



Managing an endemic taxon at the verge of extinction: factors driving population persistence and larval microhabitat selection of *Zygaena angelicae elegans* (Lepidoptera, Zygaenidae)

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Abstract

The shift towards “close-to-nature forestry” in Central Europe led to an area-wide decrease of open forest structures and a decline of many photophilous species or taxa. One of them, the endemic taxon *Zygaena angelicae elegans*, only occurs on the western margin of the Swabian Alb, Germany. Five of only 37 (mostly small) populations became extinct since 2000; hence, this evolutionary significant unit is at the verge of extinction. We assessed landscape-scale drivers of population persistence by comparing contemporary surveys with data from the 1990s and analysed larval microhabitat selection to provide target values for habitat management, which we tested in a case example. While population size was highest in open, south-exposed slopes, population persistence strongly decreased with increasing distance to the next occupied patch, with high extinction risk above 1.3–1.5 km. Occurrence and abundance of larvae was mostly driven by afternoon insolation (> 135 min) and the availability and height of the larval host plant *Coronilla coronata* (> 15 and > 25 cm for occurrence and abundance, respectively), which in turn depended on low canopy (< 61%) and shrub cover (< 26%).

Implications for insect conservation Habitat management reducing forest encroachment based on these thresholds resulted in an immediate boost of local population size. Management plans targeting a stable metapopulation must focus on the expansion of current relict habitats and creation of new habitats in close vicinity (1.5 km) to existing populations, with rapid population responses indicating that a consequent implementation may save the highly endangered taxon from extinction.

Keywords Endangered burnet moth · Forest species conservation · Open canopy forest · Population dynamics · Connectivity

Introduction

Insects are key organisms in most ecological processes in natural and man-made habitats, as they are responsible for pollination, nutrient cycling, herbivory and detritivory, and serve as a source of nutrients for many other animals (Yang and Gratton 2014). The globally reported decline of both insect species richness and abundance (Sánchez-Bayo and Wyckhus 2019; Raghavendra et al 2022) therefore has a significant impact on ecosystem functions and services. Also in temperate latitudes, insect populations are seriously declining (van Strien et al. 2019). Hallmann et al. (2017) found a sharp decline of more than 75% in flying insect biomass over a period of 27 years in different protected areas in Germany. The number of moth species in the state of Baden-Württemberg, Germany, declined from 1970 to 2020 by 20% up to 60% (depending on altitude and location) and

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also the abundance of many species decreased dramatically (Karbiener and Trusch 2022).

Several studies show that habitat loss is one of the main reasons for insect decline (Habel et al. 2019; Sánchez-Bayo and Wyckhuys 2019; Kohoe et al. 2021; Warren et al. 2021).

In forest ecosystems, habitat loss traces back to the change in forest management from diverse types of forest use (e.g. coppicing, forest grazing)—which leads to extended sparse forests and ecotones – to continuous cover forestry (Bauhus et al. 2013), shaping rather homogenous, dark and dense forests which are no longer suitable for many insects (Freese et al. 2006; Hermann 2021; Kozel et al. 2021; Warren et al. 2021). In addition, as these forest are managed for stability against natural disturbances, non-equilibrium states, which are among the key drivers for high biodiversity (Connell 1978), are lacking.

Forest gaps and stands with low canopy cover provide habitat to many—especially photophilic—species, through heterogenous structures and within-forest ecotones with favourable light conditions. While in unmanaged forests such structures are shaped by natural disturbances, in the cultural forest landscapes of Central Europe these structures were present over a very long time period due to land use practices such as firewood and timber harvesting, forest grazing and litter raking (Kirby and Watkins 2015).

Forest grazing dates back to the neolithic (Ellenberg 1996) and traditional forest uses such as coppice with standards were widespread in Europe for several millennia (Vollmuth 2022). Coppicing is the periodic cutting of trees or shrubs in a rotating system of predefined sections, mainly for the production of firewood and timber. This ancient form of forest management provides open canopy and forest edge structures in early successional stages and promotes high biodiversity, with many highly endangered butterfly species benefitting from this silvicultural treatment (Fartmann et al. 2013), especially in areas where this management has a long-term tradition and thus provides habitat continuity over a long period of time (Treiber 2003). However, coppicing was gradually abandoned in the nineteenth and twentieth century (Vollmuth 2022). In Germany, for example, it declined by 98.7% between 1927 and 2020 (Kamp 2022), and also livestock farming was banned from the forests in the nineteenth century (Hartel and Plieninger 2014). The abandonment of various traditional forest management practices and the shift toward high-forest silviculture and „close-to-nature forest management“ (Bauhus et al. 2013) led to a loss of nutrient-poor open forest habitats in favour of darker, denser, cooler and more moist microclimates in fertile closed-canopy habitats (Warren et al. 2021; Vild et al. 2024). German forests are thus mainly inhabited by shade-tolerant species, while photophilic and ecotone-species decline (Hermann 2021; Roth et al. 2022),

the latter also suffering from the recent sharp spatial segregation of forest and farmland, which is exclusively man-made (Vos and Meekes 1999). Due to the rarity of open forest structures and forest ecotones, their creation and management has increasingly become a tool for forest species conservation over the last two decades (Dolek et al. 2018).

In forests, butterflies are among the species groups most affected by the lack of open forest structures, because they are ectotherms and most of them depend on their larval host plants situated in sunny conditions (Warren et al. 2021). As a consequence, some butterflies, especially highly specialized species like *Euphydryas maturna*, *Limenitis reducta* or *Coenonympha hero* are currently at the verge of extinction in Germany (Rennwald et al. 2011; Hermann 2021). For threatened species, viable metapopulations, i.e. population systems connected by migration (Hanski 1998), are of particular importance for persistence. In the case of endemic taxa, the extinction risk is further exacerbated by their local restriction, and the habitat requirements of their small and often highly specialized populations are mostly not sufficiently known to counteract their decline. One example is the burnet moth subspecies *Zygaena angelicae elegans* (Burgeff, 1914) which only occurs on the Swabian Alb, a low mountain range in Germany.

This burnet moth, the target species of our study, is classified as “threatened with extinction” on the German national Red List (Rennwald et al. 2011) and the state of Baden-Württemberg bears global responsibility for its conservation. As many endemics, this taxon has a small distribution range and consists of relict populations with small numbers of individuals.

Throughout its range, *Z. angelicae* exhibits a close association with open forest habitats. The Swabian Alb was once covered by heterogenous open canopy forests and transition zones between woodland and heathland due to traditional land use practises (Poschlod 2017). However, open forest structures and, thus, the habitats of *Z. angelicae elegans* have been heavily degraded due to the changes in land use, such as a strong reduction of forest grazing and an increased afforestation with spruce. In addition, atmospheric nitrogen deposition promotes forest succession even in extreme sites, such as steep slopes and brims of the Swabian Alb (Hermann 2021), which make up many of the remaining habitats. To counteract the loss of the relict populations, *Z. angelicae elegans* was included in the state’s conservation action programme as a target species with highest priority in the early 1990s (Hofmann 1994, 1997) and became a focal species for open forests in the state’s forests’ conservation agenda (ForstBW 2015). Potential habitats were mapped in the 1990s and expert-based conservation interventions, in the form of small-scale cutbacks of overgrowing forest habitats, subsequently implemented (Hofmann and

Ebert 2000; Hofmann 2005). However, evidence-based conservation interventions were lacking and the species' decline continued (Rennwald et al. 2011).

We use the habitat mapping of the 1990s, which provides a unique data set across the entire range of the endemic target species, as a baseline for analysing these population changes. Specifically, we

- (1) compare the current population status and distribution to that of the 1990s,
- (2) analyse the effects of landscape-scale habitat configuration on population size, stability, and persistence and
- (3) examine larval microhabitat selection. Based on the results, we
- (4) provide target values for evidence-based habitat management aimed at metapopulation development, and
- (5) apply and evaluate these target values in a case example.

Methods

Study species

Zygaena angelicae elegans is the westernmost subspecies of the Ponto-Mediterranean *Z. angelicae*. It occurs in open forest habitats and is associated with *Coronilla coronata* as most important larval host plant (Hofmann 1994). The southern Balkans are assumed to be the glacial refugium from where *Z. angelicae* spread postglacially to the north and west. Currently, the species has an eastern European distribution from Thrace (Greece) to southern Germany (Hofmann and Tremewan 2017). Within this wide range, intraspecific differentiation is weak, but becomes more pronounced at the edge of the westernmost part. While *Z. angelicae* is five-spotted on the forewings, the individuals of the Swabian Alb populations are predominantly six-spotted with distinctly different markings, a reason why the taxon *elegans* (Burgeff, 1914) was long regarded as a bona species. Today, it is regarded as a localized subspecies of *Z. angelicae* (Hofmann 1994; Reumont et al. 2011), but as an ecological significant unit. This classification is supported by the fact, that the larvae of the five-spotted populations in the Balkans feed on *Securigera varia*, while those of the mainly six-spotted populations of the Swabian Alb have switched mostly to *Coronilla coronata* as larval host plant.

Study region

The distribution of *Z. angelicae elegans* is restricted to the Swabian Alb in the state of Baden-Württemberg, Germany,

a low mountain range of mostly Jurassic limestone, which is about 200 km long and 20 to 40 km wide, with elevations up to 1016 m a.s.l.. The Swabian Alb belongs to the temperate climate zone, with average annual temperatures between 4 and 7 °C and 800–1200 mm of annual precipitation. In parts of its northwestern margin, the terrain drops steeply resulting in very steep cliffs. The deciduous forests on the hillsides are dominated by beech; on more extreme sites with high relief energy and soil erosion, steppe heath forests (dry and sparse beech and oak forest) occur. The distribution of the target species currently ranges from the south-western to the central Swabian Alb (Fig. 1).

Species distribution and population stability

Species data

The first mapping (MAP1) of all potential patches inhabited by the target species (half-open forest structures with *C. coronata*) along the northern margin of the Swabian Alb was performed between 1994 and 2000, as part of the species conservation action programme of the nature conservation authority in Baden-Württemberg (Hofmann 2005), resulting in the recognition of 32 patches with confirmed species occurrence. Between 2017 and 2023 (MAP2), we revisited all mapped patches of MAP1. In addition, we used aerial images to identify open forest patches on south- to southwest-facing hillsides and cliffs in up to 3 km distance (maximum dispersal ability of *Zygaena* spp. according to Franzén and Nilsson 2007) from known occupied patches as potential habitats, which were also controlled for species presence.

Patches were mainly mapped during the species' flight season in summer (last week of June until mid July (Hofmann 1994)), preferably during the flight seasons of several years, and some patches were additionally visited during larval time in May (Table 1). In flight season we used Pollard walks (Pollard and Yates 1993), i.e. slowly walking transects covering the total area that was delineated during MAP1 or as potential habitat based on the aerial photographs in MAP2 and counting all individuals along the transect (2.5 m to each side, 5 m above, 5 m ahead). Transects were arranged to cover the entire accessible area of the patch, i.e. transect length was adapted to the patch size, and survey dates were chosen to capture the time of the flight peak as well as possible. When we found no imagines during the flight season, we visited the patch at least once again at larval time to avoid false absences. We searched for feeding traces on the larval host plant and counted the larvae, thereby also covering the total area of the patch. Imagines were recorded in sunny weather between 10 a.m. and 5 p.m.,

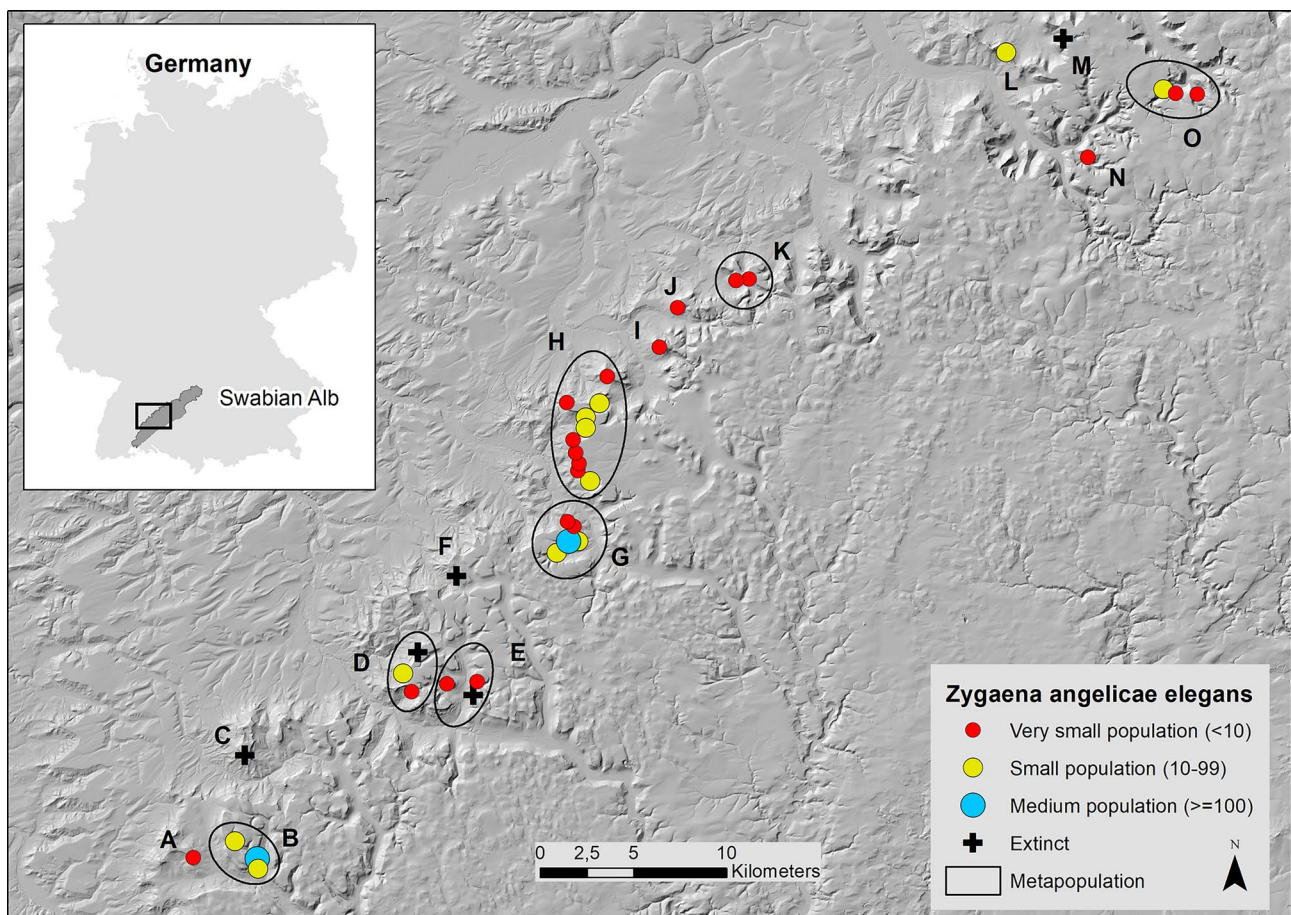


Fig. 1 Overview of all patches occupied by *Zygaena angelicae elegans* in the mapping period MAP2 (2017–2023) and patches with populations that became extinct since the previous mapping period (MAP1 1994–2000). Population size classes are based on the daily

maximum of counted individuals in MAP2. Based on the next-neighbour distance-threshold resulting from this study, we defined patches with ≤ 1528 m distance to each other as metapopulation. Program: ArcMap 10.8.1

larvae in any weather between 10 a.m. and 8 p.m. We used the maximum count of individuals per day as a proxy for population size. For patches that were mapped multiple times per mapping period, we used the maximum count (best year) in the mapping period to account for inter-annual variance. Based on these numbers, we categorized the patches in four categories: very small populations (< 10 individuals/survey day), small populations (10–99 individuals/survey day) and medium populations (100 or more individuals/survey day). Patches occupied in MAP1 were classified as “extinct” in MAP2, if we could not provide evidence for species occurrence on at least two consecutive control visits (covering both flight and larval season). In the following analyses we used the difference in the maximum number of individuals per day between MAP1 and MAP2 as a proxy for population stability, calculated for the developmental stage that was available

for both mapping periods (when available, we preferred moths).

Predictor variables

For each patch mapped in both MAP1 and MAP2, we derived the average slope, elevation and exposition (the cosine and sine of aspect as northness and eastness, respectively) within a 50 m buffer around the patch center from a LiDAR-based digital terrain model (LGL 2020) using the *terra* package in R (Hijmans 2025).

In addition, we measured the distance of the patch centroid to that of the next occupied patch (Table 2).

Data analyses

For all statistical analyses, we used R software version 4.3.1 (R Core Team 2023) with R-Studio version 2023.06.1. We

Table 1 Patches inhabited by *Zygaena angelicae elegans*, mapped in the years 1994–2000 (MAP1) and 2017–2023 (MAP2) and classified into very small (< 10 individuals as daily maximum in peak season), small (10–99) and medium (≥ 100 individuals) populations

Patch Nr	(Meta-) Population	MAP1 (1994–2000)			MAP2 (2017–2023)			Microhabitat analyses N presence/absence plots [N grid cells]
		Population size	N visits (at larval / flight time)	Max N of individuals per day (larvae/imagines)	Population size	N visits (at larval / flight time)	Max N of individuals per day (larvae/imagines)	
1	A	No data	0	No data	Very small	2/1	0/9	
2	B	Small	0/1	0/10	Small	1/2	36/45	9/10 [53]
3	B	Medium	0/2	0/185	Medium	5/5	350/145	7/7 [52]
4	B	Very small	1/4	6/1	Small	5/5	10/12	3/3 [21]
5	C	Small	0/2	0/15	Extinct	2/1	0/0	
6	D	Small	0/4	0/20	Small	1/3	15/49	1/12 [19]
7	D	Very small	1/0	4/0	Extinct	1/1	0/0	
8	D	Very small	1/0	4/0	Very small	1/1	2/1	
9	E	Small	1/1	5/20	Very small	1/1	1/1	1/3 [17]
10	E	Very small	2/1	4/5	Very small	1/1	1/3	1/3 [68]
11	E	Very small	1/0	15/0	Extinct	1/1	0/0	
12	F	Small	0/4	0/100	Extinct	1/3	0/0	
13	G	Very small	1/0	2/0	Small	0/1	0/43	
14	G	Very small	0/1	0/1	Medium	0/2	0/180	3/3 [75]
15	G	Small	1/0	20/0	Small	1/1	23/7	
16	G	Very small	1/0	2/0	Very small	0/1	0/5	
17	G	Very small	1/0	7/0	Very small	0/1	0/9	
18	H	Very small	1/0	3/0	Small	0/1	0/16	
19	H	Very small	0/3	0/2	Very small	0/2	0/1	
20	H	Very small	0/1	0/3	Very small	0/2	0/3	2/1 [21]
21	H	Small	0/1	0/25	Very small	0/2	0/5	
22	H	Small	0/1	0/15	Small	0/2	0/12	2/4 [23]
23	H	Small	0/1	0/15	Very small	0/2	0/8	
24	H	Very small	0/1	0/4	Small	0/2	0/28	
25	H	Very small	0/1	0/1	Very small	0/2	0/3	
26	H	No data	No data	No data	Small	1/1	9/13	
27	H	Small	0/2	0/20	Very small	0/1	0/1	
28	I	Small	1/0	10/0	Very small	1/1	6/8	
29	J	Very small	1/0	9/0	Very small	1/1	8/1	
30	K	No data	No data	No data	Very small	0/1	0/1	
31	K	Very small	0/1	1	Very small	0/1	0/4	
32	L	Small	2/1	14/17	Small	1/1	11/2	
33	M	Very small	0/2	0/3	Extinct	1/1	0/0	
34	N	Small	0/4	0/52	Very small	1/2	7/3	1/9 [63]
35	O	Small	0/1	12	Small	1/1	26/1	
36	O	No data	No data	No data	Very small	1/0	1/0	
37	O	No data	No data	No data	Very small	1/0	2/0	

The number (N) of visits per larval and flight time is indicated for MAP1 and MAP2

Patches without proof of existence of the target species at two or more consecutive controls are categorized as „extinct“, patches newly detected in MAP2 are indicated with „no data“ in MAP1

The maximum number (Max N) of individuals per day shows larvae and imagines

In addition, the number of presence and absence plots included in the microhabitat analyses and the total number of grid cells per patch

Based on our results, we defined patches with ≤ 1528 m distance to each other as metapopulation

Table 2 Environmental variables used for the analyses at landscape scale (LS) and microhabitat scale (MS)

Environmental variable	Unit	Reference surface	Abbreviation	Range	Correlation with
LS Landscape scale					
Distance to next patch	m		Distance	384–7145	
Slope	%	50 m buffer	Slope	15–41	
Elevation a.s.l	m	50 m buffer	Height	560–980	
Northness (cosine exposure)		50 m buffer	Northness	1 (north) to -1 (south)	
Eastness (sine exposure)		50 m buffer	Eastness	1 (east) to -1 (west)	
Connectivity					Distance to next patch
MS Microhabitat scale					
Cover of larval host plant	%	5×5 m	CC_cov	0–40	CC_height (0.6)
Height of larval host plant	cm	5×5 m	CC_height	0–50	CC_cov (0.6)
Cover of grass	%	5×5 m	Grass	0–90	
Cover of other vascular plants	%	5×5 m	Plants	0–95	
Cover of litter	%	5×5 m	Litter	0–90	
Cover of bare ground or rubble	%	5×5 m	Bare_ground	0–90	
Canopy cover (trees ≥ 5 m)	%	10×10 m	Canopy	0–95	Sun_day (0.64)
Shrub cover (≥ 1.3 < 5 m)	%	10×10 m	Shrub	0–80	
Cover of Nectar plants	%	10×10 m	Nect_pl	0–30	
Potential insolation before 12 p.m	Min	Plot center	Sun_morning	0–360	Sun_day (0.73)
Potential insolation after 12 p.m	Min	Plot center	Sun_afternoon	0–360	Sun_day (0.79)
Potential insolation whole day	Min	Plot center	Sun_day	16–480	Canopy (0.64) Sun_morning (0.73) Sun_afternoon (0.79)

fitted generalized linear mixed models (GLMMs) using the function *glmmTMB* in the homonymous R package (Brooks et al. 2017) to examine the effect of the predictor variables at landscape level (LS) (Table 2) on population size (LS1) as the maximum number of individuals counted in MAP2, population stability (LS2) as the difference in maximum numbers of individuals between MAP1 and MAP2 and population persistence (extinct (0) vs. occupied (1)) (LS3) between MAP1 and MAP2. For LS1, we additionally included the number of visits as predictor variable in the models. Since population size and stability were calculated based on different development stages (larvae or imagines), we accounted for this potential bias by including the development stage as random effect in the models and, in addition, ran all models including and excluding the populations where individual numbers in MAP1 and MAP2 were obtained from different stages.

First, we checked for correlations between predictor variables. From pairs or clusters of univariately significant, but correlated variables (Spearman's $r > 0.6$) (Spearman 1904), we chose the best performing based on the AIC and integrated them in multivariate models, fitted with the function *buildglmTMB*, determining the most parsimonious models using backward selection based on the AIC (models AIC $\Delta \leq 2$ included). For LS1 we assumed a negative binomial, for LS2 a normal and for LS3 a binomial error distribution. Residual

diagnostics were performed with the DHARMA R package (Hartig 2022).

In addition, we used Conditional inference trees (CIT) to identify variable thresholds. This method, similar to classification and regression trees, uses recursive partitioning to select significant predictor variables in a hierarchical way and to identify the best cut-off values that split the dataset so as to predict the occurrence of the target species. We calculated CITs for population size, stability and persistence of *Z. angelicae elegans* using the function *ctree* of the R package *partykit* (Hothorn and Zeileis 2015; Hothorn et al. 2006), including all variables that were significant in the respective GLMMs (Online Resource SI2). Finally, we used the next-neighbour distance that best separated populations with high and low stability as a threshold to calculate the number of “connected populations” within this distance for each population. This number was then additionally tested as a predictor for population size, persistence and stability according to the process described above. In addition, we tested the next-neighbour distance which best separated persisting populations from extinct populations as a predictor.

Larval microhabitat

Species data

For the analysis of larval microhabitat selection, ten patches with target species presence were selected (Table 1), buffered with 25 m and then subdivided into grid cells with an edge-length of 25 m (412 cells in total). All cells were preselected in either potential presence cells (presence of larvae likely) or absence cells (presence of larvae not likely), based on a 10 min search for occurrence of the larval host plant, characteristic feeding marks and larvae. Cells were classified as presence when at least one larva was found. Larvae and habitat variables were sampled in May and June 2015. For this purpose, 10×10 m plots were established in the centers of the 25×25 m grid cells, located using a handheld GPS and orientated parallel to the slope. On each 10×10 m plot in the 40 grid cells classified as potential presence, we searched for 10 min for larvae and counted them. Absence plots were chosen randomly from the remaining grid cells and we planned to map the same amount as presence plots, however, 10 potential presence plots turned out as absence as we could not find larvae, and some plots were inaccessible, resulting in 30 presence plots (7% of all grid cells) and 55 absence.

Predictor variables

Habitat variables (Table 2) were also collected during larval season. For the 10×10 m plots, we estimated canopy cover (trees ≥ 5 m) and shrub cover ($\geq 1.3 < 5$ m) in 5% steps, as well as the cover of nectar plants (estimation in 5% steps) like *Knautia dipsacifolia* or *Origanum vulgare* according to Hofmann (1994). As the larvae of *Z. angelicae elegans* feed nearly exclusively on *C. coronata*, we recorded the cover (estimation in 5% steps) and average height (in cm) of the host plant on a 5×5 m plot quarter. For presence plots, the quarter with the highest abundance of larvae or feeding marks was selected, for absence plots, the quarter was randomly selected. On the same plot quarter we also assessed the cover of grass, other vascular plants, litter and bare ground or gravel (estimation in 5% steps). In addition, we used a horizontoscope developed by Tonne (Tonne 1954) at the plot center to measure the duration of potential insolation per day (in minutes), and before and after 12 pm, respectively.

Data analysis

To examine the effects of the environmental predictor variables on occurrence (MS1) and abundance (MS2) of larvae of *Z. angelicae elegans* as well as (MS3) occurrence of the essential larval host plant *C. coronata*, we fitted

GLMMs using the same procedure as described above. For MS1 and MS3 we assumed a binomial and for MS2 a negative binomial error distribution and included the patch as a random factor to account for potential effects of spatial clustering. The fit of the occurrence models (MS1, MS3) was evaluated based on 100 iterations of a twofold cross validation (random folds) calculating the area under the receiver operating characteristics (ROC) curve (AUC) with the R package pROC (Robin et al. 2011).

In addition, variable thresholds were identified by calculating CITs for the occurrence of larvae (MS1_CIT), abundance of larvae (MS2_CIT) as well as for the occurrence of the larval host plant (MS3_CIT), taking into account all variables that showed significance in the respective GLMMs.

Case example: effects of habitat management

We used the variable thresholds obtained from the larval microhabitat analyses as target values for habitat management in a case example performed in a southwestern population of *Z. angelicae elegans*. This population (patch Nr. 3, Table 1), located to both sides of a forest road, is one of two remaining populations with more than 100 observed imagines per day. For this population, we used the maximum number of imagines before the habitat management intervention in MAP2 for modelling population size and stability.

Habitat management, i.e. logging in order to provide open forest structures and remove shrub cover, was implemented by the state forest administration ForstBW in the winters 2015/16 and 2021/22. Above and below the machine pathway, glades of a size of approximately 20–30 m width and 30–40 m length were cut clear. Logging in 2015/16 included the eastern part of the forest road on a length of approximately 250 m, logging in 2021/22 the remaining western part of the forest road with another 250 m, resulting in a total length of 500 m managed habitat. In 2021/22, in addition to logging, the machine pathway was broadened by a digger causing the excavation of calcareous rubble.

The response of the target species population size was observed by counting larvae (in May) and imagines (in July) before the intervention in 2015 (imagines) and after management in 2017 (both), 2018 (both), 2019 (larvae), 2021 (imagines), 2022 (both) and 2023 (both), using transect counts of 500 m (total length of the forest road) standardized in time. We spent one hour walking along the machine pathway, and one hour walking back, and recorded the result with the higher number of individuals. Imagines were counted in sunny weather between 10 a.m. and 5 p.m., larvae in any weather between 10 a.m. and 8 p.m.

Results

Target species distribution

The distribution of *Zygaena angelicae elegans* extends over about 70 km between the westernmost (population A, Table 1) and the easternmost patches (O) (Fig. 1), at elevations between 560 and 980 m a.s.l.. Exposure ranges from east to west (101 to 308°), with the majority of occupied patches facing southwest (Online Resource SI1). In total, we mapped 37 patches (Table 1). In MAP1 and MAP2, we found *Z. angelicae elegans* in 32 patches, including five newly mapped patches (visited only in MAP2) and five extinctions. In MAP1, 17 population were classified as very small, 14 as small and two as medium-sized whereas in MAP2, 20 were classified as very small, 10 as small and two as medium-sized populations.

Population stability

The most parsimonious model explaining population size included northness and the distance to the next occupied patch, both negatively affecting population size (LS1) (Table 3, Fig. 2a, b), while the number of visits had no significant effect (see Online Resource SI2 where results of the univariate models are provided). Population stability (LS2) and persistence (LS3) between MAP1 and MAP2 were only explained by a negative effect of the next-neighbour distance (Table 3, Fig. 2). Median next-neighbour distances for medium-sized populations were 530 m, 879 m for small populations, 896 m for very small populations and 3169 m for extinct populations (Online Resource SI3). The CITs revealed a substantial decrease in population stability when distance to the next patch exceeded 1528 m, with the distances above 1308 m significantly increasing the risk for local extinction (Online Resource SI4). In GLMMs for population size and stability, development stage as random effect was negligible (random effect standard deviation was < 0.001% of fixed

Table 3 Results of the final GLM(+M)s, explaining population size (LS1), population stability (LS2) and population persistence (LS3) at the landscape scale (with a and b marking separate models), and

the occurrence (MS1) and abundance (MS2) of larvae as well as the occurrence of the larval host plant *Coronilla coronata* at the micro-habitat scale

Final models		Estimate	Standard Error	z-value	p-value	AIC	AUC
LS1+ Landscape scale: <i>Zygaena angelicae elegans</i> – population size (MAP2) (multi- and univariate model)							
LS1a+	Distance	– 1.9856	0.6360	– 3.122	0.0018**	272.7	
	Northness	– 1.5916	0.6454	– 2.466	0.0137*		
LS1b+	Connectivity ¹	0.4391	0.1890	2.323	0.0202*	275.9	
LS2+ Landscape scale: <i>Zygaena angelicae elegans</i> – population stability (MAP1 vs. MAP2)							
LS2a+	Distance	– 45.17	19.82	– 2.279	0.0227*	328.5	
LS2b+	Connectivity ¹	10.062	4.618	2.179	0.0293*	328.9	
LS3 Landscape scale: <i>Zygaena angelicae elegans</i> – population persistence (MAP1 vs. MAP2)							
LS3a	Distance	– 3.991	1.736	– 2.299	0.0215*	26.6	0.85
LS3b	Connectivity ^a	1.5996	0.7761	2.061	0.0393*	28.2	
MS1+ Microhabitat scale: <i>Zygaena angelicae elegans</i> larvae – occurrence (multivariate models)							
CC_height		0.0894	0.0254	3.521	0.0004***	67.1	0.86
Sun_afternoon		0.0107	0.0044	2.422	0.0154*		
Bare_ground		0.0267	0.0161	1.659	0.0971 n.s		
MS2+ Microhabitat scale: <i>Zygaena angelicae elegans</i> larvae – abundance (multivariate model)							
CC_height		0.0880	0.0223	3.945	8e-05***	195.3	
Sun_afternoon		0.0062	0.0031	1.978	0.0479*		
MS3 Microhabitat scale: <i>Coronilla coronata</i> (larval host plant) – occurrence (multivariate model)							
Shrub		– 0.0751	0.0241	– 3.119	0.0018**	99.4	0.73
Canopy		– 0.0346	0.0116	– 2.970	0.0029**		

In LS1 and LS2, developmental stage (mapping of larvae or imagines) was included as random factor and in MS1 and MS2 the patch, respectively. For the second best model of MS1 (AIC $\Delta \leq 2$), see Online Resource SI5

AUC values were calculated only for logistic models (LS3, MS1, MS3). Asterisks indicate significance levels with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = non-significant

^aThe variable “connectivity” represents the number of populations within the distance threshold of 1528 m (Online Resource SI4) calculated for population stability, which was tested a-posteriori in separate models

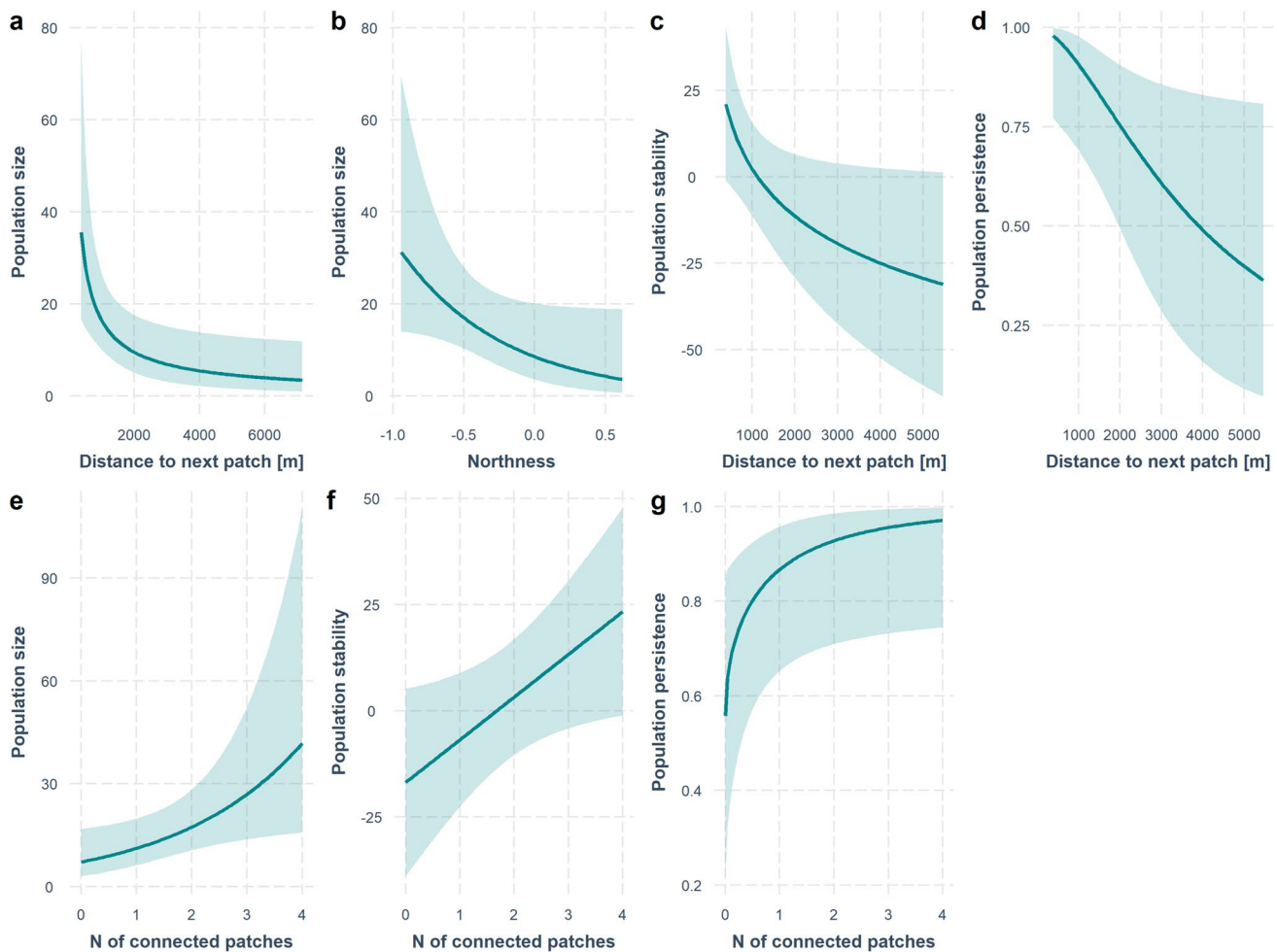


Fig. 2 Landscape scale: effect plots for the variables significantly explaining population size (**a**, **b**), population stability (**c**) and population persistence (**d**) of *Z. angelicae elegans*. Effects of the number of connected patches on **e** population size, **f** stability and **g** persistence are presented below. Shading displays 95% confidence intervals of the marginal effects. Population size: number of individuals in the second

survey phase (MAP2), population stability: change in the number of individuals between first and second survey phase (MAP1 vs MAP2) and population persistence: probability of extinction between MAP1 and MAP2). Variable definitions are presented in Table 2. Details of the models are presented in Table 3. Program: R Software 4.3.1

effect intercept (Online Resource SI5)). Excluding populations with data from different development stages between MAP1 and MAP2 did not change variable significance, and CIT split for next-neighbour distance stayed consistent at 1528 m, but CIT for connectivity resulted in no significant split (Online Resource SI4).

An increasing number of connected patches (i.e. within a distance of 1528 m or less) significantly increased population size, stability and persistence (Fig. 2e–g), with a critical threshold of at least one connected patch required for persistence and stability (Online Resource SI4). Connectivity based on patches within distance of 1308 m or less only significantly affected population stability (Online Resource SI2).

Larval microhabitat

Occurrence and abundance of *Z. angelicae elegans* larvae were best explained by the height of the larval host plant *Coronilla coronata* and the potential insolation after 12 p.m. (Table 3, MS1 and MS2, Fig. 3a–d), both showing positive effects. The best model for occurrence additionally included a positive relationship with the cover of bare ground. The presence of *C. coronata* was best explained and negatively affected by canopy and shrub cover (Table 3, MS3). The occurrence of larvae and their host-plant were predicted with an AUC of 0.86 and 0.73, respectively, showing an excellent and moderate discrimination ability of the models (Hosmer et al. 2013). Effect

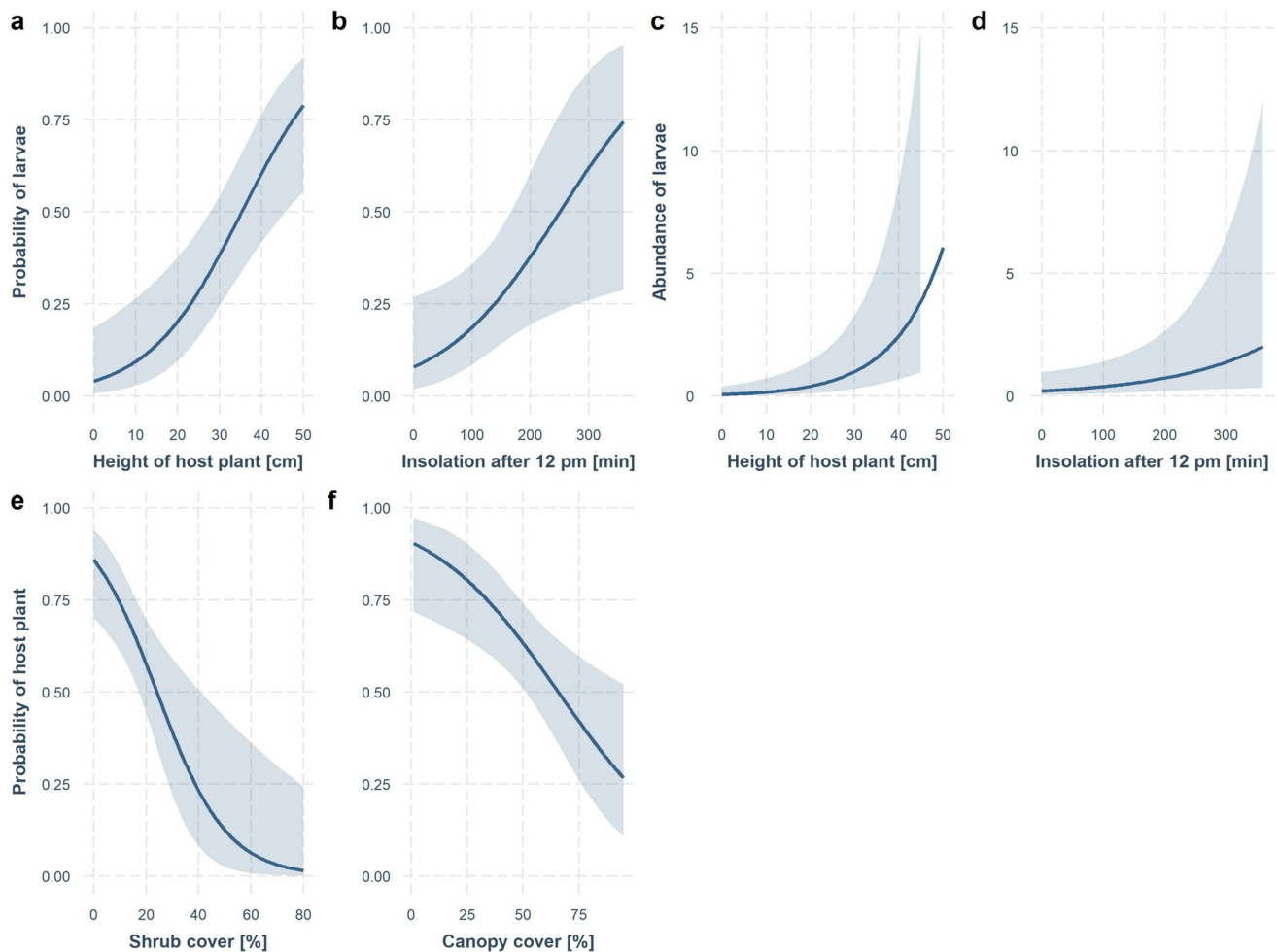


Fig. 3 Microhabitat scale: effect plots for the variables significantly explaining the occurrence probability (**a**, **b**) and the abundance (**c**, **d**) of larvae and the occurrence probability of the larval host plant *Coronilla coronata* (**e**, **f**). Shading displays the 95% confidence interval

of the marginal effects. Variable definitions are presented in Table 2. Details of the models are presented in Table 3. Program: R Software 4.3.1

plots for all significant variables of the multivariate models are presented in Fig. 3 (for results of the univariate models see Online Resource SI2).

CITs showed that a significant threshold for the occurrence probability of larvae only existed for the height of the larval host plant, with *C. coronata* of at least 15 cm height being more likely to be occupied by larvae (Fig. 4a). The abundance of larvae was highest on host plants of more than 25 cm. On smaller plants, the species still occurred in small numbers when the potential afternoon-insolation exceeded 135 min (Fig. 4b).

The occurrence of the larval host plant *C. coronata* was mainly determined by the potential insolation. Presence probability was highest, when the potential afternoon-insolation exceeded 105 min and shrub cover was below 26%, however, it could still be found when insolation was less than 105 min, but canopy cover was lower than 61% (Fig. 4c).

Case example: effects of habitat management

Management measures at the case study site were conducted in line with the results of our larval microhabitat analysis: canopy and shrub cover were reduced below 61% and 26%, respectively via targeted logging in order to increase insolation. In addition an excavator was used to expose bare ground, as this variable was univariately significant (Online Resource SI2), and still contained in the best candidate model (Table 3). The measures resulted in strong a population increase (Fig. 5), with a peak (maximum of 350 larvae, 145 imagines per day) two years after the first habitat management (logging in winter 2015/16) and another peak (400 larvae, 586 imagines) in the year after a second intervention (logging and ground disturbance in winter 2021/22). Figure 6 shows imagines (a) and larvae (b) of the target species at the case study site,

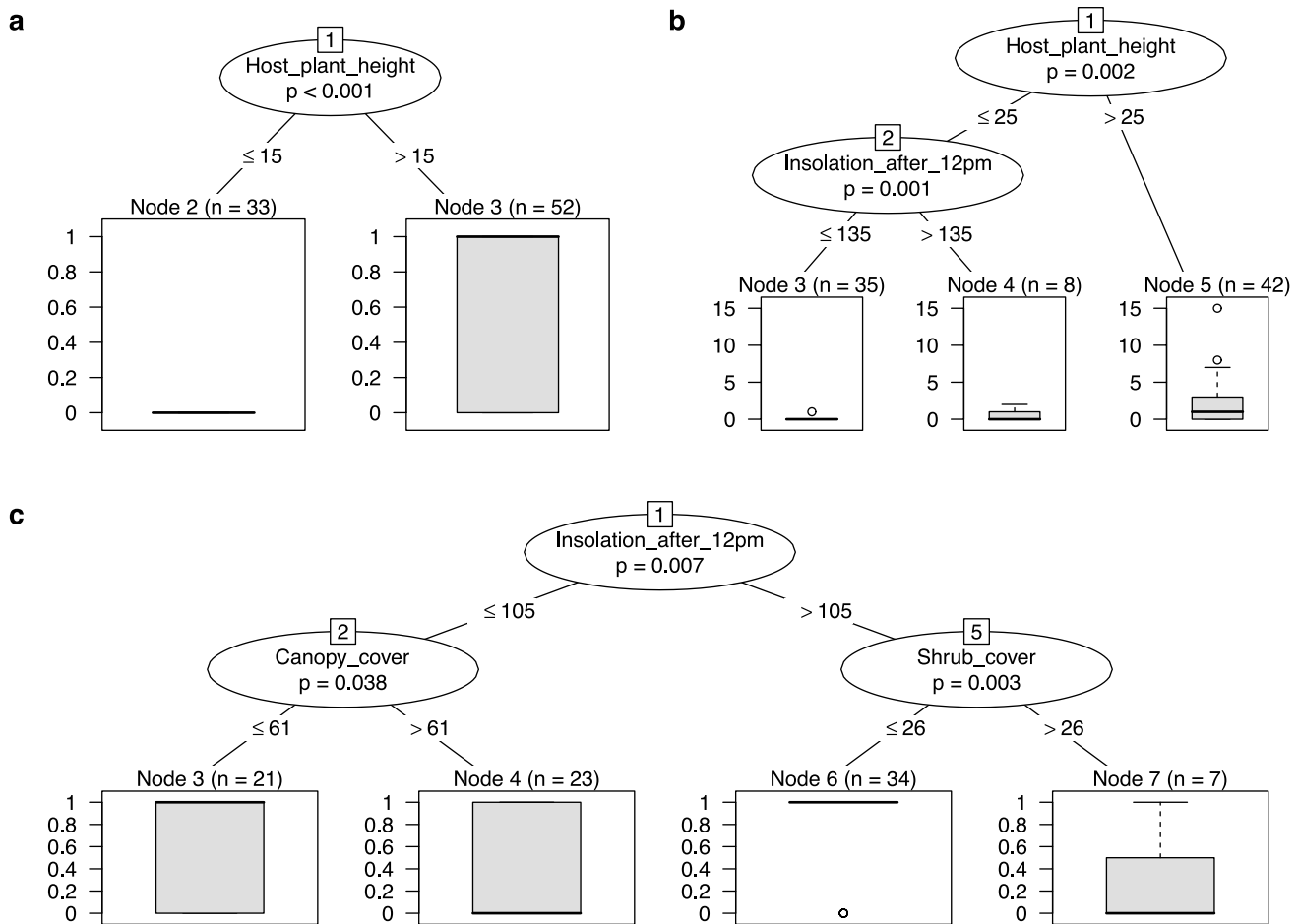


Fig. 4 Conditional inference trees (CIT) for **a** occurrence of larvae (boxes show probability of occurrence between 0 and 1), **b** abundance of larvae (boxes show number of larvae) and **c** occurrence of the lar-

val host plant *Coronilla coronata* (boxes show probability of occurrence between 0 and 1). Program: R Software 4.3.1

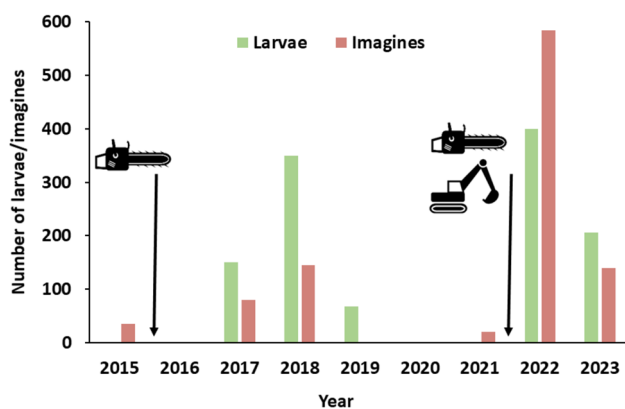


Fig. 5 Recorded number of larvae (green) and imagines (red) at the case study site for habitat management (Patch Nr. 22, Table 1, Fig. 1) in the southwestern Swabian Alb. Habitat management was undertaken in winter 2015/16 (logging) and winter 2021/22 (logging and ground disturbance). Missing bars mean that no data were collected in the respective season/year. Program: Excel 2016

as well as the habitat in the year before (c) and five months after the management intervention (d).

Discussion

Our study on the endemic taxon *Zygaena angelicae elegans* reports

- (1) That the small number of remaining relict populations with mostly very few individuals, decreasing population sizes and the extinction of five populations since the 1990s is most probably a result of habitat degradation and increasing isolation
- (2) Threshold values for distances between populations at the landscape level and habitat variables at the microhabitat level as a basis for conservation management, and



Fig. 6 **a** Imagines and **b** larva of *Zygaena angelicae elegans* (on the larval host plant *Coronilla coronata*). Westfacing view of habitat at a machine pathway in the case study site (Patch Nr. 22, Table 1) on the southwestern Swabian Alb **c** before conservation intervention (June 4th 2021) and **d** after conservation intervention (May 13th 2022) of

logging (to reduce canopy and shrub cover and increase insolation) and digging (increasing the cover of bare ground and enhancing microhabitat conditions and facilitate germination of the larval host plant). **e** Characteristic habitat of *Z. angelicae elegans* on a very steep brim (Patch Nr. 8, Table 1). Program: PowerPoint 2016

- (3) Results of a case example of conservation management which resulted in a strong increase in population size after these evidence-based measures had been implemented

Population stability and connectivity

Our results show that most of the relict habitats of *Z. angelicae elegans* only support a very limited number of individuals, and in the majority of these small habitats, only a few individuals were found during all our field campaigns. This becomes clear despite the limitations that not all occupied patches could be mapped multiple times at the peak of each flight season (few patches were even mapped only once per mapping period), and thus the recorded number of individuals may not always reflect the actual maximum population size in each patch. In addition, evaluating population stability over a period of 30 years, we identified inter-population distance as a key factor for population persistence. According to metapopulation theory, there is a maximum distance to the next patch and a minimum number of neighbouring patches within this distance, beyond which long-term survival is unlikely (Hanski 1998). Our study resulted in a maximum distance of 1528 m for inter-patch distance, and at least one connected patch, as threshold for subpopulation stability. When

applying these thresholds while referring to connectivity as spatial arrangement of patches, we identified seven existing metapopulations, consisting of two up to ten subpopulations. Only two metapopulations include patches with more than 100 individuals, while the other remaining metapopulations contain only small or very small subpopulations and, thus, only a very limited number of potential dispersers. This is alarming since connectivity is of particular importance for specialized butterfly species (Brückmann et al. 2010). According to Hanski (1998), 15–20 well-connected patches are required for the long-term persistence of a metapopulation, which, however, are only functional if there are source populations producing enough dispersers to ensure inter-patch movements.

In our study, the metapopulations consist mainly of potential sink populations, hence, our target species occurs under very insufficient conditions and the isolated patches may be “living dead”, i.e. not only at the verge of extinction, but doomed to it, if habitat loss and fragmentation are not reversed (Hanski 1998; Bulman et al. 2007). This extinction debt represents a great challenge for species conservation, yet still offers a chance for management interventions, as long as the species is still present (Kuussaari et al. 2009). Habitat area and habitat quality are main drivers of metapopulation dynamics as their synchronized decline reduces both the carrying capacity and the connectivity

of the system (Thomas et al. 2001; Hodgson et al. 2011). Although we have detailed habitat information only for a subset of patches, we assume, in line with Warren et al. (2021), that the decrease of open habitats due to progressive shrub or forest encroachment is the main driver of population decline. This assumption is supported by the low proportion of grid cells used for our microhabitat analysis that were occupied by larvae (7%), while the vast majority was characterized by conditions, especially in terms of vegetation (shrub and canopy) cover and insolation, that were unsuitable for the species.

Five subpopulations could not be confirmed during the second mapping period (MAP2) and thus mapped as extinct. For two of them (Nr. 7 and 11, Table 1) the distance to the next patch is less than 1.5 km and therefore, a repopulation could be possible, if the habitat would be improved and if a potential source population would be large enough to enable recolonization (Dias 1996). For the other extinct populations, recolonization seems less likely since they are at distances of about 3 km (Nr. 33) and about 5 km (Nr. 5 and 12) from occupied patches. Six populations are isolated (Nr. 1, 28, 29, 32, 34) and are thus severely threatened by extinction, which worsens over time since without management, habitat quality decreases and in addition, dispersion from old isolated populations is far less likely than from new isolated populations (Hanski et al. 2006).

The threshold for significant population decline at distances greater than 1.5 km to the next neighbour fits the picture of maximum dispersal distances of different *Zygaena* spp., determined based on mark–release–recapture studies, ranging from 250 to 3300 m (mean distances between 33 and 400 m) (Franzén and Nilsson 2007). Nevertheless, we assume that our approach tends to underestimate the actual dispersal ability of our target species, as we expect viable populations with numerous individuals to have a higher likelihood of dispersal and thus a higher probability of individuals reaching patches at greater distances than the small relict populations we mapped. For this reason, we used the higher distance threshold based on population stability to define metapopulations and assess connectivity, which affected population size, stability and persistence. Franzén and Nilsson (2007) also showed that dispersal distances derived from small *Zygaena* populations need to be interpreted carefully, and when studying larger populations, they recorded dispersal distances up to 5600 m. As mentioned by Hermann (2021), also the habitat requirements of our target species (i.e. sparse forests at south-west exposed steep cliffs and hillsides) suggest that *Z. angelicae elegans* is adapted to repopulate new habitats created through natural disturbances, like earthslides occurring along the brim of the Swabian Alb; this may indicate that the taxon has distinct dispersal abilities. The rapid positive effect of our habitat management interventions (imitation of a disturbance by

logging and ground disturbance) also supports the species' adaptation to periodic disturbances and its ability to respond rapidly with population growth.

Larval microhabitat

We show that insolation in the afternoon is a key factor for both larval microhabitat selection and the presence of *C. coronata*, which was negatively affected by canopy and shrub cover.

In addition to open forest structures, the larval microhabitat analysis revealed a strong dependence of *Z. angelicae elegans* on the presence and height of *C. coronata*, its most important larval host plant. Only when there is a shortage of food (in our case example, post-diapause larvae devoured almost all available *C. coronata* by the end of May 2018), we found larvae also on *Hippocrepis comosa* and *Lotus corniculatus*.

Our results confirm earlier findings showing the importance of semi-open forests and ecotones with forest edge-type stages (Hofmann 1994, 2005) for *Z. angelicae elegans*, and the threshold of 60% maximum canopy cover for occurrence of *C. coronata* is in line with the species' classification by Ellenberg (1992). Yet, for evidence-based habitat management, quantitative target values are essential, especially for habitat variables that are directly manageable, like canopy cover. Conditional inference trees are a valuable tool for deriving variable thresholds above or below which a significant change in species occurrence or abundance is to be expected, and which can therefore serve as minimum target values (Müller and Büttler 2010). However, for small and declining relict populations, species-habitat relationships are often derived from habitats with insufficient habitat conditions and therefore may not record the species' true range and optimum (Braunisch et al. 2008). This may have been the reason why our models show a continual increase of larval occurrence and abundance with afternoon insolation with only a lower threshold of at least two hours, despite *Z. angelicae elegans* is known to mainly occur in semi-open conditions, which would also make a higher threshold likely.

On the other hand, this finding may reflect the species' actual requirements: it often occurs syntopical with *Zygaena fausta*, which occupies the fully open areas with larvae also feeding on *C. coronata* (Hofmann 1994). As their niches overlap and their larvae can sometimes be found on plants in close vicinity, the occurrence of *Z. angelicae elegans* in semi-open conditions could therefore also be a result of local resource competition and a shift of the species' larval niche to more shaded conditions.

One main limitation of our study is the small sample size, a common problem with rare species (Hernandez 2006) and particularly problematic for endemic species, as

there is no possibility to supplement with—or extrapolate from—data from other regions. In addition, as open forests naturally occur mainly under extreme conditions, the habitats of *Z. angelicae elegans* are often located on steep brims (Fig. 6e), which makes area-wide, systematic data collection difficult, as some habitats are hardly accessible. As butterfly populations can strongly fluctuate, driven by various factors such as weather, habitat quality and mortality factors, e.g. parasitism or diseases (Franzén et al. 2013), our count data need to be interpreted with caution. However, we neither found a significant effect of the number of visits on population size nor of developmental stage on population size and stability, indicating that number of counted larvae is not systematically exceeding the number of imagines. We are, therefore, confident that our data are robust enough for identifying general patterns.

Habitat management—case example

According to Franzén et al. (2013), diet specialists are more often threatened and require more specific conservation efforts than generalists. Applying our target values for management in a case example resulted in a rapid increase in local population size. Measures to increase the insolation by reducing shrub and canopy cover and creating multiple small clearcuts were supplemented by the widening of the machine path with a digger. The latter was beneficial since the excavation of bare ground facilitates the germination of *C. coronata* while reducing other competitive plants. In addition, the change in microclimate caused by the bare ground may have positively influenced larval development (Stuhldreher and Fartmann 2018). Interestingly, we observed the strong population increase to peak two and a half years after the habitat management in winter 2015/16, while the even larger population boost up to more than 400 recordable larvae and more than 580 imagines after the second habitat management in winter 2021/22 occurred just half a year later in the following season. In 2016, right after the first habitat management, we did not visit the patch since we did not expect an immediate effect, as in other examples of managing open forest butterflies, effects on local abundance became obvious only one or two years later (Bergman et al. 2020; Dalüge et al. 2022; Sielezniew et al. 2024). The management in winter 2021/22 however, showed an intense immediate effect. This can only be explained by the *Zygaena*-specific larval diapause, which can last multiple years and may have amplified the observed population increase. An extended larval stage can be caused by endogenous as well as exogenous factors. In our case, we assume that two factors lead to the surprisingly steep increase in individual numbers: first, a very rainy spring and summer in 2021 resulting in a very low number of imagines (Fig. 5) and a disproportionally high number of larvae

extending their larval stage diapause (exogenous reason) until 2022. Second, a combination of habitat improvement and favourable weather conditions in the following season, which resulted in a disproportionally high number of larvae terminating diapause and fully developing into imagines in 2022. Density-dependence processes or reduced mortality factors could have additionally contributed to this peak.

Conclusions and management recommendations

While afternoon insolation, and the availability and height of the larval host plant determine microhabitat quality for *Z. angelicae elegans*, habitat connectivity at the landscape level is key for population persistence.

In order to save the last relict populations of *Z. angelicae elegans* from extinction, we therefore strongly suggest immediate evidence-based management measures to improve habitat quality with the short-term goal of enlarging the existing populations, and the long-term goal of developing stable metapopulations. While the improvement and enlargement of existing habitats benefits of the advantage that the larval host plant is already present and can be propagated, the development of metapopulations requires the creation of new habitat patches within a maximum distance of 1.5 km around the source patches, where the larval host plant needs to be sown. As we comprehend our thresholds for habitat variables as minimum requirements of *Z. angelicae elegans*, and because our target species often occurs syntopical with other red-listed and even more light-demanding burnet moth species (e.g. *Z. fausta*, *Z. osterodensis*, *Z. transalpina*) we suggest to create habitat gradients, ranging from semi-open ecotones to completely open areas (i.e. multiple small clearcuts up to a size of about 0.5 hectares, which may be established in rotation, or larger open areas with an average canopy cover of 30%). Recent studies underline the importance of clearcuts as habitat for many endangered butterflies (Ram et al. 2020; Viljur et al. 2020; Hermann 2021; Sielezniew et al. 2024), and Bergmann et al. (2020) specifically state clearcuts to provide suitable habitat for various *Zygaena* spp., including endangered grassland burnet moths. The approach of multiple small clearcuts implemented in our case example resulted in a strong increase to more than 500 recorded imagines which shows that strong population boosts within very short timeframes are possible (Fig. 5). Although this population size is still far from the size of a minimum viable population, which consists of thousands of individuals (Flather et al. 2011) distributed over at least 15–20 patches (Hanski 1998), our results give reason to hope that intensive habitat management is able to increase population sizes significantly, so that one day they will reach the critical size for viable populations. Identifying potential key areas for efficient restoration, reestablishment

and connection of habitats would be an important aspect of future research.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-025-00673-9>.

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Author contributions N.D.: Data collection, data analysis, data visualisation, writing main manuscript text. V.B.: Conceptualization, review of data analyses, main editing of manuscript. A.H.: Data collection, writing, editing. G.M.: manuscript draft, writing, editing. V.K.: Data collection, preliminary data analysis. All authors reviewed the manuscript.

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Data availability The data that support the findings of this study are available from the corresponding author upon request, as the data contain sensitive information on the occurrence sites of a highly endangered taxon.

Declarations

Competing interests The authors declare no competing interests.

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