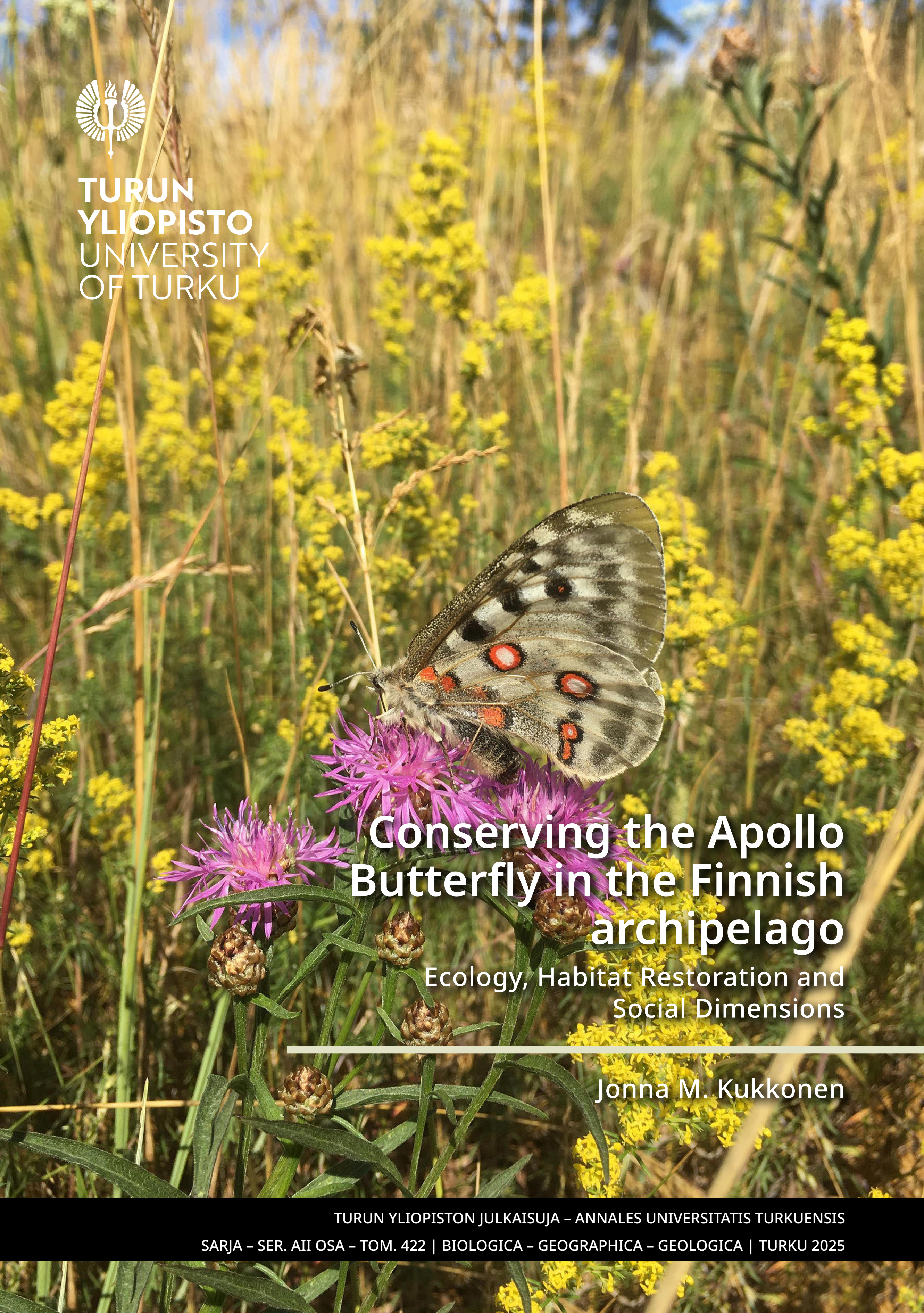

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Conserving the Apollo Butterfly in the Finnish archipelago

Ecology, Habitat Restoration and Social Dimensions

Jonna M. Kukkonen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
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University of Turku

Faculty of Science
Department of Biology
Biology
Doctoral programme in Biology, Geography and Geology (BGG)

Supervised by

Professor Jon Brommer
Department of Biology
University of Turku
Turku, Finland

Docent Mikael von Numers
Environmental and Marine Biology
Åbo Akademi
Turku, Finland

Reviewed by

Professor Marjo Saastamoinen
Organismal and Evolutionary Biology
Research Programme
University of Helsinki
Helsinki, Finland

Docent Maria Hällfors
Finnish Environment Institute (SYKE)
Helsinki, Finland

Opponent

Senior Researcher Robert J. Wilson
The National Museum of Natural Sciences (MNCN-CSIC)
Madrid, Spain

Cover Image: Jonna M. Kukkonen

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“Olen merkittävä! Huusi pölyhiukkanen universumissa…” - Lassi

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ABSTRACT

Land-use change and climate change are reshaping ecosystems across Europe, where traditional low-intensity land-use practices once maintained open habitats rich in biodiversity. Specialist species, such as the Apollo butterfly (*Parnassius apollo*), which depends on semi-open, sunny habitats with its larval host plant, orpine (*Hylotelephium telephium*), and nearby nectar plants, are especially vulnerable. In Finland, the Apollo butterfly has declined severely, yet its outer archipelago population have long been considered a national stronghold for the species. This thesis combines the use of long-term monitoring, habitat analyses, restoration experiments, and social surveys to assess ecological and social dimensions of Apollo conservation in the southwest Finnish archipelago.

First, I compared historical survey data (1997, 1999–2003) with recent data (2019–2020) to quantify possible changes in the Apollo butterfly occupancy and host plant abundance. Occupancy declined from ~75% of islands to ~20%, despite stable host plant abundance, suggesting that other factors, such as habitat quality and demographic constraints, now play stronger roles in shaping the butterfly's persistence than host plant abundance alone. Second, I surveyed 327 rocky outcrops in the coastal population. Occupancy was linked to host plant abundance, lower tree volume, higher elevation, and proximity to nectar patches, but not patch size or connectivity, showing that in dense habitat networks, habitat quality currently outweighs spatial configuration. Third, I evaluated restoration outcomes on 49 islands where junipers were cleared and burned. Occupancy continued to decline even after management. The population may have declined too much for habitat improvements to lead to colonisation in the short term. Vegetation, however, responded quickly: restored sites gained plant species richness, shifted toward nectar-rich communities, and showed higher functional diversity, thereby presumably supporting butterflies and other insects. The results indicate a lag between vegetation recovery and the butterfly response. Finally, a survey of 230 residents, visitors, and landowners in SW Finland showed that pro-environmental values predicted support for ecological management. However, support was weaker for local interventions such as juniper removal or conservation of the Apollo butterfly.

Together, these results show that Apollo conservation requires maintaining critical resources, open habitats, and stakeholder engagement. This thesis integrates ecological monitoring, restoration, and social acceptance, offering a holistic perspective on conserving an emblematic butterfly in a changing archipelago.

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TIIVISTELMÄ

Maankäytön muutokset yhdessä ilmastonmuutoksen kanssa muokkaavat ekosysteemejä kaikialla Euroopassa, joissa perinteinen maanviljelys ja karjanhoito ovat historiallisesti ylläpitäneet avoimia, biologisesti monimuotoisia elinympäristöjä. Erityisen haavoittuvia muutoksille ovat erikoistuneet lajit, kuten apolloperhonen (*Parnassius apollo*), joka on riippuvainen puoliavoimista, aurinkoisista elinympäristöistä, joissa kasvaa toukkien isäntäkasvia isomaksaruohoa (*Hylotelephium telephium*) ja mesikasveja. Suomessa apolloperhosen kanta on taantunut voimakkaasti, mutta ulkosaariston populaatiota on pitkään pidetty kansallisena kulmakivenä. Väitöskirjassani yhdistän pitkäaikaista populaatioiden seurantaa, elinympäristöanalyysiä, ennallistamistoimien seurantaa ja kyselytutkimusta arvioidakseni apolloperhosen suojelun ekologisia ja sosiaalisia ulottuvuuksia Lounais-Suomen saaristossa.

Ensin vertasin historiallisia tutkimustietoja (1997 ja 1999–2003) tuoreisiin tietoihin (2019–2020) kvantifioidakseni mahdolliset muutokset apolloperhosen esiintyvyydessä ja isäntäkasvien runsaudessa. Lajin esiintyvyys vähentyi ~75% saarista ~20%, vaikka isäntäkasvin määrä pysyi vakaana, mikä viittaa siihen, että nykyisin muut tekijät, kuten elinympäristön laatu ja demografiset rajoitteet, ovat tärkeämpiä kuin isäntäkasvien määrä yksinään. Toiseksi tutkin 327 kallioaluetta rannikon populaatiossa. Lajin esiintyvyys oli yhteydessä isäntäkasvien määrään, puiden vähäisyyteen, kallion korkeuteen ja mesikasvien läheisyyteen, mutta ei kallioiden kokoon tai kytkeytyvyyteen, mikä osoittaa, että tiheissä elinympäristöverkostoissa elinympäristön laatu on sijaintia tärkeämpää. Kolmanneksi arvioin ennallistamistoimien tuloksia 49 saarella, joilta oli raivattu ja poltettu katajia. Apolloperhosen esiintyvyys jatkoi taantumista. Kyseinen populaatio on saattanut taantua niin alhaiselle tasolle, jotta elinympäristön laadun parantaminen johtaisi kolonisaatioon lyhyellä aikavälillä. Kasvillisuus reagoi kuitenkin nopeasti: ennallistetuilla alueilla kasvilajien runsaus, toiminnallinen monimuotoisuus ja mesipitoisuus lisääntyi, luultavasti hyödyttäen apolloperhosta ja muita hyönteisiä. Tulos viittaa viiveeseen kasvillisuuden elpymisen ja perhosten reagoinnin välillä. Lopuksi, 230 Lounais-Suomen asukasta, vierailijaa ja maanomistajaa koskeva kyselytutkimus osoitti, että ympäristömyönteiset arvot ennustivat tukea luonnonhoidolle, mutta tuki heikkeni paikallisten esimerkkien, kuten katajien poistamisen tai apolloperhosen suojelun, osalta.

Yhdessä tulokset osoittavat, että apolloperhosen suojelu edellyttää tärkeiden resurssien ja avoimien elinympäristöjen ylläpitämistä sekä sidosryhmien osallistumista. Väitöskirjani tarjoaa kokonaisvaltaisen näkökulman symbolisen perhosen suojeluun muuttuvassa saaristossa.

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Abbreviations

spp.	Species
SW	Southwest / Southwestern
EU	European Union
DEM	Digital Elevation Model
F	Frequency
MPH	Mean Host Plants per rocky outcrop
MA (ha)	Mean Area in hectares
m a.s.l.	metres above sea level
AIC	Akaike's Information Criterion
GLMM	Generalised Linear Mixed Model
LMM	Linear Mixed Effects Model
BACI	Before–After–Control–Impact
ILR	Isometric Log-ratio
NMDS	Non-Metric Multidimensional Scaling
FD	Functional Diversity
FRic	Functional Richness
Fdiv	Functional Divergence
EFA	Exploratory Factor Analysis
MLR	Maximum Likelihood Estimation with Robust Standard Errors
CFA	Confirmatory Factor Analysis
SEM	Structural Equation Analysis
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Kukkonen, J.M., Mussaari, M., Fred, M.S., Brommer, J.E. A strong decline of the endangered Apollo butterfly over 20 years in the archipelago of southern Finland. *Journal of Insect Conservation,* 2022; 26(4), 673–681. https://doi.org/10.1007/s10841-022-00413-3

II Kukkonen, J.M., von Numers, M. & Brommer, J.E. Conserving apollo butterflies: habitat characteristics and conservation implications in Southwest Finland. *Journal of Insect Conservation,* 2024; 28, 1199–1210. https://doi.org/10.1007/s10841-024-00617-9

III Kukkonen, J.M., von Numers, M. & Brommer, J.E. Habitat restoration and vegetation responses in relation to the endangered Apollo butterfly in the archipelago of southwest Finland. Manuscript.

IV Kukkonen, J.M., Tuominen, L.S. & Brommer, J.E. Pro-environmental values foster support for both general and local ecological management. *Restoration Ecology,* 2025; 33(4): e70018. https://doi.org/10.1111/rec.70018

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Data curation	M.F, J.E.B., J.M.K., M.M.	J.M.K.	J.M.K.	J.M.K.
Investigation	J.M.K., J.E.B.	J.M.K., J.E.B.	J.M.K., J.E.B.	J.M.K., J.E.B., L.T.
Statistical analysis	J.M.K., J.E.B.	J.M.K., J.E.B.	J.M.K.	J.M.K.
Writing the original draft of the manuscript	J.M.K., J.E.B.	J.M.K.	J.M.K.	J.M.K.
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List of the coauthors (in alphabetical order):
Jon E. Brommer (J.E.B.), Marianne S. Fred (M.F.), Jonna M. Kukkonen (J.M.K.), Maija Mussaari (M.M.), Laura S. Tuominen (L.T.), Mikael von Numers (M.N.)

1 Introduction

The ongoing biodiversity crisis underscores the urgency of conserving species and ecosystems in the face of accelerating environmental change (Dirzo et al. 2014; Seddon et al. 2016; Ceballos et al. 2020; Marselle et al. 2021). Extinction is a natural process, but current species extinction rates are far higher than background levels, threatening ecosystem services and human well-being (Ceballos & Ehrlich 2002; Barnosky et al. 2011). Insects, which form a dominant component of biodiversity in most ecosystems, are among the taxa most affected, with widespread evidence of sharp declines in abundance, diversity, and distribution across Europe and beyond (Sánchez-Bayo & Wyckhuys 2019; Cardoso 2020; van Klink et al. 2020; Wagner et al. 2021).

Butterflies (Rhopalocera) have experienced pronounced reductions in population size and range due to their ecological specialisation, which makes them vulnerable to environmental changes (Thomas et al. 2004; Van Swaay et al. 2010). Many species rely on specific habitats that are increasingly threatened, such as flower-rich grasslands and open semi-natural areas (Thomas 2016; Warren et al. 2021). Therefore, butterflies serve as both model organisms in conservation biology and as umbrella species, with their protection benefiting wider insect communities (Erhardt & Thomas 1991; Ehrlich 2003; Parmesan 2003; Thomas 2005; Settele et al. 2008). Across Europe, the above-mentioned butterfly declines reflect the cascading effects of agricultural intensification (Thomas 2016; Habel et al. 2019). Intensification has led to habitat degradation and pollution, while simultaneously driving the abandonment of low-intensity grasslands that were once maintained through traditional practices. These interacting processes, together with ongoing habitat loss and climate change, exacerbate butterfly declines (WallisDeVries et al. 2012; Oliver et al. 2015; Thomas 2016; European Environment Agency 2020; Warren et al. 2021).

1.1 The Apollo Butterfly as a Conservation Case Study

The Apollo butterfly (*Parnassius apollo*) is an example of these broader challenges. Once widespread across Europe, the species has undergone severe declines, particularly in lowland populations, and is now endangered in many regions

(Descimon et al. 2005; Nakonieczny et al. 2007; Nadler et al. 2021; Bonin et al. 2024; Stojanović et al. 2025). Although listed globally and at the European level as "Least Concern" in the IUCN Red List assessments (Nadler et al. 2021; Van Swaay et al. 2025), it is nationally endangered in Finland (Hyvärinen et al. 2019) and strictly protected under the EU Habitats Directive (Annex IV) and listed in CITES. Finland hosts the northernmost populations of the Apollo, which are currently restricted to the Åland Islands and fragmented strongholds along the southwest coast, as well as a small inland population in Lohja (Marttila et al. 1991; Nieminen & Ahola 2017). Populations have contracted significantly since the mid-20th century, with some already extinct, and the species generally occurs at low densities, with the probability of colonisation being very low outside its range (Marttila et al. 1991; Fred & Brommer 2010).

Apollo butterflies illustrate the vulnerabilities of sedentary, habitat specialists that overwinter as eggs (Sunde et al. 2023). While mountainous populations indicate that Apollo larvae are capable of adapting their microhabitat use and host plant selection in response to temperature variations (Ashton et al. 2009), as well as exhibiting phenological shifts under changing climates (Descimon et al. 2005), Finnish populations are tightly linked to orpine (*Hylotelephium telephium*), and nearby nectar plants (Fred & Brommer 2003, 2010). In southern Finland, the species inhabits nutrient-poor rocky outcrops and archipelago islets, habitats historically shaped by grazing, burning, and other low-intensity practices. The abandonment of these practices has led to encroachment by shrubs and trees, notably low-profile dense juniper (*Juniperus communis*) scrubs, accompanied by a decrease in plant species richness (Lindgren & Metsähallitus 2000; Bakker & van Diggelen 2006). This shift is degrading the habitat suitability for the Apollo butterfly by diminishing sunny areas, reducing the abundance of host plants, and limiting nectar availability. Consequently, the species does not persist under passive protection and requires active habitat management (Nakonieczny et al. 2007; Dolek et al. 2017). Metapopulation theory provides a framework for understanding the persistence of the Apollo butterflies: local populations depend on patch size, connectivity, and habitat quality, with even unoccupied patches contributing to long-term viability (Hanski 1999). This pattern is mirrored elsewhere in Europe: for example, in the Pieniny Mountains of Poland, Apollo populations collapsed despite strict protection, with afforestation, genetic erosion, and climatic extremes contributing to their decline (Witkowski & Adamski 1996; Witkowski et al. 1997). Such examples highlight that conservation efforts cannot rely solely on on-site protection, but active restoration and management of habitats are needed.

Conserving the Apollo butterfly in Finland, therefore, hinges on both protecting and restoring suitable habitats. While many of the habitat requirements of this threatened species are known, identifying which characteristics most strongly influence occupancy and persistence helps prioritise management and ensure that conservation measures are effectively targeted. Previous studies have highlighted the importance of host plant abundance, nectar resources, and habitat connectivity at the landscape scale (Brommer & Fred 1999; Fred & Brommer 2003; Fred et al. 2006). Yet, despite this knowledge, Apollo populations continue to decline, and conservation-driven translocations have not achieved long-term establishment (Fred & Brommer 2015, Fred pers. comm.). This highlights the need to prioritise in situ conservation efforts that maintain and enhance habitats within the butterfly's remaining range. Lessons from recovery programmes also reveal risks. In Poland, supplementing local populations with captive-reared individuals temporarily boosted numbers but reduced subpopulation stability in some cases (Adamski & Witkowski 2007; Adamski & Ćmiel 2022). In Bavaria, recovery required decades of targeted management, long-term monitoring, and cooperation with landowners and industry (Dolek et al. 2017). These examples demonstrate that Apollo conservation necessitates carefully tailored, long-term strategies founded on detailed ecological knowledge.

Climate change further compounds conservation challenges faced by the Apollo butterfly populations in some locations. Apollo butterflies are sun-basking, sensitive to both drought and rain, with weather extremes disrupting larval development, reducing survival, and lowering adult fecundity (Ashton et al. 2009; Łozowski et al. 2014; Johansson et al. 2020). At a continental scale, winter precipitation has emerged as a key predictor of persistence, as overwintering eggs require insulation from cold provided by snow cover (Kebaïli et al. 2021). In Finland, where winters are warming rapidly, reduced snow cover (Luomaranta et al. 2019) may therefore pose a threat to egg survival. Lowland populations, such as those in Southwest Finland, may face amplified risks as drought reduces host plant quality and thermal buffering capacity, further limiting larval survival. While climate change is not the primary focus of this thesis, these sensitivities make Apollo butterflies and related Arctic–Alpine species particularly vulnerable to climate change, underscoring the need for proactive, adaptive management.

Habitat restoration offers one of the most promising conservation approaches. In the southwest Finnish archipelago, efforts have focused on removing junipers and reintroducing controlled burning to recreate heterogeneous habitats that support the Apollo butterfly and related biodiversity. Such measures align with the goals of the EU Biodiversity Strategy for 2030 and the Nature Restoration Law, which emphasise the restoration of degraded habitats and the maintenance of ecosystem services (European Commission 2021; European Parliament 2024). However, evidence for the effectiveness of restoration in supporting the Apollo butterfly in Finland remains limited, both in the short term and in the long term. Insights from landscape ecology suggest that improving local habitat quality, such as increasing host plant and nectar abundance, can enhance metapopulation persistence and functional connectivity, even in fragmented landscapes (Jones et al. 2023).

Restoration and conservation are not solely ecological challenges; they are also social. Stakeholder engagement is a critical component of effective ecological restoration because long-term success depends on public understanding, acceptance, and participation (Burger 2010; Gann et al. 2019; DeAngelis et al. 2020). Landscape-scale changes, such as clearing shrubs and prescribed burning, are visible and can be readily observed and questioned. Public support is therefore essential (Burger 2010; Gann et al. 2019). Pro-environmental values refer to the attitudes and concerns that motivate individuals to support and engage in behaviours that favour environmental protection (Stern & Dietz 1994; Harring & Jagers 2013). Sense of place encompasses the emotional, spiritual, and cognitive connections that people form with specific locations, shaping how they perceive and evaluate environmental change (Jorgensen & Stedman 2001; Hausmann et al. 2016). Both pro-environmental values and sense of place strongly influence how individuals perceive and accept ecological management (Stern & Dietz 1994; Hausmann et al. 2016). These factors provide a context that can be used to measure public support for ecological restoration efforts. For the Apollo butterfly, fostering local engagement and understanding is crucial, as restoration actions can be disruptive yet are vital to the species' survival. The Apollo butterfly could also serve as a flagship species whose conservation can benefit other taxa dependent on open, nutrient-poor habitats, and whose cultural value could mobilise public support, similar to the monarch butterfly in North America (Preston et al. 2021).

1.2 The Aims of the Thesis

In this thesis, I examined the conservation ecology of the Apollo butterfly in Southwest Finland, focusing on both ecological and social factors shaping its persistence in fragmented archipelago landscapes. First, I have studied the current status of the Apollo butterfly's stronghold population by comparing more recent survey data to data collected approximately 20 years ago (**Chapter I**). This research aimed to support targeted restoration efforts and design effective monitoring plans for the species.

In **Chapter II**, I investigated how environmental factors, such as resource abundance and spatial distribution, along with other habitat characteristics, influence the occupancy of the Apollo butterfly, aiming to provide conservation advice for habitat restoration. **Chapter III** expands upon the conservation narrative, as I assess the outcomes of habitat restoration efforts done by clearing and burning junipers to support the Apollo butterfly. Finally, in **Chapter IV**, I explore the societal dimensions of Apollo conservation by analysing how pro-environmental values and local attitudes influence public support for restoration and management actions identified as necessary in **Chapters II** and **III**.

Together, these chapters show that the Apollo butterfly conservation in SW Finland is constrained by a triad of factors that operate at different scales and time frames: (i) demography: small, declining, and spatially isolated subpopulations (**Chapter I**); (ii) habitat quality: occupancy correlates with host and nectar resources and site openness (**Chapter II**); and (iii**)** time lags and scale mismatch: while vegetation responds quickly to restoration, the butterfly's response is slower, and under conditions of low abundance and limited dispersal, they may not translated into demographic benefits at all (**Chapter III**). Overarching these factors, social acceptance influences the feasibility and sustainability of conservation actions (**Chapter IV**). This thesis argues that effective conservation requires aligning these four dimensions, demography, habitat quality, and societal support, rather than treating any single factor as sufficient.

Through these chapters, I aim to provide a comprehensive understanding of the multifaceted challenges facing the conservation of the Apollo butterfly in Finland. By combining ecological monitoring, spatial analysis, habitat restoration assessment, and social science methods, I aim to contribute to the discourse on insect conservation and highlight effective management strategies. I emphasise the importance of collaborative efforts among researchers, practitioners, and communities to ensure the survival of the Apollo butterfly and other endangered species within their ecosystems. Finally, I discuss the implications of my findings and future prospects for conserving the species in Finland.

2 Materials and Methods

2.1 Study Species

The Apollo butterfly is a univoltine species of the Papilionidae family, native to Europe and parts of Asia. Adults are large (wing span 62–94 mm) and capable of moving several kilometres (Brommer & Fred 1999; Fred & Brommer 2003; Franzén et al. 2024). Despite being a good flyer, the Apollo butterfly is considered a sedentary species. In Finland, the species inhabits sun-exposed rocky outcrops, islands and islets in the southwestern archipelago and the Åland Islands, with one small, inland population in the Lohja area. The Apollo butterfly typically occurs only in low densities (Marttila et al. 1991).

The Apollo butterfly overwinters as an egg; in Finland, females usually place their eggs near the host plant, the perennial orpine, rather than directly on it (Fred & Brommer 2003). Instead of ovipositing on the host plant, the females place the eggs either one at a time on the ground or drop the eggs from a height onto vegetation (Fred & Brommer 2010). In other parts of the Apollo butterfly's range, oviposition behaviour varies, and the host plant may differ. On the Baltic island of Gotland, for instance, females only occasionally alight on the host plant (*Sedum album*) before laying eggs, typically placing them one to two metres away (Wiklund 1984). In contrast, in southern Poland, females lay small batches of eggs directly on or beside the host plant, orpine (Adamski, as cited in Fred & Brommer 2003). Orpine generally grows on dry, nutrient-poor soils on bedrock and is a relatively common plant in Southern Finland.

Larvae emerge in early spring, have five larval instars, and pupate on the ground in moss or vegetation. Adults emerge in June, males first (Fred & Brommer 2003). They are active in mid-to-late summer and feed on a variety of nectar-rich plants, such as thistles (*Cirsium* spp.). The Apollo butterfly is characterised by limited dispersal, particularly among females, and exhibits classic metapopulation dynamics in fragmented landscapes (Brommer & Fred 1999; Fred et al. 2006; Franzén et al. 2024). Male Apollo butterflies engage in patrolling behaviour to locate newly emerged females, which explains their greater movement compared to females (Rutowski 1991; Brommer & Fred 1999; Baz 2002; Adamski & Witkowski 2006).

2.2 Study Area

The SW Finland archipelago is the world's largest in terms of island count (Visit Finland 2024), comprising thousands of islands across the autonomous Åland region and mainland Finland, including 30 municipalities. Two municipalities, Parainen and Kemiönsaari, are the focal points of my research and host populations of the Apollo butterfly. Parainen covers approximately 900 km^2 of land, and Kemiönsaari spans around 700 km^2, both surrounded by extensive water areas that define their archipelagic character.

I conducted the fieldwork for **Chapters I** and **III** in Kemiönsaari, primarily within the Archipelago National Park, on both protected and privately owned islands (Figure 1). My research focused on the outer archipelago population and the islands surrounding Örö (59°48′37.973″N, 22°19′27.732″E). Several islands are part of the Natura 2000 network (Habitat type 1620: outer rocky islands and islets). Vegetation forms a mosaic of open bedrock, juniper scrubs, coniferous forest patches, heaths, and semi-natural meadows, shaped historically by low-intensity grazing and mowing. In recent decades, large portions of previously open habitats have undergone overgrowth, resulting in successional changes.

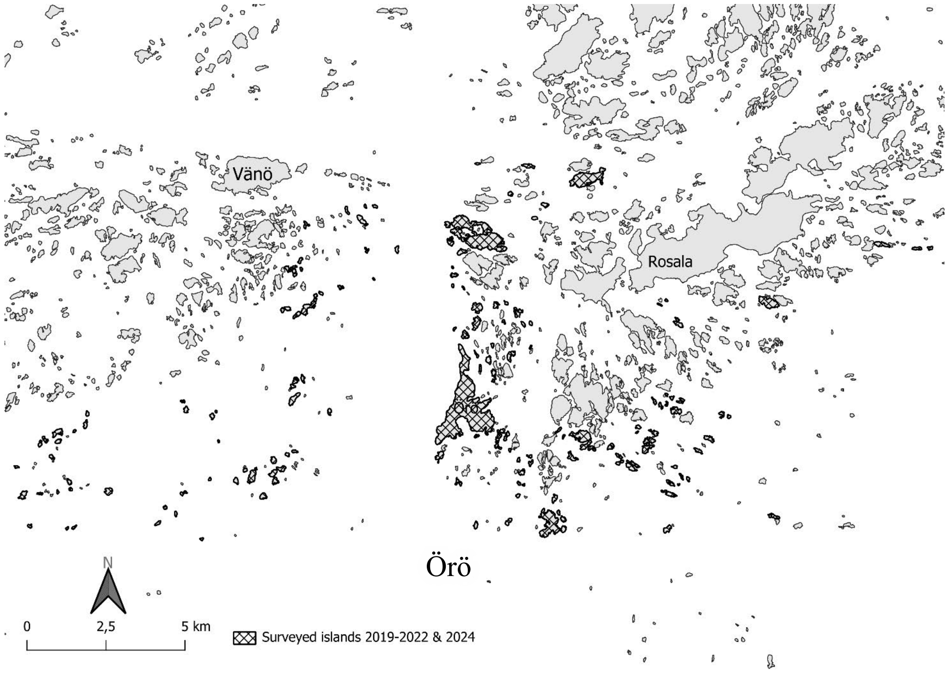

Figure 1. The study area for **Chapters I and III** focuses on the outer archipelago population in Kemiönsaari. The islands and islets surveyed from 2019 to 2022, as well as in 2024, are marked. Selection based on historical data (Fred and Brommer 2003; Fred et al. 2006). Kemiönsaari was included in the survey conducted for **Chapter IV**. ©Finnish Environment Institute (Syke), MeriSaari10 2021, CC By 4.0. Modified: Jonna M. Kukkonen 2024.

In **Chapter II**, I focused on the coastal population in Parainen (Fred & Brommer 2003). The study area, approximately 22 km², included three relatively large islands with agricultural land, forests, and settlements, interspersed with rocky outcrops that support orpine and nectar plants along roadsides, field margins, and power lines. The area was divided into four survey blocks (Figure 2), with the aim of surveying circa 40 rocky outcrops (potentially suitable habitat) in each block and thereby assessing the potential for spatial variation.

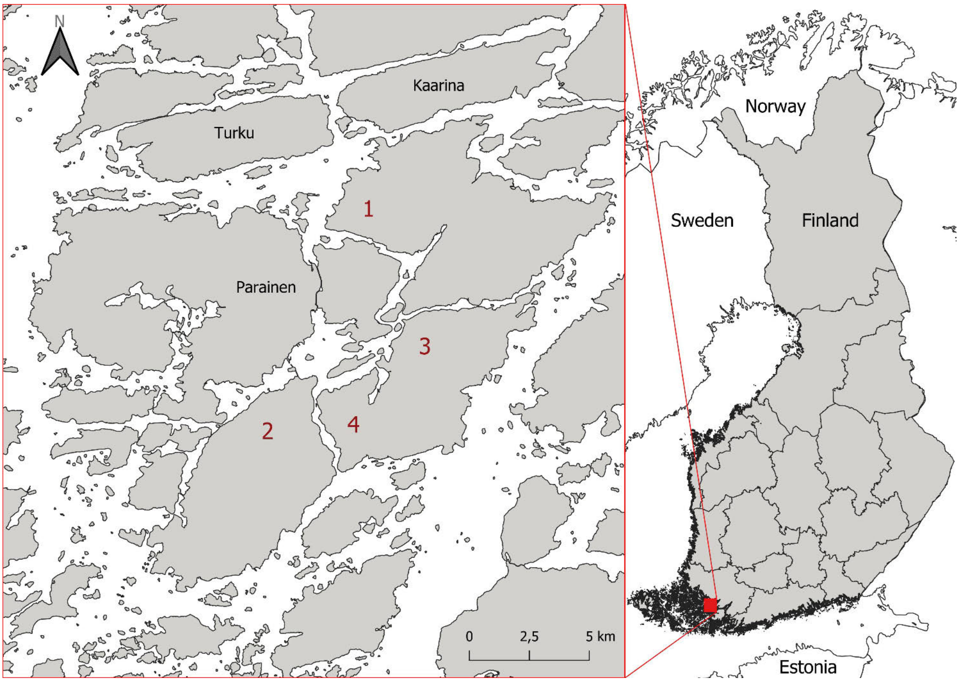

Figure 2. The study area and survey blocks for **Chapter II**, the coastal population in Parainen. Red numbers indicate blocks. Parainen was also part of the surveys done for **Chapter IV**. Figure issued from Kukkonen et al. (2024), **Chapter II**.

Both study areas primarily fall within the southern boreal/hemiboreal zone**.** The average growing season lasts approximately 190 days (Climateguide 2022). The average annual precipitation is approximately 500 mm, and the snow cover typically lasts around 40 days per year (Climateguide 2022).

The archipelago includes multiple Natura 2000 sites, a national park, and a UNESCO biosphere reserve, making it an ecologically significant area. Its mix of residents, tourists, entrepreneurs, and farmers, together with a history of EU-supported restoration projects (e.g. one presented in **Chapter III**), makes it an ideal case study for ecological management perceptions in **Chapter IV**.

2.3 Larval Survey Protocol

I surveyed larvae, as their presence indicates reproductive habitat use, and patch occupancy is more reliable in describing the population than larval abundance when densities are low (Fred & Brommer 2003). Surveys were conducted in May–early June in both the outer archipelago and coastal populations. Larvae (>0.5 cm, black–orange aposematic colouring) were detected visually, aided by foraging signs on host plants. Surveys were primarily conducted under warm and dry conditions to maximise detectability, while cloudy/rainy days were avoided. If a survey was performed in unfavourable weather conditions (cloudy), a possible re-survey under more optimal (sunny) conditions was conducted, subject to time and weather permitting.

A patch was considered suitable for the species if host plants were present (Brommer & Fred 1999). In **Chapters I** and **III**, patches were defined as islands or islets, and in **Chapter II**, as a rocky outcrop delineated on a topographical map (Fred & Brommer 2003; Fred et al. 2006). Surveyors walked systematically through each patch, counting host plants and inspecting for larvae with approximately equal effort per unit area. A patch with at least one larva sighted was classified as “occupied” for that survey year. The total survey time depended on the patch size and the number of host plants.

2.4 Status of Outer Archipelago Population (I)

For **Chapter I**, I used historical data collected in 1997 and between 1999 and 2003 by Fred and Brommer as a baseline for the archipelago population (Fred & Brommer 2003; Fred et al. 2006). Additionally, more recent data on the Apollo butterfly larvae and host-plant abundance were collected from 2019 to 2022 and 2024 from the same islands and islets as in the historical years. The same larval survey protocol was used in both historical and recent surveys to ensure methodological comparability. In the historical data, the host-plant abundance was scored in four categories during the larval surveys (1 = 1–10 host-plants; 2 = 11–100 host-plants; 3 = 101–1,000 host-plants; 4 > 1,000 host-plants). For **Chapter I**, I compared historical and recent occupancy using both broad (all surveyed islands with a historical reference) and focused (50 consistently surveyed islands) approaches to assess the population's status and possible changes in host plant abundance in the outer archipelago. The total data comprises 743 site observations from 8 years (Table 1). Repeated surveys were conducted to estimate the accuracy of the method and the detection probability and to correct possible observation errors using occupancy modelling (MacKenzie et al. 2017). 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, with re-surveys conducted in 18 of these. The islands selected for surveys were based on the historical surveys, and the number of islands surveyed was determined by the time and weather permitting. The sites chosen for repeated surveys were based on their occupancy status. This included locations where larvae were detected in the first survey, as well as sites where larvae were not detected. All chosen sites had to be considered occupied for at least one year according to historical data.

Table 1. Summary table of the Chapter I data. 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. The more recent data is separated from the historical data with a dotted line.

Year	n	Occupied	Naïve est	n larvae	Mean larvae	> 10 larvae
1997	127	77	0.61	551	4	27% (21)
1999	84	48	0.57	330	4	25% (12)
2000	83	57	0.69	678	8	35% (20)
2001	84	61	0.73	792	9	30% (18)
2002	83	52	0.63	338	4	17% (9)
2003	74	39	0.53	708	10	36% (14)
2019	118	22	0.19	125	1	22% (4)
2020	90	15	0.17	160	2	27% (4)

2.5 Habitat and Landscape Metrics (II)

To understand habitat quality and landscape context, for **Chapter II,** I combined field surveys with GIS-based spatial analysis in the coastal population. Surveys of Apollo larvae in this region were conducted around 20 years ago and again 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 Parainen. In 2022, I surveyed 124 outcrops. The following year, 203 outcrops were surveyed (including 99 new ones). I timed the surveys to cover most of the larval period (May–mid-June), when larvae of varying ages are present, reducing the risk of false absences. Some outcrops were visited more than once within a season; however, the number of revisits was too limited to support formal occupancy models with detection probability estimation, as in **Chapter I**. Instead, I used a stacked data structure, where each survey visit was treated as a separate row in the dataset, with outcrop identity included as a random effect to account for repeated surveys of the same site. This approach allows the inclusion of information from revisits, while acknowledging that detection is imperfect but reasonably high under the chosen survey protocol. In total, 327 rocky outcrops were surveyed, averaging 16.4 ha in size, with larvae found on 46% of sites (Table 2).

In the coastal population, most host-plant patches do not contain a nectar-plant patch (Fred et al. 2006). I used the same classification as Fred et al. (2006) to qualify an area as a nectar patch. An area must have at least 10 stems with large inflorescences grouped or a smaller cluster of large and conspicuous plants, each having multiple flowers, such as *Cirsium vulgare* (Fred et al. 2006). In Parainen, the nectar-producing plant patches were generally quite extensive, often extending several meters along roadways and field margins.

Table 2. Summary table of the **Chapter II** data. The number of surveyed rocky outcrops (n) is given for each year, together with the number of rocky outcrops where larvae were detected (Occupied). For 2023, the total number of rocky outcrops surveyed is provided, with the number of "new" outcrops not surveyed in 2022 included in brackets, as well as the number of new occupied outcrops. F (*Frequency*) denotes the ratio of occupied rocky outcrops to the total number of surveyed rocky outcrops. MHP (*Mean Host Plants per outcrop*) represents the average number of host plants in the surveyed rocky outcrops, and MA (ha) (*Mean Area in hectares*) represents the average size of the surveyed rocky outcrops in hectares, with column Density indicating the average density of host plants per hectare (plants/ha).

Year/block	n	Occupied	F	MHP	MA (ha)	Density
2022	124	56	0.45	35	18.65	1.9
Block 1	18	7	0.39	25	32.79	0.76
Block 2	41	9	0.22	26	21.98	1.16
Block 3	44	28	0.64	49	9.31	5.28
Block 4	21	12	0.57	35	19.6	1.78
Year/Block	n (new)	Occupied (new)	F	MHP	MA (ha)	Density
2023	203 (99)	94 (37)	0.46	46	14.96	3.09
Block 1	40 (23)	16 (6)	0.40	72	22.05	3.27
Block 2	68 (35)	31 (15)	0.46	36	16.18	2.25
Block 3	54 (18)	31 (11)	0.57	46	7.94	5.78
Block 4	41 (23)	16 (5)	0.39	38	15.27	2.47

I implemented two isolation metrics to evaluate the connectivity of rocky outcrops within the study area. Distances were measured between patch centroids in units of 100 m, as described by Hanski et al. (1994).

$$-\sum \exp\left(-\alpha D_{in}\right) \tag{1}$$

The first metric (1) quantifies how isolated rocky outcrops are from nectar patches, where D_{in} denotes the Euclidean distance (100 m) between outcrop i and nectar patch n, and α serves as a scaling factor (Hanski 1994). I used a value based on the capture-mark-recapture of Apollo done in the study area for the α parameter (0.27; Brommer & Fred, 1999). A higher value indicates greater isolation from nectar sources.

$$-\sum\left(\exp\left(-\alpha D_{ij}\right) * \text{patch size (j)}\right) \tag{2}$$

The second metric (2) assesses the interpatch isolation. I computed the isolation measure, α (0.27), as a scaling factor for the Euclidean distance (100 m) between a rocky outcrop i and all other patches j, weighted by the patch size j (in hectares). This metric accounts for both the spatial proximity and the differences in size between outcrops, with larger values indicating increased isolation among outcrops.

The landscape features I used in the analysis included the growing stock volume for all tree species (16 m x 16 m raster, Luke 2021) and elevation (2 m x 2 m DEM; NLS 2023). I used the DEM to calculate the insolation (Wh/m^2, May 2022) using ArcGIS Pro (ESRI, 2023) analysis tool “area solar radiation”.

2.6 Restoration Interventions (III)

For **Chapter III**, I analysed larval data (2019-2022 and 2024) from a set of 49 islands to test restoration effects. Restoration was carried out as part of the EU LIFE (Coastnet LIFE) project, implemented by the state-owned enterprise Metsähallitus Parks & Wildlife Finland. The restoration actions consisted of juniper removal and occasional burning. The restoration actions were conducted in August, following the larval season. I applied a before–after–control–impact (BACI) design. As the restoration efforts took place over three years (2020-2022), the classification of “before” and “after” depended on when restoration was carried out. The survey encompassed a set of 49 islands divided into three treatment categories:

1. restored islands (n = 8)
2. control islands (n = 23)
3. positive controls (n = 18)

The restored islands are islands where junipers were cleared and, in some cases, also burnt. Control islands are adjacent islands that are similar in size and habitat but have not undergone any removal or burning of junipers. Positive control islands are located farther away, where Apollo larvae occurrence was relatively high, offering insights into the species dynamics that are independent of the islands being studied.

Islands were grouped into nine clusters (six with local restored + control islands, three positive-control groups). Occupancy was recorded at the island level. The total data comprises 152 site observations from 5 years (Table 3). Of these 45 % (69/152) were surveyed more than once during the season to account for imperfect detection.

However, instead of occupancy modelling, I have used a stacked data structure, where each survey visit was treated as a separate row in the dataset, with island identity included as a random effect to account for repeated surveys of the same site, as in **Chapter II**.

Table 3. Summary table of the **Chapter III** data. The number of surveyed sites (n) from the set of 49 islands 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.

Year	n	Occupied	Naïve est	n larvae	Mean larvae	> 10 larvae
2019	30	13	0.43	77	3	15% (2)
2020	13	6	0.46	91	7	33% (2)
2021	16	2	0.13	127	8	100% (2)
2022	46	11	0.24	83	2	27% (3)
2024	47	4	0.09	15	0	0% (0)

I also conducted vegetation surveys on nine islands (six restored, three controls). Restored patches were cleared in strips from the shoreline upward. I therefore used linear transects consisting of 1 m² quadrats (3–56 per site, with a mean of ~20) spaced at 1 m intervals; on longer transects, I sampled every other metre to balance coverage and effort. Within the quadrats, I recorded the species cover, bare ground, herbaceous/woody vegetation, detritus, and moss. I conducted vegetation surveys in July 2022, 2023 and 2024, covering 15 restored and control sites. I surveyed the restored patches twice (1–2 and 2–4 years post-restoration), whereas I surveyed controls once, as I expected little temporal change. I aggregated the data at the transect level to reduce relocation uncertainty. Additionally, I chose to use the transect level to reduce zero inflation and represent vegetation more robustly, because early post-restoration sites had extensive bare ground and very low plant abundance. I accounted for the hierarchical structure of the data by fitting the site and island as a random effect where appropriate. This dataset enabled me to assess 1) ground cover dynamics, 2) orpine cover, 3) species richness and composition, and 4) functional trait shifts. The trait values were derived from Tyler et al. (2021). Functional traits, such as nectar production, are fundamental because Apollo butterfly adults depend on nectar-rich forbs for foraging. By analysing traits linked to pollinator resources and microhabitat conditions, I was able to evaluate whether restoration not only increased plant diversity but also enhanced the ecological functions most relevant to the butterfly and likely to other nectar-reliant insects.

Different subsets of islands were used for the vegetation and larval surveys due to variation in the restoration treatments applied across sites. Vegetation recovery was evaluated only on islands where prescribed burning occurred, while the Apollo butterfly surveys included both burned and juniper-cleared restoration sites to capture a broader range of management outcomes with more controls to capture occupancy dynamics.

2.7 Social Survey of Public Attitudes (IV)

To investigate the social dimension of restoration described in the previous chapter, in **Chapter IV**, I conducted a questionnaire on ecological management targeting residents, landowners, and visitors in Southwest Finland. In this study, I applied the concept of pro-environmental value orientation to measure stakeholders' support for ecological management and restoration actions, recognising that the long-term success of such efforts depends on public understanding, acceptance, and participation (Burger 2010; Gann et al. 2019; DeAngelis et al. 2020)

I administered the questionnaire online via Webropol (2020) software between May and August 2023. The survey was available in the national languages Finnish and Swedish, as well as in English. With this multilingual approach, I tried to ensure inclusivity of the region’s bilingual population and international visitors. I distinguished between residents, tourists, and visitors—the latter referring to people who frequently use the archipelago for work or leisure but do not identify as tourists. Recruitment of participants was conducted through a combination of flyers, email newsletters, and advertisements, with an emphasis on Kemiönsaari and Parainen.

The survey was open to individuals aged 15 years or older and yielded 230 responses (Table 4). Most participants lived in Finland (97%), with 61% from the Southwest archipelago region.The questionnaire included mandatory statements and questions designed to examine pro-environmental value orientation (ISSP Environment IV items), general attitudes toward ecological management, and specific perceptions of clearing, burning, and Apollo conservation. Response options were on a five-point Likert scale.

The survey began with an explanation of ecological management (e.g. sanctuary upkeep, invasive species removal), followed by an image of Apollo and background information (Figure 3). Participants were also shown pictures of three site types: unmanaged, recently restored, and restored over a year ago.

To assess survey clarity and cultural relevance, I pre-tested the survey with 10 respondents, which led to minor refinements. Average completion time was 12 minutes. Participants provided informed consent before beginning the survey, having been informed of the purpose of the study, their rights, and the anonymity of responses.

Table 4. Frequencies (F) of the responses to sociodemographic questions in "The Apollo Butterfly and Nature Management in the Archipelago" survey in **Chapter IV**. The total numbers and percentages are presented in the row "Total" and by question groups. The survey yielded 230 responses.

Gender	**F**	**%**
Woman	119	52
Man	99	43
Missing	12	5
Age (range 15-78)	**F**	**%**
15-29 years old	47	20
30-59 years old	131	57
over 59 years old	52	23
Home municipality in South-West Finland	**F**	**%**
Yes	140	61
No	90	39
Higher level education; University (bachelor or higher)	**F**	**%**
Yes	167	73
No	63	27
Primary role in the archipelago (resident or not)	**F**	**%**
Yes; resident (or summer resident or entrepreneur)	120	52
No; other (etc. tourist/visitor)	110	48
Member of any group whose main aim is to preserve or protect the environment	**F**	**%**
Yes	79	34
No	151	66
Total	**230**	**100**

Figure 3. This picture of the Apollo butterfly was used in the questionnaire with the information: "This is a picture of an Apollo butterfly (*Parnassius apollo*). The Apollo butterfly is an endangered species in Finland. It is Finland's largest butterfly, with a wing span of 62–94 mm (2.48–3.76 in.). The Apollo butterfly is easy to recognise and difficult to confuse with other Finnish butterfly species. The Apollo butterfly's habitats include semi-open rocky areas and archipelago islets where orpine grows. Adult butterflies can be seen in meadows near the cliffs, feeding on, for example, thistles and star thistles." to introduce the species and its habitats to participants. Figure issued from Kukkonen et al. (2025), **Chapter IV.**

2.8 Statistical Analyses

For **Chapter I**, I first quantified naïve occupancy for every survey year. Naïve occupancy is the proportion of occupied islands of the number of suitable islands surveyed. To compare larval abundance between historical and recent periods, I used a Kruskal–Wallis test on island-level mean larval count on the subset of 50 islands surveyed every year.

All occupancy models for **Chapter I** were performed using the PRESENCE program (Hines 2006). I used occupancy modelling because simple presence–absence surveys can underestimate true occupancy when species are rare or cryptic; the models explicitly account for imperfect detection, reducing the risk of false absences (MacKenzie et al. 2017). For 2019–2020, single-season models estimated occupancy (ψ) with constant detection (p). (MacKenzie et al. 2018a, b). Because historical surveys used removal counts instead of repeated visits, I approximated uncertainty in historical occupancy by correcting naïve occupancy with detection probability $p = 0.97$ from prior work (Fred & Brommer 2003).

To examine short-term occupancy dynamics in **Chapter I**, I fitted two-season (multiple-season) occupancy models for 2019–2020, estimating initial occupancy (ψ_1), colonisation (γ), extinction (ε), derived ψ_2, and population growth λ (MacKenzie et al. 2018c, d). I evaluated covariate effects on occupancy and detection probability by building a candidate set that added 1) island-level orpine abundance (≤ 100 vs >100 plants) on occupancy probability and 2) survey month (May/June), weather (sunny/cloudy), start time (AM/PM), and expert observer conducted the survey (yes/no) on detection probability. I compared models using Akaike's Information Criterion (AIC), favouring the more parsimonious model. To test for a change in host-plant abundance, I compared the four-class orpine categories between historical and recent surveys using a chi-square test.

In **Chapter II**, to connect the occurrence of Apollo with the characteristics of rocky outcrops across two seasons, I fitted a binomial GLMM with a logit link using glmmTMB (Brooks et al. 2017). The response was an outcrop-level occupancy variable (unoccupied = 0, occupied = 1). I included the patch ID as a random intercept. Fixed effects included host-plant number, patch size, tree (growing-stock) volume, nectar isolation, elevation, inter-patch isolation, insolation (modelled solar radiation Wh/m^2, calculated for May 2022), survey date, survey year (with two levels), and block (with four levels), as well as the year × block interaction. I standardised continuous predictors to have a mean of zero and a standard deviation of one (Z-scores) to enable meaningful comparison of effect sizes. I used the restricted maximum likelihood (REML) approach and the Wald test for hypothesis testing.

In **Chapter III**, to test whether restoration actions of clearing junipers improved the Apollo butterfly's status, I modelled island-level larval occupancy (0/1) across years using a binomial GLMM (glmmTMB). Fixed effects captured the BACI structure (year, before/after, treatment, and interactions), while random intercepts were specified for island and cluster. I assessed convergence and fit with standard plots and DHARMa (Hartig 2024). I evaluated the significance of fixed effects using Wald tests, and I report effect size estimates with their associated 95% confidence intervals.

To describe the restoration effects on vegetation in **Chapter III**, I modelled changes in ground cover using beta regression (glmmTMB). I tested the species richness with GLMMs (Poisson model provided the best fit). Changes in community composition were tested with PERMANOVA (adonis2, vegan, Oksanen et al. 2024), and homogeneity of dispersions was checked with betadisper (Anderson 2006). I analysed functional diversity using two indices: functional richness (FRic), which measures the range of trait values present in the community, and functional divergence (FDiv), which quantifies how different species' traits diverge from the community centroid. In addition, I computed community-weighted means (CWMs) for ecological traits (Tyler et al. 2021) with LMMs. I used indicator species analysis to identify species associated with restoration status or time since restoration.

In **Chapter IV**, I first conducted Exploratory Factor Analysis (EFA) on 25 survey items addressing ecological management, restoration, and Apollo conservation to explore the structure of attitudes and values. Because of the limited sample size and model complexity, I chose 16 items with strong loadings for further analyses (Table 5). I performed EFA using maximum likelihood estimation with robust standard errors (MLR), applying geomin rotation under the assumption that latent variables were correlated. The maximum number of latent variables was set at four based on the preliminary hypothesis and variable content.

Next, I applied Confirmatory Factor Analysis (CFA) to construct a measurement model of pro-environmental value orientation. Finally, I used Structural Equation Modelling (SEM) to examine the relationship between pro-environmental value orientation, attitudes toward nature management in general, local habitat restoration examples of clearing and burning, and a target species of the restoration, the Apollo butterfly. SEM allows for the simultaneous estimation of measurement and structural models, accounts for measurement error, and tests hypothesised causal relationships (Kline 2016). The hypothesised SEM specified pro-environmental value orientation as a latent predictor of (i) general management support, (ii) support for local actions (clearing/burning), and (iii) support for the focal species; correlations among attitudinal variables were allowed.

The EFA, CFA and SEM analyses in **Chapter IV** were done in Mplus version 8.4 (Muthén & Muthén 2017) using the full-information missing data method. Model fit was evaluated using standard indices: χ^2, the Comparative Fit Index (CFI), the Tucker–Lewis Index (TLI), the Root Mean Square Error of Approximation (RMSEA), and the Standardised Root Mean Square Residual (SRMR).

Table 5. The 16 questions used in **Chapter IV** as indicator variables, with their reliability test results (Cronbach's α). The respondents could choose an option on a five-point Likert scale (Scale), e.g., from 1 = strongly disagree to 5 = strongly agree with a statement presented. The variables with reversed scales are presented in the column Scale with code rev, where a higher value indicates stronger disagreement with the statement. The mean values of variables are presented in column Mean, and the number of answers, i.e., sample size, in column n.

Latent & Reliability	Indicator variable (i.e. statements) and their codes		Scale	Mean	n
Pro-environmental value orientation	*11c.	How willing would you be to accept cuts in your living standard to protect the environment?	1-5	3.85	226
	12e.	Many of the claims about environmental threats are exaggerated	1-5 rev	4.25	223
	*6.	Generally speaking, how concerned are you about environmental issues?	1-5	4.25	229
	*12a.	It is just too difficult for someone like me to do much about the environment	1-5 rev	4.35	229
Cronbach's α=0.767	*12b.	I do what is right for the environment, even when it costs more money or takes more time	1-5	3.95	227
Ecological management in general	R1	I am interested in visiting a site where nature management is carried out	1-5	4.18	222
	R2	The coastal nature needs nature management	1-5	4.65	218
	R3	Nature management should be avoided	1-5 rev	4.66	221
Cronbach's α=0.692	R4	Nature management is important	1-5	4.79	225
Restoration actions of clearing & burning	CB1	Clearing and burning as part of nature management should be avoided	1-5 rev	3.98	202
	CB2	Clearing and burning are harmful to nature	1-5 rev	3.75	197
	CB3	Clearing and burning as part of nature management is acceptable	1-5	4.18	223
Cronbach's α=0.805	CB4	I am interested in visiting a site where clearing and burning have taken place	1-5	3.80	212
Conservation of the Apollo butterfly	A1	The Apollo butterfly is an important species to protect	1-5	4.82	221
	A2	The Apollo butterfly is a valuable part of Finnish nature	1-5	4.86	222
Cronbach's α=0.812	A3	I'm interested in seeing the Apollo butterfly in the wild	1-5	4.83	227

* Indicator variables have been used in previous studies (Franzen & Vogl 2013; Davidovic et al. 2020) to measure environmental concern and/or pro-environmental value orientation.

3 Results and Discussion

3.1 Severe Decline in Occupancy (I)

In **Chapter I**, I investigated the long-term trends in larval occupancy of the Apollo butterfly population in the southwest Finnish archipelago, using 2019 and 2020 field surveys in comparison with datasets from 1997 and 1999–2003. The results revealed a dramatic decline in occupancy. Historically, larvae were present on approximately 75% of the surveyed islands, declining to about 20% in recent years, indicating a significant contraction.

This downward trend was reinforced when analysing the näive occupancy estimate of a subset of 50 islands that were consistently surveyed across both recent and historical years. In this subset, the proportion of occupied islands more than halved (based on naïve estimates). Furthermore, declines were observed across the study area. Larval counts were also lower in recent years (Figure 4).

To address issues of imperfect detection, I employed single-season occupancy models for the dataset of 50 islands (2019-2020) and compared them with historical occupancy. Despite accounting for uncertainty and historical fluctuations, recent occupancy remained significantly lower (Figure 5). Collectively, these results suggest a significant and ongoing decline in the Apollo butterfly population. This aligns with broader declines in butterfly populations (Warren et al. 2021), and is alarming, considering that this metapopulation had previously been regarded as a stronghold for the species in Finland, with no immediate threats from anthropogenic stressors (Fred 2004).

The decline in the presence of larvae was not associated with a corresponding change in the abundance of the larval host plant, orpine. More than half of the islands in both periods had over 100 orpine plants, and the abundance scores remained relatively stable ($\chi^2 = 3.8$, df = 3, $p = 0.3$). Two-season models for 2019–2020 showed only a weak link between occupancy and host-plant abundance (**Chapter I**, Table 3A). This contrasts earlier findings that emphasised host plants as the primary habitat parameter and crucial for Apollo butterfly larval survival (Fred & Brommer 2003, 2010; Fred et al. 2006). This suggests a decoupling of this anticipated relationship, indicating that other ecological factors now play a more significant role in shaping occupancy dynamics than host plant density in the outer archipelago.

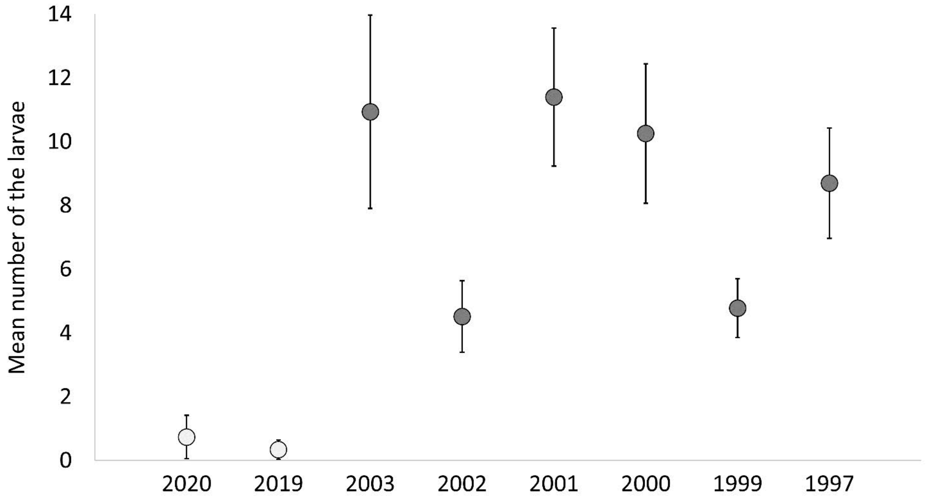

Figure 4. The mean number, ± SE, of larvae detected per survey year. Years are presented in reverse order (from most recent to past) on the x-axis. Sample size and number of detected larvae are reported in **Chapter I,** Table 1B. Figure issued from Kukkonen et al. (2022), **Chapter I**.

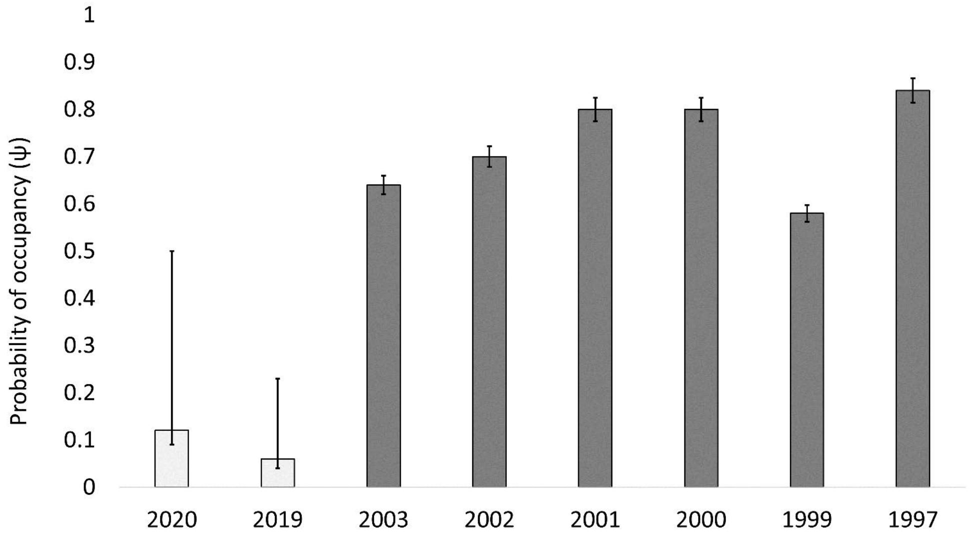

Figure 5. Modelled probability of occupancy (ψ) for 50 islands across survey years (see also **Chapter I**, Table 1B). Years are presented in reverse order (from most recent to past) on the x-axis. Figure issued from Kukkonen et al. (2022), **Chapter I**.

3.1.1 Turnover rates

Turnover remained substantial, with extinction probabilities for occupied islands and colonisation probabilities for empty ones estimated at 8% and 9%, respectively (Table 6). Historically, turnover was estimated at approximately 8% annually (Fred & Brommer 2009); thus, the results suggest the Apollo butterfly has persisted as a metapopulation. According to Hanski (1999), the probability of colonisation is influenced by connectivity to local populations in the surrounding landscape. Additionally, the dynamics of colonisation and extinction can be affected by habitat quality (Thomas et al. 2001; Fleishman et al. 2002). Hence, the contemporary decline in occupancy, combined with limited recolonisation, indicates that this metapopulation is vulnerable to stochastic extinction (Hanski et al. 1995). However, it is worth noting that these findings are based on only two years of survey data; consequently, continued monitoring and data collection on the population will be valuable for verifying current turnover rates.

The occupancy model results also revealed that in 2019–2020, baseline detection probability (measured in May) was approximately 67% (Table 6), down from around 97% in the early 2000s. However, the latter was estimated using a different method (Fred & Brommer 2003). This underscores the need for repeated surveys and timing surveys later in the larval season to reduce false absences. The lower detection probability in recent years is most plausibly linked to reduced larval abundance: detection at the island level is effectively a cumulative function of the probability of detecting an individual larva. When larval numbers are much lower, the chance of detecting at least one declines accordingly.

Table 6. Parameter estimations for the top-ranked two-season single species model. The reported parameters are the probability of occupancy (ψ), colonisation (γ), extinction (ε) and detection probability in May (pMay). Top-ranked model and more details presented in Kukkonen et al. (2022), **Chapter I,** Table 3.

Parameter	Estimate
ψ1	0.22
γ1	0.09
Ɛ1	0.08
pMay	0.62

3.1.2 Factors Influencing Decline

Although no reduction was found in the critical resource for the Apollo butterfly, the causes of the observed decline in occupancy remain unresolved. Agricultural pesticide exposure is a major driver of global insect decline (Sánchez-Bayo & Wyckhuys 2019) and is relevant in the coastal population (**Chapter II**), where agricultural land is interspersed with rocky outcrops. However, the Archipelago Sea area is remote, with minimal direct agricultural activity, suggesting that local environmental degradation, specifically reduction in habitat quality, and climate-related stress, are more plausible drivers of change. The reasons for decline may involve multiple mechanisms, including the following:

1. **Habitat Quality**: Cessation of traditional land use leads to encroachment, reducing nectar plant diversity and impacting microhabitat quality. Previous studies have demonstrated that encroachment negatively affects butterfly habitat by decreasing floral resources (WallisDeVries et al. 2012). **Chapter II** findings underscore the importance of nectar resource proximity for Apollo butterfly occupancy, consistent with earlier research (Fred & Brommer 2003). In **Chapter III**, I continue to discuss habitat restoration through the removal and burning of junipers, aimed at reducing woody encroachment and enhancing vegetation diversity and supporting the Apollo butterfly.
2. **Limited Dispersal**: Low recolonisation rates may reflect a limited dispersal potential and functional isolation of the remaining populations. The Apollo butterfly is known for its limited dispersal, particularly in fragmented landscapes where nectar resources co-occur with host plants and the sea separates suitable habitat patches (Brommer & Fred 1999; Fred et al. 2006; Franzén et al. 2024). As overall occupancy declines, suitable habitats become increasingly fragmented and disconnected, further limiting gene flow and colonisation events—issues related to spatial extinction thresholds (Fahrig 2003). Moreover, there is evidence that females tend to disperse away from deteriorating islands (Fred et al. 2006). This behaviour means that local extinctions may be exacerbated rather than rescued if females leave but fail to find suitable nectar-rich sites. Reduced nectar availability could therefore depress fecundity, lowering reproductive output even in otherwise suitable patches. Additionally, experimental work on other butterflies shows that limited nectar resources constrain egg production and lifetime reproductive success (Boggs & Ross 1993; Mevi-Schütz & Erhardt 2005); similar mechanisms are likely crucial for the Apollo butterfly.
3. **Potential Geographic Shift:** I considered, but did not test, the possibility that the observed decline reflects a geographic shift in population distribution

rather than an actual decline. However, broader surveys from 1997 to 2019, covering over 120 islands, indicate actual contraction rather than spatial shift. In recent surveys, the population appeared to be more concentrated on islands closer to the mainland, with only a few exceptions persisting in the historical outer range. While larval host plants are present throughout the archipelago, nectar plant abundance was not assessed, which may further limit colonisation potential. Dispersal constraints and functional isolation likely play a role, as movement across sea barriers is less frequent than in the coastal population (Fred & Brommer 2003). Furthermore, the Apollo butterfly is often associated with dry, calcareous grasslands and rocky calcareous substrates, which suggests that soil alkalinity or lime content could influence habitat suitability. More broadly, studies in boreal and semi-natural grasslands have shown that soil pH is correlated with plant species richness and community composition (Raatikainen et al. 2018; Tammaru et al. 2023). If lime, alkalinity, or other soil properties affect host-plant or nectar-plant quality or abundance, then even where the host plant is present, the soil substrate could be a hidden constraint on larval performance and butterfly occupancy. Together, these factors may explain why the Apollo butterfly in the archipelago has not shifted its range northward, despite climate change creating expectations of poleward shifts in many butterfly species. This lack of northward shift suggests that while climate change may be driving habitat suitability in parts of the range, other constraints, such as dispersal barriers, resource availability, and habitat quality, could be preventing compensatory range expansion.

4. **Climatic Challenges**: Environmental conditions, including extreme weather events, may also contribute to the observed decline. For example, in England, pluvials during the larval, pupal, and adult stages, as well as heatwaves during the hibernation, egg, and larval stages, negatively impacted butterfly abundance (Shan et al. 2024). Notably, an extreme 2018 drought preceded surveys, and such events can depress butterfly populations due to impacts on host plant quality and nectar availability (Carnicer et al. 2019; Johansson et al. 2020; van Bergen et al. 2020). Additionally, evidence suggests that habitat specialists in drought-susceptible environments can experience significant population declines in the event of drought (WallisDeVries et al. 2011). While some species can recover relatively quickly from extreme weather events, recurrent droughts or shifts in seasonal precipitation patterns resulting from climate change may have lasting adverse effects on butterfly populations (Oliver et al. 2015; van Bergen et al. 2020; Warren et al. 2021). The Apollo adults heavily rely on nectar-rich forbs, which are naturally scarce, and their presence is stochastic. Flowering plants may be vulnerable to drought stress in shallow, rocky soils. Thus, temporary drought-induced reductions in nectar

sources could lead to emigration or failed reproduction, particularly on peripheral islands (Fred et al. 2006). Furthermore, warmer and wetter winters are likely detrimental for an Arctic–Alpine species such as the Apollo butterfly. Overwintering eggs are typically protected by snow cover; however, warmer winters with reduced snowfall may expose them to freezing or fluctuating conditions, which can increase mortality (Kebaïli et al. 2021). Together, these climatic changes could undermine both overwinter survival and summer reproduction, compounding the species' vulnerability.

5. **Biotic Pressures**: Beyond habitat and climatic stressors, biotic pressures may compound these effects. For example, in *Pieris napi*, high larval densities lead to reduced survival and smaller pupae (Kivelä & Välimäki 2008). Analogous patterns were noted by Fred & Brommer (2003) regarding resource depletion in host plant patches. Disturbances, such as herbivory or grazing, have also been shown to decrease larval survival (Park et al. 2023). For the Apollo butterfly, reduced nectar availability may impair fecundity, and predation (Bauer & Feurle 2017) or herbivory may further increase mortality, both critical concerns in low-abundance populations. Historical declines in Finnish Apollo populations during the 1940s could have been exacerbated by viral or microbial pathogens (Marttila et al. 1991).

Given the current situation, there is an urgent need for targeted conservation actions, including habitat restoration and landscape management. Management techniques that promote habitat openness, such as juniper removal, controlled burning, and potentially rotational grazing, may help reverse local extinctions. Additionally, enhancing functional connectivity between habitat patches will be critical for maintaining recolonisation potential and genetic flow (Park et al. 2024). When suitable habitats are available, low-effort conservation approaches, such as reinforcement with minor releases, can boost local populations of threatened butterflies (Dunskis et al. 2024).

While targeted conservation efforts are essential, their effectiveness relies on timing and context. In **Chapter III**, I analyse the outcomes of restoration actions shortly after implementation in a scenario where the starting population numbers are very low. The findings demonstrate that while restoration is crucial, it may not be sufficient if populations fall below a functional threshold. In such cases, demographic reinforcement and/or improved landscape connectivity may be necessary to realise the benefits of habitat restoration efforts fully.

3.2 Habitat Characteristics Predict Occupancy (II)

In **Chapter II**, I focused on identifying the habitat characteristics that influence the current occupancy of Apollo butterfly larvae in the coastal population. The results revealed that larval occupancy on rocky outcrops was positively associated with the abundance of the larval host plant, lower tree volume, higher elevation (Figure 6), and greater connectivity to nectar plant patches. The Apollo butterfly larvae occurred on 46% (150/327) of surveyed rocky outcrops, and the proportion of occupied rocky outcrops did not differ between years ($\chi^2_1 = 0.07$, $df = 1$, $p = 0.79$). Still, nearly one-third of the rocky outcrops changed their status over the years, indicating changes in occupancy dynamics.

3.2.1 Resources

Results from **Chapter I** revealed a decoupling of the relationship between host plants and larval occupancy in the outer archipelago population. In contrast, **Chapter II** demonstrated a strong correlation between Apollo butterfly occupancy and resource availability in the coastal population. This divergence suggests that the importance of host and nectar resources may vary contextually, changing with time, space, and population dynamics.

The limited influence of host plant abundance I observed in **Chapter I** likely stems from potential decoupling during periods of low occupancy, when other factors such as nectar proximity, habitat openness, connectivity, and weather play more pronounced roles. In **Chapter II**, broader multi-predictor analyses I conducted within a more intact coastal rocky outcrop network reaffirmed the anticipated strong relationship between resources and occupancy. Together, these findings emphasise the context-dependent nature of ecological interactions; in small, isolated populations, demographic and dispersal factors may obscure the resource-occupancy dynamics that are more evident in healthier systems.

Specifically, the model results in **Chapter II** confirmed that Apollo butterfly occupancy is closely tied to available resources in the coastal population. Outcrops with more larval host plants (Figure 6) and closer proximity to nectar plant patches (**Chapter II**, Table 3) were more likely to be occupied. These findings replicate and extend the results of earlier work (Brommer & Fred 1999; Fred & Brommer 2003, 2009, 2010; Fred et al. 2006), reinforcing the need for conservation measures to secure both larval and adult resources. The importance of nectar resources is discussed more broadly in **Chapter I** results. Nevertheless, larvae were detected on three outcrops with fewer than five host plants at the time of the survey, suggesting that while host plant abundance strongly influences occupancy, reproduction can occasionally occur under low host plant abundance. However, abundance remains the dominant driver.

Management strategies should prioritise maintaining abundant host plants and ensuring the persistence of nectar sources in the surrounding landscape. Because nectar plants occur in ephemeral habitats, such as road verges, field margins, and disturbed patches, the proximity of these resources to rocky outcrops can change from year to year. Consequently, the suitability of Apollo's habitat is not static. It fluctuates with short-term vegetation dynamics, underscoring the importance of maintaining a network of potential breeding sites rather than solely focusing on the protection of isolated outcrops.

3.2.2 Habitat Openness

A key negative predictor of Apollo butterfly occupancy was the volume of trees on rocky outcrops (Figure 6). The results suggest that encroachment is already limiting larval occupancy and should be prioritised in conservation planning with resources. This pattern echoes findings from other Apollo butterfly populations, where opening the landscape is considered a successful way to conserve and restore habitats (Bonin et al., 2024; Descimon et al., 2005; Dolek & Geyer, 2002; Nakonieczny et al., 2007; Stojanović et al., 2025; Witkowski & Adamski, 1996). The result is part of a broader European trend where abandonment of grazing and traditional land use has led to forest expansion at the expense of grasslands and open habitats (Kuussaari et al. 2007; Nilsson et al. 2013; Warren et al. 2021; Sunde et al. 2023), and aligns with evidence from similar habitats, where active management, such as shrub removal, controlled burning, and re-introduction of grazing, has successfully restored open habitats for declining butterfly species (Munguira and Martín 1993; Vogel et al. 2007; Bubová et al. 2015; Bussan 2022; Geest et al. 2023). For the Apollo butterfly, which depends on sun-exposed conditions, maintaining openness is essential.

3.2.3 Elevation and behavioural ecology

Elevation, despite its modest range in the study area (from 7 to 56 m above sea level with a median of 31.7 m a.s.l.), proved to be a significant predictor of occupancy (Figure 6). Higher outcrops were more frequently occupied, a pattern that may be explained by male mate-locating behaviour. Many patrolling butterflies, including the Apollo butterfly, employ “hilltopping,” where males circle on elevated terrain to encounter receptive females (Adamski & Witkowski, 2006; Baz, 2002; Rutowski, 1991; Rutowski et al., 1989; Takeuchi, 2019). While the functional role of elevation is most likely less pronounced in lowland populations compared to mountainous habitats, the behavioural ecology of Apollo likely contributes to this pattern. Nonetheless, elevation alone is not sufficient to predict occupancy; resource availability and openness remain stronger drivers of larval occupancy.

3.2.4 Spatial variation and Land management

Occupancy patterns varied spatially across the four survey blocks. In particular, one block showed higher occupancy (Figure 6), likely due to local practices (grazing, delayed road verge mowing, small-scale restoration efforts) improving resources/connectivity. Additionally, organic farming in surrounding fields can indirectly benefit butterflies, as these farms typically create more favourable habitats compared to conventional agricultural systems (Goded et al. 2019).

There is evidence that increased nitrogen loads can have adverse effects on plants and butterflies (Öckinger et al. 2006; Kurze et al. 2018; Roth et al. 2021; Bobbink et al. 2022). Generally, nutrient-poor habitats promote butterfly diversity (Löffler et al. 2023). Furthermore, chemical pollution, including pesticides, is associated with the decline of insect populations, such as butterflies (Geiger et al. 2010; Sánchez-Bayo and Wyckhuys 2019; Van Deynze et al. 2024). These challenges can occur mainly within the agricultural and forest landscapes where Apollo butterfly habitats are found.

3.2.5 Connectivity and patch size

Contrary to expectations from metapopulation theory (Hanski et al. 1995; Hanski 1998) and global butterfly studies (Haddad & Tewksbury 2005; Binzenhöfer et al. 2008; Brückmann et al. 2010; Jangjoo et al. 2016; Popović & Nowicki 2023), neither connectivity nor patch size significantly influenced occupancy in the coastal population (**Chapter II**, Table 3). This is likely explained by the relatively high density of rocky outcrops within the study area, where the maximum nearest-neighbour distance was less than 800 m. Under these conditions, habitat quality probably outweighs spatial configuration as a determinant of the Apollo butterfly's persistence. This result is supported by Graser et al. (2023) for other light-demanding butterflies, Jones et al. (2023) for landscape-scale butterfly conservation, and Poniatowski et al. (2018) for habitat specialist insects in fragmented landscapes.

Although connectivity may seem less significant to the preservation of the Apollo butterfly in some contexts, it remains crucial overall. Its importance varies depending on the spatial scale and the structure of the surrounding environment. In more fragmented areas, like the outer archipelago, increased distances between patches and water barriers restrict dispersal, as indicated by the limited recolonisation observed in **Chapters I** and **III**. Therefore, while connectivity does not appear to have a significant impact on occupancy in the coastal population, it remains a critical factor in highly fragmented archipelago landscapes, where greater distances and water barriers may limit dispersal.

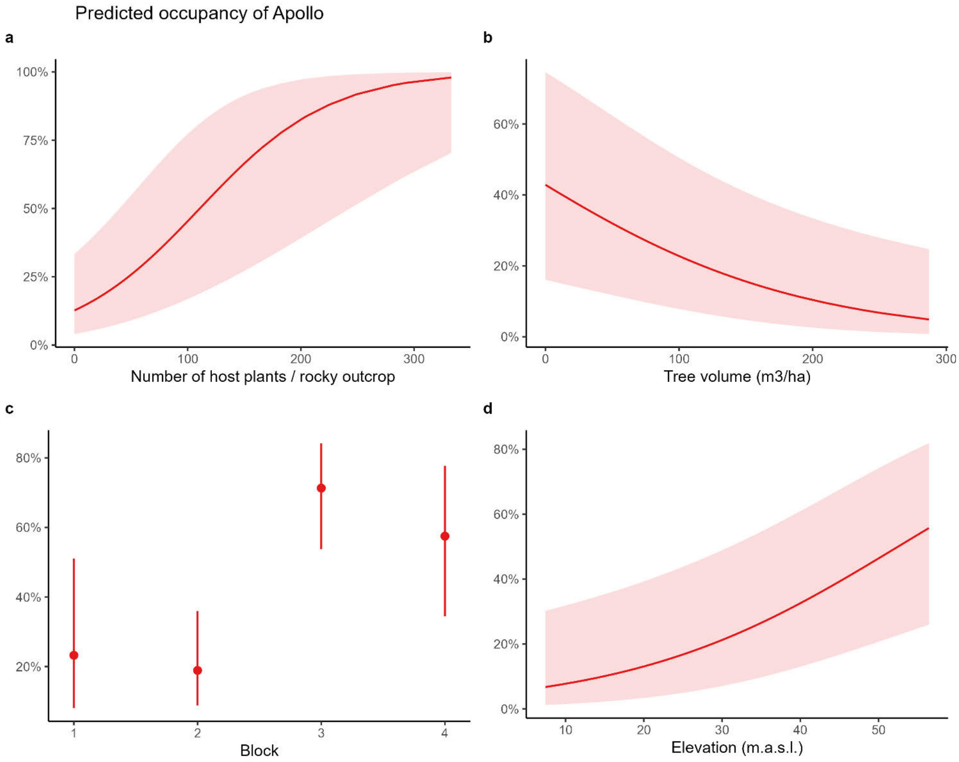

Figure 6. GLMM marginal effects for (a) host-plant number, (b) tree volume, (c) survey block, and (d) elevation on predicted occupancy. Figure issued from Kukkonen et al. (2024), **Chapter II**.

3.3 Apollo Decline Amid Vegetation Recovery (III)

In **Chapter III**, I evaluated the restoration (juniper removal and prescribed burning) effects on the Apollo butterfly occupancy in the Archipelago Sea National Park. The results revealed that, across the study period (2019-2022 & 2024), Apollo butterfly occupancy declined after the 2019 surveys on restored, control, and positive control islands, and continued to decline after restoration measures were initiated in August 2020 (Figure 7). This was confirmed by statistical analysis using GLMM, which showed significantly lower probabilities of occupancy over time. By 2024, Apollo occupancy had reached its lowest observed level, despite interventions. While positive control sites consistently maintained higher occupancy than restored or control sites, even these sites experienced reductions over time. Restoration status itself was not a significant predictor of occupancy. The last restoration work was completed in 2022; therefore, the post-restoration analysis of Apollo's dynamics in **Chapter III** focuses solely on short-term effects.

The observed decline adds to the long-term evidence that Apollo populations in the Southwest Finnish archipelago have been in steady retreat since historical times (**Chapter I**). Restoration was intended to counteract this trend by reversing juniper encroachment and enhancing larval and adult resources, as woody encroachment may limit the larval occupancy (**Chapter II**). Instead, the persistence of the decline suggests that the Apollo population may now be too small and fragmented to respond directly to habitat improvements. As McIntire et al. (2007) suggest, connectivity is influenced more by population size within habitat patches than by their location or size, along with the movement behaviour of the species. If local population sizes have become critically low, dispersal into newly restored sites may not occur despite improved habitat conditions. This possibility highlights the risk of restoration arriving too late, when demographic constraints rather than habitat availability become the limiting factor (Schrott et al. 2005).

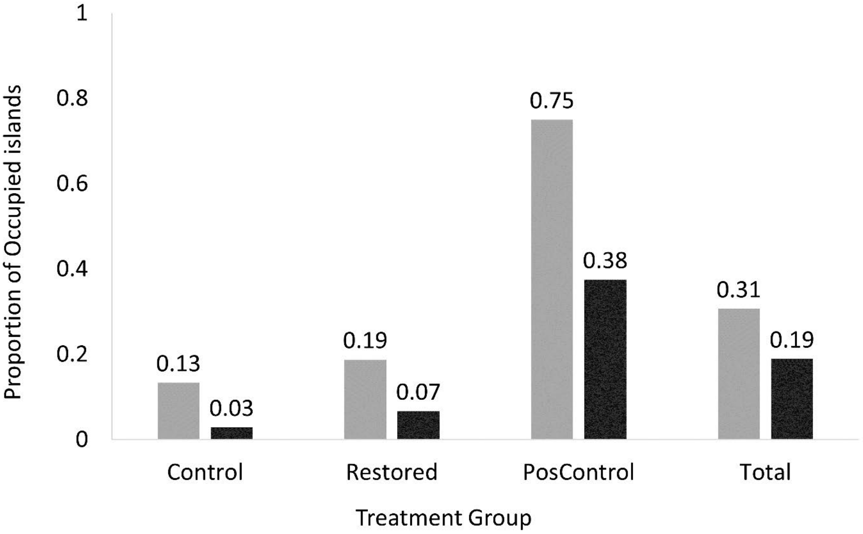

Figure 7. Larval monitoring before (grey) and after (black) restoration. Totals across treatment groups are shown (Total).

3.3.1 Vegetation responses to restoration

Although restoration efforts did not halt the decline of the Apollo butterfly, they had a measurable impact on vegetation. The removal of junipers shifted ground cover (less bare soil, more vegetation/detritus), and restored sites had higher vascular plant richness, increasing with time since restoration, consistent with studies showing restoration enhances plant diversity (Kotiluoto 1998; Benayas et al. 2009; Atkinson et al. 2022). The community composition of restored sites diverged from juniper-dominated control sites, with nectar-producing forbs (e.g., *Galium verum* and *Achillea millefolium*) characterising 2–4-year sites, while controls remained dominated by junipers and *Polypodium vulgare*. These results suggest that restoration promotes a transition toward more flower-rich, pollinator-supporting communities, even if this trajectory is still in its early stages.

I also observed the appearance of opportunistic, alien species such as horseweed (*Conyza canadensis*) in early restored sites. While alien species may temporarily provide nectar, they could displace native flora if left unchecked (D'Antonio et al. 2016; He et al. 2024). Additionally, invasions of alien plants can alter the movement behaviour of butterflies (Kajzer-Bonk et al. 2024). Appearance of alien species, along with the decline of the Apollo butterfly, underscores the need for continuous monitoring of restored habitats. With monitoring and adaptive management, it is possible to prevent unintended consequences and sustain the long-term quality of restored habitats.

Functional diversity (FD) indices supported the pattern I observed in community composition between restored and control sites. Functional richness increased over time since restoration, reflecting the expansion of ecological niches as vegetation recovered. In addition, functional divergence was higher in restored than control sites, indicating broader trait diversity that can enhance ecosystem resilience (Díaz & Cabido 2001). CMW trait analyses showed higher nectar production and pollinator dependence in restored sites. Thus, restoration is improving the ecological context (discussed in **Chapter I** results) necessary for supporting species like the Apollo butterfly, even if the Apollo butterfly has not (yet) responded demographically.

3.3.2 Lagged responses and ecological constraints

The contrast between declining Apollo butterfly occupancy and improving vegetation highlights a potential temporal mismatch between restoration outcomes and species responses. Similar patterns have been documented before. For instance, Vogel et al. (2007) found that the responses of individual butterfly species to restoration practices were highly variable. However, in their best predictive model, total butterfly abundance was negatively associated with greater bare ground cover and increased with higher forb abundance. In my study, restoration enhanced the richness and functional diversity of vascular plants, as well as traits such as nectar production. However, I did not observe that these improvements resulted in higher Apollo butterfly occupancy during the monitored period. Such lag is consistent with ecological expectations, as populations of specialist butterflies often respond slowly to habitat recovery, particularly when dispersal limitations or demographic bottlenecks constrain colonisation (Marttila et al. 2000; Kuussaari et al. 2015).

Together, **Chapters II** and **III** demonstrate a potential temporal mismatch: while restoration successfully improves vegetation characteristics known to support the Apollo butterfly, these ecological gains have not yet translated into demographic benefits for the species, likely due to dispersal limits and small population size. The absence of a positive short-term response by the Apollo butterfly to restoration echoes the findings in **Chapter I**, which demonstrated widespread declines even in habitats that appeared suitable based on vegetation surveys. Moreover, the limited influence of habitat quality on occupancy (**Chapter II**) supports the interpretation that other factors, rather than vegetation alone, are limiting recovery in the restored islands.

Connectivity likely remains one obstacle in the outer archipelago population. Although restored habitats now offer more suitable vegetation, their benefits depend on the Apollo butterfly's ability to reach and exploit them. Given the butterfly's sedentary tendencies and fragmented distribution in the archipelago, restored sites may remain underutilised until populations expand or dispersal corridors improve (Schtickzelle et al. 2006; Bubová et al. 2015). In an archipelago context, "corridors" could refer to closely spaced stepping-stone islands that enable short-distance movements between suitable habitats. Enhancing connectivity would therefore involve maintaining or restoring resource-rich patches on nearby islets, forming a network that facilitates movement between different habitat patches (Dennis et al. 2013; Fourcade et al. 2021). A further complication is that in this study system, restoration was carried out only on governmental land within the Archipelago National Park. These sites were selected based on land ownership and, thus, were not located in the currently strongest remaining parts of the population. As a result, even though vegetation quality improved, restored sites may have offered limited demographic benefit because the Apollo butterfly populations there were already sparse or absent. Enhancing functional connectivity between high-quality sites will therefore require not only ecological planning but also coordination across landowners and stakeholders, which can pose a challenge (Jones et al. 2023).

Maintaining openness and nectar resources necessitates visible interventions, such as shrub removal and controlled burning, making societal support a critical factor for ecological success. Therefore, in **Chapter IV**, I explore how values and place-based attachments influence support for these necessary actions, as well as how engagement strategies might help overcome the connectivity challenges identified earlier.

3.4 Public Support Depends on Values, Local Context, and Perceived Validity (IV)

Building on the ecological constraints I identified in **Chapters I–III**, in **Chapter IV,** I tested whether and how pro-environmental values and local context translate into support for the same restoration actions needed to recover the Apollo butterfly. The results revealed a positive relationship between pro-environmental values and support for ecological management in general, but this association weakened when attitudes towards specific restoration measures, juniper removal and burning on the local islands, and conservation of the Apollo butterfly, were examined. These findings indicate that while pro-environmental values foster broad support for ecological management, they do not translate seamlessly into acceptance of localised interventions.

The results, however, should be interpreted with caution, as the sample was skewed toward women and highly educated respondents, which may have amplified the strength of pro-environmental values. Future work should strive for more representative samples.

3.4.1 Associations between values and attitudes

EFA identified and supported a four-factor solution: (F1) pro-environmental value orientation, (F2) general ecological management, (F3) clearing and burning, and (F4) conservation of the Apollo butterfly. CFA further supported the structure, with acceptable model fit indices. In this context, pro-environmental value orientation emerged as an underlying concept, significantly correlated with gender and membership in environmental organisations.

SEM showed that pro-environmental values were positively associated with attitudes toward ecological management. The association was strongest with general ecological management and weaker, though still significant, for attitudes toward clearing and burning, as well as the conservation of the Apollo butterfly. This finding is consistent with previous research that has linked pro-environmental values to support for environmental policies and conservation initiatives (Harring & Jagers 2013; McCright et al. 2016; Nilsson et al. 2016). It highlights a divergence between general policy-level support and local acceptance of specific, sometimes disruptive, restoration practices. General ecological management was accepted more broadly by the respondents. In contrast, localised restoration actions, including clearing, burning, and single-species conservation, received more cautious support, likely reflecting their visible impact and contested ecological effectiveness (Matzek & Wilson 2021).

In future, it would be interesting to track how support evolves, particularly as restoration outcomes become visible, to clarify whether scepticism diminishes once ecological benefits are apparent. Additionally, comparative studies across different regions and taxa would also help assess whether the patterns observed here are generalizable beyond the Finnish archipelago.

3.4.2 Social and demographic dimensions

In my dataset, women and respondents who were members of environmental groups exhibited a stronger pro-environmental value orientation than men and non-members. However, I did not find indications that age, education level, and residency in the archipelago significantly affected the pro-environmental value orientation.

Gender differences were consistent with global patterns, in which women tend to express stronger environmental concern (Chodorow 1974; Zelezny et al. 2000; Schultz 2001). Membership in environmental organisations also correlated with higher pro-environmental values, potentially reflecting greater awareness and ecological knowledge associated with environmental concern, as well as greater support for conservation (Schahn and Holzer 1990; Gifford and Nilsson 2014).

Surprisingly, residency in the archipelago did not significantly affect support. This finding suggests that emotional and cognitive connections to the landscape extend beyond residents to visitors, many of whom may hold strong attachments to the archipelago through cultural traditions, recreation, or heritage values.

3.4.3 Place attachment and conservation

The concept of sense of place provides a valuable lens to interpret the moderate support observed for localised restoration actions. The SW Finnish archipelago's unique biodiversity and cultural significance likely contribute to residents' and visitors' place attachment (Hausmann et al. 2016; Nasir et al. 2024). Place attachment has been shown to enhance civic engagement and support for conservation (Buta et al. 2014; Nasir et al. 2024). In this case, it may explain why residency status was not a significant predictor, as non-residents may also experience emotional and symbolic ties to the archipelago’s uniqueness. These ties may inhibit support for restoration actions, such as juniper removal and burning, especially if the interventions are perceived as intrusive or misaligned with local traditions.

The Apollo butterfly plays a symbolic role in this dynamic. As a nationally endangered and emblematic species restricted to islands and islets in the region, it presents an opportunity to strengthen public engagement. Strong public sentiment and a symbolic connection to charismatic species can significantly enhance involvement in conservation efforts and funding (Preston et al. 2021). However, my findings suggest that symbolic value alone does not automatically guarantee support for all conservation measures. Instead, public acceptance depends on how well management practices are communicated and aligned with local cultural values and emotional aspects (Pueyo-Ros et al. 2019).

3.4.4 Toward participatory restoration and conservation

Although the moderate support for localised actions did not reflect outright “NIMBYism,” it does indicate a cautious stance toward visible management interventions. This underscores the importance of transparent communication and stakeholder involvement. Explaining the ecological rationale behind clearing and burning, and linking these actions directly to tangible benefits such as increased biodiversity or Apollo survival, may reduce scepticism. Perceived intrusiveness and issues related to a lack of communication are significant factors contributing to public opposition (Boyle et al. 2019). Similarly, involving local stakeholders in the design and implementation of management actions can foster shared ownership, enhance legitimacy, and bridge the gap between values and acceptance (Rodgers & Willcox 2018).

In Slovenia, a successful case of reviving an endangered butterfly species illustrates the importance of a comprehensive approach to conservation (Čelik et al. 2025). This project required a thorough understanding of the butterfly's ecological needs, which laid the groundwork for developing a long-term management plan. Key to their project’s approach was adaptive management, which allowed for flexibility and refinement of protocols during the implementation phase. Moreover, the project emphasised thorough documentation and evaluation of all activities. A strong collaboration among various stakeholders was crucial for bolstering the project. This project demonstrated that integrating ecological knowledge with cooperative and adaptive management strategies can enhance the effectiveness of conservation efforts and contribute to the recovery of threatened species (Čelik et al. 2025).

These insights are relevant for conservation in the archipelago landscape, where the Apollo butterfly depends on a mosaic of small, open habitat patches that are often privately owned islands and islets. Ensuring the species’ persistence requires not only preventing encroachment and securing host and nectar resources but also building social acceptance for visible actions through transparent communication and co-creation. Engaging local stakeholders, such as landowners, recreational users, and volunteer groups, in small-scale habitat restoration, as described in **Chapters II** and **III**, could help achieve broader coverage of suitable habitat patches while fostering a sense of ownership and stewardship. Moreover, the Apollo butterfly has the potential to serve as a flagship species for nature-based recreation in the Archipelago National Park.

4 Conclusions

4.1 Key Findings

In this thesis, I investigated the ecology, restoration, and conservation context of the Apollo butterfly (*Parnassius apollo*) in the Southwest Finnish archipelago, combining field-based ecological studies (**Chapters I–III**) with social research on public attitudes and pro-environmental values (**Chapter IV**). These chapters collectively provide insights into the possible reasons for the decline of this iconic butterfly, how to enhance its habitat quality, and the importance of ecological interventions alongside public support for its conservation.

Efforts to conserve the Apollo butterfly in SW Finland are ineffective when approached in a fragmented manner. While habitat improvements can quickly enhance resources (**Chapter III**), small and isolated subpopulations (**Chapter I & III**) are unable to benefit from these advances without adequate functional connectivity and demographic support. The feasibility of such initiatives largely depends on public acceptance (**Chapter IV**). Consequently, successful conservation demands the coordination of (1) site-level openness and resource availability, (2) network-level connectivity, (3) demographic safeguards where necessary, and (4) proactive and transparent engagement with stakeholders from the outset.

In **Chapter I**, I documented a dramatic long-term decline in the Apollo butterfly occupancy in the outer archipelago population. Whereas around 75% of islands were historically occupied, fewer than 20% were occupied in 2019–2020. This decline was not explained by the reduced abundance of the larval host plant, orpine, which remained stable over decades. Instead, the results suggest that other drivers, such as habitat encroachment reducing nectar availability, extreme weather, and climate variability, have contributed to the collapse of this once-strong metapopulation. Although turnover between occupied and unoccupied islands indicated persistence of a metapopulation structure, the very low occupancy rates increase the risk of stochastic extinction. The results highlight the urgent need for conservation actions for the Apollo butterfly.

In **Chapter II**, I explored the habitat associations of Apollo in a coastal population inhabiting rocky outcrops embedded in a more heterogeneous landscape. Here, I found that occupancy was positively associated with host plant abundance, proximity to nectar sources, and higher elevation, while tree volume strongly reduced the likelihood of occurrence. These findings highlight the importance of both larval and adult resources, as well as the threat posed by encroachment. The Apollo butterfly's dependence on specific habitats, particularly those characterised by nutrient-poor rocky outcrops and an abundance of its sole larval host plant, highlights the intricate relationship between biotic and abiotic factors in its environment. As historical practices such as grazing and controlled burning have diminished, the resultant encroachment of shrubs and trees has severely altered these habitats. This necessitates a proactive strategy that integrates habitat management techniques that mimic previous land-use practices to maintain open landscapes conducive to the Apollo butterfly's lifecycle. The results are consistent with broader butterfly ecology, where resource availability and habitat quality are key factors in determining persistence.

In **Chapter III**, I assessed whether restoration efforts aimed at the Apollo butterfly, the urgent conservation actions which mimic traditional land-use practices discussed in **Chapters I** and **II**, could effectively reverse encroachment and benefit the Apollo butterfly in the outer archipelago. These efforts involved strategies such as juniper removal and prescribed burning. Vegetation responded rapidly, with significant increases in vascular plant richness, functional diversity, and nectar production. However, the Apollo butterfly occupancy continued to decline across all surveyed islands, including restored sites. This mismatch reflects a pattern in specialist butterflies: while habitat quality may improve quickly, population-level responses are often delayed (Marttila et al. 2000; Kuussaari et al. 2015). Such time lags, combined with low population size and limited dispersal capacity, may mean that recolonisation does not occur within short monitoring windows, or may not occur at all if source populations are too depleted. Thus, while restoration has laid the ecological groundwork for improved habitat quality, the recovery of Apollo butterflies will likely require not only suitable habitat but also stronger source populations, improved connectivity, and time. These results underscore the importance of long-term monitoring and adaptive management, including consideration of reinforcement or other targeted measures when natural recolonisation is unlikely.

Building on the ecological findings from **Chapters I–III**, which showed both the importance of habitat quality and the limits of restoration success under low population size and weak connectivity, **Chapter IV** shifts focus to the social dimension of conservation. In this chapter, I examined how pro-environmental values and demographic factors shape attitudes toward ecological management. The results showed that pro-environmental value orientation was positively associated with support for general ecological management and, less strongly, for specific actions such as juniper clearing, burning, and conservation of the Apollo butterfly.

The findings highlight that while the public generally supports ecological management, visible and intrusive restoration actions require clear communication and participatory processes to gain legitimacy.

By connecting ecological monitoring, habitat modelling, restoration experiments, and social attitudes, this thesis demonstrates that Apollo butterfly conservation requires both ecological and social strategies. Additionally, the relative importance of habitat characteristics can vary depending on spatial context, temporal scale, and population status. In summary, conserving the Apollo butterfly in Finland, or any threatened species, requires a multifaceted approach that combines ecological knowledge and collaboration among stakeholders. By addressing both the immediate needs and the broader ecological context of this butterfly, we contribute not only to its survival but also to the preservation of the intricate web of life it represents.

4.2 Future Perspectives and Recommendations

These suggestions for future research and recommendations for conservation practice are based on the findings of this thesis and the literature:

4.2.1 Enhance habitat quality and promote small-scale heterogeneity

My results confirm that vegetation openness, host plant, and nectar resources are critical for the persistence of the Apollo butterfly. However, broader evidence shows that butterfly populations also benefit from fine-scale habitat heterogeneity that supports foraging, thermoregulation, and reproduction (Benton et al. 2003; Oliver et al. 2010). Creating and maintaining such heterogeneity requires interventions at multiple levels. At the local level, volunteer groups and landowners can contribute to conservation efforts through restoration practices. Heterogeneity could be maintained with such practices as selective shrub and invasive alien species removal, rotational grazing, and delayed mowing of roadsides, all of which increase structural and floral diversity. At the landscape scale, agri-environmental schemes that incentivise organic farming, wider field margins, and rotational grazing can substantially enhance matrix quality and facilitate interpatch movement (Vandermeer & Perfecto 2007; Rundlöf et al. 2008; Piccini et al. 2024; Lehikoinen et al. 2024). In some systems, coppice management and temporary habitats created by forest clearings have also been shown to sustain threatened butterflies (Fartmann et al. 2013; Graser et al. 2023; Sielezniew et al. 2024). At the regional and national level, management planning should explicitly integrate heterogeneity as a conservation goal. Additionally, it is crucial to ensure that environmental impact assessments and ecological compensation measures account for sensitive species and habitats. Research from Sweden suggests that while ecological compensation is being implemented, significant challenges persist, including weak integration into planning processes, a narrow species focus, and a lack of monitoring standards (Blicharska et al. 2022); similar issues have been documented in Poland’s faunistic reserves (Ginszt & Laskowska-Ginszt 2024). Finally, at the EU level, policy frameworks such as the Common Agricultural Policy, the EU Biodiversity Strategy for 2030, and the Nature Restoration Law provide opportunities to support and guide member states in restoring heterogeneity at larger scales. Taken together, fostering heterogeneity across these levels can buffer butterfly populations against climatic extremes, enhance population stability, and improve long-term persistence.

4.2.2 Monitoring populations and restoration outcomes

The significant decline of the outer archipelago population went unnoticed for nearly two decades due to the absence of systematic monitoring, leaving the drivers of decline open to speculation. Regular monitoring is therefore essential for detecting subtle or delayed ecological changes, distinguishing natural variability from real declines, and understanding the complex dynamics (Lindenmayer & Likens 2010; Magurran et al. 2010) of butterfly populations. For univoltine species, such as the Apollo butterfly, annual surveys with repeated visits during the short larval period are likely the minimum requirement to ensure reliable information (Van Swaay et al. 2015). Less frequent monitoring (e.g. once per decade) risks overlooking rapid changes, as demonstrated by the sharp contraction of Apollo distribution that remained undocumented between the early 2000s and 2019. Long-term butterfly schemes across Europe indicate that consistent annual data are essential for detecting population trajectories and identifying the drivers of change (Thomas et al. 2004; Van Swaay et al. 2012). When resources are scarce, intermittent monitoring may be a cost-effective compromise. Even if surveys are not conducted annually, repeated visits within the same season can still yield valuable insights into population dynamics and environmental drivers, such as temperature-related shifts in phenology (Goded et al. 2024).

For species that occupy many habitat patches, patch occupancy monitoring provides a practical and effective approach for assessing trends (WallisDeVries 2004; MacKenzie et al. 2017). In particular, larval surveys can be effective for conspicuous species, such as the Apollo butterfly, where larvae can be reliably observed (Wahlberg et al. 2002; Nowicki et al. 2008). The Apollo butterfly’s distinctive larval colouration and unique adult appearance make misidentification unlikely, thereby increasing the potential for involving volunteers in monitoring. In Austria, the LIFE Apollo2020 project is currently training dogs to monitor the Apollo butterfly, especially to cover areas that are inaccessible to humans (Vancura

2024). Citizen science offers a cost-effective complement to expert surveys (Taron & Ries 2015; Dennis et al. 2017). Additionally, participation in butterfly monitoring has been shown to increase nature connection, nature noticing, and pro-conservation attitudes, while also improving overall well-being (Butler et al. 2024). Thus, using expert-led and citizen-based monitoring could provide robust long-term data while simultaneously strengthening public engagement and support for management actions. The information needs and costs associated with different approaches will ultimately determine the optimal strategy (Haddad et al. 2008; Taron & Ries 2015).

Positively, Metsähallitus has released a management plan for the Archipelago Sea that emphasises the importance of ongoing monitoring of the Apollo butterfly (Metsähallitus 2025). While the plan does not prescribe specific intervals for the Apollo butterfly monitoring, it notes that other sensitive species, such as *Parnassius mnemosyne*, should be monitored every 1–3 years, and that monitoring of endangered species should be updated regularly. In the management plan, the Apollo butterfly is recognised as a species of urgent conservation concern under the Habitats Directive, and the restoration and management of its habitats are expected to benefit numerous other endangered species (Metsähallitus 2025). However, the only existing management plan in Finland remains at a rather general level and is focused on the declining and currently low-numbered population of the Archipelago Sea. This highlights a gap between recognition at the policy level and the development of detailed, population-specific monitoring protocols. Strengthening this framework provides an opportunity to integrate systematic and cost-efficient Apollo butterfly monitoring into ongoing and future management programs while ensuring consistency across all remaining populations.

Monitoring is also essential for evaluating the restoration outcomes. My results demonstrate that juniper removal and prescribed burning produced rapid effects on vegetation: bare ground decreased, vascular plant richness increased, and functional diversity shifted toward traits beneficial for pollinators. However, these ecological improvements had not yet translated into demographic benefits for the Apollo butterfly during the short monitoring period. Therefore, continued monitoring is essential to determine whether Apollo butterfly populations eventually respond to the improved vegetation structure and resource availability. Annual or biennial monitoring with repeated within-season visits is needed to detect recovery lags and rule out false absences.

Without systematic monitoring and an understanding of what constitutes ecological success, there is a risk of misallocating resources, overestimating the success of restoration or failing to detect delayed responses of species (Palmer et al. 2005; Ruiz-Jaen & Aide 2005; Wortley et al. 2013). Connecting population and habitat monitoring would provide the most informative evaluation, ensuring that conservation actions are both ecologically effective and adaptive over time.

4.2.3 Active and adaptive site management

My results show that despite vegetation improvements, the Apollo butterfly occupancy continued to decline in the outer archipelago population. This suggests that habitat improvements alone may not be sufficient when populations are already very small and fragmented. Therefore, active and adaptive management should be considered. Repeated interventions (e.g., grazing, selective clearing, small-scale burning) are necessary to maintain open, sun-exposed conditions and prevent juniper encroachment. This is supported by earlier studies on Apollo butterfly conservation (Dolek & Geyer 2002; Bubová et al. 2015). In cases where populations remain critically low despite improved habitat, reinforcement through small, carefully planned releases could be an option to enhance local persistence. There are successful examples of assisted migration in Finland with *Parnassius mnemosyne* (Kuussaari et al. 2015) and reinforcement of a tiny existing *Scolitantides orion* population with minor release, circa 200 individuals, in Sweden (Dunskis et al. 2024). This approach has also been applied in Poland, where captive rearing and releases have contributed to the recovery of several Apollo butterfly populations (Witkowski & Adamski 1996; Adamski & Witkowski 2007; Adamski & Ćmiel 2022). However, these required decades of intensive effort, close integration of rearing with large-scale habitat management, and long-term monitoring. Any consideration of reinforcement in the Finnish archipelago must therefore be approached cautiously. It is essential to ensure that possible reinforcement complements habitat improvements and is guided by both ecological evidence and stakeholder engagement. Engaging stakeholders is important because restoration is not solely an ecological process but also a social one that depends on public acceptance, transparency, and collaboration (Burger 2010; Bodin 2017; Gann et al. 2019; DeAngelis et al. 2020). Local communities and other stakeholders often hold valuable ecological and cultural knowledge that can enhance project design and legitimacy, while their involvement reduces opposition linked to NIMBY attitudes and strengthens long-term commitment to conservation goals (Boyle et al. 2019; Rodrigues dos Santos 2021; Pearson and Gorman 2023). In the case of the Apollo butterfly, such stakeholder engagement is particularly vital, as the species' conservation relies on continued management of privately owned land where local cooperation determines the feasibility and sustainability of restoration measures. More broadly, adaptive management in conservation should be based on continuous ecological monitoring and feedback from stakeholders to ensure that interventions are both practical and socially acceptable (Rodgers & Willcox 2018; Gann et al. 2019). Adaptive actions would also align with the goals of the EU Biodiversity Strategy for 2030 and the Nature Restoration Law, which emphasise restoring open habitats and safeguarding endangered species through adaptive, evidence-based management.

4.2.4 Connectivity and landscape planning

A comparison of the two study populations highlights the importance of landscape context. Whereas the archipelago population showed signs of functional isolation, with restored islands seldom colonised, the coastal population still occupies a denser network of rocky outcrops embedded in an agricultural–forest matrix. In the coastal population, the spatial arrangement of host and nectar plant patches appears more favourable. These differences underline that restoration success cannot rely solely on improving individual sites but must be planned at the scale of entire habitat networks.

For the archipelago population, dispersal constraints across water barriers limit recolonisation, meaning that even high-quality restored patches may remain underutilised if they are not spatially connected to current strongholds. In this context, prioritising restoration on islands that are well connected to occupied patches is likely to be more effective than focusing on isolated sites. Therefore, network-scale planning for connectivity, such as prioritising restored sites within colonisation distance of sources, is essential for ensuring that vegetation gains lead to successful recolonisation. In the longer term, if functional isolation persists, strategies such as reinforcement or assisted colonisation may need to be considered to maintain metapopulation viability.

Such explicit landscape-level planning is essential not only for the persistence of the Apollo butterfly but also for the many other species that depend on open, nutrient-poor habitats. By accounting for connectivity, management strategies can help buffer populations against local extinctions, enhance dispersal opportunities, and promote overall ecosystem resilience.

4.2.5 Social engagement and communication

Conservation actions must be framed in ways that resonate with community values and cultural or place-based attachments. My results highlight the importance of transparent communication about why interventions such as burning or juniper removal are necessary, and how they benefit both the Apollo butterfly and broader biodiversity (Matzek & Wilson 2021). Clear communication can reduce scepticism and provide legitimacy, but long-term success also depends on the active involvement of local stakeholders. Engaging communities in restoration fosters shared ownership, enhances trust, and strengthens a sense of place (Hausmann et al. 2016).

Educational initiatives, such as those in White Carpathians (Rossberg 2024), that emphasise the Apollo butterfly's ecological role and its cultural significance can further mobilise public support. At the same time, landowners and managers should be encouraged to adopt sustainable practices that align conservation with land use goals, ensuring that management efforts are both practical and beneficial locally.

Citizen science provides a particularly promising avenue. Monitoring the Apollo butterfly populations is relatively straightforward, and butterfly monitoring more broadly has been shown to increase nature connectedness, nature noticing, and pro-conservation attitudes (Butler et al. 2024). By integrating local knowledge, volunteer participation, and public engagement into restoration projects, conservation strategies can achieve dual benefits: strengthening ecological outcomes while also deepening social commitment to biodiversity protection.

4.2.6 Conservation Actions and Research Possibilities

To support the recovery of the Apollo butterfly, actionable steps should be tailored to the specific ecological and landscape contexts of each population. In the outer archipelago, restoration efforts should focus on islands within demonstrable colonisation distance of existing populations. This may include engaging private landowners and volunteers, synchronising shrub removal with the enhancement of nectar resources (e.g. sowing native wildflower mixes), and considering reinforcement only after habitat quality and functional connectivity have been sufficiently improved.

In the coastal population, where rocky outcrops are embedded in a rapidly developing landscape, the maintenance of open habitats and nectar-rich areas within 0–300 m of host plant patches remains crucial for supporting the Apollo butterfly. Increasing host plant density (e.g. sowing local orpine seeds) could enhance the habitat quality. However, recent land-use changes, including infrastructure and housing development, have resulted in some irreversible loss of habitats, a concerning trend given that the Apollo butterfly is listed under Annex IV of the EU Habitats Directive, which provides strict protection for the species' breeding and resting sites. To prevent further habitat degradation and loss, systematic larval monitoring should be implemented across the coastal population range to identify potential breeding habitats. These areas should be prioritised for strict protection or, where avoidance is not feasible, for mandatory habitat compensation as part of land-use planning.

Future research could strengthen conservation efforts in several key areas. First, functional connectivity analyses would help assess how landscape features facilitate or constrain movement and genetic exchange, allowing for the identification of key areas for restoration and land protection. Second, incorporating metapopulation modelling would clarify the roles of different outcrops or islands as source or sink habitats, helping to prioritise management where it matters most (e.g. Fred et al. 2006).

Understanding the butterfly's vulnerabilities across life stages is also essential. Targeted studies should assess the survival of overwintering eggs, larvae, and adults under varying climatic conditions to identify which stage is most affected by stressors. The potential role of extreme events, such as the 2018 drought, should be revisited to determine whether it triggered demographic bottlenecks.

Finally, although reinforcement from other populations has proven effective elsewhere, it should only be explored in Finland after habitat improvements and connectivity prerequisites are met. Collectively, these coordinated actions and research directions would help address the interconnected ecological and demographic challenges facing the Apollo butterfly and guide evidence-based conservation planning.

4.3 Final reflections

The Apollo butterfly serves both as a symbol and a sentinel: a species that reflects the fragility of specialised habitats in a changing world, while signalling the health of broader ecological systems. This thesis has demonstrated that conserving such a species is a complex endeavour. On the one hand, the ecological requirements of the Apollo butterfly are relatively well understood, and restoration can rapidly improve vegetation structure and resource availability. On the other hand, population responses remain constrained by demographic limits, dispersal barriers, and time lags, meaning that ecological gains do not automatically translate into recovery.

My findings also highlight that conservation is not solely an ecological endeavour. Public support, stakeholder engagement, and cultural connections to place are equally crucial for ensuring that restoration efforts are accepted and sustained. I acknowledge that challenges remain, including resource constraints (funding), implementation issues, demographic bottlenecks, and social uncertainties. However, they also may present opportunities. By integrating ecological knowledge with adaptive management, transparent communication, and participatory approaches, such as citizen science, the conservation of the Apollo butterfly could serve as one example of how ecological and social dimensions can be successfully bridged in biodiversity protection.

Ultimately, ensuring the persistence of the Apollo butterfly in Finland will require a long-term commitment to maintaining open, heterogeneous landscapes, as well as fostering collaboration among researchers, landowners, practitioners, policymakers, and local communities. If achieved, such an approach will not only support the Apollo butterfly but also strengthen the resilience of fragmented landscapes and the many species that depend on them.

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