



The importance of dynamic open-canopy woodlands for the conservation of a specialist butterfly species

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Abstract

Context Intensification of land-use caused a reduction of ecosystem heterogeneity and diversity, and subsequently led to dramatic decrease of biodiversity. Species depending on dynamic ecosystems are particularly affected from this trend of land-use intensification, landscape homogenization, and the optimization of land-use. Forest species suffer under the intensification of forest management, in the worst case transforming light and heterogeneous deciduous forests into species-poor intensively used deciduous forests optimized for wood production. This lead to

the destruction of a mosaic consisting of various successional stages in parallel.

Objective In this study we analyse the relevance of forest heterogeneity, forest disturbance and microhabitat preferences of egg oviposition and larval development for a highly endangered butterfly species, *Euphydryas maturna*. This butterfly species mainly occurs in light and moist deciduous forests, such as riparian forests along mountain streams in northern Austria.

Methods We combine detailed field observations with high resolution aerial pictures taken with an Unmanned Aerial Vehicle (UAV) to build ensemble habitat suitability models from GAM, GBM, GLM, and Maxent models.

Results We found that egg ovipositions take place exclusively on the tree species *Fraxinus excelsior*, preferably exposed to the south, partly shaded, and at medium height (3 m). Our habitat suitability models based on high resolution aerial pictures indicate that egg ovipositions are clustered and accumulate along forest edges and at sites with high forest heterogeneity.

Conclusion Our study underlines the high relevance and importance of light deciduous forest structures with environmental dynamics creating the preconditions of specific microhabitat structures for endangered species, such as *E. maturna*. Our study shows that UAV-captured high precision aerial imagery are well suited to optimally connect two spatial scales, the ecosystem and microhabitat scale.

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Keywords Habitat dynamics · Ecosystem heterogeneity · Open-canopy woodlands · Ecotone · Habitat demands · *Euphydryas maturna* · Unmanned aerial vehicle · Aerial pictures · Habitat suitability model

Introduction

The transformation of natural habitats into anthropogenic landscapes such as intensively used pastures, agricultural fields, settlements and forests optimized for wood production caused a dramatic loss of habitats and biodiversity during the past decades (Maxwell et al. 2016). These land-use changes frequently lead to the destruction of heterogeneous and species rich ecosystems into homogenous and species-poor landscapes (Gámez-Virués et al. 2015). Apart from the complete loss of natural and near natural ecosystems, the remaining habitats frequently suffer under the deterioration of habitat quality through increased atmospheric nitrogen depositions and the influx of pesticides, among others (Thomas et al. 2016). This deterioration of habitat quality negatively impacts local plant and animal populations (Dennis and Eales 1997). Particularly sensitive species demanding specific habitat conditions suffer under reduced habitat quality, as documented for various butterfly species across Central Europe (Thomas et al. 2011; Thomas 2016; Habel et al. 2021).

A very relevant prerequisite to the existence of many plant and animal species are ecosystem dynamics and the co-existence of various successional stages (Kuuluvainen 2009). However, human demographic pressure and increasing life-standards caused a rising demand for more land to settle and to cultivate for the production of food and energy crops (Steffan-Dewenter et al. 2007). This trend also affects forests, which are frequently transformed from natural forest into forests for intense wood production (Kirby and Watkins 2015). This counteracts natural dynamics such as forest succession, natural rejuvenation, and the availability of ecotones (Skrajna 2020). As a result, dynamic environments exist today only sporadically. However, many species rely on such dynamic environments (Bubová et al. 2015). Last remnant ecosystems shaped by strong environmental dynamics can still be rarely found along non-regulated streams and

ivers (Naiman et al. 1993; Ward et al. 1999; Trockner and Stanford 2002).

Forest biodiversity suffers in particular under management intensification across major parts of Central Europe (Seibold et al. 2015), turning light and heterogeneous deciduous forests into comparatively dark and uniform monocultures of coniferous trees (Nau-mov et al. 2018). However, most forest species rely on light forests and heterogeneous vegetation structures consisting of various (deciduous) trees species, shrubs, and herbs, and the co-existence of various successional stages (Kozák et al. 2021). A prominent example is the scarce fritillary butterfly *Euphydryas maturna*. This butterfly depends on light and humid deciduous forests with *Fraxinus excelsior* (Freese et al. 2006) and is usually found along transitions of forest and open land, along forest pastures, and in light forests creating mosaics of trees, shrubs and grassland (Fartmann et al. 2013). Such forest structures are known to be hotspots of biodiversity (Horák et al. 2018).

In this study we analyse ecosystem structures and microhabitat preferences for oviposition of the scarce fritillary *E. maturna*, across sparse deciduous riparian forests along the highly dynamic Taugl River in northern Austria (close to the village Hintersee). We assessed caterpillar nests and habitat parameters (manually) across our study region and took high-resolution aerial photographs with a UAV. We combined these datasets to calculate habitat suitability models to project the occurrence of larvae of this butterfly and to quantify ecosystem structures and microhabitat preferences. Based on our data and results we will answer the following questions:

1. Which ecosystem structures are preferably used for oviposition of *E. maturna*?
2. Which microhabitat conditions are of relevance for oviposition and successful larval development?
3. What conservation conclusions can be derived from our findings for this butterfly species, and for forest biodiversity in general?
4. What are the advantages and limitations of using high-resolution aerial imagery through drones?

Material and methods

Study species

The scarce fritillary butterfly, *E. maturna*, is a typical continental woodland butterfly and occurs across the Palaearctic region (Kudrna et al. 2011). This butterfly species is mainly found in open, sunny, humid, and sheltered gaps of open, sparse deciduous woodlands (Freese et al. 2006; Dolek et al. 2013), being on the wing mainly in June, in one generation (Ebert and Rennwald 1991). Oviposition usually takes place in batches (one batch consists out of about 250 eggs) (Eliasson and Shaw 2003) mainly on *Fraxinus excelsior* (with some exceptions observed, e.g. *Ligustrum vulgare* in eastern Austria, see Straka 2014, or different species of herbs in Sweden, see Eliasson 2001b). Females mostly prefer small trees and oviposit at heights between 1.5 and 3 m above the ground, along forest edges, at forest clearings and along road verges (Gros 2002; Dolek et al. 2006). Mortality of larvae increases under full sun (Dolek et al. 2006) and with increasing duration of sunshine (Weidemann 1985; Ebert and Rennwald 1991; Wahlberg 1998, 2000, 2001; Eliasson 2001a). Preference of sites for oviposition not only depends on habitat structures, but also on female behaviour. Studies showed that the more nests of larvae in a tree the higher is the survival probability of larvae. In consequence, females often oviposit in trees where already eggs have been laid by other females (Dolek et al. 2013). This behaviour might be related with parasitoid pressure survival probabilities. Pre-hibernation mortality rates are very high due to various parasitoids (Dolek et al. 2006; Freese et al. 2006). Thus, population fluctuations of *E. maturna* are very high (Dolek et al. 2006; John et al. 2021). The silk web around the larvae may act as a shelter against predators and parasitoids (Fitzgerald 1993). Early larval stages hibernate and complete its development in the following spring (first on various herbs, shrub and tree species, later on *Fraxinus excelsior* after the opening of the leaf buds, see Gros 2002; Dolek et al. 2006). Due to intensification in forestry, open-canopy woodlands become very scarce. Typical habitats are early successional stages of deciduous woodland, historically maintained by coppicing and forest pastures. Due to changes in management as well as habitat destruction, this butterfly species is ranked among the most threatened

European butterfly species (van Swaay and Warren 1999; van Swaay et al. 2010). Specific and locally adapted conservation management (e.g. coppicing of forest stands, creation of early-successional stages in deciduous and humid forests) support this butterfly, among many other taxa (Gros 2008; Fartmann et al. 2013; Dolek et al. 2018; Vrabec et al. 2019; Bubová et al. 2015).

Data collection

We assessed sites with egg ovipositions of *E. maturna* based on the sightings of caterpillar nests during June and July 2021. For each of these caterpillar nests, we recorded the following parameters: Exact geographic location (GPS coordinates, with a handheld GPS device, Trimble Juno SB, accuracy ± 3 m); height of *Fraxinus excelsior* trees (the single tree species on which caterpillar nests could be found, classified into < 5 m, 5–10 m, 10–15 m, > 15 m); height of caterpillar nests (m); cardinal direction; and shading (grouped into the categories completely shaded, partly shaded, predominantly unshaded).

Aerial pictures

The study area was mapped with a UAV equipped with a multispectral camera system. For the purpose of detailed mapping, the following requirements were considered for flight planning. Based on local relief and flight restrictions a flight height of 80 m above ground level (AGL) was used and resulted in a geometric resolution of 7 cm ground sampling distance for the final orthomosaic. The used camera sensor system, a multispectral MicaSense RedEdge-MX Dual, was configured with a front and lateral overlap of 75% to successfully create the orthomosaic. As flight platform we used the quadcopter DJI Inspire 2 (<https://www.dji.com/de/inspire-2>). Flight route planning was done using DJI Pilot app on the remote controller with precompiled KML files of the target ground coverage. Sensor system details were saved to DJI Pilot app, flight route planning was automatically calculated and checked with the settings of the MicaSense RedEdge MX Dual web configuration concerning capture mode, front overlap and AGL.

The MicaSense camera system was chosen, because it simultaneously captures 10 spectral bands (with central wavelength in nm and band width in

brackets: Coastal blue 444(28), blue 475(32), green 531(14), green 560(27), red 650(16), red 668(14), red edge 705(10), red edge 717(12), red edge 740(18), NIR 842(57)). The arrangement of the spectral bands follows the well-known satellite platforms LANDSAT and Sentinel-2 and thus allows the calculation of several vegetation indices, which can be used by subsequent habitat suitability modelling on coarser scales, e.g. from local to regional or even national scale. To ensure data quality and usability before and after the flight, images of a spectral reference plate were recorded to consider the influence of radiation and changes during the flight when processing the data. Irradiance values were recorded during flight mission through the Downwelling Light Sensor of the sensor system (Mamaghani and Salvaggio 2019).

Based on the captured imagery, a digital surface model and a multispectral orthomosaic were calculated. Georeferencing was done using meta-data of imagery and manual referencing of prominent terrain points, which were equally spread across the study area. Thus, the resulting high resolution multispectral orthomosaic was exported as a GeoTIFF file with 10 bands for further processing in QGIS software. QGIS version 3.4.5 was used to prepare the data for habitat suitability modelling (HSM) and besides the multispectral orthomosaic, the commonly used vegetation index NDVI. A digital surface model (DSM) was exported from Agisoft Metashape Professional as GeoTIFF file and then was used to generate derived variables for the HSMs using QGIS. The variables aspect, topographic position index (TPI), terrain ruggedness index (TRI), and roughness (Wilson et al. 2007) were considered potentially relevant to describe the preferred habitat of the species. The TPI is calculated as the difference between the value of a cell and the mean value of its eight surrounding cells. The TRI is the mean of the absolute differences between the value of a cell and the value of its eight surrounding cells. Roughness is the maximum value of a cell and its eight surrounding cells minus the respective minimum value. Before calculating these variables, the resolution of the DSM was decreased, by building the mean of 20×20 pixels (1.4 m \times 1.4 m) in each horizontal and vertical direction. This way the variables captured topographical variation introduced by whole trees, shrubs, and similar, instead of single branches or even leaves. The resolution of all variables was subsequently rescaled such that one pixel represented

the mean of 5×5 pixels of the original resolution, which corresponds to pixel sizes of 35×35 cm.

Habitat suitability modelling

To avoid possible effects of inter-correlation, we calculated pairwise Pearson correlation coefficients among all variables. In case of $r > 0.7$ (Dormann et al. 2013), only the biologically putatively more relevant variables were used for modelling. Habitat suitability models were then inferred based on spectral bands 4 (green@560 nm) and 9 (red edge@740 nm), the NDVI, aspect, TPI, and roughness. We calculated ensemble models of habitat suitability with presence only data using the biomod2 package version 3.5.1 in R (Thuiller et al. 2013), using GAM, GBM, GLM, and the built-in Maxent algorithms. Eighty percent of the presence records were randomly chosen to build the models, while the remaining 20% were used for model evaluations by the relative operating curve (ROC). Three sets of 1000 pseudo-absences were generated using the disk-method and dis-allowing pseudo-absence points to be closer than 3 m to presence points. We ran three repeats for evaluation to make up 36 single models (three repeats \times four model algorithms \times three pseudo-absence sets). Variable importance was estimated in three permutations. biomod2 implements the evaluation strip method (Elith et al. 2005), which permits a direct comparison of predicted responses across all model algorithms used. All model predictions were scaled for better comparability. Single models were considered for the ensemble model if ROC scores were > 0.7 . Final ensemble models were calculated as weighted mean of single models, where weightings of single models were determined by the area under the receiver operator curve (ROC).

Results

In total we recorded 296 nests of *E. maturna*, which were distributed to 170 *F. excelsior* trees throughout the study area (Supplement Table S1). Most of them were exposed to the south, south-west, or south-east, at a mean height of 3 m (ranging from 1–8 m) (Fig. 1). The vast majority of nests was found at partly shaded branches, as opposed to fully shaded and fully exposed places (Fig. 2). Young trees smaller

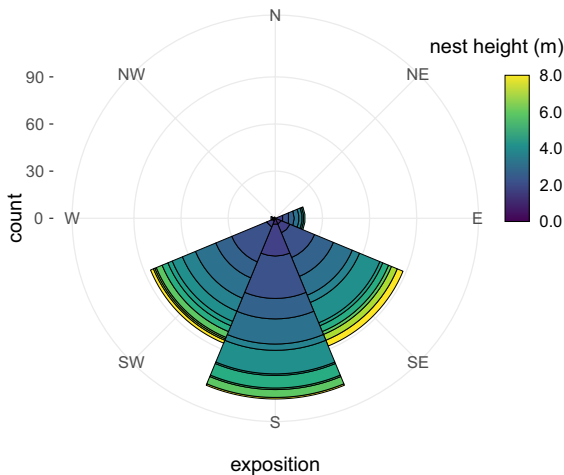


Fig. 1 Exposition and height of nests relative to host trees

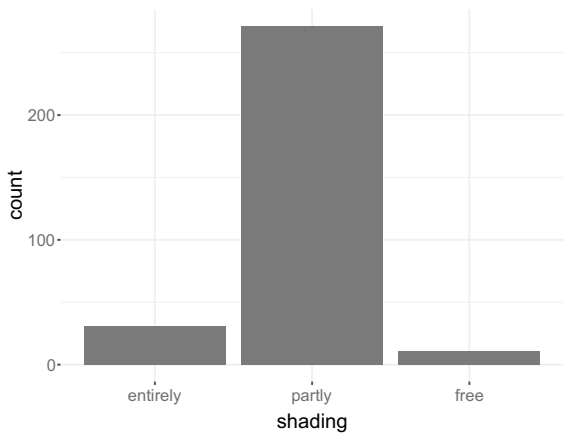


Fig. 2 Number of nests in entirely, partly, and unshaded locations

than 10 m in height were preferentially used for oviposition (Fig. 3). The habitat suitability model clearly favoured forest edges with southern, south-western, or south-eastern expositions, as suitable nesting-habitats, whereas it did not matter whether the edge was adjacent to the river or the surrounding meadows (Fig. 4). Likewise, somewhat isolated trees within the forest were determined to be suitable. The model thus well reflected the occurrences of caterpillar nests of *E. maturna* throughout the area, as also indicated by the evaluation metrics (Supplement Table S2). Topographical variables had the highest influence on the model according to the variable response plots

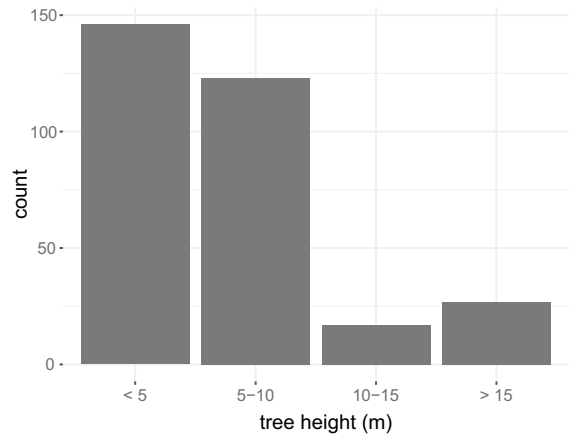


Fig. 3 Distribution of nests at trees of different height

(Fig. 5). Values around zero were favoured for the topographical position index (TPI), in combination with the aspect reflecting the favouring of trees with open space to the south, including forest edges. In the present case, high TPI values either indicate tree-tops that protrude from the surrounding terrain or such positions that are surrounded by higher trees (at a resolution of 1.4 m; see methods section), which were both modelled to be unsuitable. The model excluded flat regions like the river and surrounding meadows by the terrain roughness, which needed to be above five for 50% habitat suitability, meaning a minimum height difference of 5 m was needed within a square of 4.2×4.2 m (3×3 pixels á 1.4 m edge length). The mandatory tree species was likely incorporated in the model by the NDVI and the two spectral bands (Fig. 5).

Discussion

We found that topographical variables had the highest influence on the model according to the variable response plots. Values around zero were favoured for the topographical position index, in combination with the aspect reflecting the favouring of trees with open space to the south, including forest edges. This is also confirmed by the manually mapped information on oviposition sites of *E. maturna*, which are mainly restricted to sunny spots of deciduous forest mostly along forest edge habitats, such as close to the River Taugl, in the transition area between forest

Fig. 4 Study area and habitat suitability model. **a** Aerial photograph of the study site as taken by the UAV. Open circles indicate records of nests of *E. maturna* that were used to model habitat suitability. **b** Projection of the inferred habitat suitability model to the study area and **c** to an enlarged section from the centre of the area. Pixels with warmer colours at the southern margin of forest edges and more isolated trees indicate better condition for *E. maturna* as inferred by the model

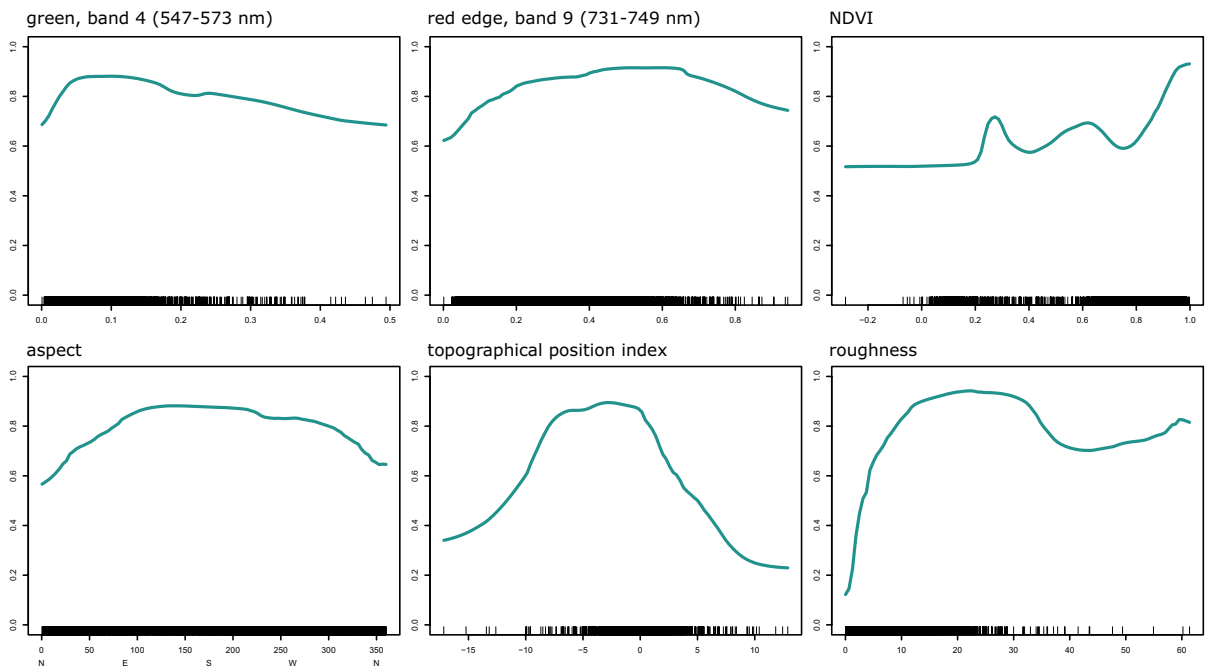
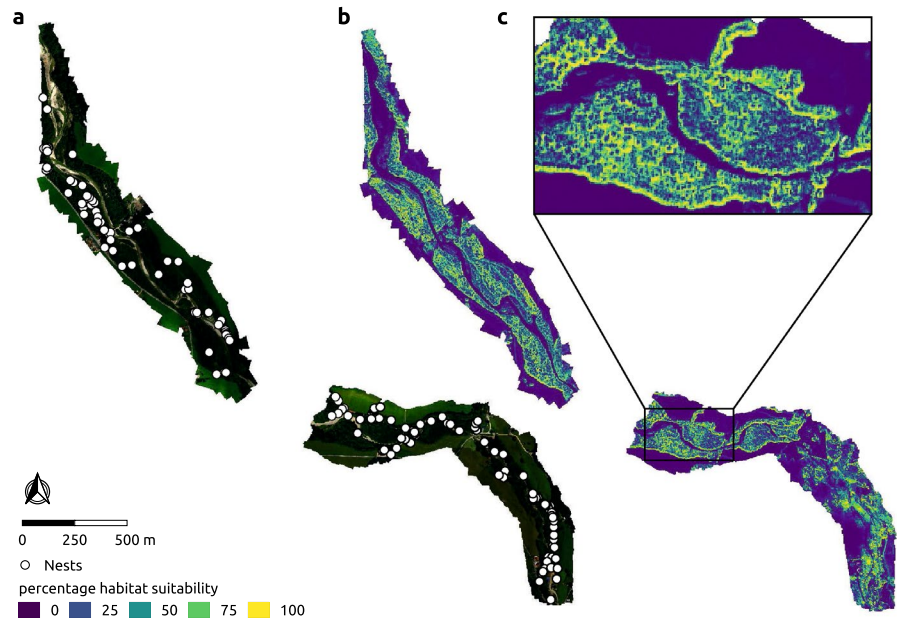


Fig. 5 Response plots of the ensemble model for all variables. Higher values indicate increased importance of the respective variable values for *E. maturna*. x-axes represent values in units of the original variables

and adjacent meadows and along forest roads, with heterogeneous and light vegetation structures. Our findings are in line with previous studies showing that nests of larvae of *E. maturna* are mainly in light

forest structures of early successional stage, along forest edges with smooth forest-openland ecotones (Gros 2002). Furthermore, our results underline that the accumulation of eggs and larvae concentrates at

spots being protected from the wind, such as forest clearings in the forest interior, or in indentations at the edge of the forest (see also Gros 2002). Due to the intensification in forestry, light, sparse, species-rich and structure-rich mixed deciduous forests become transformed into monocultures of trees. With the combination of very detailed data recorded manually in the field through observations and the larger scale ecosystem information recorded using UAV, it is possible to very precisely project detailed information onto the landscape and to identify areas of high conservation value (see Habel et al. 2016, 2019; Leitao & Santos 2019).

Apart of these ecosystem structures, further micro-habitat preconditions are of relevance for successful larval development of *E. maturna*. Our habitat suitability model clearly favoured forest edges with southern, south-western, or south-eastern exposures as suitable nesting habitats, whereas it did not matter whether the edge was adjacent to the river or the surrounding meadows. Also isolated trees within the forest, e.g. forest glades, were determined to be suitable. Our results using habitat suitability models (based on accurate aerial imagery) are consistent with previous studies that clearly state that egg oviposition of this butterfly species usually occurs at forest edges, or in sparse forest clearings, and is mostly in a southerly orientation (Gros 2002). This might be that eggs and subsequently larvae are exposed to the sun (already during morning), and thus warm up more quickly and thus there are higher rates of successful larval development (Gros 2002). In addition to sky orientation, there was also a clear preference of oviposition on medium height (mean height of 3 m) on *Fraxinus excelsior* trees (assessed manually in our study), which matches well with earlier observations in another *E. maturna* population in northern Austria (average 3.2 m, Gros 2002). At this height, there might exist a very specific microclimate, with presumably high levels of humidity (close proximity to the ground), but is in parallel well exposed to solar radiation (and thus high temperatures). In addition to ecosystem structures and microclimatic conditions, further behavioural factors may drive the accumulation of egg oviposition at specific sites. Studies found that females of *E. maturna* lay more eggs at sites that have already been visited by other females and where egg deposition has already occurred. Such a behaviour and subsequent mass ovipositions may reduce

parasitic pressure (Freese et al. 2006; Dolek et al. 2006, 2013).

According to our modelling results, oviposition mostly occurred along forest edges and forest roads. Such forest clearings are comparatively humid and frequently characterized by intense sun-exposure, and are at the same time comparatively windless (Weidemann 1985). Strong environmental dynamics create numerous early successional stages in ecosystems, and thus enable the growth of herbs and diverse flowering plants, shrubs and diverse pioneer tree species, as well as young *Fraxinus excelsior* trees, which is of high relevance for the successful larval development of *E. maturna* (Gros 2002). Sunny sites in the forest and a smooth transition of the forest into adjacent openland habitats are essential—not only for *E. maturna*, but for a large number of animal and plant species (Kozel et al. 2021). For example, numerous species depend on the combination of sunshine and a moist forest climate, or feed on and develop on herbs growing in open disturbance areas in or along the forest. Thus, the detected habitats for *E. maturna* development generally represent valuable structures for a variety of now rare animal and plant species (Vojta and Drhová 2012; Hartel et al. 2014). Prescribed forest grazing may be an efficient management strategy to promote forest biodiversity adapted to light, moist heterogeneous deciduous forests.

Conclusion

Our study supports the relevance of sparse deciduous forests that provide valuable moist and sunny habitats through moderate disturbance (Kirby et al. 1995). The identification of such valuable ecosystems and specific ecosystem structures and its projection across landscapes is possible using high-resolution aerial imagery and modelling approaches (Perepenova and Skalos 2019). The high resolution of recent camera systems (e.g., submeter resolution) already makes it possible to determine not only vegetation composition (distinguishing among plant species), but also study accurate vegetation topographies and structural diversity for forests and landscapes (Marvin et al. 2016; Librán-Embida et al. 2020). Nevertheless, the investigation of details on the occurrence, ecology and behaviour of species is essential to provide the basis for the calculation of the models, and

to correctly interpret the results derived from habitat suitability models.

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Declarations

Conflict of interest The authors have not disclosed any competing interests.

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