J Insect Conserv (2017) 21:129–136
DOI 10.1007/s10841-017-9961-7

ORIGINAL PAPER

Larval habitat preferences of a threatened butterfly species in heavy-metal grasslands

Alexander Salz[1] **· Thomas Fartmann**[2,3]

Received: 11 November 2016 / Accepted: 3 February 2017 / Published online: 26 February 2017

Abstract Understanding the factors that determine habitat quality is of vital importance in ensuring appropriate habitat management. Here we used the Niobe fritillary (*Argynnis niobe*) as a study system to analyse the larval habitat preferences in a small network of heavy-metal grasslands in western Germany. The data were compared with the results of a previous study in coastal dune grasslands of the German North Sea. Based on this knowledge, we give management recommendations for the conservation of this threatened species. The key factors for the survival of *A. niobe* in heavy-metal grasslands were (i) open vegetation with a warm microclimate and (ii) sufficient host plants for the larvae. This reflects similar results from the previous study in coastal grey dune grasslands. However, in the heavy-metal grasslands, physiological stress generally slows down succession and favours the fritillary's host plant, the metallophyte *Viola calaminaria*. As a result, the cover of the host plant was nearly twice as high in heavy-metal grasslands compared to the dune grasslands. Heavy-metal grasslands are of great significance for the conservation of *A. niobe* and overall butterfly diversity. Usually, the speed of succession in heavy-metal grasslands is slow and, hence, sites with high heavy-metal concentrations are characterised by relatively stable plant composition and vegetation structure. However, on soils with low heavy-metal content a loss of habitats of *A. niobe* and associated species of conservation concern may occur without management. On those sites sheep grazing seems to be an appropriate way to keep the habitats open and rich in violets.

Keywords *Argynnis niobe* · Coastal dune · Conservation management · Host plant · Microclimate · Vegetation structure

✉ Alexander Salz
Alexander.Salz@web.de

[1] Ostpreußenstr. 30, 48167 Münster, Germany

[2] Department of Biodiversity and Landscape Ecology, Faculty of Biology/Chemistry, Osnabrück University, Barbarastr. 13, 49076 Osnabrück, Germany

[3] Institute of Biodiversity and Landscape Ecology (IBL), Hafenweg 31, 48155 Münster, Germany

Introduction

Recently, global biodiversity has experienced a dramatic decline (De Vos et al. 2014). This trend is predicted to continue and it has been hypothesised that we are heading for the sixth global extinction crisis (Chapin et al. 2000; Thomas et al. 2004). In contrast to previous mass extinction events, the recent collapse of global biodiversity is induced by man-made alterations of the environment (Tilman et al. 2001). In this context, land-use change has been identified as the most severe driver of terrestrial biodiversity loss (Sala et al. 2000; Tilman et al. 2001). However, conservation measures are frequently still inadequate in maintaining ecosystems and their biodiversity (Walker 1992). Thus, there is an urgent need to detect the key factors that determine the occurrence of species of conservation concern.

Butterflies exhibit high host-plant specificity (Munguira et al. 2009), their niches are often narrow (Fartmann and Hermann 2006; García-Barros and Fartmann 2009) and many species form metapopulations that depend on a network of suitable habitat patches (Thomas et al. 2001; Anthes et al. 2003; WallisDeVries 2004; Eichel and Fartmann 2008; Stuhldreher and Fartmann 2014). Due to these complex requirements, their decline exceeds those of many other taxonomic groups (Thomas et al. 2004; Thomas

2005). Consequently, they can function as sensitive indicators for environmental change (Thomas and Clarke 2004; Thomas et al. 2004; Thomas 2005).

Understanding the factors that determine habitat quality is of vital importance in ensuring appropriate habitat management (Thomas et al. 1998, 2001). Most studies on butterflies define habitat quality on the basis of the niche of the pre-adult stages, because it is narrower than those of the adults (Thomas et al. 2011). This is due to low or absent mobility and the usually longer lifetime of the immature stages in comparison to the adult stage (Fartmann 2004; Fartmann and Hermann 2006). Generally, only a fraction of the total host-plant population in a patch is suitable for successful development of the pre-adult stages (Dennis et al. 2006). Selection of a host plant often reflects a complex trade-off between several biotic and abiotic factors. Hence, a large body of research has examined the environmental conditions that influence larval habitat selectivity. In Central and north-western Europe, many threatened butterfly species depend on a warm microclimate for successful development (Thomas 1991; Beneš et al. 2002; Fartmann 2006; García-Barros and Fartmann 2009).

Here we used the Niobe fritillary (*Argynnis niobe*) as a study system to analyse larval habitat preferences in a small network of heavy-metal grasslands in western Germany. *Argynnis niobe* has suffered a dramatic decline throughout Central Europe (Fric and Konvička 2002; Bos et al. 2006; Salz and Fartmann 2009). In Germany, its last remaining strongholds are the Bavarian Alps, the southern parts of the Black Forest and the East Frisian Islands (Fig. 1). One isolated metapopulation still exists in the western part of North Rhine-Westphalia, around the city of Stolberg. Here, *A. niobe* inhabits heavy-metal grasslands, a rare habitat that is protected by the EU Habitats Directive (EC 2007) due to its importance for biodiversity conservation.

The main objective of this study was to assess larval habitat preferences in order to define habitat quality for *A. niobe*. The data were compared with the results of a previous study on *A. niobe* in coastal dune grasslands of the German North Sea (Salz and Fartmann 2009). Based on these findings, we give management recommendations for the conservation of this threatened species.

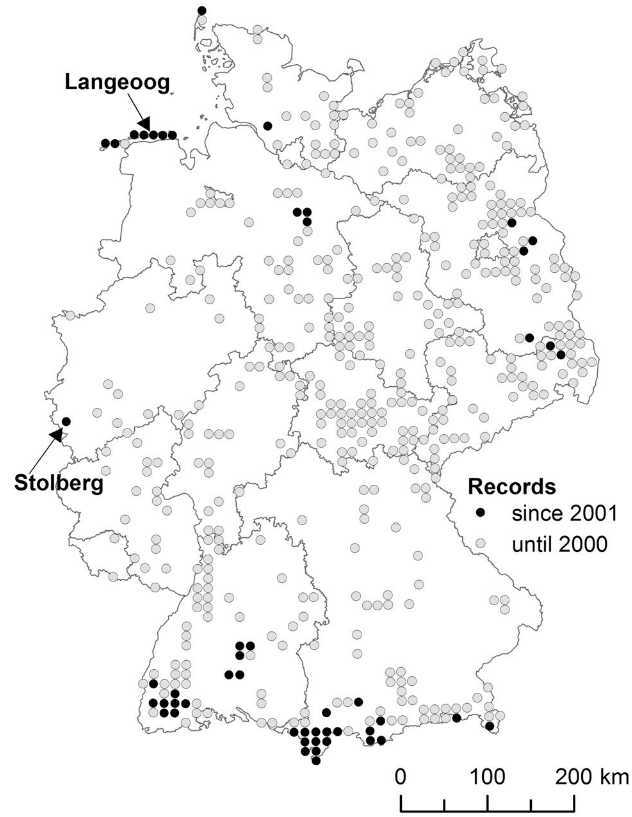

Fig. 1 Distribution of *Argynnis niobe* in Germany and location of the two study areas (Stolberg and Langeoog). *Data sources*: Bräu et al. (2013), Brockmann (1989), Ebert and Rennwald (1991), Föhst and Broszkus (1992), Kraus (1993), Lederer and Künnert (1963), Lobenstein (2003), NLWKN (2006), Reinhardt (1983, 2005), Stamm (1981) as well as Aquazoo – Löbbecke Museum, H. Andretzke, S. Buchholz, S. Caspari, J. Gelbrecht, S. Hafner, H. G. Joger, J. Kleinekuhle, D. Koelman, D. Kolligs, A. C. Lange, D. Lück, P. Mansfeld, B. Nannen, A. Nunner, R. Ohle, R. Reinhardt, F. Röbbelen, A. Schmidt, P. Schmidt, M. Sommerfeld, R. Trusch (all pers. comm.)

Materials and methods

Study species

Argynnis niobe is a univoltine butterfly species, with a flight period ranging from June to August. Following hibernation in the egg stage, larvae hatch in spring and develop between mid-April and the end of June (Bink 1992). Habitat characteristics of *A. niobe* have recently been studied for coastal dunes (Salz and Fartmann 2009). For inland populations, however, our knowledge is still poor (cf. Hafner 2005; Spitzer et al. 2009). In Central Europe, *A. niobe* occurs from sea level up to the sub-alpine belt of the Alps in nutrient-poor grasslands that are rich in violets (*Viola* spp.; SBN 1987; Fric and Konvička 2002; Bos et al. 2006; Salz and Fartmann 2009). Formerly, *A. niobe* was widespread and occurred in all German federal states (Fig. 1). However, during the past 100 years it has declined severely. Until 2001, the German range of *A. niobe* decreased by 90% (based on a 10′ × 6′ geographic grid). Consequently, the fritillary species is considered endangered in Germany (Reinhardt and Bolz 2011).

Study area

We studied larval habitat preferences of *A. niobe* in an inland metapopulation and compared larval habitats with those of a coastal island population in Germany. The inland study area was located around the city of Stolberg ("Stolberg", 250–280 m a.s.l., 50°46′26″N and 6°13′30″E) in the western part of the federal state of North Rhine-Westphalia (Fig. 1). The climate of the study area is sub-Atlantic with a mean annual temperature of 9.5 °C and a mean annual precipitation of 854 mm (weather station Aachen–Orsbach, 231 m a.s.l., DWD 2016a). Stolberg is characterised by a small, but well-connected, network of heavy-metal grasslands [area size = 40 ha (LANUV 2016); mean [±SE] distance between the grassland patches = 3.5 ± 1.7 km]. The heavy-metal soils contain a high quantity of zinc, but also elevated concentrations of lead, cadmium, and copper, which result in physiological stress for plants occurring on these sites (Ernst 1974; Brown 1993). Consequently, vegetation is generally characterised by low cover and slow succession speed. Only plant species adapted to heavy-metal stress—metallophytes and pseudometallophytes—can thrive under such conditions. One of the metallophytes that has a competitive advantage is *Viola calaminaria*, a violet species endemic to the border triangle between Germany, the Netherlands and Belgium (Brown 1993; Pardey 1999; Pardey et al. 1999). This species is the regional host plant of *A. niobe* and occurs in high density in the heavy-metal grasslands. Additionally, it is the character species of the plant community *Violetum calaminariae* which is dominant on the metalliferous soils of the study area. The parts of the grasslands with lower heavy-metal content in the soil and, consequently, a higher vegetation cover, are grazed by sheep. Moreover, on these parts of the grasslands, invading pines (*Pinus sylvestris*) are regularly cut and removed. The study took place in the three largest nature reserves ("Schlangenberg", "Brockenberg" and "Napoleonsweg") with heavy-metal grassland in the study area. The mean (±SE) area size of the three grassland patches was 7.9 ± 6.5 ha and the mean (±SE) distance between the patches was 3.0 ± 1.2 km.

The studied island population of *A. niobe* was located on the East Frisian Island of Langeoog in the North Sea ("Langeoog", 0–20 m a.s.l., 53°44′55″N and 7°29′31″E, Lower Saxony; Salz and Fartmann 2009). Langeoog has an Atlantic climate with a mean annual temperature of 8.7 °C and a mean precipitation of 737 mm (weather station Langeoog; DWD 2016a). The island is about 11 km long and has an area of 20 km^2 (Petersen and Pott 2005). The main larval habitat of *A. niobe* on Langeoog is grey dune grassland (*Koelerion albescentis* and *Ammophilion arenariae*) with *Viola canina* as the main host plant (Salz and Fartmann 2009). In total, continuous grey dune grasslands cover 248 ha on Langeoog. Only a small area of grey dune vegetation is grazed by cattle.

Larval microhabitat

From May to June 2010 we systematically searched in Stolberg for larvae of *A. niobe* in heavy-metal grassland vegetation adjacent to the potential host plant *V. calaminaria*. The following parameters were measured to characterise the larval habitats: aspect (°) and slope (°) were recorded using a compass with an inclinometer; potential sunshine duration (h) was measured during the peak of caterpillar development in June using a horizontoscope (Tonne 1954). The following parameters were recorded in a circle of 50 cm around the observed larva: turf height (cm) and cover (%) of shrubs, herbs, mosses, lichens, litter, bare ground and host plants (*V. calaminaria*).

In order to detect larval habitat preferences, we selected the nearest potential host plant to a randomly thrown stick (cf. Anthes et al. 2003), and at each of these available microhabitats, the same parameters were measured as described above. The number of available microhabitats corresponded to the proportional area of each patch (Krämer et al. 2012; Löffler et al. 2013). Moreover, larval microhabitats occupied by *A. niobe* in Stolberg were compared with larval microhabitats of the previously published study from Langeoog (Salz and Fartmann 2009). Methods used in both studies were identical (cf. Salz and Fartmann 2009). Climatic conditions were also similar during both study periods (Langeoog, weather station Norderney: May 2006: 12.9 °C, 57 mm; June 2006: 15.2 °C, 21 mm; Stolberg, weather station Aachen: May 2010: 10.6 °C, 97 mm; June 2010: 17.2 °C, 21 mm; DWD 2016b).

Statistical analysis

As the distance between the three studied grassland patches in Stolberg was low and soil conditions were identical (Brown 1993), data were analysed together. To compare continuous variables, we used a Mann–Whitney *U* test (MWU). To derive preferences from observed and expected frequencies of categorical variables, a χ^2 test was conducted. To assess which parameters had the highest explanatory power for larval habitat electivity, a binominal generalised linear model (GLM) was performed. In order to avoid multicollinearity, a bivariate correlation analysis of environmental variables was conducted using Spearman's rank correlation (r_s). However, no intercorrelation ($|r_s| > 0.7$) was detected. Statistics were performed using Sigma Plot 13.0 statistical package and R 2.12.0.

Results

Larval microhabitats in heavy-metal grasslands

In total, we found 33 caterpillars of *A. niobe* at 32 microhabitats in the heavy-metal grasslands at Stolberg. All larvae were observed close to the host plant *V. calaminaria* (mean distance ± SE = 2 ± 3 cm, maximum distance = 10 cm). Most larvae were hidden on the ground between grass, litter or moss, or under the host plant. Two of the caterpillars were observed feeding on the leaves of *V. calaminaria*.

Occupied microhabitats of *A. niobe* in heavy-metal grasslands were generally characterised by short turf, open vegetation with a considerable amount of litter, and a long sunshine duration (Table 1). In comparison to unoccupied sites, they had a significantly lower herb/grass cover and higher cover of host plants. Occupied microhabitats were generally flat and aspect did not differ between occupied and unoccupied sites (Fig. 2; Table 2). The occurrence of *A. niobe* larvae in the heavy-metal grasslands was best explained by (i) a low cover of the herb layer and (ii) a high host-plant abundance (Table 3; Fig. 3).

Comparison of larval microhabitats between heavy-metal and dune grasslands

In comparison to the larval microhabitats of *A. niobe* in the dune grasslands of Langeoog, the occupied heavy-metal grasslands of Stolberg were characterised by significantly higher cover of the herb and litter layer, a higher host-plant density and lower cover of mosses (Table 1). All further sampled environmental parameters did not differ between occupied microhabitats at Stolberg and Langeoog (Tables 1, 2).

Discussion

Occupied microhabitats of *A. niobe* in heavy-metal grasslands were generally characterised by short turf, open vegetation with a considerable amount of litter, and a long sunshine duration. The occurrence of *A. niobe* larvae in the heavy-metal grasslands was best explained by (i) a low cover of the herb layer and (ii) a high host-plant abundance.

Sparse and low-growing vegetation that is rich in litter, in combination with high solar irradiation, results in a warm microclimate (cf. Stoutjesdijk and Barkman 1992). The high litter cover promotes the heating up of the microsites, resulting in temperature differences between the litter and the air that can exceed, under such conditions, values of up to 20 °C (Stoutjesdijk and Barkman 1992; WallisDeVries 2006). Measurements from coastal dunes showed that the vegetation in the larval habitats of *A. niobe* can reach temperatures of over 50 °C during sunny summer days (Salz and Fartmann 2009). Additionally, caterpillars of *A. niobe* elevate their body temperature during cool weather by basking, as is the case for most fritillary species (Salz and Fartmann 2009).

High host-plant abundance is usually important for butterfly species with gregarious larvae (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). *Argynnis niobe* is not a true gregarious species, however, females often clump eggs together at favourable microsites (Salz and Fartmann 2009). In coastal dunes, a maximum of 22 eggs in a single microhabitat was observed. Indeed, under

Table 1 Mean values ±SE of all numerical parameters for sites occupied by *A. niobe* at Stolberg and Langeoog as well as of unoccupied sites at Stolberg

Parameter	Stolberg			Langeoog	
	Occupied (N = 32)	Unoccupied (N = 25)	P	Occupied (N = 66)	P[b]
Turf height (cm)	12.8 ± 4.4	13.4 ± 5.7	n.s	11.9 ± 5.1	n.s
Cover (%)					
Shrubs	2.0 ± 7.5	1.7 ± 4.9	n.s	0.6 ± 3.2	n.s
Herbs/grasses	45.2 ± 12.5	55.2 ± 14.3	**	37.1 ± 15.0	**
Litter	48.3 ± 20.2	45.0 ± 18.4	n.s	19.4 ± 15.3	***
Mosses	19.0 ± 22.6	12.9 ± 19.8	n.s	58.5 ± 22.8	***
Lichens	2.8 ± 6.5	1.7 ± 4.0	n.s	2.6 ± 6.7	n.s
Bare ground	1.0 ± 1.7	0.6 ± 1.4	n.s	4.9 ± 12.6	n.s
Host plants	10.1 ± 5.7	6.3 ± 6.3	**	6.2 ± 6.4	**
Daily sunshine duration (h)[a]	14.0 ± 1.8	13.9 ± 1.6	n.s	14.6 ± 0.9	n.s

Differences between groups were tested using a Mann–Whitney U test

n.s. not significant

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$

[a]Mean daily sunshine duration in June

[b]Comparison between occupied sites at Stolberg and Langeoog

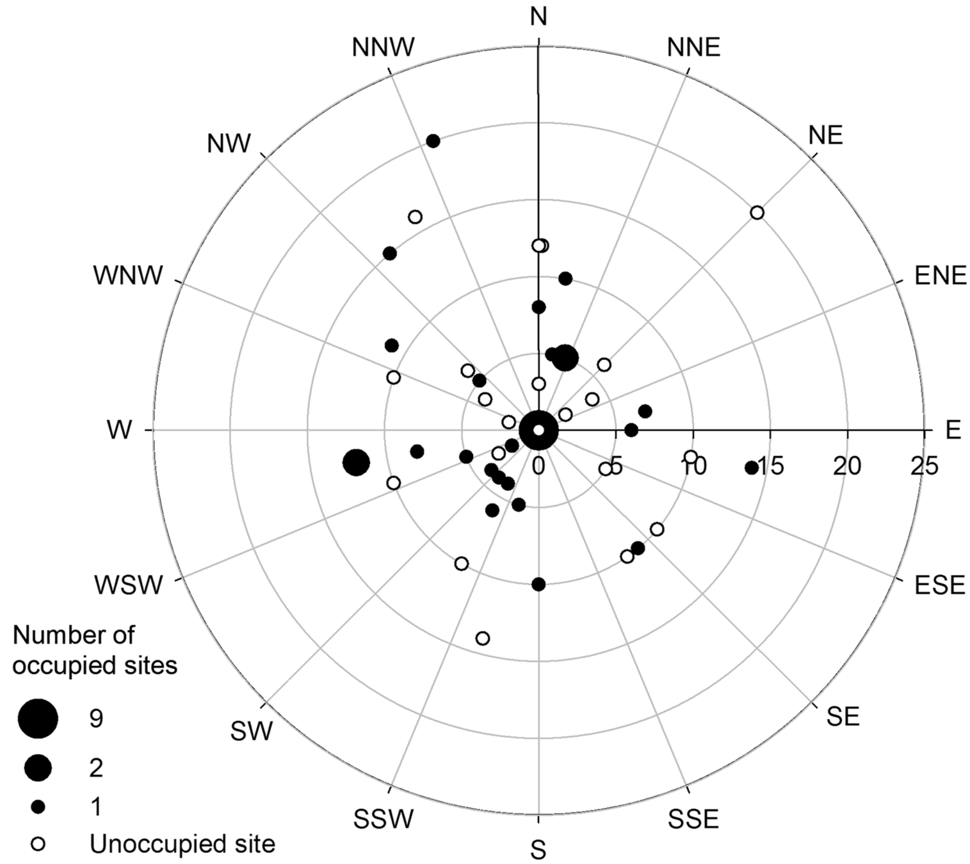

Fig. 2 Aspect and slope at sites occupied ($N=32$) and unoccupied ($N=25$) by larvae of *A. niobe* in Stolberg. For clarity, data for unoccupied sites with no aspect and slope ($N=5$) are shown as one site

Table 2 Aspect of sites occupied by *A. niobe* at Stolberg and Langeoog as well as of unoccupied sites at Stolberg

Aspect	Stolberg				Langeoog	
	Occupied ($N=32$)		Unoccupied ($N=25$)		Occupied ($N=66$)	
	N	%	*N*	%	*N*	%
N	3	9.4	4	16.0	3	4.6
E	1	3.1	2	8.0	4	6.1
S	2	6.3	3	12.0	5	7.6
W	2	6.3	2	8.0	4	6.1
Flat[a]	24	75.0	14	56.0	50	75.8
Total	32	100	25	100	66	100

Differences in absolute frequencies between groups were analysed using χ^2 test

Occupied versus unoccupied sites at Stolberg: $\chi^2=2.486$, $df=4$, $P=0.65$; occupied sites at Stolberg versus Langeoog: $\chi^2=1.241$, $df=4$, $P=0.87$

[a]Slopes less than 10° to the horizontal were classified as flat (Warren 1993)

such conditions, it seems likely that in some cases food shortage due to intraspecific competition will occur, as is observed for gregarious species.

In comparison to the larval microhabitats of *A. niobe* in the dune grasslands of Langeoog, the occupied heavy-metal grasslands had a higher cover of the herb and litter layer, a higher host-plant density and a lower cover of mosses. Despite some differences in vegetation structure, the microclimatic conditions of the microhabitats at Langeoog and Stolberg seem to be very similar (see above; Salz and Fartmann 2009). In contrast, the cover of *Viola* host plants was nearly twice as high at Stolberg than at Langeoog (mean cover: 10% vs. 6%). *Viola canina*, the main host plant of *A. niobe* in the coastal dunes of the North Sea, has a clumped distribution and relatively low cover in the grey dunes (Salz and Fartmann 2009). Consequently, Salz and Fartmann (2009) described the habitat quality of the grey dune grasslands for *A. niobe* as low, which explained the

Table 3 Statistics of the GLM: relationship between the occurrence of *Argynnis niobe* larvae at Stolberg [binomial response variable: occupied ($N=32$) versus unoccupied sites ($N=25$)] and several environmental parameters (predictor variables)

Parameter	Estimate	SE	Z	*P*
Cover of herbs/grasses	−0.06668	0.02492	−2.675	**
Cover of host plants	0.12949	0.05501	2.354	*

The following non-significant ($P>0.05$) predictors were excluded from the final model by stepwise backward-selection: turf height, cover of shrubs, mosses, lichens, litter and bare ground, and the daily sunshine duration in June

**$P<0.01$, *$P<0.05$; Pseudo R^2 [McFadden] = 0.18

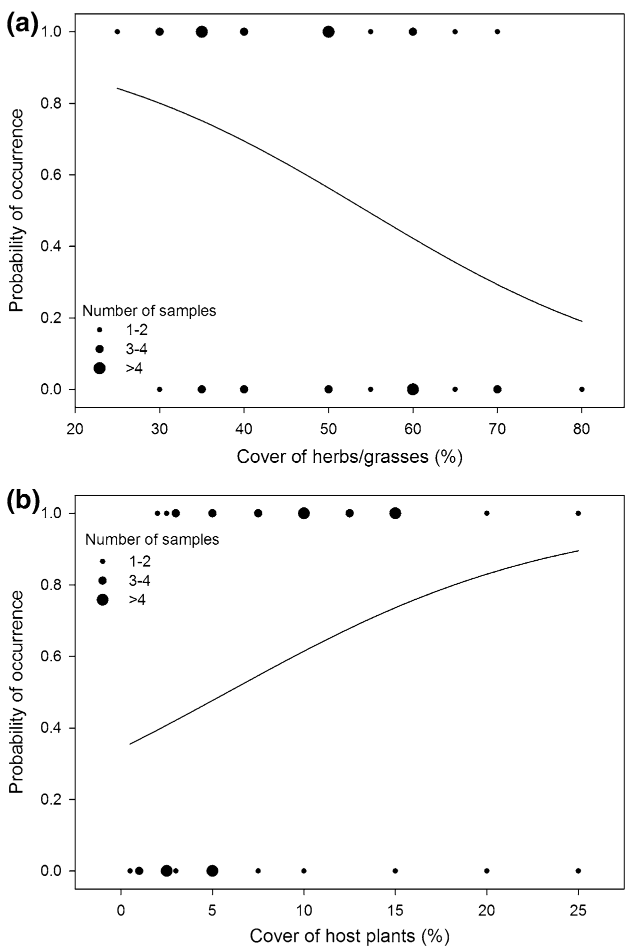

Fig. 3 Relationship between the occurrence of *Argynnis niobe* larvae at Stolberg [binomial response variable: occupied ($N=32$) versus unoccupied sites ($N=25$)] and significant environmental parameters assessed in the multivariate GLM (Table 3). The regression slopes were fitted using single predictor GLM: **a** $y=3.08907-0.05668\times$cover of herbs/grasses, $P<0.01$, Pseudo R^2 [McFadden] = 0.10; **b** $y=-0.65289+0.11195\times$cover of host plants, $P<0.05$, Pseudo R^2 [McFadden] = 0.07

large area required by this species in the dunes of the North Sea islands. Presence of *A. niobe* on North Sea islands was restricted to those with at least 100 ha of connected grey dune vegetation. In contrast, at Stolberg, *A. niobe* was able to persist in a much smaller habitat network of only 40 ha. We assume that this is the result of a much higher habitat quality due to a higher cover of the host plant, *V. calaminaria* (cf. Salz and Fartmann 2009).

However, it could be argued that the feeding of *A. niobe* caterpillars on zinc-accumulating *V. calaminaria* has negative effects on the butterfly species. A study on another fritillary species, *Issoria lathonia*, showed that caterpillars feeding on zinc-contaminated *V. calaminaria* are able to regulate their internal zinc concentration through the excretion of highly metal-concentrated faeces (Noret et al. 2007). *Issoria lathonia* not only has the ability to cope with high heavy-metal concentrations in its host plants, but it also has its largest populations in Belgium on heavy-metal grasslands with *V. calaminaria* as the only host plant. The authors also explain these strong populations by the high habitat quality of the grasslands due to high cover of the host plant *V. calaminaria*.

In conclusion, the key factors for the survival of *A. niobe* in heavy-metal grasslands were (i) open vegetation with a warm microclimate and (ii) sufficient host plants for the larvae. This reflects similar results from a previous study in coastal grey dune grasslands (Salz and Fartmann 2009). However, in the heavy-metal grasslands, physiological stress generally slows down succession and favours the host plant of *A. niobe*, the metallophyte, *V. calaminaria* (Ernst 1974; Brown 1993). As a result, the cover of the host plant was nearly twice as high in heavy-metal grasslands compared to dune grasslands.

Implications for conservation

Despite the relatively small habitat size, the heavy-metal grasslands around Stolberg host a large metapopulation of *A. niobe*, which is the last one in North Rhine-Westphalia (Fig. 1). There is further evidence that heavy-metal grasslands are generally of great significance for the conservation of butterfly diversity. *Boloria selene*, another fritillary species of conservation concern that also feeds on *V. calaminaria*, regularly occurs in the heavy-metal grasslands of the study area (own observation). Additionally, the largest populations of *I. lathonia* in Belgium thrive in this grassland type (Noret et al. 2007) and heavy-metal grasslands in southern North Rhine-Westphalia are home to strong populations of *Hipparchia semele* (Leopold 2006).

Usually, the speed of succession in heavy-metal grasslands is slow and, hence, sites with high heavy-metal concentrations are characterised by a relatively stable plant composition and vegetation structure (cf. Pardey 1999). However, on soils with low heavy-metal content and faster succession speed a loss of habitats of *A. niobe* and associated species of conservation concern may occur without management. Sheep grazing, as practised in the study area around Stolberg, seems to be an appropriate way to keep these habitats open and rich in violets. Where pine forests occur adjacent to the grasslands, additional removal of the pine saplings is necessary. For optimal conservation of the grasslands, most of the neighbouring pine forests should be cleared to suppress pine encroachment in the long term. The first results on the restoration of heavy-metal grasslands on areas of former pine forests by removing the trees and topsoil are very promising in stopping the spread of pine saplings and, additionally, creating suitable larval habitats for *A. niobe* (cf. Raskin 2008).

This study highlights the importance of early successional (warm) microhabitats which contain high densities of host plants to benefit threatened butterfly species. On soils with high heavy-metal contents such microhabitats can occur due to physiological stress without regular management for longer time periods. However, with decreasing heavy-metal concentrations disturbance becomes increasingly important for the maintenance of the microsites.

Acknowledgements We are grateful to J. Dover, C. Haaland, D. Lück, B. Theißen and two anonymous reviewers for valuable comments on an earlier version of the manuscript. Moreover, we would like to thank D. Lück and A. Deepen-Wiezcorek for providing information about the butterfly assemblages in the heavy-metal grasslands around Stollberg. We are also grateful to R. Altmüller, H. Andretzke, R. Bolz, M. Bräu, S. Buchholz, S. Caspari, J. Gelbrecht, F. Goosmann, S. Hafner, H. G. Joger, J. Kleinekuhle, D. Koelman, D. Kolligs, A. C. Lange, D. Lück, P. Mansfeld, B. Nannen, R. Ohle, R. Reinhardt, F. Röbbelen, A. Schmidt, P. Schmidt, M. Sommerfeld, R. Trusch, J. Voith and H. Wegner for providing distribution data of *Argynnis niobe*.

References

Anthes N, Fartmann T, Hermann G, Kaule G (2003) Combining larval habitat quality and metapopulation structure—the key for successful management of pre-alpine *Euphydryas aurinia* colonies. J Insect Conserv 7:175–185

Beneš J, Kepka P, Konvička M (2002) Limestone quarries as refuges for European xerophilous butterflies. Conserv Biol 17:1058–1069

Bink FA (1992) Ecologische atlas van de dagvlinders van Noordwest-Europa. Schuyt, Haarlem

Bos FG, Bosveld MA, Groenendijk DG, van Swaay CAM, Wynhoff I (2006) De dagvlinders van Nederland. Verspreiding en bescherming. Nederlandse Fauna 7. KNNV Uitgeverij, Leiden

Bräu M, Bolz R, Kolbeck H, Nunner A, Voith J, Wolf W (2013) Tagfalter in Bayern. Eugen Ulmer, Stuttgart

Brockmann, E (1989) Schutzprogramm für Tagfalter in Hessen (Papilionoidea und Hesperioidea). Stiftung Hessischer Naturschutz, Reiskirchen

Brown G (1993) Pflanzensoziologische, vegetationsökologische und ökophysiologische Untersuchungen der Schwermetallrasen der Eifel. Dissertation, Rheinische-Friedrich-Wilhelms-Universität Bonn

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE (2000) Consequences of changing biodiversity. Nature 405:234–242

De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL (2014) Estimating the normal background rate of species extinction. Conserv Biol 29:452–462

Dennis RLH, Shreeve TG, van Dyck H (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodivers Conserv 15:1943–1966

DWD (Deutscher Wetterdienst) (2016a) Langjährige Mittelwerte. http://www.dwd.de. Accessed 24 Sep 2016

DWD (Deutscher Wetterdienst) (2016b) Archiv Monats- und Tageswerte. http://www.dwd.de. Accessed 24 Sep 2016

Ebert G, Rennwald E (1991) Die Schmetterlinge Baden-Württembergs. Band 1, Tagfalter I. Eugen Ulmer, Stuttgart

EC (European Commission) (2007) Interpretation manual of European union habitats—EUR27. European Commission, DG Environment, Brussels

Eichel S, Fartmann T (2008) Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation and patch area. J Insect Conserv 12:677–688

Ernst W (1974) Schwermetallvegetation der Erde. Gustav Fischer Verlag, Stuttgart

Fartmann T (2004) Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales. Abh Westf Mus Naturkde 66:1–256

Fartmann T (2006) Welche Rolle spielen Störungen für Tagfalter und Widderchen?. In: Fartmann T, Hermann G (eds) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa, vol 68. Abh Westf Mus Naturkde, Münster, pp 259–270

Fartmann T, Hermann G (2006) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa—von den Anfängen bis heute. In: Fartmann T, Hermann G (eds) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa, vol 68. Abh Westf Mus Naturkde, Münster, pp 11–57

Föhst P, Broszkus W (1992) Beiträge zur Kenntnis der Schmetterlingsfauna (Insecta: Lepidoptera) des Hunsrück-Nahe-Gebiets (BRD), Rheinland-Pfalz. Fauna und Flora in Rheinland-Pfalz Beih, vol 3. Ges. für Naturschutz und Ornithologie Rheinland-Pfalz, Mainz, pp 5–334

Fric Z, Konvička M (2002) Perleťovec maceškový *Argynnis niobe* (Linnaeus, 1758). In: Beneš J, Konvička M, Dvořak J, Fric Z, Havelda Z, Pavlíčko A, Vrabec V, Weidenhoffer Z (eds) Motýli České republiky: Rozšíření a ochrana I. Butterflies of the Czech Republic: distribution and Conservation I. SOM, Prague, pp 409–411

García-Barros E, Fartmann T (2009) Butterfly oviposition: sites, behaviour and modes. In: Settele J, Konvicka M, Shreeve T, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 29–42

Hafner S (2005) Neue Beobachtungen zum Vorkommen von *Fabriciana niobe* im Schwarzwald und auf der Schwäbischen Alb. In: Ebert G (ed) Die Schmetterlinge Baden-Württembergs. Band 10, Ergänzungsband. Eugen Ulmer, Stuttgart, pp 46–47

Krämer B, Kämpf I, Enderle J, Poniatowski D, Fartmann T (2012) Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. J Insect Conserv 16:857–865

Kraus W (1993) Verzeichnis der Großschmetterlinge (Insecta: Lepidoptera) der Pfalz. Selbstverlag, Bad Dürkheim

LANUV (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen) (2016) Excerpt from the habitat register of North Rhine-Westphalia. Accessed 24 Sep 2016

Lederer G, Künnert R (1963) Beiträge zur Insektenfauna des Mittelrheins und der angrenzenden Gebiete. Entomol Z 73:237–243

Leopold P (2006) Larvalökologie der Rostbinde Hipparchia semele (Linnaeus, 1758; Lepidoptera, Satyrinae) in Nordrhein-Westfalen. Die Notwendigkeit raumzeitlicher Störungsprozesse für den Arterhalt. Dissertation, Westfälische Wilhelms-Universität Münster

Lobenstein U (2003) Die Schmetterlingsfauna des mittleren Niedersachsens. Bestand, Ökologie und Schutz der Großschmetterlinge in der Region Hannover, der Südheide und im unteren Weser-Leine-Bergland. NABU, Bonn

Löffler F, Stuhldreher G, Fartmann T (2013) How much care does a shrub-feeding hairstreak butterfly, *Satyrium spini* (Lepidoptera: Lycaenidae), need in calcareous grasslands?. Eur J Entomol 110:145–152

Munguira M, García-Barros E, Cano JM (2009) Butterfly herbivory and larval ecology. In: Settele J, Shreeve TG, Konvicka M, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 43–54

NLWKN (Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz) (ed) (2006) *Argynnis niobe*. Auszug aus den Funddaten des Tierarten-Erfassungsprogramms der Fachbehörde für Naturschutz. Stand: 13.03.2016

Noret N, Josens G, Escarre J, Lefebvre C, Panichelli S, Meerts P (2007) Development of *Issoria lathonia* (Lepidoptera: Nymphalidae) on zinc accumulating and nonaccumulating *Viola* species (Violaceae). Environ Tox Chem 26:565–571

Pardey A (1999) Grundlagen des Naturschutzes auf Schwermetallstandorten in Nordrhein-Westfalen. Abiotische Verhältnisse, Flora, Vegetation, Fauna aktuelle Schutzsituation und zukünftige Zielsetzungen. In: LANUV (ed) Naturschutzrahmenkonzeption Galmeifluren NRW. LÖBF-Schriftenr Bd 16:7–48

Pardey A, Hacker E, Schippers B (1999) Schutzgebiets- und Biotopverbundplanung für Schwermetallstandorte im Raum Aachen-Stolberg (Nordeifel). In: LANUV (ed) Naturschutzrahmenkonzeption Galmeifluren NRW. LÖBF-Schriftenr. Bd 16:99–128

Petersen J, Pott R (2005) Ostfriesische Inseln. Landschaft und Vegetation im Wandel. Schriften zur Heimatpflege. Veröffentl Niedersächs Heimatbd. 15:1–160

Raskin R (2008) Möglichkeiten und Grenzen der Regeneration von Schwermetallfluren. In: Lennartz G (ed) Renaturierung: Programmatik und Effektivitätsmessung. Academia Verlag, Sankt Augustin, pp 60–76

Reinhardt R (1983) Beiträge zur Insektenfauna der DDR. Lepidoptera—Rhopalocera et Hesperiidae. Entomol Nachr Ber, Beih 2

Reinhardt R (2005) Beiträge zur Tagfalterfauna Sachsens. Teil 2: Familie Nymphalidae (Edelfalter)—Unterfamilien Heliconiinae und Nymphalinae. Mitteilungen Sächs Entomol Suppl 3:1–210

Reinhardt R, Bolz R (2011) Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands. Natursch Biol Vielfalt 70:167–194

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Salz A, Fartmann T (2009) Coastal dunes as important strongholds for the survival of the rare Niobe fritillary (*Argynnis niobe*). J Insect Conserv 13:643–654

SBN (Schweizerischer Bund für Naturschutz – Lepidopteren-Arbeitsgruppe) (ed) (1987) Tagfalter und ihre Lebensräume. Arten, Gefährdung, Schutz. Fotorar AG, Egg/ZH

Spitzer L, Beneš J, Konvička M (2009) Oviposition of the Niobe fritillary (*Argynnis niobe* (Linnaeus, 1758)) at submountain conditions in the Czech Carpathians (Lepidoptera, Nymphalidae). Nachr Entomol Ver Apollo 30:165–168

Stamm K (1981) Prodomus der Lepidopteren-Fauna der Rheinlande und Westfalens. Selbstverlag, Solingen

Stoutjesdijk P, Barkman JJ (1992) Microclimate, vegetation and fauna. Opulus Press, Uppsala

Stuhldreher G, Fartmann T (2014) When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. J Insect Conserv 18:965–979

Thomas JA (1991) Rare species conservation: case studies of European butterflies. In: Spellerberg IF, Goldsmith FB, Morris MG (eds) The scientific management of temperate communities for conservation. Blackwell Scientific, Oxford, pp 149–197

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos Trans Roy Soc B 360:339–357

Thomas JA, Clarke RT (2004) Extinction rates and butterflies. Science 305:1563–1564

Thomas JA, Simcox DJ, Wardlaw JC, Elmes GW, Hochberg ME, Clarke RT (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. J Insect Conserv 2:39–46

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc Roy Soc B 268:1791–1796

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds and plants and the global extinction crisis. Science 303:1879–1881

Thomas JA, Simcox DJ, Hovestadt T (2011) Evidence based conservation of butterflies. J Insect Conserv 15:241–258

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. Science 292:281–284

Tonne F (1954) Besser Bauen mit Besonnungs- und Tageslichtplanung. Hofmann, Schondorf

Walker BH (1992) Biodiversity and ecological redundancy. Conserv Biol 6:18–23

WallisDeVries MF (2004) A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. Conserv Biol 18:488–499

WallisDeVries MF (2006) Larval habitat quality and its significance for the conservation of Melitaea cinxia in northwestern Europe. In: Fartmann T, Hermann G (eds) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. Abh Westf Mus Naturkde 68:281–294

Warren MS (1993) A review of butterfly conservation in central southern Britain: II. Site management and habitat selection of key species. Biol Conserv 64:37–49