

RESEARCH ARTICLE

Ellenberg's indicator values support prediction of suitable habitat for pre-diapause larvae of endangered butterfly *Euphydryas aurinia*

Remigiusz Pielech¹, Krzysztof Zając², Marcin Kadej^{2*}, Marek Malicki³, Adam Malkiewicz², Dariusz Tarnawski²

1 Department of Forest Biodiversity, Institute of Forest Ecology and Silviculture, University of Agriculture, Kraków, Poland, **2** Department of Invertebrate Biology, Evolution and Conservation, Institute of Environmental Biology, University of Wrocław, Wrocław, Poland, **3** Department of Botany, Institute of Environmental Biology, University of Wrocław, Wrocław, Poland

* marcin.kadej@uwr.edu.pl



OPEN ACCESS

Citation: Pielech R, Zając K, Kadej M, Malicki M, Malkiewicz A, Tarnawski D (2017) Ellenberg's indicator values support prediction of suitable habitat for pre-diapause larvae of endangered butterfly *Euphydryas aurinia*. PLoS ONE 12(6): e0179026. <https://doi.org/10.1371/journal.pone.0179026>

Editor: Manuela Pinzari, Università degli Studi di Roma Tor Vergata, ITALY

Received: November 14, 2016

Accepted: May 23, 2017

Published: June 8, 2017

Copyright: © 2017 Pielech et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was supported by the University of Wrocław no. 1076/S/IBS/2017 to DT and MK. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abstract

In spite of the great popularity of Ellenberg's Indicator Values (EIVs) in plant ecology, animal ecologists seldom use EIVs to address ecological questions. In this study we used EIVs to test their potential usefulness for the prediction of suitable habitat for pre-diapause larvae of the endangered butterfly species *Euphydryas aurinia*. Nine transects crossing grasslands in SW Poland with abundant populations of *E. aurinia* were designed. We sampled 76 vegetation plots along the transects. In addition, the presence of the larval webs of *E. aurinia* in sampled plots was also recorded. We then calculated the mean community EIVs of light, nitrogen, soil reaction, moisture and temperature for each sample plots. Generalized linear mixed-effects models (GLMMs) were used to assess which factors determine the local occurrence of larval webs of *E. aurinia*. We found the larval webs only in 12 plots, while the host plant was present in 39 of the examined plots. The presence of the host plant was the most important predictor in both models including all plots or including only plots with host plants. The other significant predictor was the mean EIV of light, and its importance increased in models considering all plots. We attributed the importance of the EIV of light to the site openness and density of the vegetation layer. A positive relationship between this predictor and the presence of larval webs indicates that sites with looser vegetation, a lower contribution of shrubs and tall herbs and better penetration of photosynthetically active radiation to lower vegetation layers are preferred by *E. aurinia* for oviposition. Moreover, the significance of EIV of light may be linked with management practices. Many light-demanding species decline after cessation of mowing as a result of litter accumulation and the dominance of tall herbs. An absence of light-demanding species decreases the community's mean EIV of light and thus indicates the influence of meadow abandonment.

Introduction

Since its introduction in the mid-70s, Ellenberg's Indicator Values (EIVs) have become an extensively used tool in ecological studies. It is especially popular in plant ecology, where EIVs are used to characterize environmental conditions when detailed site-specific measurements are absent. The application of EIVs includes research on vegetation change [1–3], interpretation of ecological gradients [4,5] and describing ecological preferences of both plant species [6,7] and plant communities [8,9]. Some authors, however, have claimed that the interpretation of analyses based on EIVs may be biased due to circular reasoning [10], weak correlations with field measurements [11–13] or inter-correlations between different EIVs [14]. In spite of these reservations, EIVs have enjoyed great popularity and are generally believed to be an important tool in applied plant ecology [15]. On the contrary, animal ecologists seldom use EIVs to address ecological questions, and only a few researchers have tested this approach so far. Significant relationships have been found between EIVs and the diversity of *Sciomyzid* flies [16], butterflies [17–20] and molluscs [21]. In addition, EIVs are sometimes used to characterize the ecological properties of habitats of studied animal assemblages, e.g. ants [22] or molluscs [23]. Some of these studies have highlighted the advantages of the utilization of EIVs in the study of animal autoecology, but this approach is still underexplored and needs more detailed examination.

In this study we used EIVs to test their potential usefulness in the prediction of suitable habitat for pre-diapause larvae of *Euphydryas aurinia*. The species is regionally endangered in many European countries and a great deal of effort has been put so far into supporting its conservation. Some research suggests that host plant abundance is the only important predictor of the presence-absence and abundance of larval webs of *E. aurinia* [24]; however, others showed that vegetation structure and habitat management were also important [18,25,26]. We share the latter opinion on the basis of the field observations of *E. aurinia* habitats in Poland. The species frequently occurs in meadows with a high density of its host plant; however, there are usually apparently-similar meadows in a close vicinity with abundant populations of known host plants and the absence of *E. aurinia*. It is obvious that the ecological niche of the individual species does not overlap exactly with the niche of their host plant [18]. The requirements of either larvae or adults may be limited to a narrower range of ecological conditions than the requirements of the host plants. Understanding this spatial pattern of species distribution at the local scale is essential for its successful conservation. The aim of this work was to examine the relation between the EIVs and the spatial distribution of the pre-diapause larvae of *E. aurinia*.

Material and methods

Studied species

The marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera: Nymphalidae) is widely distributed in the Palearctic from Ireland in the West to Yakutia in the East and to North-west China and Mongolia in the South. In many European countries it is reported to be experiencing declines in distribution or population size [27] and the species has become included in Annex II of the Bern Convention on the Conservation of European Wildlife and in Annexes II and IV of the EEC/EU Habitat Directive (92/43 EU of 21 May 1992), and it is legally protected in many European countries. However, both at the level of the Europe and the European Union [28] as well as worldwide [27] it is listed under the least concern category. In Poland, *E. aurinia* is listed as endangered in the Polish red list [29].

The species occurs in different types of open or semi-open habitats, such as pastures [30], hay meadows [18,25] or woodland clearings [31]. *E. aurinia* has a univoltine life cycle. Adults fly from the third week of May until the third week of June in western Poland. In June (the first three weeks) females lay eggs in batches on the underside of the leaves of the Devil's-bit scabious, *Succisa pratensis* (probably the only initial host plant for pre-diapause caterpillars in western Poland). Young larvae live together in webs that are built by them directly on the host plant. At the end of the summer or early in the autumn, the caterpillars of the IV instar build stronger webs, located low to the ground, in which they hibernate until spring. They pupate around beginning/mid-May [32,33].

Study area

All field investigations were carried out within the rural district of Lwówek Śląski in Lower Silesia (SW Poland), covering a total area of approximately 10 km² (50° 57'N, 15° 22'E). The study area is located in the western part of the mountainous region of the Sudetes, at the foot of the massif of the Izerskie Mts. (see [34] for details). The altitude above sea level ranges from 360 to 420 m. The annual average temperature in the research area is 7.5°C, yearly precipitation is ca. 800 mm and the vegetation period is 180 days [35]. The research area is characterized by a large proportion of arable land and forest, which is interposed with patchily distributed fragments of grassland. The different grassland community types within the research area were investigated. Some of the investigated grasslands had been abandoned for up to 10 years, while the others were still managed with various intensities (sporadic to intensive mowing). All grasslands were developed on moderately acid and nutrient poor soils, which had been developed by draining former marshland. According to the phytosociological nomenclature [36,37], the vegetation of the investigated grassland is classified as *Molinion caeruleae* and *Calthion palustris* meadows, while small fragments of *Violion caninae* grasslands may also occur. Some of abandoned meadows are colonized by communities dominated by tall nitrophilous herbs (communities of *Aegopodion podagrariae*) and shrub (communities of *Sambuco-Salicion capreae*) with domination by *Rubus* spp., *Rosa canina*, young individuals of *Betula pendula* and *Populus tremula*. The study area is located in a Special Area of Conservation, Łąki Gór i Pogórza Izerskiego (PLH020102), which was established within the Natura 2000 network. This area is one of the most important refuges of *E. aurinia* in south-western Poland [38].

Data collection and processing

During a few years preceding this study, field surveys had been conducted within the study area. The surveys were aimed at making an inventory of larval webs by *E. aurinia*, and they yielded a detailed map of its distribution. We then used this map to design nine linear transects with lengths between 100 and 260 m, which were randomly placed within meadows with a known occurrence of *E. aurinia* in previous years. In effect, each transect crossed patches with high densities of *S. pratensis*, as a known host plant of pre-diapause larvae in this region, as well as patches without its presence. Along each transect we sampled vegetation plots (2 m × 2 m) placed every 20 meters. In total, 76 plots were sampled in August 2014. Due to the particular phenology of the *Molinion* meadows, we sampled vegetation plots ca. two months after the females of *E. aurinia* laid their eggs on the host plants. At the beginning of June, when the eggs are laid, many of the plant species that compose these meadow communities are at an early stage of their development and lack some important diagnostic features. Thus, at this stage it is impossible to differentiate among some species of *Asteraceae*, *Apiaceae*, *Juncaceae* or *Poaceae* families, but the proper determination of all plant

species within the sampled plots is crucial to calculate the mean EIVs. Within each plot we recorded all vascular plants and estimated their cover using the Braun-Blanquet scale (r—solitary; +—< 1%; 1—1–5%; 2—6–25%; 3—26–50%; 4—51–75; 5—76–100%). In addition, the presence of the larval webs of *E. aurinia* in the sampled plots was also recorded. All collected samples were entered into a Turboveg database [39]. The average means of the EIVs were calculated for each sample [40]. When calculating the community means of the EIVs, we took only the presence/absence data into consideration. We did not use the weights determined from the abundance of each plant species because the abundance of each species could have change between the eggs laid (June) and the vegetation being sampled (August). Finally, the abundance of host plant (*S. pratensis*) was transformed into an ordinal scale using the method proposed by van der Maarel [41].

Statistical analyses

To assess which factors determine the local occurrence of the larval webs of *E. aurinia*, generalized linear mixed-effects models (GLMMs) with a binomial error distribution and log-link function were performed. We made two separate models that took into account (1) all the studied plots of vegetation samples and (2) only the plots with the presence of *S. pratensis*. For the purpose of both analyses we included six potential predictors of larval web occurrence: abundance of the host plant (variable “Succisa”) and the average community means of the EIVs of “light,” “moisture,” “nutrients,” “soil reaction” and “temperature.” The interpretation of the ecological meaning of the EIVs was presented, e.g. as by Horsák et al. [21]. The transect was used in our analyses as a random effect. Prior to modeling we checked all variables for collinearity using the Spearman rank correlation matrix and the variance inflation factor (VIF). Acceptable levels of correlation were assumed at $r_s < |0.6|$ and VIF values below 3 [42,43]. Due to the high correlation between “soil reaction” and “nutrients” and, for the data set based only on relevés with the occurrence of *S. pratensis*, between “soil reaction” and “moisture” also (S1 Table), we decided to exclude the “soil reaction” variable from both multivariate models. After this step, we did not find any significant collinearity between the remaining variables (all VIF scores were below 2; see S1 Table). All explanatory variables were standardized to a mean of 0 and standard deviation of 0.5 before inclusion in the models to allow for comparisons of their respective effect sizes [44,45].

To identify factors affecting the pre-diapause larvae of marsh fritillary presence in the study plots we used a model selection procedure based on information theory [46]. We used Akaike Information Criterion (AICc) to select the best reduced model. We ranked all subsets of models according to their ΔAICc values together with the associated weight value (w_i). Models with an $\Delta\text{AICc} < 2$ were considered to be equally good [46]. To assess whether the final models provided a good fit to the data we calculated the conditional and marginal R^2_{GLMM} [47,48]. The conditional R^2 value showed the proportion of the variance in the raw data explained by the model, including both fixed and random effects, while the marginal R^2 value showed the proportion of the variance explained only by the fixed effects.

The relative importance of each variable was estimated, on a scale 0–1, by summing the AICc weights across all models that included the explanatory variable of interest [46]. To derive the parameter estimates (β) we used model averaging over the 95% confidence set (thus we used all models with sum of Akaike weights ≤ 0.95 [46]). Only beta coefficients in which the 95% confidence intervals (95% CI) did not overlap with zero were considered as significant. Additionally, we used principal component analysis (PCA) for the visualization of vegetation samples in relation to explanatory variables.

Table 1. Best generalized linear mixed models ($\Delta AICc < 2$) describing the presence of the larval webs of *Euphydryas aurinia* in study plots.

| No. | Model | df | R^2_m | R^2_c | AICc | $\Delta AICc$ | w_i |
|---------------------------------------|---|----|---------|---------|--------|---------------|-------|
| All plots | | | | | | | |
| 1 | ~ <i>Succisa</i> + Light + (1 Transect) | 4 | 0.81 | 0.81 | 43.567 | 0 | 0.343 |
| 2 | ~ <i>Succisa</i> + Light + Temperature + (1 Transect) | 5 | 0.82 | 0.82 | 44.840 | 1.272 | 0.182 |
| Plots with host plant presence | | | | | | | |
| 1 | ~ <i>Succisa</i> + Light + (1 Transect) | 4 | 0.54 | 0.54 | 43.369 | 0 | 0.299 |
| 2 | ~ Light + (1 Transect) | 3 | 0.36 | 0.36 | 45.205 | 1.837 | 0.119 |
| 3 | ~ <i>Succisa</i> + Light + Temperature + (1 Transect) | 5 | 0.58 | 0.58 | 45.271 | 1.903 | 0.116 |

R^2_m —the marginal R^2 value shows the proportion of the variance explained only by the fixed effects, R^2_c —the conditional R^2 value shows the proportion of the variance in the raw data explained by the model, including both fixed and random effects.

<https://doi.org/10.1371/journal.pone.0179026.t001>

All statistical analyses were performed in open source statistical software R (version 3.2.2, <http://www.r-project.org/>), with the packages: *arm* (version 1.8–6) [49], *lme4* (version 1.1–10) [50] and *MuMIn* (version 1.15.1) [51]. Plots were performed using the packages *plotrix* (version 3.6) [52] and *ggbiplot* (version 0.55, downloaded from <https://github.com/vqv/ggbiplot>, December 2015). The variance inflation factor (VIF) was calculated using the ‘vif.mer’ function (downloaded from <https://github.com/aufrank/R-hacks/blob/master/mer-utils.R>, December 2015) in R.

Results

The presence of the larval webs of *E. aurinia* was found in 12 out of 76 studied vegetation samples (relevés), only on *S. pratensis*. The host plant was present in 39 examined plots. The key importance of the presence of *S. pratensis* (as the host plant) for the occurrence of larval webs of *E. aurinia* was confirmed by the results of the GLMMs. The model selection showed that, taking into account all samples, the two models’ explanations of the presence of larval webs were equally good (Table 1).

The best models explained over 80% of the variation and included three explanatory variables. The abundance of the *S. pratensis* was the most important variable explaining the presence of larval webs, followed by “light” and “temperature” factors (Fig 1).

Only the positive relation of the first two predictors with the occurrence of larval webs was statistically significant (Fig 2).

The same three predictors were present in the best three models explaining the presence of larval webs in the second model for vegetation samples only with the occurrence of *S. pratensis* (Table 1). However, in this model the relative importance of the *S. pratensis* abundance was much lower, and the most important predictor was “light” (Fig 1), which explained 36% of the variation alone (Table 1). “Light” was also the only variable in the second model with a statistically significant effect, although the larval webs tended to be more frequent with an increase in the abundance of the host plant (Fig 2). For both groups of models, “transect” as a random effect was not a significant term in the GLMM. The distribution of the sampled plots with the occurrence of the larval webs and those without the species, in relation to a gradient of explanatory variables, is shown in Fig 3.

Discussion

Our research has shown that the distribution of the larval webs of marsh fritillary is closely associated with the presence of *S. pratensis*, which seems to be the only initial host

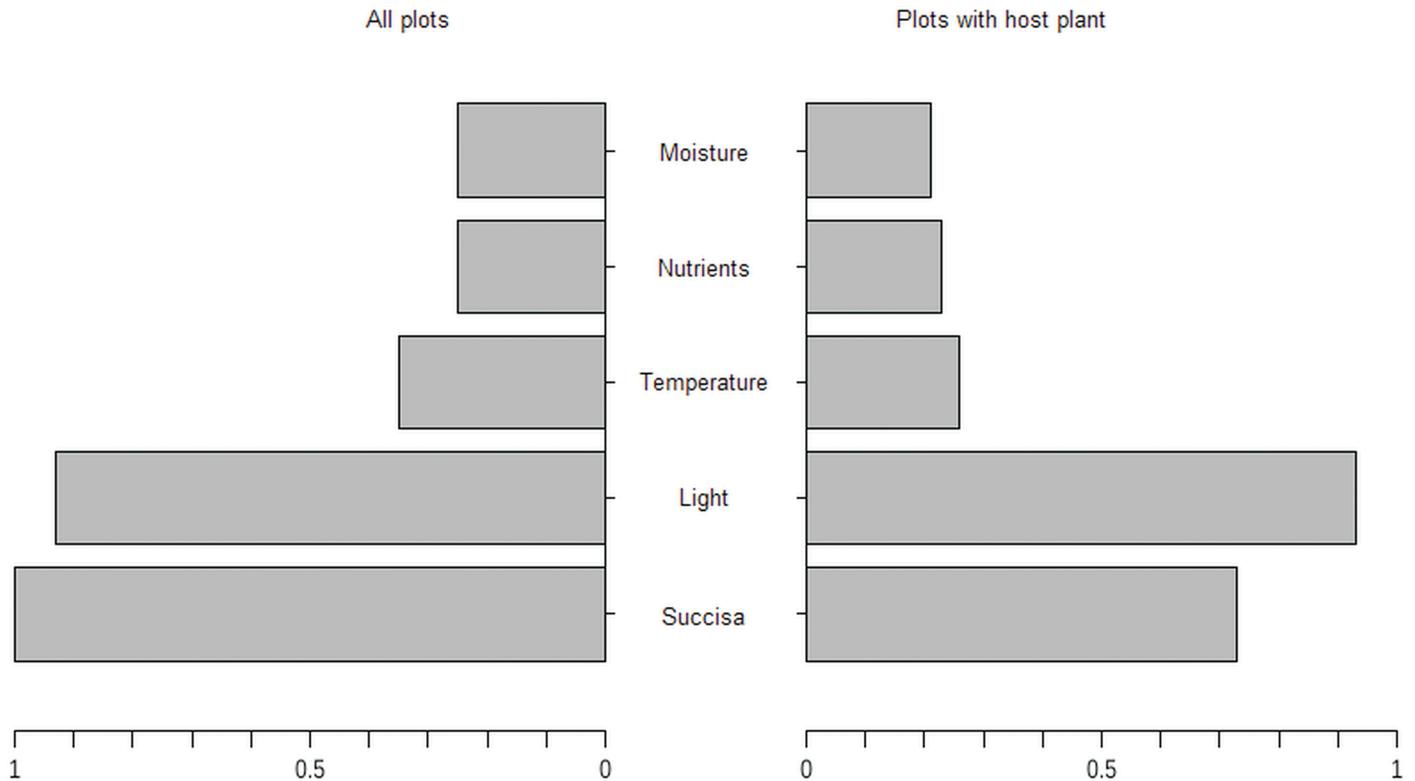


Fig 1. Comparison of the relative variable importance (RVI) used to explain the presence of larval webs of *Euphydryas aurinia* in two data sets: Including all plots and only those with the presence of *Succisa pratensis*. The RVI was computed as the sum of the AICc weights over all models including the explanatory variable.

<https://doi.org/10.1371/journal.pone.0179026.g001>

plant of the caterpillars in the study population, as in many other regions of central Europe [53]. As we expected, based on the results of other authors [18,26,30,54–56], the abundance of the host plant was an important determinant of the occurrence of pre-dia-pause larvae. However, our results indicated that after taking into account only samples with the presence of the host plant, the importance of this factor decreased, in favor of the EIV of “light”.

This factor should not be linked with the total solar radiation reaching the site, but rather with the site openness and density of the vegetation layer [21]. A positive relation between this predictor and the presence of larval webs indicates that sites with looser vegetation, decreasing representation of species characteristic of forests and shrubs and better penetration of photo-synthetically active radiation to lower vegetation layers are preferred by marsh fritillary for ovi-position. Moreover, the significance of the EIV of “light” may be attributed to management practices. Many light-demanding species decline after the cessation of mowing as a result of litter accumulation and the dominance of tall herbs [57–61]. The absence of light-demanding species decreases the community mean EIV of “light” and thus indicates the influence of meadow abandonment.

Based on this ecological interpretation, our results are consistent with those reported by other researchers, who showed that the females of *E. aurinia* chose individual *S. pratensis* in open vegetation structures that were fully exposed to the sun and surrounded by lower

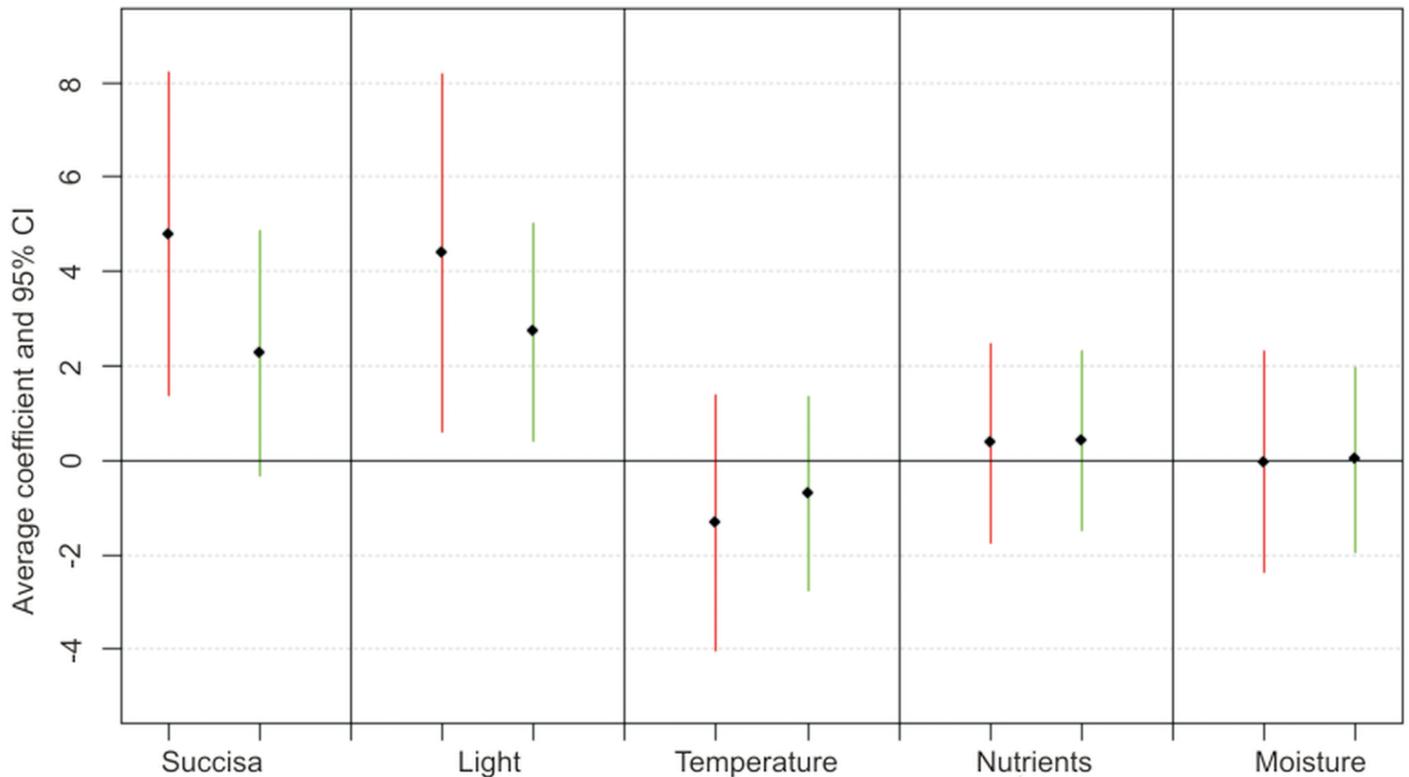


Fig 2. Average parameter estimates and 95% confidence intervals (CIs) for all standardized variables in two data sets. One group includes all plots (red color) and one only those with the presence of *Succisa pratensis* (green color). Parameters were averaged for the 95% confidence set of the models.

<https://doi.org/10.1371/journal.pone.0179026.g002>

vegetation as host [18,25,26]. Larvae of *E. aurinia* may increase their growth rate behaviorally by sun basking, thus microclimate conditions shaped by the looser structure of the vegetation and better access for the light may be particularly important in the case of a low temperature environment [62]. Moreover, the rosette of *Succisa* leaves is situated close to the ground and is easily accessible for egg-depositing females in an open vegetation structure [25]. The accessibility and sun-exposure of the host plants are, next to visibility, the most important factors determining the female oviposition in the Mediterranean subspecies *E. a. provincialis* [63].

The presence or abundance of the host plant is of course the most important factors determining habitat quality for *E. aurinia*. However, there are also some other environmental requirements that have to be met to enable its successful reproduction. Assessing habitat quality only on the basis of the number of host plants may be somewhat misleading. For example, individuals of *S. pratensis* in abandoned populations have higher growth rates and produce more flower heads per plant (in spite of higher mortality rates and lower seedling establishment) [64]. As we stated above, these abandoned sites are at the same time unfavourable for *E. aurinia*. Thus, various variables related to the vegetation structure and dynamics can both fine-tune the prediction of the insect's distribution and habitat quality assessment. As we show in this research, EIVs may be a useful tool in that field.

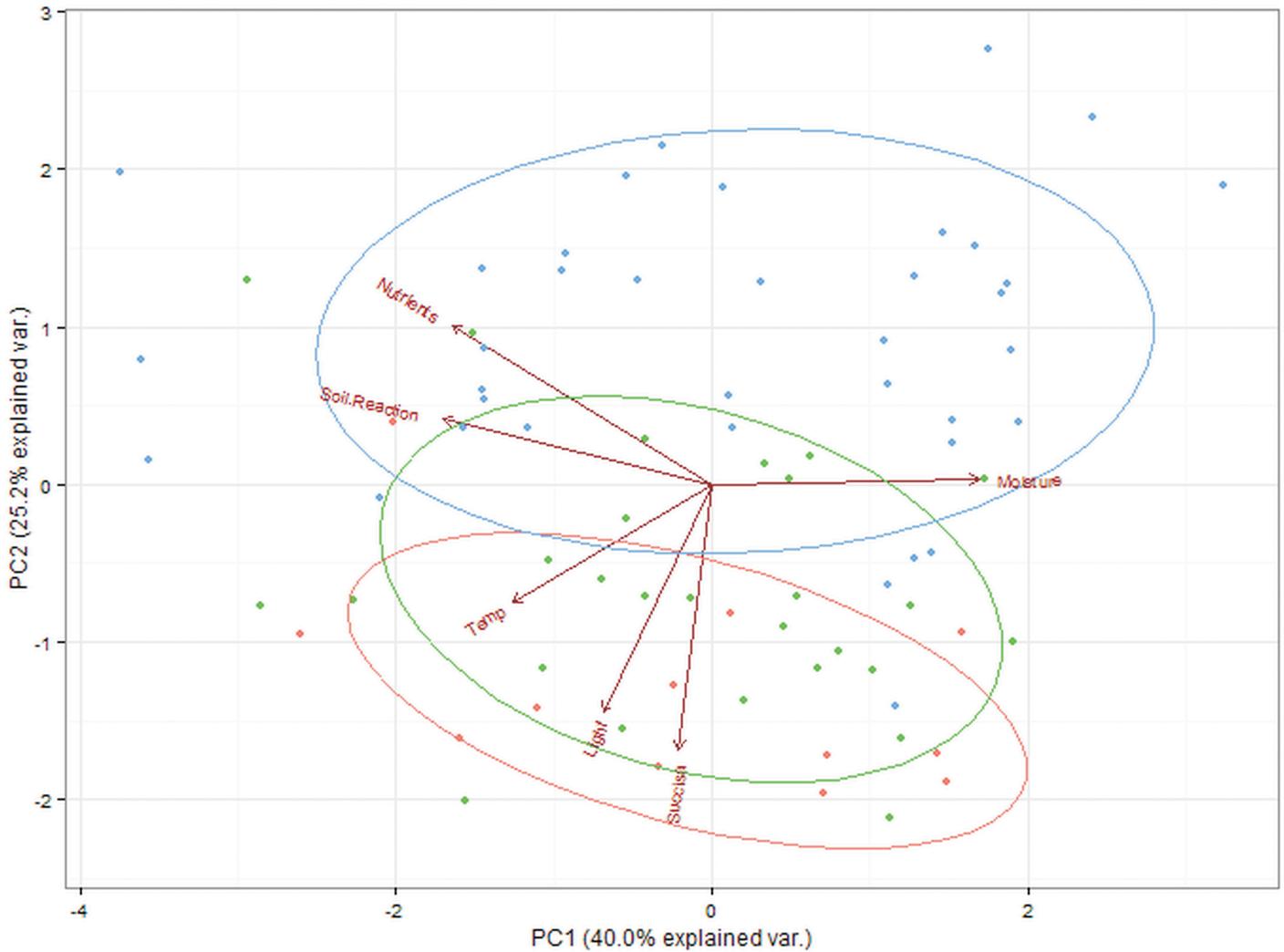


Fig 3. PCA ordination diagram of all 76 study plots of vegetation based on six explanatory variables, with differentiation of the three groups of plots presented with different colors and circled with 95% confidence interval ellipses. Red points and ellipsoid represents plots with *Euphydryas aurinia* occurrence; green points and ellipsoid represents plots with *Succisa pratensis* occurrence and without *E. aurinia*; and blue points and ellipsoid represent plots without *S. pratensis* and *E. aurinia*. Arrows indicate the direction of the explanatory variables. Eigenvalues: PC1–2.397, PC2–1.514.

<https://doi.org/10.1371/journal.pone.0179026.g003>

Supporting information

S1 Table. Spearman correlation coefficients between explanatory variables and variance inflation factors (VIFs) for variables in final models. Significant correlations ($p < 0.05$) are indicated in bold.

(DOC)

Acknowledgments

This research was supported by a grant from the University of Wrocław no. 1076/S/IBŚ/2017. The field work was conducted with the permission of the General Directorate for Environmental Protection in Poland (permit no. DOP-OZGZ.6401.35.2012.JRO).

Author Contributions

Conceptualization: KZ RP DT MK.

Data curation: KZ RP.

Formal analysis: KZ RP.

Funding acquisition: DT MK.

Investigation: AM DT MK MM.

Methodology: KZ RP.

Project administration: DT MK.

Resources: AM DT MK MM KZ RP.

Supervision: DT MK KZ RP.

Validation: KZ RP MK AM DT MM.

Visualization: KZ.

Writing – original draft: KZ RP.

Writing – review & editing: RP KZ DT MM AM MK.

References

1. Durak T, Holeksa J. Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of managed beech stands. *For Ecol Manag.* 2015; 351: 47–56. <https://doi.org/10.1016/j.foreco.2015.05.001>
2. Šebesta J, Šamonil P, Lacina J, Oulehle F, Houška J, Buček A. Acidification of primeval forests in the Ukraine Carpathians: Vegetation and soil changes over six decades. *For Ecol Manag.* 2011; 262: 1265–1279. <https://doi.org/10.1016/j.foreco.2011.06.024>
3. Stevens CJ, Ceulemans T, Hodgson JG, Jarvis S, Grime JP, Smart SM. Drivers of vegetation change in grasslands of the Sheffield region, northern England, between 1965 and 2012/13. Hölzel N, editor. *Appl Veg Sci.* 2016; 19: 187–195. <https://doi.org/10.1111/avsc.12206>
4. Škodová I, Janišová M, Hegedúšová K, Borsukevych L, Smatanová J, Kish R, et al. Sub-montane semi-natural grassland communities in the Eastern Carpathians (Ukraine). 2015;
5. Zelený D, Schaffers AP. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. Palmer M, editor. *J Veg Sci.* 2012; 23: 419–431. <https://doi.org/10.1111/j.1654-1103.2011.01366.x>
6. Puchałka R, Wyborska D, Rutkowski L, Piwczyński M. *Pilosella bauhinii* (Schult.) Arv.-Touv. and *P. cymosa* subsp. *vaillantii* (Tausch) S. Bräut. & Greuter (Asteraceae) from new localities in north-central Poland. *Acta Soc Bot Pol.* 2015; 84: 449–451. <https://doi.org/10.5586/asbp.2015.043>
7. Tomaselli M, Petraglia A, Rossi G, Adorni M. Contribution to the environmental ecology of *Cryptogramma crista* (L.) R. Br. ex Hooker in the Alps. *Flora—Morphol Distrib Funct Ecol Plants.* 2005; 200: 175–186. <https://doi.org/10.1016/j.flora.2004.04.002>
8. Reczyńska K. Diversity and ecology of oak forests in SW Poland (Sudetes Mts.). *Phytocoenologia.* 2015; 45: 85–105. <https://doi.org/10.1127/phyto/2015/0021>
9. Šumberová K, Hrivnák R. Formalised classification of the annual herb vegetation of wetlands (Isoëto Nano—Juncetea class) in the Czech Republic and Slovakia (Central Europe). *Phytocoenologia.* 2013; 43: 13–40. <https://doi.org/10.1127/0340-269X/2013/0043-0529>
10. Roo-Zielińska E. Fitoindykacja jako narzędzie oceny środowiska fizycznogeograficznego. Podstawy teoretyczne i analiza porównawcza stosowanych metod. Warszawa: Institute of Geography and Spatial Organization Polish Academy of Sciences; 2004.
11. Hill MO, Carey PD. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *J Veg Sci.* 1997; 8: 579–586. <https://doi.org/10.2307/3237210>

12. Szymura TH, Szymura M, Macioł A. Bioindication with Ellenberg's indicator values: A comparison with measured parameters in Central European oak forests. *Ecol Indic.* 2014; 46: 495–503. <https://doi.org/10.1016/j.ecolind.2014.07.013>
13. Wagner M, Kahmen A, Schlumprecht H, Audorff V, Perner J, Buchmann N, et al. Prediction of herbage yield in grassland: How well do Ellenberg N-values perform? *Appl Veg Sci.* 2007; 10: 15. [https://doi.org/10.1658/1402-2001\(2007\)10\[15:POHYIG\]2.0.CO;2](https://doi.org/10.1658/1402-2001(2007)10[15:POHYIG]2.0.CO;2)
14. Pakeman RJ, Reid CL, Lennon JJ, Kent M. Possible interactions between environmental factors in determining species optima. *J Veg Sci.* 2008; 19: 201–208. <https://doi.org/10.3170/2007-8-18353>
15. Diekmann M. Species indicator values as an important tool in applied plant ecology—a review. *Basic Appl Ecol.* 2003; 4: 493–506. <https://doi.org/10.1078/1439-1791-00185>
16. Williams CD, Moran J, Doherty O, Mc Donnell RJ, Gormally MJ, Knutson LV, et al. Factors affecting Sciomyzidae (Diptera) across a transect at Skealaghan Turlough (Co. Mayo, Ireland). *Aquat Ecol.* 2009; 43: 117–133. <https://doi.org/10.1007/s10452-007-9149-4>
17. Feest A, van Swaay C, van Hinsberg A. Nitrogen deposition and the reduction of butterfly biodiversity quality in the Netherlands. *Ecol Indic.* 2014; 39: 115–119. <https://doi.org/10.1016/j.ecolind.2013.12.008>
18. Konvicka M, Hula V, Fric Z. Habitat of pre-hibernating larvae of the endangered butterfly *Euphydryas aurinia* (Lepidoptera: Nymphalidae): What can be learned from vegetation composition and architecture? *Eur J Entomol.* 2003; 100: 313–322. <https://doi.org/10.14411/eje.2003.050>
19. Oostermeijer JGB, van Swaay CAM. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biol Conserv.* 1998; 86: 271–280. [https://doi.org/10.1016/S0006-3207\(98\)00040-8](https://doi.org/10.1016/S0006-3207(98)00040-8)
20. Tiitsaar A, Kaasik A, Lindman L, Stanevičs T, Tammaru T. Host associations of *Coenonympha hero* (Lepidoptera: Nymphalidae) in northern Europe: microhabitat rather than plant species. *J Insect Conserv.* 2016; 20: 265–275. <https://doi.org/10.1007/s10841-016-9861-2>
21. Horsák M, Hájek M, Tichý L, Juříčková L. Plant indicator values as a tool for land mollusc autecology assessment. *Acta Oecologica.* 2007; 32: 161–171. <https://doi.org/10.1016/j.actao.2007.03.011>
22. Weber S. Faunistisch-ökologische Untersuchungen der Ameisenfauna (Hymenoptera, Formicidae) einer Wildflusslandschaft im Salzburger Tennengau. *Myrmecol Nachrichten.* 2003; 5: 15–30.
23. Kappes H, Kopeč D, Sulikowska-Drozd A. Influence of Habitat Structure and Conditions in Floodplain Forests on Mollusc Assemblages. *Pol J Ecol.* 2014; 62: 739–750. <https://doi.org/10.3161/104.062.0416>
24. Tjørnløv RS, Kissling WD, Barnagaud J-Y, Bøcher PK, Høye TT. Oviposition site selection of an endangered butterfly at local spatial scales. *J Insect Conserv.* 2015; 19: 377–391. <https://doi.org/10.1007/s10841-014-9747-0>
25. Anthes N, Fartmann T, Hermann G, Kaule G. Combining larval habitat quality and metapopulation structure—the key for successful management of pre-alpine *Euphydryas aurinia* colonies. *J Insect Conserv.* 2003; 7: 175–185.
26. Betzholtz P-E, Ehrig A, Lindeborg M, Dinnéty P. Food plant density, patch isolation and vegetation height determine occurrence in a Swedish metapopulation of the marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera, Nymphalidae). *J Insect Conserv.* 2007; 11: 343–350. <https://doi.org/10.1007/s10841-006-9048-3>
27. van Swaay C, Wynhoff L, Verovnik R, Wiemers M, López Munguira M, Maes D, et al. *Euphydryas aurinia*. The IUCN Red List of Threatened Species 2010: e.T174182A7024283 [Internet]. 2010 [cited 28 Feb 2016]. <http://www.iucnredlist.org/details/174182/1>
28. van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, et al., editors. European red list of butterflies. Luxembourg: Publications Office of the European Union; 2010.
29. Głowaciński Z, editor. Red list of the threatened animals in Poland. Kraków: Polish Academy of Sciences, Institute of Nature Conservation; 2002.
30. Smees M, Smyth W, Tunmore M, French-Constant R, Hodgson D. Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (*Euphydryas aurinia*) in SW England. *J Insect Conserv.* 2011; 15: 153–163. <https://doi.org/10.1007/s10841-010-9334-y>
31. Wahlberg N, Klemetti T, Hanski I. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography.* 2002; 25: 224–232.
32. Kadej M, Malicki M, Malkiewicz A, Smolis A, Suchan T, Tarnawski D. Trwałe zachowanie zagrożonych siedlisk łąkowych i ich motyli w sieci Natur 2000 w południowo-zachodniej Polsce. Wrocław: Stowarzyszenie Ekologiczne EKO-UNIA; 2014.
33. Sielezniew M. Przeplatka *aurinia* *Euphydryas aurinia* w Puszczy Knyszyńskiej. *Chrońmy Przyr. Ojczystą.* 2015; 71: 221–228.
34. Kondracki J. Geografia regionalna Polski. Warszawa: Wydawnictwo Naukowe PWN; 2002.

35. Staffa M, Mazurski KR, Czerwiński J, Pisarski G. Pogórze Izerskie. Słownik geografii turystycznej Sudetów. Wrocław: Wydawnictwo I-BIS; 2003.
36. Chytrý M, editor. Vegetation of the Czech Republic 1. Grassland and heathland vegetation. Praha. 526: Academia; 2007.
37. Chytrý M, editor. Vegetation of the Czech Republic 4., Forest and scrub vegetation. Praha: Academia; 2013.
38. Reczyńska K, Tarnawski D, Kadej M, Świerkosz K. Łąki Gór i Pogórza Izerskiego. In: Świerkosz K, Liberačka H, Lysiak M, Zając K, editors. Obszary Natura 2000 na Dolnym Śląsku. Wrocław: RDOŚ we Wrocławiu; 2012. pp. 174–176.
39. Hennekens SM, Schaminée JHJ. TURBOVEG, a comprehensive data base management system for vegetation data. *J Veg Sci.* 2001; 12: 589–591. <https://doi.org/10.2307/3237010>
40. Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D. Zeigerwerte von Pflanzen in Mitteleuropa. *Scr Geobot.* 1991; 18: 1–248.
41. van den Maarel E. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio.* 1979; 39: 97–114. <https://doi.org/10.1007/BF00052021>
42. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography.* 2013; 36: 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
43. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems: Data exploration. *Methods Ecol Evol.* 2010; 1: 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>
44. Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol.* 2011; 24: 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x> PMID: 21272107
45. Schielzeth H. Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. *Methods Ecol Evol.* 2010; 1: 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
46. Burnham KP, Anderson DR. Model selection and multimodel inference a practical information-theoretic approach [Internet]. New York: Springer; 2002. <http://site.ebrary.com/id/10047705>
47. Nakagawa S, Schielzeth H. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol.* 2013; 4: 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
48. Johnson PCD. Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods Ecol Evol.* 2014; 5: 944–946. <https://doi.org/10.1111/2041-210X.12225> PMID: 25810896
49. Gelman A, Su Y-S, Yajima M, Hill J, Pittau MG, Kerman J, et al. Package “arm”: data analysis using regression and multilevel/hierarchical models [Internet]. 2015 [cited 6 Dec 2015]. <ftp://204.45.83.126/cran/web/packages/arm/arm.pdf>
50. Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, et al. Package “lme4”: linear mixed-effects models using “Eigen” and S4 [Internet]. 2015 [cited 6 Dec 2015]. <http://pbil.univ-lyon1.fr/CRAN/web/packages/lme4/lme4.pdf>
51. Bartoń K. Package “MuMIn”: multi-model inference [Internet]. 2015 [cited 10 Mar 2015]. <ftp://155.232.191.229/cran/web/packages/MuMIn/MuMIn.pdf>
52. Lemon J, Bolker B, Oom S, Klein E, Rowlingson B, Wickham H, et al. Package “plotrix”: various plotting functions [Internet]. 2015 [cited 6 Dec 2015]. <ftp://152.19.134.44/CRAN/web/packages/plotrix/plotrix.pdf>
53. Meister H, Lindman L, Tammaru T. Testing for local monophagy in the regionally oligophagous *Euphydryas aurinia* (Lepidoptera: Nymphalidae). *J Insect Conserv.* 2015; 19: 691–702. <https://doi.org/10.1007/s10841-015-9792-3>
54. Hula V, Konvicka M, Pavlicko A, Fric Z. Marsh fritillary (*Euphydryas aurinia*) in the Czech Republic: monitoring, metapopulation structure, and conservation of an endangered butterfly. *Entomol Fenn.* 2004; 15: 231–241.
55. Liu W, Wang Y, Xu R. Habitat utilization by ovipositing females and larvae of the Marsh fritillary (*Euphydryas aurinia*) in a mosaic of meadows and croplands. *J Insect Conserv.* 2006; 10: 351–360. <https://doi.org/10.1007/s10841-006-9009-x>
56. Botham MS, Ash D, Aspey N, Bourn NAD, Bulman CR, Roy DB, et al. The effects of habitat fragmentation on niche requirements of the marsh fritillary, *Euphydryas aurinia*, (Rottemburg, 1775) on calcareous grasslands in southern UK. *J Insect Conserv.* 2011; 15: 269–277. <https://doi.org/10.1007/s10841-010-9344-9>
57. Huhta A-P, Rautio P, Tuomi J, Laine K. Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. *J Veg Sci.* 2001; 12: 677–686. <https://doi.org/10.2307/3236908>

58. Jensen K, Meyer C. Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. *Plant Ecol.* 2001; 155: 169–181. <https://doi.org/10.1023/A:1013270628964>
59. Öckinger E, Eriksson AK, Smith HG. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol Conserv.* 2006; 133: 291–300. <https://doi.org/10.1016/j.biocon.2006.06.009>
60. Janeček Š, de Bello F, Horník J, Bartoš M, Černý T, Doležal J, et al. Effects of land-use changes on plant functional and taxonomic diversity along a productivity gradient in wet meadows. Acosta A, editor. *J Veg Sci.* 2013; 24: 898–909. <https://doi.org/10.1111/jvs.12012>
61. Májeková M, Janeček Š, Mudrák O, Horník J, Janečková P, Bartoš M, et al. Consistent functional response of meadow species and communities to land-use changes across productivity and soil moisture gradients. Schwabe-Kratochwil A, editor. *Appl Veg Sci.* 2016; 19: 196–205. <https://doi.org/10.1111/avsc.12223>
62. Porter K. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos.* 1982; 38: 308. <https://doi.org/10.2307/3544670>
63. Pinzari M, Pinzari M, Sbordoni V. Egg laying behaviour, host plants and larval survival of *Euphydryas aurinia provincialis* (Lepidoptera Nymphalidae) in a Mediterranean population (central Italy). *Boll Della Soc Entomol Ital.* 2016; 148: 121. <https://doi.org/10.4081/BollettinoSEI.2016.121>
64. van der Meer S, Dahlgren JP, Mildén M, Ehrlén J. Differential effects of abandonment on the demography of the grassland perennial *Succisa pratensis*. *Popul Ecol.* 2014; 56: 151–160. <https://doi.org/10.1007/s10144-013-0400-7>