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ORIGINAL PAPER

Conserving apollo butterflies: habitat characteristics and conservation implications in Southwest Finland

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Abstract

The conservation of insects, particularly endangered species such as the Apollo butterfly, is a pressing global concern. Understanding the habitat requirements and factors influencing species occupancy is crucial for designing effective conservation strategies. We focused on investigating the habitat characteristics expected to affect the occupancy of the nationally endangered Apollo butterfly in Southwest Finland. We conducted field surveys and GIS analysis to assess the impact of larval host plant and adult nectar resources, habitat encroachment, elevation, connectivity, and spatial variation on Apollo larval occupancy in rocky outcrop habitats. We found that rocky outcrops with abundant host plants and those less isolated from nectar patches play a significant role in supporting Apollo reproduction, whereas encroachment, specifically increased tree volume, negatively affected occupancy. We additionally observed spatial variation in occupancy across different blocks within the study area. Our findings emphasise the importance of resource availability for Apollo butterflies and highlight the dynamic nature of their habitat requirements. Maintaining a network of intact rocky outcrops with suitable resources is essential for the long-term persistence of the Apollo butterfly population in the region.
Implications for insect conservation: Our research underscores the critical need to protect and restore habitats for the Apollo butterfly, particularly by addressing threats such as habitat encroachment and construction projects that pose risks to their breeding sites.

Keywords Apollo · Butterfly · Endangered · Habitat · Restoration · Host plant

Introduction

Biodiversity conservation is currently one of the most significant challenges facing our society and ecosystems (Cardinale et al. 2012). Anthropogenic actions, climate change, and habitat loss are among the primary factors causing biodiversity loss and documented declines in terrestrial insects (Sánchez-Bayo and Wyckhuys 2019; Wagner 2020; Cardoso 2020; Ceballos et al. 2020). Conserving biodiversity and insect diversity is essential for maintaining ecosystem services, stability and functioning (Börschig et al. 2013; Potts et al. 2016; Cardoso 2020; Sollai and Solari 2022). Butterflies (*Rhopalocera*) are among the best-studied groups of insects and are valuable environmental indicators because they react quickly to changes in their habitat. Nevertheless, European butterflies, particularly those of the grassland species, are facing a general decline (Warren et al. 2021). Although climate change is considered a significant global threat, habitat loss is known to be the most destructive threat to biodiversity, especially for butterflies and threatened species (Newbold et al. 2015; McWilliams et al. 2019; Horváth et al. 2019; Warren et al. 2021; Hogue and Breon 2022). Hanski (2005) identified four main types of habitat loss: loss of habitat quality, loss of habitat area, loss of habitat connectivity, and loss of habitat continuity. Direct human action has transformed almost half of the land, with negative consequences for biodiversity (Fischer et al. 2007). Agricultural intensification, leading to monocultures and habitat fragmentation, further exacerbates this issue (Raven and Wagner 2021).

Like many other regions, Finland has experienced significant habitat loss and changes in land use due to human activities (Ruuska and Helenius 1996; Millennium Ecosystem

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Assessment 2005; Hanski 2011; Kontula and Raunio 2019; Sunde et al. 2023). The disappearance of cultural habitats created and maintained by traditional agriculture, including various kinds of meadows and pastures, is the second most significant threat to biodiversity after forestry in Finland (Hyvärinen et al. 2019). In general, in the EU (Warren et al. 2021), these open habitats suffer from overgrowth, a direct consequence of changes in agriculture such as abandoning land, reducing grazing, and reaping and burn-clearing. Eutrophication caused by fertilisers and long-range transboundary deposits, combined with a warming climate, facilitates habitat overgrowth. Regardless of habitat type, land use changes and habitat loss have caused declines in several insect species and populations, particularly butterflies (Sánchez-Bayo and Wyckhuys 2019; Wagner 2020; Cardoso 2020; Wagner et al. 2021).

This study focuses on the Apollo butterfly (*Parnassius apollo,* L.*)*, a species similar to many other butterflies that are susceptible to environmental changes due to their restricted and specialised habitats (Van Swaay and Warren 1999; Crone and Schultz 2003; Wiens and Graham 2005). Although classified as "Least Concern" on the IUCN Red List due to its wide distribution and minor estimated decline worldwide (Nadler et al. 2021), the Apollo butterfly is declining worldwide, particularly in European lowlands (Nakonieczny et al. 2007; Van Swaay et al. 2010; Nadler et al. 2021). Protected under the EU Habitats Directive (Annex IV), the Apollo butterfly's habitat management is crucial for its conservation. Yet, many areas lack proper management, leading to population declines (Nadler et al. 2021). Finland represents the lowland population in the northernmost range of Apollo, and the known populations occupying only the country's southwestern corner are small and declining (Marttila et al. 1991; Hyvärinen et al. 2019). Furthermore, the species generally occurs at low densities, and the probability of colonisation is very low outside its range (Marttila et al. 1991; Fred and Brommer 2010). The conservation-driven translocation of the Apollo butterfly within Finland initially showed some success (Fred and Brommer 2015), but no long-term establishment was achieved (M. Fred pers. comm.). According to Hyvärinen et al. (2019), Apollo is considered an endangered species at the national level. The remaining strongholds of the Apollo butterfly are on the Åland Islands and the coast of Southwest Finland (Marttila et al. 1991). However, in the archipelago of Southwest Finland, the abundance and probability of occupancy of Apollo butterflies have decreased by 50% over the last two decades (Kukkonen et al. 2022).

Describing species' habitats can be challenging, but in Finland, Apollo butterflies are mainly found on rocky outcrops, where their sole host plant, orpine (*Hylotelephium telephium*), grows. These rock outcrops are threatened by overgrowth and construction (Kontula and Raunio 2018; Hyvärinen et al. 2019). Characterised by their chemical composition, steep topography, microclimates, proximity to water bodies, natural conditions, and various combinations (Ministry of the Environment 2017), rocky outcrops are a critical habitat. In this paper, we study a coastal population around the city of Parainen, which, based on recorded observations, has endured from the early 20th century to the present day (Häkkinen 1976; NAFI 2023). In this population, Apollo butterflies occur on rocky outcrops scattered in an agricultural landscape. Given the declining Apollo population, the threat to its habitats from construction (Nieminen and Ahola 2017, pers. obs.), and the risk of regional extinction as a sedentary habitat specialist overwintering in the egg stage (Sunde et al. 2023), conservation efforts benefit from a better understanding of which rocky outcrops Apollo uses in the landscape. In patchy populations, such as the coastal population in Parainen (Brommer and Fred 1999), many suitable outcrops exist for Apollo, but not all are equally important. Recognising the most important breeding and resting habitats for Apollo and protecting them with proper management plans is crucial, as the species does not thrive under passive protection (Nakonieczny et al. 2007). For the Apollo and many butterflies, adult and larval feeding requirements typically require different plant species, resulting in spatial decoupling (Janz 2005). For butterflies, the nectar supply is one of the primary resources determining habitat quality (Wallisdevries et al. 2012). The quantity of nectar flowers also influences the movement patterns of Apollo butterflies, affecting the next generation; female Apollo butterflies lay more eggs in suitable habitats near nectar resources (Brommer and Fred 1999; Fred and Brommer 2003; Fred et al. 2006). Additionally, the survival of the Apollo butterfly, both globally and nationally, is heavily reliant on the availability of its larval host plant (Nakonieczny et al. 2007; Fred and Brommer 2010).

In this study, we investigate the habitat requirements of the Apollo butterfly, focusing on the presence/absence of Apollo larvae on rocky outcrops. We survey Apollo larvae, as the presence of larvae indicates that the rocky outcrop is reproductively important to the population. We surveyed 327 rocky outcrops for Apollo larvae in the spring of 2022 and 2023. The surveys were carried out in four spatially separate networks of rocky outcrops that are presumably semi-independent of each other. We hypothesise that Apollo butterflies are more likely to occur in rocky outcrops that are open, well-connected, well-lit, and larger in size, with abundant orpine and close proximity to nectar plants. Using a combination of Geographic Information Survey (GIS) data and field-based mapping, we analyse the characteristics of rocky outcrops and other landscape elements that may affect the Apollo butterfly. Specifically, we consider (1) the number of Apollo butterfly host plants (orpine) on rocky outcrops, (2) the encroachment and openness of rocky outcrops,

(3) the potential exposure of rocky outcrops to sunlight to describe their microclimate, (4) proximity of rocky outcrops to adult nectar resources, (5) elevation of rocky outcrops, as more highly elevated outcrops could contain fewer trees and more open areas (Macias-Fauria and Johnson 2013), (6) the distance between surveyed outcrops (connectivity), and (7) whether the survey date affects the presence of larvae, as early-season larvae may go undetected due to their small size.

By understanding these factors, we aim to inform conservation strategies that can be applied not only to the Apollo butterfly but also to other specialised butterfly species facing similar ecological challenges.

Materials and methods

Study system

The coastal population of Southwest Finland resides on the islands that comprise the Parainen archipelago municipality. For more than 100 years, several Apollo observations have been made in this area (Häkkinen 1976; FinBIF 2023). For parts of this region, detailed surveys of Apollo larvae were carried out approximately 20 years ago and in 2020 (Fred 1998; Laaksonlaita 2023). The information on presence from the abovementioned previous studies was used to select a study area of approximately 22 km^2 within the Parainen coastal archipelago (Fig. 1). The study area comprises three relatively large islands containing agricultural landscapes, forests, and human settlements. The study area was divided into four semi-independent blocks (Fig. 1), with the objective of surveying all rocky outcrops (potentially suitable habitat) in each block and thereby assessing the potential for spatial variation. Block 1 (3 km^2) is located on the northernmost island, closest to the mainland. Block 2 (9 km^2) is located on the southernmost island of the three islands surveyed. The middle survey island between blocks 1 and 2 was divided into two blocks, blocks 3 and 4 (both 5 km^2). The central island was divided into two blocks to separate one large landowner's estate from the rest of the island. This landowner has performed small-scale restoration work for Apollo by opening meadows and rocky outcrops and, in general, favours agricultural and forestry practices that promote biodiversity and reduce the effects of climate change (P. Heikkinen, pers. comm.). For instance, fields are

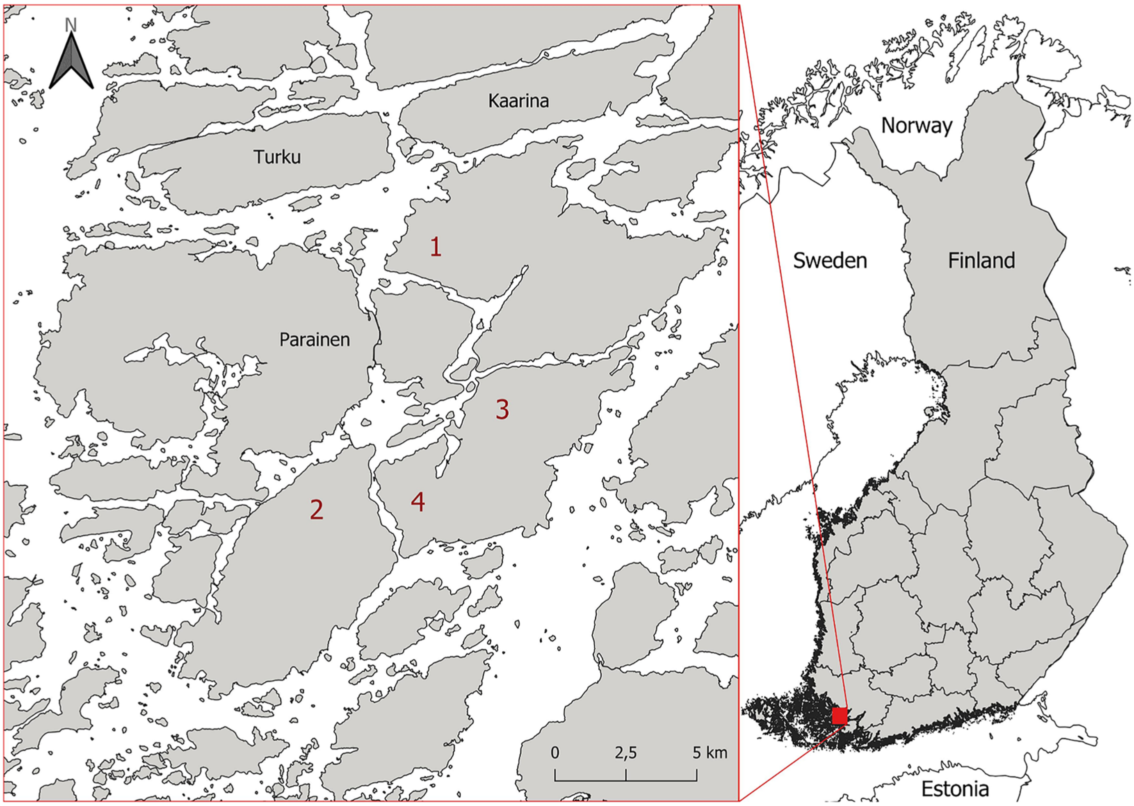

Fig. 1 The study area is in southwest Finland's municipality of Parainen. The survey blocks are presented with numbers (1–4) inside the islands. ©National Land Survey of Finland (NLS), the regions of Finland 2021, CC By 4.0 DEED and Natural Earth, Admin 0—Countries version 5.1.1, Free vector and raster map data @ naturalearthdata.com. Modified: Jonna M. Kukkonen 25.6.2024

cultivated biologically and organically. Furthermore, Apollo's occurrence was previously recorded multiple times in the estate area (NAFI 2023).

The Apollo butterfly has a yearly life cycle in the northernmost part of its range, with larvae and adult butterflies present mainly from May to August (Marttila et al. 1991). The presence of larvae is a sure sign that a host-plant patch is being used for breeding (Fred et al. 2006); thus, the detection of Apollo larvae was the focus of our surveys. Apollo overwinters as an egg (Marttila et al. 1991; Fred and Brommer 2003). The larvae start to hatch in May, and after three to four weeks, they form a cocoon in the undergrowth and become pupae (Fred and Brommer 2003). Larvae occur singly but can be observed relatively effectively due to their aposematic colouration (orange and black). In addition, the grazing patterns on host plants can aid in finding larvae even when they have taken cover in the surrounding vegetation. Development to pupation is not synchronous for all larvae. Throughout most of the larval period, some individuals have not yet hatched from their eggs and others that have already pupated (Fred and Brommer 2003). This allows the detection of Apollo larvae of varying ages from the beginning of May to mid-June, when the surveyor(s) visited rocky outcrops in the study area to count Apollo larvae and the host plants. When searching for host plants, all areas were surveyed by walking through them as consistently as possible, with approximately equal searching effort per unit area. The total time spent surveying for larvae was proportional to the total amount of host plants present. The larval survey season was considered to last approximately 1.5 months (46 days). However, surveys were not conducted daily throughout this time period.

The surveys focused on areas outlined as rocky outcrops on a topographical map, i.e., habitat patches. Our sampling approach aimed to survey both documented occurrences of Apollo larvae from a previous, recent study (Laaksonlaita 2023) and nearby outcrops that were previously unsurveyed to capture habitat characteristics across the landscape comprehensively. In 2022, 124 outcrops were surveyed. The following year, 203 outcrops were explored, of which 99 were not surveyed in 2022. Consequently, 223 unique rocky outcrops were surveyed over the course of these two years. The geographical information system QGIS (version 3.22, 2022) was used to estimate the total patch area sizes of the rocky outcrops.

Apollo depends on two significant resources: larval host plants and flowering nectar plants for the adult stage (Brommer and Fred 1999; Fred and Brommer 2003; Fred et al. 2006). The larval host plant, perennial orpine, can grow one or multiple stems and can be found singularly around a rocky outcrop or in more dense patches. These patches of the host plant were marked on the map, and the number of host plants in each patch was counted. During the larval surveys and during the adult Apollo season, from July to early August, nectar plant patches were also marked on the map of the survey area. In the coastal population, most host-plant patches do not contain a nectar-plant patch (Fred et al. 2006). The Apollo butterfly is not a specialist in nectar plants (Fred 2004) but favours large, bright-coloured flowers that are relatively common species in Finland, such as *Cirsium* spp., *Centaurea* spp., *Hieracium* spp., *Trifolium pratensis, Chamaenerion angustifolium,* and *Valeriana officinalis* (Marttila et al. 1991; Fred 2004). For an area to be designated as a nectar site, it should contain a minimum of 10 stems with large inflorescences clustered together or a smaller group of very large and conspicuous plants, each bearing several flowers, such as *Cirsium vulgare* (Fred et al. 2006). In Parainen, patches of nectar-producing plants were typically extensive (Fred et al. 2006), often stretching several meters along roadsides and field margins.

We employed two isolation measures to assess the connectivity of rocky outcrops within the study area. The first measure,$-\sum exp\left(-\alpha D_{in}\right)$, quantifies the isolation of rocky outcrops from nectar patches, where D_{in} represents the Euclidean distance between outcrop i and nectar patch n, and α is a scaling parameter (Hanski 1994). This measure assigns the greatest weight to patches in close proximity. For the parameter α, we used a value based on the capture-mark-recapture of Apollo done in the study area (0.27; Brommer and Fred 1999). A higher value indicates greater isolation from nectar sources. The second measure, $-\sum(exp\left(-\alpha D_{ij}\right) * patch\ size(j))$, evaluates the interpatch isolation, incorporating the size of each neighbouring outcrop j. This measure accounts for both spatial proximity and size disparities between outcrops, with larger values indicating increased isolation among outcrops. Both D_{in} and D_{ij} were measured from the centre to the centre of a patch in units of 100 m, as described by Hanski et al. (1994). These measures collectively provide a robust evaluation of spatial isolation in relation to both nectar sources and neighbouring rocky outcrops within the study landscape.

Geographical information systems (GIS) data

The landscape features used in the analysis are the raster layer (16 m × 16 m) of the growing stock volume for all tree species (1 m^3/ha) (Luke 2021) and the raster layer (2 m × 2 m) of the digital elevation model, DEM (NLS 2023). The patch size area and distances between rocky outcrop centroids and nectar patches were calculated, and the values were extracted from the raster layers via QGIS (version 3.22, 2022). Because the slope and aspect of a rocky outcrop affect its potential exposure to sunlight, we used the digital elevation model (NLS 2023) to calculate the insolation (WH/m^2) of each rocky outcrop to describe its microclimate. Insolation was computed using ArcGIS

Pro (version 3.1.0, ESRI 2023) with the analysis tool "area solar radiation". The time period used for calculating the insolation was May 2022.

Statistical analyses

The presence/absence of Apollo was recorded in several rocky outcrops in two seasons, and we, therefore, applied a generalised linear mixed-effects model (GLMM) in which the patch ID was used as a random intercept to account for the dependency among observations made on the same rocky outcrop. The binomial GLMM model was implemented with a logit function in the R package glmmTMB (Brooks et al. 2017). We used a rocky outcrop's occupancy (unoccupied 0 or occupied 1) as the response variable. The fixed effects included the number of host plants (continuous), the size of the patch (continuous), the mean value of the tree volume of the growing stock in a patch (continuous), the nectar isolation (continuous), the mean value of the elevation of a patch (continuous), the interpatch isolation (continuous), and the insolation of a patch (continuous). Temporal variation was captured by including the survey date (continuous), the survey year (categorical with two levels), and spatial variation by including the survey block (categorical with four levels). We considered meaningful interactions survey year × block number to capture spatial–temporal interactions at the above-patch level. We chose not to utilise stepwise model selection methods due to well-documented concerns about their reliability and interpretability (Mundry and Nunn 2009). Instead, we present the full model with all predictor variables included simultaneously. This approach allows for a comprehensive evaluation of each variable's effect while minimising the risk of erroneous conclusions associated with stepwise techniques. All estimates were standardised to facilitate interpretation, ensuring that effect sizes were comparable across predictors. We used the restricted maximum likelihood (REML) approach and the Wald test for hypothesis testing. All analyses were performed with the R program (R Core Team 2023), version 4.3.1.

Results

The data comprised 327 rocky outcrops surveyed over two years (Table 1). The size of the outcrops averaged 16.36 ± 1.30 SE ha (Table 2). Apollo larvae were detected on 46% (150/327) of these rocky outcrops (Table 1), and this proportion did not differ between years (Table 1; $X^2_1 = 0.07$, $P = 0.79$). Of the 327 patches surveyed in two years, 50 patches (15%) had fewer than five host plants at the time of the survey. However, in 3 of these patches, in one patch in 2022 and two in 2023, an Apollo larva was detected. In most blocks, especially in 2023, approximately 40 rocky outcrops were surveyed (Table 1). The number of host plants in the surveyed outcrops over two years varied, averaging 42 host plants per outcrop

Table 1 Descriptive statistics of the survey findings

Year/block	N	OC	F	MHP	MA (ha)	Density
2022	124	56	0.45	35	18.65	1.90
Block 1 (north)	18	7	0.39	25	32.79	0.76
Block 2 (south)	41	9	0.22	26	21.98	1.16
Block 3 (middle north)	44	28	0.64	49	9.31	5.28
Block 4 (middle south)	21	12	0.57	35	19.60	1.78
Year/Block	**N (new)**	**OC (new)**	**F**	**MHP**	**MA (ha)**	**Density**
2023	203 (99)	94 (37)	0.46	46	14.96	3.09
Block 1 (north)	40 (23)	16 (6)	0.40	72	22.05	3.27
Block 2 (south)	68 (35)	31 (15)	0.46	36	16.18	2.25
Block 3 (middle north)	54 (18)	31 (11)	0.57	46	7.94	5.78
Block 4 (middle south)	41 (23)	16 (5)	0.39	38	15.27	2.47

The column Year/Block denotes the two survey years (totals per year) and specific numbers for each block within each year

For each block, the block's location within the study area (see Fig. 1) is denoted within brackets

We further report the number of surveyed rocky outcrops (N), where for 2023, the total number of rocky outcrops surveyed is given with inside brackets the number of "new" rocky outcrops not surveyed in 2022

The number of occupied rocky outcrops (where Apollo larvae were detected) is reported in column OC, with–for 2023–the number of occupied new rocky outcrops inside brackets

F denotes the ratio of occupied rocky outcrops to the total number of surveyed rocky outcrops

MHP represents the average number of host plants (*H. telephium*) in the surveyed rocky outcrops, and MA (ha) represents the average size of the surveyed rocky outcrops in hectares, with density indicating the average density of host plants per hectare (plants/ha)

Table 2 Descriptive statistics of the surveyed rocky outcrop characteristics

Variable	Data 2022–2023				Mean/block			
	Min	Max	Median	Mean	1	2	3	4
Number of host plants	0	333	27	42	57	32	47	37
Mean tree volume (m^3/ha)	0	287.0	97.4	97.3	103.0	80.6	115.1	109.8
Nectar isolation (100 m)	− 19	− 3.7	− 13.7	− 13.6	− 13.8	− 13.4	− 14.7	− 13.1
Distance to a nectar patch (m)	0.2	889.9	134.9	158.6	146.4	167.3	121.5	170.3
Area of outcrop (ha)	0.009	156.0	6.4	16.4	21.9	17.1	8.5	15.0
Mean elevation (m.a.s.l)	7.4	56.4	31.7	32.0	42.5	31.8	26.1	32.2
Insolation (kWH/m2)	102.4	128.3	117.7	117.6	116.3	118.8	117.5	116.5
Interpatch isolation (100 m)	− 1642	− 117	− 673	− 749	− 1053	− 682	− 675	− 611
Distance between rocky outcrops (m)	34.9	14,288.7	5690.4	5563.8	6992.7	6022	4851.3	4540.2

The column "Variable" denotes the variables used in the model as rocky outcrop characteristics and fixed effects

However, with the nectar and interpatch isolation values, we provide the distances from a rocky outcrop to a nectar patch (Distance to a nectar patch) and between rocky outcrops for clarity (Distance between rocky outcrops)

We provide the minimum (min), maximum (max), median (median), and average (mean) values of each of the survey datasets (Data 2022–2023)

The insolation values were calculated for the time period of May 2022

In addition to the analysis variables, we also present the average values of the variable for each block

(Table 2). The growing stock volume for all tree species in the surveyed outcrops also showed variation, as did the isolation measure of nectar patches and interpatch (i.e. between rocky outcrops) (Table 2). The elevation of the surveyed outcrops ranged from low to moderate levels above sea level. Insolation values were relatively consistent but displayed some variation, and the distance to the nearest neighbouring rocky outcrop also varied (Table 2). The correlation coefficients among habitat characteristics (number of host plants, patch size, tree volume, insolation, nectar isolation, and interpatch isolation) ranged from − 0.44 to 0.46, where the highest correlation (0.46) was between host plant number and patch size. These findings indicate no strong correlations among the variables examined in our study, and we, therefore, included all as explanatory variables when modelling patch occupancy.

Of the 104 rocky outcrops surveyed in both years, 36 (35%) were occupied, and no larvae were detected in 39 (38%). Occupancy changed between years in 29 (28%) rocky outcrops, indicating occupancy dynamics. Apollo was more likely to occur on rocky outcrops with more abundant host plants and closer to nectar plant patches but was less likely to occur on rocky outcrops with a large growing stock volume of trees (Table 3, Fig. 2). In addition, we found ($P < 0.05$) that outcrops with higher elevations were more likely to be occupied (Table 3, Fig. 2). Finally, there was an indication of spatial variation in occupancy across the study area ("Block" in Table 3; $P < 0.05$), with occupancy being exceptionally high in one block (Table 3, Fig. 2).

Discussion

We examine characteristics of the rocky outcrops and other landscape elements supporting the occupancy of the nationally endangered Apollo butterfly in the coastal population of Southwest Finland. We find that rocky outcrops with a higher abundance of host plants and nearby nectar plants are significant for Apollo. Moreover, we observed that elevated rocky outcrops also play a significant role in the butterfly's habitat. We also find that the encroachment of rocky outcrops, in terms of a greater tree volume of growing stock, lowers the probability of the rocky outcrop being used for reproduction by Apollo. Finally, we find spatial variation (included here by surveying four "blocks" of 20–40 rocky outcrops in this population) in Apollo occupancy.

Our finding that the abundance of larval resources (host plant) and proximity of adult resources (nectar plants) are essential for Apollo is consistent with results obtained some 20 years ago in one part of this population (Brommer and Fred 1999; Fred and Brommer 2003, 2009, 2010; Fred et al. 2006), roughly coinciding with block 2. Our finding that these two resources are crucial for Apollo when considering a larger area two decades later underlines their importance in this Apollo population. This is consistent with broader butterfly ecology, where the availability of these resources is crucial for many species (Boggs et al. 2003; Dennis et al. 2003, 2006; Hardy et al. 2007; Wallisdevries et al. 2012; Curtis et al. 2015). Previous research in other Apollo populations (Nakonieczny et al. 2007;

Table 3 Estimated regression parameters, standard errors, Z values, and P values for the fixed effects in a binomial generalised linear mixed model (GLMM) on the occupancy of rocky outcrops by the Apollo butterfly

Parameter	Estimate	Std. error	*z* value	Chisq	Df	P value
Intercept	– 1.421	0.910	– 1.562			0.118
Number of host plants	0.913	0.295	3.095	9.577	1	**0.002**
Area of patch	0.210	0.279	0.752	0.566	1	0.452
Mean tree volume (m^3/ha)	– 0.597	0.264	– 2.266	5.133	1	**0.023**
Nectar isolation	– 0.484	0.245	– 1.978	3.912	1	**0.048**
Mean elevation (m.a.s.l.)	0.627	0.305	2.053	4.216	1	**0.040**
Insolation	– 0.140	0.219	– 0.639	0.408	1	0.523
Date of the survey	– 0.254	0.222	– 1.141	1.302	1	0.254
Interpatch isolation	0.248	0.282	0.880	0.775	1	0.379
Block				8.665	3	**0.034**
Block 2	– 0.294	1.080	– 0.273			
Block 3	2.612	1.178	2.217			
Block 4	1.501	1.127	1.332			
Year				0.395	1	0.530
Year x block				6.019	3	0.111
Year x block 2	1.684	1.078	1.562			
Year x block 3	– 0.205	1.066	– 0.192			
Year x block 4	– 0.170	1.193	– 0.143			

On the right side of the vertical line is the analysis of the deviance table (Type II Wald test), which includes chi-square values (Chisq) with their corresponding degrees of freedom (Df) and P values (P value)

The variables block and year were included as categorical variables. The other (continuous) variables were scaled to zero means and unit SDs to make their effect sizes (estimates) comparable

The estimated variance across host-plant patches $\sigma^2 = 3.29$

P values less than 0.05 are in bold

Adamski and Ćmiel 2022; Sbaraglia et al. 2023) highlights similar dependencies, demonstrating that conservation strategies focused on these resources are widely applicable. For example, Baz (2002) emphasised that successful conservation management requires habitat management and restoration focused on host and nectar plants. This principle applies broadly across butterfly species (Smallidge and Leopold 1997; Dennis et al. 2006; Hardy et al. 2007; Wallisdevries et al. 2012; Curtis et al. 2015), making our findings relevant to general butterfly ecology and conservation.

We found that tree encroachment on rocky outcrops significantly lowers the probability of Apollo occupancy. This phenomenon is not unique to the Apollo butterfly; many butterfly species are sensitive to habitat structure changes caused by encroachment and succession. Encroachment reduces the open habitats required by many specialised butterflies, as seen with the Clouded Apollo butterfly (Parnassius mnemosyne) (Konvička and Kuras 1999; Välimäki and Itämies 2005). Encroachment is a significant threat to European butterflies in general, particularly those dependent on grasslands that become forests due to land abandonment or the cessation of grazing (Kuussaari et al. 2007; Warren et al. 2021; Sunde et al. 2023). Our findings contribute to the broader understanding that managing open habitats is crucial for conserving many specialised butterfly species.

The elevation of the outcrop, despite its seemingly unremarkable range from 7 to 56 m a.s.l., was found to be a significant factor influencing Apollo occupancy. This unexpected finding could be attributed to the mate-locating behaviour of male butterflies, who use hilltops as landmarks for finding potential mates (Rutowski 1991). This hill-topping behaviour, exhibited by various patrolling butterflies and species of Papilionidae (Rutowski et al. 1989; Takeuchi 2019), including Apollo (Baz 2002; Adamski and Witkowski 2006), could explain the significance of the elevation. However, our findings suggest that the openness of the outcrop is a more significant characteristic for the Apollo larvae than its elevation in this lowland population.

We find strong evidence for spatial differences in Apollo occupancy within our relatively small study area. As this spatial heterogeneity is apparent in a model that also considers the effect of all the above-discussed landscape elements, this finding implies that—in addition to these landscape elements—there are other factors affecting Apollo occupancy that we did not consider here. Within our study area, the most favourable part for Apollo is located in the northern part of the central island (Fig. 1; block 3). In this part of the study area, biodiversity is promoted by managing the

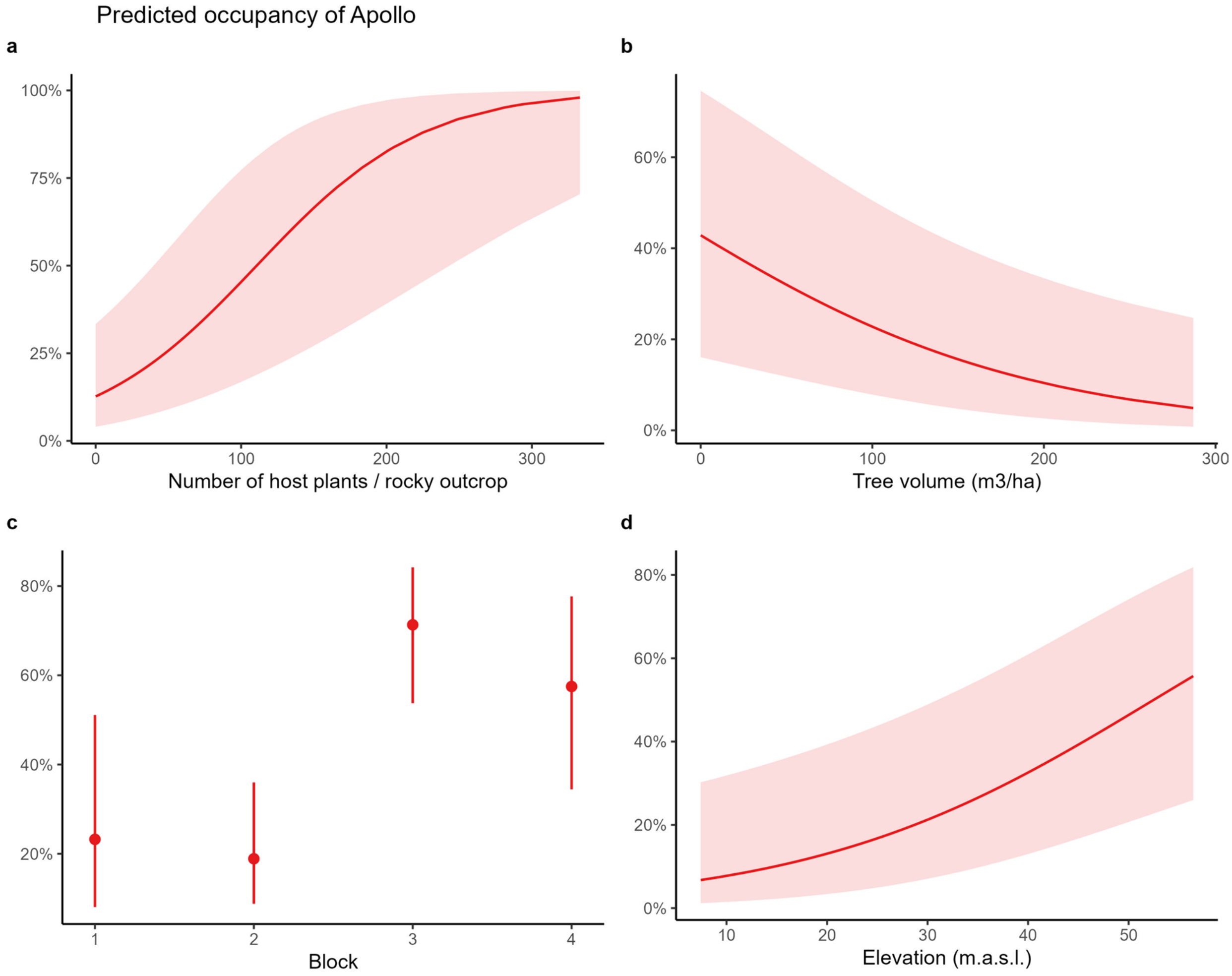

Fig. 2 Marginal effects for four significant model terms of a GLMM on the predicted probability of Apollo occupancy (Table 3). The marginal effects of **a** the number of host plants/rocky outcrop, **b** the average tree (growing stock) volume of an outcrop, **c** within-study-area spatial differences (between survey blocks) and **d** elevation of a rocky outcrop are plotted here

land. For instance, unpaved roadsides with nectar flowers are mowed once relatively late in the summer (Valtonen and Saarinen 2005), and sheep graze on some outcrops after the larval season, which could benefit Apollo in terms of critical resources. Furthermore, the above-described small-scale restoration work has been performed for the Apollo in the area. It seems likely that the details of land management related to aspects other than larval and adult resources and encroachment benefit Apollo. Another aspect is that the fields are cultivated biologically and organically in block three. There is evidence that organic farms offer higher-quality habitat for butterflies than conventional farms (Goded et al. 2019; Van Deynze et al. 2024). More research is thus needed to identify which aspects of land management favour Apollo.

We did not observe any significant impact of connectivity on Apollo occupancy in our study area, likely due to the relatively high density of rocky outcrops within the survey blocks (the longest distance to the nearest neighbour was < 800 m). A recent study by Graser et al. (2023) also concluded that habitat quality is a more influential factor than patch connectivity for two light-demanding butterfly species. Although our research did not identify habitat connectivity and patch size as significant factors, we acknowledge that these elements are well-established determinants influencing butterfly populations globally (e.g., Haddad and Tewksbury 2005; Binzenhöfer et al. 2008; Brückmann et al. 2010; Jangjoo et al. 2016; Paterson et al. 2019; Stilley and Gabler 2021; Popović and Nowicki 2023).

Implications for conservation

The Apollo butterfly is a species listed in Annex IV of the EU Habitats Directive that requires strict protection (Council Directive 92/43/EEC). The Habitats Directive mandates that all Member States establish a strict protection regime for the species listed in Annex IV within and outside protected areas (European Commission 2024). In particular, Member States must prohibit the deterioration or destruction of these species' breeding or resting sites (European Commission 2024). Despite strict protection, a major threat to Apollo in this and other populations is the deterioration of its breeding habitats. In our study population, one threat is that both large and smaller construction projects are carried out on the rocky outcrops (breeding habitat) of Apollo (The Supreme Administrative Court 1999, Nieminen and Ahola 2017). This Apollo population is scattered across various rocky outcrops. In this patchy population (Brommer and Fred 1999), Apollo adults move across several rocky outcrops in the landscape, and arguably, the importance of a single outcrop for the entire population is relatively small. However, habitat quality at a specific location in a given year is determined by its inherent spatial attributes and ever-changing environmental conditions (Hanski 2005). Rocky outcrops not used in one year may be crucial in another year and vice versa. In particular, our finding that rocky outcrops near nectar plants are more likely to produce the next generation of Apollo implies that the system is very dynamic, as nectar plants grow on ephemeral sites and are likely to change location from year to year. Hence, a network of intact outcrops with host plants near nectar resources is needed for Apollo to persist in this area. Chipping away rocky outcrops from this network for infrastructure development likely will, at some point, make the network unsuitable for Apollo, and more research is needed to understand better whether and where a critical threshold exists.

Our findings suggest strategies for restoring or offsetting Apollo's habitat loss. Offsets are a way to achieve additional or equivalent biodiversity benefits to compensate for the losses caused by development. In general, offsetting is the last resort in the mitigation hierarchy. First, developers must try to avoid, minimise, and reverse the predicted impacts of biodiversity. Our findings imply that it may be possible to offset Apollo by opening previously suitable habitats and ensuring high host plant abundance and the presence of nearby nectar resources (cf. Nieminen and Ahola 2017).

Rocky outcrops form potential breeding habitats for Apollo in SW Finland, and conveniently, these can be readily delineated. Importantly, however, we find that the area of the rocky outcrop itself has little importance, but it is the number of host plants that affect Apollo occupancy. Thus, not only large rocky outcrops are important for Apollo reproduction since even small rocky outcrops can contain a relatively high (to their area) abundance of host plants. The ramification of this finding is that responsible infrastructure development in this Apollo population requires knowledge of host plant numbers on rocky outcrops and taking this information into consideration. However, as far as we know, this detailed information is not easily obtained through remote sensing, but field surveys are needed. The Apollo butterfly is, in that sense, one of many butterfly species that Dennis et al. (2006) describe as relying on resources found in small or even tiny pockets that are widely dispersed. Surveying for these small resources can be challenging due to limited access, search time, and the number of surveyors compared to the area being covered. Nevertheless, orpine is a perennial herb that is easy to census in early spring, as it is one of the first to grow after snow melts. Thus, orpine will likely persist in the same area if conditions remain favourable.

The Apollo butterfly is facing a concerning future, as its populations show declining trends at all levels—global, European, and national (Swaay et al. 2010; Hyvärinen et al. 2019; Nadler et al. 2021). Furthermore, the cold-adapted, sedentary nature of Apollo, along with its specialisation in habitat and host plants, all predict that this declining trend will continue (Pöyry et al. 2009; Eskildsen et al. 2015; Sugimoto et al. 1971; Shirey et al. 2024). Translocation of Apollo in Finland to other suitable sites has proven challenging (Fred and Brommer 2015), and the few Apollo populations remaining thus warrant conservation actions.

Our study's findings provide insights into the general principles of butterfly ecology and conservation. Resource availability, habitat structure, and spatial configuration are relevant to many specialised and threatened butterfly species. Conservation actions should focus on preserving and enhancing these critical habitat features. This includes ensuring the availability of host and nectar plants, managing habitats to prevent encroachment, and maintaining habitat connectivity.

Furthermore, our research underscores the complex interplay of various factors in determining the occupancy dynamics of the Apollo butterfly, with broader implications for the conservation of other specialised butterflies. The importance of specific resources and habitat characteristics identified in our study can inform general conservation strategies, making this study relevant for a wider audience interested in butterfly ecology and conservation. Efficient conservation efforts require a multifaceted approach, considering the specific needs of butterflies throughout their life cycles and addressing the challenges posed by habitat loss and fragmentation.

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(supporting); GIS analyses—review (lead) and writing—review and editing (supporting). JEB: Conceptualisation (lead); methodology (lead); supervision (lead); formal analysis (supporting); investigation (equal); visualisation (supporting); writing—original draft (supporting); writing—review and editing (lead).

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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