



The relevance of transition habitats for butterfly conservation

Jan Christian Habel¹ · Viktoria Angerer¹ · Patrick Gros² · Mike Teucher³ · Jonas Eberle¹

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Abstract

Biodiversity is declining across the globe. Main drivers causing the vanishing of species are habitat destruction and the transformation of former heterogeneous landscapes into homogeneous and intensively used landscapes. Modern land management focuses on the creation of landscape configuration with sharp boundaries between ecosystems. In consequence, transition zones between two ecosystems such as between forest and open grassland are rare, as it counteracts the efficient and commercial use of space. However, there are many species relying on such transition zones between habitats, as the Clouded Apollo butterfly *Parnassius mnemosyne*. This highly endangered butterfly species occurs in light deciduous forests, interspersed with extensively used grasslands. In our study, we analysed habitat requirements of this butterfly species. We recorded larvae and feeding marks at its primary larval food plant, *Corydalis cava*, and assessed microhabitat characteristics, including microclimatic conditions. We captured high-resolution multispectral aerial imagery with an unmanned aerial vehicle. We subsequently combined ground-truthing data with information from high resolution aerial pictures to calculate habitat suitability models. We found that *P. mnemosyne* larvae mainly occur in the transition zone between deciduous light forest and extensively used grasslands with *C. cava*. Caterpillars of *P. mnemosyne* are particularly found around trees, basking on foliage and grass to rapidly reach high operation temperatures. Results from Species Distribution Models underline the relevance of transition zones between habitats for *P. mnemosyne*, and for biodiversity in general. The Clouded Apollo may serve as excellent indicator species for light deciduous forests, and as flagship to promote the conservation and restoration of transition zones between habitats in nature conservation.

Keywords Transition zone · Forest · Grassland · *Parnassius mnemosyne* · Microhabitat structures · Microclimate · Unmanned aerial vehicle · Species Distribution Model

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✉ Jan Christian Habel
Janchristian.habel@plus.ac.at

Extended author information available on the last page of the article

Introduction

The Anthropocene is characterized by a dramatic decline of biodiversity (Maxwell et al. 2016). Recent studies have shown that, especially since the industrialization of agriculture, there has been a severe decline in species diversity and abundance (Emmerson et al. 2016). This has recently been particularly evident for insects, which have declined severely in diversity and abundance over the last few decades (Wagner et al. 2021). This decline in insect diversity also affects other organisms at higher trophic level, such as insectivorous birds (Hallmann et al. 2014). In addition, declining insect diversity causes a deterioration of ecosystem functions, of which some are of key relevance to humans, in particular in respect to agricultural production (Klein et al. 2007).

Agricultural intensification have caused the destruction of numerous natural and semi-natural habitats, and diminished habitat quality, due to supra-regional influx of various substances, such as nitrogen (Pe´er et al. 2014) and pesticides (Zaller and Brühl 2019). This negatively affects habitat availability and habitat quality, and subsequently biodiversity. In addition, the configuration of entire landscapes have changed significantly during the past decades (Batáry et al. 2017); Heterogeneous landscapes were often transformed into homogenous ones, which can be efficiently cultivated with large agricultural machinery. As a result, transition zones between habitats have largely vanished from our landscapes. However, such transition zones provide home for a large number of taxa, including various highly specialized species, which are on the need of both habitats, including the transition zone itself (see Endler 1980; Smith et al. 2001).

Species, which require more than one habitat type, suffer particularly under current landscape homogenization. For example, most butterflies are on the need for very specific microhabitat structures, larval food plants and further resources (e.g. ant species, Thomas et al. 1989) for successful development of larvae, and for the existence of the imagoes (Dennis et al. 2003). However, habitats of the two developmental stages (larvae and adult) frequently differ considerably (Hekkinen et al. 2005). Therefore, efficient butterfly conservation needs to include the entire life cycle (Radchuk et al. 2013). As many butterflies show a rather restricted movement behaviour (but not all butterflies in general, see De Ro et al. 2021), specific habitat structures and resources should occur in close geographic proximity. Examples include butterfly species that require the microclimate of a forest, but also microhabitat opportunities for warming up in the sun, and profiting from nectar sources of neighbouring grasslands (Kudrna and Seufert 1991; Hekkinen et al. 2005). Studies on the larval ecology of butterflies have shown that for numerous species, the presence of a species-specific larval food plant is far from being sufficient for successful species development. Studies showed that further and important demands are specific microclimatic conditions, availability of litter, bare soil, or a specific vegetation structure (e.g. density and height) (Habel et al. 2016).

To better understand the relevance of transition zones between habitats for butterfly, and biodiversity conservation in general, we studied the larval ecology of the Clouded Apollo butterfly *Parnassius mnemosyne*. This butterfly species inhabits sparse deciduous forests and forest edges interwoven with extensively used grasslands (Kudrna and Seufert 1991; Konvicka and Kuras 1999; Nunner and Seufert 2013; Maes et al. 2014; Dickens et al. 2019). This large, iconic and charismatic butterfly species stands at the forefront of the conservation of the transition zones between two ecosystems—forest and open grasslands. For this butterfly species we assessed the occurrence of the larvae and species´ specific feeding marks, as well as microhabitat conditions along the forest edge (integrating forest interior,

forest fringe, and open grassland). We integrated microclimatic conditions assessed with iButton temperature loggers. We combined these acquired ground data with high-resolution aerial images, captured with an unmanned aerial vehicle (UAV). The application of this new technique allows us to calculate Species Distribution Models identifying relevant explanatory variables for the occurrence of larvae, and thus for successful development of *P. mnemosyne*. With the combination of these various techniques (including UAV), we integrate the micro- and landscape scales (Habel et al. 2016; Mukhamediev et al. 2021; Sun et al. 2021). Based on the obtained results, we will elaborate on the following research questions:

1. Which microhabitat structures are preferred for egg oviposition and by larvae of *P. mnemosyne*?
2. What habitat and landscape structures are preferred by *P. mnemosyne* during the larval stage?
3. Which conclusions can we derive from our findings for practical nature conservation?

Materials and methods

Study species

Parnassius mnemosyne, the Clouded Apollo, is a comparatively large butterfly (55–65 mm wing span), mainly found in montane to subalpine grassland-forest mosaics across the Palaearctic region (Tolman 2009). Its global distribution extends from disjunct areas in Western Europe (e.g. Pyrenees and Massif Central) to the Caucasus, parts of the Near East to central Ural and the Tian Shan region (Tolman 2009). In the area north of the Alps, this butterfly is on the wing from about mid-May until July, and hibernates as developed caterpillar in the egg (Ebert and Rennwald 1993). The larvae hatch in early spring and feed mainly on species of the herbs *Corydalis* (lark spur) as *C. intermedia* and *C. cava* (Ebert and Rennwald 1993). Larvae can frequently be observed while basking in the sun on foliage, mainly dead dry leaves, to increase their body temperature (Välimäki and Itämies 2005). This behaviour accelerates development speed (but might also increase the exposure to predation and thus predation rates) (Välimäki and Itämies 2005). Typical habitats of *P. mnemosyne* are extensively used grasslands (pastures with low stocking, meadows with mowing once a year, Konvicka and Kuras 1999) being in contact with light deciduous and mixed forests and single groups of trees and shrubs (Konvicka and Kuras 1999; Luoto et al. 2001; Bergström 2005; Kuusemets et al. 2005; Bolotoy et al. 2013; Kask 2015; Szigeti et al. 2015). The main threats that have led to the decline of this butterfly species are agricultural intensification, land consolidation and landscape clearing (van Swaay and Warren 1999). This caused the destruction of numerous heterogeneous transition zones between habitats over the past decades (Konvicka and Kuras 1999). In the meanwhile, this butterfly species can be found on various regional, national and international red lists (Huemer et al. 2022; van Swaay et al. 2012). For successful preservation of the Clouded Apollo, the conservation of structurally rich forest edges with extensive fringe sites as well as clearings and sparse forests with lark spur occurrences is essential (Sebek et al. 2013; Kuussaari et al. 2015; Westin et al. 2018; Cini et al. 2020). In addition, adults require flowering, nectar-rich grasslands growing close to its larval habitat. The creation of such a habitat mosaic can usually only be ensured by targeted management measures, such as extensive grazing

and alpine pasture management, and adapted forestry with spatially limited clear-cutting (Trusch 2005; Cini et al. 2020). These management strategies are covered by EU conservation guidelines, and favour many other (endangered) species (van Swaay et al. 2012).

Study area and data collection

Our study area is located about 15 km east of Salzburg city, Austria, close to Lake Fuschl. This habitat is comparatively small (< 1 ha) and consists of an extensively used grassland (mown once a year in late summer, no fertilizers and pesticides), with stands of single trees, bordering a light deciduous forest (Fig. 2A). Plants of the genus *Corydalis* grow in high density across the grassland. The transition zone is indicated in yellow, the forest in blue (remark that the second small forest patch in the south consists of only some few single trees, and thus does not create a typical transition zone between forest and open grassland). The transition zone in our study area consist of a variety of small (young) trees and shrubs, e.g. *Corylus avellana*.

During spring 2021, we studied the presence of *P. mnemosyne* larvae for $1 \times 1 \text{ m}^2$ study plots equally distributed across the three habitat types (deciduous forest, transition zone between forest and grassland, grassland). These study plots (in total 183) were set with minimum distances among single plots of about 4 m (mean distance 4.36 m). Multiple occurrences of larvae or feeding traces were counted as a single presence per plot. This study set-up was selected to minimize potential effects from autocorrelation on models and cross-validation approaches (Dormann et al. 2007). Each study plot was located with a high precision GPS device (Geoexplorer 6000 series, Trimble). The points measured with this GPS device represent the centre of the respective study plot. For each of these study plots we recorded the following details: Date, time and habitat type (classified into forest, transition zone, grassland). We recorded caterpillars of *P. mnemosyne*, and typical feeding marks from caterpillars of *P. mnemosyne*. The patterns of feeding marks of caterpillars from this butterfly species are species-specific and very easy to recognize, and to distinguish from feeding marks of other organisms (such as snails). We only considered the presence/absence of feeding marks, but did not incorporate the number of feeding marks per plant individual (because it is not possible to make further statements about the number of caterpillars, because several feeding traces can come from one and the same caterpillar). We measured the distance of each study plot to the next tree/shrub (in cm). We assessed the following microhabitat parameters for each study plot (measured for 1 m^2 study plots): Distribution of *Corydalis* plants (very loose, loose, regular, clumped, and very clumped, coded as 0, 1, 2, 3, 4 and 5, respectively), proportion of bare soil (rounded to 5%, 10%, 20%, 30%, 40%, 50%, and 60%), proportion of moss cover (rounded to 0%, 10%, 40%, and 70%), depths of litter (rounded to 0 cm, 1 cm, 3 cm, 10 cm), and kind of litter (dead grass, dead grass with foliage, foliage, coded as 0, 1, and 2). These data were collected once towards the end of the larval development phase (24.4.–1.6.2021). In addition to the assessment of caterpillars, feeding marks, and microhabitat structures, we measured microclimatic conditions with the iButton temperature and humidity logger (model DS1923-F5). These very compact data loggers were deployed in small housings to minimize potential artefacts from external radiation. These external housings were attached to wooden sticks, so that they were freely swinging about 2 to 5 cm above the ground. Data were collected every 10 min over a period of two weeks, from May 4th to May 18th 2021. Data from iButtons were combined by spatial kriging using packages *fields* (version 12.5, Nychka et al. 2017)

and *raster* version 3.4-5 (Hijmans 2021) for R 4.0.2 (R Core Team 2020). Resolution and extent were chosen according to the UAV-data as described below.

Drone-based habitat assessment

The study area was mapped with an UAV in combination with a multispectral camera system. Based on local relief and restrictions a flight altitude of 80 m was used and in combination with the used camera sensor resulted in a geometric resolution of the final orthomosaic of 7 cm ground sampling distance. A precise flight path was not programmed, as the study area was manageable and could therefore be flown manually. The camera sensor system, a Micasense RedEdge-MX Dual, was configured with a forward and lateral overlap of 75% to successfully create the orthomosaic. As the carrying platform we used a DJI Inspire 2 (<https://www.dji.com/de/inspire-2>), which is a multirotor copter.

The Micasense camera system was chosen, because it simultaneously captures 10 spectral bands (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. Here we used the NDVI—Normalized Difference Vegetation Index (Rouse et al. 1974). To ensure data quality and usability before and after the flight, images of a spectral reference plate were recorded in order to be able to consider the influence of radiation and radiation changes during the flight when processing the data. In total 3350 10-band images were acquired.

Processing was conducted using the software Agisoft Metashape Professional version 1.7.3. Based on the captured imagery, a digital surface model and a multispectral orthomosaic were calculated. Georeferencing was done using the high precision GPS data of the individual study plots, 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, and a digital surface model (DSM) was calculated. The DSM was used to generate a variable for the HSMs that described the slope in the study area, which was considered potentially relevant in terms of water drainage. We refrained from using the typically calculated variables aspect, topographic position index (TPI), terrain ruggedness index (TRI), and roughness, since they were indifferent for the studied area and would have over-parameterised the model.

Since transition zones between forest and grassland were hypothesized to determine habitat quality for *P. mnemosyne* larvae, we marked each tree in the study area in QGIS. The resulting points were saved as a shape file and converted to raster format using the *raster* package version 3.4-5 for R 4.0.2 so that the position of each tree was represented by one pixel with value 0. Two variables describing tree configurations were calculated based on this layer: 1. A distance-to-tree variable was created by assigning all pixels that did not represent trees the value of the distance to the nearest tree in meters, using the *distance*-function in the *raster* package; 2. A tree-density variable was calculated using the *sp.kde*-function in the R-package *spatialEco* version 1.3-7 by estimating the unweighted Gaussian kernel density.

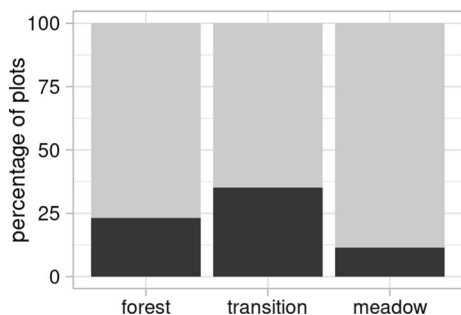
Habitat suitability modelling

To avoid possible negative effects of inter-correlation, we calculated pairwise Pearson correlation coefficients among all variables. In case of $r^2 > 0.75$, biologically putatively more relevant variables were preferred. Habitat suitability models were then inferred based on spectral bands 4 and 8, the NDVI, slope, distance-from-trees, tree-density, mean and standard deviation of temperature and humidity, host plant density, raw soil proportion, litter depth, and litter type. Presence and absence data were taken from the plots, counting the presence of larvae and feeding marks as presences. We calculated ensemble models of habitat suitability with the *biomod2* package version 3.5.1 in R (Thuiller et al. 2013), using two commonly applied regression based approaches (generalized linear models, GLM and generalised additive models, GAM, which allow for more complex response curves), a generalized boosting model (=boosted regression trees; GBM), and built-in maximum entropy (Maxent) algorithms. Different models might predict habitat suitability better under certain conditions. The idea of ensemble modelling is, to merge a range of models with different statistical properties, weighing individual models based on their fit to the data. Eighty percent of the presence/absence records were randomly chosen to build the models, while the remaining 20% were used for model evaluations by the relative operating characteristic (ROC). We ran three repeats for evaluation to make up twelve single models (three repeats $\times$ four model algorithms). 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 mean, median, and weighted mean of single models, where weightings of single models were determined by the area under the receiver operator curve.

Results

During the observation period (24.4.2021–1.6.2021) we recorded five plots with larvae and 43 plots with species specific feeding marks in a total of 179 plots (56, 71, and 52, in forest, transition, and meadow, respectively). All larvae were observed while feeding on *Corydalis cava* at the northern margin of the transition zone and at the light edge of the adjoining forest. Feeding marks were found in all habitat types, but predominantly in the transition zone between forest and grassland (ca 57%) (Figs. 1–2).

Fig. 1 Distribution of *P. mne-mosyne* records among habitat categories. Dark grey portions of bars are percentages of plots in the respective habitats category where either larvae or feeding traces were recorded, light grey portions indicate plots without records



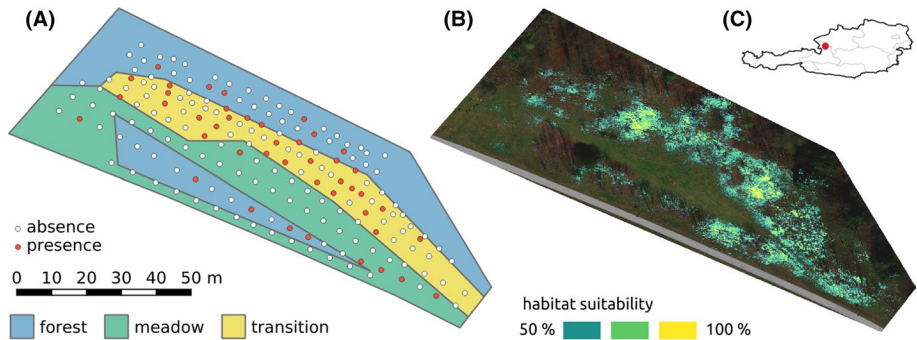


Fig. 2 Study site and habitat suitability model. **A** Orthophoto of the study site captured by the UAV, overlaid by sampled plots with and without records of larvae and habitat types. **B** Median ensemble habitat suitability model for *P. mnemosyne*. Areas with suitability below 50% are not shown

The caterpillars were found feeding on the forage plants as well as hiding deep in the litter. Some caterpillars were found in the litter, 30 cm beyond the next food plant. Small caterpillars (10–20 mm) moved increasingly over longer distances (up to 30 cm) from their food plants, while large caterpillars (40 mm) were observed exclusively feeding on food plants. Even when disturbed, these animals did not stop feeding or immediately started feeding again. Caterpillars in the early stages of their development (about 1–2 cm in size) moved very quickly when startled. Larger caterpillars (ca. 3–4 cm) continued to feed despite disturbance. The caterpillars are very sedentary, and mostly remained on the same plant for several hours and over days, or occurred within a very restricted radius (about 10–20 cm radius). Most caterpillars were found in the immediate vicinity of a tree. Caterpillar's feeding and activity period depends on sunny weather. Active caterpillars could be observed from about 12:30 pm, and then until early evening (until about 5:30 pm).

Habitat suitability models (HSMs) matched our field observations well. Sensitivity and specificity were 84.09 and 83.70, respectively, for the median ensemble model (mean: 90.91 and 80.00, weighted mean 90.91 and 81.48, respectively) (Supplement Table 2). The transition zone between the forest at the northern margin of the study area and the central grassland was inferred to harbour the most suitable microhabitat for *P. mnemosyne* larvae. Most relevant variables for larval habitat were identified to be host plant density, the NDVI, and distance from the nearest tree, while climate, microhabitat, and terrain variables played a minor role for the model (Table 1).

Host plant density was estimated to be a crucial factor for larval development with proportional increase in habitat suitability with increasing plant density (Fig. 3). However, neither feeding marks nor larvae were found in strongly clumped plots, which was reflected by a drop in the response curve. Also higher proportions of bare soil were predicted to be beneficial for larvae. Potentially linked with host plant density, although not strongly correlated, increasing NDVI values clearly indicated higher occurrence probabilities. The third of the most conspicuous response curves was found for the distance from trees variable (Fig. 3). Here, highest probabilities for the occurrence of larvae was predicted in close proximity to trees. At distances greater than about four meters, occurrence probabilities nearly ceased. On the other hand, high tree densities as they occurred inside the forest patches were predicted to be unsuitable, indicating the importance of transition zones for *P. mnemosyne*. Further notable predictions were that steep slopes seem to be less suited and

Table 1 Summarized variable importance from twelve single models. Given are values of mean, median and standard deviation

Variable	Mean	Median	SD
Plant_density	0.27	0.24	0.21
NDVI	0.22	0.19	0.14
Distance from nearest tree	0.20	0.14	0.20
Spectral band 9 (726–754 nm)	0.13	0.07	0.13
Slope	0.12	0.08	0.11
Litter type	0.10	0.06	0.12
Raw soil	0.10	0.03	0.15
Tree density	0.09	0.05	0.11
Spectral band 4 (546.5–573.5 nm)	0.09	0.02	0.16
Mean humidity	0.08	0.02	0.14
Litter depth	0.07	0.03	0.09
Standard deviation of humidity	0.05	0.00	0.10
Mean temperature	0.04	0.01	0.07
Standard deviation of temperature	0.03	0.00	0.08

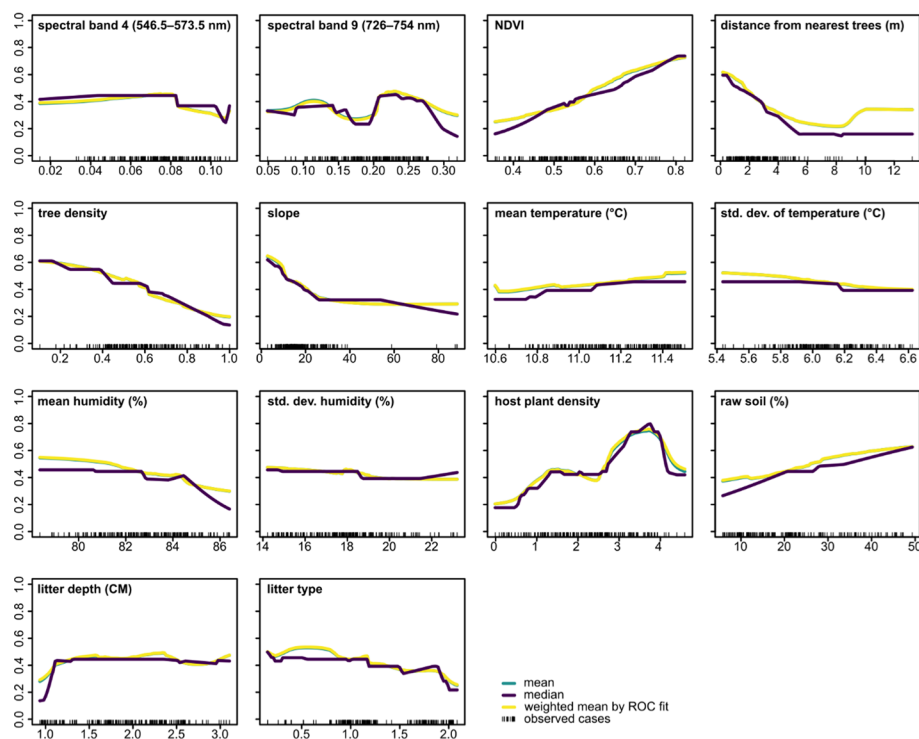


Fig. 3 Evaluation strip response plots of all variables based on mean, median, and weighted mean ensemble models. Y-axes show probability of the species' occurrence. X-axes show variable values in the respective units

that a certain amount of litter seems to be needed by the larvae. The latter corresponds with our field observation that no larvae or feeding marks were found in plots without litter. The preferred litter type seemed to be dead grass.

Discussion

Our results show that, in our study area, the presence of *P. mnemosyne* larvae strongly depends on the abundance of its larval food plant *Corydalis cava*. The occurrence of this plant species correlates with the presence of solitary trees. This might be due to specific mesoclimatic conditions created through the shadowing from the leaves of the tree. And, in addition, these spots were characterized by comparatively dense vegetation. Increasing distance from the trees negatively impacts the occurrence of larvae. We found that the occurrence of larvae depend on a moderate layer of litter, consisting of old grass and foliage, which frequently build up in the transition zone between forest and grassland. This habitat structure was mainly found in the transition zone between forest and grassland. Here, about 30% of all plants studied had feeding marks, about 57% of all feeding marks, and all larvae found were restricted to this transition zone between forest and grassland. Our results clearly demonstrate the relevance of transition zones for *P. mnemosyne*. In this transition zone there is light shade conditions and leaves i.e. foliage, as well as further microhabitat structures such as old grass with foliage and specific microclimatic conditions suitable to this endangered butterfly species.

The transition zone between creates a mosaic consisting of various habitats and ecological niches, and provides a large variety of different conditions in respect of solar radiation (light), temperature and humidity, if compared with pure forest stands and the adjoining grassland. Thus, transition zones are characterized by very specific climatic conditions, which subsequently impacts plant species community (König 2014), and provides unique microhabitat structures (Bollmann et al. 2009). Various studies showed that biodiversity is particularly high in transition zones (Hendry et al. 2000; Korol et al. 2000; Schluter 2000; Schilthuizen 2000).

We found high numbers of individuals of *C. cava* in the transition zone, and only few in the adjacent forest or grassland. Foliage increases with topographic proximity to trees, and obviously the climate with appropriate soil and air humidity due to the shading in the transition zone, near trees, seems to be the precondition for optimal growth of *C. cava*, as well as for the development of the larvae of *P. mnemosyne*. Spatial structure and the surrounding microclimate play a critical role in the oviposition and subsequent larval development for numerous butterfly species (Fartmann and Hermann 2006). Studies showed that most butterfly larvae prefer warm to hot larval habitats with low vegetation height and density, in order to develop as quickly as possible, as documented for the butterfly species *Phengaris (Maculinea) arion*, *Hesperia comma*, *Chazara briseis*, *Lycaena alciphron*, *Melitaea didyma*, *Parnassius apollo* (Fartmann and Hermann 2006) and other Lycaenid butterflies (Habel et al. 2016). It seems to be of key relevance for the caterpillars of *P. mnemosyne* to find sites with different levels of sunlight, with surface temperatures between 35 and 40 °C (Arbeitsgemeinschaft Bayerischer Entomologen 2013). Such microhabitat preconditions guarantees fast larval development and a reduced potential fungation of larvae. The creation of such microhabitat structures frequently rely on ongoing disturbances (Fartmann and Hermann 2006).

However, not all butterfly larvae prefer high solar radiation. For example, butterflies from calcareous grasslands are even at risk of desiccation due to excessive solar insolation. Similar behaviour as *P. mnemosyne* can also be observed for butterflies living in mesophilic grasslands and ruderal stands with comparatively high herb layer as well as a certain amount of litter (well-developed moss or litter layer), such as *Erebia medusa* or *Hamearis lucina*. These species are also frequently found close to forest edges with high humidity produced by appropriate shading, but at the same time high temperatures (Fartmann and Hermann 2006). However, there are also species like *Euphydryas maturna* that prefer younger and medium old middle forests with high humidity, but in parallel also with high temperatures as larval habitat (Fartmann and Hermann 2006). Dependence on the occurrence of the appropriate larval food plant obviously plays a corresponding role in the selection of suitable larval habitats, in combination with specific microhabitat structures and microclimatic conditions (Stuhldreher and Fartmann 2018).

Our study underlines the relevance of an interplay of various factors: 1. The occurrence of the larval food plant, 2. Specific microhabitat structures, and 3. Appropriate microclimatic conditions. In addition, there is also a generally montane climate, not too dry, that makes this butterfly a species of the higher regions, at least in major regions around the Alps. We found that, *C. cava* in high densities, the existence of individual trees (and subsequently light shadow and leaves i.e. foliage), and the existence of a layer of litter consisting of fallen leaves and dead grass might produce different microclimatic niches, and provide a suitable habitat for this butterfly species. Due to these very specific environmental requirements, we argue that *P. mnemosyne* underlines the relevance of transition zones between two habitat types, as already indicated for our study species (Konvicka et al. 2006) and other taxa (Simberloff 1998; Peyras et al. 2013; Lindenmayer and Westgate 2020). Furthermore, this species might act as umbrella for a large number of other specialized and endangered species being restricted to the light and moist conditions of forest-grassland-transitions (see also Dulli 2002; Spörri 2014), at least for our study region, and major parts around the Alps. It must be kept in mind that this study is representative of only a limited area, and the data were collected over a single larval phase. Nevertheless, it can be assumed that the found correlations and trends are of general validity.

In this study we bring together different spatial scales, the micro-habitat scale with the landscape level. This was only made possible by the acquisition of high-resolution aerial images, and the use of UAVs. The benefits of this combination of different spatial scales, and the resulting added value for ecology and nature conservation have been demonstrated in some, initial studies in recent years (Habel et al. 2016; de Vries et al. 2021). Nature conservation should pay more attention to transition zones between different habitats (Spörri 2014), as there exist hardly any such transition zones between different habitats. In potentially settable regions, abrupt forest edges should be partially thinned, artificially planted trees as spruce trees removed and replaced by natural, sparse deciduous forest structures with open tree seams and single trees in the directly adjacent open land, which should be managed gently enough to enable the use of resources and other structures needed by the imagoes (Grosser 2004; Trusch and Hafner 2005). Mowing under the trees should only occur sporadically at intervals of several years to encourage, rather than destroy, the accumulation of litter from old grass and fallen leaves. This would create a mosaic of habitats enabling settlement for a variety of organisms (Grosser 2004; Trusch and Hafner 2005).

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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References

- Batáry P, Gallé R, Riesch F, Fischer C, Dormann CF, Mußhoff O, Császár P, Fusaro S, Gayer C, Happe A-K, Kurucz K, Molnár D, Rösch V, Wietzke A, Tschamtké T (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nat Ecol Evol* 1:1279–1284. <https://doi.org/10.1038/s41559-017-0272-x>
- Bergström A (2005) Oviposition site preferences of the threatened butterfly *Parnassius mnemosyne* ? implications for conservation. *J Insect Conserv* 9:21–27. <https://doi.org/10.1007/s10841-004-3204-4>
- Bollmann K, Bergamini A, Senn-Irlet B, Nobis M, Duelli P, Scheidegger C (2009) Konzepte, Instrumente und Herausforderungen bei der Förderung der Biodiversität im Wald. *Schweizerische Zeitschrift für Forstwesen* 160:53–67
- Bolotov IN, Gofarov MY, Rykov AM, Frolov AA, Kogut YE (2013) Northern boundary of the range of the Clouded Apollo butterfly *Parnassius mnemosyne* (L.) (Papilionidae): climate influence or degradation of larval host plants. *Nota Lep* 36:19–33
- Cini A, Barbero F, Bonelli S, Bruschini C, Casacci LP, Piazzini S, Scalercio S (2020) The decline of the charismatic *Parnassius mnemosyne* (L.) (Lepidoptera: Papilionidae) in a Central Italy national park: a call for urgent actions. *J Insect Biodivers* 16:47–54. <https://doi.org/10.12976/jib/2020.16.2.2>
- De Ro A, Vanden Broeck A, Verschaeye L, Jacobs I, T'Jolyn F, Van Dyck H, Maes D (2021) Occasional long-distance dispersal may not prevent inbreeding in a threatened butterfly. *BMC Ecol Evol* 21:1–12
- de Vries JPR, Koma Z, WallisDeVries MF, Kisslin WD (2021) Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. *Divers Distrib* 27:1251–1264
- Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* 102:417–426
- Dickens JK, McMahon L, Binnie SE (2019) The butterflies of a Cerrado-Atlantic Forest ecotone at Laguna Blanca reveal underestimation of Paraguayan butterfly diversity and need for conservation. *J Insect Conserv* 23:707–728
- Dormann CF, McPherson M et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Duelli P, Obrist MK, Flückiger PF (2002) Forest edges are biodiversity hotspots—also for Neuroptera. *Acta Zool Acad Sci Hung* 48:75–87
- Ebert G, Rennwald E (eds) (1993) *Die Schmetterlinge Baden-Württembergs*. E. Ulmer, Stuttgart

- Elith J, Ferrier S, Huettmann F, Leathwick J (2005) The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. *Ecol Model* 186:280–289. <https://doi.org/10.1016/j.ecolmodel.2004.12.007>
- Emmerson M, Morales MB, Oñate JJ, Batáry P, Berendse F, Liira J, Aavik T, Guerrero I, Bommarco R, Eggers S, Pärt T, Tscharrntke T, Weisser W, Clement L, Bengtsson J (2016) Chapter two - how agricultural intensification affects biodiversity and ecosystem services. *Adv Ecol Res* 55:43–97
- Endler JA (1980) Geographic variation, speciation, and clines, 2. print., with corr. Princeton Univ. Press, Princeton
- Fartmann T, Hermann G (2006) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa – von den Anfängen bis heute. In: *Fartmann T, Hermann G (eds) Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. Abhandlungen aus dem Westfälischen Museum für Naturkunde*, pp 11–57
- Grosser N (2004) *Parnassius mnemosyne* (Linnaeus, 1758) – Schwarzapollo. Die Tier- und Pflanzenarten nach Anhang IV der Fauna-Flora-Habitat-Richtlinien im Land Sachsen-Anhalt. In: *Naturschutz im Land Sachsen-Anhalt, Sonderheft*, pp 9–12
- Habel JC, Teucher M, Ulrich W, Bauer M, Rödder D (2016) Drones for butterfly conservation: larval habitat assessment with an unmanned aerial vehicle. *Landsc Ecol* 31:2385–2395. <https://doi.org/10.1007/s10980-016-0409-3>
- Hallmann CA, Foppen RPB, van Turnhout CAM, de Kroon H, Jongejans E (2014) Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511:341–343. <https://doi.org/10.1038/nature13531>
- Heikkinen RK, Luoto M, Kuussaari M, Pöyry J (2005) New insights into butterfly–environment relationships using partitioning methods. *Proc R Soc B* 272:2203–2210. <https://doi.org/10.1098/rspb.2005.3212>
- Hendry AP (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–518. <https://doi.org/10.1126/science.290.5491.516>
- Hijmans RJ (2021) raster: Geographic data analysis and modeling. Version R package version 3.4-13. <https://CRAN.R-project.org/package=raster>
- Huemer P, Rüdiger J, Hiermann U, Lechner K, Mayr T, Ortner A, Friebe JG (2022) Rote Liste gefährdeter Schmetterlinge Vorarlbergs (Neubearbeitung) – Rote Listen Vorarlbergs 11: 210 S, Dornbirn (inatura)
- Kask K (2015) Distribution and habitat preferences of the Clouded Apollo butterfly (*Parnassius mnemosyne*) in Estonia. Tartu, PhD Thesis
- Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharrntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proc R Soc B* 274:303–313. <https://doi.org/10.1098/rspb.2006.3721>
- König S (2014) Der blühende Waldrand. In: *Bodensee Akademie (ed) Netzwerk blühendes Vorarlberg*
- Konvicka M, Kuras T (1999) Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelské Pomoraví L. Czech Republic. *J Insect Conserv* 3:211–223
- Konvicka M, Vlasanek P, Hauck D (2006) Absence of forest mantles creates ecological traps for *Parnassius mnemosyne* (Papilionidae). *Nota Lep* 29:145–152
- Korol A, Rashkovetsky E, Iliadi K, Michalak P, Ronin Y, Nevo E (2000) Nonrandom mating in *Drosophila melanogaster* laboratory populations derived from closely adjacent ecologically contrasting slopes at “Evolution Canyon.” *Proc Nat Acad Sci* 97:12637–12642. <https://doi.org/10.1073/pnas.220041397>
- Kudrna O, Seufert W (1991) Ökologie und Schutz von *Parnassius mnemosyne*. *Oedippus* 2:1–44
- Kuusemets V, Meier K, Luig J, Liivamägi A (2005) Habitat and landscape structure requirements of Clouded Apollo (*Parnassius mnemosyne*). Studies on the ecology and conservation of butterflies in Europe. In: *Kühn E, Feldmann R, Thomas JA, Settele J (eds) Studies on the ecology and conservation of butterflies in Europe, vol 1*, pp 18–21
- Kuussaari M, Heikkinen RK, Heilölä J, Luoto M, Mayer M, Rytteri S, von Bagh P (2015) Successful translocation of the threatened Clouded Apollo butterfly (*Parnassius mnemosyne*) and metapopulation establishment in southern Finland. *Biol Conserv* 190:51–59
- Lindenmayer DB, Westgate MJ (2020) Are flagship, umbrella and keystone species useful surrogates to understand the consequences of landscape change? *Curr Landsc Ecol Rep* 5:76–84. <https://doi.org/10.1007/s40823-020-00052-x>
- Luoto M, Kuussaari M, Rita H, Salminen J, von Bonsdorff T (2001) Determinants of distribution and abundance in the clouded apollo butterfly: a landscape ecological approach. *Ecography* 24:601–617. <https://doi.org/10.1034/j.1600-0587.2001.d01-215.x>
- Maes D, Jacobs I, Segers N, Vanreusel W, Van Daele T, Laurijssens G, Van Dyck H (2014) A resource-based conservation approach for an endangered ecotone species. *J Insect Conserv* 18:939–950

- Maxwell SL, Fuller RA, Brooks TM, Watson JEM (2016) Biodiversity: the ravages of guns, nets and bulldozers. *Nature* 536:143–145. <https://doi.org/10.1038/536143a>
- Mukhamediev RI et al (2021) Review of some applications of unmanned aerial vehicles technology in the resource-rich country. *Appl Sci* 11:10171. <https://doi.org/10.3390/app112110171>
- Nunner A, Seufert W (2013) Schwarzer apollo (*Parnassius mnemosyne*). In: Bräu M et al (eds) Tagfalter in Bayern, Ulmer Verlag
- Nychka D, Furrer R, Paige J, Sain S (2017) fields: tools for spatial data
- Pe'er G, Dicks LV, Visconti P et al (2014) EU agricultural reform fails on biodiversity. *Science* 344:1090–1092. <https://doi.org/10.1126/science.1253425>
- Peyras M, Vespa NI, Bellocq MI, Zurita GA (2013) Quantifying edge effects: the role of habitat contrast and species specialization. *J Insect Conserv* 17:807–820
- R Core Team (2020) R: A language and environment for statistical computing. Version R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Radchuck V, Turlure C, Schtickzelle N (2013) Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *J Anim Ecol* 82:275–285
- Rouse JW, Haas RH, Scheel JA, Deering DW (1974) Monitoring vegetation systems in the Great Plains with ERTS. In: Proc. 3rd earth resource technology satellite (ERTS) symposium, vol 1, pp 48–62
- Schilthuizen M (2000) Ecotone: speciation-prone. *Trends Ecol Evol* 15:130–131. [https://doi.org/10.1016/S0169-5347\(00\)01839-5](https://doi.org/10.1016/S0169-5347(00)01839-5)
- Schluter D (2000) The ecology of adaptive radiation. Oxford University Press, Oxford
- Sebek P et al (2013) Effect of active conservation management on biodiversity: multi-taxa survey in oak woodlands of Podyji National Park, Czech Republic. In: Conference volume, 5th symposium for research in protected areas, Mittersill, pp 717–720
- Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol Conserv* 83:247–257. [https://doi.org/10.1016/S0006-3207\(97\)00081-5](https://doi.org/10.1016/S0006-3207(97)00081-5)
- Smith TB, Kark S, Schneider CJ, Wayne RK, Moritz C (2001) Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends Ecol Evol* 16:431. [https://doi.org/10.1016/S0169-5347\(01\)02201-7](https://doi.org/10.1016/S0169-5347(01)02201-7)
- Spörri K, Babbi M, Krüsi BO (2014) 20 Jahre ökologische Aufwertung von Waldrändern im Kanton Aargau: erste Erfolgskontrolle. *Schweizerische Zeitschrift Fur Forstwesen* 165:313–320. <https://doi.org/10.3188/szf.2014.0313>
- Stuhldreher G, Fartmann T (2018) Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient—implications for conservation in times of climate change. *Ecol Ind* 94:83–98. <https://doi.org/10.1016/j.ecolind.2018.06.043>
- Sun Z, Wang X, Wang Z, Yang L, Xie Y, Huang Y (2021) UAVs as remote sensing platforms in plant ecology: review of applications and challenges. *J Plant Ecol* 14:1003–1023
- Szigeti V et al (2015) Habitat use, larval host-plant and nectar-plant distribution in the Clouded Apollo butterfly *Parnassius mnemosyne*. *Természetvédelmi Közlemények* 21:311–320
- Thomas JA, Elmes GW, Wardlaw JC, Woyciechowski M (1989) Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* 79:452–457
- Thuiller W, Georges D, Engler R (2013) biomod2: ensemble platform for species distribution modeling. Version R package version 3.5.1
- Tolman T (2009) Collins butterfly guide: the most complete guide to the butterflies of Britain and Europe, New. Collins, London
- Trusch R, Hafner S (2005) Neue Beobachtungen zu *Parnassius mnemosyne* auf der Schwäbischen Alb. In: Ebert G (ed) Die Schmetterlinge Baden-Württembergs, Ergänzungsband. Ulmer-Verlag, Stuttgart, pp 38–41
- Välimäki P, Itämiä J (2005) Effects of canopy coverage on the immature stages of the Clouded Apollo butterfly [*Parnassius mnemosyne* (L.)] with observations on larval behaviour. *Entomol Fennica*. <https://doi.org/10.33338/ef.84244>
- van Swaay C, Warren M (1999) Red data book of European butterflies (Rhopalocera). In: Nature and environment. Council of Europe Publishing
- van Swaay C, Collins S, Dušej G et al (2012) Dos and Don'ts for butterflies of the Habitats Directive of the European Union. *Nat Conserv* 1:73–153. <https://doi.org/10.3897/natureconservation.1.2786>
- Wagner DL, Grames EM, Forister ML et al (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proc Natl Acad Sci USA* 118:e2023989118. <https://doi.org/10.1073/pnas.2023989118>
- Westin A, Lennartsson T, Björklund J-O (2018) The historical ecology approach in species conservation—identifying suitable habitat management for the endangered clouded Apollo butterfly (*Parnassius mnemosyne* L.) in Sweden. *AIMS Environ Sci* 5:244–272. <https://doi.org/10.3934/environsci.2018.4.244>

Zaller JG, Brühl CA (2019) Editorial: Non-target effects of pesticides on organisms inhabiting agroecosystems. *Front Environ Sci* 7:75. <https://doi.org/10.3389/fenvs.2019.00075>

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Authors and Affiliations

Jan Christian Habel¹  · Viktoria Angerer¹ · Patrick Gros² · Mike Teucher³ · Jonas Eberle¹

¹ Evolutionary Zoology, Department of Environment and Biodiversity, University of Salzburg, 5020 Salzburg, Austria

² Haus der Natur, Museumsplatz 5, 5020 Salzburg, Austria

³ Department of Geoecology, Institute of Geosciences and Geography, Faculty of Natural Sciences III, Martin Luther University Halle-Wittenberg, 06099 Halle (Saale), Germany