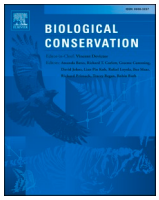
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Challenges and bottlenecks for butterfly conservation in a highly anthropogenic region: Europe's worst case scenario revisited

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ABSTRACT

The recent decline in insect diversity and abundance and the consequences for associated ecosystem functioning and services have attracted growing attention. Especially highly anthropogenic regions are affected by rapid biodiversity changes including significant losses. Two decades ago, we suggested that Flanders (northern Belgium) was Europe's worst case scenario for butterfly diversity loss with habitat destruction, fragmentation and nitrogen deposition as major causes (Maes and Van Dyck, 2001). To analyse changes since the second half of the 20th century, we used >2.5 million distribution records to calculate trends in distribution during the last three decades. By linking these trends to the species' ecology using multi-species indicators for a set of ecological and life-history traits, we determined the most important drivers policy makers and nature managers should focus on. Species showing the strongest expansion are woodland specialists and polyphagous species. On the other hand, sedentary species of nutrient-poor biotopes such as heathlands and semi-natural grasslands showed a decreasing trend, despite the ongoing policy focus and conservation efforts. We discuss our results with regard to challenges and bottlenecks for the conservation of butterflies and other insects in anthropogenic regions.

1. Introduction

Biodiversity is rapidly declining worldwide (Díaz et al., 2019; IPBES, 2019). Three major, interacting drivers have been identified as responsible for this decline: habitat loss (Brooks et al., 2002), invasive alien species (Early et al., 2016) and climate change (e.g., Román-Palacios and Wiens, 2020). Many international species-based indicators such as the IUCN Red List (Rondinini et al., 2014) and the Living Planet Index (WWF, 2020) largely focus on vertebrates to assess the state of biodiversity, despite the fact that invertebrates make up for the largest, but far less-studied part of global biodiversity (Stork, 2018). Recently, many researchers have illustrated important declines in insect diversity and abundance (e.g., Hallmann et al., 2017; Seibold et al., 2019; Cardoso et al., 2020; Wagner et al., 2021). The current knowledge on the effect of declines on ecosystem services provided by insects, however, is still scarce and biased (Luck et al., 2009; Noriega et al., 2018). The data quality of insect trends worldwide is often criticised (Thomas et al., 2019; Desquilbet et al., 2020) and shows the importance of establishing regional and global insect monitoring schemes for a wide variety of taxonomic and functional invertebrate groups (Hausmann et al., 2020). The most extensive existing monitoring scheme for an insect group is the European Butterfly Monitoring Scheme (van Swaay et al., 2020) which reported strong declines from highly anthropogenic regions in NW Europe (Netherlands: van Strien et al., 2019; Germany: Laussmann et al., 2021; UK: Warren et al., 2021). Here, habitat (quality) loss has long been the major cause of changes in insect diversity (e.g., Maes and Van Dyck, 2001) but more recently, climate change has become increasingly important as a driver of change often interacting with habitat loss (Segan et al., 2016). With the abandonment of traditional small-scale farming and an increasing intensification of agricultural practices since the 1950s in NW Europe, many (semi-)natural habitats have been lost and have become strongly fragmented. The associated increase in

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nitrogen deposition, together with changing management practices (Thomas et al., 2015), had a major impact on the habitat quality of nutrient-poor biotopes in Flanders (e.g., heathlands, chalk grasslands, dunes; Van Landuyt et al., 2008). The impact of current climate change is less straightforward than that of changes in land use and can be both positive (e.g., range expansion – Parmesan et al., 1999; warmer microclimate for thermophilous species – De Frenne et al., 2013) and negative (e.g., maladaptive host plant shifts – Singer and Parmesan, 2019; range retraction – Warren et al., 2018; developmental traps – Van Dyck et al., 2015) depending on the habitat, the species and the region considered.

Flanders (northern Belgium) is a highly anthropogenic region in NW Europe and was called "Europe's worst case scenario" regarding butterfly diversity loss in the beginning of the century (Maes and Van Dyck, 2001), without much improvement in the following decade (Maes et al., 2012). During, the 20th century, Flanders has undergone a rapid intensification of agricultural practices and a fast urban and infrastructural sprawl, both leading to the loss of many natural habitats. In addition, due to a poor spatial planning policy, Flanders is also the region with the highest degree of natural landscape fragmentation in Europe (e.g., woodlands, semi-natural grasslands, heathlands; European Environment Agency, 2011). Furthermore, only 2 % of the area is protected as a strict nature reserve (IUCN category Ia) and as habitat/species management area (IUCN category IV; Dudley, 2013; Vught et al., 2020). Flanders has one of the highest nitrogen deposition loads in Europe (Vivanco et al., 2018). Consequently, many of the habitats of the European Habitats Directive (Council Directive 92/43/EEC) that are important for the conservation of threatened butterflies and other species are currently in an unfavourable conservation state (Paelinckx et al., 2019). This has, in turn, led to a large number of species being assessed as threatened in the most recent Red List of butterflies (39 out of 75 species are Regionally Extinct or threatened; Maes et al., 2021a), but also in other terrestrial insect groups such as ladybirds (11 out of 36 species are Regionally Extinct or threatened; Adriaens et al., 2015), saproxylic beetles (nine out of 15 species are Regionally Extinct or threatened; Thomaes et al., 2015) and hoverflies (136 out of 288 species are Regionally Extinct or threatened; Van de Meutter et al., 2021).

Here, we use Flanders as an extreme case of *human induced rapid environmental change* (Sala et al., 2000). We analysed changes in butterfly composition and distribution in Flanders during the three most recent decades (1991–2000, 2001–2010 and 2011–2020) compared to a reference period in the 20th century (1951–1990). To examine the effect of possible drivers of changes in butterfly distribution, we related them to species-specific ecological and/or life-history traits such as biotope preference, nutrient level of the biotope, mobility, climate suitability, overwintering stage, voltinism, host plant specialism and host plant form (cf. Eskildsen et al., 2015). To account for spatial and temporal biases in the dataset spanning almost 70 years, we applied a correction method to estimate relative distribution ranges in different periods and subsequently calculated a change index for every species. In a next step, we merged these species' change indices into a multi-species change index per trait. Based on these results, we discuss challenges and bottlenecks for the conservation of butterflies in highly anthropogenic region using Flanders as a well-documented example.

2. Materials and methods

2.1. Study area

Flanders (total area 13,522 km^2) is the northern administrative region of Belgium (Fig. 1). It is under an intense anthropogenic pressure with 492 inhabitants/km^2 (https://statbel.fgov.be/nl/themas/bevolking/structuur-van-de-bevolking) which is >14 times higher than the European average (https://www.worldometers.info/world-population/europe-population/). More than half of the territory of Belgium is agricultural land with a very high Gross Nitrogen Balance (136 kg N/ha/year) and phosphorous use (60 kg P_2O_5/ha/year). In addition, Belgium has 94 cows and 422 pigs per km^2, which is, respectively five and 13 times higher than the European Union average (ec.europa.eu). Regarding pesticides, Belgium is among the most intensive users in Europe (8–10 kg/ha/year; Reif and Hanzelka, 2020). All these figures are even higher for Flanders, since most intensive agriculture is situated in the north of Belgium. A further 28 % of Flanders is urbanised (i.e., artificial surfaces; Poelmans et al., 2019). The total area of sites with a nature management plan in Flanders (e.g., nature reserves, private woodlands, some military areas) is 94,060 ha (i.e., 7 % of the total area; Vught et al., 2020). Nature conservation is the competence of the three regional administrative authorities in Belgium (Flanders, Wallonia and the Brussels Capital Region) and we, therefore, analyse data on the scale of Flanders instead of Belgium.

2.2. Data

For a new regional Red List assessment of butterflies in Flanders (Maes et al., 2021a), we compiled butterfly distribution data from four different sources:

1. The database of all museum and literature data, but also observations from the period 1830–2014 (658,859 records – Maes et al., 2016);

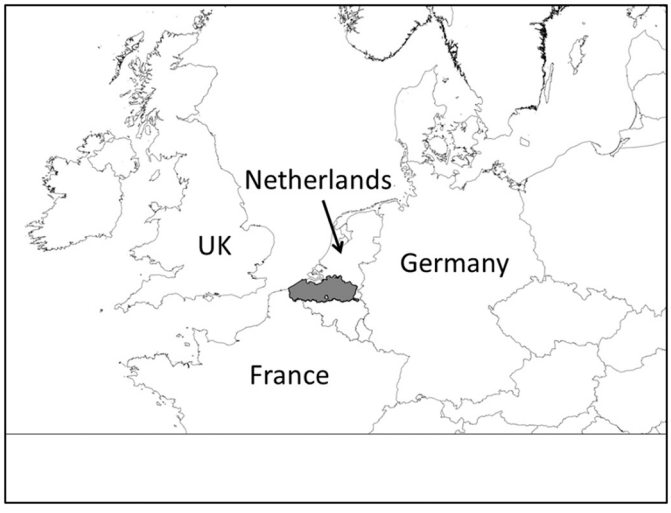


Fig. 1. Location of Flanders in Europe (in grey).

2. Distribution data from the online data portal waarnemingen.be with records between 1902 and 2020; this database is managed by Natuurpunt, the largest nature NGO in Flanders (1,781,854 records – partly published in Maes et al., 2016);
3. Data from butterfly monitoring schemes in Flanders:
   a. The Flemish Butterfly Monitoring Scheme in which butterfly transects are counted since 1991 (138,828 records – Maes et al., 2021b);
   b. The meetnetten.be monitoring scheme in which twelve species of conservation concern in Flanders are monitored since 2016: *Apatura iris*, *Cyaniris semiargus*, *Erynnis tages*, *Euhpydryas aurinia*, *Hesperia comma*, *Hipparchia semele*, *Lasiommata megera*, *Melitaea cinxia*, *Phengaris alcon*, *Pyrgus malvae*, *Pyronia tithonus* and *Satyrium ilicis* (22,206 records – Piesschaert et al., 2022a; Piesschaert et al., 2022b; Piesschaert et al., 2022c);
4. Since 2017, the data portal waarnemingen.be includes an application to register opportunistically walked transects (i.e., they are not part of a butterfly monitoring scheme) and to link all butterfly observations to that transect. This is similar to the Flemish Butterfly Monitoring Scheme but differs from it in the fact that the transect is not in a fixed location and that it is not necessarily walked on a regular (weekly) basis. In total, 69,044 records have been collected using such opportunistic transects (n = 4866; total length = 12,219 km).

In total, this resulted in 2,668,791 distribution records (species, date, location, observer). All observations were attributed to a grid cell of 5 × 5 km^2 of the Universal Transverse Mercator (UTM) projection, hereafter called "grid cell". The full dataset was subsequently condensed to "species-year-grid cell" records (n = 222,838). The number of condensed records per year since 1951 is given in Fig. 2.

2.3. Analysis

For the compilation of the most recent Red List, 75 species were assessed in Flanders (Maes et al., 2021a). For further analysis, we only used species that regularly breed in Flanders and that are able to successfully overwinter here since 1951. Three migrant species were excluded from the analysis: *Colias crocea*, *C. hyale* and *Vanessa cardui*. *Vanessa atalanta* is also a migrant in Flanders, but was included since it is overwintering here since the beginning of the 2000s. Two more species (*Nymphalis antiopa* and *N. polychloros*) were excluded because the majority of the records concern vagrant individuals and not established populations. Finally, species that went extinct in Flanders before 1950 (*Boloria euphrosyne*, *Coenonympha hero*, *Fabriciana adippe*, *Hipparchia statilinus*, *Pontia edusa/daplidice* and *Spialia sertorius*) were not used for further analysis.

With the condensed data set, we calculated a change in distribution between a reference period (1951–1990) and three recent decades: 1991–2000, 2001–2010 and 2011–2020. To compensate for the increased mapping intensity compared to the reference period, we first calculated a relative distribution range p_{ip} by dividing the number of grid cells of each species i in each period p by the sum of the grid cells of every individual species in each period, i.e., 6309 in the reference period 1951–1990 and 10,726, 12,584 and 15,606 in the decades 1991–2000, 2001–2010 and 2011–2020, respectively (cf. Maes et al., 2012; see Supplementary material 1). This corresponds to a 1.70 times higher relative mapping coverage in the decade 1991–2000 compared to the reference period 1951–1990, 1.99 for the decade 2001–2010 and 2.47 in the decade 2011–2020 (see Supplementary material 2). We used this relative distribution range to calculate a species change index (SCI) between the three recent decades and the reference period (Buckland et al., 2011 – formula (1)).

$$SCI_{ip} = p_{ip}/p_{i1} \quad (1)$$

With p_{ip} being the relative distribution range of species i in period p (1991–2000, 2001–2010 or 2011–2020) and p_{i1} being the relative distribution range in the reference period 1951–1990. To detect more general patterns and underlying causes of changes in distribution in Flanders, we calculated so-called Multi-Species Change Indices (MSCI – Buckland et al., 2011) by calculating a geometric mean per ecological and life-history trait using formula (2)

$$MSCI_p = exp\left(\frac{1}{S}\sum_{i=1}^{S}\log SCI_{ip}\right) \quad (2)$$

With S being the number of species per period and per trait. We calculated P% confidence intervals for $MSCI_p$ by bootstrapping the log-transformed SCI_{ip} and calculating the (arithmetic) mean for each bootstrap sample. An equal-tail confidence interval was calculated based on the exponentiated $(1 - P) / 2$ and $(1 + P) / 2$ quantiles from the distribution of the means calculated from 1000 bootstrap samples. Since the MSCI cannot be calculated if any of the relative distribution ranges are zeroes (Buckland et al., 2011), we excluded eleven species that went extinct and six species that colonised Flanders since the reference period. This reduced the number of species in the analyses to 47. We express the MSCI as a percentage change compared to the reference period 1951–1990. We calculated MSCIs for eight ecological and life-history traits (Table 1). The classification of species in the different

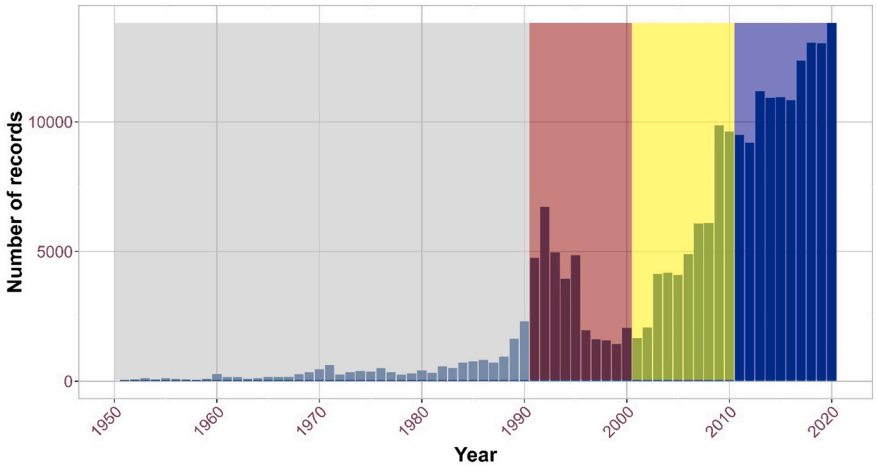


Fig. 2. Number of condensed records per year since 1951 in Flanders. The period 1951–1990 was used as a reference period (in grey) and was compared with the decades 1991–2000 (red), 2001–2010 (yellow) and 2011–2020 (blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Classes of the ecological and life history traits used in the analysis and the reference that was used for the classification.

Trait	Classes	Reference
Biotope preference	Ubiquitous generalists	Bos et al. (2006)
	Grassland generalists	
	Woodland generalists	
	Heathland specialists	
	Grassland specialists	
	Woodland specialists	
Nutrient level of the biotope	Oligotrophic (low nutrient level)	Oostermeijer and van Swaay (1998)
	Mesotrophic (intermediate nutrient level)	
	Eutrophic (high nutrient level)	
Mobility	Sedentary (<500 m)	Bink (1992)
	Mobile (>500 m)	Bos et al. (2006)
		Dennis (2010)
Climate suitability in Flanders in 2050	Less suitable	Settele et al. (2008)
	Equally or more suitable	Maes et al. (2010)
Voltinism	Univoltine spring (one generation in spring)	Bos et al. (2006)
	Univoltine summer (one generation in summer)	
	Bivoltine (two generations per year)	
	Multivoltine (more than two generations per year)	
Overwintering stage	Egg	Bink (1992)
	Caterpillar	
	Pupa	
	Adult	
Host plant specialization	Monophagous (single host plant species)	Bink (1992)
	Oligophagous (single family host plants)	Dennis (2010)
	Polyphagous (host plants from different families)	
Host plant form	Grass	Dennis (2010)
	Herb	
	Shrub/tree	

ecological or life-history traits is given in Supplementary material 3. To avoid overinterpretation of the results, we used relatively stringent thresholds to decide whether a species increased or decreased in relative distribution range: +100 % as threshold for an increase (a twofold increase of the relative distribution range compared to the reference period) and −50 % as threshold for a decrease (a halving of the relative distribution range compared to the reference period; Onkelinx et al., 2021). We express changes in relative distribution ranges using the classes as defined in the R package *effectclass* (Onkelinx, 2022; see Supplementary material 4). For example, a change in relative distribution range is labelled as "strong increase" if the confidence interval is completely above the +100 % threshold.

3. Results

3.1. Changes in species richness

In Flanders, the number of butterfly species dropped from 58 in the reference period 1951–1990, to 49 in the decade 1991–2000 and 48 in the decade 2001–2010 but increased to 53 in the decade 2011–2020. Ten species were no longer observed in the period 1991–2000 compared to the reference period 1951–1990: *Pyrgus armoricanus* (last year of observation 1952), *Melitaea diamina* (1954), *Limenitis populi* (1957), *Euphydryas aurinia* (1959), *Aporia crataegi* (1965), *Melitaea athalia* (1968), *Speyeria aglaja* (1971), *Fabriciana niobe* (1977), *Phengaris teleius* (1980) and *Plebejus idas* (1984), while one species (re)colonised Flanders during that period (*Cupido minimus* – 1991). During the decade 2001–2010, *Coenonympha tullia* (1994) and *Heteropterus morpheus* (1995) went extinct and one species colonised Flanders (*Carcharodus alceae* – 2009). During the decade 2011–2020, no more species went extinct and four species colonised Flanders: *Cupido argiades* (first observation in 2012), *Brenthis daphne* (2015; Cuvelier and Spruytte, 2011), *Pieris mannii* (2015; Vantieghem, 2018) and *Apatura ilia* (2017). One species (*Euphydryas aurinia*) was (illegally) reintroduced in a nature reserve in 2016 and is still present to date.

3.2. Changes in distribution in relation to ecological and life-history traits

3.2.1. Biotope preference

For ubiquitous generalist species, the relative distribution range was stable compared to the reference period, but moderately decreased in the last two decades. For generalist grassland and woodland species, there were no significant changes in relative distribution range. In biotope specialists, heathland and grassland species showed a (potential) decrease in relative distribution range compared to the reference period during the three recent decades. Woodland specialists, on the other hand, showed a decrease in relative distribution range in the first period after the reference period, but gradually increased their relative distribution range towards the most recent decades (Fig. 3a).

3.2.2. Nutrient level of the biotope

Compared to the reference period, the relative distribution range of species of oligotrophic biotopes showed a decrease in the two subsequent decades but this trend changed into a potential decline in the most recent decade. The relative distribution range of species of mesotrophic biotopes remained stable compared to the reference period. Species of eutrophic biotopes showed a stable trend in the first two decades after the reference period, but potentially increased in relative distribution range during the most recent decade (Fig. 3b).

3.2.3. Mobility

Sedentary species showed a decrease in relative distribution range in the three decades since the reference period, while mobile species remained stable compared to the reference period (Fig. 3c).

3.2.4. Climate suitability

Species for which the climate in Flanders is predicted to become less suitable in the future (Maes et al., 2010) showed a potential decrease in relative distribution range in the first two decades after reference period, but a potential increase in the most recent decade. Species for which Flanders was predicted to stay equally or more suitable, showed a moderate decrease in relative distribution range at first, but showed a stable trend in the two subsequent decades compared to the reference period (Fig. 3d).

3.2.5. Voltinism

The relative distribution range of species with only one generation in spring potentially decreased compared to the reference period, while that of species with one generation in summer at first remained stable, but potentially increased during the most recent decade. The relative distribution range of bivoltine species at first decreased compared to the reference period, but showed a potential decrease in the two most recent decades. Multivoltine species remained stable in relative distribution range compared to the reference period (Fig. 3e).

3.2.6. Overwintering stage

Compared to the reference period 1951–1990, species that overwinter as egg showed a decrease in relative distribution range at first, with a trend becoming stable and potentially increasing in the subsequent decades. Species that overwinter as caterpillar showed a decrease in relative distribution range in the first two decades after the reference period, but a potentially decreasing trend in the most recent decade. The relative distribution range of species overwintering as pupa remained stable compared to the reference period. Species overwintering as adults

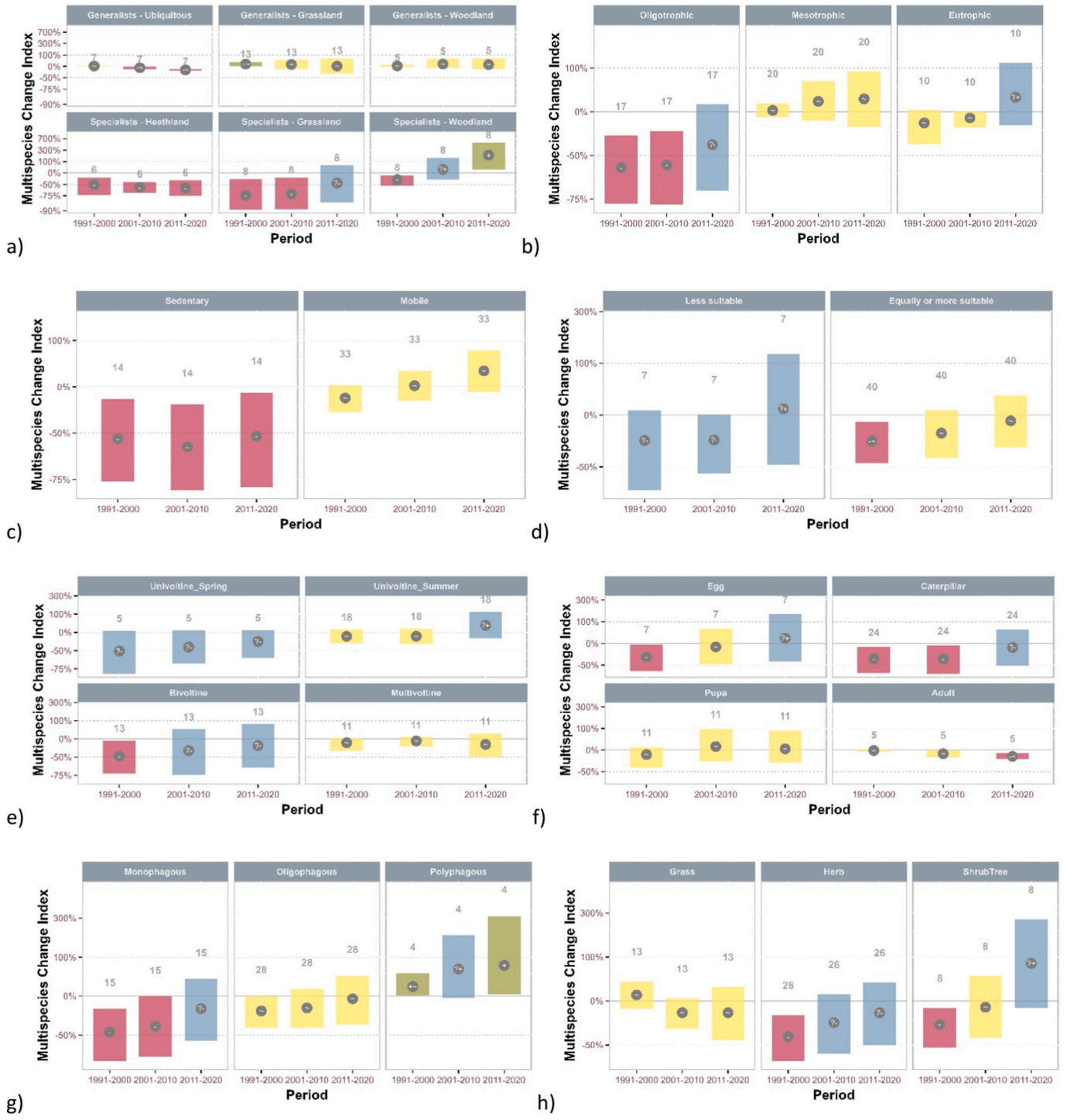


Fig. 3. Multispecies Change Index (±95 % CI s, i.e., ca. 2 * se) in three decades compared to a reference period (1951–1990) per a) biotope class, b) nutrient level of the biotope, c) mobility class, d) climate suitability, e) voltinism, f) overwintering stage, g) host plant specialism and h) host plant form. The dashed lines indicate the threshold for increases or decreases compared to the reference period 1951–1990. The figures in grey indicate the number of species in each period and each biotope class. The grey dots indicate the mean MSCI and the trend is given in white in the dots: ++ = strong increase, + = increase, +~ = moderate increase, ~ = stable, −~ = moderate decrease, − = decrease, −− = strong decrease, ?+ = potential increase, ?− = potential decrease, ? = unclear.

showed a moderate decrease in relative distribution range in the most recent decade compared to the reference period (Fig. 3f).

3.2.7. Host plant specialism

Monophagous species showed a decrease in relative distribution range in the first two periods after the reference period, but a potentially decreasing trend in the most recent decade. The relative distribution range of oligophagous species remained stable compared to the reference period. Polyphagous species increased in relative distribution range towards the most recent decade (Fig. 3g).

3.2.8. Host plant form

The relative distribution range of species feeding on grasses remained stable compared to the reference period. Species feeding on

herbs decreased in relative distribution range in the first decade after the reference period, but this trend changed into a potential decrease in the most recent decades. Scrub and tree feeding species first showed a decrease in relative distribution range compared to the reference period, became stable in the subsequent decade and was potentially increasing in the most recent decade (Fig. 3h).

4. Discussion

With 20 species that went regionally extinct since the 19th century, Flanders was called the "worst-case scenario for butterfly diversity loss in Europe" (Maes and Van Dyck, 2001). Especially sedentary species and species of nutrient-poor biotopes (e.g., heathlands, semi-natural grasslands) have further decreased compared to the reference period 1951–1990. On the other hand, woodland specialists (e.g., *Apatura iris*, *Argynnis paphia*) expanded their distribution range, particularly during the last decade.

4.1. Calculating changes in distribution

Detecting changes in distribution over long periods is challenging due to spatial and temporal differences in survey intensity and coverage (Isaac et al., 2014). The development of smartphone applications and a rapidly increasing number of volunteers recording butterflies (*citizen scientists*) resulted in databases in which the number of recent records outnumbers historical records by orders of magnitude (MacPhail and Colla, 2020). In Flanders, for example, the number of distribution records in the most recent decade (2011–2020) is 50 times higher than in the reference period (1951–1990). Additionally, historical butterfly recorders (often collecting for museum specimens) targeted their surveys much more on rare species making common species relatively underrepresented in historical records (Dennis et al., 1999; Dennis and Thomas, 2000). On the other hand, a lower number of volunteers in the early periods could result in an incomplete coverage of the distribution of rare species as well. Different methods have been proposed to correct for such biases in the number of records between recent and historical periods and here, we corrected for differences in mapping intensity and coverage by calculating relative distribution ranges per period (cf. Maes et al., 2012). Spatial bias could be excluded by only using grid cells that are well-sampled in the periods compared (Maes and Van Dyck, 2001), but since the sampled grid cells are spatially well-spread over Flanders, we used all the available data to calculate changes in distribution between recent decades and the reference period. Given the probable underestimation of the distribution of rare species in the reference period, the outcome of our analyses has to be seen as a rather cautious interpretation of changes in butterfly diversity and its drivers. Site Occupancy Models (Kéry et al., 2013) are often used to correct for differences in mapping coverage or intensity, but need sufficient repeated visits to do so. Especially in the reference period in which mostly museum specimens were used in the dataset, we did not have a large enough number of repeated visits to apply Site Occupancy Model here (Shirey et al., in press). The ecological and life-history traits of the large number of species that went extinct compared to the reference period or the few species that colonised Flanders can greatly contribute to detect general patterns in changes in butterfly diversity.

We used a relatively long reference period as a benchmark and are aware that during this long reference period a lot of changes have occurred (e.g., agricultural intensification, increasing human population and building) leading to an increasing anthropogenic impact on the landscape (Poelmans and Van Rompaey, 2009). But, by using a long reference period, we wanted to avoid the shifting baseline syndrome effect (Papworth et al., 2009) and illustrate the potential species composition in Flanders in the second half of the previous century as a possible goal in nature conservation (cf. Hallman et al., 2021).

For this analysis, we calculated changes in *relative distribution ranges* during the last three decades compared to the period 1950–1990. Changes in *abundances*, however, would be a more sensitive measure to reflect the state of butterfly populations, but such data are rarely available over long time periods (van Strien et al., 2019). The use of distribution data usually underestimates population trends since all individuals within a grid cell have to disappear before the grid cell is no longer occupied, while in the meantime, the number of individuals could have dropped strongly. Conversely, species' increases in area of occupancy are signalled faster with methods that focus on changes in distribution area (Wilson et al., 2004), whereas this pattern could be largely decoupled from changes in abundance (Van Dyck et al., 2009). *Pyronia tithonus*, for example, shows an increase in distribution range and is filling in gaps in its range in Flanders, but the abundance on butterfly monitoring transects has dropped with 33 % in Flanders (Maes et al., 2020). Although a butterfly monitoring project is running in Flanders since 1991 (van Swaay et al., 1997), the number of transects is too low and includes too few rare species to yield usable numbers for a long-term analysis of changes in abundances for all species in Flanders. Since 2016, however, twelve so called Flemish priority butterfly species are monitored in a species-tailored monitoring scheme Meetnetten.be and these data will be very useful to calculate changes in abundance for these threatened species (Westra et al., 2022).

4.2. Changes in species richness

In NW Europe, butterfly diversity loss is probably among the strongest globally (Maes et al., 2012; van Strien et al., 2019; Laussmann et al., 2021). This is due to the very high anthropogenic impact (intensive agriculture and industry, high population density and dense road and infrastructure network) on the landscape which converted (semi-)natural habitat into other land uses and lowered the quality of the remaining fragmented (semi-)natural areas. This has led to the extinction of 20 butterfly species in Flanders (27 %), making it still Europe's worst case scenario regarding butterfly loss (Maes and Van Dyck, 2001; Maes et al., 2021a). Natural recolonisation of most of the Regionally Extinct and/or threatened species is unlikely due to insufficient remaining habitat, the low landscape connectivity (Maes and Van Dyck, 2022) and distant and often small, potential source populations.

4.3. Changes in relation to ecological and life-history traits

By comparing the distribution of butterflies in Flanders during the last three decades with that in a reference period in the 20th century, we showed that woodland specialists have expanded their range especially during the most recent decade. Heathland, specialist grassland species and sedentary species, on the other hand, continue to show a decrease. Patterns in other ecological and life-history traits such as voltinism, overwintering stage and host plant specialism were less clear.

Woodland specialists showed a steady increase in relative distribution range compared to the reference period 1951–1990. This is also reflected in the host plant form as shrub and tree feeding species potentially increased (Fig. 3h; cf. Mattila et al., 2009). Due to a change towards a more ecologically favourable management, woodlands now have more variation in tree age structure (Govaere, 2020) and are better buffered against extreme weather events than open biotopes (Zellweger et al., 2020). This development has probably benefitted the larval development of typical woodland species such as *Apatura iris*, *Argynnis paphia* and *Limenitis camilla*. In Finland, a similar suite of butterflies inhabiting woodland edges and using woody plants as larval host plants, showed the strongest expansion northwards in recent decades (Pöyry et al., 2009). In the UK, macro-moths species of woodlands fared better than grassland species (Conrad et al., 2004) and in Central Europe, species of closed woodland also tended to be less threatened than species of open habitats (Potocký et al., 2018). A more recent study in the UK, however, showed that 50 % of the declining macro-moths had woody larval food sources (Coulthard et al., 2019). For specialist woodland butterflies, Flanders is not at the northern distribution limit and instead

of expanding northwards, these species are expanding to locally available suitable habitats (*range filling*; Mattila et al., 2011). Woodland specialists that went extinct in Flanders in the second half of the 20th century such as *Boloria euphrosyne*, *Melitaea athalia* and *M. diamina* are species of open areas in large woodlands feeding on herbs rather than trees or shrubs (cf. Bergman and Kindvall, 2004). Due to the cessation of coppicing, these habitats were, and still are, very scarce in woodlands (Gorissen et al., 2004).

In general, specialist grassland species showed a decline compared to the period 1951–1990 which is also the case for Lepidoptera in general in other regions (Franzén and Johannesson, 2007; Valtonen et al., 2017; Coulthard et al., 2019), mostly due to habitat quality loss and fragmentation. Two grassland specialists (*Issoria lathonia* and *Melitaea cinxia*), however, expanded their distribution range recently, but are still restricted to more natural areas. *Issoria lathonia* used to have a very restricted distribution range in Flanders (coastal dunes), but during recent decades, it strongly expanded on the sandy soils in the northeast of Flanders. Thanks to its high dispersal capacities and an increased use of *Viola arvensis* as a host plant, the expansion might be explained by similar factors as for *A. agestis* in the UK (i.e., regional warming and a shift of hostplant – Pateman et al., 2012). *Melitaea cinxia* used to be a widespread species until the 1970s, but rapidly declined to only a few sites in the northeast of the region. Local conservationists translocated overwintering caterpillar nests from sites at risk (e.g., building areas) to safer sites (e.g., nature reserves) and strongly contributed to the regional conservation of the species. In intense anthropogenic and strongly fragmented regions, intensive care actions such as translocations and/or reintroductions will be increasingly needed to lower the regional extinction risk of threatened species (see further).

Specialist heathland species keep showing a decreasing trend during the last three decades (cf. Coulthard et al., 2019; van Strien et al., 2019). Heathlands have suffered the most from habitat destruction during the 20th century (transformation into pine forests or agricultural fields) and have become increasingly fragmented in Europe (Fagúndez, 2013). This resulted in small populations and a strongly reduced gene flow between populations which, in turn, caused inbreeding effects in local populations of typical heathland butterflies (e.g., *Phengaris alcon*, *Hipparchia semele*, *Plebejus argus*). Additionally, they strongly suffer from nitrogen deposition leading to grass encroachment (Friedrich et al., 2011) and extreme climate events such as long drought periods during the last years (Satoh et al., 2022) resulted in a very low quality of host plants and a limited nectar availability (Oliver et al., 2015; Kuppler and Kotowska, 2021). Although management plans increasingly focus on heathland restorations, this is not yet reflected in the recovery of heathland butterflies, mainly due the fact that the nitrogen deposition is still far above the critical load in many regions. Present-day policy changes will take years, if not decades, to have tangible effects on the ground (Stevens, 2016) and emphasises the need for species-specific management measures to bridge this time lag.

Four typical marshland and wetland species could not be taken into account in this analysis because they went extinct in Flanders since 1950 (*Euphydryas aurinia* – 1959, *Phengaris teleius* – 1980, *Heteropterus morpheus* – 1995 and *Boloria selene* – 2016; Maes et al., 2013). The main reason for their disappearance is the draining of wetlands for agriculture or building purposes, which can have detrimental effects over large distances including nature reserves, especially in highly fragmented landscapes (cf. Franzén and Johannesson, 2007).

Sedentary species show an ongoing decrease in distribution range. Surprisingly, species that, according to most butterfly literature, are classified as being (very) sedentary such as *Satyrium w-album* and *Thecla betulae* also managed to expand their distribution considerably. Dispersal kernels (i.e., the combination of distances a species can fly, but also the frequency with which it covers certain distances) are challenging to estimate reliably and they also depend on the landscape configuration (Hodgson et al., 2022) and the size of populations in a given region (Nowicki and Vrabec, 2011). Literature sources often classify species in different mobility classes based on expert opinion of local butterfly experts, but an objective classification of butterfly mobility is yet to be determined. Genetic research has recently shown that distances over which exchanges between populations occur are often (strongly) underestimated (*Phengaris alcon* – Vanden Broeck et al., 2017; *Hipparchia semele* – De Ro et al., 2021; *Plebeius argus* – Vanden Broeck et al. unpublished data). But, even when species can move longer distances than previously estimated in fragmented landscapes (Fourcade et al., 2021), gene flow is often too low to result in sustainable populations (Saarinen et al., 2016; De Ro et al., 2021). Furthermore, dispersal is also dependent on the size of populations with larger populations resulting in more frequent dispersers which increases the probabilities of successful gene flow between populations (e.g., *Melitaea cinxia* – Enfjäll and Leimar, 2005). The building-up of larger populations of some of the abovementioned woodland species might have resulted in a spill-over to other woodland areas, explaining their rapid regional range expansion and filling.

Contrary to other areas (Hickling et al., 2006; Pöyry et al., 2009; Devictor et al., 2012), climate suitability did not show clear patterns in changes in distribution range, probably because of the very narrow latitudinal range in climate variables in Flanders. Some individual species for which Flanders was predicted to become more suitable in 2050 (Maes et al., 2010), strongly expanded their distribution and colonised Flanders during the last decade(s): *Carcharodus alceae*, *Apatura ilia* and *Brenthis daphne* (cf. Reinhardt et al., 2020 in Germany). These species are/were at the northern edge of their distribution range in Flanders and probably benefitted from a regionally warming climate. Since the northward shift in temperature is going faster than the change in distribution of butterflies (i.e., climate debt; Devictor et al., 2012), more southerly species are expected to move further northward in the (near) future. Some species for which the climate is predicted to become more suitable will not be able to (re)colonise Flanders due to the lack of suitable habitat and the distance to possible source populations relative to their presumed limited dispersal capacity (e.g., *Melitaea athalia*, *Phengaris teleius*, *Pyrgus armoricanus*). Additionally, the lack of landscape conductance and an insufficient area of suitable habitat in the strongly fragmented NW European landscape hamper the northward expansion or range filling of species (Maes and Van Dyck, 2022). This can eventually cause strongly disrupted regional or continental distribution ranges in the future, making it even more difficult to conserve threatened species on a continental scale.

Monophagous species decreased in distribution area, while polyphagous species expanded their distribution range (cf. Öckinger et al., 2010; Valtonen et al., 2017). Especially species of nutrient-poor habitats such as heathlands (e.g. *Hesperia comma*, *Phengaris alcon*) and semi-natural grasslands (e.g., *Lycaena tityrus*) showed strong declines in distribution. Most of the monophagous species use host plants that are typical of oligotrophic biotopes (e.g., *Lycaena tityrus* in nutrient-poor grasslands, *Hesperia comma* or *Phengaris alcon* in heathlands) and suffer from an excess of nitrogen deposition, leading to the disappearance or lower quality of their host plants (WallisDeVries and van Swaay, 2006; WallisDeVries and van Swaay, 2017). *Aglais urticae*, one of the monophagous species that uses the very common and nutrient-tolerant *Urtica dioica* as host plant, is strongly declining in Flanders in recent decades (Maes et al., 2021a), but the reasons for its decline remain to be studied.

4.4. Implications for butterfly conservation in highly anthropogenic regions

The strong impact of human activities on nature and the environment in highly anthropogenic regions leads to small and highly fragmented butterfly habitats suffering from high nitrogen depositions, climate change and most likely pesticide loads. This makes butterfly conservation in such highly impacted regions not as straightforward as in more natural areas (Hülber et al., 2020). Many of the present-day

nature management measures are based on traditional/historical techniques. Given the increasing environmental changes, nature management needs to adopt novel insights on a changing species' ecology and/or behaviour (Van Dyck, 2012; Maes et al., 2014). Here, we discuss some challenges and bottlenecks for butterfly conservation in highly anthropogenic regions, using Flanders as a case study.

Some threatened species have recently colonised man-made biotopes as a surrogate for natural biotopes. For example, *Leptidea sinapis*, *Hipparchia semele* and *Hesperia comma* have a large proportion of their populations in sites that are not designated as natural areas (e.g. military areas, coal mine slag heaps, industrial grounds or former quarries). Acquisition as nature reserve and/or an appropriate management agreement with the private-owners of these man-made biotopes can, therefore, help the conservation of threatened species in strongly industrialised regions (e.g., Beneš et al., 2003; Lenda et al., 2012; Tropek et al., 2017; Münsch and Fartmann, 2022). Moreover, efforts to invest into nature-friendly management in an agricultural landscape matrix and in gardens will have a favourable pay-off for the wider community of butterflies and other insects (Ellis and Wilkinson, 2020).

Nitrogen deposition was assumed to be one of the main causes of butterfly diversity declines in Flanders (Maes and Van Dyck, 2001). The lack of any recovery of specialist species of oligotrophic biotopes confirms that its effects are ongoing (Kurze et al., 2018; Klop et al., 2015) and other countries also report strong negative impacts of nitrogen (Roth et al., 2021). Although the levels of nitrogen deposition are declining in recent decades in the whole of Europe (Erisman et al., 2015), they are still far above the critical load of all oligotrophic biotopes such as heathlands (critical load 11–17 kg/ha/year) and nutrient-poor grasslands (critical load 10–12 kg/ha/year; Hettelingh et al., 2017). A reduction of the nitrogen deposition at the source (i.e., agriculture, traffic, industry) through a transition towards more environmental-friendly and renewable energy sources is slowly being implemented, but the recovery of nutrient-poor biotopes and their butterfly communities will take decades (Walker et al., 2004; Stevens, 2016; Nijssen et al., 2017). It is, therefore, unlikely that the measures taken at-present will result in timely solutions, given the pace at which species of nutrient-poor biotopes are declining or being lost. Intensifying nature management in open biotopes such as nutrient-poor grasslands and heathlands to remove accumulated nitrogen more rapidly has been suggested to reduce nitrogen content in threatened biotopes (Jones et al., 2017). This is, however, not an efficient solution for invertebrates such as butterflies. More intensive management (e.g., more frequent and/or large-scale mowing regimes, more intensive grazing), especially in small nature reserves that are embedded in an agricultural landscape, reduces both vegetation structure and available nectar sources for butterflies and ecological resources for other insects (Maes et al., 2017).

Climate change is increasingly causing extreme weather events (e.g. prolonged droughts) which is especially impacting species of open habitats (i.e. nutrient-poor grasslands, heathlands and marshes). During such extreme weather events (Hill et al., 2021), species change their behaviour and habitat use and management plans need to take this into account. *Hipparchia semele*, for example, is a species of open biotopes such as heathlands and dunes in NW Europe, but avoids open terrain during the hottest moments of the day. During heat waves, individuals of *H. semele* are almost exclusively found in woodland edges or small groups of trees to avoid overheating (Tropek et al., 2017). Hence, such woody habitat components become key elements of this typically open-biotope species under climate change pointing at the increasing role of environmental heterogeneity, including in particular microclimatic heterogeneity (de Vries et al., 2021). Apart from the abovementioned pressures, the effects of pesticide use (Braak et al., 2018) and its possible spread into natural areas need to be studied more thoroughly. Given the large area of intensive agriculture and the proximity of mostly small nature reserves embedded in an agricultural matrix in NW Europe, it can be assumed that pesticides contributed to the decline of butterflies in agricultural areas (Hallmann et al., 2017; Warren et al., 2021). Another poorly studied potential pressure for butterflies is artificial light at night (ALAN), which is usually associated with nocturnal insects such as moths and fireflies (Owens and Lewis, 2018). ALAN can, however, also have an impact on the behaviour, physiology and ecology of (larvae of) butterflies and it is, therefore, advocated to include the effects light pollution as an increasingly important factor in butterfly conservation (Seymoure, 2018; Giavi et al., 2021).

In highly fragmented regions where distances between populations of threatened species become increasingly large, translocations and/or reintroductions can be applied to spread the extinction risk over multiple sites and/or to increase gene flow (IUCN/SSC, 2013). Not only very sedentary species (e.g., *Phengaris alcon* – Vanden Broeck et al., 2017) but also relatively mobile species (e.g., *Hipparchia semele* – De Ro et al., 2021) could benefit from such translocations. Whenever threatened species occur on unprotected sites that will be developed in the near future (e.g., industrial grounds, building activities), a translocation to a safe site (e.g., a protected nature reserve) could prevent such populations from going extinct. Recently, guidelines for the translocation of species have been compiled for Flanders (Mergeay and Verbist, 2021), based on the IUCN guidelines (IUCN/SSC, 2013). Such guidelines are needed to avoid well-intentioned, but illegal reintroductions or translocations. They contain risk assessments and advice on how to perform translocations or reintroductions (e.g., number of individuals, origin of source populations). For most of the threatened species, source populations in regions under high environmental pressure are usually not large enough (or even absent) and international collaboration is needed to find suitable sites to harvest individuals from (cf. Maes et al., 2019 for the reintroduction of *Carterocephalus palaemon* in England using Belgian individuals).

5. Conclusions

With 20 extinct species and a further 19 species threatened, the situation of butterflies in Flanders is still one of the worst-case scenarios in Europe. Although some new (generalist) species colonised Flanders and specialist woodland species increased in the most recent decade, sedentary specialist species of nutrient-poor grasslands and heathlands continue to decline. Creating and/or maintaining large populations through appropriate management measures within nature reserves and landscape-scale restoration measures are not easily achievable in a strongly fragmented and intensively cultivated region such as Flanders. High nitrogen deposition loads and a poor spatial planning make it difficult to sustainably conserve populations of threatened butterfly species with conventional conservation measures. Therefore, embracing man-made biotopes as a surrogate for natural biotopes, species-tailored adaptive management approaches creating heterogeneous vegetations and climate refugia and targeted translocations or reintroductions need to be adopted to tackle the continuing pressures on butterflies. We urge for an evidence-based action plan to improve efforts of butterfly conservation within the challenging environmental context of Flanders, that could become an instructive case for insect conservation plans in other highly anthropogenic regions.

CRediT authorship contribution statement

DM and HVC conceived the analysis; all authors contributed to the writing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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