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ORIGINAL PAPER

The last of the maculineans: can we save the emblematic Alcon Blue butterfly *Phengaris alcon* under climate change when its habitat continues to deteriorate?

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Abstract

In the NW-European region of Flanders (northern Belgium), wet heathlands harbour several threatened species among which the emblematic Alcon Blue butterfly *Phengaris alcon* is rapidly declining. Since 1990, the number of occupied grid cells in Flanders has decreased from 61 to only six in 2023, a decline of 90%. Due to the loss of many populations, the mean distance between populations tripled from 9 km in the period 1950–1990 to 27 km now. Site-wide egg counts in one of the strongholds of the Alcon Blue in Flanders revealed a strong increase after some initial intensive care conservation measures in the 2000s, but since 2013 a steep decline of 99% has been observed. The standardised egg counts in the remaining six Flemish populations (i.e., monitoring within the framework of the Natura2000 reporting) showed a yearly decrease of 18% since 2016. Despite increased conservation attention and targeted management since the end of the 1990s, the current situation of *P. alcon* in Belgium is more precarious than ever. Causes of this rapid decline are manifold and they are likely to be amplified by extreme weather conditions caused by climate change. More efficient intensive care measures and more intense cooperation across national borders are now quickly required to regionally preserve this habitat specialist with a unique eco-evolutionary profile.

Implications for insect conservation By analysing the causes of the decline of the threatened Alcon Blue butterfly in Flanders, we suggest management and policy measures in an attempt to conserve this and other threatened heathland species in a highly anthropogenic region.

Keywords Conservation · Threatened species · Management · Reintroduction

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Introduction

Several recent studies have shown that biodiversity and especially insects are in strong decline (e.g., Hallmann et al. 2017; Seibold et al. 2019; Wagner et al. 2021). Insects play a vital role in almost every biotope in the world by providing healthy soils, recycling nutrients, pollinating flowers and crops and controlling pests. The major threats that are causing these rapid declines are habitat (quality) loss and fragmentation, pollution by fertilisers and pesticides, climate change and invasive alien species (Cardoso et al. 2020). Solutions pointing at the importance of maintaining or increasing suitable habitat area and quality (Samways et al. 2020) and tackling habitat fragmentation (e.g., Mony et al. 2022) have been proposed, but are not always easy to implement in a highly anthropogenic environment (Maes et al. 2022). Through the loss of populations, distances between

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the remaining sites become larger resulting in less likely dispersal among populations. This, in turn, leads to genetic erosion, increasing the extinction risk of the remnant populations (Vanden Broeck et al. 2017). Habitat quality in NW Europe is under pressure by a very high nitrogen deposition causing encroachment of grasses and bushes, especially in nutrient-poor biotopes (Friedrich et al. 2011), eventually leading to an impoverished insect fauna (Schirmel et al. 2011; Ubach et al. 2020).

Butterflies are among the most popular invertebrates and are, therefore, often used as flagships in nature conservation (Preston et al. 2021). Despite ample attention in nature management and policies, declines of butterfly numbers or the extinction of local emblematic species have been reported from many European countries (Maes et al. 2019b; Warren et al. 2021). Especially species of oligotrophic and/or wet biotopes such as nutrient-poor semi-natural grasslands, heathlands and/or marshes show the strongest declines (van Swaay et al. 2011). Heathlands, for example, harbour several threatened and unique habitat and resource specialist species with complex mutualistic or parasitic life styles (e.g., myrmecophily – Thomas et al. 1989; De Graaf et al. 2009). The majority of the heathlands in Flanders, but also in the rest of NW Europe, were transformed into arable land or were planted with coniferous trees for use in the coal mining industry during the early 20th century (De Smidt 1966; De Keersmaeker et al. 2024).

The Alcon Blue butterfly *Phengaris alcon* is one of the flagship species of wet heathlands in NW Europe (Maes and Van Dyck 2005), but is facing strong and fast declines (Maes et al. 2019b). As a larva, the Alcon Blue is an obligate social parasite of red ant colonies (*Myrmica* spp.) and the species is confined to wet heathland and nutrient-poor grasslands where host ants and its unique host plant, *Gentiana pneumonanthe*, co-occur (Bink 1992). Although *P. alcon* has been a focal species for conservation in Flanders since the end of the 1990s when it was one of the first species for which a species action plan was developed (Vanreusel et al. 2000), local site managers have recently reported worrying trends about the poor conditions of the few remaining populations. Therefore, we used historical and recent distribution data, as well as samples of local abundance data (i.e., egg count data) of *P. alcon* in Flanders to quantify the species distribution and abundance trends. Such a test is significant as *P. alcon* has the ecological profile of a species for which more general structural habitat-based conservation strategies may not be able to compensate climate-change induced losses (Wessely et al. 2017) and (in)direct nitrogen-driven impacts on small local, often isolated populations (Vogels et al. 2023). We report a strong recent decline, discuss the management and policy measures that were undertaken during the last decades and reflect on urgent actions to be taken (e.g., reintroductions in restored suitable sites).

Materials and methods

Study area

Flanders (area 13,625 km², northern Belgium – Fig. 1) is a highly anthropogenic region in NW Europe. With more than 500 inhabitants/km² (Statistiek Vlaanderen 2023) and more than three quarters of its territory being agricultural land or urbanised (i.e., artificial surfaces such as built-up areas, industrial grounds, transport infrastructure; Poelmans et al. 2019), the environmental pressure on natural areas, including nature reserves under European protection (i.e., Natura2000), is recognised to be very high (Michels et al. 2023). The majority of these European habitats are in an unfavourable state in Flanders (Paelinckx et al. 2019). The total area of legally protected natural sites in Flanders is 94,060 ha (i.e., 7% of the total area) and a further 12% is managed as nature reserve (Vught et al. 2020). Furthermore, Flanders is characterised by very high nitrogen deposition values within European standards (Vivanco et al. 2018) and natural areas are among the most severely fragmented in Europe (European Environment Agency 2011).

The nature reserve Hageven – De Plateaux used to harbour one of the largest populations of the Alcon Blue in Flanders and site-wide egg counts have been done here since 1995 (see further). It is a transnational nature reserve of more than 600 ha and is situated at the border of the north of Flanders (Pelt) and the south of The Netherlands (Valkenswaard; Fig. 1). It consists of dry and wet heathlands, inland dunes, marshes and nutrient-poor grasslands. Nature management in the nature reserve here is strongly focused on the conservation of the Alcon Blue, amongst other target species, following the publication of the species action plan in 2000 (Vanreusel et al. 2000). Management measures consisted of a series of interventions over the last two decades:

- Rewetting of heathlands to increase the abundance of one of the most important nectar sources *Erica tetralix*;
- Combing litter of Purple moor-grass *Molinia caerulea* to create suitable germination sites for the host plant on the one hand and to make access to fresh leaves of the same grass more easily available for grazers (e.g., sheep, cattle and/or horses);
- Mowing Purple moor-grass at different heights to create different microclimates and suitable nesting conditions for *Myrmica* host ants;
- Sod-cutting at both large scales (up to 8000 m²) in unsuitable sites such as former arable land, strongly

Fig. 1 Location of Flanders (black) in NW Europe (top left), the location of the Hageven – De Plateaux nature reserve (top right) and the distribution of extinct (light grey) and existing populations (black) of *Phengaris alcon* in Flanders (bottom)

encroached Purple moor-grass locations, but also at a very small scale (50–70 cm wide in the immediate vicinity of *G. pneumonanthe* plants) in more suitable areas to create better circumstances for the germination of the host plant;

- Small-scale mulching of unsuitable habitat and manually combing of vegetations in late autumn to remove dry blades of Purple moor-grass in suitable zones for *P. alcon*;
- Removing or cutting down young and older trees (especially *Pinus sylvestris*, *Betula pendula*) in wet heathlands;
- Placing exclosures to temporarily prevent grazers during the flight season from eating *G. pneumonanthe* plants with Alcon Blue eggs.

Study species

Phengaris alcon is a large blue lycaenid butterfly species with a scattered distribution from NW Europe to Japan (Bink 1992). The species occurs in nutrient-poor habitats such as wet heathlands with *Erica tetralix* (main habitat in NW Europe) and fen-meadows (elsewhere in Europe). Wet heathlands are a conservation priority habitat in Europe (habitat type 4010 in the European Habitats Directive). The flight period in Flanders is from mid-July to mid-August (Maes et al. 2013). Eggs are laid on the Marsh gentian *Gentiana pneumonanthe* Linnaeus 1753, the exclusive host plant in NW Europe (Van Dyck and Regniers 2010). Elsewhere in Europe *Gentiana cruciata* Linnaeus 1753 is used as a host plant as well. The young caterpillars do not eat the egg shells, that remain on the host plant after hatching (Thomas et al. 1991). Every female lays on average about 140 eggs (Bink 1992) and by counting the number of eggs (or egg shells) on the host plant, it allows to calculate the number of females per population and by multiplying it by two (assuming a 1:1 female: male ratio), the estimated total number of individuals in the population. Although young larvae start eating the internal parts of gentian flower buds, they leave this resource and obligatory switch to a parasitic ‘cuckoo’ life style in *Myrmica* ant nests (Thomas et al. 1991). Through chemical (Nash et al. 2008) and acoustic mimicry (Sala et al. 2014), the small larvae get adopted by worker ants, that will transport them to the brood chambers of the ant colony where the caterpillars are fed as if they were ant brood (Thomas and Elmes 1998). Depending on the geographic region, *P. alcon* may parasite a variety of host ants from the genus *Myrmica*, but in NW Europe the most used host ant is *Myrmica ruginodis* Nylander 1846 although *M. scabrinodis* Nylander 1846 and *M. rubra* (Linnaeus 1758) are also used (Tartally et al. 2019b).

P. alcon is Critically Endangered in Flanders due to the strong decline in distribution, the low number of populations and a very low estimated number of individuals (i.e., less than 300; Maes et al. 2021). The species is threatened in other NW European countries or regions (the Netherlands – van Swaay 2019; Germany – Reinhardt and Bolz 2011; North Rhine Westphalia – Schumacher and Vorbrüggen 2021; Denmark – Helsing 2019), but also in many other European countries (Maes et al. 2019b). In Europe as a whole, *P. alcon* was assessed as being of Least Concern (van Swaay et al. 2010), but it was classified as a Species of European Conservation Concern according to van Swaay et al. (2011).

Climate data

To align with the flight period of *P. alcon* in Flanders, we collected mean summer (July and August) temperature and rainfall data from the central weather station in Uccle (Brussels) during the period 1991–2023 from the Royal Meteorological Institute (KMI) website. We used the long-term mean summer temperature (i.e., 18.5 °C) and rainfall (i.e., 82.4 mm) to calculate the difference between the yearly observed values with the long-term average. This difference was standardised around the mean to make differences in temperature and rainfall comparable.

Distribution data

We collected all available distribution data of *P. alcon* in Flanders coming from historical museum specimens, entomological literature and more recently, also opportunistic observations (Maes et al. 2016). All records were attributed to grid cells of 1 × 1 km² of the Universal Transverse Mercator (UTM) coordinate system. We counted the number of occupied grid cells per year to assess changes in distribution since 1990.

Egg counts

In the Hageven – De Plateaux nature reserve, eggs/egg shells were counted site-wide by volunteers since 1995 except for the years 2007–2010 (Palmans and Pardon 2015). In 2016, a structured monitoring network was developed for regional priority species in Flanders, including *Phengaris alcon* (Maes et al. 2023). This standardised monitoring consists of counting the conspicuous eggs on *G. pneumonanthe* plants in plots of 100 m² after the flight period of *P. alcon* (i.e., end of August; Maes et al. 2019a). Although it has been suggested that phenological time windows for ovipostion on individual flower buds and gentians are very narrow (2–3 days) in *Phengaris* species (Thomas and Elmes 2001), it has been shown that this is not necessarily true in Flemish populations (up to 40 days with an average of 9.5 days; Van Dyck and Regniers 2010).

Results

Changes in climate

When looking at the climate in Flanders since 1991 (Fig. 2) and comparing that with the trend in the number of occupied grid cells by *P. alcon*, we see that the period 1991–1998 (corresponding with a moderate decline in the number of occupied grid cells; Fig. 3), the climate was drier and colder than the long-term average values. Between 1999 and 2013 (corresponding with a relatively stable number of occupied grid cells; Fig. 3), the climate was on average rainier and

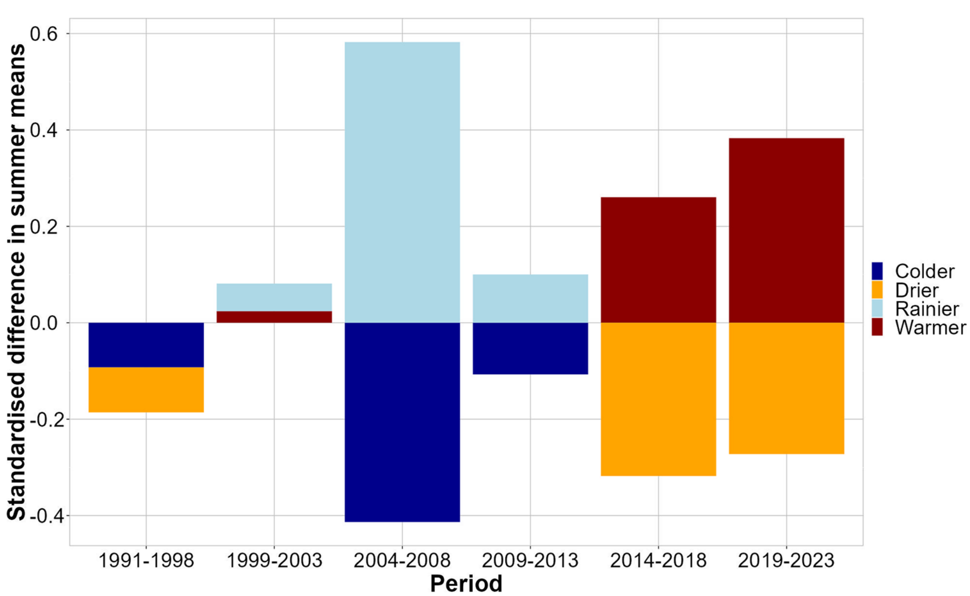

Fig. 2 Difference in standardised mean summer (July and August) temperature and rainfall compared to the long-term average since 1991. Dark blue indicates a colder and dark red a warmer than average summer, orange indicates a drier and light blue a rainier summer than average

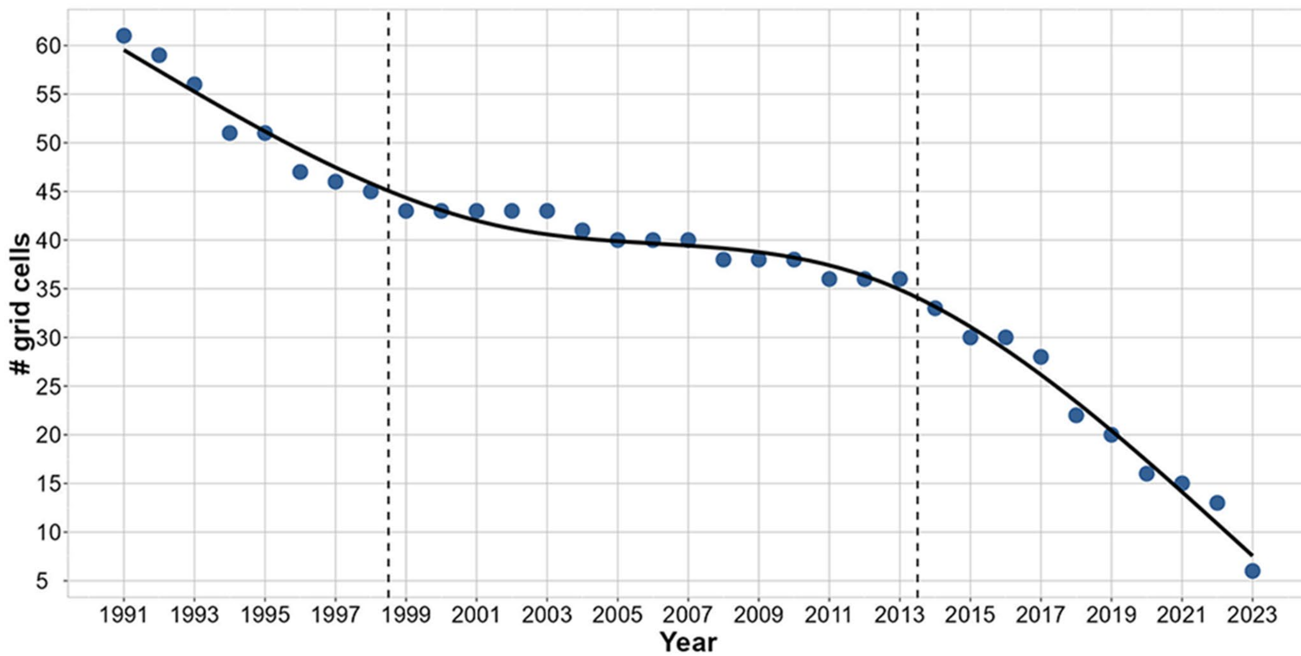

Fig. 3 Number of grid cells (blue dots) in which *Phengaris alcon* was observed in Flanders between 1991 and 2023 together with a fitted trend (smoother; black). The number of grid cells does not necessarily correspond to the number of populations since populations can cover more than one grid cell. Vertical dashed lines delimit periods of decline (1991–1999 and 2014–2023) from a period with a more stable distribution (1999–2013)

colder (except for the period 1999–2003 which was rainier but warmer). From 2014 onwards (corresponding with a steep decline of the number of occupied grid cells; Fig. 3), however, the climate was markedly warmer and drier than the long-term average.

Changes in distribution

In Flanders, the number of grid cells (1 × 1 km²) occupied by *P. alcon* decreased from 61 in 1991 to six in 2023, a decrease of 90% (Fig. 3). During the first decade, a relatively strong decline was observed followed by a relatively stable distribution from 2000 onwards. Since 2013, however, a steep decline started towards 2023 with only six occupied grid cells left. Most of the (very) small sites and sites that are relatively isolated went extinct and all extant populations, with one exception, occur now in sites > 3 ha. Some extinctions, however, also occurred in a few larger wet heathland areas. Three of the extant populations (Mathiashoeven, Panoramaduinen and Katersdelle) are located within the dispersal distance of *P. alcon* and are part of a metapopulation (distances between these three sites range from 800 to 1800 m). The three other remaining populations are located in relatively large wet heathlands, but are completely isolated from all other populations. The mean distance to the three nearest population increased from 9.4 km in the period 1950–1990 to 26.8 km in 2023 (Fig. 4). Mean distances to the nearest populations per individual population are given in SuppMat 1.

Changes in egg numbers

Changes in egg numbers of *P. alcon* were measured in two different ways and in different time frames, namely in the Hageven – De Plateaux nature reserve, where eggs are counted since 1995 and in the seven extant populations using standardised plot in the meetnetten.be monitoring scheme since 2016.

In the Hageven – De Plateaux population, the number of eggs at first showed a strong increase until 2003, remaining at relatively high levels until 2014. Since 2014, however, there is a steep decline in the number of eggs (-99%; Fig. 5), with the most recent count in 2023 totalling only 151 eggs in the whole area, indicating the presence of only a couple of females.

In the standardised plots of the meetnetten.be monitoring scheme in the seven extant populations, the mean number of eggs decreased by 18% per year since 2016 (Fig. 5; Westra et al. 2022), with decreases observed in all surveyed populations (SuppMat 2). One of the populations (Achter de Witte Bergen) even went extinct in 2022. In the first two years after the start of the monitoring scheme (2017 and 2018), the decrease in egg number was called probable according to the *effectclass* package of Onkelinx (2023), since the

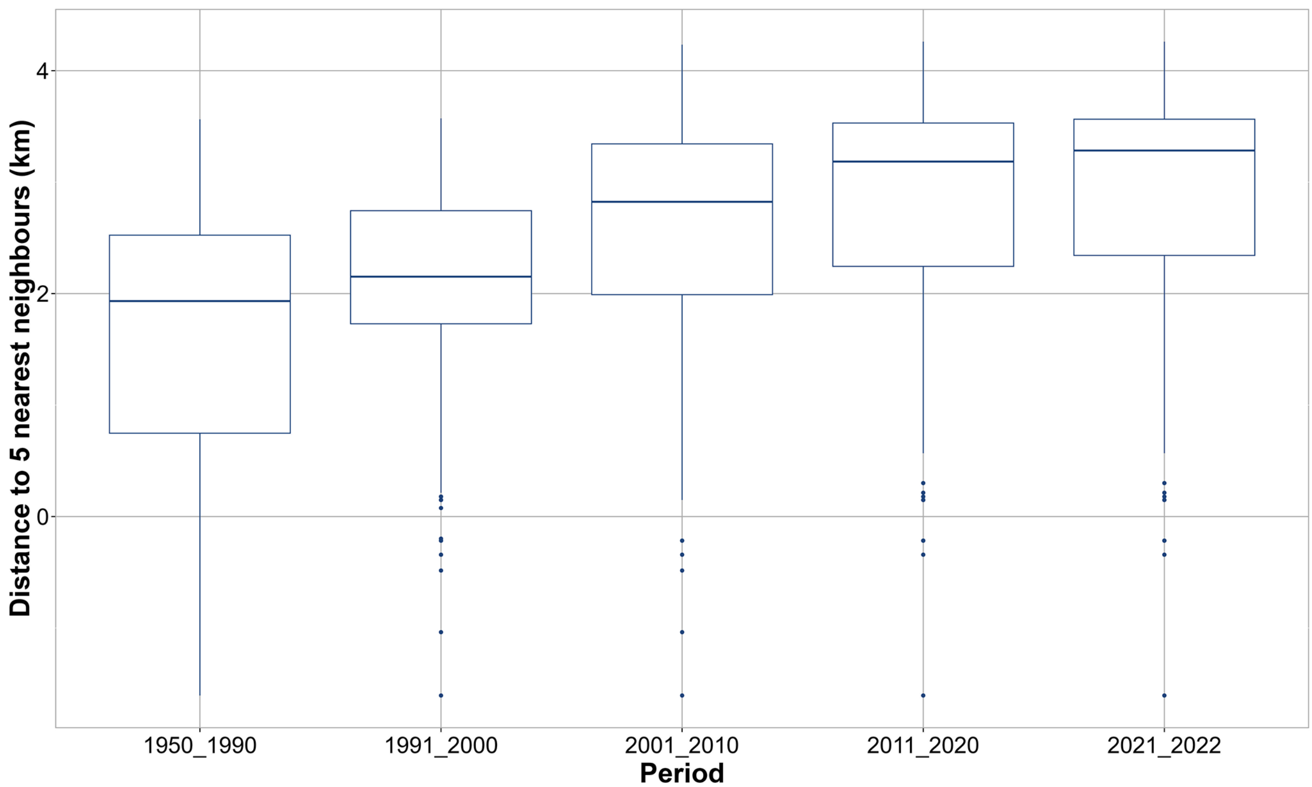

Fig. 4 Mean distance to the five nearest extant *P. alcon* populations (y-axis, log-transformed) in five periods (x-axis) in Flanders

confidence interval still overlapped with the zero-line (no change), but since 2019, this decrease is confirmed and, therefore, no longer called 'probable'.

Discussion

Despite the fact that the Alcon Blue *Phengaris alcon* is a focal species in nature conservation policy in Flanders since several decades (Vanreusel et al. 2000), it continues to decline at an accelerating speed. Here, the number of occupied grid cells decreased from 61 in the beginning of the 1990's to only six in 2023, after a relatively stable distribution between 2000 and 2013, following the publication of the species action plan in 2000 (Vanreusel et al. 2000). The number of eggs counted in the remaining sites is also steadily declining and indicates a very low number of individuals persisting in the extant populations. Overall, our quantitative results confirm the very negative impressions of several local site managers: the current condition of *P. alcon* in Flanders is more precarious than ever.

Causes of decline

Habitat loss and fragmentation of heathlands (Piessens et al. 2005; De Keersmaeker et al. 2024) are two of the main reasons for the rapid decline of *P. alcon* in Flanders. This decline is confirmed in other lowland populations elsewhere (Cerrato et al. 2016; Boe et al. 2022; Kajzer-Bonk and Nowicki 2022). In the Netherlands, for example, the number of populations dropped from 132 to 15 (-89%) in recent decades (WallisDeVries et al. 2024) and the number of eggs in the monitoring plots is now 75% lower than in 1998 (van Swaay et al. 2022). In Denmark, only one third of the 10 × 10 km² squares from which it was previously observed remain present after 2000 (Boe et al. 2022). This is probably an underestimation since many small populations could have gone extinct within the relatively coarse 10 × 10 km² grid cells. The main causes of this decline are the loss of suitable habitat, a lower habitat quality, habitat fragmentation and climate change (Fagúndez 2013). The shrinking area and lowering quality of heathlands also lead to the decline of other typical heathland butterflies, though with less complex life cycles as *P. alcon*, such as the Silver-studded Blue (*Plebejus argus*).

Apart from habitat loss, a decreasing habitat quality caused by nitrogen deposition and desiccation, is recognised to be another negative key factor (Maes and Van Dyck 2001; WallisDeVries 2004). Heathlands can only support a very low nitrogen load (10–17 kg/ha/year; Hettelingh et al. 2017). Although there has been a slight decrease in nitrogen deposition levels, current average nitrogen deposition

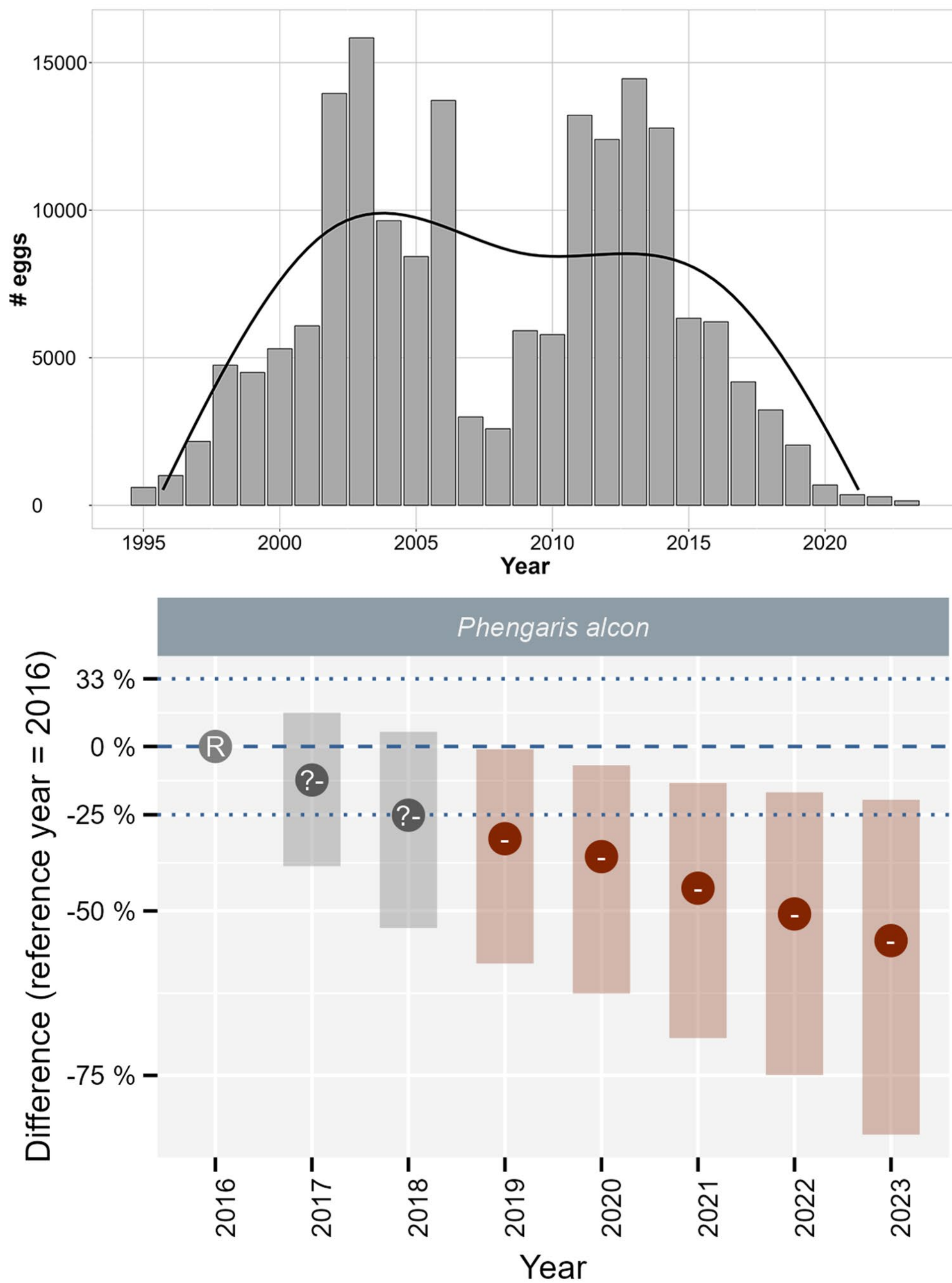

Fig. 5 The number of counted eggs (grey) and trend (black line) in the Hageven nature reserve in Neerpelt (northern Flanders) between 1995 and 2023 (left) and in the seven plots of the meetnetten.be monitoring scheme since 2016 (right; R = Reference year, ?- = probable decrease, - = decrease, according to the terminology used in the *effectclass* R-package of Onkelinx 2023)

values in Flanders of ≥ 22.5 kg/ha/year (with local extremes of > 50 kg/ha/year in northern Flanders; Cools et al. 2015) still exceed the critical load of many nutrient-poor biotopes such as heathlands. The role of such factors is widely recognised across *P. alcon* populations in NW-Europe. For example, one of the main nectar sources for *P. alcon* is the Cross-leaved Heath *Erica tetralix* and high atmospheric nitrogen deposition levels caused a decline of its cover in Denmark (Damgaard et al. 2014). Nitrogen deposition also leads to soil acidification that can prevent the seeds of the Marsh Gentians from germination (Van Den Berg et al. 2005). In some nature reserves, liming has been applied after sod cutting to buffer or increase the soil pH to facilitate the germination of gentian seeds. Nitrogen deposition additionally causes an increase in the local dominance of Purple Moor-grass *Molinia caerulea* to the detriment of other plants (e.g., host and nectar plants) and of open spaces in the vegetation nearby gentians, which are key for larval adoption by red ants. A higher and denser vegetation can lead to less-accessible host plants for egg laying (Arnaldo et al. 2014), to a lesser accessibility to nectar plants, a lower amount of bare ground for the germination of the host plant, but also to cooler microclimates for thermophilous *Myrmica* ants (WallisDeVries and van Swaay 2006). Hence, homogenization of vegetations by increasing dominance by Purple Moor-grass is disadvantageous for functional reproductive habitat of *P. alcon*.

Climate change can have negative and interacting effects on local populations of *P. alcon* in two ways: average regional warming as such, but also extreme weather events such as long droughts and/or excessive rainfall in short time periods. The distribution of *P. alcon* is predicted to decrease with 74% (mainly in central Europe) in the worst-case climate change scenario (mean expected increase in temperature of 4.1 °C) and is, therefore, classified as being of high climate risk (Settele et al. 2008). Long droughts lead to desiccation effects (Oliver et al. 2015), particularly in small wet heathland patches that have little hydrological buffering. Soil desiccation has, in turn, a negative effect on both the hygrophilous host ants (e.g., *Myrmica ruginodis*, the major host ant of *P. alcon* in NW Europe (Tartally et al. 2019a) and on the seedling recruitment of the host plant, *G. pneumonanthe* (Kesel and Urban 1999). At the other extreme, excessive rainfall can cause flooding of ant nests, but the ants are less affected by flooding then the caterpillars (Kajzer-Bonk et al. 2013). Flooding during the flight season may reduce adoption chances if zones with gentians are flooded and, therefore, do not allow the passage of host ants. Additionally, mating and oviposition can be postponed during long rainy periods resulting in suboptimal egg-laying behaviour and reduced egg laying and spreading (Van Dyck and Regniers 2010). Especially small populations can be highly sensitive to such extreme weather effects. Climate-change-induced population losses are very difficult to compensate for by habitat management (Wessely et al. 2017), and this is thus particularly so in small, ill-buffered areas.

Further adapted conservation program

Due to its precarious status, spatially explicit species action plans were compiled in both Flanders (Vanreusel et al. 2000; Maes et al. 2004) and in the Netherlands (WallisDeVries 2004; Radchuk et al. 2012). Thanks to local managers conscientiously applying most of the management measures suggested in these plans, the species was able to persist in most of the locations in the early 2000's, although some further local extinctions have been reported. During the second decade of the 20th century, however, the number of populations rapidly declined, despite the management measures being continued in all populations. Hence, the application of the species action plan of 2000 (Vanreusel et al. 2000) has probably slowed down the decline, but did not stop or reverse the negative trend.

Phengaris alcon is a very sedentary species and conservation measures need to be employed within the colonisation distance of the butterfly (i.e., 3 km – Maes et al. 2004; Vanden Broeck et al. 2017). However, colonisation is not only a matter of maximum reachable distance, but also concerns probabilities of different dispersal distances (i.e., dispersal kernel; Hovestadt et al. 2011) and hence the probability of ending up in a suitable site. Increasing again the total habitat area for the Alcon Blue in Flanders needs large-scale interventions such as large-scale sod-cutting of degraded wet heathlands combined with rewetting heathlands on a landscape scale (Schwieger et al. 2022). However, if executed in an inadequate way, large-scale sod cutting may result in a levelled site that will take a long time to recover into functional *P. alcon* habitat (Mouquet et al. 2005). Soil humidity is very important for both the germination of the host plant and for the functional habitat of the host ants, especially for butterfly species of cool and wet habitats (Klockmann and Fischer 2017). *Myrmica* ants are very sensitive to changes in soil humidity and changes therein can cause a shift towards ant species that prefer drier or wetter soils, in turn causing a mismatch during the adoption of the Alcon Blue caterpillars (Soares et al. 2012). Furthermore, the restoration of wet heathlands takes time since many typical heathland plants, such as *G. pneumonanthe*, do not persist in the seed bank and will not appear spontaneously after sod-cutting (Dorland et al. 2005a). Hence, there is a considerable colonisation debt for the habitat and community restoration in such systems (Cristofoli and Mahy 2010). Liming of acidified wet heathlands in combination with reintroducing *G. pneumonanthe* can lower the soil pH and improves the germination possibilities of Marsh Gentians (Dorland et al. 2005b; Cools et al. 2020). This technique was successfully applied in one of the former sites of *P. alcon* (Vallei van de Ziepbeek, Zutendaal) and could be considered for a reintroduction project of *P. alcon* in the near future (see further). In Flanders, a few sites have been restored showing again good-looking wet heaths with gentians, but detailed data on the responses of *Myrmica* ants are currently not available. An additional research effort in this regard is now highly recommended.

To tackle nitrogen deposition, intensive on-site management has been proposed (Jones et al. 2017), but this can be detrimental for typical heathland species such as the Alcon Blue (Maes et al. 2017). An important issue when managing wet heathlands is to create vegetation heterogeneity at both very local and somewhat wider scale (Webb 1998; Van Eupen et al. 2024), e.g., small-scale sod-cutting and/or choppering (WallisDeVries et al. 2019; Byriel et al. 2023), but with different intensities depending on the presence of *P. alcon* (Maes et al. 2004). Habitat heterogeneity in wet heathlands (e.g., variation in vegetation height, vegetation cover and micro-relief, a combination of cooler shaded and warmer sunny areas) is moreover of major and even growing significance to deal with consequences of climate change (e.g., long lasting droughts, heavy rainfall in short time periods; Gunderson 2024) for the butterfly, its host plant and especially host ants (Soares et al. 2012).

Grazing is an often applied management measure in wet heathlands (often integrated with grazing blocks of other vegetation types like nearby dry heathland), but can also have negative effects when done too intensive (Bullock and Pakeman 1997; Vanreusel et al. 2000; Lake et al. 2001; Piessens et al. 2006; Newton et al. 2009; Rosa García et al. 2013; Denton 2014; Moschetti et al. 2020). The use of exclosures to temporarily prevent grazers from eating gentians with butterfly eggs during a few weeks in the summer has proven to be an adequate intensive care solution and it actually contributed to boosting the Hageven population between 2000 and 2014 as was advised in the species action plan (Vanreusel et al. 2000).

Can reintroductions and translocations contribute to ultimately rescuing *P. alcon* in Flanders?

Reintroduction of *P. alcon* is not as straightforward as in other species because of the complex life cycle (Als et al. 2004) on the one hand and the lack of sufficiently large local source populations on the other. The obligate myrmecophilous life cycle makes ex-situ breeding very difficult. Some sites have been adequately managed and now hold large *G. pneumonanthe* populations, the host plant of *P. alcon*. A reintroduction using individuals from local populations remains to be investigated due to lack of sufficiently large source populations in Flanders (IUCN/SSC 2013). The relation with specific local host ants demands for thorough prior research of host ant compositions in potential reintroduction sites (Maes et al. 2003). In NW Europe, both the Netherlands and Denmark have populations where *M. ruginodis* is the main host ant as is the case in most of the populations in Flanders (Tartally et al. 2019b) and a collaboration on a wider range than the country's or region's borders would be more efficient (Boe et al. 2022). Mixing of individuals of different populations is often advocated (Zecherle et al. 2021; Parmesan et al. 2023), but it remains to be seen whether this is also advisable for *P. alcon*. The genetic population structure of the Alcon Blue in Flanders showed clearly isolated populations (Vanden Broeck et al. 2017), that are locally adapted to the optimal *Myrmica* host ant (Tartally et al. 2019b). Bringing in individuals from other sites, potentially being adapted to only one *Myrmica* host ant species (most likely *M. ruginodis* in Flanders), could lead to a lower adoption rate by other *Myrmica* ants and subsequently to a lower number of adult butterflies. One of the present populations (Zwart Water) was established after a reintroduction of only five females from a Dutch population situated about 20 km northward of the reintroduction site (Vanreusel et al. 2000; Maes et al. 2004). This suggests that large numbers are not necessarily needed for a successful reintroduction of this ecologically complex species. On the other hand, using a low number of individuals for reintroductions may lead to low genetic diversity making it more susceptible for stochastic events, especially in the light of extreme weather conditions due to climate change (Vanden Broeck et al. 2017).

Conclusions

Despite species-specific management measures and local species action plans, habitat (quality) loss and fragmentation, nitrogen deposition and climate change (e.g., intense rainfall causing flooding and extreme droughts) are creating extremely unfavourable conditions for the critically endangered wet heathland specialist *Phengaris alcon*. Without a more pro-active nature conservation policy dealing with the strong anthropogenic pressures, the species is doomed to disappear from the lowland heathlands in Flanders, but possibly also in other NW European regions.

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Data availability Standardised egg counts of the Alcon Blue in the meetnetten.be monitoring project are published on GBIF (Piesschaert et al. 2022).Piesschaert F, Brosens D, Westra T, Maes D, Desmet P, Ledegen H, Veraghtert W, Van de Poel S & Pollet M (2022) Meetnetten.be - Egg counts for butterflies in Flanders, Belgium. Version 1.17. Brussels. https://doi.org/10.15468/hsfq2u.

Declarations

Competing interests The authors declare no competing interests.

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