rennwald, 1991). In the Czech Republic, oviposition was observed on *Carex fritschii* and *C. michelii* (Konvička et al., 2008). The habitats of *L. achine* are open and light forests with high grass cover (Ebert and Rennwald, 1991). In southern Bavaria, bog, mixed and dry pine forests are the core habitats (Hermann, 2005).

2.2. Study region

The study region, the Loisach and Isar Valley in the district of Garmisch-Partenkirchen, is located in the southern Bavarian Alps at an elevation of 660 to 1050 m a.s.l. (southern Germany) (Fig. 2). It has a typical mountain climate with a mean annual temperature of 6.7 °C (weather station Garmisch-Partenkirchen; Müller-Westermeier, 1996). Compared to the surrounding mountains, the valleys and their adjacent hillsides have a relatively mild climate, functioning as corridors for warm and dry foehn winds (BayFORKLIM, 1996; Hölzel, 1996). Precipitation is high with an annual mean of 1400 mm (BayFORKLIM, 1996).

Among the full range of potential *L. achine* habitats, 13 study areas were randomly selected within pine and mixed forests. On foehn wind-influenced, south-facing steep slopes, as well as on

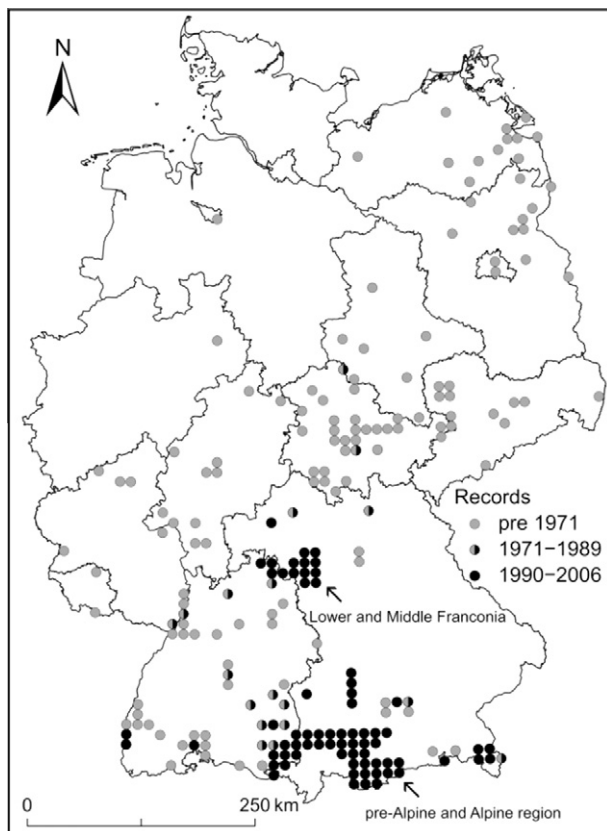


Fig. 1. Historical and recent distribution of *Lopinga achine* in Germany. The two recent strongholds, Lower and Middle Franconia as well as the pre-Alpine and Alpine region, are highlighted by arrows. The distribution is plotted using a 12.5 × 8.5 km grid. Data sources: see Material and methods section.

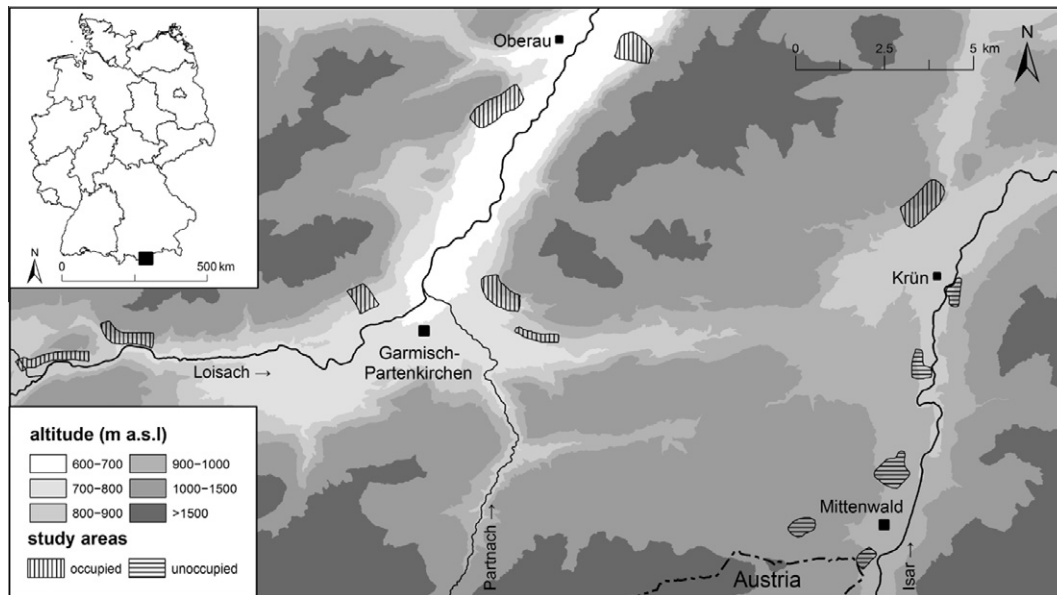


Fig. 2. Location of the study region in Germany (inset) and the study areas both occupied and unoccupied by *Lopinga achine* situated along the Loisach and Isar valley in the district of Garmisch-Partenkirchen, Bavaria.

alluvial gravel with shallow soils, primary pine forests (*Calamagrostio-Pinetum*) occur under extremely nutrient-poor and dry conditions (Hölzel, 1996). These forests exhibit a light tree layer and a high cover of herbs and grasses. Compared with pine forests, mixed forests occur under less extreme conditions, e.g. on less inclined slopes and more developed soils. However, on these sites grazing can favour pine forests at the expense of mixed forests (=secondary pine forests, Fig. 3a). Mixed forests are the dominant forest type within the study region. Here, sites were mostly chosen within formerly grazed areas where the spruce-dominated *Seslerio-Fagetum* association (Fig. 3b), with *Brachypodium rupestre* (according to Ewald, 1997), is widespread. It also represents a vegetation type adapted to dry conditions; therefore, it shares a great amount of the ground flora with the *Calamagrostio-Pinetum* association and exhibits a similar vegetation structure.

2.3. Sampling design

2.3.1. Adult habitats

At the 13 study areas, 52 transect plots with a size of 500 m² were selected to assess density of adult *L. achine*. All the plots had, according to descriptions in literature (Bergman, 2000, 2001; Hermann, 2005; Konvička et al., 2008), a vegetation structure typical of *L. achine* habitats (i.e. cover of tree layer below 80%, low shrub cover, as well as a cover of herbs and grasses >50%).

All plots were visited twice during warm (>18 °C) and sunny days without precipitation, between the end of June until mid-July 2010. All adult individuals present were counted by walking slowly in sinuous lines and for a standardized time of 15 min along the plot. On 13 plots, situated along the Isar valley south of Krün, the species was not detected (Fig. 2).



Fig. 3. Impressions of typical light forest stands preferred by *Lopinga achine* within our study region: (a) pine forest and (b) mixed forest.

On all plots, vegetation and climate data were collected to assess the habitat preferences of *L. achine*. The coverage of the tree and shrub layers was estimated for the whole plot. Land use was classified into the categories 'grazed' and 'ungrazed'. The structure of the herb layer was examined on 100 m² in the centre of each transect plot. The following parameters were estimated: cover of herb, moss and litter layers, as well as of all grasses, Poaceae and Cyperaceae. In addition, the cover of all plant species within the shrub and herb layer with a nitrogen indicator value ≥ 5 according to Ellenberg et al. (2001) (hereafter referred to as nitrophytes) was estimated. This value was selected as the majority of plants occurring in the *Calamagrostio-Pinetum* and the *Seslerio-Fagetum* associations possess nitrogen indicator values < 5 (cf. Ewald, 1997; Hölzel, 1996). Vegetation density was recorded using a frame of 20 cm depth and 40 cm width in six layers of 5 cm from 5 to 30 cm height above ground level. Aspect and inclination were ascertained using a compass with inclinometer. Altitude was assessed using a GPS. For further analyses, aspect was converted into 'northness' and 'eastness' by cosine and sine transformation (northness: $360^\circ = 1$; $180^\circ = -1$; eastness: $90^\circ = 1$; $270^\circ = -1$). Potential daily sunshine duration for the months May to September was measured using a horizonscope by Tonne (1954) with an accuracy of $\frac{1}{4}$ h. The mean height of the herb layer was calculated from height measurements at 10 random points within each plot.

2.3.2. Oviposition sites

In order to observe egg-laying, females of *L. achine* were studied in the field from the end of June until mid-July on the four plots with the highest adult density. Only observations where the egg was seen when falling were classified as an oviposition. Available microhabitats were selected within the same plots by a randomly thrown stick (Anthes et al., 2003).

Apart from the cover of nitrophytes, vegetation and climate data were assessed using the same methods as described in Section 2.3.1. The cover of the tree and shrub layer as well as land use, were determined on a plot of 100 m² in size with the oviposition site in the centre. All other variables (see Section 2.3.1.) were ascertained within a radius of 25 cm around the oviposition site.

2.3.3. Range retraction and climate

To detect potential climate effects on the range retraction of *L. achine* in Germany, climatic parameters were related to historical and recent distribution data. The distribution data were classified into three categories reflecting the extinction history (pre-1971, 1971–1989, 1990–2006; cf. Fig. 1). The historical and recent distribution of *L. achine* was assessed according to the following sources: BfN (2007), BfU (2001), Brockmann (pers. comm.), Ebert and Rennwald (1991), Engel (1987), NLÖ (2001), Reinhardt (pers. comm.), Reinhardt et al. (2007), Retzlaff (1973), Schulte et al. (2007), Stamm (1981), Thust et al. (2006) and Werno (2011). Climate data comprised the mean temperature for January, the mean annual number of frost days (minimum daily temperatures below 0 °C) and the mean annual temperature (data for the period 1961–1990, Deutscher Wetterdienst, pers. comm.). Distribution and climate data were based on a 12.5 × 8.5 km grid.

2.3.4. Statistical analysis

If the data were normally distributed and had homogeneous variances, differences between numerical variables were tested using the *t* test. If these requirements were not fulfilled, the Mann–Whitney *U* test served as an alternative method. Differences of frequencies of nominal variables were detected using *Chi*² tests.

Two generalized linear mixed-effects models (GLMMs: lmer, Bates et al., 2008) were applied to reveal which environmental parameters possess the highest explanatory power for the density of adult *L. achine* (adult habitats) and for an oviposition (oviposi-

tion sites) (for details see Crawley, 2007). In all mixed models, 'study area' functioned as a random factor. In the first case, due to overdispersion, a GLMM with a quasi-Poisson error structure with the maximum number of individuals counted during the two transect surveys was used as the response variable. A binomial GLMM was used for oviposition sites. To reduce the number of predictor variables and to avoid intercorrelations, Spearman rank correlations (r_s) between the variables were calculated. Correlations with r_s values $> |0.7|$ were regarded as strongly intercorrelated and only non-intercorrelated parameters were entered into the regression analysis. The selection of the final model was based on backward selection using likelihood ratio tests with a significance level of $\alpha = 0.05$.

In both cases, we undertook a pre-analysis: therefore, two GLMMs (quasi-Poisson for adult habitats; binomial for oviposition sites) were calculated with the independent variables as simply the coverage of grass species appearing in more than 50% of the occupied sites (adult habitats: *B. rupestre*, *Calamagrostis varia*, *C. alba*, *C. flacca*, *C. humilis*, *C. montana*, *C. sempervirens*, *Melica nutans*, *Molinia arundinacea*, *Sesleria varia*; oviposition sites: *B. rupestre*, *C. alba*, *C. montana*, *S. varia*). The selection of the final model followed the methods mentioned above. In addition to the other environmental parameters, the significant grass species of the final model (adult habitats: *B. rupestre*, *C. alba*; oviposition sites: *C. alba*) were entered into the two main GLMMs mentioned above.

The potential effects of climate on the range retraction of *L. achine* were analyzed by using a generalized linear model (GLM). Due to overdispersion, a model with quasi-Poisson error structure was carried out with the number of the three extinction categories (1–3) as the response variable. A principal component analysis (PCA) was performed to summarize the strongly intercorrelated climate parameters into one variable, and this variable was incorporated into the model as an independent variable, hereafter called 'climate factor'. The variable represented an independent principal component with an eigenvalue of 2.9. It explained 97% of the total variance in the data set. The component was positively correlated with mean annual temperature (Spearman rank correlation, $r_s = 0.98$, $P < 0.001$), mean temperature in January ($r_s = 0.98$, $P < 0.001$) and negatively with the mean number of frost days ($r_s = -0.98$, $P < 0.001$).

All GLMM and GLM were applied using R 2.11.1 (R Development Core Team, 2009). Further statistical analyses were performed with PASW 18.

3. Results

3.1. Adult habitats

Occupied plots were situated at an altitude of 660–1000 m a.s.l. (Table 1). They were mostly SSW- to SSE-facing and moderately to highly inclined (Tables 1 and 2, Fig. 4). Potential daily sunshine duration was generally low at 2.6–2.8 h per day during the growing season (Table 1). Two thirds of the occupied plots were ungrazed, and one third grazed (Table 2). The tree cover ranged from 15% to 60% with a mean of 36% (Table 1). The cover of the shrub layer was low with an average of 10%: however, the herb and litter layer had a high cover of about 80%. Grasses were the dominant plants in the herb layer with a mean cover of 69%. The most abundant grass species, showing a positive correlation with the abundance of *L. achine* (cf. 'Materials and methods'), were *B. rupestre* and *C. alba*, covering on average 21% and 10%, respectively, of the ground surface. Nitrophytes had a low cover at 9%. Vegetation was generally dense up to a height of 15 cm. The mean vegetation height was 25 cm.

Table 1

Mean values \pm SD, minimum and maximum (in brackets) of all numerical parameters at occupied ($N = 39$) and unoccupied transect plots ($N = 13$) of *Lopinga achine*. Comparison between groups by t test and Mann–Whitney U test, respectively. Significant differences between groups are indicated by bold type.

Parameter	Occupied sites		Unoccupied sites		t	U
<i>Climate</i>						
Altitude (m)	830.8 \pm 79.4	(660–1000)	933.5 \pm 72.6	(850–1050)	–	79.0***
Northness ^a	–0.70 \pm 0.4	(–1.0 to 0.5)	–0.27 \pm 0.3	(–0.77–0.17)	–	65.5**
Eastness ^a	–0.08 \pm 0.6	(–1.0 to 0.99)	0.57 \pm 0.7	(–0.98–1.0)	–	73.5**
Inclination (°)	20.4 \pm 10.0	(2.5–50)	20.4 \pm 14.4	(0–40)	0.007 ^{n.s.}	–
<i>Daily sunshine duration (h)</i>						
September	2.7 \pm 1.3	(0.75–6.75)	2.7 \pm 1.6	(1.25–6.5)	–0.167 ^{n.s.}	–
August	2.8 \pm 1.4	(1–8)	3.1 \pm 1.6	(1.25–6.5)	0.551 ^{n.s.}	–
May/July	2.8 \pm 1.6	(1–8)	3.2 \pm 1.6	(1–6)	0.943 ^{n.s.}	–
June	2.6 \pm 1.8	(0.5–7)	3.1 \pm 1.4	(0.75–6)	1.484 ^{n.s.}	–
Sum June/July	5.3 \pm 3.3	(2–15)	6.3 \pm 2.9	(1.75–12)	0.974 ^{n.s.}	–
<i>Vegetation cover (%)</i>						
Tree layer	35.8 \pm 11.2	(15–60)	39.2 \pm 8.1	(30–60)	1.024 ^{n.s.}	–
Shrub layer	9.6 \pm 9.6	(0–35)	6.8 \pm 7.5	(0–25)	–0.652 ^{n.s.}	–
Herb layer	83.5 \pm 8.1	(60–95)	80.0 \pm 8.2	(65–90)	–	190.5 ^{n.s.}
Litter layer	79.5 \pm 15.8	(30–95)	86.2 \pm 8.9	(70–95)	–	185.0 ^{n.s.}
Moss layer	17.5 \pm 23.3	(1–90)	8.8 \pm 10.0	(0–25)	–0.999 ^{n.s.}	–
All grasses	69.1 \pm 10.6	(45–85)	67.7 \pm 15.5	(30–85)	–0.368 ^{n.s.}	–
Poaceae	50.6 \pm 15.5	(15–75)	53.5 \pm 15.9	(20–70)	0.564 ^{n.s.}	–
Sedges	27.6 \pm 11.3	(5–55)	23.8 \pm 8.9	(10–45)	–1.082 ^{n.s.}	–
<i>Brachypodium rupestre</i>	21.2 \pm 14.5	(0–60)	20.8 \pm 17.3	(0–60)	–0.089 ^{n.s.}	–
<i>Carex alba</i>	10.1 \pm 10.6	(0–35)	11.4 \pm 11.5	(0–35)	0.364 ^{n.s.}	–
Nitrophytes	9.0 \pm 10.3	(0–40)	7.3 \pm 7.4	(0–25)	–0.264 ^{n.s.}	–
<i>Turf height (cm)</i>						
Herb layer	25.3 \pm 6.6	(15.4–47.3)	25.3 \pm 3.6	(20–30.7)	–0.02 ^{n.s.}	–
<i>Horizontal cover (%)</i>						
5 cm	89.0 \pm 8.8	(60–100)	86.9 \pm 7.8	(75–100)	–	200.5 ^{n.s.}
10 cm	65.5 \pm 13.3	(40–90)	66.2 \pm 10.4	(45–85)	0.158 ^{n.s.}	–
15 cm	36.2 \pm 14.0	(10–75)	36.5 \pm 13.6	(15–60)	0.086 ^{n.s.}	–
20 cm	17.2 \pm 11.1	(1–40)	17.5 \pm 13.2	(2.5–40)	–0.375 ^{n.s.}	–
25 cm	6.3 \pm 6.8	(0–25)	5.5 \pm 8.1	(0–30)	–0.753 ^{n.s.}	–
30 cm	2.1 \pm 4.4	(0–25)	3.1 \pm 8.1	(0–30)	–	235.0 ^{n.s.}

n.s. = not significant.

^a $N = 10$ unoccupied sites.

** $P < 0.01$.

*** $P < 0.001$.

Table 2

Absolute and relative frequencies of all nominal variables at occupied ($N = 39$) and unoccupied transect plots ($N = 13$) of *Lopinga achine*. Comparisons between groups was undertaken by χ^2 Test.

Parameter	Occupied sites		Unoccupied sites		Chi	df	P
	Absolute	%	Absolute	%			
Aspect					33.5	3	***
E	2	5.1	8	61.5			
S	28	71.8	1	7.7			
W	9	23.1	1	7.7			
Flat	0	0.0	3	23.1			
Land use					1.02	1	n.s.
Grazed	15	38.5	3	23.1			
Ungrazed	24	61.5	10	76.9			

n.s. = not significant.

*** $P < 0.001$.

In comparison with available sites, adult *L. achine* significantly preferred sites at a lower altitude (Table 1). The aspect of occupied and unoccupied sites also differed significantly (Tables 1 and 2). Unoccupied sites were predominantly found on east-facing slopes or under flat conditions (Tables 1 and 2; Fig. 4). Land use and vegetation structure did not differ between occupied and unoccupied sites (Tables 1 and 2). The same was true for the abundance of *L. achine* in grazed and ungrazed sites ($t = -0.426$, $P = 0.67$), as well as between pine and mixed forests ($t = 0.529$, $P = 0.60$).

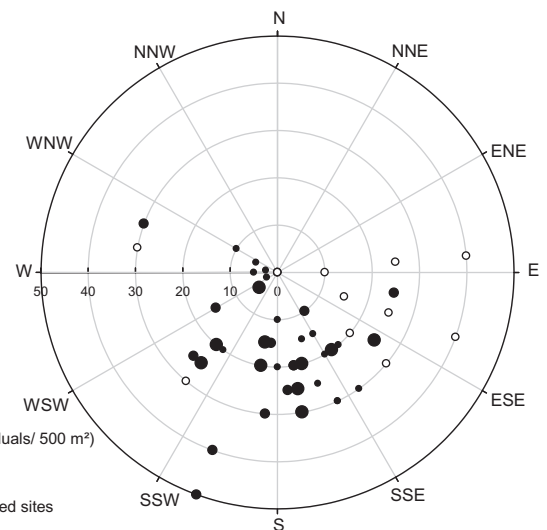


Fig. 4. Aspect and inclination of transect plots occupied ($N = 39$) and unoccupied ($N = 13$) by *Lopinga achine*.

Abundance of adult *L. achine* was best explained by a combination of the coverage of certain grass species, vegetation structure and climate parameters: abundance was positively correlated with the cover of *B. rupestre* and *C. alba*, vegetation height and southern aspects (Table 3a). In contrast, a high cover of nitrophytes affected density negatively.

Table 3
 Statistics of GLMM: (a) quasi-Poisson error-structured, relationship between the abundance of *Lopinga achine* and environmental parameters ($N = 39$ occupied sites and $N = 10$ unoccupied sites, three flat sites were not included in analysis), (b) binomial, relationship between the probability of oviposition by *L. achine* and environmental parameters ($N = 21$ oviposition sites and $N = 20$ available sites). The following variables entered into the analysis were not significant: (a) altitude, eastness, inclination, cover of tree, shrub, herb, moss and litter layer, land-use, potential daily sunshine duration June/July; (b) cover shrub layer and tree layer. Non-significant predictors were excluded from the models by stepwise backward-selection ($P > 0.05$).

Variable	Estimate	SE	T/Z	P
<i>(a) adult habitats</i>				
Cover				
<i>Brachypodium rupestre</i>	0.02402	0.00596	4.028	***
<i>Carex alba</i>	0.02634	0.0115	2.291	**
Nitrophytes	-0.0195	0.00596	-2.105	*
Vegetation height	0.04302	0.01541	2.792	***
Northness	-0.62457	0.29094	-2.213	**
Pseudo R^2 [Nagelkerkes] = 0.37				
<i>(b) oviposition sites</i>				
Cover				
<i>Carex alba</i>	0.14625	0.05887	2.484	**
Herbs	0.16303	0.08828	1.847	*
Moss	-0.24923	0.11373	0.330	***
Litter	-0.17629	0.10514	1.677	*
Vegetation height	0.26315	0.1501	1.753	*
Sunshine duration				
June/July	-1.53511	0.7149	-2.147	**
Pseudo R^2 [Nagelkerkes] = 0.62				

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 4
 Mean values \pm SD, minimum and maximum (in brackets) of all numerical parameters at oviposition sites ($N = 21$) and available sites ($N = 20$) of *Lopinga achine*. Comparison between groups by t test and Mann-Whitney U test, respectively. Significant differences between groups are indicated by bold type.

Parameter	Oviposition sites		Available sites		t	U
<i>Climate</i>						
Altitude (m)	850.0 \pm 32.2	(780–945)	861.0 \pm 27.5	(820–925)	1.173 ^{n.s.}	–
Northness	-0.84 \pm 0.3	(-1.0–0.0)	-0.75 \pm 0.4	(-1.0–0.5)	–	191.0 ^{n.s.}
Eastness	-0.03 \pm 0.5	(-1.0–0.77)	-0.08 \pm 0.5	(-1.0–0.64)	–	200.5 ^{n.s.}
Inclination (°)	18.6 \pm 9.1	(5–35)	18.3 \pm 10.0	(5–45)	-0.18 ^{n.s.}	–
Daily sunshine duration (h)						
September	1.5 \pm 0.7	(0.25–3.5)	1.9 \pm 0.9	(1–4)	0.639 ^{n.s.}	–
August	1.5 \pm 0.6	(0.5–3)	2.0 \pm 0.8	(0.75–3.75)	0.833 ^{n.s.}	–
May/July	1.5 \pm 0.8	(0.5–3.5)	1.9 \pm 0.8	(0.75–3.5)	0.347 ^{n.s.}	–
June	1.3 \pm 0.7	(0.5–3.5)	1.9 \pm 0.9	(1–4)	–	151.5 ^{n.s.}
Sum June/July	2.9 \pm 1.4	(1–7)	3.8 \pm 1.6	(2–7.5)	0.174 ^{n.s.}	–
<i>Vegetation cover (%)</i>						
Tree layer	40.5 \pm 22.0	(10–75)	38.8 \pm 15.7	(25–70)	-0.288 ^{n.s.}	–
Shrub layer	6.3 \pm 9.3	(0–35)	1.1 \pm 1.4	(0–5)	–	148.0 ^{n.s.}
Herb layer	72.6 \pm 11.8	(55–90)	69.3 \pm 12.5	(50–95)	-0.888 ^{n.s.}	–
Litter layer	81.9 \pm 22.5	(30–95)	82.5 \pm 22.2	(25–95)	–	183.5 ^{n.s.}
Moss layer	9.1 \pm 13.3	(0–50)	17.3 \pm 25.1	(0–75)	0.916 ^{n.s.}	–
All grasses	58.8 \pm 16.5	(15–90)	53.0 \pm 14.8	(25–80)	-1.184 ^{n.s.}	–
Poaceae	34.0 \pm 23.7	(0–80)	37.3 \pm 18.2	(5–70)	0.483 ^{n.s.}	–
Sedges	30.5 \pm 16.8	(2.5–60)	19.0 \pm 9.4	(5–40)	-1.035 ^{n.s.}	–
<i>Carex alba</i>	21.5 \pm 16.6	(0–50)	8.5 \pm 9.6	(0–35)	–	112.0*
<i>C. montana</i>	6.3 \pm 9.3	(0–30)	7.9 \pm 7.2	(0–25)	–	158.0 ^{n.s.}
<i>Turf height (cm)</i>						
Herb layer	25.5 \pm 4.5	(19–36)	20.5 \pm 4.8	(14–30)	–	100.0*
<i>Horizontal cover (%)</i>						
5 cm	91.2 \pm 9.2	(70–100)	87.8 \pm 10.3	(60–95)	–	155.0 ^{n.s.}
10 cm	68.8 \pm 21.1	(30–95)	54.3 \pm 18.7	(25–90)	–	128.0*
15 cm	32.9 \pm 17.2	(10–70)	21.4 \pm 17.6	(1–60)	–	123.0*
20 cm	14.5 \pm 14.6	(1–60)	5.8 \pm 5.7	(0–20)	–	110.5**
25 cm	7.3 \pm 14.9	(0–70)	1.1 \pm 1.5	(0–5)	–	109.0**
30 cm	3.1 \pm 8.6	(0–40)	0.1 \pm 0.3	(0–1)	–	125.0**

n.s. = not significant.

* $P < 0.05$.

** $P < 0.01$.

3.2. Oviposition sites

In total, 21 ovipositions were observed. Oviposition sites were mostly found on moderately inclined slopes having a southern as-

pect (Tables 4 and 5). Potential daily sunshine duration was generally low at 1.3–1.5 h per day during the growing season (Table 4). The vast majority of sites were ungrazed (Table 5). Vegetation structure was similar compared to that of the adult habitats

Table 5

Absolute and relative frequencies of all nominal variables at oviposition sites ($N = 21$) and available sites ($N = 20$) of *Lopinga achine*. Comparisons between groups was undertaken using χ^2 Test.

Parameter	Oviposition sites		Available sites		Chi	df	P
	Absolute	%	Absolute	%			
Aspect					1.15	2	n.s.
E	1	4.8	0	0.0			
S	17	81.0	16	80.0			
W	3	14.3	4	20.0			
Land use					0.66	1	n.s.
Grazed	4	19.0	6	30.0			
Ungrazed	17	81.0	14	70.0			

n.s. = not significant.

(Tables 1 and 4). As in the adult habitats the cover of sedges was high with a mean of 31%. The most abundant sedges were *C. alba* and *C. montana*. *C. alba* occurred in 86% ($N = 18$) and *C. montana* in 57% ($N = 12$) of the oviposition sites. The cover of *C. alba* (22%) was three times higher than that of *C. montana* (Table 4). In comparison with available sites, oviposition sites had a higher cover of *C. alba*, a higher turf height and a denser herbaceous layer.

The oviposition pattern of *L. achine* was best explained by host plant quantity, vegetation structure and microclimate (Table 3b): High cover of *C. alba* and herbs, as well as high vegetation, promoted oviposition. In contrast, the likelihood of a site being accepted for oviposition decreased with the cover of litter and mosses as well as the potential sunshine duration in June/July.

3.3. Range retraction and climate

L. achine once had a scattered distribution throughout eastern and southern Germany (Fig. 1). Thus far, it has been recorded in 214 12.5×8.5 km grid cells across Germany. Before 1990, *L. achine* had disappeared from 67% of its previously occupied cells. Nowadays, only a few populations remain in two (Baden-Wuerttemberg, Bavaria) of the formerly 13 Federal States hosting populations of *L. achine*. The last two strongholds are the 'Steigerwald' in Lower and Middle Franconia, as well as the pre-Alpine and Alpine region.

The GLM revealed that the likelihood of extinction of *L. achine* was negatively correlated with the climate factor (Table 6). The risk of extinction was therefore highest in areas with a high annual temperature in January as well as a low number of annual frost days. However, the explanatory power of the model was very low with an adjusted pseudo R^2 [McFadden] value of 0.09.

4. Discussion

4.1. Habitat preferences in the northern Alps

Vegetation structure, microclimate and host-plant availability were the most crucial factors explaining adult densities and oviposition site selection. In our study region, spruce and pine dominated forests on south-facing slopes with a light canopy (Fig. 3), ideally covering about 40%, were preferred. They had a medium-high and dense herbaceous layer with a high cover of small sedges and litter. The abundance of adult *L. achine* was positively

correlated with vegetation height and the cover of *B. rupestris* and *C. alba*. In contrast, the cover of nitrophytes and northern aspects negatively affected abundance. The likelihood of oviposition increased with turf height and the cover of *C. alba* and herbs. However, it decreased with potential sunshine duration in June/July and the cover of litter and mosses.

In comparison with *L. achine* habitats in Sweden and the Czech Republic, the canopy cover of adult and oviposition habitats was clearly lower in our study. In Sweden *L. achine* occurred in woodlands with a tree and shrub cover of about 80% (Bergman, 2001) and in the Czech Republic habitats had an average canopy cover of 60% (Konvička et al., 2008). Both study regions were in the lowlands (<200 m a.s.l.) and are characterized by relatively warm and dry conditions during the growing season (Bergman, 2001; Konvička et al., 2008). In contrast, our study region has a relatively cold and wet mountain climate (BayFORKLIM, 1996). Hence, *L. achine* seems to compensate for the relatively unfavourable macroclimatic conditions by colonizing habitats with a lower canopy cover, preferentially on south-facing slopes having a warm microclimate (cf. Stoutjesdijk and Barkman, 1992). In fact, geographically shifting microhabitats along a macroclimatic gradient across Europe have been observed among other butterfly species, too (Thomas et al., 1998).

Despite occurrence of *L. achine* in the upper Isar valley south of Krün (own observation) and a similar vegetation structure, we were not able to detect the species in our study areas along this section of the valley. This might also be explained by the preference for extraordinarily warm microclimates near the altitudinal range limit. The combination of a greater altitude and east-facing slopes in these study areas may lead to unfavourable climatic conditions, compared with occupied sites on south-facing slopes at lower altitudes.

Generally, desiccation is a major threat to eggs of terrestrial insects (Porter, 1992). This would appear to be especially true for *L. achine*. Laboratory studies showed that egg mortality of *L. achine* is extremely high under a relative humidity below 80% (Bergman, 1999; Karlsson and Wiklund, 1985). The eggs of this species therefore differ considerably from that of other satyrine butterflies that are able to survive under drier conditions (Karlsson and Wiklund, 1985). Because *L. achine* always drops its eggs to the ground, embryonic development is highly dependent on the microclimate near the soil surface. Microclimate near the ground differs extremely between high and short turf, with high swards having a cooler and more humid microclimate (Stoutjesdijk and Barkman, 1992). Accordingly, a medium-high and dense herbaceous vegetation, with a high cover of litter, found at the oviposition sites of *L. achine* should be crucial for successful development of the eggs. The negative relationship between the potential daily sunshine duration in June/July and the occurrence of eggs might also be interpreted as a strategy to avoid egg desiccation.

Besides a suitable microclimate, oviposition sites need to provide sufficient food for the larvae (García-Barros and Fartmann, 2009). *L. achine* is a grass-feeding butterfly with caterpillars found on different species of Cyperaceae, Juncaceae and Poaceae (Bergman, 2000). Experiments by Bergman (2000) showed that *L. achine* is able to develop successfully from larvae to adult butterflies at least on Cyperaceae and Poaceae species. However, survival was by far highest on the only Cyperaceae investigated in his study,

Table 6

Statistics of GLM: relationship between extinction of *Lopinga achine* and climate variables. Strongly intercorrelated climatic parameters (mean annual temperature, mean temperature January, mean annual number of frost days) were summarized by PCA into one factor which was used as the independent variable (Climate factor).

Variable	Estimate	SE	Z	P
Climate factor	-0.13429	0.02317	0.00097	<0.001
Pseudo R^2 [Nagelkerke]	= 0.09			

C. montana. Despite a variety of observed grass host plants, *L. achine* clearly seems to prefer low-growing and fine-leaved sedges as larval food. In southern Sweden *C. montana* was identified as the main host plant (Bergman, 2000), and for the Czech Republic *C. fritschii* and *C. michelii* were mentioned (Konvička et al., 2008). For our study region, we assumed *C. alba* as the preferred host plant. The cover of *C. alba* in *L. achine* habitats was generally high, and adult abundance, as well as the likelihood of a site being used for oviposition, increased with the cover of this *Carex* species. The second most common sedge, *C. montana*, was also widespread: however, abundance was relatively low. Although it is a known host plant of *L. achine*, in our study region its relevance seems to be clearly inferior to that of *C. alba*. However, egg deposition also occurred on sites without any adjacent *Carex* species or where only other small sedges, such as *C. humilis* or *C. flacca*, occurred. So, in some cases, further grass species might also be used by the larvae. With reference to Poaceae, it is difficult to estimate which role species such as *B. rupestre* play. Due to its superabundance within the study region, *B. rupestre* occurred within oviposition and available sites to the same extent, similarly to other grass species, such as *S. varia*. However, as there are larvae observations on other *Brachypodium* species (Ebert and Rennwald, 1991; SBN, 1994), it appears to be a possibility that *B. rupestre* sometimes serves as a food source. In contrast, *L. achine* may be solely dependent on this species, as it is a relatively high growing grass and creates the preferred vegetation structure.

As freshly-hatched larvae have to locate their food source, it is a general rule that egg-dropping butterflies depend on dense stands of host plants (Wiklund, 1984). Accordingly, the observed high cover of host plants is not only crucial because of microclimatic aspects, but also in order to avoid time-consuming searching behaviour of the caterpillar (cf. Wiklund, 1984).

Although the cover of nitrophytes is generally low in our *L. achine* habitats, abundance of butterflies was negatively affected by the cover of nitrophytes. Nitrophytes are antagonists of low-competitive host plant sedges (Konvička et al., 2008). According to Fabian (1990), atmospheric nitrogen deposition in our study region is so low that it does not affect species composition of the vegetation. However, natural nutrient content and availability in the pine and mixed forests depend on slope and soil thickness (Ewald, 1997; Hölzel, 1996). Hence, less inclined sites with more mature soils favour nitrophytes and discriminate against small sedges and *L. achine*. A too-dense moss and litter layer might also oppress *C. alba* and low-competitive herbs. This possibly explains the negative relationship between the cover of litter and mosses and the likelihood of a site being used for oviposition, whereas the probability increased with increasing cover of *C. alba* and herbs.

In summary, although we have no feeding observation, in our study area *C. alba* seems to be the main host plant of *L. achine*. The high density of the host plant is necessary to fulfill the humidity requirements of the eggs and to allow easy access by the larvae. The preference for particularly light forests on warm south-facing slopes most probably reflects a compensation for the cold mountain climate near the altitudinal range limit.

4.2. Drivers of the decline throughout Germany

The decline of *L. achine* was positively correlated with the mean annual temperature and mean January temperature. Correspondingly, the likelihood of extinction decreased with the annual number of frost days. More generally speaking, *L. achine* populations have become extinct in regions with a mild climate while most of the remaining colonies are restricted to areas with relatively cold winters. However, the explanatory power of the model was very low.

Therefore, we have to be cautious in assuming global warming as the main reason for the decline, as has been observed for some northern butterfly species that retracted their ranges at lower latitudes and elevations (Franco et al., 2006; Wilson et al., 2005). The two remaining strongholds in Germany are not only characterized by cold winters but also by the continuation of traditional forest management promoting *L. achine* (Konvička et al., 2008). In Lower and Middle Franconia, coppicing, and coppicing with standards, is still relatively widespread. With an area of about 6000 ha, it is the largest remnant of this forest management technique in Germany (Bärnthol, 2003). Larger areas of wood pastures in Germany are restricted to the second stronghold, the pre-Alpine and Alpine region (Sachteleben, 1995). Moreover, there are still strong populations of *L. achine* in areas with mild winters (e.g. woodlands in the southern Upper Rhine Valley and the adjacent French Alsace, own observation). These areas are also characterized by the continuation of traditional woodland management, including coppicing and coppicing with standards.

In the Czech Republic eutrophication has recently been identified as a very serious risk for the last population of *L. achine*. Nitrogen depositions alter the vegetation and affect butterflies negatively by supporting high growing species that repress low-competitive host plants (Konvička et al., 2008; Pollard et al., 1998; Weiss, 1999). Except for the Alpine region, where nitrogen deposition is still low (Fabian, 1990), eutrophication of woodlands in recent times by atmospheric nitrogen might have additionally promoted the extinction in Germany. However, detailed studies are so far absent.

In nearly 90% of all grid cells where the species has become extinct, it disappeared before 1971. In contrast to the more recent global warming and atmospheric nitrogen depositions, the abandonment of coppicing and wood pasture also mainly took place before the mid-20th century (Ellenberg and Leuschner, 2010), assuming that the cessation of traditional woodland management has been the major driver of the range retraction of *L. achine* in Germany.

4.3. Implications for conservation

Suitable woodlands for *L. achine* are characterized by: (i) a light canopy (Fig. 3); and (ii) a medium-high and dense herbaceous layer rich in low-competitive sedges. The preservation of the preferred vegetation structure depends, in the majority of the Central European habitats, on management. Exceptions are naturally light woodlands having dense carpets of low-growing *Carex* species, such as some bog forests, particularly in the pre-Alps, and primary pine forests on alluvial gravel, screes or steep and shallow soils in the Alps.

Besides coppicing or litter raking, forest grazing is a suitable technique to maintain open woodland structures (Vera, 2000). In Sweden, simulations showed that, without the application of grazing, canopy closure can lead to the extinction of a complete metapopulation within 100 years of abandonment (Bergman and Kindvall, 2004). Wood pasture has also been recommended as a suitable option to prevent the invasion of competitive plant species into the ground vegetation and to save the last *L. achine* population in the Czech Republic (Konvička et al., 2008).

In our study region, abundance of *L. achine* did not differ between grazed and ungrazed sites. This is probably explained by the fact that some of the occupied sites were primary pine forests which naturally exhibit a light canopy cover. Nonetheless, there were ungrazed mixed forests and secondary pine forests still possessing vegetation structures suitable for *L. achine*. The high impact of overstocking game animals on natural woodland regeneration, a problem for large parts of Europe and North America (Côté et al., 2004), was also present in these forests, with the result of slowing

down succession (cf. Hölzel, 1996). However, in the longer term, these sites are also at risk of becoming overgrown by invading shrubs and canopy closure.

In the pine and mixed forests of the northern Alps large growing grasses, such as *B. rupestre*, *C. varia* or *M. arundinacea*, typically become dominant after the abandonment of grazing (Hölzel, 1996). *L. achine* seems to tolerate a high cover of *B. rupestre*. Nonetheless, it is important to prevent dominance of these grasses, in particular of the much taller *C. varia* and *M. arundinacea* that repress the low-competitive host plant sedges. Forest grazing by cattle is suitable for controlling the growth of coarse grasses and reducing litter accumulation. In small patches, or on steep slopes where the introduction of cattle grazing is logistically difficult, it is necessary to remove single trees and scrubs manually. Within the remaining wood pastures in our study area, grazing influence is mainly found from the bottom of the valleys up to 200 m higher on the slope (own observation). This is particularly true for wood pastures where the more massive cattle breeds avoid steep slopes, compared to traditional races (e.g., the Murnau–Werdenfelser cattle) (Hölzel, 1996).

Alternatively, the introduction of goat pastures is a viable alternative. Goats are suitable for mountainous regions and belong to the intermediate feeding type of ruminants (Hofmann, 1989). Accordingly, they do not graze on grasses as intensively as do sheep, but rather consume woody species to a higher degree (Jáuregui et al., 2009).

In order to enhance long-term population viability of *L. achine*, new habitats should be created adjacent to occupied patches. According to Bergman and Landin (2001), a network of 15–20 patches connected by distances below 700 m counteracts the risk of extinction of a metapopulation.

The results of our study suggest it is conceivable that *L. achine* will shift its range upwards rather than moving on to more northern exposed slopes to compensate for climate change. Given this is a butterfly species included in Annex IV of the EU Habitats Directive (Ssymank et al., 1998), there is a general responsibility to monitor it and, if necessary, to adjust conservation measures; e.g. on sites possibly becoming suitable at higher elevations.

This study clearly highlighted the special role of a light canopy for the threatened and strongly declining woodland butterfly *L. achine*. There are other studies that also show that many woodland butterfly species of conservation concern depend on open conditions (Anthes et al., 2008; Fartmann, 2006; Freese et al., 2006; Konvička and Kuras, 1999; Slamova et al., 2011). However, it is not only butterflies that are known to benefit from light woodlands. Among other species, birds (Fuller and Henderson, 1992) or saproxylic beetles (Vodka et al., 2009) are further examples.

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