A 20-year study of a threatened butterfly: The importance of management across space and time for long-term persistence in dynamic landscapes

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ABSTRACT

Biodiversity loss is accelerating at an unprecedented rate, with land-use change being the primary driver globally. This crisis is particularly acute for European semi-open woodland specialists, which have declined dramatically following the abandonment of traditional management practices that historically maintained dynamic landscape mosaics. We examined population dynamics and habitat preferences of the threatened woodland brown butterfly (*Lopinga achine*) in Sweden, combining habitat quality assessments of 139 patches in the core area with 21-year population surveys and metapopulation modeling. We modified the Incidence function model to incorporate habitat quality and projected future dynamics under four management scenarios. The number of occupied patches remained stable until 2010 but then decreased by over 40 % by 2020. Butterfly numbers were highest in ungrazed patches with approximately 70 % tree and shrub cover. Intensive grazing significantly reduced population sizes; however, the absence of management allows succession from open woodlands to closed forests to proceed, eventually leading to local extinctions. Future projections predicted drastic declines in patch occupancy and distribution over the next century without intervention. Strategic management, including selective clearing of overgrown patches every decade, can stabilize metapopulation dynamics even with limited resources. Cost-effective conservation of semi-open woodland specialists requires balancing local habitat quality enhancement with landscape connectivity maintenance, highlighting the importance of evidence-based management strategies for restoring and maintaining the habitat mosaics upon which these species depend.

1. Introduction

Biodiversity loss is accelerating at an unprecedented rate, with extinction risks now estimated to be 100–1000 times higher than historical baselines (Ceballos et al., 2015; Pimm et al., 2014). Land-use change, including habitat destruction, fragmentation, and degradation caused by intensification of agriculture and forestry, are the primary drivers of biodiversity loss globally (IPBES, 2019; Maxwell et al., 2016; Sala et al., 2000). This crisis is particularly acute in European temperate landscapes, which were historically dynamic mosaics of semi-open woodlands and grasslands maintained by large herbivore grazing and natural disturbances—now recognized as Europe's natural state rather than continuous closed forests (Vera, 2000; Pearce et al., 2023; Pearce et al., 2025). These semi-open woodlands supported a rich fauna of specialist species adapted to the structural complexity and microhabitat diversity of partially open environments. The transition from natural large herbivore systems to human-managed pastoral landscapes maintained many of these mosaic characteristics, sustaining the specialized communities that had evolved within them (Vera, 2000).

However, the dramatic intensification of land use over the past century has fundamentally altered these traditional landscape mosaics. The abandonment of extensive grazing systems has led to woodland closure and homogenization, while agricultural intensification has resulted in the fragmentation and degradation of remaining semi-open habitats (IPBES, 2019; Plieninger et al., 2003). Across Europe, wood-pasture systems and semi-natural grasslands have suffered severe declines, with many traditional silvopastoral systems now occurring only as vanishing relics of historical land-use (Bergmeier et al., 2010; Poschlod and WallisDeVries, 2002). This habitat loss represents a particular threat to specialist fauna that depend on the specific microclimatic conditions, structural diversity, and resource availability provided by semi-open woodland environments.

Butterflies associated with semi-open woodlands are among the most vulnerable to these landscape changes, as they typically require specific

combinations of microclimatic conditions, host plants, and nectar sources that occur at the interface between woodland and open areas (Konvička et al., 2008a; Öckinger and Smith, 2006). European species like the scarce fritillary (*Euphydryas maturna*) and clouded apollo (*Parnassius mnemosyne*) exemplify this vulnerability, both depending on semi-open woodland mosaics (Freese et al., 2006; Luoto et al., 2001). The woodland brown butterfly (*Lopinga achine*) represents another clear example of this ecological group—despite its common name suggesting woodland habitat, it actually depends on the complex mosaic of semi-open woodlands, forest edges, and adjacent grasslands that characterize these dynamic systems (Bergman and Kindvall, 2004; Streitberger et al., 2012). Across Central Europe, populations have declined dramatically due to the abandonment of traditional forest management practices such as coppicing and wood pasture, with the species now requiring forests with light canopy and dense herbaceous layers rich in sedges (Streitberger et al., 2012). This decline is exemplified by the Czech Republic, where *L. achine* distribution has contracted from 30 different areas before 1950 to just one remaining population (Konvička et al., 2008b).

In Sweden, *L. achine* populations have declined dramatically and are now restricted to just two isolated metapopulations, reflecting the broader European pattern of decline among semi-open woodland specialists (Bergman and Kindvall, 2004). This decline mirrors broader patterns observed in semi-natural habitats across Europe, where both the intensification and abandonment of traditional management practices further threaten specialist species (Maes and Van Dyck, 2001; Nilsson et al., 2008). Like other specialized butterflies, *L. achine* faces the dual challenge of habitat loss and fragmentation, which disrupts both local population dynamics and the connectivity necessary for metapopulation persistence (Hanski, 1999; Ovaskainen and Saastamoinen, 2018). Understanding the habitat requirements and population dynamics of such species is crucial not only for their conservation but also for informing the management of semi-open woodlands more broadly.

Here, we present a comprehensive analysis of *L. achine*'s habitat preferences and metapopulation dynamics in Sweden's largest remaining population, using long-term monitoring data to inform targeted conservation management recommendations. By using a unique time-series of population data spanning over 20 years, integrating detailed field observations with a metapopulation framework, we aim to (i) elucidate the roles of patch characteristics, habitat quality, and management regimes in determining local population sizes, (ii) model the colonization–extinction dynamics across a fragmented semi-open woodland landscape, and (iii) evaluate how different management scenarios affect long-term population viability. Our work not only provides concrete recommendations for the conservation of *L. achine* but also offers a transferable framework for the conservation of other semi-open woodland specialists in dynamic, human-modified landscapes. Given the growing recognition of the historical importance of semi-open woodlands in European ecosystems, such research is essential for developing evidence-based strategies to restore and maintain the habitat mosaics upon which many specialist species depend.

2. Methods

2.1. Study area and species

The study was conducted south of Linköping, Sweden, in a metapopulation representing one of the species' last strongholds in northern Europe with a network of patches covering approximately 770 km² (Fig. 1). The study area encompassed the core distribution range south of Linköping and all known peripheral populations. The study landscape included 254 habitat patches that varied in size from 0.19 to 24.6 ha (mean = 3.50), with a 165 km² core area of 139 patches with extensive data on patch occupancy, local population sizes, and management regimes (see below, Fig. 1).

2.2. Study species

The woodland brown (*Lopinga achine*) requires semi-open deciduous forest habitats. In Östergötland, where *Carex montana* is the main host
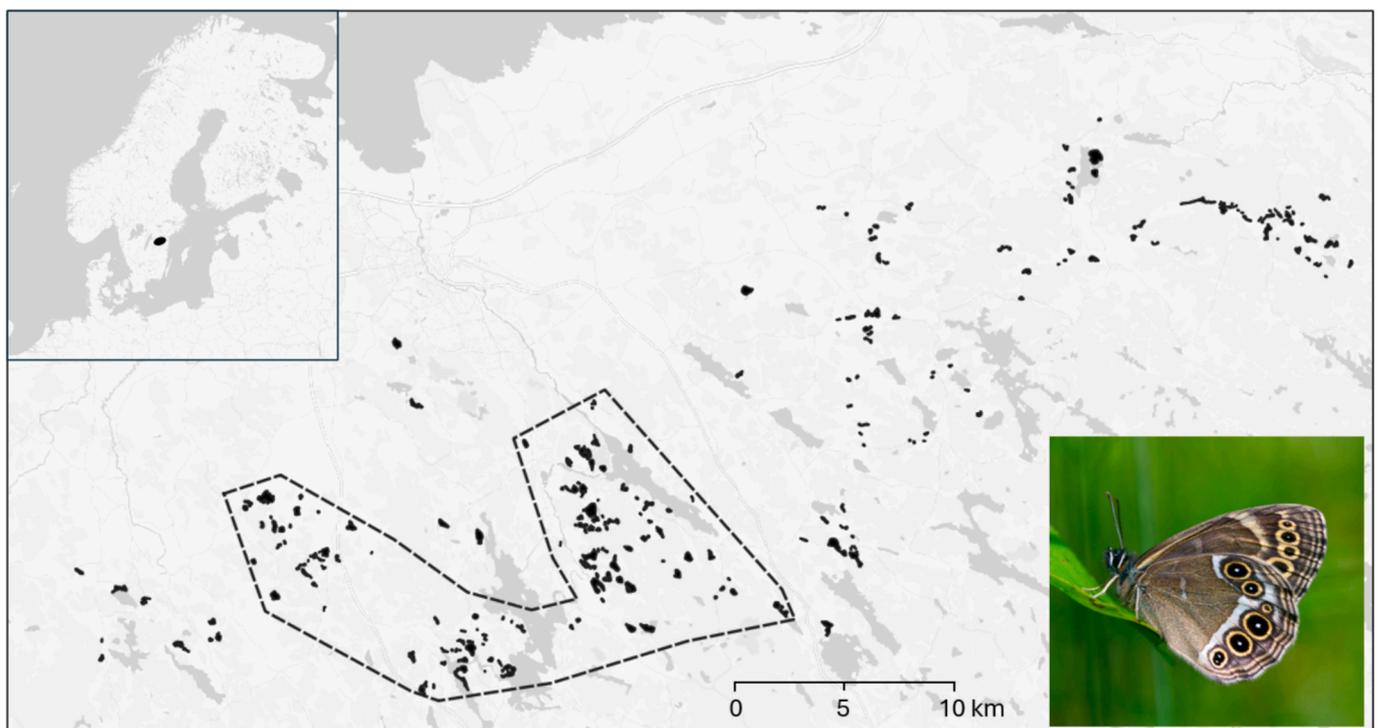

Fig. 1. The study area in the county of Östergötland, southeastern Sweden, with 254 patches of habitat (black polygons) for the woodland brown (*Lopinga achine*). The dashed boundary marks the core area containing 139 of these patches. Photo: Karl-Olof Bergman. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

plant (Bergman, 2000), the butterfly frequents glades within oak (*Quercus robur*) woodlands interspersed with hazel (*Corylus avellana*). Females lay their eggs at the edges of the glades (Bergman, 1999). The woodland brown produces one generation in June–July and hibernates in the larval stage. Based on patch occupancy data, the metapopulation maintained a relatively stable occupancy at the end of the last century (Bergman and Kindvall, 2004); however, the species has since declined for reasons that remain unclear, and no in-depth analysis of its population dynamics has been conducted.

2.3. Data collection and habitat assessment

This study utilizes data from four comprehensive surveys (1999, 2010, 2015, and 2020) of *L. achine* populations in the county of Östergötland (Fig. 1). For all 139 patches in the core area (Fig. 1) we had data on patch size, butterfly occupancy (from 1999 to 2020), number of observed butterflies (2010–2020), and grazing regimes (no grazing, light grazing, or heavy grazing, 2010–2020). In each of the four survey years all patches within the core area were visited during the peak flight period of the woodland brown (a ten-day period between mid-June and mid-July depending on the phenology of the year). The surveys were done along transects covering the entire patch area where all observed individuals were recorded. The surveyor also judged the grazing intensity based on the sward height. For data on tree and shrub cover in each patch we utilized National Land Cover Data (NMD) which is based on laser scanning (LIDAR) and covers all of Sweden (Naturvårdsverket, 2018). As the NMD data was from 2018 we corrected for the succession of vegetation (in ungrazed patches) by estimating the vegetation cover retrospectively for 2010 and 2015 (calculating backwards) and prospectively for 2020 (calculating forward) using documented canopy cover rates for the area (Bergman, 2001). For details see supplementary material (Appendix A, Fig. A1).

2.4. Statistical analysis

To assess habitat quality of patches we modelled local population size (here number of butterflies at peak flight) based on patch size, grazing regime (as a factor with three levels: no grazing, light grazing, and heavy grazing), and tree- and shrub cover using a generalized linear model with a negative binomial distribution (overdispersed count data). For tree- and shrub cover we included the squared term as we expected an optimum (Bergman and Kindvall, 2004).

2.5. Metapopulation modeling

To model the colonization-extinction dynamics of the woodland brown we used a modified version of the classical Incidence function model (IFM, Hanski, 1994). The original IFM uses patch area as a proxy for the local population size, and assumes that all patches have equal quality. The IFM can, however, include habitat quality by adjusting the 'effective area' of the patch based on different patch characteristics (Moilanen and Hanski, 1998; Johansson et al., 2019). Here we account for habitat quality by adjusting the area of patches based on the estimated difference between different grazing categories (following the method described in Johansson et al., 2019) and the optimum tree- and shrub cover from the regression model of local population size. In practice, we calculated the 'effective area' of patches (A_{eff}) as:

$$A_{eff} = A_p \times G_p \times e^{b(T_p - T_{opt})2} \qquad (1)$$

where A_p is the geometric patch area of patch p. The grazing regime of patch p, denoted as (G_p), is defined as 1 for ungrazed patches, $1/Q_{light}$ for lightly grazed patches, $1/Q_{heavy}$, for heavily grazed patches. The values Q_{light} and Q_{heavy} represent the ratios of habitat quality in ungrazed patches relative to lightly and heavily grazed patches, respectively, as derived from the regression model. The parameter b is

the quadratic coefficient for tree cover in the regression analysis (see above), T_p the current tree- and bush cover (expressed as proportion) in patch p, and T_{opt} the optimal cover. For ungrazed patches with an optimum tree and shrub cover the 'effective area' (A_{eff}) = the actual patch area (A_p).

The IFM was parameterized based on the patch occupancy from 2010 in the core area, where we assume that the metapopulation is still in equilibrium based on the similar patch occupancy as in 1999, following Oksanen (2004). For the full IFM formulation and details about the parameterization process see Hanski (1994, 1999) and Oksanen (2004). Below we only describe the functions for the local extinction and colonization probabilities.

The extinction probability of patch i (E_i) was modelled as a function of "effective patch area" (A_i) as:

$$E_i = \frac{e}{A_i^x} \qquad (2)$$

where e and x are model parameters. The colonization probability of patch i (C_i) was modelled as a function of connectivity (S_i):

$$C_i = \frac{S_i^2}{S_i^2 + y^2} \qquad (3)$$

where y is a model parameter. Connectivity was further modelled as:

$$S_i = \sum_{j=1}^{n} e^{-d_{ij} \times \alpha} A_j p_j \qquad (4)$$

where d_{ij} is the distance in meters between focal patch i and source patch j, A_j is the 'effective area' of patch j, and $p_j = 1$ if the butterfly is present in patch j and $pj = 0$ if the butterfly is absent. The 'effective area' is here, as in the function for E_i, used as a proxy for the local population size (i.e. like regular area is used in the original IFM). It does not mean any changes to patch geometry that may affect distances between patches. The spatial scaling parameter α was set to 0.003, based on earlier studies of patch occupancy patterns and capture-mark-release for the species (Bergman and Landin, 2001, 2002), which give very little weight to patches further away than 1.5 km. The remaining parameters were estimated when fitting the IFM (e = 0.066, x = 0.91, and y = 137.8).

2.6. Future scenarios of management

Using the parameterized model, we simulated future population dynamics for the entire patch network (254 patches). Four management scenarios (S0, S1, S2, and S3) were tested, varying in grazing intensity and vegetation clearing regimes:

S0: "With grazing". The current management regime continues, allowing natural vegetation succession in all ungrazed patches.

S1: "Without grazing". Grazing is discontinued, leading to natural succession across all patches.

S2: "Clearing all patches". Every 10 years, patches with vegetation cover exceeding 90 % are cleared down to 68 % to optimize habitat quality.

S3: "Clearing top ranked". Every 10 years, 20 of the "top ranked" patches with vegetation cover exceeding 90 % are cleared down to 68 % to optimize habitat quality. The ranking of patches was based on metapopulation capacity (the potential to contribution to the long-term persistence of the entire metapopulation, Hanski and Ovaskainen, 2000).

For each scenario, we used the observed occupancy and management data from 2020—collected in the most recent survey that covered all patches—as our starting point. Then, we ran 100 replicates projecting the system 100 years into the future.

2.7. Observed population dynamics 2010 to 2020

Based on the observed population turnovers between 2010 and 2020 we analysed local extinction probability and colonization probability (two different models) in relation to patch area, effective patch area, tree cover, grazing pressure, local population size (t-1) and connectivity (t-1) using generalized linear mixed models (GLMMs) with time period as random effect to account for the two observation periods (2010 to 2015 and 2015 to 2020).

3. Results

3.1. Habitat requirements and population response

The observed number of butterflies in different patches 2010 ranged from 0 to 219 (mean of occupied patches = 22.6). The number of butterflies increased with increasing patch area, and it peaked at a tree- and shrub cover of 68.1 % (Fig. 2). Based on the parameter estimates (Table 1) ungrazed patches supported populations 2.45 times larger than lightly grazed areas (even if not significantly different, $p = 0.055$) and 211 times larger than heavily grazed areas ($p < 0.001$). Based on these values the 'effective patch area' was on average 0.52 (SE = 0.027) of its potential (i.e. ungrazed and with optimal tree- and shrub cover).

In total 76 patches were occupied in 2010 (78 in 1999) within the core area (139 patches), while the corresponding numbers for 2015 and 2020 were 50 and 46, respectively (Table 2). This means that the metapopulation within the core area has decreased with over 40 % compared to the occupancy in 1999, with the main decrease between 2010 and 2015 (Table 2).

Local extinction probability decreased with increasing patch area, local population size, and connectivity, while colonization probability increased with increasing connectivity (Table 3).

3.2. Current status of the metapopulation and projected future trends

In 2020, the Woodland brown occupied 106 of 254 patches (42 %). Under the current management regime (scenario S0), projections indicate that succession will drive a steep decline in the number of occupied patches and the spatial extent of the metapopulation over the coming century (Fig. 3). By 2120, the average number of occupied patches is expected to drop to just four patches dispersed over roughly 50 km^2, although the overall extinction risk remained relatively low at 1 %. In contrast, if grazing is terminated (scenario S1), the decline becomes even more pronounced, with the extinction probability for the entire

Table 1
Parameter estimates (with SE) and *p*-values of the model for local population size (number of observed butterflies at peak flight).

Parameter	Est (SE)	p-Value
Intercept	−9.65 (4.08)	0.018
Patch area	0.62 (0.18)	<0.001
Light grazing	−0.90 (0.47)	0.055
Heavy grazing	−5.35 (1.44)	<0.001
Tree and shrub cover	37.0 (11.9)	0.002
Tree and shrub cover^2	−27.2 (8.52)	0.001

Table 2
The total number of occupied patches in the core area (139 patches) between 2010 and 2020 (and the difference compared to 1999), and the number of observed colonisations and extinctions as well as the number of grazed patches.
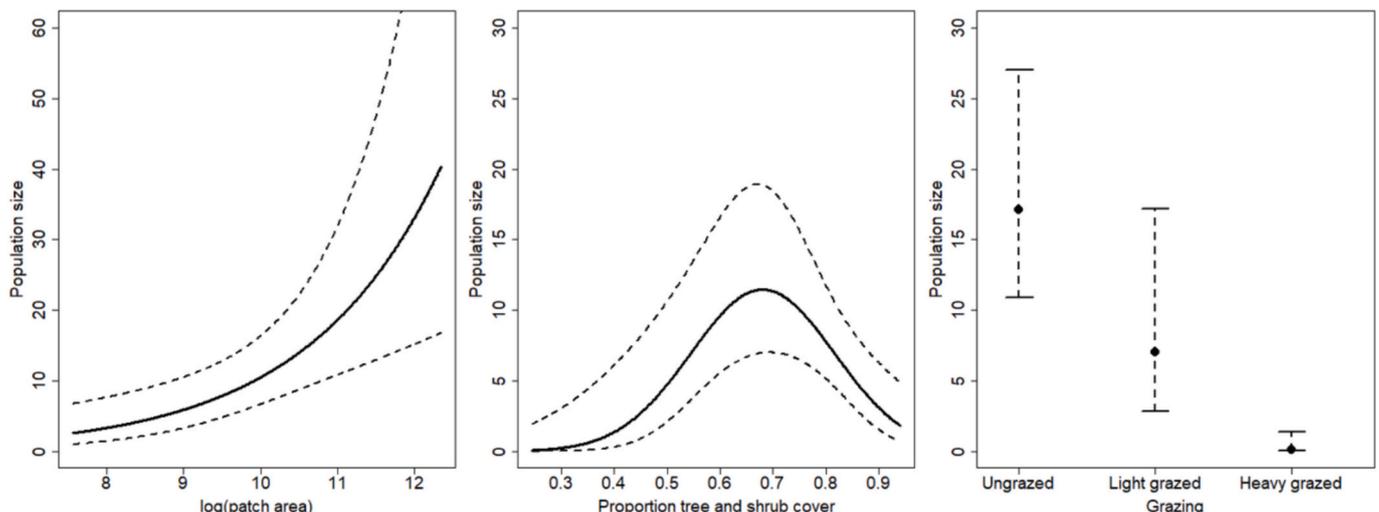
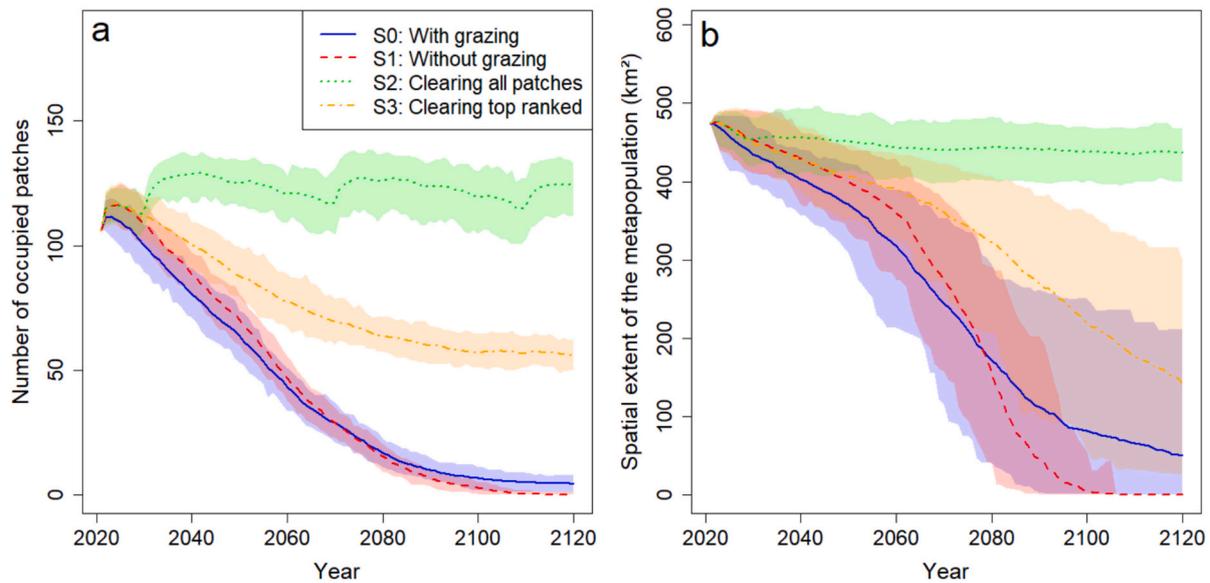|	Occupied patches (decrease in relation to 1999)	Colonizations	Extinctions	Grazed (heavy)
2010	76 (−3 %)	–	–	33 (9)
2015	50 (−36 %)	3	29	37 (5)
2020	46 (−41 %)	6	10	27 (11)

Table 3
Parameter estimates (with SE) and *p*-values of the generalized linear mixed models for extinction probability and colonization probability.

Parameter	Extinction probability		Colonization probability	
	Est (SE)	p-Value	Est (SE)	p-Value
Intercept	15.3 (5.77)	0.008	−2.77 (0.51)	<0.001
log(patch area)	−6.18 (2.47)	0.012		
log(local population size)	−0.78 (0.21)	<0.001		
log(connectivity)	−0.50 (0.19)	0.007	0.83 (0.33)	0.012

metapopulation of 96 %. Under a management regime that includes clearings of glades in heavily overgrown patches every 10 years (S2), the number of occupied patches and the extent of the metapopulation remains relatively stable over time (Fig. 3). With glade clearings focusing on the 20 "top ranked" patches (S3), the patch occupancy was reduced to 53 % (56 occupied patches) of the occupancy in 2020 with none of the replicates going extinction. However, the spatial extent decreased to only 30 % of the initial extent.

Fig. 2. The observed number of butterflies (here called population size) in relation to patch area, tree and shrub cover, and grazing intensity.

Fig. 3. (a) The number of occupied patches and (b) the spatial extent of the metapopulation over time, based on projections from four management scenarios for *Lopinga achine* over the coming century. The lines represent the mean, and the shaded areas indicate the 95 % confidence intervals.

4. Discussion

Our study provides clear evidence that cost-effective conservation of semi-open woodland specialists such as the woodland brown (*Lopinga achine*) requires detailed management measures to increase local habitat quality in targeted patches to maintain landscape connectivity. The species' unique preference for semi-open woodland conditions—with optimal conditions occurring at approximately 70 % tree and shrub cover—exemplifies the habitat requirements of species that depends on partially open forest environments maintained by traditional management practices. These habitat preferences are consistent with findings from the Czech Republic, where the last remaining population inhabits mature deciduous woodland with approximately 60 % canopy cover (Konvička et al., 2008b), and Germany, where populations require light canopy forests with dense ground vegetation (Streitberger et al., 2012). The habitat preferences of the woodland brown contrast with many other grassland butterflies, which typically thrive in more open environments (Thomas et al., 2009), underscoring the need for management approaches that foster habitat heterogeneity across a landscape to preserve general butterfly diversity (Wenzel et al., 2006). These findings align with conservation challenges faced by other semi-open woodland specialists across Europe, such as the scarce fritillary (*Euphydryas maturna*) and clouded apollo (*Parnassius mnemosyne*), which similarly require heterogeneous landscapes combining semi-open woodlands with diverse ground vegetation (Freese et al., 2006; Luoto et al., 2001). The consistent patterns observed across these species highlight the importance of maintaining the dynamic semi-open woodlands that historically characterized European temperate landscapes.

Our results show that it is possible to keep the patch occupancy stable in the metapopulation with regular management measures such as clearing of glades every ten years. Similar management cycles have been shown to be successful for other species dependent on successional stages in woodlands (Warren, 1987; Robertson et al., 1995). Grazing could be an option to halt the successional changes and keep the glade structure that *L. achine* requires. However, our results demonstrate that intensive grazing has a profoundly negative impact on *L. achine*, with heavily grazed patches supporting considerably smaller populations compared to ungrazed or lightly grazed areas. This agrees with other species (Jerrentrup et al., 2014; Johansson et al., 2017; Johansson et al., 2019; Kruess and Tscharntke, 2002) and aligns with a growing body of evidence suggesting that current agricultural practices and agri-

environmental policies in the EU may lead to too intense management that may harm biodiversity (Kindvall et al., 2022; Marques et al., 2019). For the woodland brown, even low intensity grazing seems harmful, but is required to prevent succession in the absence of regular clearing of trees and shrubs. In light of these results, it is imperative to reconsider grazing regimes in conservation planning, where low intensity rotational grazing systems might serve as a viable compromise (Johansson et al., 2019; Ravetto Enri et al., 2017). Our approach aligns with management strategies used elsewhere in Europe, where populations benefit from selective logging and tree removal to maintain light canopy cover (Streitberger et al., 2012; Konvička et al., 2008b).

It is evident, both from the fitted Incidence function model and observed population turnovers, that the woodland brown displays a metapopulation structure where habitat patch area, quality, and connectivity jointly drive the population dynamics. This metapopulation structure has been documented across *L. achine*'s European range, from the Czech Republic (Konvička et al., 2008b) to Germany (Streitberger et al., 2012), highlighting the species' consistent dependence on dynamic semi-open woodlands maintained through appropriate management. This finding also aligns with research on many other specialized butterflies (e.g., Hanski, 1994; Fleishman et al., 2002; Schtickzelle et al., 2005; Johansson et al., 2019). Our results underscore the importance of considering habitat quality—not just patch area—when predicting local population sizes (Fleishman et al., 2002; Thomas et al., 2001; Johansson et al., 2019). On the other hand, patch area per se seems to contribute with something more (than a proxy for local population size) based on the model for the observed extinctions probability. One possible reason could be that larger patches harbour more heterogeneity which reduce the local extinction probability by buffering the effects of for example weather extremes (Oliver et al., 2010; Johansson et al., 2020).

We show that targeted management of key habitat patches can sustain viable populations in fragmented landscapes, demonstrating that conservation can under some circumstances as e.g. restricted budgets for management, if needed, focus on the most critical for maintaining connectivity and population sizes (Moilanen et al., 2005; Hodgson et al., 2011). Strategic interventions—like regular clearing of the potentially "top ranked" overgrown patches—can maintain stable metapopulations. However, concentrating management on the best patches may reduce the metapopulation's spatial extent (as shown in S3). This contraction increases vulnerability to stochastic events, such as extreme weather, and places greater risk on the population if a key landowner changes

management practice (Liebhold et al., 2004). Maintaining a large distribution area with spatial heterogeneity and diversified stewardship may be crucial to ensure long-term resilience (Lindenmayer et al., 2012; Fletcher et al., 2018).

Our study provides general insights for conserving specialist species in human-modified landscapes by demonstrating the importance of high-quality local habitats and connectivity to maintain viable populations in dynamic landscapes. By adapting practices—whether through regular habitat clearing, reducing grazing intensity or implementing rotational grazing—we can establish a resilient framework for conservation planning in fragmented, human-dominated landscapes. For semi-open woodland specialists like *L. achine*, this framework must recognize their dependence on the partially open conditions that characterized pre-industrial European landscapes and can be maintained through carefully designed management interventions.

CRediT authorship contribution statement

Victor Johansson: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Markus Franzén:** Writing – review & editing, Methodology, Conceptualization. **Karl-Olof Bergman:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Ethics approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve readability and language quality. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111367.

Data availability

All data and R code used and/or analysed during the current study are available from the corresponding author on reasonable request.

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