

The larval ecology of the butterfly *Euphydryas desfontainii* (Lepidoptera: Nymphalidae) in SW-Portugal: food plant quantity and quality as main predictors of habitat quality

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Abstract Corresponding to theory, the persistence of metapopulations in fragmented landscapes depends on the area of suitable habitat patches and their degree of isolation, mediating the individual exchange between habitats. More recently, habitat quality has been highlighted as being equally important. We therefore assess the role of habitat area, isolation and quality for the occupancy of larval stages of the regionally threatened butterfly *Euphydryas desfontainii* occurring in grassland habitats comprising the host plant *Dipsascus comosus*. We put a special focus on habitat quality which was determined on two spatial scales: the landscape (among patches) and the within-patch level. On the landscape level, occupancy of caterpillars was determined by a presence-absence analysis at 28 host plant patches. On the within-patch level, oviposition site selection was studied by comparing 159 host plants with egg clutches to a random sample of 253 unoccupied host plants within six habitat patches. The occupancy of caterpillars and presence of egg clutches on host plants was then related to several predictors such as patch size and isolation on the landscape level and host plant characteristics and immediate surroundings on the within patch level. On the landscape level, only host plant

abundance was related to the presence of caterpillars, while size and isolation did not differ between occupied and unoccupied patches. However, the weak discrimination of larval stages among patches changed on the within-patch level: here, several microclimatic predictors such as sunshine hours and topography, host plant morphology and phenology as well as further potential host plants in the immediate surroundings of the plant chosen for oviposition strongly determined the presence of egg clutches. We strongly suggest promoting the presence of the host plant in topographically and structurally rich habitat patches to offer potential for microclimatic compensation for a species considered threatened by climate change.

Keywords Conservation · Landscape level · Larval ecology · Mediterranean region · Metapopulation · Resource-based habitat concept · Within-patch level

Introduction

Biodiversity is decreasing worldwide with unprecedented rates of species' extinctions (Sala et al. 2000). Habitat loss and fragmentation as well as decreasing habitat quality were determined as important drivers of population declines. Butterflies are frequently used as an indicator group to assess the effects of anthropogenic global change on biodiversity due to their rapid response to alterations of their habitats (Thomas 2005). Among butterflies, checkerspot butterflies are long recognized as excellent model systems and have a primordial role for studies of natural population dynamics and the impact of environmental change as habitat fragmentation and degradation (Ehrlich and Murphy 1987; Ehrlich 1992; Ehrlich and Hanski 2004). Due to their association with semi-natural habitats,

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many checkerspots are threatened by land-use changes and are nowadays of particular conservation concern, for instance *Euphydryas aurinia*, listed in Annex II of the EEC/EU Habitat and Species Directive.

Checkerspot populations are often structured in networks of spatially separated sub-populations connected by individual exchanges commonly referred to as metapopulations, exemplified by *Euphydryas editha bayensis* or *Melitaea cinxia* (Harrison et al. 1988; Hanski 1998). Metapopulation structure is believed to mitigate the detrimental effects of fragmentation and habitat loss due to individual exchanges maintaining gene flow and allowing recolonisation of vacant habitats once a population went extinct (Fahrig 2003). However, only metapopulations with higher recolonisation rates than patch extinction rates are viable. The viability of butterfly metapopulations therefore strongly depends on factors like patch size, degree of isolation, but also habitat quality (Dover and Settele 2009). Although metapopulation theory emphasizes the influence of landscape structure on viability, several studies have shown that habitat quality is at least as important as patch size and geometry (Murphy and Weiss 1988; Thomas et al. 2001; Anthes et al. 2003). Habitat quality mostly influences local population dynamics, but can thereby modify important population processes as patch emigration which is subsequently influencing regional dynamics (Mortelliti et al. 2010).

Particularly important aspects of habitat quality for butterfly species are the conditions for larval survival because juvenile stages are the dominant life phase of most insects, spanning the majority of the organisms' entire life time (García-Barros and Fartmann 2009). The mortality of eggs and larvae has strong effects on population dynamics, leading to explosive growth under suitable conditions of resource availability and low parasitism and predation rates, while high egg and larval mortality can lead to population extinction (Ehrlich and Hanski 2004). Due to the extended time of susceptibility to various threats during earlier stages of the life cycle, larval habitats are carefully chosen by female butterflies to maximize survival chances of their offspring (Renwick and Chew 1994).

The choice of the appropriate larval habitat has to include several spatial scales (García-Barros and Fartmann 2009): after mating, females have to find an appropriate location where conditions for oviposition and consequently caterpillar development exist. Although adult distribution and host plant patches overlap in many cases, individuals might disperse depending on their own physical condition and the external context (Bowler and Benton 2005). In case of emigration from the natal patch, the probability to encounter an appropriate patch for reproduction is strongly influenced by the landscape configuration (e.g. patch sizes and their degree of isolation), while the decision to settle

depends on the quality level of the habitats (Tschamtko and Brandl 2003).

For example, the landscape occupancy of *E. aurinia* imago was most significantly explained by patch size in a dynamic landscape in Southeast Finland (Wahlberg et al. 2002). However, Anthes et al. (2003) found that patch size was an important predictor, but inasmuch landscape connectivity and habitat quality explained 82 % of the variation in landscape occupancy. A study on *E. aurinia* in Sweden emphasized the importance of patch isolation as crucial determinant of metapopulation dynamics, but also the influence of habitat quality with host plant density and sward height as occupancy predictors (Betzholtz et al. 2007).

Once having encountered an appropriate site at the landscape level, local patch characteristics have the highest importance, and a searching sequence is started by the female butterfly to find its host plant in an appropriate microclimate (Renwick and Chew 1994): this behavioural sequence commonly involves searching, orientation, encounter, landing, surface evaluation and, finally, acceptance or rejection of a host plant in a given environment. Different sensory cues are used in this sequence to orient towards the host plant and especially for the evaluation of plant's properties and its surroundings. In determining suitability of the host plant for oviposition, visual cues are believed to be predominant during searching, orientation and encounter, while chemical and physical cues become paramount after landing (Renwick and Chew 1994). Characteristics as the amount of available plant biomass is of particular importance (Wiklund 1984), especially in species laying egg clutches with hundreds of eggs leading to the eventual defoliation of the entire host plant initially chosen for oviposition (Eichel and Fartmann 2008), and even specific parts of host plants might be preferred (Rabasa et al. 2005).

Besides the characteristics of the host plant, microclimatic parameters are essential to guarantee a successful larval development (Weiss et al. 1988; Anthes et al. 2008), but also to avoid desiccation of eggs due to excessive insolation. Therefore, the combination of microclimate, the presence and abundance of host plants and the respective conditions of the surrounding vegetation are known to strongly influence the females' oviposition decisions (Fartmann and Hermann 2006).

A successful management of rare and endangered butterfly species therefore has to consider all of its life stages and the entire spectrum of necessary habitat requirements (i.e. a resource-based habitat definition) (Dennis et al. 2003). Therefore, knowledge on oviposition preferences of target species is vital for designing effective conservation concepts, especially in strongly human influenced landscapes as in Europe. One example underlining the

paramount importance of understanding the larval habitat to stop population decline is the case of the Heath fritillary *Melitaea athalia*. While adults have rather broad habitat requirements, the niche of the larvae is considerably narrower, depending on specific extensive anthropogenic influence (Warren 1987). The recognition of these specific larval requirements helped in developing an action plan to appropriately manage the sites where *M. athalia* occurred, hereby safeguarding remnant populations (New et al. 1995).

Due to the vital role of larval habitats, we conducted a study to determine the characteristics necessary for the development of *E. desfontainii* caterpillars and egg clutches. This species is considered an Atlanto-Mediterranean faunal element having its centre of distribution on the Iberian Peninsula (Kudrna 2002). In Portugal, *E. desfontainii* is considered one of the rarest butterflies, only found in very restricted areas of the Lower Alentejo and Algarve provinces (Maravalhas 2003). Based on the results of the Climatic Risk Atlas of European Butterflies, the species is facing an extremely high risk due to climate change (HHHR), with more than 95 % loss of its current grid cells under at least one of the three simulated scenarios (Settele et al. 2008). Due to the elevated risk from climate change, the conservation status of *E. desfontainii* has recently been upgraded to the near threatened category of the IUCN (van Swaay et al. 2011). While the species is at present not yet considered threatened in the centre of its distribution in Spain, its marginal populations in France and Portugal are already reported to decline (van Swaay and Warren 1999; Maravalhas 2003).

The conservation status of *E. desfontainii* leads to a strong interest in unravelling the habitat requirements to develop management strategies for its conservation in the face of habitat and climate change. Our study was conducted on two spatial scales, the landscape (among patch comparisons) and the within-patch level, to identify the necessary conditions for successful egg and larval development of these vulnerable populations at the southwestern margin of Iberia.

Materials and methods

Study species

Euphydryas defontainii (Godart 1819) belongs to the family Nymphalidae and is scattered over the Iberian Peninsula and very locally in adjacent France (Eastern Pyrenees). Additionally, the species is distributed in Northwestern Africa, with localized populations in the Atlas Mountains (Morocco and Algeria). A total of five subspecies is described with *E. desfontainii baetica* (Rambur 1858)

inhabiting the southern parts of Spain and Portugal (Tolman and Lewington 1998). The adult butterflies are on the wing from April to June in one discrete generation (Maravalhas 2003). The species is found from sea level up to 1,800 m asl on hot rocky slopes and in dry river beds (Tolman and Lewington 1998). As in many congeneric species, eggs are usually laid in clutches on the host plants *Cephalaria leucantha* and two species of Dipsacaceae, *Dipsacus fullonum* and *Dipsacus comosus* (Maravalhas 2003). Caterpillars have a development time of 1 year with the first instars showing gregarious behaviour and inhabiting a silken web (Tolman and Lewington 1998). In our study area, only the biannual *D. comosus* was used as host plant. This plant species is common in Southern Portugal, but mainly in habitats with fluctuating soil moisture content.

Study area

The study was conducted from 17th of March to 27th of May 2009 in the Algarve and the adjacent Lower Alentejo province (Southern Portugal). For the analysis of larval habitats, our study area covered the region between Portimão in the South, São Marcos da Serra in the East, São Teotónio and Saboia in the North and Aljezur in the West (Fig. 1), and a subset of six of these patches close to Pereiras-Gare (central position at 37°25'N, 8°28'W) for the study of oviposition sites. This study area consists of a mosaic of extensively used meadows, maquis shrublands (mainly *Cistus ladanifer*) and some *Eucalyptus globulus* plantations. The hilly topology (up to 300 m asl) is marked by small and temporary river beds with *Rubus* hedges and meadows used for extensive cattle grazing. The high clay content of the soils favours the retention of water in the lower parts and creates a suitable environment for the larval host plant, *D. comosus*. The Mediterranean climate is characterized by mild wet winters and long dry summers, with normally little rain between April and October. The mean annual temperature for the region ranges from 15.5 to 17.5 °C (Mabberley and Placito 1993).

Larval habitat analyses

From 17th of March to 2nd of April 2009, caterpillars were systematically searched in patches with abundant *Dipsacus* plants. A patch was defined as a group of at least 10 plant individuals. In case of more than 10 m distance to the next plant, a new patch was delimited; however, mean distance between two patches was 717 m (Fig. 1). Caterpillars were searched for a given duration depending on the habitat size (<2,000 m²: 20 min, >2,000 m²: 40 min). Searching was stopped as soon as one caterpillar was detected. Several environmental variables were collected for all patches:

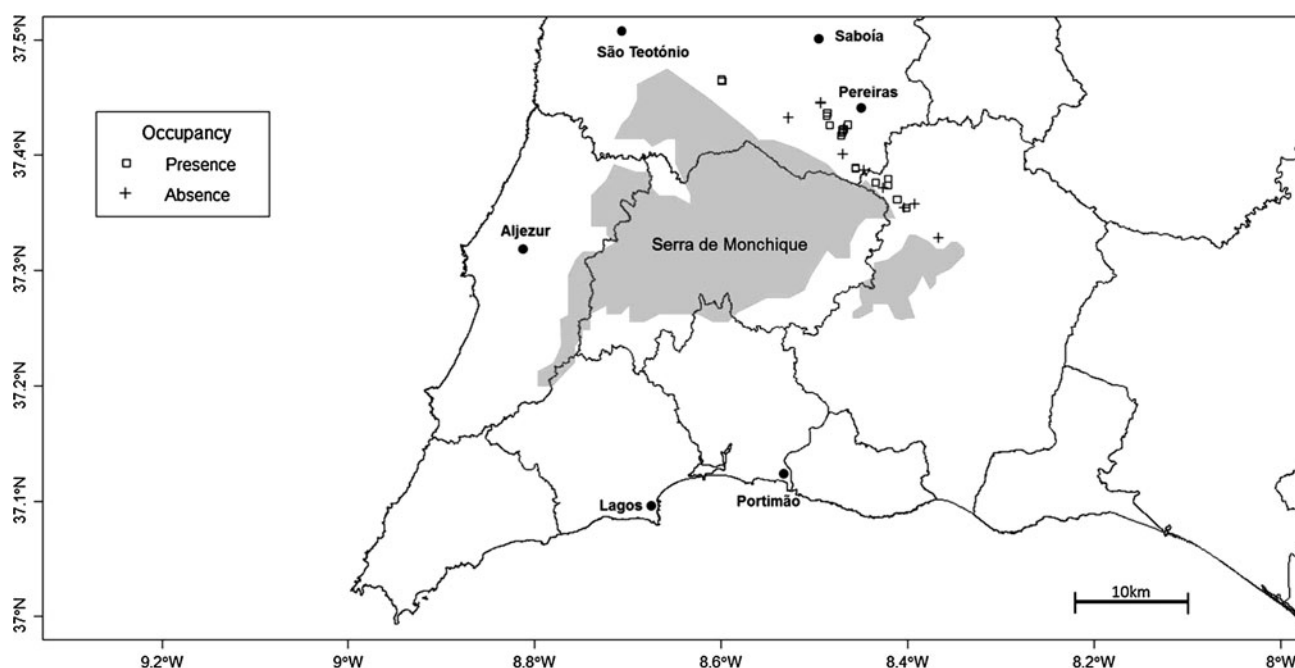


Fig. 1 Map of the Algarve and the Lower Alentejo region showing the study area for the presence-absence analysis of *E. desfontainii* on the landscape level. Altitudes above 200 m asl are given in grey

surface area (in m^2), degree of shading (three classes: without shade, partially shaded, fully shaded), soil humidity (three classes: dry, moist, wet), inclination measured in degrees, exposition, daily mean temperature, daily mean minimum and maximum temperatures recorded by Tinytag dataloggers (Gemini Data Loggers Ltd., UK) between 3rd of April till 28th of May 2008, mean vegetation height, absolute number of host plants in the patch, mean diameter of host plant rosette, cover of bare soil, herb and shrub layer (estimated in 5-% steps), presence of water bodies and whether the area was used for grazing or not. Given that the host plant patches are relatively small compared to the whole study area, Euclidean distances between patches were calculated based on the centroid position of each patch to all other patches, and the minimum distance to the nearest habitat patch and the nearest occupied habitat patch determined.

Oviposition site analyses

Besides caterpillar habitats, the oviposition sites chosen by the female butterflies were studied between 12th and 27th of May 2009 in a subset of six patches that were also studied for the larval habitat requirements. Egg clutches were searched on *D. comosus* plants irrespective of their habitus or location. If a clutch was found, the following variables concerning the host plant and its 50 cm radius were collected. For microclimatic characterization, maximum hours of sun (± 0.5 h) measured with a horizonscope

(Tonne 1954) for 37° N and the month of May, inclination and exposition as well as soil humidity (see above) were determined. The vegetation structure was measured by density estimations in vertical layers of 10, 20, 30, 50 and 80 cm, the estimated horizontal coverage of bare soil, stones, detritus or vegetation, as well as mean and maximum sward height (in cm). Furthermore, we recorded the size of the host plant itself, the number of rosette leaves and rosette diameter as well as the number and cover with additional host plants in the 50 cm radius. The clutch was characterized by measuring the height above the soil, the position on leaf or stem, its position inwards or outwards from the stem, if situated on leaves, and the number of further clutches on the same plant. A random sample of plants, selected by throwing a stick over the shoulder and choosing the closest unoccupied plant to the place where the stick fell to the ground, was characterized in the same way to compare occupied and unoccupied plants.

Statistical analyses

Non-parametric Wilcoxon tests were performed to compare single variables to characterize occupied and unoccupied larval patches and host plants. Non-metric multidimensional scaling (NMDS) was applied to display similarity between sample units and subsequently test for difference with ANOVA of similarities (ANOSIM). The two axes of the NMDS were consequently correlated with

the explanatory variables to determine the factors influencing the discrimination between sites.

The relationship between presence/absence of an egg clutch on host plants and the microhabitat was assessed by logistic regression. A correlation matrix of all explanatory variables was built based on pairwise comparisons with Spearman's Rho to identify correlated variables prior to applying the logistic regression. All pairs were checked for a correlation coefficient <0.6 , otherwise one of the variables was discarded. After checking for collinearity, the logistic regression model was used to assess the association between egg clutches and descriptors of host plants and their surroundings. AIC model selection was used to assess the importance of each variable in predicting clutch presence, and the model with the lowest AICc was chosen for interpretation (if models differed by a delta AICc of <2 , the model with the smallest number of parameters is selected, i.e. the most parsimonious model) (Johnson and Omland 2004).

Statistical analyses were performed in SAS Enterprise Guide 4.2, save multivariate non-metric multidimensional scaling and ANOSIM analysis conducted in the software package Primer 6.0 (Clarke and Gorley 2006).

Results

Larval habitats

Twenty-eight patches with host plants were found, and parameters on structure and host plant availability were

collected (Table 1). The majority of patches was occupied ($N = 18$).

The patches occupied by caterpillars only differed significantly in having a higher number of host plants. There was a trend for occupied patches towards larger areas and host plants with smaller leaf rosettes. A multivariate analysis using NMDS to represent patches according to their similarity and a subsequent analysis of similarities (ANOSIM) detected no significant differentiation between occupied and unoccupied patches based on environmental characteristics of the patches (Fig. 2). The first axis of the NMDS correlated most strongly and negatively with patch area, number of host plants and humidity, while the second axis was negatively associated with the distance to the nearest available patch, the nearest occupied patch and shade level.

Oviposition sites

A total of 159 *D. comosus* plants with 246 egg clutches was found and compared to a random sample of 253 host plants without eggs. Except for one host plant, all plant individuals used for oviposition were in the 2nd year of their development, i.e. their year of flowering. The mean number of egg clutches per plant was 1.55, ranging from one to eight clutches. To test whether plants with already present egg clutches of conspecifics are avoided for subsequent oviposition, the observed number of egg clutches per plant was compared to a Poisson distribution with a mean number of one clutch per plant. The observed distribution significantly differed from the expected distribution, if females laid only one clutch per plant ($X^2 = 819.29$, $p < 0.001$). 56.1 % of

Table 1 Comparison between occupied and unoccupied patches for caterpillars of *E. desfontainii*

	Unoccupied patches (N = 10)		Occupied patches (N = 18)			
	Mean	SD	Mean	SD	H test	p value
Area	1030.86	2164.50	2077.84	2,507.28	3.32	*
Degree slope	6.90	14.55	2.28	3.48	0.13	ns
Shade	2.50	0.53	2.61	0.50	0.31	ns
Humidity	1.30	0.67	1.17	0.38	0.11	ns
Mean temp	16.38	1.16	16.83	1.45	0.42	ns
Max temp	19.45	2.25	19.77	2.29	0.13	ns
min temp	13.96	0.98	14.53	0.98	2.14	ns
Number HP	104.70	105.44	278.50	237.99	4.66	**
Density HP	9.64	9.57	6.84	4.76	0.06	ns
Mean rosette	47.86	12.33	39.26	13.26	2.9	*
Mean sward	39.10	11.47	32.08	11.68	1.81	ns
Cover soil (%)	3.50	5.30	2.78	3.52	< 0.01	ns
Cover herb (%)	55.50	24.99	66.39	20.64	1.47	ns
Cover shrub (%)	41.00	22.83	31.11	21.04	1.46	ns
min. patch (m)	1,210.12	1,454.90	443.38	349.83	0.83	ns
min. occ. patch (m)	1,477.73	1,426.55	722.40	751.56	2.07	ns

ns not significant, HP host plants

* $p < 0.10$; ** $p < 0.05$

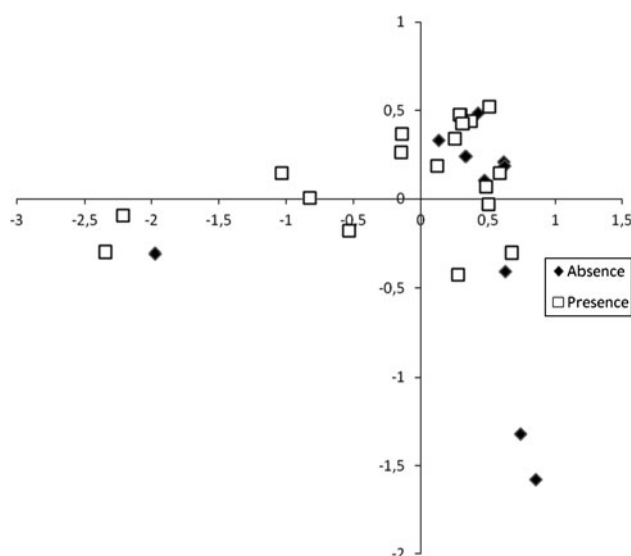


Fig. 2 Non-metric multidimensional scaling of occupied and unoccupied patches for caterpillars of *E. desfontainii*. The first axis is negatively correlated with patch size, host plant number and humidity, while the second axis is negatively associated with distances to next occupied and unoccupied patches and shade level

the clutches were found on leaflets close to the stem, 39.4 % in the middle of the leaf while <5 % were found on the outer tip of the leaflets. We found a significant positive correlation between the position of clutches above the ground and sward height ($r = 0.77$, $p < 0.01$).

Univariate comparison of occupied and unoccupied host plants revealed several highly significant differences (Table 2): occupied host plants were higher, but had less rosette leaflets, they were situated on more inclined sites, received more hours of sun in the month of May, and had more individuals and a higher cover of potential host plants in the 50 cm radius. The sward height and maximum vegetation height was lower around occupied plants. We found a trend towards less dense vegetation around host plants in 30 cm height and highly significant differences in 80 cm height.

A logistic regression model was constructed to assess the factors explaining the use of a given plant for oviposition. Variables included in the analysis were exposition and inclination, hours of sunshine in the month of May, height of the host plant, diameter of rosette leaflets, cover of potential host plants surrounding the plant, mean vegetation height and additionally the quadratic term of hours of sunshine and sward height to check for unimodal relationships between predictor and response variables. Due to their high correlation with other variables maximum vegetation height, vegetation density from 10 to 80 cm, and number of host plants in the vicinity of the target plant were excluded. The variables soil moisture and the different types of cover around the target plant were dropped for their low discriminatory power as revealed by univariate comparisons.

Table 2 Univariate comparison between *D. comosus* plants used and not used for oviposition

	Random plants (N = 253)		Occupied plants (N = 159)			
	Mean	SD	Mean	SD	H test	p value
Inclination (°)	0.71	2.64	1.73	4.27	7.44	***
Moisture	1.18	0.48	1.21	0.52	0.16	ns
Insolation (h)	10.41	1.74	11.56	1.58	47.42	***
Host plant height (cm)	51.23	22.23	62.28	28.60	11.99	***
No. rosette leaflets	8.08	3.37	7.06	3.54	8.31	***
Rosette diameter (cm)	43.17	16.20	43.78	14.26	2.68	ns
No. surrounding HP	2.56	2.86	3.28	3.07	8.88	***
Cover surrounding HP (%)	5.17	7.70	8.31	9.86	15.86	***
Cover soil (%)	4.44	8.74	3.92	7.49	0.38	ns
Cover stones (%)	0.63	2.23	0.45	2.04	1.22	ns
Cover detritus (%)	2.18	4.99	1.69	3.92	0.32	ns
Cover vegetation (%)	92.73	12.00	93.88	10.01	0.80	ns
Sward height (cm)	29.58	11.08	25.84	11.20	14.38	***
Max vegetation (cm)	92.97	19.87	80.92	20.12	31.82	***
Density 10 cm	87.78	18.46	86.28	17.62	0.93	ns
Density 20 cm	73.92	25.70	71.46	26.28	0.54	ns
Density 30 cm	53.60	27.98	48.78	30.52	3.06	*
Density 50 cm	17.89	18.62	16.92	18.76	1.31	ns
Density 80 cm	4.26	6.94	3.27	6.62	12.19	***

ns not significant, HP host plants

* $p < 0.10$; *** $p < 0.01$

Table 3 Results of the AICc model comparison showing the five most supported models to explain oviposition site selection

Factors	Number of parameters	Log likelihood	AICc	Delta AICc
Inclination, exposition, sunshine hours, sunshine hours ² , HP height, rosette diameter, HP cover (%), sward	11	−213.65	449.97	0.00
Inclination, exposition, sunshine hours, sunshine hours ² , HP height, rosette diameter, HP cover (%), sward, sward ²	12	−213.28	451.35	1.38
Inclination, sunshine hours, sunshine hours ² , HP height, rosette diameter, HP cover (%), sward	8	−217.90	452.15	2.19
Inclination, exposition, sunshine hours, sunshine hours ² , HP height, HP cover (%), sward	10	−216.24	453.04	3.07
Inclination exposition, sunshine hours, HP height, rosette diameter, HP cover (%), sward	10	−216.33	453.21	3.25

Model comparisons based on AICc revealed that the best model was including all variables and the quadratic term of hours of sunshine in the month of May (Table 3). The next best model included all terms and the quadratic terms of sunshine hours and the sward height. According to the best model (Table 4), well developed host plants in sun exposed microhabitats had an increased probability to be chosen by females for oviposition. Increasing inclination and exposition further positively influenced the selection of a host plant for egg-laying, especially if further host plant individuals were present in the immediate surroundings. On the contrary, increasing sward height and number of rosette leaves negatively influenced the probability of host plants to bear egg clutches. The model classified 73.8 % of all cases correctly. However, the predictive ability of the model differed between the two classes. While 83 % of the plants without egg clutches were correctly classified as unsuitable, only 59 % of the host plants that showed clutches were classified as appropriate for oviposition.

Discussion

Our study revealed that environmental parameters influence the presence of *E. desfontainii* larval stages, but the strength of the relationship differs between the two spatial

Table 4 Estimates of the logistic regression model to model the probability that a host plant is used for oviposition

Parameter	Estimate	SE	Wald	p value
Intercept	−0.4689	1.1156	0.0385	ns
Host plant height	0.0352	0.00651	28.7464	***
Insolation (h)	−0.7726	0.0828	2.699	ns
Insolation (quadratic term)	0.0588	0.0233	6.3877	**
Inclination	0.2621	0.1065	6.2577	**
Rosette diameter	0.0232	0.038	4.9726	**
Cover surrounding HP	0.0358	0.0145	5.9593	**
Sward height	−0.0768	0.0146	21.9728	***
Exposition WNW	−1.7165	1.2157	1.9764	ns
Exposition NW	−3.2493	1.3194	5.996	**
Exposition N	−0.5111	1.2757	0.1555	ns
No exposition	0	0	0	–

ns not significant, HP host plants

** $p < 0.05$; *** $p < 0.01$

scales considered. While occupied and unoccupied patches on the landscape level only differed significantly in the abundance of host plants, the difference between occupied and unoccupied host plants on the microhabitat level was much stronger. Indeed, several characteristics of the host plant and the surrounding microhabitat differed significantly between plants chosen for oviposition and those not selected. These differences in the strength of the relationship between presence of larval stages and the environment on the different spatial scales studied are similar to the pattern found by Rabasa et al. (2005). These authors showed that egg incidence of the lycaenid butterfly *Iolana iolas* was more influenced by fruit-to-fruit variation within plants than by patch-to-patch variation, although both levels explained significant parts of the observed variation.

Larval habitats

At the landscape level, patch size and geometry are generally considered most important in determining the presence or absence of a species (Dover and Settele 2009). Wahlberg et al. (2002) found that patch area was the most important predictor of landscape occupancy for *E. aurinia* in Finland and a study on the same species in Southern Germany also identified patch size as an important predictor of occupancy (Anthes et al. 2003). In our study, we found only a marginally significant trend that occupied patches are larger. Betzholtz et al. (2007) equally failed to identify patch area as a significant predictor of *E. aurinia* occupancy. Nevertheless, patch size and host plant abundance often are linked. In our study, we also found a positive relationship between host plant abundance and patch size, corroborating the hypothesis that patch size and

quality are interrelated in many cases (cf. Dover and Settele 2009).

Regarding the patch geometry, neither a difference was found between the mean Euclidean distance between all occupied and unoccupied patches, nor between the mean distances to the next occupied patch. This result suggests that the presence of larval stages is not determined by the connectivity of the studied habitat network. This finding is in contrast to the predictions of metapopulation theory emphasizing the importance of habitat isolation for occupancy (Hanski and Gaggiotti 2004). In our habitat network, the dispersal ability of *E. desfontainii* seems sufficient to allow some exchange between the different host plant patches, given that unoccupied patches are not more isolated than occupied ones. On the other hand, if fragmentation is a quite recent phenomenon in our study region, the effect of patch isolation might only be delayed. If so, already isolated populations may merely persist due to high local population sizes, but in case of local extinctions no recolonisation may follow.

The habitat quality in terms of available host plants proved to be the only factor significantly differing between occupied and unoccupied patches. Consequently, the presence of host plants most probably is used by females to detect suitable larval habitats, and only a sufficient amount of host plants matters as a prerequisite for successful development. Several other studies on checkerspot butterflies also emphasize the role of host plant abundance or density for patch occupancy (Anthes et al. 2003; Konvicka et al. 2003; Fowles and Smith 2006; Betzholtz et al. 2007; Smee et al. 2011). Further host plants within the reach of caterpillar mobility is crucial especially for butterfly species with egg clutches and gregarious caterpillars because they have the capacity to completely defoliate a host plant and subsequently die from starvation, if no other host plants are nearby. Indeed, starvation is considered as one of the main natural sources of larval mortality in checkerspot butterflies besides parasitism (Kuussaari et al. 2004).

The mean diameter of the host plant rosettes showed a marginally significant difference between occupied and unoccupied patches. Surprisingly, occupied patches were characterized by host plants with smaller leaf rosettes. However, this finding is counterintuitive given that host plants with smaller leaf rosettes offer less food resources for caterpillars and should therefore be avoided. The detailed study on oviposition sites moreover revealed that plants with bigger leaf rosettes were preferentially selected for oviposition. On the other hand, the size of the host plants is influenced by the surrounding vegetation: in patches with high sward, only those plants that are especially prominent and large are able to survive. On the contrary, in patches with lower sward, also smaller plants are able to survive. This pattern is underlined by the strong positive

correlation between sward height and mean rosette diameter across sites ($r = 0.77$, $p < 0.01$). Therefore, the observation of plants having smaller leaf rosettes in occupied patches is probably confounded by the fact that the sward height in occupied patches is lower.

In our study system, habitat quality (e.g. host plant abundance) seems indeed to be more important for the occupancy of *E. desfontainii* caterpillars than patch size and connectivity. This result clearly confirms findings of studies on the closely related sibling species *E. aurinia* underlining that habitat quality has to be taken into account to predict landscape occupancy in checkerspot butterflies (Anthes et al. 2003; Betzholtz et al. 2007).

Oviposition sites

Host plants are carefully chosen by females to deposit their eggs. Thus, with one exception, only plants of the 2nd year were selected for oviposition. *Dipsacus comosus* is a biannual plant developing its large inflorescence usually in the 2nd year of its life cycle. The age of the plant is well distinguishable by the appearance of the inflorescence stem and the development of spines on the underside of the main leaf vein. Due to the conspicuous visual aspect of the 2nd year plants with their emerging inflorescence, the females most likely rely on their vision to find appropriate host plants.

Besides visual cues, chemical properties may play a role in detecting an appropriate host plant. The majority of checkerspot butterflies feed on host plants that produce iridoid glycoside metabolites (Wahlberg 2001). The ingestion of the metabolites makes larvae unpalatable and therefore unattractive for predators (Kuussaari et al. 2004). Besides their function in protecting caterpillars through ingestion, the chemical properties of plants might be involved in the host recognition in *E. desfontainii*. No information could be obtained whether the concentration of metabolites changes with the phenology of *D. comosus*.

A further explanation for the striking pattern that only 2nd year plants were selected for oviposition might be that only these individuals develop inflorescences that remain upright even after the plants' death. Novoa Pérez and García-Villanueva (1996) observed that *E. desfontainii* populations in Southwestern Spain used inflorescences to construct their overwintering nests. A similar behaviour of caterpillars was observed in our study area where caterpillars constructed their overwintering nests within the dried flower heads (EM, personal observation). The elevated position of the overwintering nests might be beneficial as it protects the larvae from flooding, which might occur in their habitats during winter rains.

Several factors were identified that influence the oviposition site choice of *E. desfontainii*. Butterflies are

known for their time-consuming oviposition site selection, even in species whose host plants are superabundant and therefore detected easily (Wiklund 1984). Thus, females search sites maximizing the survival chances of their offspring and show great exigencies not only requiring the presence of the specific host plant, but also regarding the encountered microclimate and host plant properties (Renwick and Chew 1994; García-Barros and Fartmann 2009).

Inclination and exposition were also found to influence the selection of oviposition sites in the butterfly species *Euphydryas editha* (Murphy and Weiss 1988; Weiss et al. 1988). As for this species, microclimatic properties are of great importance for the Spanish fritillary. Both, the exposition and inclination of the sites where host plants exist, influenced the probability to encounter eggs. An increasing inclination positively affected the likelihood to find egg clusters on a plant because slopes usually get more direct sunlight, especially if exposed in southern direction. Selection of microhabitats is strongly influenced by the thermal requirements of eggs and caterpillars to optimize development, and warm microsites should enhance larval development and therefore should be preferred (Weiss et al. 1988). Regarding the exposition of sites, we observed that sites with northern and northwestern exposition negatively affected the probability for oviposition compared to sites with no exposition.

Another microclimatic characteristic was the amount of sun hours at a given site. More hours of sunshine increased the probability for eggs present on a given host plant. The negative estimate of the linear term and the small but positive quadratic term of sunshine hours show that the relationship is not linear, but the probability to receive egg clutches increases even stronger with increasing amounts of sunlight. Temperature heavily impacts the developmental time of caterpillars with usually increasing temperatures having positive effects on development (Fartmann and Hermann 2006). On the other hand, excessive insolation might cause desiccation of eggs and thus decrease the survival of egg clutches, if exposed to direct sunlight.

In checkerspot butterflies, eggs are laid in clusters of different sizes with varying numbers of egg layers. We only encountered egg clusters to be laid on the underside of the leaves probably to avoid desiccation, but possibly also to escape predation and parasitism. Besides laying clusters on the underside of leaves, clusters were preferentially deposited on the inner side of leaves, relatively close to the stem and therefore probably better buffered against fluctuations of the humidity level. Northern and western expositions in general receive less sunlight. Therefore, the decreased probability for sites exposed to these directions corresponds with the results that the amount of sunlight increases the oviposition site selection. Nevertheless, the

use of different microhabitats by the same butterfly species can provide an insurance against climatic variability, especially in variable Mediterranean ecosystems; if droughts reduce the availability of appropriate host plants in some years, increasing egg and larval mortality, eggs laid at colder microclimates guarantee survival of immature stages and the species persistence at a given site.

Another important predictor of egg presence is the mean vegetation height around the chosen host plants. This matches well what is known for the sibling species *E. aurinia*, with sward height being crucial in determining habitat quality (Liu et al. 2006; Botham et al. 2011; Smees et al. 2011). Generally, the vegetation was lower around plants with eggs. Two reasons possibly explain the preference for lower sward height.

First, the surrounding vegetation affects the microclimatic properties. Normally, shorter vegetation allows faster warming of a given site, whereas higher vegetation is buffering humidity and therefore lowering temperature. Due to the positive correlation between the height of the clutch above ground and the sward height, females in general lay their eggs just below the top of the surrounding vegetation, hereby encountering oviposition sites where the temperature is still high, but eggs are not directly exposed to wind and are less accessible to possible predators and parasitoids.

The second aspect of sward height is the prominence of host plants. The lower the surrounding vegetation, the easier females manage to visually track their host plants (Wiklund 1984; Renwick and Chew 1994). Size and prominence of host plants was shown to influence the oviposition behaviour of *E. aurinia* and *Melitaea aurelia*, whose larvae are both gregarious and therefore require larger amounts of host plant tissue (Anthes et al. 2003; Eichel and Fartmann 2008). The same is true for *E. desfontainii*. The height of the host plant and the rosette diameter both positively influenced the probability to be selected for oviposition.

Two explanations are usually put forward to explain the preference of large host plants against small and inconspicuous host plants. As discussed above, big plants provide more food than host plants with smaller leaf rosettes. Bigger host plants guarantee that caterpillars encounter enough food resources before reaching larval instars with elevated movement abilities allowing movements between host plants after the original host plant is depleted. Besides food availability, the appearance of bigger host plants was mentioned as a reason just because females use to orient towards their potential hosts first by visual cues and only afterwards by assessing their other (i.e. chemical) properties. As mentioned before, 2nd year plants were almost exclusively selected for oviposition. Due to their easily recognizable inflorescences, they are much easier to detect than the flat, 1st-year rosette-only plants.

The number of egg clutches per plant differed significantly from the expected distribution, if females would avoid plants already bearing eggs. Up to eight egg clutches were found on a single host plant indicating that competition for food resources might get severe as soon as caterpillars reach later larval instars with high demand of plant tissue to satisfy their energy demands. Moreover, not only large plants with big leaf rosettes, but also plants with higher amounts of potential host plants around them were preferred for oviposition. This further supports the idea that the actual amount of food is the decisive force behind selecting huge plants with potential alternative host plants in proximity after depletion of the original food source.

The model that best explained the chosen host plants for oviposition included all predictor variables. Host plant quality and quantity, but also vegetation structure and microclimatic parameters as inclination, exposition and sunshine hours are important predictors of oviposition site selection. Interestingly, our final model predicted considerably better whether a host plant is not appropriate for egg-laying than whether the host plant is appropriate for oviposition. We propose that this result is due to the fact that besides vegetation structure and microclimate further factors as chemical cues are of high importance for the selection of host plants. Moreover, host plants were very abundant in the study site suggesting that plants suitable for larval development were not selected in many cases because they were in surplus, while a plant that does not provide the appropriate microclimatic characteristics and vegetation structure is definitely ignored by females.

Our findings underline the importance of vegetation structure and topography for the egg-laying decisions of the females and the resulting role of microclimatic conditions around the oviposition sites, i.e. a resource-based habitat definition (Dennis et al. 2003, 2006; Turlure et al. 2010). According to the resource-based habitat concept, habitat patches must be based on the requirements of all life stages of a butterfly and include not only suitable host plants, but further resources and utilities, among others the appropriate microclimate for successful larval development, nectar sources and shelter for adult butterflies.

When habitat quality was assessed on the landscape level, host plant abundance alone was the only significant factor, contradicting the resource-based habitat definition stating that information about a biotope comprising the host plant might suffice to predict butterfly presence (Dennis et al. 2003, 2006). However, detailed analysis of the oviposition site selection of females revealed the importance of vegetation structure that did not seem to matter on the landscape level (e.g. host plant size or sward height). We hypothesize that this is due to the heterogeneity of the landscape level patch characteristics. Patches can vary considerably in their characteristics on a small

spatial scale, a variety that might be difficult to capture for patches as a whole, e.g. representative sward height for larger patches. On the contrary, if detailed information on oviposition sites or larval habitat is collected, highly specialized microclimatic requirements of larval stages are likely to emerge. As a corollary, we have to consider the precise requirements of all life stages and then to define the habitat as areas where all these resources and utilities co-occur or are within the movement range of a given species (Dennis et al. 2003).

Conservation implications

The present study adds to the findings that habitat quality can be of key importance for the occurrence of a given species, in some cases maybe being even more important than isolation and size of the habitat patches (cf. Thomas et al. 2001). Especially the within site availability of suitable host plants in appropriate microclimatic conditions is crucial for the successful reproduction and thus the persistence of a species in the studied habitat network (Murphy and Weiss 1988; Anthes et al. 2003; Thomas et al. 2010). Conservation plans for *E. desfontainii* therefore should aim at propagation of its host plant, e.g. maintaining habitats with an appropriate disturbance regime to allow occurrence of the ruderal host plant, as well as providing the complementary resources crucial for completing the butterflies' life cycle.

Studies on *E. aurinia* have shown that the management of sites can have beneficial effects on the habitat quality (e.g. host plant density), and consequently on the butterflies, if the larval and adult requirements are acknowledged by a balanced light grazing (i.e. low stock number) (Fowles and Smith 2006; Smee et al. 2011). For the sibling species *E. desfontainii*, we identified some important characteristics for caterpillar presence and oviposition site selection, but more research is still needed for this species to elucidate how to integrate an appropriate grazing regime in a successful habitat management strategy.

In the face of climate change, increasing ambient temperature and variability of precipitation are expected for the Mediterranean region. A recent modelling approach based on the climate envelope of *E. desfontainii* indicates its high sensitivity to the predicted climatic changes (Settele et al. 2008). We show that the species additionally relies on a single host plant species, which is associated with temporal inundations in winter and spring and resulting fluctuations in soil moisture content. The dependency on a host plant using such special soil conditions is probably rendering this butterfly even more susceptible. However, possibilities exist to buffer butterfly populations against the detrimental effects of climate change. One such strategy provides areas with diversified microclimates (Murphy and Weiss 1988;

Ehrlich 1992; Hodgson et al. 2009) by means of topographic and structural diversity of the vegetation. Hence, populations could persist in areas that are currently sub-optimal, but turn suitable when macroclimatic conditions change, thus allowing the persistence of the host plant and the associated butterfly under a warmer and drier climate.

Also larval mobility has some potential to buffer against environmental fluctuations, when alternative host plant species are available that are less affected by environmental change (Hellmann 2002). For example, *E. editha bayensis* caterpillars switch between different host plant species depending on their respective senescence status, which is affected by temperature and exposition. In the case of *E. desfontainii*, this seems rather unlikely, given that no alternative host plant species to *D. comosus* were used in the study area, although some are known from other parts of the distribution.

Finally, we have to acknowledge that our study only covers a limited number of sites, although representative for the type of habitat covered by the species in Portugal. While the spatial variation in conditions of larval habitat is accounted for, only a single season was studied, limiting the wider generalization of the observed patterns. Several studies report that resource use might change according to the conditions in a given survey period (Dennis and Sparks 2006). Complementary assessments could reveal whether the observed habitat use of *E. desfontainii* larval stages are stable over time and therefore valid as a basis to develop management strategies for this endangered butterfly species.

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