J Insect Conserv (2014) 18:111–120
DOI 10.1007/s10841-014-9619-7

ORIGINAL PAPER

Coastal heathland succession influences butterfly community composition and threatens endangered butterfly species

Jens Schirmel · Thomas Fartmann

Received: 7 August 2013 / Accepted: 3 February 2014 / Published online: 14 February 2014

Abstract Succession has a strong influence on species diversity and composition of semi-natural open terrestrial ecosystems. While several studies examined the effects of succession on butterflies in grassland and forest ecosystems, the response of heathland butterflies to succession had not been investigated so far. To address this issue we sampled butterfly abundance and environmental parameters on the Baltic island of Hiddensee (NE Germany) along a gradient of coastal heathland succession from grey dunes to birch forest. Our results provide evidence that succession of coastal heathland has a strong influence on butterfly diversity, abundance, and species composition. Thereby grass and tree encroachment present the main threats for heathland butterflies. Diversity and abundance of butterflies were highest in shrub-encroached heath directly followed by early stages of coastal heathland succession (dwarf-shrub heath, grey dune). Both observed threatened species (*Hipparchia semele*, *Plebeius argus*) were negatively affected by succession: abundance decreased with increasing vegetation density (both species) and grass cover (*P. argus*); consequently, the two later successional stages (shrub, birch forest) were not occupied. Our findings highlight the importance of the preservation of early stages of coastal heathland succession for endangered butterfly species. For coastal heathland management we therefore suggest to maintain early successional stages by sheep grazing, mowing or, in case of high nutrient contents, intensive techniques such as sod-cutting or choppering. To a lower extend shrub-encroached sites should also be present, which might be beneficial for overall species richness.

Keywords *Calluna vulgaris* · Grass encroachment · *Hipparchia semele* · Land-use change · *Plebeius argus* · Vegetation structure

J. Schirmel (✉)
Biological Station of Hiddensee, University of Greifswald, Biologenweg 15, 18565 Isle of Hiddensee, Germany
e-mail: schirmel@uni-landau.de

Present Address:
J. Schirmel
Institute for Environmental Sciences, University of Koblenz-Landau, Fortstr. 7, 76829 Landau, Germany

T. Fartmann
Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany

Present Address:
T. Fartmann
Ecology Group, Department of Biology and Chemistry, University of Osnabrück, Barbarastr. 13, 49076 Osnabrück, Germany

Introduction

Succession has a strong influence on species diversity and composition of semi-natural open terrestrial ecosystems. Invertebrates respond differentially to successional processes showing both positive (butterflies: Balmer and Erhardt 2000) and negative effects (Orthoptera: Marini et al. 2009; Fartmann et al. 2012). In Europe, most studies have concentrated on grassland succession (e.g. Balmer and Erhardt 2000; Baur et al. 2006; Kruess and Tscharntke 2002; Marini et al. 2009; Öckinger et al. 2006; Skórka et al. 2007), while studies of successional influences on heathland fauna are still rare (but see Schirmel et al. 2011; Schirmel and Buchholz 2011).

European heathlands are important ecosystems for biodiversity conservation protected by the EU Habitats Directive (EC 2007). Land-use changes including agricultural intensification, afforestation and the abandonment of traditional land use are the main threats for heathlands. As a consequence, the formerly widespread heathland areas in many parts of Central Europe are nowadays fragmented and restricted to small and isolated remnants (Rose et al. 2000; Webb 1998). Heathlands depend on traditional land use such as sheep grazing, sod cutting and burning (Webb 1998; Provoost et al. 2009). If management measures are stopped, nutrient depletion is inhibited and heathland vegetation undergoes succession towards shrub- or tree-dominated vegetation (Webb 1998; Britton et al. 2001; Provoost et al. 2009). In addition, increasing amounts of atmospheric nitrogen deposition result in a eutrophication of nutrient-poor heathland ecosystems often causing grass encroachment (Heil and Diemont 1983; Britton et al. 2001; Roem et al. 2002; Remke et al. 2009a, b). Both succession and grass encroachment can reduce the number of specialised and endangered species (Littlewood et al. 2006; Schirmel et al. 2011; Schirmel and Buchholz 2011).

Butterflies are known to be useful and rapidly responding indicators for the effects of land-use change (Balmer and Erhardt 2000; Fartmann et al. 2013). Most species are very specific concerning local habitat requirements, such as the need of specific host plants (Munguira et al. 2009) and microhabitats for their immature stages (Dennis et al. 2003; García-Barros and Fartmann 2009; Dennis 2010). While several studies examined the effects of succession on butterflies in grassland and forest ecosystems (Balmer and Erhardt 2000; Kruess and Tscharntke 2002; Öckinger et al. 2006; Skórka et al. 2007; Fartmann et al. 2013), the response of heathland butterflies to succession had not been investigated so far.

To address this issue we conducted a field survey on the Baltic island of Hiddensee, NE Germany. We sampled butterfly abundance and environmental parameters in five stages of coastal heathland succession (from grey dunes to birch forest). We were interested in how succession influences butterfly composition and how endangered species react to this process. In particular we tested the hypotheses that (1) coastal heathland succession influences butterfly diversity, abundance, and species composition and (2) endangered butterfly species are negatively affected by succession and the environmental parameters associated with it. Based on our findings we will give implications for butterfly conservation in coastal heathlands.

Materials and methods

Study area and site selection

The study area was a coastal heathland on the Baltic island of Hiddensee, Germany (54°32'N, 13°5′E) (Fig. 1). The north–south extent of the island is about 19 km with a maximum width of about 3 km (total area approx. 16 km^2). Mean annual temperature in this region is 8.0 °C and mean annual precipitation is 564 mm (world climate data, station Greifswald). The coastal heathland was traditionally used as grazing ground for domestic animals and as fuel and building material until World War II (Mecklenburg-Vorpommern 2003). In recent times the coastal heathland is partly managed by manual shrub clearing and since 2004 also by sheep grazing. The coastal heathland area is therefore characterised by a mosaic of different successional stages. We selected a total of 31 sites (500 m^2) stratified to the five main successional stages and their respective area fraction in the study area: (1) 'grey dune' with a high proportion of bare ground (N = 6), (2) 'dwarf-shrub heath' dominated by *Calluna vulgaris* (N = 10), (3) 'grassy heath' with a high cover of tall graminoids (*Carex arenaria*, *Deschampsia flexuosa*) (N = 7), (4) 'shrubs', mainly *Betula pendula*, *B. pubescens*, and *Prunus serotina* (N = 4), and (5) young 'birch forest' (N = 4). Sites had a minimum distance of 50 m to each other.

Vegetation and temperature

Vegetation sampling was done three times during the growing season 2008 (May, June/July, August) at two randomly chosen plots per site. Plots had a specific size depending on the vegetation type and were 25 m^2 in grey dunes and dwarf-shrub heath, 50 m^2 in grassy heath and shrubs and 100 m^2 in birch forest. We recorded seven vegetation parameters: cover (%) of vertical field layer, *C. vulgaris*, grasses, shrubs, and trees and the proportion (%) of bare ground. Horizontal field layer cover (%) was estimated in the vegetation heights 0–10, 10–20, 20–30, 30–40, and 40–50 cm using a 50 × 50 cm frame placed in front of a white board (Sundermeier 1998) and values were summed up for further analyses (maximum value = 500). Data of the three sampling dates were averaged for statistical analyses.

Air temperature was recorded hourly from June to October 2008 with micro-weather stations ('i-buttons', DS 1923 Maxim/Dallas, USA). We exposed one i-button in the centre of each site at the mean vegetation height of the field layer. For statistical analysis, mean values of the daylight period (8:00–18:00 h) were used.

Butterfly sampling

Butterflies were sampled using standardised transect walks in each site under suitable weather conditions (Pollard 1977; Pollard and Yates 1993). Transects had a standardised length of 70 m and were 4 m width (= 280 m^2 per site). Each transect walk took exactly 15 min, excluding

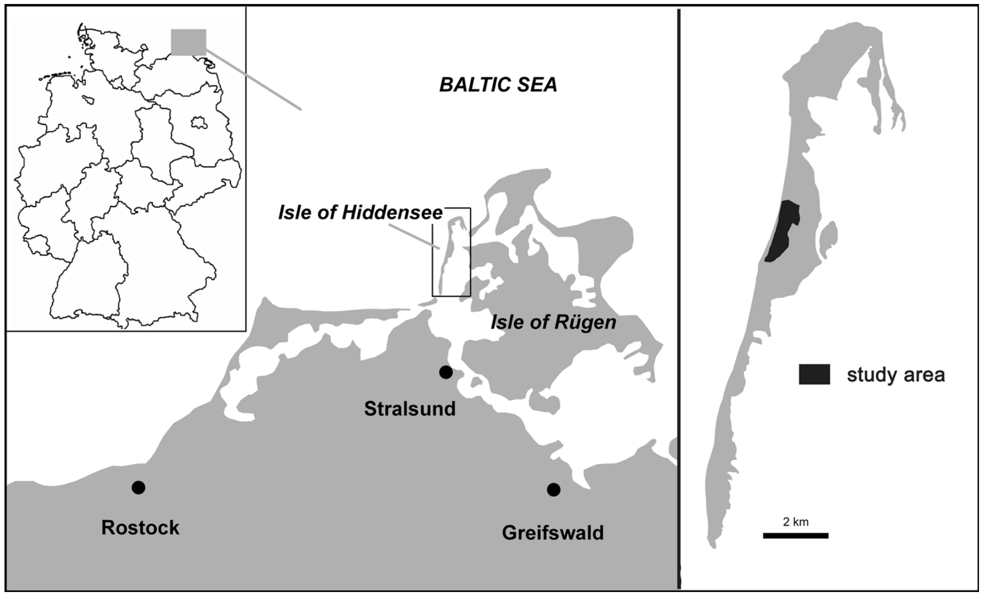

Fig. 1 Location of the study area on the Baltic island of Hiddensee in Germany

time for species identification (Krämer et al. 2012; Fartmann et al. 2013). All sites were sampled six times between May and August 2008 (6–8 May, 21–23 May, 18–20 June, 2–4 July, 22–24 July, 1–3 August). For statistical analyses, data of the six samplings were summed up to obtain one dataset per site. Butterflies were identified according to Settele et al. (2005). Scientific nomenclature follows Karsholt and Razowski (1996). The status of endangerment of butterflies was taken from Reinhardt and Bolz (2011).

Data analysis

All statistical analyses were done in R 2.12.2 (R Development Core Team 2011).

Differences of Simpson diversity (1-D), total butterfly abundance, and abundance of the two threatened species *Hipparchia semele* and *Plebeius argus* among the five successional stages were tested with ANOVA using permutation tests (command 'aovp' in the package 'lmPerm', Wheeler 2010). Data was log10(x + 1) transformed and exact permutation test *P* values were given. Multiple comparisons of means were done by Tukey HSD post hoc tests. We are aware that comparison of diversity among sites with uneven number of replicates might be crucial (species–area-relationship). However, since prior analysis on a reduced dataset with a standardised replicate number ($N = 4$ per stage) showed similar results, we used the complete dataset ($N = 31$) for the analysis of Simpson diversity. Moreover, we choose the Simpson diversity, because this index is robust and relatively unaffected by sample size (Magurran 2004).

Because of collinearity of the parameters vertical field layer cover, horizontal field layer cover, and the proportion of bare ground (Pearson's $r > |0.7|$), we used a principal component analysis (PCA) to reduce the number of continuous predictors to one component axis. The summarized principal component 'vegetation density' explained 60 % of the overall variation and was used as a predictor variable in all models (component relations: horizontal vegetation cover +, vertical vegetation cover +, proportion of bare ground −).

The relationships between Simpson diversity and total butterfly abundance to environmental variables were tested with linear models on log10(x + 1) transformed data to meet model assumptions. Model selection was based on the Akaike information criterion (AIC) with combined backward and forward selection. Model performance was checked graphically using diagnostic plots (Zuur et al. 2010). Effects of environmental parameters on the abundances of the two threatened species *H. semele* and *P. argus* were analysed using Poisson GLM's for count data. Because overdispersion was detected we corrected the standard errors using a quasi-Poisson GLM model (Zuur et al. 2009). For model selection non-significant predicator variables were excluded stepwise from the models using the 'drop1' command. Significance of *P* values was based on F-statistics (Zuur et al. 2009). Predictor variables in all models were vegetation density, cover of *C. vulgaris*, grass cover, shrub cover, tree cover, and temperature.

Butterfly species composition was analysed using non-metric multidimensional scaling (NMDS). Species occurring as singletons were omitted from ordination analyses (see Table 4) as well as sites where only one individual was detected. Finally, 13 butterfly species and 28 sites were subjected to the NMDS. The Bray Curtis distance was used as a distance measure and environmental parameters were fitted afterwards onto the ordination. Explaining vectors were vegetation density, cover of *C. vulgaris*, grass cover, shrub cover, tree cover, and temperature. As an explaining factor successional stage (grey dune, dwarf-shrub heath, grassy heath, shrubs, birch forest) was used. Significance of environmental parameters was analysed by a Monte-Carlo randomisation test with 1,000 permutations. To evaluate the performance of the NMDS we used Kruskal's stress formula multiplied by 100 (McCune and Grace 2002). NMDS ordination was applied using the command 'metaMDS' in R package 'MASS' (Venables and Ripley 2002).

Results

Butterfly diversity, abundance and species composition

Simpson diversity significantly differed among the stages: it was higher in shrubs, grey dunes and dwarf-shrub heath than in birch forest; grassy heath had an intermediate diversity (permutational ANOVA, $df = 26$, $P = 0.002$; Fig. 2a). Diversity was significantly determined by three predictors: shrub cover had a positive, grass and tree cover a negative effect (Table 1). Total butterfly abundance patterns were similar: abundance was significantly higher in grey dune, dwarf-shrub heath and shrub compared to grassy heath and birch forest (permutational ANOVA, $df = 26$, $P < 0.001$; Fig. 2b). It was significantly explained by four environmental predictors: vegetation density and grass cover had negative effects while the cover of *C. vulgaris* and shrubs had a positive influence (Table 1).

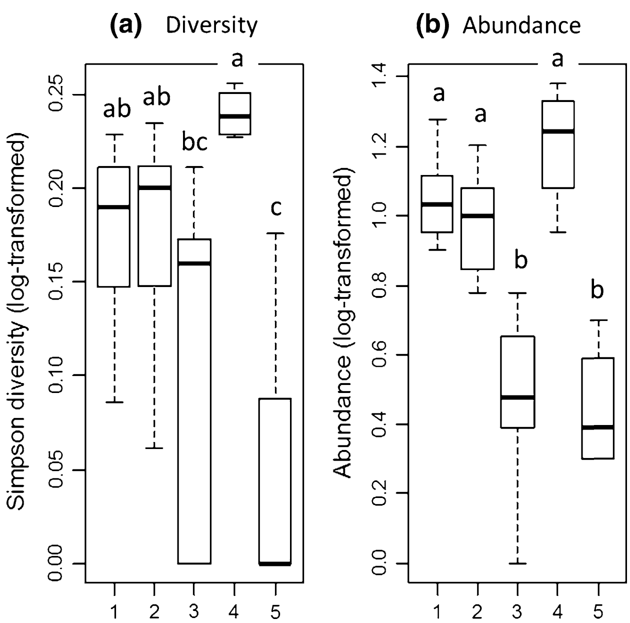

Fig. 2 Differences in **a** Simpson diversity (1-D) and **b** total abundance of butterflies among five successional stages along a coastal heathland successional gradient. *1* grey dune, *2* dwarf-shrub heath, *3* grassy heath, *4* shrubs, *5* birch forest. Differences among successional stages were tested with ANOVA using permutation tests. *Different letters* indicate significant differences among successional stages (multiple comparisons of means by Tukey HSD post hoc tests at $P < 0.05$). *Box-plots* show 10th and 90th percentile (*whiskers*), 25th and 75th percentile (boundary of the *box*), and median (*thick line*)

Based on butterfly species composition, three successional groups were clearly separated: (1) open heathlands (grey dunes, dwarf-shrub heath, grassy heath), (2) shrubs and (3) birch forest (Fig. 3a). Successional stage as well as five environmental vectors had a significant effect on butterfly species composition (Table 2; Fig. 3b). Grey dune, dwarf-shrub heath, and grassy heath sites were correlated with high temperature and a low vegetation density. Butterfly species associated with these habitats were *Coenonympha pamphilus*, *H. semele*, *Lycaena phlaeas*, and *P. argus*. Shrub-encroached and birch-forest sites were characterised by dense vegetation and a high cover of shrubs and trees, respectively. Typical species in shrub-encroached sites were *Aphantopus hyperanthus*, *Celastrina argiolus*, *Melanargia galathea*, *Nymphalis io*, *Ochlodes sylvanus*, and *Vanessa atalanta.* No butterfly species was associated with birch forest.

Response of threatened species to succession

Abundance of both threatened species *H. semele* (permutational ANOVA, $df = 26$, $P < 0.001$) and *P. argus* (permutational ANOVA, $df = 26$, $P < 0.001$) significantly differed among the five successional stages and both species were absent in shrub-encroached heath and birch forest. Abundances of *H. semele* were significantly higher in

Table 1 Relationship of total butterfly Simpson diversity and abundance to environmental factors [linear model with log10(x + 1) transformed data]

Parameters	Estimate	SE	t	P
Simpson diversity ($R^2 = 0.45$)				
Grasses	−0.001	0.000	−2.055	0.050
Shrubs	0.002	0.001	2.635	0.014
Trees	−0.002	0.001	−2.915	0.007
Butterfly abundance ($R^2 = 0.67$)				
Vegetation density	−2.433	0.566	−4.299	<0.001
Calluna vulgaris	0.068	0.031	2.190	0.038
Grasses	−0.067	0.022	−2.995	0.006
Shrubs	0.218	0.041	5.365	<0.001

Model selection was based on the AIC (backward and forward selection) with only significant variables in the final model

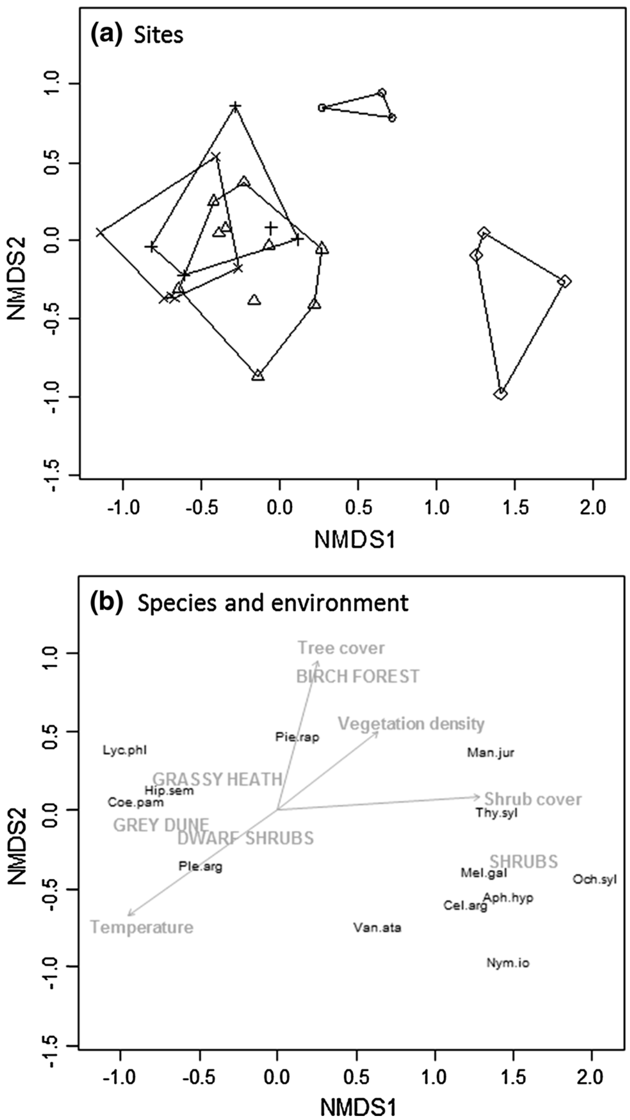

Fig. 3 NMDS on butterfly species composition in five successional stages of a coastal heathland: **a** sites with convex hull volume and **b** butterfly species and significant environmental parameters (vectors as *arrows*). Further information for ordination statistics see Table 2. *x* grey dune, *triangles* dwarf-shrub heath, *crosses* grassy heath, *diamonds* shrubs, *circles* birch forest. Aph.hyp = *Aphantopus hyperantus*, Cel.arg = *Celastrina argiolus*, Coe.pam = *Coenonympha pamphilus*, Hip.sem = *Hipparchia semele,* Lyc.phl = *Lycaena phlaeas*, Mel.gal = *Melanargia galathea*, Man.jur = *Maniola jurtina*, Nym.io = *Nymphalis io,* Och.syl = *Ochlodes sylvanus*, Ple.arg = *Plebeius argus*, Pie.rap = *Pieris rapae*, Thy.syl = *Thymelicus sylvestris*, Van.ata = *Vanessa atalanta*

grey dunes than in the four other successional stages (Fig. 4a) while abundances of *P. argus* were highest in both grey dunes and dwarf-shrub heath (Fig. 4b).

The only remaining significant predictor variable in the final GLM model for *H. semele* abundance was vegetation density which had a negative effect (Table 3; Fig. 5a). Predictors in the final model for *P. argus* abundance were

Table 2 Results of NMDS ordination of butterfly species in five successional stages of a coastal heathland (Bray Curtis distance, three dimensions, stress = 6.8)

	NMDS1	NMDS2	R^2	*P*
Vectors				
Vegetation density	−0.79	0.61	0.32	0.007
Calluna vulgaris	0.13	−0.99	0.05	0.503
Grasses	0.21	0.97	0.20	0.057
Shrubs	0.10	0.06	0.81	<0.001
Trees	0.25	0.97	0.47	0.003
Temperature	−0.819	0.57	0.66	<0.001
Factor				
Habitat type			0.75	<0.001
Grey dune	−0.65	0.11		
Dwarf-shrubs	−0.19	0.13		
Grassy heath	−0.33	0.14		
Shrubs	1.45	−0.32		
Birch forest	0.55	0.86		

Environmental parameters were fitted afterwards onto the ordination. Significance of *P* values was analysed by a Monte-Carlo randomisation test with 1,000 permutations

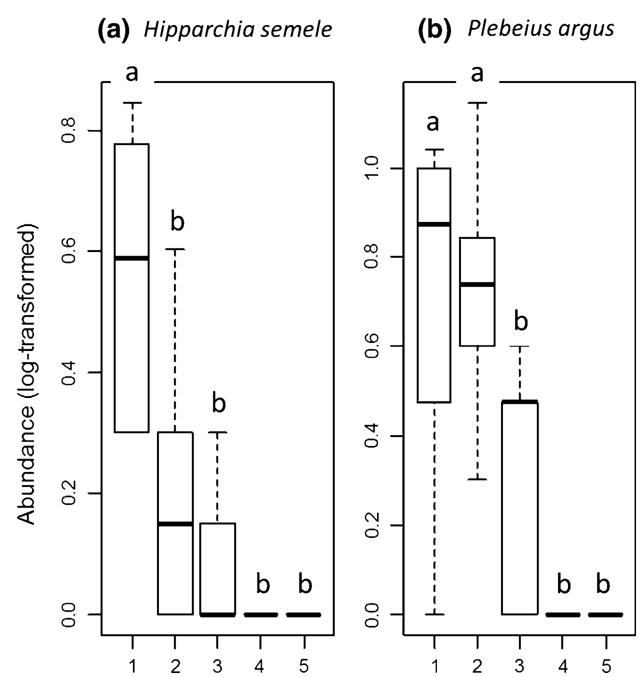

Fig. 4 Differences in abundance of the threatened butterfly species **a** *Hipparchia semele* and **b** *Plebeius argus* in five successional stages along a coastal heathland successional gradient. *1* grey dune, *2* dwarf-shrub heath, *3* grassy heath, *4* shrubs, *5* birch forest. Differences among successional stages were tested with ANOVA using permutation tests. *Different letters* indicate that successional stages differed in abundances (multiple comparisons of means by Tukey HSD post hoc tests at $P < 0.05$). *Box-plots* show 10th and 90th percentile (*whiskers*), 25th and 75th percentile (boundary of the *box*), and median (*thick line*)

Table 3 Relationship of abundances of the two threatened species *Hipparchia semele* and *Plebeius argus* to environmental factors (GLM with quasi-Poisson error structure)

Parameters	Estimate	SE	*t*	*P*
Hipparchia semele				
Vegetation density	−0.417	0.085	−4.933	<0.001
Plebeius argus				
Vegetation density	−0.215	0.071	−3.052	0.005
Grasses	−0.018	0.005	−3.265	0.003

Non-significant predictors were excluded from the final model by stepwise deleting non-significant variables using the drop1 command (F-test, $P > 0.05$)

vegetation density and grasses (Table 3; Fig. 5b). Both had a negative effect.

Discussion

Our results provide evidence that succession of coastal heathland has a strong influence on butterfly diversity, abundance, and species composition. Thereby grass and tree encroachment present the main threats for heathland butterflies. Both observed endangered species (*H. semele*, *P. argus*) were negatively affected by succession: abundance decreased with increasing vegetation density (both species) and grass cover (*P. argus*); consequently, the two later successional stages (shrub, birch forest) were not colonized.

Succession influence butterfly diversity, abundance and species composition

Diversity and abundance of butterflies were highest in shrub-encroached heath directly followed by early stages of coastal heathland succession (dwarf-shrub heath, grey dune). Grass-encroached sites and birch forest had clearly reduced values. In line with this, in our GLM models shrub cover had a positive and grass cover a negative effect on butterfly diversity and abundance.

We interpret a certain amount of shrubs within the heathlands as a measure of heterogeneity. Such heath stands consist of a heterogeneous mixture of different plant life forms with different heights (dwarf shrubs, grasses, shrubs) (cf. Schirmel et al. 2011; Mantilla-Contreras et al. 2012). Habitat heterogeneity is well-known to be beneficial

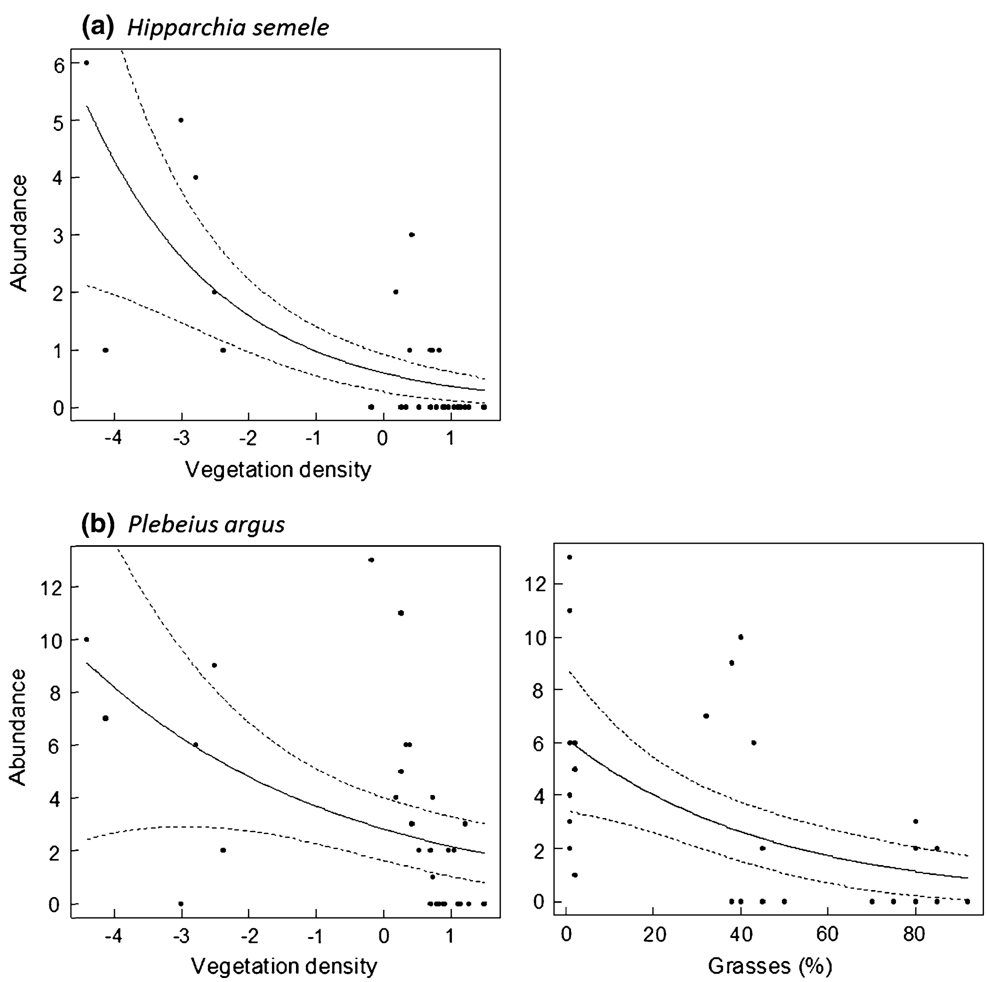

Fig. 5 Relationship of **a** *Hipparchia semele* and **b** *Plebeius argus* abundances (individuals/90 min) to significant environmental factors (for test statistics see Table 3). Vegetation density is a principal component of the variables vertical field layer cover, horizontal field layer cover, and the proportion of bare ground. High values indicate dense vegetation with high field layer cover and low proportion of bare soil

for animal diversity in generally (Tews et al. 2004) and butterfly diversity and abundance in particular (Fartmann et al. 2013).

In contrast, heathlands encroached by grasses, like *C. arenaria*, form homogenous stands with a dense field layer and are poor in other life forms (cf. Fig. 1b in Schirmel et al. 2011). Consequently, the diversity of potential host plants and the abundance of nectar-providing plants are low. The same is true for heathlands with a high vegetation density (dense and high-growing heath stands) that also had a negative effect on butterfly abundance. Grass encroachment and dense vegetation in heathlands is often caused by high (atmospheric) nutrient deposition (Heil and Diemont 1983). Hence, eutrophication of nutrient-poor heathlands presents a major threat to heathland butterflies (cf. WallisDeVries and Van Swaay 2006; WallisDeVries et al. 2012).

Tree cover had also a negative effect on butterfly diversity. Shading has been identified as an important driver of butterfly diversity (Warren 1985; Greatorex-Davies et al. 1993; Fartmann et al. 2013). Shading affects butterflies indirectly by altering the microclimatic conditions and the quantity of host plants and nectar resources (Warren 1985; Sparks et al. 1996). Consequently, dense and shady forest usually provides relatively poor conditions for butterflies (Fartmann et al. 2013). However, some species such as *H. semele* use trees and bushes to look for shelter on very warm days and for sleeping (Dennis 2010). For these species the occurrence of single trees and bushes might therefore be necessary elements for a viable population.

A further determinant of butterfly abundance was the cover of *C. vulgaris* having a positive influence. *C. vulgaris* is one of the main larval host plants of *P. argus* in heathlands (Asher et al. 2001) and an important nectar source for many butterfly species (Dennis 2010). The latter is especially relevant as other nectar-providing plants are usually rare in heathlands.

Butterfly communities of open heathland, shrub-encroached heathland and birch forests were clearly different. Birch forests were lacking any characteristic species. Dense forests are known for their poverty in butterflies (see above). The number of typical species was highest in shrub-encroached heath most likely due to the heterogeneity of the stands (see above). However, all of the species are more or less widespread generalists (cf. Ebert and Rennwald 1991a, b; Bräu et al. 2013) and none is threatened (cf. Reinhardt and Bolz 2011). In contrast, the number of characteristic species was lower in open heathlands but among them were the two endangered habitat specialists *H. semele* and *P. argus* (cf. Ebert and Rennwald 1991a, b; Reinhardt and Bolz 2011; Bräu et al. 2013). Open stages of coastal heathland succession providing a warm microclimate are known to be beneficial for threatened butterflies (WallisDeVries and Raemakers 2001; Maes and Bonte 2006; Salz and Fartmann 2009). Similar results were also found for other invertebrate groups such as carabid beetles (Schirmel and Buchholz 2011) and grasshoppers (Schirmel et al. 2011).

Open successional stages as important habitats for endangered butterfly species

Hipparchia semele and *P. argus* are endangered target species for nature conservation in Germany and typical for dunes and heathlands (Asher et al. 2001; Bräu et al. 2013). Both species are strongly negatively affected by succession. Within the open stages of coastal heathland succession especially grey dunes (both species) and dwarf-shrub heath (*P. argus*) were important habitats.

Hipparchia semele is adapted to sparsely vegetated habitats with high temperatures that allow a successful egg and larval development (Leopold 2007). Both conditions are fulfilled in grey dunes. Moreover, they offer sufficient suitable larval host plants (e.g. *Corynephorus canescens*, *Festuca rubra*, *F. ovina*). In line with this, an increasing vegetation density and a decreasing proportion of bare ground had a negative effect (Maes et al. 2006).

Plebeius argus abundance was also negatively affected by increasing vegetation density and, moreover, by grass encroachment. Consequently, the species was almost absent in densely grass-covered heathland sites (>60 %, Fig. 3b). In contrast, the cover of the host plant *C. vulgaris* was not correlated with *P. argus* numbers, indicating that the host-plant quantity is not a limiting resource in the open stages of heathland succession in our study. As studies from Great Britain show *P. argus* depends in heathlands on sufficient bare ground and at least one of the two black ant species (*Lasius niger* or *L. alienus*) associated with the immature stages of the butterfly also preferring warm microhabitats (Thomas 1985; Ravenscroft 1990).

Implications for butterfly conservation in coastal heathlands

Our findings highlight the importance of the preservation of early stages of coastal heathland succession for endangered butterfly species. Early successional stages with sparse vegetation and dry and hot microclimate are basic requirement not only for the endangered butterfly species *H. semele* and *P. argus* but for many other specialized and endangered species. This pattern is in accordance to findings of carabids, spiders and Orthoptera (Buchholz et al. 2013; Schirmel et al. 2011; Schirmel and Buchholz 2011; Wünsch et al. 2012). For biodiversity conservation the presence of shrub-encroached sites is also important. However, most species occurring on these sites are widespread generalists. For coastal heathland management we therefore suggest to maintain early successional stages by sheep grazing. Sheep are known to be best for heath grazing as they feed on grasses in summer and on dwarf-shrubs in winter (Gimingham 1992). In case of high nutrient contents mowing or intensive techniques such as sod-cutting or choppering are suitable management measures for (re)opening heathlands (cf. Buchholz et al. 2013; Borchard et al. 2013; Schirmel et al. 2011). To a lower extent shrub-encroached sites should also be present, which enhance habitat heterogeneity and might be beneficial for other target species (e.g. birds such as *Lanius collurio* or the viper *Vipera berus*). Moreover, single trees and shrubs are important habitat elements for some butterfly species (e.g. *H. semele*) during unfavourable weather conditions. Management therefore should not completely remove these important ecological resources. In contrast, succession to forest must be prevented for the conservation of heathland butterflies.

Acknowledgments We thank Jasmin Mantilla-Contreras for help with the field work and the national park 'Vorpommersche Boddenlandschaft' for the permission to conduct the study in the protected area. The study was partly funded by the 'Bauer-Hollmann-Stiftung'. Moreover, we a grateful to two anonymous referees for valuable comments on an earlier version of the manuscript.

Appendix

See Table 4.

References

Asher J, Warren M, Fox R, Harding P, Jeffcoate G, Jeffcoate S (2001) The millennium atlas of butterflies in Britain and Ireland. Oxford University Press, Oxford

Balmer O, Erhardt A (2000) Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. Conserv Biol 14:746–757

Baur B, Cremene C, Groza G, Rakosy L, Schileyko AA, Baur A, Stoll P, Erhardt A (2006) Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania, Romania. Biol Conserv 132:261–273

Borchard F, Schulte AM, Fartmann T (2013) Rapid response of Orthoptera to restoration of montane heathland. Biodivers Conserv 22:687–700

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

Britton AJ, Pakeman RJ, Carey PD, Marrs RH (2001) Impacts of climate, management and nitrogen deposition on the dynamics of lowland heathland. J Veg Sci 12:797–806

Buchholz S, Hannig K, Schirmel J (2013) Losing uniqueness—shifts in carabid species composition during dry grassland and heathland succession. Anim Conserv 16:661–670

Dennis RLH (2010) A resource-based habitat view for conservation. Butterflies in the British landscape. Wiley, Chichester

Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102:417–426

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

Ebert G, Rennwald E (eds) (1991b) Die Schmetterlinge Baden-Württembergs. Vol 2, Tagfalter II. Eugen Ulmer, Stuttgart

Table 4 List of observed butterfly species in five successional stages of a coastal heathland on the Baltic island of Hiddensee, NE Germany

Butterfly species	Grey dune (N = 6)		Dwarf-shrub heath (N = 10)		Grassy heath (N = 7)		Shrubs (N = 4)		Birch forest (N = 4)		Total individuals
	Ind.	%	Ind.	%	Ind.	%	Ind.	%	Ind.	%	
Aphantopus hyperantus	0	0	0	0	0	0	4	100	0	0	4
Callophrys rubi	0	0	1	100	0	0	0	0	0	0	1
Celastrina argiolus	0	0	3	14	0	0	19	86	0	0	22
Coenonympha pamphilus	8	89	1	11	0	0	0	0	0	0	9
Gonopteryx rhamni	0	0	1	100	0	0	0	0	0	0	1
Hipparchia semele	19	66	8	28	2	7	0	0	0	0	29
Lycaena phlaeas	1	50	1	50	0	0	0	0	0	0	2
Maniola jurtina	0	0	0	0	0	0	17	85	3	15	20
Melanargia galathea	0	0	0	0	1	17	5	83	0	0	6
Nymphalis io	0	0	0	0	0	0	2	100	0	0	2
Nymphalis urticae	0	0	1	100	0	0	0	0	0	0	1
Ochlodes sylvanus	0	0	0	0	0	0	5	100	0	0	5
Pieris brassicae	0	0	1	100	0	0	0	0	0	0	1
Pieris rapae	2	6	17	49	5	14	6	17	5	14	35
Plebeius argus	34	35	55	56	9	9	0	0	0	0	98
Thymelicus sylvestris	0	0	0	0	0	0	4	100	0	0	4
Vanessa atalanta	1	20	2	40	0	0	2	40	0	0	5
Total individuals	65		91		17		64		8		245

Ind. = number of individuals, % = percent of total individuals

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

Fartmann T, Krämer B, Stelzner F, Poniatowski D (2012) Orthoptera as ecological indicators for succession in steppe grassland. Ecol Indic 20:337–344

Fartmann T, Müller C, Poniatowski D (2013) Effects of coppicing on butterfly communities of woodlands. Biol Conserv 159:396–404

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

Gimingham CH (1992) The lowland heathland management handbook. English Nature Science, Peterborough

Greatorex-Davies JN, Sparks TH, Hall ML, Marrs RH (1993) The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biol Conserv 63:31–41

Heil GW, Diemont WH (1983) Raised nutrient levels change heathland into grassland. Vegetatio 53:113–120

Karsholt O, Razowski W (1996) The Lepidoptera of Europe: a distributional checklist. Apollo Books, Stentrup

Krämer B, Poniatowski D, Fartmann T (2012) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. Biol Conserv 152:253–261

Kruess A, Tscharntke T (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conserv Biol 16:1570–1580

Leopold P (2007) Larvalökologie der Rostbinde *Hipparchia semele* (Linnaeus, 1758; Lepidoptera, Satyrinae) in Nordrhein-Westfalen. Die Notwendigkeit raumzeitlicher Störungsprozesse für den Arterhalt. Abh Westf Mus Naturkde 69:1–146

Littlewood NA, Pakeman RA, Woodin SJ (2006) The response of plant and insect assemblages to the loss of *Calluna vulgaris* from upland vegetation. Biol Conserv 128:335–345

Maes D, Bonte D (2006) Using distribution patterns of five threatened invertebrates in a highly fragmented dune landscape to develop a multispecies conservation approach. Biol Conserv 133:490–499

Maes D, Ghesquiere A, Logie M, Bonte D (2006) Habitat use and mobility of two threatened coastal dune insects: implications for conservation. J Insect Conserv 10:105–115

Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford

Mantilla-Contreras J, Schirmel J, Zerbe S (2012) Influence of soil and microclimate on species composition and grass encroachment in heath succession. J Plant Ecol 5:249–259

Marini L, Fontana P, Battisti A, Gaston KJ (2009) Response of orthopteran diversity to abandonment of semi-natural meadows. Agric Ecosyst Environ 132:232–236

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

Mecklenburg-Vorpommern U (ed) (2003) Die Naturschutzgebiete in Mecklenburg-Vorpommern. Demmler, Schwerin

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

Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol Conserv 133:291–300

Pollard E (1977) Method for assessing changes in abundance of butterflies. Biol Conserv 12:15–134

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London

Provoost S, Jones MLM, Edmondson SE (2009) Changes in landscape and vegetation of coastal dunes in northwest Europe: a review. J Coast Conserv 15:207–226

Ravenscroft NOM (1990) The ecology and conservation of the silver-studded blue butterfly *Plebejus argus* L. on the sandlings of East Anglia, England. Biol Conserv 53:21–36

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reinhardt R, Bolz R (2011) Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands. Natursch Biol Vielfalt 70(3):167–194

Remke E, Brouwer E, Kooijman A, Blindow I, Esselink H, Roelofs JGM (2009a) Even low to medium nitrogen deposition impacts vegetation of dry, coastal dunes around the Baltic Sea. Environ Pollut 157:792–800

Remke E, Brouwer E, Kooijman A, Blindow I, Roelofs JGM (2009b) Low atmospheric nitrogen loads lead to grass encroachment in coastal dunes, but only on acid soils. Ecosystems 12:1173–1188

Roem WJ, Klees H, Berendse F (2002) Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. J Appl Ecol 39:937–948

Rose RJ, Webb NR, Clarke RT, Traynor CH (2000) Changes on the heathlands in Dorset, England, between 1987 and 1996. Biol Conserv 93:117–125

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

Schirmel J, Buchholz S (2011) Response of carabid beetles (Coleoptera: Carabidae) and spiders (Araneae) to coastal heathland succession. Biodivers Conserv 20:1469–1482

Schirmel J, Mantilla-Contreras J, Blindow I, Fartmann T (2011) Impacts of succession and grass encroachment on heathland Orthoptera. J Insect Conserv 15:633–642

Settele J, Steiner R, Reinhardt R, Feldmann R (2005) Schmetterlinge: die Tagfalter Deutschlands. Ulmer, Stuttgart

Skórka P, Settele J, Woyciechowski M (2007) Effects of management cessation on grassland butterflies in southern Poland. Agric Ecosyst Environ 121:319–324

Sparks TH, Greatorex-Davies JN, Mountford JO, Hall ML, Marrs RH (1996) The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. For Ecol Manag 80:197–207

Sundermeier A (1998) Methoden zur Analyse der Vegetationsstruktur. In: Traxler A (ed) Handbuch des vegetationsökologischen Monitorings. Teil A: Methoden. Umweltbundesamt, Wien, pp 123–158

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thomas CD (1985) The status and conservation of the butterfly *Plebejus argus* L. (Lepidoptera: Lycaenidae) in North West Britain. Biol Conserv 33:29–51

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

WallisDeVries MF, Raemakers I (2001) Does extensive grazing benefit butterflies in coastal dunes? Restor Ecol 9:179–188

WallisDeVries MF, Van Swaay C (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Glob Chang Biol 12:1620–1626

WallisDeVries MF, Van Swaay CAM, Plate CL (2012) Changes in nectar supply: a possible cause of widespread butterfly decline. Curr Zool 58:384–391

Warren MS (1985) The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white *Leptidea sinapis*. Biol Conserv 33:147–164

Webb NR (1998) The traditional management of European heathlands. J Appl Ecol 35:987–990

Wheeler B (2010) lmPerm: permutation tests for linear models. R package version 1.1-2. http://CRAN.R-project.org/package=lmPerm

Wünsch Y, Schirmel J, Fartmann T (2012) Conservation management of coastal dunes for Orthoptera has to consider oviposition and nymphal preferences. J Insect Conserv 16:501–510

Zuur AF, Ieno IN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, Berlin

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14