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Limestone quarries are the most important refuge for a formerly widespread grassland butterfly

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Abstract. 1. Calcareous grasslands have an outstanding value for nature conservation. However, during the last century, they have suffered from severe area loss, fragmentation and degradation.

2. Here, we studied the influence of macroclimate, landscape quality and habitat quality on populations of the Silver-studded Blue, *Plebejus argus*, in calcareous grasslands and limestone quarries in a Central European landscape.

3. Our study revealed that limestone quarries, especially those being actively managed, are the most important refuge for *P. argus*. Originally, the species was common in calcareous grasslands across the study area. More recently, however, patch occupancy was five times higher at quarries compared to calcareous grasslands and mean adult abundance nearly four times higher at occupied quarries than at occupied grasslands. The key driver of patch occupancy and adult abundance was a high abundance of the host plant. Adult abundance, additionally, increased with a sparse vegetation and a high cover of bedrock.

4. The deterioration of habitat quality due to abandonment and decreasing grazing intensity has resulted in a strong decline of *P. argus* in calcareous grasslands. In contrast, quarries exhibit a very low successional speed due to their shallow soils. Hence, they are characterised by a high habitat quality for *P. argus*, i.e. dense stands of the host plant *L. corniculatus*, which grow on skeletal soils providing warm microclimatic conditions.

5. Preserving limestone quarries with their early-successional stages is of crucial importance for the conservation of *P. argus*.

Key words. Calcareous grassland, early-successional stage, habitat quality, host-plant abundance, microclimate, patch connectivity.

Introduction

Calcareous grasslands are among the most species-rich habitat types across Europe (Poschlod & Wallis de Vries, 2002; Wallis de Vries *et al*., 2002). However, during the last century, agricultural intensification, eutrophication, afforestation and abandonment of traditional land use have caused a severe loss, fragmentation and degradation of calcareous grasslands (Poschlod & Wallis de Vries, 2002; Wallis de Vries *et al*., 2002; Veen *et al*., 2009). Due to their status as biodiversity hotspots and the threats they face, they are protected by the EU Habitats Directive (European Commission, 1992). They are of prime importance for plants and many groups of insects (Wilson *et al*., 2012; Bonari *et al*., 2017; Löffler *et al*., 2020; Poniatowski *et al*., 2020; Helbing *et al*., 2021). For example, about 50% of all native European butterfly species occur in calcareous grasslands (van Swaay, 2002; van Swaay *et al*., 2006).

Butterflies are characterised by very specific habitat requirements (García-Barros & Fartmann, 2009; Dennis, 2010). Host-plant availability and microclimatic conditions are the most important predictors of butterfly habitat quality (García-Barros & Fartmann, 2009; Curtis *et al*., 2015). The microclimate within a butterfly habitat is mainly influenced by vegetation structure (García-Barros & Fartmann, 2009; Scherer *et al*., 2021), which usually depends on land use (Dover & Settele, 2009). Most thermophilous habitat-specialist butterflies require warm microhabitats for oviposition

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(e.g. Roy & Thomas, 2003; Krämer *et al*., 2012a). This is especially true for regions with a cool macroclimate, such as most of western or Central Europe. Here, they often depend on the earliest successional stages (Thomas, 1993; Roy & Thomas, 2003) and are among the most strongly declining species (Eskildsen *et al*., 2015; Habel *et al*., 2019). Besides habitat quality, the distribution of habitat-specialist butterflies in cultivated landscapes usually depends on patch size and patch connectivity (Eichel & Fartmann, 2008; Stuhldreher & Fartmann, 2014; Poniatowski *et al*., 2018b).

The Silver-studded Blue, *Plebejus argus* (Linnaeus 1758), is a thermophilous habitat specialist, and calcareous grasslands are one of its main habitats (Asher *et al*., 2001; Nunner, 2013). In western and Central Europe, the species has disappeared from many areas in recent decades (Bos *et al*., 2006; Fox *et al*., 2006; Meineke, 2020). Habitat loss and the deterioration of habitat quality due to the abandonment of traditional land use are assumed to be the main drivers of the decline (Asher *et al*., 2001; Stefanescu *et al*., 2009). For Great Britain, detailed studies on the habitat requirements of *P. argus* in calcareous grasslands are available (Thomas 1985a, 1985b; Lewis *et al*., 1997; Dennis & Sparks, 2006). Based on this research, the species depends on early-successional habitats, which provide warm microclimatic conditions for larval development.

In this article, we studied patch occupancy and abundance of *P. argus* in calcareous grasslands and limestone quarries in a Central European landscape with intensive agriculture and forestry. We analysed the influence of macroclimate, landscape quality and habitat quality on patch occupancy and abundance of the species. The aim of our study was to compare the environmental conditions of occupied and vacant habitat patches to determine the drivers of local population extinctions. Based on our results, we make management recommendations for the conservation of *P. argus* in Central European landscapes.

Materials and methods

Study area

The study area, the Diemel Valley and directly adjoining Brilon Plateau, is about 510 km^2 large and located in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°22'N/8°28'E and 51°38'N/9°28'E) (Fig. 1). It exhibits the largest area of semi-dry calcareous grasslands (~775 ha) in the northern half of Germany (Fartmann, 2004, 2006). Open limestone quarries are also widespread (~205 ha). Both calcareous grasslands and limestone quarries are surrounded by a matrix of intensively used agricultural land and forests (Fartmann, 2004; Poniatowski *et al*., 2020).

The climate is subatlantic and varies greatly with elevation (Fartmann, 2004). The Brilon Plateau (360–600 m a.s.l.) is the coolest (annual mean temperature: 7.9 °C) and wettest (annual precipitation: 1073 mm) part of the study area [meteorological values are long-term means (1981–2010) and were derived from 1-km^2 grid datasets; Germany's National Meteorological Service, pers. comm.]. The Upper Diemel Valley (200–600 m a.s.l.) is similarly cool (8.1 °C), but the precipitation is lower

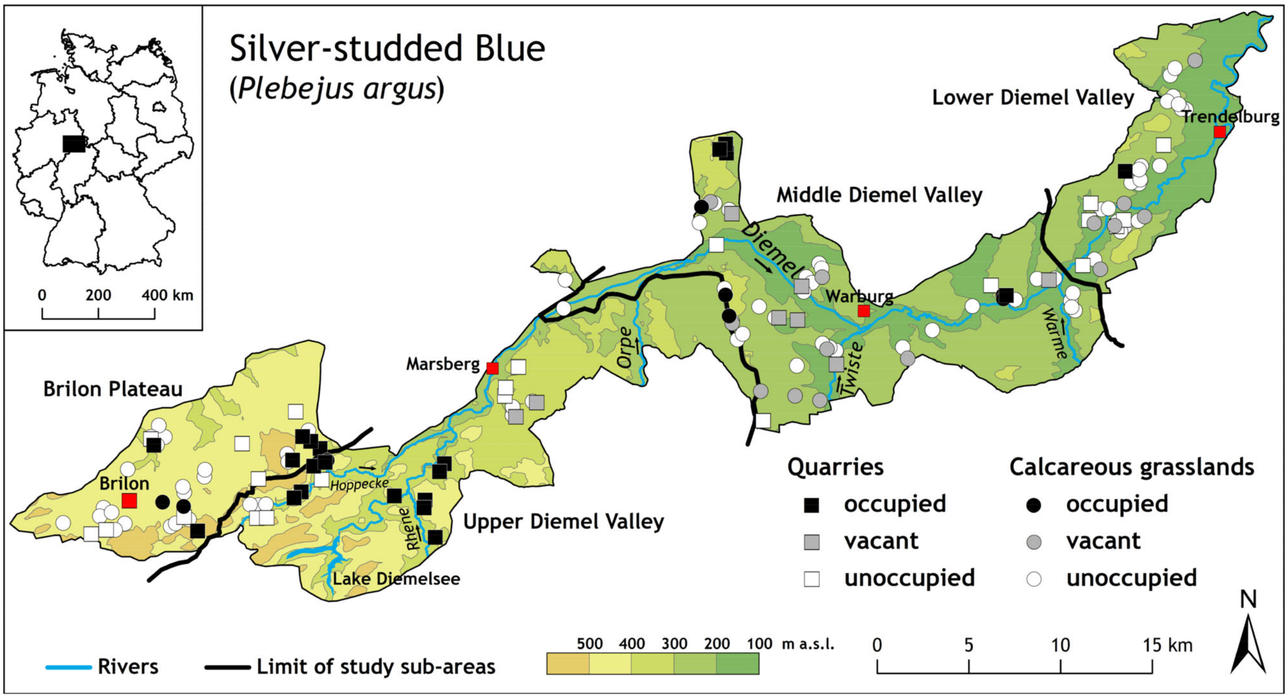

Fig 1. Location of the study area in Germany (inlay) and distribution of quarries ($n = 51$) and calcareous grasslands ($n = 99$) in the study area. Towns are indicated by red squares.

(845 mm). In the Middle Diemel Valley (140–400 m a.s.l.), the precipitation is even lower (737 mm) and the temperature is higher (8.8 °C). The Lower Diemel Valley (100–375 m a.s.l.) is the warmest (9.0 °C) part of the study area. Here, precipitation (788 mm) is slightly higher compared to the Middle Diemel Valley (Stuhldreher & Fartmann, 2018).

Calcareous grasslands are widespread in all four subareas (Glöckner & Fartmann, 2003; Fartmann, 2004, 2006). However, almost two-thirds (61%) of the limestone quarries are situated in the coolest subareas, the Brilon Plateau and the Upper Diemel Valley. Additionally, except three, all quarries still used for active mining are located in these subareas. Further information on the Brilon Plateau is available in the study by Glöckner and Fartmann (2003). A detailed description of the Diemel Valley is given by Fartmann (2004, 2006).

Study species

The Silver-studded Blue, *Plebejus argus* (Linnaeus 1758), is a lycaenid butterfly with a Palearctic distribution ranging from England eastwards across temperate Asia and Siberia to Japan, and from the Mediterranean region (36° N) to Fenno-Scandinavia (69° N) (Nunner, 2013; Meineke, 2020). In our study area, the species is univoltine and has a flight peak between mid-June and mid-July (Fartmann, 2004).

Plebejus argus colonises nutrient-poor, open habitats, such as degraded raised bogs, heathlands and calcareous grasslands (Nunner, 2013; Schirmel & Fartmann, 2014). Within its habitats, the species is dependent on early-successional stages with low-growing, sparse vegetation and a high proportion of bare ground or bedrock for oviposition (Thomas, 1985a, 1985b; Asher *et al*., 2001; Schirmel & Fartmann, 2014). Females deposit their eggs singly close to their host plants (Thomas, 1985b; Asher *et al*., 2001). On calcareous soils, *Lotus corniculatus* is the main host plant (Thomas, 1985a; Thomas *et al*., 1999; Asher *et al*., 2001). Within our study area, the occurrence of *P. argus* is restricted to calcareous grasslands and limestone quarries with *L. corniculatus* as the most important host plant (Fartmann, 2004). *Plebejus argus* hibernates in the egg stage, and larvae hatch towards the end of March (Bos *et al*., 2006). Both the caterpillars and pupae have a strong mutualistic relationship with ants of the genus *Lasius* (Hymenoptera: Formicidae). On calcareous soils, *Lasius alienus* is usually the main host (Jordano *et al*., 1992; Jordano & Thomas, 1992). From the end of May to early June, the larvae pupate near or most often within the ant nests (Asher *et al*., 2001). Adults hatch after 13–20 days of pupation (Bos *et al*., 2006).

In the first half of the 20th century, *P. argus* was common and widespread in calcareous grasslands of the Diemel Valley (Retzlaff, 1973). However, already by the end of the last century, the species had become very rare in calcareous grasslands in this part of the study area (Fartmann, 2004). In contrast, in limestone quarries, *P. argus* still occurred regularly in high densities. For the Brilon Plateau, no data on the distribution of *P. argus* during the last century are available (Glöckner & Fartmann, 2003). In Hesse and North Rhine-Westphalia, the species is considered vulnerable and endangered, respectively (Lange & Brockmann, 2009; Schumacher, 2011).

Sampling design

In this study, we surveyed a total of 150 patches: 99 calcareous grasslands (GRASS) and 51 limestone quarries (QUARRY). Data on the occurrence of GRASS and QUARRY in the study area were derived from Glöckner and Fartmann (2003), Fartmann (2004) and Stuhldreher and Fartmann (2018). Data on historic records of *P. argus* were taken from Retzlaff (1973), Glöckner and Fartmann (2003) and Fartmann (2004). The data were used to identify all formerly occupied patches in the study area. Patches were regarded as discrete if they were separated from each other by more than 50 m of non-habitat, such as forest, improved grassland and arable fields (e.g. Krämer *et al*., 2012b; Poniatowski *et al*., 2018b). Additionally, we distinguished the habitat patches based on their occupancy by *P. argus* (cf. ‘Patch occupancy’ section) into the six following habitat types: (i) occupied QUARRY, (ii) occupied GRASS, (iii) vacant QUARRY, (iv) vacant GRASS, (v) unoccupied QUARRY and (vi) unoccupied GRASS (Fig. 1). Vacant patches were occupied by *P. argus* in the past whereas the former status of the unoccupied patches is unknown. In order to determine the drivers of local population extinction only occupied and vacant patches were used for the analysis of the species' habitat characteristics. Further details on the sampling of *P. argus* and its patch occupancy are given in the ‘Butterfly sampling’ section.

Environmental conditions

Macroclimate. Characteristics of the local climate of each patch (mean number of frost days, mean annual precipitation and mean annual temperature) were derived from 1-km^2 grid datasets of Germany's National Meteorological Service (pers. comm.), which contain 10-year (2010–2019) mean values. The mean elevation (m a.s.l.) of the patches was calculated from topographic maps using ArcGIS 10.2.

Landscape and habitat quality. For each occupied and vacant patch, we assessed several parameters of landscape and habitat quality (Tables 1 and 2). Landscape quality parameters were ascertained for unoccupied patches as well (Supporting Information Table S1 and Table S2). Concerning land-use of GRASS and QUARRY, we distinguished between managed and abandoned patches. The former comprised grasslands regularly grazed by sheep and goats (at least once per year) and quarries still used for mining (Table 1; Supporting Information Table S1). In managed quarries, partly shrub removal was also regularly carried out to avoid excessive shrub encroachment.

The landscape-quality parameters patch size and patch connectivity were determined on the basis of aerial photographs using ArcGIS 10.2 (Table 2; Supporting Information Table S2). The size of the patches varied between 0.2 and 15.8 ha (mean: 2.6 ± 0.3 ha). Connectivity of the patches was measured as the geometric mean of the next three populated patches (Eichel & Fartmann, 2008; Scherer *et al*., 2021). Edge-to-edge distances from the focal patch to the three other patches were computed using the proximity-analysis tool ‘near table’ in ArcGIS 10.2.

Table 1. Absolute and relative frequencies of the nominal variables 'habitat type' and 'land use' at occupied and vacant patches of *Plebejus argus*.

	Occupied ($n = 29$)		Vacant ($n = 22$)		
Parameter	*N*	%	*N*	%	*P*
Habitat type					*
QUARRY	21	72.4	8	27.6	
GRASS	8	36.4	14	63.6	
Land use					
QUARRY					*
Managed	9	100.0	0	0.0	
Abandoned	12	60.0	8	40.0	
GRASS					*
Managed	8	57.1	6	42.9	
Abandoned	0	0.0	8	100.0	

Differences in absolute frequencies between habitat types were analysed with Fisher's exact test. Significance levels are indicated as follows: *$P < 0.05$.

Connectivity of the patches varied between 0.3 and 12.7 km (mean: 4.2 ± 0.2 km).

We sampled habitat-quality parameters once at the beginning of July 2019 (Table 2). On each occupied and vacant patch, we recorded several vegetation-structure parameters, abundance of the main host plant (*L. corniculatus*) and soil depth at three randomly selected plots of 4 m^2 (2 m × 2 m). The following parameters of horizontal vegetation structure were estimated (in 5% steps): the cover of herbs, grasses, litter, mosses, small shrubs (<0.5 m) and bare ground as well as gravel, stones and rocks (hereinafter termed 'bedrock'). In cases where cover was above 95% or below 5%, 2.5% steps were used. The mean value of the average vegetation height was calculated from measurements at three random points within each plot. Vegetation density was estimated using a wire-framed box (50 cm × 30 cm × 30 cm), which was open on all sides except the back. Horizontal wires on the front side of the box divided it into six height layers of 5 cm each to estimate the vegetation density between 0 and 30 cm above ground. The cover of each layer was viewed horizontally against the bright back of the box, using the same classes as for the horizontal vegetation structure (Fartmann *et al*., 2012; Löffler & Fartmann, 2017). Soil depth was measured at the centre of each plot using a metal rod with length marks (Poniatowski *et al*., 2020). For further analyses, we calculated mean values of the three plots.

We sampled sunshine duration and air temperature as microclimatic parameters. The potential daily sunshine duration for the month June was measured in the field with an accuracy of ¼ h using a horizontoscope (Streitberger & Fartmann, 2015). Air temperature was ascertained for each of the four habitat types. The patches were randomly selected and the number of replicates per habitat type was five. We installed Hygrochron temperature data loggers (iButton, Maxim/Dallas, DS1923, USA) 10 cm above ground. They were placed in a self-constructed radiation shield to protect the sensor from direct sunlight and precipitation (Stuhldreher & Fartmann, 2018). The radiation shield consisted of a white metal case with an integrated Styrofoam insulation (1 cm thick) to prevent the data loggers from overheating on sunny days. The data loggers recorded air temperature once every hour with an accuracy of 0.5 °C for 14 days from 23 July until 5 August 2019.

Since the data loggers were placed in distinct patches, we treated them as statistically independent units. The values recorded by one and the same data logger, however, were not independent of each other. Hence, we averaged the hourly recorded values of each logger over the entire measurement period and used these averages for our analyses. Accordingly, differences between the mean values of distinct data loggers reflect the microclimatic differences between patches (Stuhldreher & Fartmann, 2018). Furthermore, we analysed microclimatic differences between habitat types for daytime and night-time separately. As the thermal effects of solar radiation are weak shortly after sunrise, but especially in summer the aftereffects last a relatively long time until sunset, daytime was defined as the period from two hours after sunrise to sunset (8:00 a.m. to 9:00 p.m.). Consequently, all recorded values within this period were assigned to daytime, while all other measurements (10:00 p.m. to 7:00 a.m.) were assigned to night-time.

Butterfly sampling

Patch occupancy. In 2018 and 2019, respectively, all patches of GRASS ($n = 99$) and QUARRY ($n = 51$) in the study area were surveyed up to two times during the peak of the species' flight period between mid-June and the beginning of July, with a time interval of at least two weeks between each survey (cf. Öckinger, 2006; Eichel & Fartmann, 2008). To assess the occupancy of *P. argus*, transect walks were done between 10 a.m. and 5 p.m. under suitable weather conditions (dry, sunny days with temperatures >18 °C and low wind speed). In every patch, adults of *P. argus* were recorded walking in loops covering all open habitat structures with a width of 5 m between each loop. Only GRASS and QUARRY without evidence for occupancy of the species during the first survey were investigated a second time. According to Poniatowski *et al.* (2018b), a patch was classified as occupied if at least three adults (as an indicator for an indigenous population) were detected.

Abundance. Based on the patch occupancy survey, we sampled the abundance of adult *P. argus* in all occupied patches in 2019. Butterflies were sampled in plots of 500 m^2 (20 m × 25 m) size at that part of the patch with the highest adult density using standardised transect counts (Pollard & Yates, 1993; Krämer *et al*., 2012b). We recorded the number of adult individuals inside the plots in loops with a width of 5 m. Each transect count took 15 min, excluding identification time for critical individuals (Krämer *et al*., 2012b). All plots were visited twice throughout the peak of the species' flight period (mid-June to early July) between 10:00 a.m. and 5:00 p.m. and only during suitable weather conditions (cf. 'Patch occupancy' section). The chronological order of the sampling of the transect plots was based on the climatic gradient across the four subareas (Lower Diemel Valley > Middle Diemel Valley > Upper Diemel

Table 2. Mean values (±SE) of all numerical environmental parameters at the four habitat types. Differences among habitat types were analysed by LMM/GLMM and subsequent Tukey contrasts, see materials and methods for details.

Parameters	Occupied ($n = 29$)		Vacant ($n = 22$)		P	r_S	Used variables
	QUARRY ($n = 21$)	GRASS ($n = 8$)	QUARRY ($n = 8$)	GRASS ($n = 14$)			
Macroclimate							
Elevation (m a.s.l.)	380.8 ± 17.7^{a}	314.1 ± 39.8^{ab}	252.9 ± 21.0^{b}	221.5 ± 10.4^{b}	***	−0.82	
Frost days[a]	80.2 ± 1.4^{a}	77.4 ± 1.9^{ab}	74.4 ± 1.6^{b}	72.7 ± 0.8^{b}	***	−0.86	► Temperature
Precipitation (mm)[b]	746.8 ± 20.4^{a}	730.4 ± 34.3^{ab}	653.3 ± 11.8^{b}	658.0 ± 7.6^{b}	**	−0.83	
Temperature (°C)[c]	9.1 ± 0.1^{a}	9.3 ± 0.2^{ab}	9.6 ± 0.1^{b}	9.7 ± 0.1^{b}	***	1.00	
Landscape quality							
Patch size (ha)	1.0 ± 0.1	0.8 ± 0.2	1.4 ± 0.2	2.7 ± 0.7	n.s.		
Patch connectivity (km)[d]	1.8 ± 0.4^{a}	3.0 ± 0.5^{ab}	4.8 ± 0.6^{b}	6.1 ± 0.7^{b}	***		
Habitat quality							
Sunshine (h)[e]	13.4 ± 0.5^{a}	12.3 ± 0.7^{a}	10.4 ± 0.8^{b}	11.8 ± 0.5^{a}	**		
Vegetation structure							
Vegetation density (%)							
0–5 cm	65.3 ± 2.7^{a}	71.0 ± 3.4^{ab}	86.7 ± 5.3^{bc}	94.6 ± 2.1^{c}	***	0.79	
10–15 cm	27.9 ± 2.7^{a}	19.0 ± 2.1^{a}	49.2 ± 8.8^{b}	52.9 ± 6.6^{b}	***	1.00	► Vegetation density, 10–15 cm
20–25 cm	5.0 ± 0.9^{ab}	2.3 ± 0.6^{a}	14.3 ± 5.7^{ab}	17.1 ± 5.5^{b}	*	0.84	
Vegetation height (cm)	14.3 ± 1.0^{a}	11.5 ± 1.2^{a}	17.3 ± 2.1^{ab}	19.8 ± 2.3^{b}	*	0.81	
Cover (%)							
Bare ground	11.0 ± 1.8^{ab}	21.7 ± 3.2^{a}	6.3 ± 1.2^{b}	4.9 ± 0.8^{b}	***		
Bedrock[f]	20.3 ± 2.4^{a}	5.7 ± 1.6^{b}	5.0 ± 1.6^{b}	2.1 ± 0.8^{b}	***		
Small shrubs (<0.5 m)	0.8 ± 0.3^{a}	0.9 ± 0.3^{ab}	2.8 ± 1.1^{ab}	3.7 ± 0.9^{b}	**		
Herbs	51.7 ± 1.8^{a}	41.1 ± 2.9^{b}	49.3 ± 1.9^{ab}	41.6 ± 1.8^{b}	***		
Grasses	15.1 ± 1.9^{a}	30.0 ± 4.9^{b}	37.1 ± 3.7^{b}	51.2 ± 2.8^{c}	***	−0.83	
Host plant *L. corniculatus*	38.1 ± 2.6^{a}	24.2 ± 3.7^{b}	15.7 ± 3.3^{bc}	8.9 ± 1.2^{c}	***	1.00	
Mosses	26.1 ± 3.4^{ab}	17.3 ± 4.1^{a}	36.5 ± 6.3^{b}	38.6 ± 5.3^{b}	*	−0.70	► *Lotus corniculatus*
Litter	4.5 ± 1.4^{a}	5.4 ± 2.7^{a}	30.4 ± 7.9^{b}	33.0 ± 6.0^{b}	***	−0.74	
Soil depth (cm)	5.3 ± 0.6^{a}	7.2 ± 0.9^{a}	10.4 ± 1.6^{ab}	18.7 ± 1.6^{b}	***	−0.73	

Habitat types without consistent letters indicate significant differences ($P < 0.05$). Significant differences between the habitat types are also indicated by bold type. Significance levels are indicated as follows: n.s. not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

[a] Mean no. of frost days/a.

[b] Mean annual precipitation (mm).

[c] Mean annual temperature (°C).

[d] Mean distance to the next three occupied patches.

[e] Mean potential duration of daily sunshine in June.

[f] Gravel, stones and rocks.

Valley > Brilon Plateau) in order to take phenological differences into account. For statistical analyses, the maximum abundance of the two counts was used (Streitberger *et al.*, 2012; Weking *et al.*, 2013).

Statistical analysis

Differences in absolute frequencies between the nominal variables 'habitat type' and 'land use' of occupied, vacant and unoccupied patches were analysed with Fisher's exact test (Table 1; Supporting Information Table S1). For detecting significant differences in environmental parameters (Table 2; Table S2; Fig. 2) and butterfly abundance between the habitat types, (generalised) linear mixed-effect models (GLMM; LMM) were applied (R packages lme4, Bates *et al.*, 2020) with 'subarea' as a random factor. Habitat type served as a nominal fixed factor, and the analysed parameters were used as dependent variables. Depending on the distribution of the variables, binomial (percentage data), Poisson (count data) or Gaussian (for square-root- or log-transformed variables with normal distribution) models were applied with the respective standard link functions. For reducing overdispersion within the models (binomial/Poisson), observation-level random effects were added as a random factor (Harrison, 2014, 2015). The overall effect of the dependent variables on habitat type was analysed by comparing the full models with reduced models without 'habitat type' as the fixed factor and applying likelihood-ratio tests. Pairwise differences between the habitat types were detected by applying Tukey contrasts (glht function, R package multcomp, Hothorn *et al.*, 2020).

To determine which environmental parameters explained patch occupancy and abundance of *P. argus*, we fitted GLMM (binomial and negative-binomial, respectively). To avoid model overfitting, in both cases, we performed three different models, each containing a different set of environmental parameters (macroclimate, landscape quality and habitat quality, Table 2; Stuhldreher & Fartmann, 2014). Finally, all significant variables

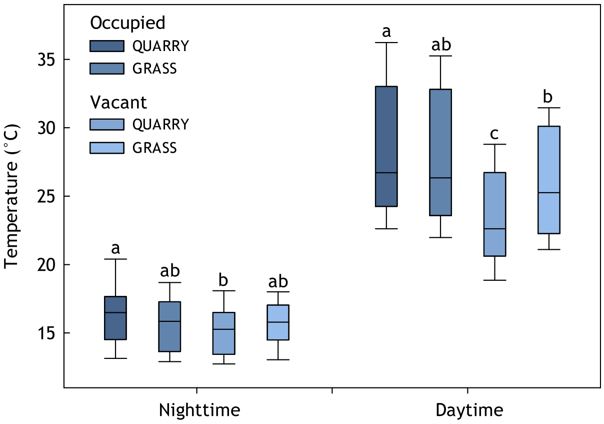

Fig 2. Differences in hourly mean air temperature during night-time (10 p.m. to 7 a.m.) and daytime (8 a.m. to 9 p.m.) between the four habitat types (measurement period: 23 July to 5 August 2019). The boxes show the median and the first and third quartile, the whiskers indicate the 10th and 90th percentile. Differences among habitat types were analysed by GLMM and subsequent Tukey contrasts, see 'Statistical analysis' section for details. Habitat types without consistent letters indicate significant differences ($P < 0.05$).

of the macroclimate, landscape-quality and habitat-quality models were incorporated into a synthesis model. For all GLMM, the variables 'habitat type' and 'subarea' were used as random factors (Crawley, 2007). In order to increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber *et al*., 2011). Model averaging was conducted using the dredge function (R package MuMIn, Bartón, 2020) and included only top-ranked models within $\Delta AIC_C < 3$ (Grueber *et al*., 2011). Prior to multivariable analyses, we implemented Spearman's rank correlations (r_S) between all numerical environmental parameters to identify possible intercorrelations. If parameters were strongly intercorrelated ($|r_S| > 0.7$), only the most important variable was used in GLMM analyses (Table 2). All statistical analyses were performed using R 3.5.2 (R Development Core Team, 2019).

Results

Patch occupancy

5wIn total, 29 (19%) of the 150 studied patches were occupied by *P. argus* and 22 (15%) were vacant. All other 99 patches (66% of all surveyed patches) were unoccupied by *P. argus*, but the former occupation status is unknown. Patch occupancy was five times higher at QUARRY ($n = 21$, 41% of all surveyed quarries) compared to GRASS ($n = 8$, 8% of all surveyed grasslands) (Table 1; Supporting Information Table S1). The frequency of occupied and vacant patches differed between QUARRY and GRASS; at QUARRY, the number of occupied patches was higher and those of vacant patches were lower. Additionally, active management favoured the occurrence of the species. Patch occupancy was higher at managed QUARRY than at abandoned QUARRY. At GRASS, even all occupied patches were managed ones (Table 1). The frequency of unoccupied patches also differed between QUARRY and GRASS, as the majority of unoccupied patches were GRASS patches (Table S1).

Except patch size, all metric environmental parameters differed among the four habitat types (Table 2; Fig. 2). Especially, occupied patches varied strongly from vacant ones; additionally, occupied QUARRY was characterised by the most extreme environmental conditions. All macroclimatic parameters were intercorrelated (Table 2). Occupied QUARRY was situated at the highest elevations and was characterised by the highest number of frost days and annual precipitation as well as the lowest temperature. Occupied QUARRY differed from vacant patches. Occupied GRASS had an intermediate position. Occupied QUARRY had the highest connectivity, differing from vacant patches. In contrast, occupied GRASS did not differ in any of the macroclimatic and landscape-quality parameters from any of the three other habitat types.

When comparing the landscape-quality parameters of all six habitat types, unoccupied patches differed from occupied patches. Unoccupied QUARRY patches were larger than occupied patches. Both unoccupied QUARRY and unoccupied GRASS were less connected than occupied QUARRY and showed similar patch connectivity values as vacant patches. Unoccupied QUARRY was situated at higher elevations than vacant patches. Unoccupied GRASS did not differ in macroclimatic parameters from any of the five other habitat types (Supporting Information Table S2).

Habitat-quality parameters were also strongly intercorrelated (Table 2). Usually, they reflected a gradient from occupied QUARRY to occupied GRASS to vacant patches. Along this gradient, vegetation density, vegetation height, the cover of small shrubs, mosses, grasses and litter as well as soil depth increased. In contrast, the cover of bare ground, bedrock, herbs and the host plant *L. corniculatus* decreased. Sunshine duration was lowest in vacant QUARRY, differing from the three other habitat types. Since vegetation structure and sunshine duration strongly differed among the habitat types, temperature in the microhabitats did so too (Fig. 2). During daytime, temperatures decreased from occupied QUARRY to vacant GRASS to vacant QUARRY. Occupied GRASS had an intermediate position. At night-time, the pattern was similar, however, only occupied QUARRY differed from vacant QUARRY.

The GLMM analysis identified macroclimate, landscape quality and habitat quality as drivers of patch occupancy of *P. argus* (Table 3). In the macroclimate model, patch occupancy of *P. argus* decreased with temperature. The landscape-quality model revealed a positive relationship between connectivity of the patches and patch occupancy. In the habitat-quality model, the occurrence of the species was best predicted by the cover of the host plant, *L. corniculatus*. In the synthesis model, the cover of the host plant remained as the only predictor variable (Table 3, Fig. 3). For all models, the explanatory power and the discriminative ability was high (R^2_{GLMMm} 0.35–0.87, AUC 0.89–0.97).

Abundance

Mean abundance of adult *P. argus* was nearly four times higher at occupied QUARRY than at occupied GRASS (Fig. 4). The GLMM analysis detected habitat quality as the driver of *P. argus* adult abundance (Table 4). In contrast, macroclimate and landscape quality had no effect on butterfly abundance. In both the habitat-quality and the synthesis model, the abundance of the species was best predicted by the cover of the host plant, *L. corniculatus*, the cover of bedrock as well as a low vegetation density (Table 4; Fig. 5). Again, the explanatory power of the models was high (R^2_{GLMMm} 0.37–0.41).

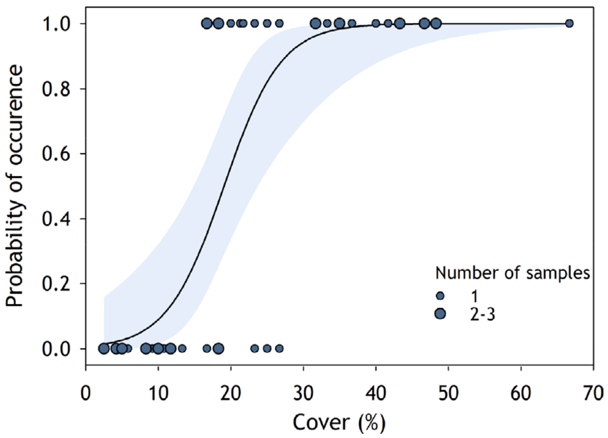

Fig 3. Relationship between patch occupancy of *Plebejus argus* and the significant parameter (cover of the host plant *L. corniculatus*) of the averaged synthesis model. The regression slope (including 95% confidence intervals) was fitted by using single predictor GLMM with binomial error structure (see Table 3): $y = 1/(1 + \exp(-(-4.87718 + 0.25596 \times L.\ corniculatus)))$, $P < 0.01$, $R^2_{GLMMm} = 0.80$, $R^2_{GLMMc} = 0.80$. R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al*., 2017).

Discussion

Our study revealed that limestone quarries are the most important refuge for the formerly widespread Silver-studded Blue. Originally, *P. argus* was common in calcareous grasslands across the study area (Retzlaff, 1973; Fartmann, 2004). More recently, however, patch occupancy was five times higher at quarries compared to calcareous grasslands and mean adult abundance nearly four times higher at occupied quarries than at occupied grasslands. Active management favoured the occurrence of *P. argus* in quarries and was even an essential prerequisite in calcareous grasslands. The key driver of patch occupancy and adult abundance in the synthesis models was a high abundance of the host plant. Adult abundance, additionally, increased with a sparse vegetation and a high cover of bedrock.

Macroclimate is an important predictor of butterfly distribution (Settele *et al*., 2008; Chen *et al*., 2011; Devictor *et al*., 2012). This has also been documented for many species across the elevational gradient of the study area (Fartmann, 2004; Stuhldreher & Fartmann, 2018). In our study, we detected a negative relationship between patch occupancy of *P. argus* and temperature in the macroclimate GLMM. Occupied patches situated at higher elevations were characterised by more frost days, higher precipitation and lower temperatures than vacant patches. However, it is unlikely that the observed patterns reflect a genuine preference for cool and wet climates. In fact, we attribute these relationships by the predominant occurrence of the main habitat, limestone quarries, especially those

Table 3. Statistics of GLMM: Relationship between patch occupancy of *Plebejus argus* [binomial response variable: Occupied ($n = 29$) versus vacant patches ($n = 22$)] and several environmental parameters (metric predictor variables). 'Habitat type' and 'subarea' were used as random factors. Model-averaged coefficients (conditional average) were derived from the top-ranked models (ΔAICC < 3).

Parameters	Estimate	SE	Z	*P*	R^2_{GLMMm}	R^2_{GLMMc}	AUC
(a) Macroclimate					0.35	0.46	0.89
(Intercept)	34.52	12.60	2.74	*			
Temperature	−3.63	1.33	−2.74	*			
(b) Landscape quality					0.72–0.77	0.75–0.79	0.94
(Intercept)	6.53	2.64	2.42	*			
Connectivity	0.85	0.30	2.78	**			
Not significant: patch size							
(c) Habitat quality					0.84–0.87	0.87–0.89	0.97
(Intercept)	−5.15	3.49	1.45	n.s.			
Lotus corniculatus	0.27	0.09	2.76	**			
Not significant: sunshine, vegetation density, bare ground, bedrock, small shrubs, herbs							
(d) Synthesis model					0.80–0.83	0.82–0.85	0.96
(Intercept)	14.82	15.45	0.95	n.s.			
Lotus corniculatus	0.24	0.08	2.70	**			
Not significant: temperature, connectivity							

R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al*., 2017), AUC = area under the curve; accuracy of model prediction (Fielding & Bell, 1997). Significance levels are indicated as follows: *n.s.* not significant, *$P < 0.05$, **$P < 0.01$.

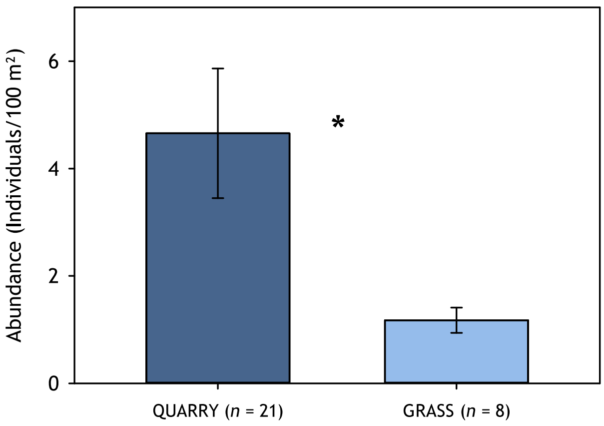

Fig 4. Mean (±SE) abundance of *Plebejus argus* in occupied QUARRY ($n = 21$) and occupied GRASS ($n = 8$). Differences between the two groups were tested using GLMM, see 'Statistical analysis' section for details; $^*P < 0.05$.

with active management, in the highest elevations of the study area (cf. 'Study area' section). In line with this, *P. argus* is known to occur across very different macroclimates throughout Europe (Nunner, 2013; Meineke, 2020) and is even considered a thermophilous species (Asher *et al.*, 2001).

Recent studies have shown that the distribution of habitat-specialist butterflies in cultivated landscapes is mainly driven by (i) habitat quality within patches, (ii) patch size and (iii) patch connectivity (Eichel & Fartmann, 2008; Stuhldreher & Fartmann, 2014; Poniatowski *et al.*, 2018b). The relative importance of these factors, however, depends on the mobility of the species, its population structure and the landscape composition (Dover & Settele, 2009; Stuhldreher & Fartmann, 2014; Münsch *et al.*, 2019). Nonetheless, habitat quality is considered the most important predictor of species survival in fragmented landscapes (Poniatowski *et al.*, 2018b).

Patch size did not affect patch occupancy and abundance in our study. *Plebejus argus* is an extremely sedentary butterfly species (Thomas & Harrison, 1992; Lewis *et al.*, 1997) and colonised patches are often small. In British calcareous grasslands, patch size varied mainly between 0.1 and 5 ha (Thomas, 1985b; Thomas *et al.*, 1992). In our study, occupied patches were also tiny and had a mean size of 1.0 (quarries) and 0.8 ha (calcareous grasslands). In contrast, unoccupied quarries with no information about a former occurrence of *P. argus* were much larger (mean size: 6.1 ha) but more isolated (mean patch connectivity: 4.1 km). Consequently, we assume that *P. argus* is able to persist in fairly small habitats if further patches occur in close proximity or habitat quality is high (cf. Münsch *et al.*, 2019). Indeed, patch occupancy increased in the landscape-quality model with connectivity.

However, habitat quality was the most important driver of patch occupancy and adult abundance. A high cover of the host plant *L. corniculatus* favoured both patch occupancy and butterfly abundance. Additionally, abundance of *P. argus* increased with early-successional stages, i.e. sparse vegetation and a high cover of bedrock. Sufficient food is of vital importance for successful development of the larvae. Consequently, a high abundance of host plants is known to determine habitat quality in many butterfly species (García-Barros & Fartmann, 2009; Curtis *et al.*, 2015).

Vegetation structure is usually interrelated with microclimate (Stoutjesdijk & Barkman, 1992). Early-successional stages characterised by a sparse vegetation and high cover of bedrock favour a warm microclimate, which is preferred by various butterfly species in general (García-Barros & Fartmann, 2009; Dennis, 2010) and *P. argus* in particular (Thomas, 1985b; Jordano *et al.*, 1992; Hodgson *et al.*, 2015) for oviposition. In

Table 4. Statistics of GLMM: Relationship between the abundance of *Plebejus argus* at occupied patches [negative-binomial response variable: Individuals/100 m^2 ($n = 29$)] and several environmental parameters (metric predictor variables). 'Habitat type' and 'subarea' were used as random factors. Model-averaged coefficients (conditional average) were derived from the top-ranked models (ΔAICC < 3).

Parameter	Estimate	SE	Z	P	R^2_{GLMMm}	R^2_{GLMMc}
(a) Macroclimate						
Not significant: temperature						
(b) Landscape quality						
Not significant: connectivity, patch size						
(c) Habitat quality					0.37–0.41	0.37–0.41
(Intercept)	0.34	0.52	0.65	n.s.		
Lotus corniculatus	0.03	0.01	3.06	**		
Bedrock	0.02	0.01	1.97	*		
Vegetation density	−0.02	0.01	2.08	*		
Not significant: sunshine, vegetation height, bare ground, small shrubs, herbs						
(d) Synthesis model					0.37–0.41	0.37–0.41
(Intercept)	0.33	0.57	0.56	n.s.		
Lotus corniculatus	0.03	0.01	2.95	**		
Bedrock	0.02	0.01	2.08	*		
Vegetation density	−0.01	0.01	2.09	*		

R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al.*, 2017). Significance levels are indicated as follows: *n.s.* not significant, $^*P < 0.05$, $^{**}P < 0.01$.

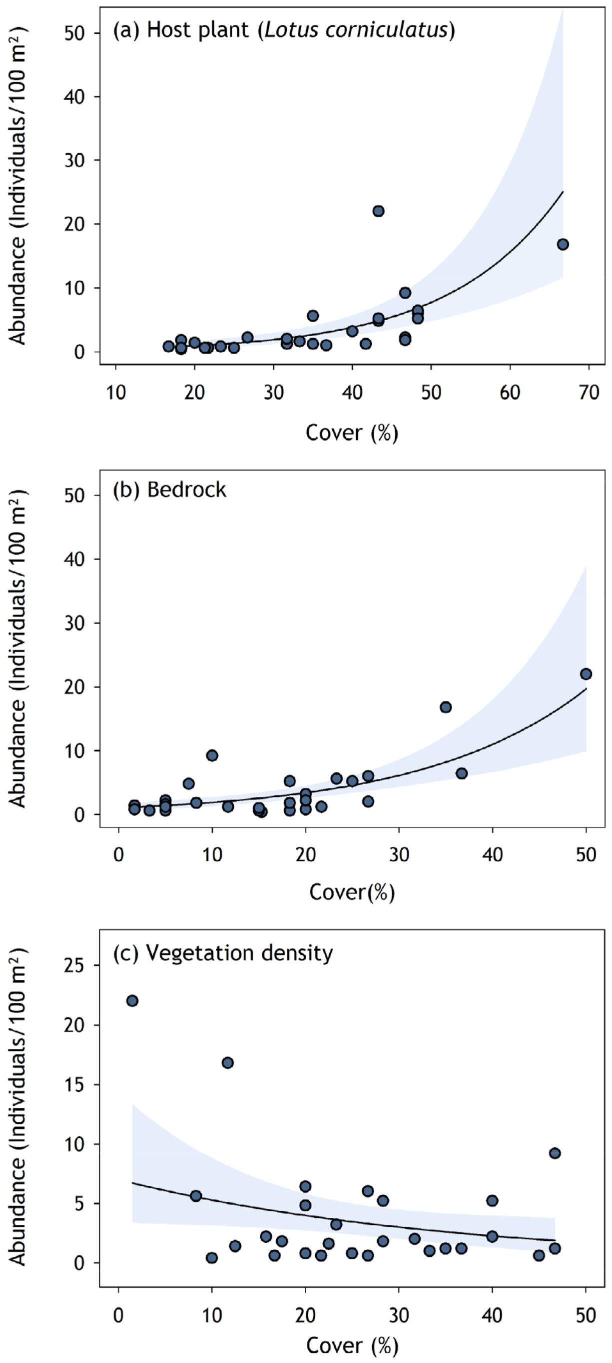

Fig 5. Relationship between abundance of *Plebejus argus* and the significant parameters of the averaged synthesis model. The regression slopes (including 95% confidence intervals) were fitted by using single predictor GLMM with negative-binomial error structure (see Table 4): (a) $y = \exp(-1.47512 + 0.07043 \times L.\ corniculatus)$, $P < 0.001$, $R^2_{GLMMm} = 0.60$, $R^2_{GLMMc} = 0.63$; (b) $y = \exp(0.06747 + 0.05826 \times \text{bedrock})$, $P < 0.01$, $R^2_{GLMMm} = 0.38$, $R^2_{GLMMc} = 0.40$; (c) $y = \exp(1.94455 – 0.02811 \times \text{vegetation density})$, $P < 0.05$, $R^2_{GLMMm} = 0.14$, $R^2_{GLMMc} = 0.14$. R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al.*, 2017).

accordance with this, occupied quarries and grasslands were characterised by higher temperatures during daytime compared to vacant quarries. Additionally, occupied quarries were also warmer than vacant grasslands. Besides the immature stages of *P. argus*, the host ants also depend on high ambient temperatures. On calcareous soils, *Lasius alienus* is usually the main host (Jordano *et al.*, 1992; Jordano & Thomas, 1992). This ant species is thermophilous and its nest density increases with shallow, skeletal soils (Jordano *et al.*, 1992; Seifert, 2018). Such soil conditions also foster the colonisation of the host plant, *L. corniculatus* (Grime *et al.*, 2007).

In recent decades, *P. argus* has strongly declined in calcareous grasslands of the study area (Fartmann, 2004), although large and well-connected calcareous grasslands with occurrence of *L. corniculatus* are still common (Fartmann, 2004; Poniatowski *et al.*, 2018a, 2018b). Dense stands of *L. corniculatus*, however, are rare today in these grasslands (Fartmann, 2004). Most of these calcareous grasslands have suffered from abandonment or a decreasing grazing intensity (Fartmann, 2004) favouring competitive, dense-growing grasses (e.g. *Brachypodium pinnatum*, *Bromus erectus*) at the expanse of poor competitors such as *L. corniculatus* (Grime *et al.*, 2007; Poniatowski *et al.*, 2018a). In line with this, the few remaining calcareous grasslands with occurrence of *P. argus* were all managed ones. The influence of atmospheric nitrogen deposition possibly also contributes to the deterioration of habitat quality in calcareous grasslands. In nutrient-poor habitats on deeper soils eutrophication promotes the establishment of taller vegetation, resulting in microclimatic cooling (Wallis de Vries & van Swaay, 2006; Roth et al., 2021).

In contrast, limestone quarries still host abundant populations of *P. argus* in the study area. We explain the higher patch occupancy and adult abundance in quarries especially by a more favourable habitat quality. Occupied quarries had a much higher cover of *L. corniculatus* and bedrock than occupied calcareous grasslands. In quarries still used for mining, early-successional stages rich in *L. corniculatus* as well as gravel, stones or rocks having a warm microclimate regularly emerge (own observation). Additionally, and in contrast to calcareous grasslands, quarries are characterised by a very low successional speed due to the shallow soils, even without further management after abandonment of mining (Poschlod *et al.*, 1997, Tropek *et al.*, 2010). Hence, they are characterised by a suitable habitat quality for much longer time periods than abandoned calcareous grasslands, which are strongly dependent on regular management. In accordance with this, *P. argus* has only disappeared from rather small (mean size: 1.4 ha) and isolated (mean patch connectivity: 4.8 km) quarries and those that have been abandoned for more than 50 years (own observations). Here, the invasion of woody plants (e.g. *Salix caprea*, *Prunus spinosa*, *Rhamnus cathartica*, *Crataegus* spp.) has led to strong shading of the herb layer (own observation) and, thus, to an adverse microclimate.

In conclusion, the deterioration of habitat quality due to abandonment and decreasing grazing intensity has resulted in a strong decline of *P. argus* in calcareous grasslands of the study area. Today, limestone quarries, especially those being actively managed, are the most important refuges for the species. Quarries exhibit a very low successional speed due to their shallow soils. Hence, they are characterised by a high habitat quality for *P. argus*, i.e. dense stands of the host plant *L. corniculatus*, which grow on skeletal soils providing warm microclimatic conditions.

Implications for conservation

Preserving limestone quarries with their early-successional stages is of crucial importance for the conservation of *P. argus*. Hence, in abandoned quarries, technical reclamation including backfilling and afforestation has to be prevented (Tropek *et al*., 2010). Although quarries are characterised by a very low successional speed (cf. 'Discussion' section), trees and shrubs have to be removed periodically to avoid shading (Poschlod *et al*., 1997). In particular in old abandoned quarries where thicker soil layers have developed, topsoil removal is important to re-create early-successional stages (Konvička & Fric, 2002). The positive effects of topsoil removal in quarries on *P. argus* colonies have already been documented by De Whalley *et al*. (2006). In their study, the cover of *L. corniculatus* increased, the host ant *L. alienus* recolonised the restoration sites and the abundance of adult *P. argus* also flourished.

In calcareous grasslands, we recommend the reintroduction of regular, rough grazing with sheep and goats. Such a grazing regime creates habitat heterogeneity and fosters the expansion of early-successional stages (Wallis de Vries *et al*., 2002; Eichel & Fartmann, 2008). Especially, grazing in winter and spring seems to be suitable to favour both the host plant and *P. argus*. *Lotus corniculatus* regenerates mainly by seeds and usually germinates in spring (Grime *et al*., 2007). Indeed, Goodenough and Sharp (2016) detected a strong positive relationship between grazing in spring and the cover of *L. corniculatus* in British calcareous grasslands. In our study area, half of the calcareous grasslands currently unoccupied by *P. argus* are still managed, but not all grasslands are grazed multiple times every year. This implies that the intensity and seasonal time interval of the present grazing regime does not favour the habitat demands of our target species. Therefore, we suggest that the intensification of the management regime of these grasslands should be adjusted at least partly.

Additionally, maintaining a dense network of suitable habitat patches appears to be crucial for the species' persistence in fragmented landscapes (Lewis *et al*., 1997; this study). Lewis *et al*. (1997) showed that the proportion of *P. argus* individuals migrating between habitat patches is generally low and that the probability of migration does increase with population density. Therefore, conservation management should focus on quarries and calcareous grasslands inhabiting large populations. Additionally, stepping stones should be restored in close vicinity (mean distance to the next three occupied patches ≤ 2 km) between these large core populations (Thomas & Harrison, 1992; Lewis *et al*., 1997; this study). Currently unoccupied patches with no historical data about a former patch occupancy but providing suitable habitat conditions should be particularly included in this network.

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Conflict of interest

The authors declare that they have no conflict of interest.

Data Availability Statement

Data are available on request from the authors.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Absolute and relative frequencies of the nominal variables 'habitat type' and 'land use' at occupied, vacant and unoccupied patches of *Plebejus argus*. Differences in absolute frequencies between habitat types were analysed with Fisher's exact test. Significance levels are indicated as follows: *n.s.* not significant, $^{*}P < 0.05$, $^{***}P < 0.001$.

Table S2 Mean values (± SE) of macroclimatic and landscape parameters at the six habitat types. Differences among habitat types were analysed by LMM/GLMM and subsequent Tukey contrasts, see materials and methods for details. Habitat types without consistent letters indicate significant differences ($P < 0.05$). Significant differences between the habitat types are also indicated by bold type. Significance levels are indicated as follows: *n.s.* not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

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