



A strong decline of the endangered Apollo butterfly over 20 years in the archipelago of southern Finland

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Received: 10 January 2022 / Accepted: 1 June 2022 / Published online: 24 June 2022
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Abstract

Insect groups are declining worldwide; Lepidoptera are among the taxa most affected in terrestrial ecosystems. The main drivers of these declines are a diverse set of factors relating to environmental change including habitat loss, pollution, and climate change. In 2019 and 2020, we surveyed 118 and 90 islands, respectively, in southern Finland's archipelago for occupancy of *Parnassius apollo* larvae and counted the abundance of their host plant *Hylotelephium telephium*. Compared with historical data (1997–2003), the occupancy of Apollo butterfly larvae has decreased remarkably from about 75% to about 20% of islands and abundance declined as well. However, the abundance of their host plant has not changed. Occupancy models showed that the present occupancy probability is not affected by host plant numbers, and shows substantial colonization-extinction dynamics making the population vulnerable to stochastic extinction.

Implications for insect conservation Our results show that this Apollo butterfly population is declining, and conservation actions are needed.

Keywords *Parnassius* · Occupancy model · Metapopulation · Plant–herbivore interaction

Introduction

Today's rapid rate of extinctions indicates that our planet is facing a catastrophic loss of biodiversity (Ceballos et al. 2020). Insects have a striking rate of decline, which is projected to lead to the extinction of large numbers of the world's insect species over the next few decades (Cardoso 2020; Sánchez-Bayo and Wyckhuys 2019; Wagner 2020). The main drivers of insect species decline are thought to be a diverse set of factors relating to environmental change including habitat loss, pollution, and climate change (Cardoso 2020; Sánchez-Bayo and Wyckhuys 2019; Wagner 2020). In terrestrial ecosystems, Lepidoptera appear to be among the taxa most affected (Sánchez-Bayo and Wyckhuys 2019; Wagner 2020). In Finland, for example, 30.3%

of the assessed Lepidoptera taxa ($n = 716$) are red listed (Hyvärinen et al. 2019). In comparison to central European countries, however, Lepidoptera in Nordic countries, such as Finland, are still doing relatively well (Hällfors et al. 2021).

Part of the taxa Lepidoptera are butterflies that have suffered significant declines in population abundance, range contractions and numerous extinctions around Europe (Thomas 2016; van Swaay and Warren 1999; Warren et al. 2021). Most butterflies inhabit restricted and special ecological niches which makes them vulnerable to environmental changes (Crone and Schultz 2003; van Swaay and Warren 1999). Many butterflies are considered to exist and behave like metapopulations (Hanski et al. 1995), which rely on networks of habitat patches (Crone and Schultz 2003; van Swaay and Warren 1999). Loss and degradation of habitat are viewed as one main reason for decline in butterflies across European countries (Warren et al. 2021). In particular, intensification of agriculture drastically reduced traditional management of habitats based on rotational grazing, hay cutting and other practices. The several resulting habitat changes include, among others, a degradation of habitat quality through a staggering high loss of nectar plants that are an important food source for adult butterflies and thereby increase extinction rates of habitat patches (WallisDeVries

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et al. 2012). Climate change is considered another threat to at least some butterfly species, where especially a projected increase in extreme weather events, such as droughts, could tip butterfly metapopulation dynamics towards extinction (Oliver et al. 2015; Kahilainen et al. 2018).

The Apollo butterfly (*Parnassius apollo*) is endangered and protected in Finland (Hyvärinen et al. 2019; Rassi et al. 2001, 2010). Further, the Apollo butterfly is mentioned in the Council Directive 92/43/EEC, Annex IV among other species of interest to Europe which are in need of strict protection (EU Council 1992). In the Archipelago Sea of southern Finland, the Apollo butterfly lives as a metapopulation occupying small islands (Fred 2004). Islands were monitored in 1997 and annually in 1999–2003 for larval occupancy. Nearly 80% of adult Apollo butterflies stayed on their natal island and extinction/colonization events happened on about 8% of islands each year (Fred and Brommer 2009). These earlier findings suggest that the population can be considered as inhabiting islands forming a metapopulation (Fred 2004). This Apollo butterfly metapopulation is relatively remote, situated around 40 km from the mainland in the outer archipelago where there is no permanent human settlement. The area has, however, historically been used for fishing and animal husbandry. Traditional management of the islands included grazing by sheep and burning of woody vegetation to retain small meadows. The archipelago was densely populated until the 1940s, but has since been largely abandoned, and no large-scale traditional management has been conducted for decades. Orpine (*Hylotelephium telephium*) is the sole host plant for the Apollo butterfly larvae in Finland and only islands where orpine grows hence are suitable for the Apollo butterfly. The amount and the density of host plant is an important habitat factor for Apollo butterfly larvae and their survival on islands in the archipelago (Fred and Brommer 2003, 2010). In addition, movement of adult butterflies over the patches is towards islands where nectar plants are more abundant (Fred and Brommer 2009) and the spatial distribution of adult food resources therefore affects metapopulation dynamics in this system (Fred et al. 2006). The biotopes where orpine grows are vulnerable to overgrowth (Hyvärinen et al. 2019) which could cause a decline in the abundance of the host plant as well as a decline in meadows with nectar plants. Climate-change associated increase in the frequency of droughts could likewise induce vegetation changes for both larval host plant and adult nectar plants in this system. In mountainous populations, microclimatic factors and overall habitat heterogeneity are found to be important for Apollo population persistence in a warming climate (Ashton et al. 2009, Wilson et al. 2015).

In this paper, we report on a recent re-survey of larval occupancy and abundance conducted in 2019 and 2020, and compare our findings to the occupancy and abundance some 20 years ago on the same islands. Additionally, we

study the current abundance of orpine and evaluate whether a change in host plant has occurred during the last two decades. Our expectation is that the abundance of the Apollo butterfly has declined, as for butterflies in general (Warren et al. 2021), possibly in connection with a decline in host plant abundance due to overgrowth. We further expect that islands with the highest abundance of host plant are those where the Apollo butterfly has persisted (Fred and Brommer 2003, 2010).

Materials and methods

Study system

We study the occupancy of the Apollo butterfly (*Parnassius apollo* Linnaeus 1758, family Papilionidae) in the islands of Archipelago Sea in southwest Finland. These islands can be classified as Natura 2000 -type boreal Baltic islets and small islands (code 1620) (EU Council 1992). The barren islands' vegetation is mainly composed of grasses, heather and crowberry with low-growing Juniper shrubs, with surrounding areas of mosses, lichens, and bare rock. Some bigger islands have small patches of trees. The study area covers, open water areas included, approximately 165 km².

At this location, the Apollo butterfly has a single generation per year; the larvae and adult butterflies occur at this northern range in general from May to August (Marttila et al. 1991). The Apollo overwinters in an egg-state and larvae hatch in the spring and start feeding on their host plant (Fred and Brommer 2003). Due to the high mobility of adult Apollo butterflies, the presence of larvae which are conspicuous, large (>0.5 cm) and have distinct warning colors, is a reliable sign of a host-plant patch having been used for breeding (Fred et al., 2006).

The historical data, collected in 1997 and annually from 1999 to 2003, acted as a baseline for this study. In the survey years starting from May and continuing to early June investigators visited several of the islands in the study area to count the numbers of the Apollo larvae. Based on removal counts, the probability of detecting at least one larva in an occupied habitat patch was 97% in the historical years (Fred and Brommer 2003). The weather conditions (sunny or cloudy) were also recorded. The surveyed area within the islands was focused in the zone near the coastline where most of the host plants grows. The total amount of time surveying Apollo butterfly larvae on each island depended on the total amount of host plant present. In the historical data, the number of orpine plants per site were scored in four categories: (1) 1–10 plants; (2) 11–100 plants; (3) 101–1000 plants; (4) > 1000 plants.

Islands were again surveyed in 2019 and 2020. Repeated surveys were conducted to estimate the accuracy of the

method and the detection probability and to correct possible observation errors using occupancy modeling (MacKenzie et al. 2018c). In 2019, a total of 118 islands were surveyed and 44 of these were included in a second (repeated) survey. In 2020, a total of 90 islands were surveyed and re-surveys were done in 18 of these. The sites for repeated surveys were chosen based on occupancy status: including sites that had and had not a detection of larvae on the first survey, and which had been considered occupied at least one year in the historical data. If the first survey had been done in sub-optimal weather conditions (cloudy), the repeated survey was done in presumably optimal weather conditions (sunny). To increase the independency of the repeated surveys, they were conducted on a different day, different time of the day and by different observer, as the first survey occasion.

The total data comprise 743 site observations from 8 years. The records include 371 observations of occupied patches. To study possible changes in the occupancy of the larvae and in the abundance of the host plant we compare the recent data, collected in 2019 and 2020, to the historical data. We first compare occupancy in a wide sense, where the islands surveyed in 2019 and 2020 all have a reference point in history (at least one previous visit on the same island or in the group of islands). That is, this wide-sense comparison concerns islands in the same general area. In addition, we compare occupancy in a narrow set of the same 50 islands surveyed in all years.

Statistical analysis

The naïve occupancy was computed as the number of occupied islands divided by the number of suitable islands surveyed for every survey year. A Kruskal–Wallis test was conducted on the average number of larvae detected on each of the 50 islands in the narrow set to determine whether the number of larvae differed between historical and recent surveys. We used single species, single-season occupancy models (MacKenzie et al. 2018c) to estimate the probability of a site being occupied by the Apollo larvae in 2019 and 2020. The single-season occupancy analysis focuses on estimating the probability that a site is occupied (ψ), along with p_i which is the probability of detecting the species on survey i , given the species is present on the site (MacKenzie et al. 2018a). The single-season occupancy analysis is based on the encounter history indicating whether one or more Apollo larvae was detected or not in each of the surveys for each sampling site. Use of a single season occupancy modeling was only possible for the recent years as there were no repeated surveys made in the historic data. The occupancy modeling was performed using constant detection probability (p). For the historical data, the naïve occupancy was corrected with detection probability of 0.97 (Fred and

Brommer 2003) to get an estimate of the uncertainty in occupancy probability (ψ).

Orpine abundance on islands were scored in the historic data using four classes. To study the possible change in abundance, we classified orpine abundance in the recent data using these same classes and used a chi-square test for testing for a possible change between the historic and recent data.

We applied multiple-season, single species occupancy modeling (MacKenzie et al. 2018b) to assess occupancy dynamics between years 2019 and 2020. Compared to the single-season occupancy model, the two-season model has two additional parameters, $\epsilon[t]$ and $\gamma[t]$. These parameters are, respectively, the probability a species becomes locally extinct or colonizes a site between seasons t and $t + 1$. Further, we used the two-season model to examine the factors affecting occupancy and detection probability by introducing covariates to the model (MacKenzie et al. 2018a).

The two-season occupancy modeling was initiated from the simplest model and then proceeded to consider other candidate models with one or more covariates. We used Akaike's Information Criterion (AIC) as a model selection technique, since the method can handle non-nested model structures and encourages parsimonious models (MacKenzie et al. 2018c). The magnitude of AIC is not relevant, but the differences in AIC among different models are the focus of model selection (MacKenzie et al. 2018c).

As covariates in the two-season occupancy model, we introduced a site-specific covariate 'Orpine' to the general two-season model to explore if abundance of orpine affects the occupancy of Apollo butterfly larvae. To estimate the detection probability (p) of the larvae, we used seasonal effect and survey specific covariates in the two-season model. Additionally, the survey specific covariates could help explain differences in detection probabilities among the surveys (MacKenzie et al. 2018a). We consider four covariates for detection probability: weather (sunny or cloudy), survey month (May or June), starting time of the survey (AM/PM) and whether an experienced observer conducted the survey (yes or no). A person who had surveyed Apollo larvae in a previous year was considered to be experienced.

All occupancy models were performed using program PRESENCE (Hines 2006). The 95% confidence limit was used in all analyses. Differences at the level of $p \leq 0.05$ were reported as significant or judged by the non-overlapping 95% confidence intervals.

Results

The historical and recent occupancy and abundance of the Apollo butterfly

The historic data consisted of a relatively wide-ranging survey in 1997 covering nearly 130 islands, followed by annual surveys of a set of approximately 80 islands in 1999–2003 (Table 1A). In 2019, again a relatively wide-ranging survey was conducted of approximately 120 islands, followed by a more focused survey of approximately 90 islands in 2020 (Table 1A). Comparison of the naïve occupancy of all islands surveyed in the historic data was never below 50% of islands, whereas naïve occupancy in the recent data was below 20% (Table 1A). Comparison of the narrow set of 50 islands that have been visited in both recent years and in historical years also indicated a clear decrease, as naïve occupancy in recent years was beneath 10% (Table 1B). Apart from naïve occupancy, there was a reduction also in the number of detected larvae in the recent data compared to historical years (Table 1, Fig. 1, Kruskal–Wallis chi-squared = 71.5, df = 1, $p < 2.2e-16$).

Using the narrow dataset of 50 islands, we conducted a single-season occupancy models for each of the two recent years to correct for imperfect detection, and compared it to occupancy in the historic years (Fig. 2). Also when accounting for uncertainty in occupancy, which is clearly large in the recent years, the probability of occupancy of an island by Apollo butterfly larvae in recent years remained well below what it was in historical years, as judged by the non-overlapping 95% confidence intervals (Fig. 2).

The abundance of orpine

The hypothesis exploring the possible decline in abundance of orpine, the larval host plant, was tested by comparing the counts of orpine categorized in four classes between the historical data and recent data (Table 2). In both the historic and the recent survey, more than half the islands contained over 100 orpine plants, and the abundance of orpine did not change when comparing the historical and recent data (Table 2, chi-square = 3.8; d.f. = 3, $p = 0.3$).

Table 1 Summary of detected Apollo butterfly larvae in (A) all surveyed islands and (B) in a set of islands that have been surveyed 2019 and 2020 and in the historical years

A						
Year	n	Occupied	Naïve est	n larvae	Mean larvae	> 10 larvae
2020	90	15	0.17	160	2	26% (4)
2019	118	22	0.19	125	1	18% (4)
2003	74	39	0.53	708	10	36% (14)
2002	83	52	0.63	338	4	17% (9)
2001	84	61	0.73	792	9	30% (18)
2000	83	57	0.69	678	8	35% (20)
1999	84	48	0.57	330	4	25% (12)
1997	127	77	0.61	551	4	27% (21)
B						
Year	n	Occupied	Naïve est	No. larvae	Mean larvae	> 10 larvae
2020	50	3	0.06	37	1	33% (1)
2019	50	3	0.06	17	0	33% (1)
2003	50	32	0.64	547	11	38% (12)
2002	50	35	0.70	226	5	23% (8)
2001	50	40	0.80	570	11	35% (14)
2000	50	40	0.80	513	10	38% (15)
1999	50	29	0.58	239	5	34% (10)
1997	50	42	0.84	435	9	43% (18)

The number of surveyed sites (n) is given for each year together with the number of islands where larvae were detected (occupied). The naïve occupancy estimation (naïve est.) is computed as (occupied/n). In addition, the total number of detected larvae on all islands (n larvae), and the mean number of larvae per island (mean larvae) are given as well as the proportion of occupied sites where more than 10 larvae were detected (> 10 larvae) and inside the brackets is the number of islands where more than 10 larvae were detected

Fig. 1 The mean number, \pm SE, of the larvae detected per survey year from the same study islands. Sample size and number of detected larvae are reported in Table 1B. Lighter colored dots represent the more recent years and dots with grey coloration represent the historical years

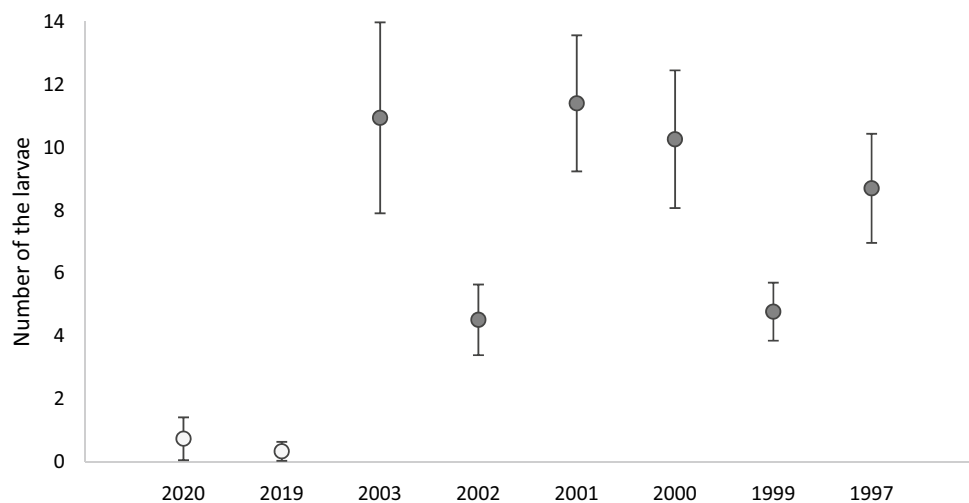


Fig. 2 Probability of occupancy (ψ) of *P. apollo* larvae on 50 islands monitored in all survey years (see also Table 1B). For the years 2019 and 2020 occupancy model estimates of ψ are presented with constant detection probability (p) with 95% confidence intervals. For the historical data (years 1997, 1999–2003) estimates of occupancy probability are based on the reported values presented in Table 1B and naïve occupancy estimates are corrected with 97% detection probability. The first two lighter colored dots with bars represent the recent survey and darker coloured dots with bars the historical survey

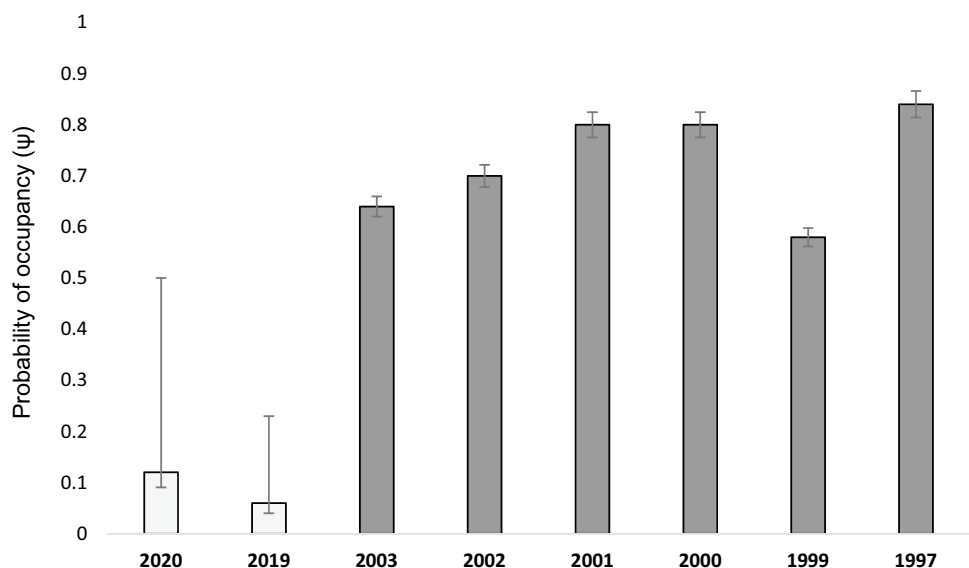


Table 2 The percentage (printed in bold) of islands with orpine *Hylotelephium telephium* abundance classified in four classes in the historic data and currently, with the number of islands in each category in brackets

N orpine	Historic % (n)	Current % (n)
1–10	5% (24)	2% (5)
11–100	41% (215)	36% (74)
101–1000	53% (279)	60% (122)
> 1000	2% (10)	1% (3)

Orpine abundance was categorized in four classes defined by a specific range of number of orpine plants per site (N orpine). Historical data was collected in years 1997, 1999–2003 in the same area as the current (2019–2020) data

Occupancy modeling

We applied a multiple-season, single species occupancy model (MacKenzie et al. 2018b) to study the occupancy dynamics based on 118 sites with 44 repeated surveys conducted in 2019 and 90 sites with 18 repeated surveys done in 2020 (Table 3). In this set of islands, 80 were surveyed both years. Because the lowest and highest abundance class of orpine were rare (Table 2), we considered the abundance of orpine in two categories, ≤ 100 vs > 100 plants/site, as covariate for occupancy of *P. apollo* larvae and a number of covariates were considered for detection probability (Table 3).

The model with orpine abundance affecting occupancy probability has low support, with a combined weight for the $\psi(\text{orpine})$ models of 27% (Table 3). We found clear evidence that detection (p) was higher when the survey

Table 3 Comparison of two-season single species occupancy models for 2019 and 2020 (A) and parameter estimates of the top model (B)

A			
Model	Δ AIC	ω	Npar
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{May})$	0.00	0.32	5
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{May} + \text{obs})$	0.86	0.21	6
$\psi(\text{orpine}), \gamma(\cdot), \epsilon(\cdot), p(\text{May})$	1.38	0.16	6
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{obs})$	1.87	0.13	5
$\psi(\text{orpine}), \gamma(\cdot), \epsilon(\cdot), p(\text{May} + \text{obs})$	2.12	0.11	7
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	5.16	0.02	4
$\psi(\text{orpine}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	6.30	0.01	5
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{AM})$	6.42	0.01	5
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{year})$	5.85	0.03	5
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{sunny})$	5.89	0.03	5
$\psi(\text{orpine}), \gamma(\text{orpine}), \epsilon(\text{orpine}), p(\cdot)$	8.51	0.01	7
B			
Parameter	Estimate		
ψ_1	0.22		
γ_1	0.09		
ϵ_1	0.08		
pMay	0.62		
ψ_2	0.27		
λ	1.24		

In (A) the models are ranked in terms of AIC. Δ AIC is the relative difference in AIC values compared with the top-ranked model; ω is the AIC model weight; Npar is the number of parameters. Models consist of probability of occupancy (ψ), colonization (γ) and extinction (ϵ) with detection probability (p), and possible covariates included in the model are written inside the brackets. A dot inside brackets (\cdot) indicates that the parameter is considered to be constant. Covariates used are site-specific covariate orpine class (orpine), and survey specific covariates weather (sunny), month (May), starting time (AM) and an experienced observer (obs). Covariates not listed (June, cloudy, PM, no experienced observer) act as a reference variable that the other variable is compared to. Seasonal effect on detection probability is indicated with $p(\text{year})$. In (B), the parameter estimations of the top model are provided. The reported parameters are the probability of occupancy (ψ), colonization (γ), extinction (ϵ) and detection in May (pMay). The derived estimates are the probability of occupancy in second year (ψ_2), and an occupancy-based population growth rate (λ) that are calculated as the ratio of successive occupancy estimates

was conducted in June as opposed to May (Table 3) likely related to Apollo butterfly larvae being bigger and easier to detect at that time. Additionally, there was some support for higher detection when an experienced observer conducted the survey.

The top-ranked two-season occupancy model inferred the probability of occupancy in 2019 (ψ_1) to be 0.22 (Table 3B). Based on these two years, the dynamics of the system appears relatively stable, as the derived probability of occupancy in 2020 ($\psi_2 = 0.27$) was very similar to the occupancy estimate in the first year and the population growth rate (λ) was around 1 (Table 3B). Nevertheless, extinction and colonization probabilities were 8% and 9% respectively (Table 3B) indicating the Apollo butterfly persisted as a meta-population. In 8 of the 80 islands surveyed in both 2019 and 2020, occupancy status changed. In half of these sites, Apollo butterfly larvae were detected in 2019 but not in 2020, and the other half was without a detection in 2019, but the species was detected in 2020.

Discussion

Compared to the historical survey years (1997, 1999–2003) the probability of occupancy of islands by the Apollo butterfly in recent years (2019 and 2020) decreased dramatically in the Archipelago Sea area of southern Finland. Whereas about 20 years ago, approximately 75% of islands were occupied, currently only about 20% of islands are occupied by the Apollo butterfly. Although the species' occupancy of islands fluctuated also in historic years, it is clear that the number of larvae and occupancy estimates are currently less than half of even the poorest years some twenty years ago. This Apollo metapopulation was considered to be a stronghold for the species in Finland. We were anticipating a decline in this Apollo butterfly population, as for butterflies in general (Warren et al. 2021), but the current results are alarming.

The decline in occupancy probability by Apollo larvae is not due to a decrease in the abundance of its host plant, because we find that the abundance of the species' only larval host plant, orpine, has not changed in the area. Furthermore, occupancy models of the recent data also showed that abundance of orpine does not affect occupancy probability. This finding is unexpected, since previous studies emphasized that the amount of host plant on a patch is the most important habitat parameter and crucial factor for Apollo butterfly larvae and their survival in the archipelago (Fred and Brommer 2003, 2010). Hence, we expected that islands with plenty of host plants would have the highest probability to be occupied. It appears that the decline of this Apollo butterfly over the last 20 years that we document here is due to other causes, causes that at present are not known.

Based on occupancy modeling, we also find that turnover rates (i.e. change in occupancy status) are substantial with both extinctions of occupied islands and colonization of empty islands. Thus, the Apollo butterfly population persists as a meta-population. Also in the historical years, turnover occurred in around 8% of islands in the Apollo butterfly metapopulation (Fred and Brommer 2009). Clearly, however, the present combination of low occupancy coupled with substantial colonization-extinction dynamics makes the system vulnerable to stochastic extinction (Hanski et al. 1995). Nevertheless, our findings are based on only two years of survey data and because the occupancy probability at present is so low, more information is needed to substantiate current turnover rates.

As part of our design, we did not repeatedly survey each island for occupancy, but instead less than half of the islands were repeatedly surveyed. Repeated surveys are important. Historically, the population abundance of the Apollo butterfly was higher and also detection was high (about 97%). Our occupancy models show that nowadays baseline detection probability (in May) is lowered to 67%. Inference of detection probability could have been enhanced by increasing the number of islands with a repeated survey. However, repeated surveys are costly and cause a reduction in the total number of sites that can be surveyed (Ewing and Gangloff 2016) and we thus believe our design is a reasonable compromise.

The decline in the occupancy probability of Apollo butterfly larvae that we observe could be partly caused by a change in the distribution of the population away from the study area. We believe such a change in distribution to be unlikely, however, because wider surveys of the area were conducted. In the year 1997, approximately 130 islands were surveyed and the Apollo butterfly larvae were detected in circa 60% of these; and again in 2019 nearly 120 islands were surveyed in the same general area and Apollo butterfly larvae were detected in only 19% of islands. Nevertheless, the even stronger decline we observed when consider the

same 50 islands (Fig. 1) underlines that extinctions have been severe on certain islands.

The decline in the occupancy probability we here document may be temporally transient. An extreme drought occurred in the area in 2018 and this drought is known to have affected the quality and availability of the host plants of the Glanville fritillary butterfly in the nearby Åland islands, causing a dramatic population decline that year (van Bergen et al. 2020). Although the Glanville fritillary butterfly population and their host plants recovered rapidly from this drought, droughts in general have the potential for long-term negative effects in butterflies (Oliver et al. 2015). Additionally, on the barren islands flowering plants are naturally scarce and their presence stochastic. Therefore, drought may negatively affect available nectar resources for the adults, which increases emigration from islands and affects the metapopulation structure (Fred et al. 2006). It is therefore important to repeat the survey for Apollo butterfly larvae in the future to verify whether the decline we recorded here is transient or not.

Reduction and degradation of habitat, pollution and negative effects of climate change are considered the main causes for butterfly decline (Warren et al. 2021). Of these, pollution (primarily through agricultural application of insecticides), is unlikely to be relevant in our study system as this population is away from permanent human settlement. Traditional habitat management of archipelago islands included grazing mainly by sheep and burning to reduce bushes and trees, but ended during the 1940s. Islands have subsequently suffered encroachment by mainly densely, low-growing Juniper shrubs and trees. Although we here find no evidence that host-plant abundance has changed during these 20 years, encroachment may have lowered habitat quality by reducing meadows with nectar plants (cf. WallisDeVries et al. 2012). Traditional management aiming to halt encroachment of small meadows in these islands is one possible conservation action that could help this Apollo butterfly population to persist. This conservation action would also increase habitat heterogeneity, a factor shown to be important for Apollo persistence in other populations (Ashton et al. 2009, Wilson et al. 2015). Apart from habitat degradation, the risk of extinction of small metapopulations may increase due to climate change as the extreme weather phenomenon strengthens (Kahilainen et al. 2018). In addition, there are several other potential mechanisms of climate change impacts, including detrimental changes in phenology and interaction with other species (Foden et al. 2019).

In the end, the reasons for decline in occupancy probability in this Apollo butterfly population might be several, biotic and/or abiotic, and provide a need for further studies. Continuing to monitor this Apollo butterfly population and its habitats as well as other insect species could provide us with valuable data on population trends, help identifying

practical conservation acts and target them in relevant locations, as the biodiversity of insects is threatened across the globe (Sánchez-Bayo and Wyckhuys 2019).

Acknowledgements We thank Olli Borg and volunteers for assistance in the surveys of 2020 and Parks and Wildlife Finland personnel for assistance in the field. Funding was provided by CoastNet LIFE (EU-LIFE+) (MM, JB), Societas pro Fauna et Flora Fennica (to JMK). Laura Tuominen is thanked for providing comments on a draft. Comments of two reviewers considerably improved the manuscript.

Funding Open Access funding provided by University of Turku (UTU) including Turku University Central Hospital.

Declarations

Conflict of interest The authors declare that they have no conflict of interest. Permission to work on islands that are privately protected was obtained from the Centre for Economic Development, Transport and the Environment and the landowners.

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