



Negative impacts of future forest succession on three threatened butterfly species

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Abstract

The dynamic interplay between anthropogenic activities and biodiversity conservation necessitates a nuanced understanding of habitat change, especially in contexts marked by transitions from grasslands to forested areas. This investigation utilised three threatened butterfly species—the Marsh Fritillary, Apollo, and Large Blue—as models to explore how grassland associated species respond to altered environmental conditions. The methodology encompassed extensive field surveys and statistical analyses with ecological niche modelling to determine their current and future distributions on the Island of Gotland. The species were surveyed under distinct years from 2017 to 2020 in a total of 3333 hectares in a 6000 hectare area—the Marsh Fritillary in 2017 (1232 hectares), Apollo in 2019 (2346 hectares), and Large Blue in 2020 (2256 hectares). Results revealed that the estimated current extents of suitable habitats were 49,104 hectares for the Marsh Fritillary (15.6% of the island), 45,646 hectares for Apollo (14.5%), and 33,089 hectares for Large Blue (10.5%). In general, increased forest and shrub cover and decreased heterogeneity negatively affected butterfly occupancy, but each species exhibited unique habitat preferences. The predictive modelling demonstrated that continued succession would reduce the amount of habitats predicted to be suitable and generated alarming forecasts—a twofold increase in forest and shrub cover suggests habitat declines of 41%, 47%, and 65% for the Marsh Fritillary, Apollo, and Large Blue, respectively. Given these findings, proactive measures are imperative for strategically managing these habitats to preserve landscape heterogeneity and accommodate diverse ecological needs. This study is important to conservation management providing, crucial insights amid anthropogenic and ecological changes.

Keywords Butterflies · Environmental change · Forest succession · Land use · Lepidoptera · Ecological niche models

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Extended author information available on the last page of the article

Introduction

The world faces an unprecedented biodiversity crisis, with extinction rates 100 to 1000 times higher than background rates (Barnosky et al. 2011; Pimm et al. 2014; Rull 2022). This global biodiversity crisis is primarily attributed to habitat loss and degradation owing to the direct and indirect effects of climate change, altered land use, the growing human population, and exploitation—and the negative trend is expected to continue (Parmesan & Yohe 2003; Rull 2022; Thomas et al. 2004). As extinction rates continue to surge, understanding how different stressors influence the availability of suitable habitats for different species, and thus their potential distributions, is pivotal for improving projections on how populations, species, and ecosystems will respond to environmental change, which will be vital for designing targeted conservation strategies that can promote successful management.

Among the organisms heavily impacted by the environmental changes are butterflies—iconic indicators of environmental health and vital pollinators in ecosystems (Cardoso et al. 2020; Wagner et al. 2021). One of the main threats to butterflies stems from widespread habitat degradation and loss (Warren et al. 2021). Many suitable habitats have already disappeared, and yet more are threatened by altered land use practices and climate change-driven transformations (Cardoso et al. 2020). Modified agricultural and forestry practices have resulted in substantial transformations in land cover through deforestation, afforestation, and succession (Reidsma et al. 2006). The discontinuation of traditional practices has had varying effects, encompassing both intensified land use following transitions to modern practices as well as decreased land use owing to abandonment of land. These transformations have had severe consequences for semi-natural grasslands and associated biodiversity (Balmer & Erhardt 2000; DeFries et al. 2004; Kuussaari et al. 2007; Öckinger et al. 2006; Young et al. 2005). Both intense grazing by livestock, such as cattle and sheep, and overgrowth of shrubs and trees as a result of natural succession following the cessation of grazing (i.e., after small farms have been abandoned) pose severe challenges for butterflies in Europe, threatening the persistence of many species (Bussan 2022; Hula et al. 2004; Johansson et al. 2019; Kindvall et al. 2022a, 2022b).

The response of butterflies to succession scenarios is complex and will vary depending on location, species characteristics and the type and magnitude of habitat changes (Kuussaari et al. 2007; Thomas 1993). Because the habitat requirements, including the type of food, shelter, and breeding sites, differ among butterfly species, a variety of resources, including forest and shrub cover, availability of host plants, and moisture levels, all influence the distribution and survival rates (Ehrlich 1992; Hanski & Gaggiotti 2004; New et al. 1995). With their specific habitat requirements, short generation times, and dispersal capability, butterflies are excellent model organisms in ecological studies aimed at investigating how biodiversity responds to altered environmental conditions (Ehrlich & Hanski 2004; Hanski 1998; Urban et al. 2016; Warren et al. 2001).

While numerous regions across the globe have witnessed declines in forest cover, particularly in tropical areas post-2000, forest cover in the colder northern territories is on the rise (SLU 2022; Soja et al. 2007; Sunde et al. 2023). This expansion has largely been attributed to the succession of grasslands and wetlands and the establishment of new forest plantations (Erdős et al. 2022; SLU 2022). One area where biodiversity is profoundly threatened by forest succession is the Island of Gotland in the Baltic Sea, Sweden. The island, characterised by extensive and interconnected grassland habitats, is experiencing a transformation of grassland habitats into forests (Jansson & Zucchetto 1978; Pettersson

et al. 2019; Pettersson 1958; Rosén & van der Maarel 2000), a succession accelerated by human activities (Löhmus et al. 2015) and climate change (McMahon et al. 2010). The challenge for many native species has been exacerbated by landscape drainage, a practice used in large parts of western and northern Europe to facilitate forest growth, which causes wetlands and semi-natural habitats to disappear. The reduction of these important habitats has had dramatic consequences for the associated flora and fauna (Löhmus et al. 2015; Saarinen et al. 2003), and the loss of flower-rich areas vital for butterflies, such as semi-natural grasslands, leads to localised or even global extinctions (Thomas et al. 2004). In Sweden, the steady increase in forest cover (SLU 2022; Sunde et al. 2023) particularly impacts species associated with rich fens and flower-rich grasslands, many of which are on the verge of extinction (Eide et al. 2020).

Three threatened butterfly species that are important in this context are the Marsh Fritillary (*Euphydryas aurinia*), the Apollo butterfly (*Parnassius apollo*), and the Large Blue (*Maculinea/Phengaris arion*). These butterfly species, as well as their host plants, require relatively open habitats, and all three butterflies are widespread on Gotland, where their ecology and spatiotemporal dynamics have been studied extensively (Franzén et al. 2022b; Johansson et al. 2019; Kindvall et al. 2022a, 2022b). While previous studies have shed light on various aspects of the ecology and spatiotemporal dynamics, such as the effects of grazing (Johansson et al. 2019; Kindvall et al. 2022a, 2022b), and factors associated with climate change (e.g., phenology, Franzén et al. 2022a; temperature, Franzén et al. 2022b; extreme weather, Johansson et al. 2020; and drought, Johansson et al. 2022), important knowledge gaps still remain. For example, it is not known how continued forest succession will impact the availability and quality of habitats for these species and to what extent it will influence their future distributions and persistence. Addressing these knowledge gaps is essential to obtain the comprehensive understanding required for formulating conservation strategies that mitigate the threat and effectively protect these threatened butterflies. For this, Ecological Niche Models (also called Environmental Niche Models; ENMs) are pivotal. ENMs relate known species occupancies to environmental characteristics to identify species-environment relationships and to project species distributions. They allow for incorporating several environmental factors when predicting habitat distributions, thus presenting a holistic view of an organism's habitat (Melo-Merino et al. 2020; Peterson 2006).

In this study, we used generalised linear models (GLMs) to determine and compare the species' habitat preferences for environmental variables associated with forest succession and drainage (forest cover, shrub cover, cover of open land, habitat heterogeneity, and ground moisture). The species-specific GLMs were subsequently used to infer the current distribution of suitable habitats (i.e., the potential butterfly distribution) and to model the distribution of suitable habitats under different hypothetical succession scenarios to project the potential future butterfly distributions.

Materials and methods

Description of the study species

The present study included three butterfly species: the Marsh Fritillary (*Euphydryas aurinia*), the Apollo butterfly (*Parnassius apollo*), and the Large Blue (*Maculinea/Phengaris arion*). These species have suffered declines and are red-listed across Europe to varying degrees (Eide et al. 2020; Gärdenfors 2015; SLU, 2020; van Swaay et al. 2010; Warren et al. 2021). They are

of considerable conservation concern and are under legal protection in the European Union (EU), covered in the Habitats Directive (Council Directive 92/43/EEC). Despite their poor statuses globally, the species are locally abundant, for example, in certain areas on the island of Gotland in the Baltic Sea (including our study area; see details in the section 'Description of the study area' further down), thus allowing comprehensive evaluations of their habitat preferences within this region.

The Marsh Fritillary is an orange-to-brown butterfly with a wing pattern of chequered markings and an average wingspan ranging from 33 to 48 mm. Its distribution spans large parts of the Palaearctic region, ranging from western Europe and northern Africa into Asia, but the species is absent in several countries within the range and is only found locally in certain areas (Stănescu et al. 2022). As indicated by its name, the Marsh Fritillary is associated with relatively wet habitats; in our study area, it inhabits damp to wet calcareous ungrazed grasslands and rich fens, where the larvae host plant devil's-bit scabious *Succisa pratensis* is found (Johansson et al. 2019, 2020). The Marsh Fritillary is a univoltine species, and in Sweden, adults are active from late May to late June (Eliasson et al. 2005; Franzén et al. 2022a). The adults feed on the nectar from different flowering plants, and the females lay their eggs under the leaves of *S. pratensis*. When the larvae hatch from July to August, they build a nest of silk webs around the host plant, where they live gregariously feeding until September, when they enter diapause after reaching the fourth instar. The larvae hibernate collectively and resume feeding in the spring until the fully-grown larvae pupate in May or June (Eliasson et al. 2005; Johansson et al. 2019, 2020).

The Apollo butterfly is a large, white butterfly with a wing pattern of variable black and red elements and an average wingspan ranging from 73 to 87 mm (Eliasson et al. 2005). Its distribution is scattered across the western Palaearctic (large parts of Europe to China). Apollo is found in our study area's alvar terrain, which is characterised by sparse vegetation and low plant establishment on limestone, aligning with its preference for bare rocks and vegetation-free surfaces. It is a univoltine species, and in Sweden, adults are active from June to August (Eliasson et al. 2005; Franzén et al. 2022a). The adults feed on the nectar from many flowering plants, and females lay their eggs on different shrubs, bushes, and vascular plants. The eggs overwinter until spring when the larvae hatch and feed on *Sedum album* (the only Apollo larvae host plant in our study area), and then pupate in May/June (Eliasson et al. 2005).

The Large Blue is a small, blue butterfly with black spots on the dorsal side of the forewings and an average wingspan ranging from 32 to 42 mm. Its distribution resembles that of Apollo, scattered across the western Palaearctic (large parts of Europe to China). The species has highly specific requirements; it is thermophilic and associated with dry grasslands, and in our study area, it is found on dry, unfertilised calcareous grasslands and naturally open alvar terrain where vegetation is limited by low establishment success. It is a univoltine species, and in Sweden, adults are active from July to August (Eliasson et al. 2005; Franzén et al. 2022a). Adults feed on nectar from many flowering plants, and females lay their eggs on the larvae host plant *Thymus serpyllum*. After hatching in August, the larvae feed exclusively on *T. serpyllum* until *Myrmica* ants adopt them into their nests. In the nests, the larvae feed parasitically on ant broods and then hibernate before pupating in June (Eliasson et al. 2005; Thomas et al. 2009).

Description of the study area

The field surveys of this study were conducted in an area of approximately 6000 hectares (10 km × 6 km) encompassing 3333 hectares located close by Slite on the island of Gotland

in the Baltic Sea, Sweden (midpoint of the area: 57° 69' N, 18° 69' E) (Fig. 2). In this region, all three butterfly species are locally abundant (Franzén et al. 2022a; Johansson et al. 2020, 2022), and it is one of few remaining landscapes where continuous populations can be found. Because the area encompasses a region where large areas of suitable habitats and relatively large numbers of the three species occur, it offers a great opportunity to comprehensively study the ecology of the species, determine their habitat requirements, and evaluate the impacts of altered future conditions.

The landscape consists of a variety of habitats, including 15 habitat types listed in the Habitats Directive. It covers sites characterised by extensive livestock grazing (which has intensified since 2000; Kindvall et al. 2022b), ungrazed areas overgrown with shrubs and trees, and old pine forests. The different habitat types are interspersed throughout the study area, making up a mosaic of differently sized habitat patches. The surrounding agricultural fields constitute a boundary towards the west and northeast (Fig. S1).

Butterfly occupancy data collection

For our study, we employed a grid-based systematic approach (Norman et al. 2023) covering the entirety of the designated study area. We overlaid a grid-net, each cell spanning 100×100 m, over our study site, thus creating a total of 3333 hectare-grids for butterfly surveys.

Owing to logistical constraints and a noticeable scarcity of Large Blue butterflies during 2018 and 2019 (due to the 2018 drought; Johansson et al. 2022), surveys for each species were conducted in distinct years. The Marsh Fritillary was surveyed in 2017, Apollo in 2019, and Large Blue in 2020.

The fieldwork methodology was designed to align with the flight periods of the target butterfly species, and surveys were initiated early in their respective flight period and extended until their culmination, effectively covering most of their active flight period. For the Marsh Fritillary, field work was initiated on the 26th of May 2017 and terminated on the 27th of June 2017, encompassing a 33-day period wherein surveys were conducted on 28 days. In the case of Apollo, field work was initiated on the 14th of June 2019 and terminated on the 5th of August 2019, encompassing a 52-day period wherein surveys were conducted on 47 days. Lastly, for Large Blue, field work was initiated on the 10th of July 2020 and terminated on the 4th of August 2020, encompassing a 26-day period wherein surveys were conducted on 23 days. To ensure comprehensive coverage across the flight period, all hectare-grids underwent daily or bi-daily surveys, predominantly between 8 a.m. and 6 p.m. on days with conducive weather conditions. Adverse weather conditions, especially rain (within one hour post-rainfall) or temperatures below 14 °C, precluded any survey activities.

The field surveys involved a team comprising up to ten proficient field personnel on any given day. In total, 14, 18, and 9 field personnel were involved in the data collection for the Marsh Fritillary, Apollo, and Large Blue, respectively. Before field deployment, each participant underwent a half-day training session focusing on butterfly capture, identification, handling, marking, and data documentation. A systematic rotation of field personnel and their schedules ensured that all grids were surveyed by different observers and during different times of the day. Fieldwork was designed to optimise the spatial coverage of hectare-grids, and butterfly observations were documented along non-linear pathways to encompass all areas of potential utilisation within each grid. Data metrics, including species, geographical coordinates, and time of capture for each specimen, were recorded in

the Collector app (Esri). Based on the capture data, each hectare-grid was categorised as either occupied or unoccupied by each of the three butterfly species. Grids were re-visited at least five times to minimise the risk of erroneously being assigned as unoccupied. The complexity and methodological rigour of our fieldwork (e.g., large study area, sampling throughout the flight period, and repeated re-visits to ensure accurate occupancy assignments) allow for comprehensive investigations of different aspects of these species' ecology and population dynamics (Franzén et al. 2022a, 2022b; Johansson et al. 2019, 2020, 2022; Kindvall et al. 2022b), and emphasises this study's valuable contribution to contemporary landscape-scaled butterfly studies.

Because absence data also carries information for ENMs, the inclusion of extended absence data can significantly improve predictive performance, especially when the actual data is collected in a climatically or spatially biased manner (Barbet-Massin et al. 2012). To increase the reliability of our models, we therefore expanded the study areas by including absence data (assigning grids as unoccupied) for the unsuitable surrounding areas, which resulted in a total of 8683 hectare-grids ($N_{aurinia} = 6594$; $N_{apollo} = 6425$; $N_{arion} = 6437$; see Fig. 2). Regarding the extended grids, none of the target species have their host plant or suitable microclimate within these grids. The grids were primarily composed of habitats unsuitable for the species in question, including dense forests, open areas lacking essential host plants (e.g., *Schoenus ferrugineus* wetlands), intensively grazed fields, and exploited areas. Systematic evaluations were conducted once in each of the expanded hectare grids to ascertain the absence of host plants and confirm the unsuitability of these habitats for supporting the studied butterfly species.

Land cover and environmental data

For this study, the Swedish Environmental Protection Agency provided high-resolution data comprising 25 distinct land cover categories covered in the national land cover data (NMD) (Naturvårdsverket 2018). NMD comprises a foundational cartography segmented into 25 thematic classes. The mapping is conducted in a raster format with a spatial resolution of 10 m and a minimum mapping unit of 0.01 hectares. In addition to this foundational cartography, we obtained data on ground moisture (ground moisture index) and shrub and forest cover (Naturvårdsverket 2018). The environmental data was extracted on a 10 m × 10 m grid scale, and several key environmental variables were averaged per hectare-grid (100 m × 100 m). These include forest cover, shrub cover, coverage of vegetated open land, coverage of non-vegetated open land, and ground moisture index. In addition, habitat heterogeneity within each grid was estimated by calculating the Simpson diversity index. These derived metrics provide a comprehensive environmental characterisation of each hectare-grid, enhancing the granularity and precision of habitat assessments.

The Simpson diversity was calculated with the formula: $D = \sum n(n - 1) / N(N - 1)$, where D denotes the Simpson diversity, ' n ' the abundance of a specific landscape characteristic (conceptualised as 'species'), and ' N ' the cumulative abundance of all landscape characteristics (sum of all 'species'). For this, all 25 land cover categories and three distinct forest growth rate classes were included, as well as a series of continuous environmental variables: ground moisture index, forest and shrub cover, and forest and shrub height. These variables were partitioned based on their quantile distribution as follows: low (smaller than the 25th quantile), medium (spanning between the 25th and 75th quantiles), and high (larger than the 75th quantile). Each landscape characteristic, interpreted as a 'species' within this context, was confined to the hectare-grid, encompassing 100 pixels,

each sized at 10 m × 10 m. The abundance metric was expressed as the total number of 10 m × 10 m segments occupied by a specific landscape element within each hectare-grid. The Simpson diversity index used in this study signifies the likelihood of two congruent landscape characteristics being randomly sampled from an identical hectare-grid (Borcard et al. 2011). Consequently, a higher Simpson diversity estimate indicates decreased environmental heterogeneity (i.e., increased uniformity) within the hectare-grid. As land cover cannot exceed 100% (i.e., complete cover) in the real world, it was imperative to ensure that the total land cover for each grid did not exceed this. When summing the values of forest cover, shrub cover, and coverage of open land 262 of the 315,665 grids on Gotland surpassed the limit. To rectify this, we recalibrated the values for these 262 grids, ensuring that the land cover categories retained their inherent relative proportions whilst their aggregate aligned to precisely 100%.

Statistical analyses

R.4.0.3 (R Core Team 2021) was used for all the statistical analyses, and data visualisations were created using ggplot (Wickham 2016). Because collinearities among predictor variables can cause model instability and loss of predictive power (Dormann et al. 2012), the modelling process commenced with collinearity testing with hierarchical cluster analysis (Varclus analysis in the Hmisc package; Harrell 2020) to select the least correlated environmental variables. To exclude highly correlated variables, we used a threshold of 0.3 for the Spearman correlation coefficient (Graham 2003), which resulted in one of the six initially included environmental variables (cover of vegetated open land) being excluded, whereas the other five (forest cover, shrub cover, cover of non-vegetated open land (henceforth referred to as just ‘open land’), habitat heterogeneity, and ground moisture) were retained for use in the subsequent analyses (Fig. S2).

Fitting GLMs to investigate habitat requirements

To investigate species’ habitat preferences, we used generalised linear models (GLMs) with a binomial response distribution, implemented in the ‘glmmTMB’ function in the ‘glmmTMB’ package (Brooks et al. 2017). Before running the real analyses, we performed model optimisation for each of the three study species separately to construct species-specific best-fit models. For this, multiple GLMs with logit link functions were run and compared. For all GLMs, butterfly occupancy was introduced as a binomial, presence/absence (1/0) response variable, and each hectare-grid (from the full dataset containing extended absence data) contributed one observation. The models differed in the included environmental variables, incorporating some or all of forest cover, shrub cover, cover of open land, habitat heterogeneity, and ground moisture—all introduced as continuous predictor variables. First, the full model, including both linear and squared terms (to encompass potential for non-linear correlations) of all five environmental variables, was run. The ‘dredge’ function in the ‘MuMIn’ package (Bartoń, 2013), which performs automated model selection was then used to compare and select the model with the lowest corrected Akaike information criterion (AICc). To further assess the best-fit GLMs identified in the model selection process, their performances were compared to those of models that included only linear terms. For this, the corresponding ‘full’ GLMs (with all five environmental predictor variables) but including only linear terms were also run and dredged. Lastly, the ‘anova’ function in base R was used to compare AIC for all of the models (null model, full linear terms

only model, optimised linear terms only model, full linear and non-linear terms model, and optimised linear and non-linear terms model). This showed that the full linear and non-linear terms model had the best fit for Apollo, whereas the optimised linear and non-linear terms models were superior (had the lowest AIC) for the Marsh Fritillary and Large Blue (Table S1), and these GLMs were thus used in the subsequent distribution predictions in the ENMs. To assess statistical significance of model terms and obtain slope estimates with standard errors, the Likelihood Ratio tests (type II) implemented in the ‘Anova’ function in the ‘car’ package (Fox et al. 2019) and the ‘summary’ function in base R were used. The ‘effect’ function in the ‘effects’ package (Fox 2003; Fox & Weisberg 2019) was used to obtain predicted means for each predictor variable separately, and results were visualised using ggplot.

Cross-validation of models

We employed the predict function in base R on the GLMs to evaluate the predictive capability of each occupancy model. For this, the full dataset containing extended absence data was analysed and tenfold cross-validation was used. Although ideally, statistically independent test data should be used for model evaluation (Araújo et al. 2005), data-splitting methods often serve as viable alternatives. In the literature, the most commonly adopted values for K are 5 or 10, which are believed to yield test error rate estimates that are minimally affected by bias or variance (Araújo & Guisan 2006; Nti et al. 2021). In K -fold cross-validation, the dataset is partitioned into K subsets. During each validation cycle, one of the subsets is reserved for validation, while the remaining $K - 1$ folds serve as the training set. Consequently, in our study, 90% of the data was used for training and 10% for validation.

Optimal threshold methods for ecological niche modelling

When predicting species distributions, many different methods for determining the threshold for assigning occupancy status (occupied/unoccupied) can be used, and the best choice depends on the properties of the specific dataset (Freeman & Moisen 2008b; Manel et al. 2001). To evaluate which method to use in this study, we compared the performance of seven threshold methods available in the ‘optimal.thresholds’ function in the ‘Presence-Absence’ package (Freeman & Moisen 2008a): (1) ‘Default’: threshold fixed at 0.5, (2) ‘Sens=Spec’: the threshold where sensitivity equals specificity, (3) ‘MaxSens+Spec’: the threshold that maximises the sum of sensitivity and specificity, (4) ‘MaxKappa’: the threshold that maximises Cohen’s Kappa, a measure of classification accuracy, (5) ‘MaxPCC’: the threshold that maximises PCC (percent correctly classified), (6) ‘Pred-Prev=Obs’: the threshold where the predicted prevalence equals the observed prevalence, and (7) ‘ObsPrev’: the observed prevalence of each species in the dataset. Sensitivity refers to the ability of the model to correctly identify true positives, and specificity to the ability of the model to correctly identify true negatives.

Model performance metrics

Model performance was evaluated, and optimal threshold method chosen based on the mean values from the tenfold cross-validations of assignment accuracy: the percentage of correctly assigned grids (both true positives and true negatives), sensitivity, specificity, area under the curve (AUC), and the true skill statistic (TSS, sensitivity + specificity

– 1; Allouche et al. 2006). Performance varied considerably among the threshold methods (see Table S2). Four of the methods (Default, MaxPCC, MaxKappa, and PredPrev = Obs) suffered from notably low sensitivity and the first two majorly underestimated occupancy, especially for Large Blue—problems likely associated with its low prevalence (Freeman & Moisen 2008b; Manel et al. 2001). The performance of the remaining three methods (Sens = Spec, MaxSens + Spec, and ObsPrev) differed somewhat among the species but were similar for dataset-specific comparisons. TSS was consistently higher for MaxSens + Spec (0.54–0.66) than for the other two methods (0.50–0.62 for both ObsPrev and Sens = Spec), and was thus selected. Using the best-fit models and the MaxSens + Spec method for the threshold, the performance was further evaluated by calculating the number of false positives and false negatives.

Constructing forest succession scenarios

To evaluate how continued forest succession may impact the occupancy of the three study species, potential future scenarios were constructed, and ecological niche modelling (based on the best-fit species-specific GLMs) was used to project the current and future distribution of predicted suitable habitats and the potential species distributions. To cover a variety of potential succession developments, we included three main types of land cover changes (succession trajectories): (1) an increase in forest cover, (2) an increase in shrub cover, and (3) an increase in both forest and shrub cover. Including all three succession trajectories allows for a more thorough understanding, enabling evaluations of both the different variables separately and their interactive effects.

For each of the three succession trajectories, multiple hypothetical scenarios with different levels of land cover change were constructed based on the grid data for the entire island of Gotland (315,665 grids). The inclusion of multiple increase scenarios was done to evaluate whether and how the magnitude of succession impacts the species' responses. We, therefore, constructed all scenarios of future land cover for increases in increments of 10% ranging from a factor of one (i.e., the current coverage, 0% increase) to a factor of three (threefold coverage, 200% increase). The scenarios up to 100% are plausible, they are within the observed increase in Sweden during the last century (107% increase during the last 100 years) (SLU 2022) and also in line with predicted future increases (Skogsstyrelsen 2022). The higher increase scenarios represent more extreme cases of succession e.g., if demand and prices for timber increase and forests become even more intensively managed. Because, as stated previously, land cover in nature can not exceed 100%, land cover values were curtailed to a maximum coverage of 100%. Even after limiting the calculated values, the total coverage (aggregate of shrub cover, forest cover, and open land coverage) frequently exceeded 100% in the grids, especially in the scenarios with more profound succession. To remedy this, we adjusted the values to sum up to a maximum of 100%. For the two types of succession trajectories where only one of the two environmental variables (either shrubs or forest) was subjected to increase, this was done by letting the land cover variable of interest keep its calculated value, whereas the two other variables were down-adjusted based on their proportional coverage (i.e., curtailing by splitting and subtracting the difference percentage-wise). For the third succession trajectory (increase in both forest and shrub cover), the adjustment was instead done by first curtailing the cover of open land (to a minimum of 0%), and then, if necessary, down-adjusting shrub cover as it is likely that forests will take over shrubs as succession progresses.

Projecting species distributions on Gotland with ENM

The 'predict function' was used for the entire Gotland dataset to predict the current and future distributions of suitable habitats across Gotland. For this, the optimised species-specific models (GLMs) were used in a separate ENM for each species and forest succession scenario combination ($N=189$, including 21 magnitudes of change for each of the three succession trajectories for each species). Presence/absence in each grid was categorised based on the species-specific threshold obtained with the MaxSens + Spec method, and the mean predicted probability across all grids on Gotland was calculated from each run.

Results

The extensive field survey revealed that the Marsh Fritillary occupied 471 hectare-grids in 2017, Apollo 1140 in 2019, and Large Blue 128 in 2020, corresponding to 38.2%, 48.6%, and 5.7% of the surveyed grids for each species ($N_{\text{aurinia}}=1232$; $N_{\text{apollo}}=2346$; $N_{\text{arion}}=2256$; Fig. 2). The corresponding numbers for the full dataset were 7.1%, 17.7%, and 2.0% of the grids in the whole study area including grids with no suitable habitat ($N_{\text{aurinia}}=6594$; $N_{\text{apollo}}=6425$; $N_{\text{arion}}=6437$; Fig. 2).

Species-specific habitat preferences

The best-fit GLMs showed that predicted butterfly occupancy was associated with both environmental characteristics (land cover variables and ground moisture) and habitat heterogeneity. For Apollo, all five environmental variables included in the model selection (forest cover, shrub cover, cover of open land, habitat heterogeneity, and ground moisture) were retained for the best-fit model and displayed significant associations with occurrence; and for both the Marsh Fritillary and Large Blue all but open land were associated with the species' occupancies (Fig. 1, Tables 1, and S3).

The results from the three best-fit, species-specific models demonstrated that, in large, the same environmental variables were associated with the predicted occupancy of all three species but that the response profiles differed, indicating differences in habitat preferences (Fig. 1, Tables 1 and S3). Some of the predicted occupancy—environmental variable relationships showed similar patterns for the different species. For example, all three species displayed curvilinear relationships with similar optima for both shrub cover (the Marsh Fritillary: 23%, Apollo: 27%, and Large Blue: 29%, $P<0.001$ for all three) and habitat heterogeneity (peaked at 0.10, towards the higher end of the range, for all three species), though the association for Large Blue fell just short of the traditional p-value cut-off for statistical significance ($P<0.01$ for the Marsh Fritillary, $P<0.001$ for Apollo, and $P=0.06$ for Large Blue). In contrast, the effect of forest cover differed among the species (Fig. 1, Table 1). The predicted occupancy of both the Marsh Fritillary and Apollo was greatest at no forest cover ($P<0.001$), whereas Large Blue displayed an optimum just below 29% ($P<0.001$), indicating a preference for moderate forest cover for this species. Nevertheless, all three species showed lower predicted occupancies at higher levels of forest cover. Similarly, the association of occupancy with ground moisture and cover of open land also differed among the species. For both Apollo and Large Blue, predicted occupancy

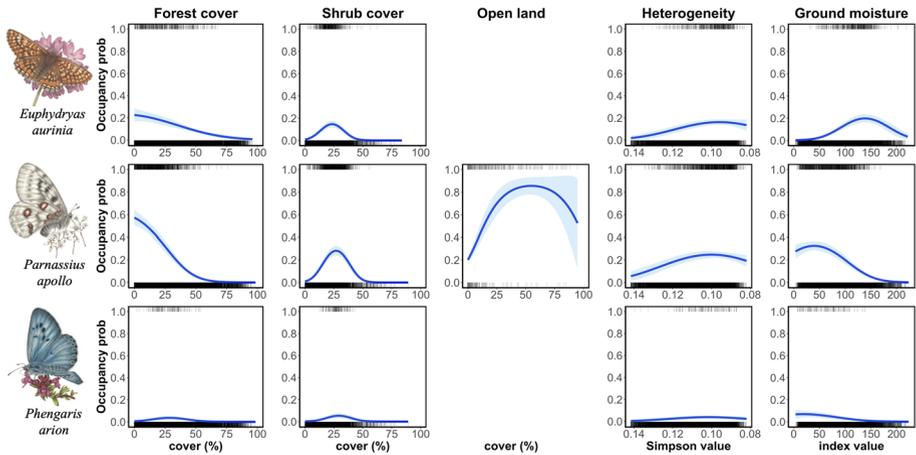


Fig. 1 Species-specific relationships of butterfly occupancy with environmental variables. This figure illustrates the environmental preferences for the three study species: the Marsh Fritillary (*Euphydryas aurinia*, top row), Apollo (*Parnassius apollo*, middle row), and Large Blue (*Phengaris arion*, bottom row). Each panel represents the estimated probability of butterfly occupancy (based on the best-fit species-specific GLMs) for one of the five environmental variables: forest cover (panel one), shrub cover (panel two), coverage of non-vegetated open land (panel three), habitat heterogeneity (panel four), and ground moisture (panel five). Please note that because higher values of Simpson diversity, counter-intuitively, indicate lower heterogeneity, the x-axis is reversed to facilitate easier interpretation. Dark blue lines and blue shading illustrate the predicted mean lines with 95% CI obtained from the best-fit species-specific GLMs, using the ‘effect’ function in the ‘effects’ package (Fox 2003; Fox & Weisberg 2019). For details on statistical significance and parameter estimates, see Table 1 and Table S3; for model selection, see Materials and Methods. The black ticks along the top and bottom of each plot represent the raw data points—one observation per hectare-grid ($N_{aurinia} = 6594$; $N_{apollo} = 6425$; $N_{arion} = 6437$)—where values of 1 indicate butterfly presence and 0 butterfly absence. Butterfly drawings by Emma Tinnert

was highest at low ground moisture (Apollo: 40, Large Blue: 18; $P < 0.001$), whereas the Marsh Fritillary had an optimum at moderate levels (139, $P < 0.001$). Cover of open land was not associated with predicted occupancy for either the Marsh Fritillary or Large Blue but showed a curvilinear relationship peaking at 55% for Apollo ($P < 0.001$).

Predicted habitat distribution across Gotland

The assessment of the prediction performance showed that with the selected optimal threshold method and best-fit GLMs (for details see Materials and Methods), prediction accuracy was relatively high for the contemporary distribution within the range of environmental conditions that the model was fitted to: for the Marsh Fritillary 76.3% of the grids (5028 of 6549) were correctly assigned, for Apollo 80.8% (5190 of 6425), and for Large Blue 73.9% (4754 of 6437). The number of false positives were generally higher than the number of false negatives: 1444 and 122 (21.9% and 1.9%), respectively, for the Marsh Fritillary, 1055 and 180 (16.4% and 2.8%) for Apollo, and 1657 and 26 (25.7% and 0.4%) for Large Blue. However, sensitivity and specificity values were similar, indicating that the predictive accuracy was comparable for true negatives and true positives (76.4% and 74.1% for the Marsh Fritillary, 80.0% and 84.2% for Apollo, and 73.7% and 79.7% for Large Blue). Projecting the ENMs to all of Gotland indicated that the island currently

Table 1 Associations between butterfly occupancy and environmental variables for the study species

Species	Predictor	Estimate	SE	z-value	P-value
<i>Euphydryas aurinia</i>	(Intercept)	-3.77	0.12	-32.68	<0.001***
	Forest cover lin	-67.39	11.13	-6.06	<0.001***
	Forest cover sq	-16.65	9.67	-1.72	0.09°
	Shrub cover lin	-4.36	7.49	-0.58	0.56
	Shrub cover sq	-108.4	11.26	-9.63	<0.001***
	Heterogeneity lin	-43.29	10.7	-4.05	<0.001***
	Heterogeneity sq	-19.01	6.88	-2.76	<0.01**
	Ground moisture lin	81.7	7.11	11.49	<0.001***
	Ground moisture sq	-54.77	7.15	-7.66	<0.001***
<i>Parnassius apollo</i>	(Intercept)	-3.1	0.12	-26.55	<0.001***
	Forest cover lin	-160.85	14.21	-11.32	<0.001***
	Forest cover sq	-38.92	11.53	-3.38	<0.001***
	Shrub cover lin	36.36	5.26	6.92	<0.001***
	Shrub cover sq	-99.49	7.46	-13.34	<0.001***
	Open land lin	33.2	3.26	10.19	<0.001***
	Open land sq	-14.16	2.71	-5.23	<0.001***
	Heterogeneity lin	-29.51	7.59	-3.89	<0.001***
	Heterogeneity sq	-17.08	4.91	-3.48	<0.001***
<i>Phengaris arion</i>	(Intercept)	-5.95	0.34	-17.3	<0.001***
	Forest cover lin	-85.79	30.62	-2.8	<0.01**
	Forest cover sq	-117.57	27.39	-4.29	<0.001***
	Shrub cover lin	52.23	17.33	3.02	<0.01**
	Shrub cover sq	-87.72	23.82	-3.68	<0.001***
	Heterogeneity lin	-34.29	18.55	-1.85	0.06°
	Heterogeneity sq	-22.83	12.2	-1.87	0.06°
	Ground moisture lin	-71.92	16.57	-4.34	<0.001***
	Ground moisture sq	-24.33	14.36	-1.70	0.09°

The table presents the results (output from 'summary' function in base R) from the best-fit species-specific GLMs (with logit link functions) for associations between butterfly occupancy and environmental variables. A separate GLM was run for each of the three study species: the Marsh Fritillary (*Euphydryas aurinia*), Apollo (*Parnassius apollo*), and Large Blue (*Phengaris arion*), in which some or all of the five environmental variables (forest cover, shrub cover, coverage of non-vegetated open land, habitat heterogeneity, and ground moisture) were included, based on the variable selection procedures (for details see Materials and Methods). Occupancy (presence/absence) was introduced as a binomial, presence/absence (1/0) response variable, and each hectare-grid contributed one observation ($N_{\text{aurinia}} = 6594$; $N_{\text{apollo}} = 6425$; $N_{\text{arion}} = 6437$). For information on overall effects see Table S3)

SE standard error

Asterisks indicate statistical significance, ° $0.05 < P < 0.1$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

hosts substantial areas of habitat predicted to be suitable for the three species (Fig. 2). The ENMs estimated that there were 49,104 hectares (15.6% of Gotland) of habitat predicted to be suitable for the Marsh Fritillary; 45,646 hectares (14.5%) for Apollo; and 33,089 hectares (10.5%) for Large Blue at their respective study year.

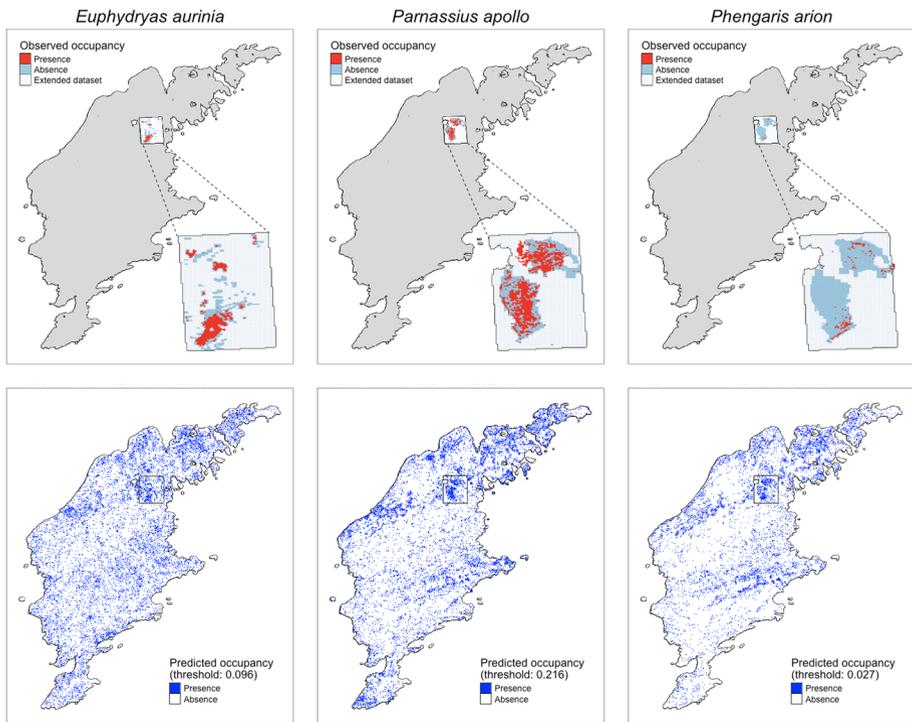


Fig. 2 Maps showing the geographic distribution of the hectare-grids in the study area and predicted contemporary occupancy of the three study species across the island of Gotland. The maps in the top row show the included grids for the three study species: the Marsh Fritillary (*Euphydryas aurinia*, left panel, $N=6594$), Apollo (*Parnassius apollo*, middle panel, $N=6425$), and Large Blue (*Phengaris arion*, right panel, $N=6437$). The colour of the grids indicates whether the grid was occupied ('Presence', red), unoccupied ('Absence', medium blue), or included in the full dataset with an extended set of unsuitable habitat absence grids used to increase the predictive power of the ecological niche models (pale blue) (for details see Materials and Methods). The maps in the bottom row show the predicted contemporary occupancies across the island of Gotland for the same three species. Predictions are based on ecological niche modelling of the best-fit species-specific GLMs, including all or some of five environmental variables: forest cover, shrub cover, coverage of non-vegetated open land, habitat heterogeneity, and ground moisture (for model selection, see Materials and Methods). Colours in the maps indicate whether the occupancy probability exceeded the species-specific threshold (indicated by blue) or not (indicated by white)

Impacts of forest succession and shrub overgrowth

The results from the predictive modelling of succession scenarios revealed that even though there is a large extent of habitats predicted to be suitable for these butterflies on Gotland in its current environmental state, continued forest succession and shrub overgrowth (Fig. S3) threaten to decrease the availability. The findings suggested that continued succession of open lands into shrubs and forests will reduce the amount of suitable habitats for all three butterflies (Figs. 3, S4 and S5). However, the magnitude of the effect depends on how far succession has progressed and also differs among the species and between forest and shrub growth. For example, a twofold increase in shrub cover forecasts a decline of 7% for the Marsh Fritillary, 16% for Apollo, and 37% for Large Blue. The numbers for a corresponding increase in forest points to far worse prospects:

– 47% for the Marsh Fritillary, – 49% for Apollo, and – 56% for Large Blue. The effects of increased forest cover were consistently negative (Fig. S4), whereas responses to increased shrub cover varied—the Marsh Fritillary and Large Blue both showed a minimal positive response (1% increase) to minor shrub increases (Fig. S5). However, the positive effect diminished and completely disappeared in scenarios with more extensive shrub cover increases and in scenarios including both shrub and forest increases (Fig. 3). Notably, the scenarios incorporating increases in both forest and shrub cover consistently demonstrated decreases in habitat availability. A twofold increase in both variables forecasted declines of 41% for the Marsh Fritillary, 47% for Apollo, and 65% for Large Blue, and the numbers were even higher in scenarios in which succession has progressed further (e.g., in response to a threefold increase: – 55%, – 61%, and – 78%, respectively).

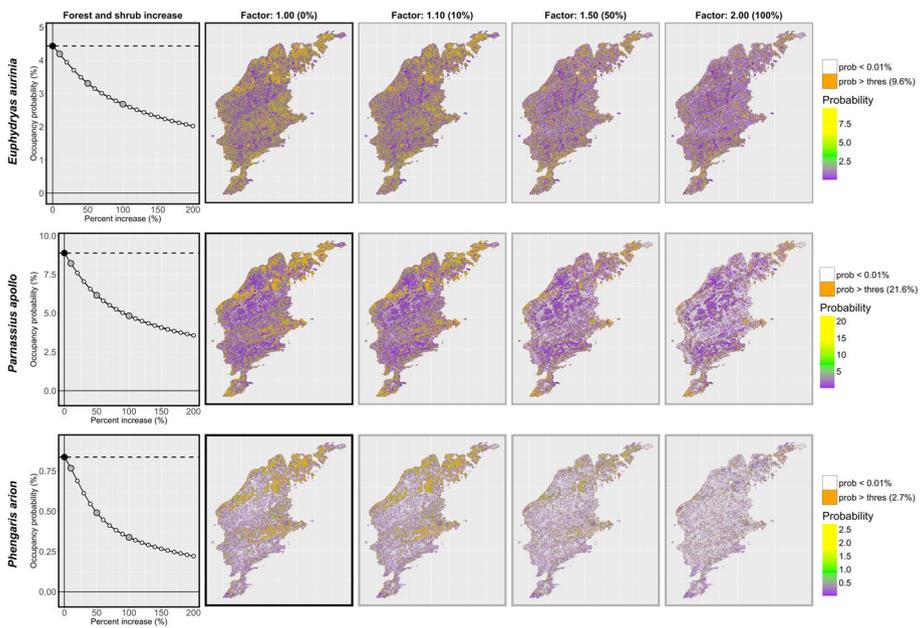


Fig. 3 Predicted occupancy probabilities for the three study species given different land cover change scenarios with continued forest succession and shrub overgrowing. The figure shows predicted occupancy probabilities for the Marsh Fritillary (*Euphydryas aurinia*, top row), Apollo (*Parnassius apollo*, middle row), and Large Blue (*Phengaris arion*, bottom row) across the island of Gotland based on ecological niche modelling. The leftmost panel of each row illustrates changes in the estimated probability of butterfly occupancy in different scenarios of continued forest succession and shrub overgrowing (i.e., increase in both forest cover and shrub cover) ranging from 0% increase (current land cover) to 200% increase, in 10% increments. Dashed lines represent the "no-difference-line", circles represent the mean occupancy probability averaged across the island of Gotland, and black lines depict fitted lines with 95% CI. Filled circles represent the scenarios visualised in the maps—black circles the current land cover, and grey the three scenarios of continued forest succession and shrub overgrowing (forest and shrub cover increase) (panel three: 10% increase, panel four: 50% increase, and panel five: 100% increase), visualised in the bottom row of Fig. S3. Colours in the maps indicate the probability of butterfly occupancy (in %), values less than 0.01% are shown in white, and values exceeding the species-specific threshold are indicated in orange. Note that the scale for all three species differs

Discussion

Our study utilised a combination of extensive field surveys and statistical analyses with ecological niche modelling to unravel the current and future distribution of suitable habitats for the Marsh Fritillary, Apollo, and Large Blue butterflies across Gotland. We show that (1) the habitat preferences of the Marsh Fritillary, Apollo and Large Blue are species-specific, 2) Gotland currently harbours large amounts of habitats predicted to be suitable for all three species, and 3) forest and shrub cover are key components determining the potential distributions of the butterflies. With predictive modelling of potential future succession scenarios, we also demonstrate that continued increases in forests and shrubs will decrease the availability of habitats predicted to be suitable and, thus, the species' potential distributions. These findings not only illustrate the current state of these butterflies but also forecast the dire consequences of further modifications to their habitats.

Species-specific habitat preferences

Examining the habitat preferences of the studied species yielded insights into their ecological requirements. Both environmental characteristics (land cover and ground moisture) and habitat heterogeneity emerged as important factors influencing the predicted occupancy of all three species (Fig. 1, Tables 1, and S3). As expected, high forest cover, shrub cover, and low habitat heterogeneity were all associated with lower predicted habitat suitability, underscoring the importance of maintaining open and diverse habitats on Gotland. Interestingly, although the studied species commonly are associated with open sunny habitats (Franzén et al. 2022a, 2022b; Johansson et al. 2019, 2020, 2022), we did not find any significant relationship between occupancy probability and the cover of open land for either Large Blue or the Marsh Fritillary, and Apollo reached a maximum at approximately 55% (Fig. 1). Thus, these butterflies appear sensitive to both succession and intense grazing (Johansson et al. 2019; Kindvall et al. 2022a, 2022b). This apparent vulnerability might appear contradictory, given that species thriving in warm habitats typically depend on grazing, mowing or hay-cutting practices (Franzén & Nilsson 2008; Nilsson et al. 2013; Pöyry et al. 2006). However, intense grazing compromises butterfly habitats by destroying host plants, which is detrimental to their eggs, larvae, and caterpillars, hindering butterfly reproduction and larval growth (Van Noordwijk et al. 2012). Many of these species, therefore, encounter difficulties completing their life cycles when habitats are excessively managed (Smallidge & Leopold 1997), exposing them to prolonged periods of intensified grazing (Johansson et al. 2020). Conversely, ecological succession alters the habitat's microclimate, often resulting in cooler, more humid conditions due to the increased vegetation density, which is unfavourable for many butterfly species, adversely affecting the development from the egg stage (Bubová et al. 2015). The contrasting responses to the environmental variables of these butterflies demonstrate the intricate interplay between species-specific preferences and habitat management practices, emphasising the urgent need for targeted and tailored conservation strategies in the face of ongoing climate change and habitat modifications (Cardoso et al. 2020; Smallidge & Leopold 1997).

Another intriguing observation concerns the role of ground moisture. Both Apollo and Large Blue were negatively impacted by higher ground moisture, which aligns with their expected habitat preferences based on previous observations (Nakoneczny et al. 2007; Thomas 1995). However, the Marsh Fritillary showed an optimum at moderate

ground moisture levels (ground moisture index value 138.7), illustrating this species specific requirement for its hydrological environment (Botham et al. 2011; Fowles & Smith 2006). This finding bears considerable importance in the face of the ongoing environmental changes associated with climate change and anthropogenic impact. Alterations in precipitation regimes are expected (IPCC 2021), and land management practices such as wetland drainage are implemented (Johnson et al. 2005), which can profoundly modify ground moisture dynamics. These insights necessitate judicious management of water resources within the habitats, underscoring the need to incorporate hydrological considerations into more comprehensive habitat management strategies for this species.

Importance of environmental heterogeneity

The findings of species-specific habitat preferences and occupancy being negatively associated with low habitat heterogeneity emphasise the importance of environmental heterogeneity. It shows that both small-scale heterogeneity (within patches) as well as large-scale landscape heterogeneity is essential for maintaining biodiversity and highlights the butterflies' reliance on a mosaic of interconnected habitats. A heterogeneous landscape presents a mixture of habitats with varying resources and microclimates, such as different temperature and humidity gradients and various nectar sources (Dennis et al. 2003; Weiss et al. 1988). They thus contain a wide variety of ecological niches, which cater to different species-specific needs (Kingsolver & Watt 1983; Rytteri et al. 2021) and favour different butterfly species, life stages and nutritional requirements (Oliver et al. 2015; Shreeve & Dennis 2011), by providing suitable breeding sites and shelter that facilitates survival and propagation (Britton et al. 2001; Hodgson et al. 2009). Heterogeneous landscapes also typically present a succession of flowering plants, providing a continuous and diverse source of nectar throughout the season (Ehrlich & Hanski 2004), which is essential for adult butterflies, impacting their longevity, fecundity, and overall population viability (Fleishman et al. 2002; McLaughlin et al. 2002). The observed preference for heterogeneous habitats aligns with the findings in previous studies showing that species in human-modified landscapes often require complex, heterogeneous habitats (Franzén & Nilsson 2008; González-Megías et al. 2007; Smallidge & Leopold 1997). Our study provides a valuable contribution to understanding this phenomenon, and the collective evidence demonstrates that conservation efforts must strive to preserve or recreate diverse landscapes to ensure the maintenance of viable butterfly populations.

Potential for widespread butterfly populations

The island of Gotland currently contains substantial areas of habitats predicted to be suitable for all three study species (Fig. 2)—49,104 hectares (15.6%) for the Marsh Fritillary; 45,646 hectares (14.5%) for Apollo; and 33,089 hectares (10.5%) for Large Blue. Surveys in potential butterfly habitats on Gotland have revealed that both Apollo and the Marsh Fritillary occupy substantial portions of their respective habitats (Franzén et al. 2022a). The finding that such large areas currently constitute habitats predicted to be suitable thus indicates that there is a great potential for abundant, widespread populations of these two species. In certain years, both the Large Blue and Apollo butterflies exhibit notable population surges on Gotland, with abundance fluctuations closely tied to varying climatic conditions.

In contrast, the Large Blue occupied only a fraction of its suitable habitats (Pettersson & Arnberg 2021). This is noteworthy as this species is typically more widespread than the

Apollo, and the situation has been attributed to the adverse impacts of the drought in 2018 (Pettersson & Arnberg 2021). A remarkable recovery has been seen in the Large Blue following the drought (Johansson et al. 2022), and given that large areas of its suitable habitats still exist, there is potential for the species to bounce back even more by recolonising patches; yet this requires urgent and proactive management. Because of the outstanding opportunity for exceptional population sizes and habitat configurations, a compelling argument exists for establishing dedicated butterfly reserves on Gotland. These reserves should integrate each species' needs and build on evidence-based conservation and adaptive management (Serrouya et al. 2019).

Field observations from 2017 to 2023 revealed significant population fluctuations in both the Marsh Fritillary and Large Blue, whereas the Apollo population remained relatively stable (M. Franzén personal obs., and citizen science data from www.artportalen.se). Such population fluctuations can critically influence ecological niche modelling and lead to both overestimations and underestimations when data from a single year is used (Santini et al. 2021; Velazco et al. 2020). Specifically, our models suggest inflated occupancy estimates for the Marsh Fritillary, which may be attributed to overestimation of the quality in isolated grids, whereas the Large Blue, observed during a low prevalence year, naturally demonstrated an underrepresentation in predicted suitable grids compared to years in which the butterfly has a higher prevalence. Overall, our model performance was robust in the cross-validation, as indicated in Table S2. However, it is important to note that this does not necessarily mean that the models are robust when extrapolated over space and time, and it would be insightful to compare various modelling algorithms, assess model performance across years, and identify core grids and regions that could be targeted for focused management and conservation efforts.

Forest succession threatens all three species

The predictive models demonstrated the vulnerability of butterfly habitats on Gotland due to ongoing forest succession and shrub overgrowth (Figs. 3, S4, and S5). Even though the magnitude of the effect differed depending on the type and extent of succession, and the species studied, the results suggest that continued forest succession will overall adversely affect the butterflies and reduce the amount of predicted suitable habitats. For instance, a twofold increase in forest cover predicts declines of 47% for the Marsh Fritillary, 49% for Apollo, and 56% for Large Blue. Low levels of shrub cover increase indicated a positive effect on the extent of predicted suitable habitat for both the Marsh Fritillary and Large Blue (Fig. S5). However, the positive effect diminished already at moderate shrub overgrowth and was also contingent on the maintenance of current forest cover levels, i.e. it was not evident in (the perhaps more realistic) scenarios where shrub increase was accompanied by increased forest cover (Fig. 3).

It is important to note that continued forest succession will not only limit the amount of suitable habitats it will also reduce the quality of the remaining habitats and cause elevated patch isolation (Ewers & Didham 2006). While habitat quality is pivotal in determining butterfly occupancy within specific patches, the consequences will reach beyond this aspect by influencing the ecological carrying capacities and meta-population dynamics (Hanski 1994, 1998; Thomas et al. 2011). High-quality habitats are associated with higher population densities, lower extinction risk, and higher colonisation success, and they also have a higher potential to generate emigrants (Clobert et al. 2009; Hanski 1994, 1998). In addition, even optimal habitat patches may remain

unoccupied if they are isolated by ecological or physical barriers (e.g., geographic distance or environmental features) (Dunham & Rieman 1999). Increased inter-patch distances accompanying forest succession will thus pose an additional challenge to these butterflies. As grassland butterflies struggle to disperse through forest habitats (Stewart et al. 2007), the effective isolation by afforestation will likely be exacerbated by the increased overgrowth restricting their dispersal. This predicament is particularly relevant for many endangered grassland butterflies suffering from long-term land-abandonment and the following succession (Bubová et al. 2015). Consequently, the accompanying declines in habitat suitability and connectivity will likely amplify the adverse impacts, resulting in even more profound negative effects than estimated in this study.

Implications for conservation and management strategies

The predicted declines in the availability of suitable habitats and associated population declines of these iconic species on Gotland reflect the broader biodiversity crisis resulting from human-modified landscapes (Cardoso et al. 2020; Pimm et al. 2014; Wagner et al. 2021). The need to understand the effects of forest succession on these butterflies extends beyond the species. Butterflies are essential components of ecosystems (as food for birds, pollinators, etc.), contributing to the broader ecological communities they inhabit (Cardoso et al. 2020; Price 1999). Therefore, the effects can transfer to other species within the ecological community and cascade through the trophic levels (Wootton 1994). The importance of the Large Blue in this context is indicated by its role as a flagship species for grassland conservation (New 1997; Thomas et al. 2009). Increased knowledge is thus not only crucial for designing conservation strategies for the specific species (Anderegg et al. 2020; Sala et al. 2000), but also imperative to understand how associated species and even entire ecosystems will be affected (Mouquet et al. 2005). Alignments between scientific understanding and conservation actions are of utmost importance (Guisan et al. 2013), not only for the persistence of these butterflies but also for the protection of these biodiversity-rich environments and to safeguard our planet's biological heritage (Cardoso et al. 2020).

The collective knowledge from this and previous studies provides support for creating a dedicated butterfly reserve on Gotland. For this to succeed, preserving a heterogeneous landscape with well-connected, high-quality habitat patches is pivotal. This may be achieved through a balanced combination of conservation-oriented management activities, allowing this region to serve as a stronghold for these species. To optimise habitat conditions, low-intensity grazing and mowing, following a mosaic pattern (Bubová et al. 2015), removal of trees and shrubs to prevent undesirable succession, and actions to maintain the hydrological integrity of habitats may be beneficial. Measures facilitating connectivity, such as establishing habitat corridors and stepping stone habitats, should also be considered (Dover & Settele 2009; Holl 2020). Collaborative efforts with stakeholders, including local communities, conservation organisations, and governmental bodies, would be essential for realising such an ambitious goal. In the UK, the successful conservation of the Large Blue butterfly provides compelling evidence that harmonious coexistence between humans and butterflies is attainable (Thomas et al. 2009), and a conservation area on Gotland could become a similar flagship initiative in European butterfly conservation.

Challenges, limitations, and future directions

While our study provides valuable insights, important questions and future avenues of research remain. It should be noted that correlative analyses (such as those used in this study) are inherently associated with some characteristics that limit the conclusions that can be drawn. One crucial aspect is that, despite the usefulness of correlative analyses for relating species occupancy to environmental characteristics, they do not inform about causality. The environmental variables found to be associated with butterfly occupancy in this study should thus not be interpreted as definitive drivers of the species distributions. The influence of unmeasured variables cannot be assessed either, reflecting inherent limitations in correlative analyses. This highlights the importance of conducting more targeted research that could integrate these missing factors to advance our understanding about the factors influencing butterfly distributions further. Experimental manipulation and intervention studies could more definitively ascertain causal links and inform targeted conservation strategies, bridging the gap between scientific understanding and practical application. It should also be noted that the type of non-independent cross validation as used in this study does not allow for evaluations of model performance for extrapolated data; and the models did not account for potential spatial autocorrelation. Given these limitations and the common assumptions of contemporary spatial equilibrium (i.e., no biotic time-lags) and temporally constant realised niches in ecological niche modelling relying on space-for-time substitutions, results should be interpreted with caution (Lovell et al. 2023). It is also important to remember that ENMs predict the distribution of suitable habitats and thus commonly cause inflated estimates of species distributions if directly translated. Incorporating mobility and dispersal constraints and information on community compositions, could refine predictions further (Mendes et al. 2020; Zhang et al. 2020) and should be considered in future studies. Lastly, because of the spatiotemporally unpredictable nature of climate change and its potential impact on succession, future research should consider long-term monitoring and studies of human-induced changes (such as limestone quarries and farming) to obtain a more holistic view of these species' threats.

Conclusions

We underscore the need to halt ongoing forest succession and demonstrate the importance of habitat heterogeneity, emphasising the need for diverse and interconnected habitats in human-modified landscapes. Additional pressures from limestone quarries, intense grazing, and agricultural intensification further exacerbate the situation, putting these threatened species under serious threat. Given these compounding challenges, targeted conservation strategies supporting the species and alleviating imminent threats are vital. We advocate for preserving environmental heterogeneity with interconnected patches of suitable habitats and propose the establishment of dedicated butterfly reserves on Gotland. Our study contributes to the broader mission of preserving biodiversity, inspiring collaborations among stakeholders to safeguard these butterflies, their habitats, and our planet's ecological heritage.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02892-z>.

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Author contributions J.S. contributed to conceptualisation, data analyses and data interpretations, and wrote the first draft of the manuscript. J.A. was instrumental in data collection, contributing to extensive field surveys. O.K. played a crucial role in designing the methodology and managing data curation, ensuring the quality and accessibility of the dataset. V.J. collected data. M.F. contributed to data collection, writing and statistical analysis. All authors have read and provided substantial comments on the manuscript and approved the final version before submission.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare that they have no competing interests.

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