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Butterflies in trouble: The effectiveness of Natura 2000 network in preventing habitat loss and population declines of endangered species in urban area

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ABSTRACT

Habitat deterioration and biodiversity decline is progressing worldwide. However, these effects may be somewhat mitigated in urban areas, which are strongly exposed to anthropogenic pressure. The protected sites may here impede habitat loss and serve as effective tool of biodiversity conservation. The aim of this study was to test if location (inside/outside Natura 2000 sites) and size of habitat fragments affect the habitat loss and population trends in metapopulations of three *Phengaris* butterflies exposed to urbanization pressure. Across 20 years of study the number of habitat patches decreased by half, mainly outside N2000 sites. Total area of available habitat decreased by 13% for *P. teleius* and *P. nausithous* butterflies, and by 21% for *P. alcon*. Negative population trends were observed for all three species at small and medium-size habitat patches located outside N2000 sites as well as at small patches inside N2000 sites. The existing populations appear to be vulnerable outside N2000 sites. Our findings indicate that N2000 sites fulfill their protective function in halting population loss of species of high conservation interest and effective protection of intact habitats may support urban biodiversity. Nevertheless, there is an urgent need to expand the existing protected areas in order to save remnant local populations from their imminent extinctions in near future, as the species legal protection is not effective beyond N2000 sites. As meadow habitats serve a whole range of ecosystem services, their remnants deserve to be effectively protected in urbanized areas.

1. Introduction

In the face of the sixth global extinction and climate crisis (Ceballos et al., 2015), protection of natural and semi natural ecosystems is one of the most urgent needs in the world. Impoverishment of biodiversity at various special scales is observed, typically as a consequence of habitat specialists decline and generalists increase (Habel et al., 2016). The scientific community worldwide has been calling for immediate changes in the management of natural resources in numerous appeals (Ehrlich and Ehrlich, 2013; Ripple et al., 2019; Cardoso et al., 2020). Alongside global initiatives in this field (cf. Bastin et al., 2019), maintaining existing ecosystems is among the most important targets for humanity.

Protected areas are being established worldwide for biodiversity conservation. One of the most important systems of protected areas is Natura 2000 network created in the European Union for the effective protection of its habitats and species, and currently covering 18.5% of the EU land area (EEA, 2020). As negative trends in protected areas intensify recently all over the world, with the cases of their downgrading, downsizing, or degazettement (Kroner et al., 2019) as well as land use and climate changes (Vogel, 2017; Forister et al., 2021), it is unclear if existing forms of protected areas still fulfill their protective function. It has been revealed that protected areas may be insufficient to provide effective conservation of flying insects (Hallman et al., 2017) or to prevent biological invasions (Guerra et al., 2018). Effectiveness of Natura 2000 sites may depend on public perception of the network (Blicharska et al., 2016), human population size, and taxonomic group considered (Trochet and Schmeller, 2013). Despite the increasing interest in ecological studies conducted in Natura 2000 sites, little is known about the actual effectiveness of Natura 2000 sites on the status and population trends of focal species in habitats vulnerable to increasing urbanisation pressure.

More than half of the world human population lives in urban areas,

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Table 1
Linear regression results concerning the decline in the number of habitat patches (n) available for the three investigated butterfly species before (a) and after (b) the establishment of the Natura 2000 sites. The average absolute change per year b and the relative rate of decline are shown. All the declines reported are statistically significant at $P < 0.05$.

(a)			Before the establishment of the N2000 sites				
	in 2001	number (proportion) of lost patches	$b \pm$ SE	rate of decline	R^2	F	P
P. teleius and *P. nausithous*							
outside Natura 2000							
small (<1ha)	n = 38	11 (28.9)	−1.21 ± 0.156	−0.037	0.87	59.64	0.0001
medium (1–10 ha)	n = 14	1 (7.1)	−0.15 ± 0.031	−0.011	0.69	0.00	0.0017
big (>10 ha)	n = 1	0 (0)	–	–	–	–	–
all patches	n = 53	12 (22.6)	−1.35 ± 0.166	−0.029	0.88	0.00	<0.0001
inside Natura 2000							
small (<1ha)	n = 7	5 (71.4)	−0.46 ± 0.066	−0.104	0.84	0.00	0.0001
medium (1–10 ha)	n = 4	0 (0)	–	–	–	–	–
big (>10 ha)	n = 6	0 (0)	–	–	–	–	–
all patches	n = 17	5 (29.4)	−0.46 ± 0.066	−0.031	0.84	0.00	0.0001
entire metapopulation	n = 70	17 (24.3)	−1.81 ± 0.152	−0.029	0.94	0.00	<0.0001
P. alcon							
outside Natura 2000	n = 8	4 (50.0)	−0.57 ± 0.065	−0.092	0.89	75.85	<0.0001
inside Natura 2000	n = 10	2 (20.0)	−0.24 ± 0.048	−0.026	0.73	25.00	0.0011
entire metapopulation	n = 18	6 (33.3)	−0.81 ± 0.095	−0.052	0.89	72.70	<0.0001
(b)		**After the establishment of the N2000 sites**					
	in 2011	**number (proportion) of lost patches**	**$b \pm$ SE**	**rate of decline**	**R^2**	**F**	**P**
P. teleius and *P. nausithous*							
outside Natura 2000							
small (<1ha)	n = 26	14 (53.8)	−1.71 ± 0.162	−0.091	0.92	110.68	<0.0001
medium (1–10 ha)	n = 13	2 (15.4)	−0.28 ± 0.042	−0.023	0.82	43.18	0.0002
big (>10 ha)	n = 1	0 (0)	–	–	–	–	–
all patches	n = 40	16 (40.0)	−1.99 ± 0.181	−0.062	0.93	120.81	<0.0001
inside Natura 2000							
small (<1ha)	n = 2	2 (100)	−0.15 ± 0.058	−0.176	0.39	6.87	0.0306
medium (1–10 ha)	n = 4	0 (0)	–	–	–	–	–
big (>10 ha)	n = 6	0 (0)	–	–	–	–	–
all patches	n = 12	2 (16.7)	−0.15 ± 0.058	−0.013	0.39	6.87	0.0306
entire metapopulation	n = 52	18 (34.6)	−2.14 ± 0.169	−0.049	0.95	159.86	<0.0001
P. alcon							
outside Natura 2000	n = 4	1 (25.0)	−0.13 ± 0.034	−0.035	0.59	14.00	0.0057
inside Natura 2000	n = 8	2 (25.0)	−0.21 ± 0.037	−0.028	0.77	31.24	0.0005
entire metapopulation	n = 12	3 (25.0)	−0.33 ± 0.051	−0.030	0.82	42.31	0.0002

and this trend is expected to increase continuously (United Nations, 2019). Impervious surface areas in urban space reflect, absorb and trap heat generated by city, leading to permanent changes of abiotic conditions (McDonnell and Hahs, 2009), and hence urban agglomerations are commonly regarded as heat islands. This effect is enhanced by pollution and chaotic settlement, and it affects vegetation growth and species phenology at different spatial scales due to higher temperatures and longer growing season compared to non-urban areas (Melaas et al., 2016). In the long term perspective cities become important evolutionary force for species living in urban environments (Alberti et al., 2017; Johnson and Munshi-South, 2017).

Sustainable urban design includes and green infrastructure (i.e. green roofs, green walls) and reduced moving frequency at lawns (Fenoglio et al., 2021). Additionally, it is necessary to halt habitat loss and fragmentation in urban areas. Maintaining ecosystems should however comply with latitudinal and historical context to incorporate different needs of society and make conservation actions adequate for local conditions. It seems that one of the ecosystems that should be primarily protected in most urbanized regions are seminatural grasslands. Grasslands are one of the most common ecosystems covering up to 40% global terrestrial surface (Blair et al., 2014), but they are also strongly impacted human activities. Nowadays, especially temperate zone grasslands exist as seminatural ecosystem remnants and are threatened by further fragmentation and habitat loss, fertilization, inappropriate management (abandonment or agriculture intensification), climate change, biological invasions (Joyce, 2014). Consequently many grassland organisms are threatened as well (Cardoso et al., 2020), and this problem in particular concerns specialist species (Habel et al., 2016).

In fragmented landscape, habitat size is among crucial factors shaping species occurrence patterns, with higher probability of small patches to be unoccupied (Salz and Fartmann, 2009) due to demographic and environmental stochasticity. This effect may be further strengthen by certain species life history traits e.g. narrow niche and low mobility (Öckinger et al., 2010). However, even small and isolated patches may persist under specific demographic conditions (Nowicki et al., 2019) and/or act as stepping stones for isolated populations (Haddad, 1999). Hence, in warming climate a high amount of seminatural habitats and their aggregation may decrease the risk of extinction of less mobile species (Fourcade et al., 2021).

Unfortunately, with some exceptions (Vladev and Stoyanova, 2021) green areas in urban space, including grasslands, are under strong anthropogenic pressure. The negative effects of urbanization have been recognized for plants, invertebrates and vertebrates, and all depend on urbanization intensity and focal taxon (McKinney, 2008). However, long-term effects and species trends in urban ecosystems are generally understudied. In the case of invertebrates previous studies have focused mostly on urban forests, parks, gardens and yards or roadsides and were limited to short-term analyses of max. 3-year duration (McIntyre, 2000).

As long-term monitoring of all biodiversity components is impractical due to costs, labour requirements and time constraints, a reasonable alternative is the monitoring of indicator species, which rapidly

Table 2

Linear regression results concerning the decline in the area of habitat patches (*A*) available for the three investigated butterfly species before (a) and after (b) the establishment of the Natura 2000 sites. The average absolute change per year *b* and the relative rate of decline are shown. All the declines reported are statistically significant at $P < 0.05$.

(a)	Before the establishment of the N2000 sites					
	area [ha] (proportion) lost	b ± SE	rate of decline	R^2	F	P
P. teleius and *P. nausithous*						
outside Natura 2000						
small (<1ha)	1.47 (13.6)	−0.16 ± 0.017	−0.016	0.90	82.21	<0.0001
medium (1–10 ha)	2.10 (5.7)	−0.31 ± 0.066	−0.008	0.69	21.33	0.0017
big (>10 ha)	0.00 (0.0)	–	–	–	–	–
all patches	3.58 (5.3)	−0.46 ± 0.069	−0.007	0.83	45.84	0.0001
inside Natura 2000						
small (<1ha)	1.33 (58.0)	−0.13 ± 0.033	−0.068	0.60	14.27	0.0054
medium (1–10 ha)	0.00 (0.0)	–	–	–	–	–
big (>10 ha)	0.00 (0.0)	–	–	–	–	–
all patches	1.33 (0.9)	−0.13 ± 0.033	−0.001	0.60	14.27	0.0054
entire metapopulation	4.91 (2.3)	−0.59 ± 0.051	−0.003	0.94	135.50	<0.0001
P. alcon						
outside Natura 2000	0.32 (24.2)	−0.05 ± 0.008	−0.037	0.80	37.12	0.0003
inside Natura 2000	0.04 (0.6)	−0.01 ± 0.001	−0.001	0.74	27.26	0.0008
entire metapopulation	0.36 (4.5)	−0.05 ± 0.008	−0.007	0.84	47.85	0.0001
(b)	**After the establishment of the N2000 sites**					
	area [ha] (proportion) lost	**b ± SE**	**rate of decline**	**R^2**	**F**	**P**
P. teleius and *P. nausithous*						
outside Natura 2000						
small (<1ha)	5.05 (55.4)	−0.64 ± 0.052	−0.095	0.94	148.77	<0.0001
medium (1–10 ha)	14.01 (42.6)	−1.37 ± 0.226	−0.056	0.80	37.03	0.0003
big (>10 ha)	0.00 (0.0)	–	–	–	–	–
all patches	19.06 (30.7)	−2.01 ± 0.245	−0.039	0.88	67.63	<0.0001
inside Natura 2000						
small (<1ha)	0.97 (100)	−0.08 ± 0.028	−0.149	0.41	7.26	0.0273
medium (1–10 ha)	0.00 (0.0)	–	–	–	–	–
big (>10 ha)	0.00 (0.0)	–	–	–	–	–
all patches	0.97 (0.7)	−0.08 ± 0.028	−0.001	0.41	7.26	0.0273
entire metapopulation	20.03 (9.7)	−2.09 ± 0.224	−0.011	0.90	86.63	<0.0001
P. alcon						
outside Natura 2000	0.10 (9.9)	−0.01 ± 0.003	−0.012	0.59	14.00	0.0057
inside Natura 2000	1.23 (18.4)	−0.15 ± 0.026	−0.024	0.79	34.64	0.0004
entire metapopulation	1.32 (17.3)	−0.17 ± 0.026	−0.023	0.81	40.54	0.0002

react to environmental disturbances and signal upcoming changes in a wide spectrum of biodiversity (Thomas, 2005). Well-known indicator species as well as flagships for grassland biodiversity conservation are endangered Large blue butterflies of the genus *Phengaris*, protected by the EU law, and their occurrence testifies to the high natural values of the meadows they inhabit (Thomas and Settele, 2004). The aim of our study was to assess changes over a two-decade period in the populations of *Phengaris* butterflies and their grassland habitats within and outside Natura 2000 sites strongly exposed to urbanization pressure. Due to such a strong anthropogenic pressure we hypothesized that the rate of decline in habitat patch numbers, habitat area and local population sizes was similar regardless of their location before, but stronger outside Natura 2000 sites after their establishment. In addition, we tested if the detected negative trends are patch-size dependent. As small patches are *a priori* assumed to comprise less viable populations (Nowicki et al., 2019), they may be regarded less valuable and destroyed more frequently. Since the urbanization is connected with climatic changes, we also checked whether local climatic conditions (temperature and precipitation) additionally affect the focal butterfly population dynamics.

2. Methods

2.1. Study area

The study was conducted in a large meadow complex, located in the Vistula River Valley on the suburban part of the Kraków city (50°01′N, 19°54′E). Across the 20th century the city grew up from the area of 6.9 km^2, comprising the old town, with 85 300 inhabitants in 1900 to 327 km^2 with 781 000 inhabitants in 2020 (Wypych, 2010; Statistical Office in Kraków, 2021). This transformation and dynamic development made Kraków the second biggest city in Poland, experiencing strong anthropogenic pressure due to industrialisation, urbanisation, melioration and the reduction of green areas (Pieńkowski et al., 2019), including precious seminatural meadows (Denisiuk, 1987; Dubiel, 1996). Together with the city location in a big river valley, this pressure results in increasing effects of urban heat island, with growing air temperatures without changes in sunshine duration (Matuszko and Piotrowicz, 2018) and decreasing air humidity (Wypych, 2010).

In particular, the investigated meadow complex was incorporated into Kraków in the years from 1946 to 1970 (Wypych, 2010), and is located in south-western part of the city. It covers ca. 800 ha of a mosaic landscape encompassing grasslands, forests, fields and moderately densely built-up settlements (Kajzer-Bonk et al., 2016a). The grassland habitats include among others humid and mesophilic meadows of the *Molinio-Arrhenatheretea* class with *Sanquisorba offcinallis* and *Gentiana pneumonathe*, which represent the only foodplants of the focal butterflies: the Scarce large blue *Phengaris teleius*, the Dusky large blue *P. nausithous* as well as the Alcon large blue *P. alcon*, respectively (Thomas et al., 1998). The aforementioned meadow habitats are regarded as highly valuable for nature conservation and have been largely included to the Natura 2000 network as two Special Areas of Conservation: “Dębnicko-Tyniecki Meadow Area” and “Skawina Meadow Area” since 2011. These two N2000 sites were designated primarily for the preservation of *Phengaris* butterflies as parts of one of

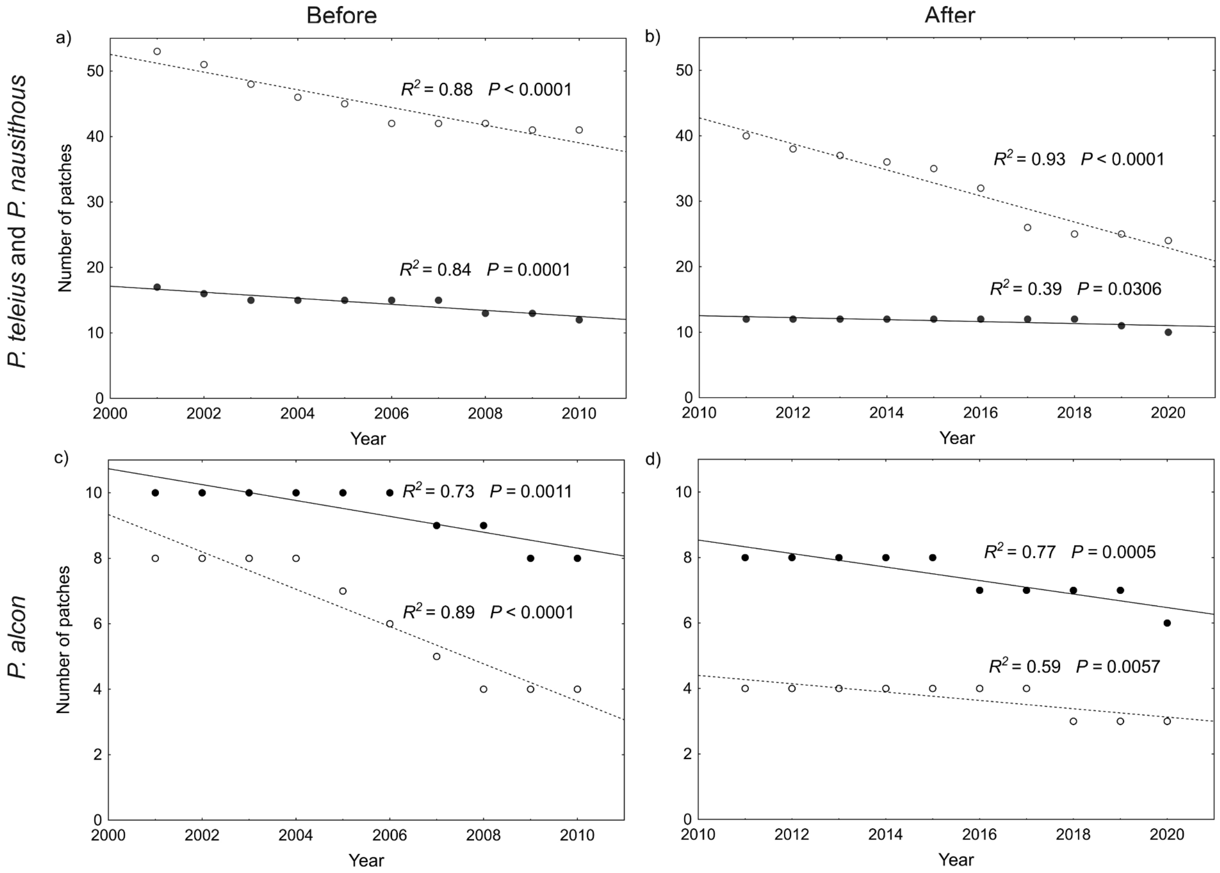

Fig. 1. Year-to-year loss in the numbers of habitat patches of *P. teleius* and *P. nausithous* (a, b), and *P. alcon* (c, d) inside (black dots, solid lines) and outside (empty dots, broken lines) Natura 2000. Regression lines with fractions of explained variation (adjusted R^2) and significance (P) are depicted. Left and right panels show trends before and after the establishment of the N2000 sites respectively.

the best-described metapopulation systems of the focal species in the world (Nowicki et al., 2007; Nowicki, 2017).

Study was carried out in 2001–2020. In the first year the distribution of both foodplants, which define the spatial limits of the investigated butterfly species (Nowicki et al., 2007; 2014), were mapped in detail using GPS with ca. 1-m accuracy (Nowicki et al., 2007). Habitats separated by a minimum of 50 m or clear barriers (such as roads, trees, fields, or reeds, which significantly decrease butterfly movement probability, Skórka et al., 2013) were assumed as discrete patches. The investigated patch system meets the conditions of a classic metapopulation (Kajzer-Bonk et al., 2016a), with limited dispersal of individuals between habitat patches (Nowicki et al. 2014).

Since 2003 the abundances of the three *Phengaris* species have been estimated every year within all existing patches. Abundances of *P. teleius* and *P. nausithous* butterflies were surveyed using catch-per-time unit method in the peak period of the flight season, while *P. alcon* abundance was evaluated with egg counts on foodplants (for details see Nowicki, 2017). These standard methods were used and presented in numerous previous works (Nowicki et al. 2005; 2007; Kajzer-Bonk et al., 2013, 2016a). The local population sizes typically reach several hundred to several thousand adults in *P. teleius* and *P. nausithous* respectively, but are much smaller in *P. alcon*, rarely exceeding a hundred adults (Nowicki, 2017).

The meteorological data (average monthly temperatures and total precipitation per month) were acquired from the Research Meteorological Station of the Department of Climatology of the Jagiellonian University in Kraków. To test the effects of temperature and precipitation on year-to-year butterfly population dynamics, their average and total values respectively were calculated for each year (starting from September in previous year to cover the life cycle of a butterfly generation) as well as for each season (autumn: Sep-Nov, winter: Dec-Feb, spring: Mar-May, summer: Jun-Aug).

2.2. *Analyses of number and area of habitat patches*

The overall number of existing habitat patches and their total area within the entire study system were calculated separately for each year. The linear regression analysis was conducted for the number of patches and their area before and after the establishment of the N2000 sites as a function of time (=year; with 2001 and 2011 as year 0, respectively), expressed as (*i*) absolute values (=number of patches, n; area, A) and (*ii*) logarithmic values ($\log_{10}(n)$; $\log_{10}(A)$). This approach allowed to estimate both the absolute rate of change in patches, with b coefficient of regression *i* expressing the average decrease in the number of patches and area per year, as well as their relative rate of change, with the percentage decrease in number of patches and area per year calculated as 100% * $(1–10^b)$ for regression *ii*.

In addition, the linear regressions were performed for the numbers of lost patches and the lost area before and after the establishment of the Natura 2000 sites as a function of time (=year; with 2001 and 2011 as year 0, respectively) separately for six groups of *P. teleius* and *P. nausithous* habitat patches defined according to their location (outside/inside N2000 sites) and size (small: <1 ha, medium: 1–10 ha, big: >10 ha). The habitat patches of *P. alcon* were categorized only according to their location as their range of area is significantly smaller (0.01–3 ha) comparing to the two other species (0.02–33 ha). Then the average loss per year for all the defined patch categories was calculated. Finally, the habitat loss (L) was also determined separately for each partly or entirely lost patch, as the actual area in the given year ($A_i = 0$ if the patch ceased to exist or > 0 if it partially survived) minus the area in

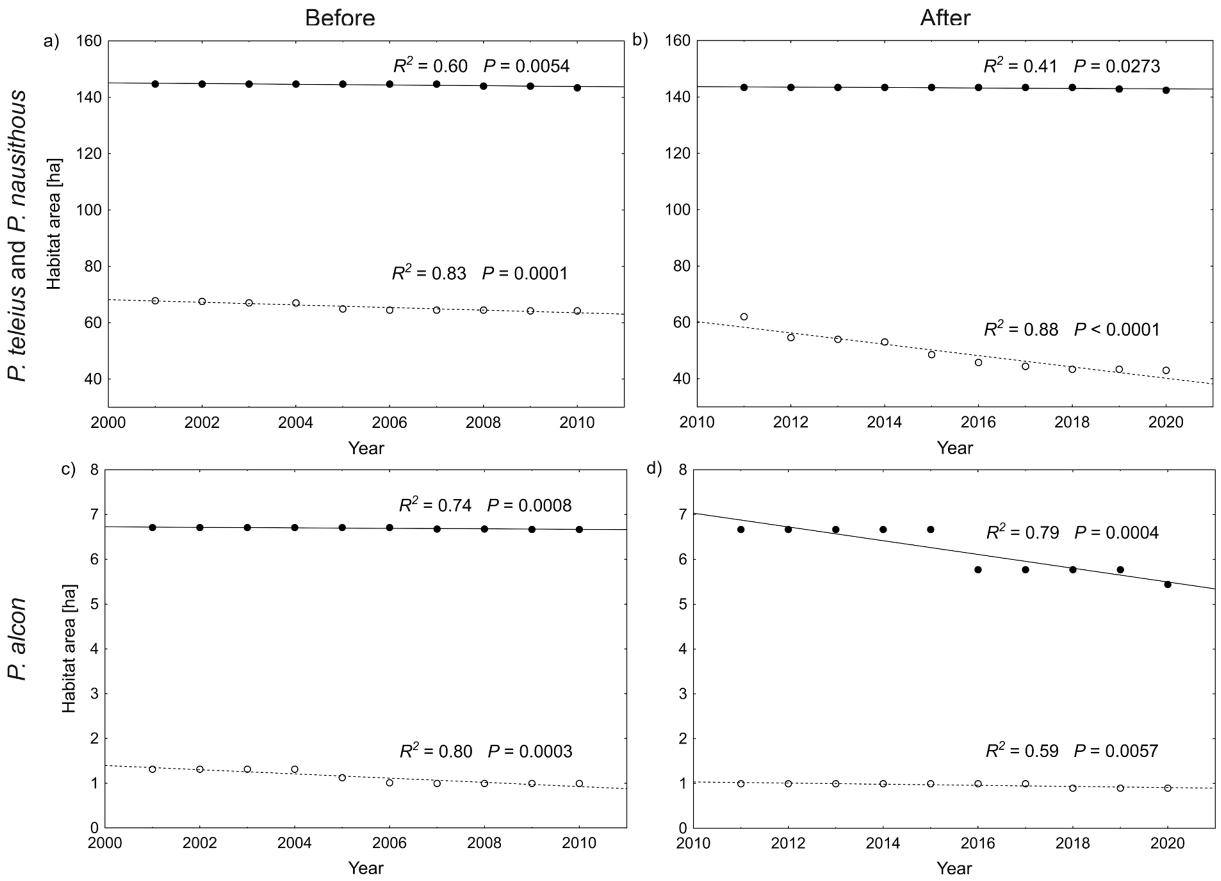

Fig. 2. Year-to-year loss in the area of habitat patches of *P. teleius* and *P. nausithous* (a, b), and *P. alcon* (c, d) inside (black dots, solid lines) and outside (empty dots, broken lines) Natura 2000. Regression lines with fractions of explained variation (adjusted R^2) and significance (P) are depicted. Left and right panels show trends before and after the establishment of the N2000 sites respectively.

previous year (A_{i-1}; $L = A_i – A_{i-1}$). Subsequently, the effect of location (outside/inside N2000 sites) on individual patch habitat loss before and after the establishment of the N2000 sites was tested with Mann-Whitney *U* test.

2.3. Analyses of butterfly abundance patterns

Analyses of butterfly abundances were performed for all three species separately. The total abundances for consecutive years within the entire metapopulations as well as within the defined categories of populations were calculated. As in the case of patch change analysis, local populations were categorized according to their location (outside vs. inside Natura 2000 site) and patch size (small/medium/big) in the case of *P. teleius* and *P. nausithous*, but only according to their location in the case of *P. alcon*. Subsequently, the linear regression analysis was conducted for the entire metapopulation size and the butterfly abundances within the defined population categories before and after the establishment of the Natura 2000 sites as a function of time (=year; with 2003 and 2011 as year 0, respectively), using the logarithmic numbers of individuals ($\log_{10}(N)$) as dependent variables.

In the next step, the estimated ‘loss’ in the number of butterflies was determined for each patch lost, either partially or entirely. The butterfly loss was determined separately for each species as the actual abundance in a given year (0 if the patch ceased to exist or > 0 if it partially survived) minus the potential abundance in this year. The latter was estimated from the predictive regression models based on the population sizes in previous years. Hence, the calculations were possible only for the local populations with population size estimates available for at least three previous years. The effect of location within or outside N2000 sites on butterfly loss before and after the establishment of the N2000 sites was tested with Mann-Whitney *U* test.

In order to verify the hypothesis that N2000 sites mitigate butterfly population declines, the linear regression analyses for the population sizes before and after the establishment of the N2000 sites as a function of time (=year; 2003 and 2011 as year 0, respectively) were performed for all the local populations. The obtained results were tested for the frequency of increasing ($b > 0$) and decreasing ($b < 0$) populations within and outside the current Natura 2000 sites using Fisher test.

Finally, the linear regression analyses were also performed for the climatic variable effects on log-transformed year-to-year change in the total metapopulation size ($\log_{10}[N_i/N_{i-1}]$) of the three investigated species, with average annual and seasonal temperature and precipitation tested as alternative predictors.

All the statistical procedures were conducted in Statistica 13.3 software (TIBCO Software Inc., 2017).

3. Results

3.1. Habitat availability

Strikingly, across the 20 years of study the number of habitat patches decreased twofold, from 70 to 33 patches in *P. teleius* and *P. nausithous*, and from 18 to 9 patches in *P. alcon* (Table 1).

Correspondingly, their total area declined by 27.12 ha (13 %) from 212.5 ha, and by 1.68 ha (21 %) from 8.02 ha, respectively (Table 2).

This implies that the habitat loss primarily derived from the vanishing of small- and medium-size patches (Tables 1 & 2). Before the establishment of the Natura 2000 sites, the negative trends in patch numbers and their area were similar regardless of the location (inside/outside the current N2000 sites), whereas afterwards the negative trends

Table 3
Linear regression results concerning the decline in abundances of the three investigated butterfly species before and after the establishment of the Natura 2000 sites. The average change per year b and the relative rate of decline are shown. Statistically significant declines (at $P < 0.05$) are bolded.

	Before the establishment of the N2000 sites					After the establishment of the N2000 sites				
	$b \pm$ SE	rate of decline	R^2	F	P	$b \pm$ SE	rate of decline	R^2	F	P
P. teleius										
outside Natura 2000										
small (<1ha)	−0.06 ± 0.022	−0.122	0.45	6.67	**0.0416**	−0.03 ± 0.013	−0.064	0.31	5.10	**0.0539**
medium (1–10 ha)	−0.01 ± 0.017	−0.029	0.00	0.54	0.4917	−0.04 ± 0.016	−0.081	0.33	5.53	**0.0465**
big (>10 ha)	−0.04 ± 0.026	−0.078	0.11	1.83	0.2250	−0.03 ± 0.031	−0.063	0.00	0.83	0.3889
all patches	−0.03 ± 0.017	−0.068	0.25	3.37	0.1162	−0.03 ± 0.016	−0.073	0.27	4.35	0.0705
inside Natura 2000										
small (<1ha)	−0.09 ± 0.022	−0.183	0.68	15.67	**0.0075**	−0.27 ± 0.078	−0.464	0.55	12.12	**0.0083**
medium (1–10 ha)	−0.03 ± 0.024	−0.075	0.12	2.00	0.2072	0.02 ± 0.017	0.058	0.11	2.10	0.1852
big (>10 ha)	−0.03 ± 0.015	−0.072	0.33	4.47	0.0790	−0.02 ± 0.012	−0.051	0.21	3.37	0.1035
all patches	−0.04 ± 0.014	−0.081	0.48	7.34	**0.0352**	−0.01 ± 0.009	−0.012	0.00	0.38	0.5540
entire metapopulation	−0.03 ± 0.011	−0.074	0.52	8.70	**0.0257**	−0.01 ± 0.009	−0.032	0.15	2.54	0.1498
P. nausithous										
outside Natura 2000										
small (<1ha)	−0.06 ± 0.023	−0.132	0.46	6.91	**0.0392**	−0.02 ± 0.017	−0.050	0.08	1.77	0.2197
medium (1–10 ha)	−0.02 ± 0.016	−0.042	0.04	1.29	0.2999	−0.02 ± 0.007	−0.052	0.54	11.51	**0.0095**
big (>10 ha)	0.17 ± 0.038	0.471	0.73	19.72	**0.0044**	−0.04 ± 0.024	−0.088	0.16	2.76	0.1351
all patches	−0.02 ± 0.018	−0.043	0.01	1.10	0.3337	−0.03 ± 0.009	−0.057	0.47	9.08	**0.0167**
inside Natura 2000										
small (<1ha)	−0.05 ± 0.039	−0.118	0.12	1.92	0.2148	−0.33 ± 0.077	−0.529	0.65	17.96	**0.0028**
medium (1–10 ha)	−0.02 ± 0.034	−0.047	0.00	0.39	0.5576	0.03 ± 0.034	0.076	0.00	0.90	0.3715
big (>10 ha)	0.01 ± 0.028	0.016	0.00	0.06	0.8102	−0.03 ± 0.015	−0.072	0.28	4.47	0.0674
all patches	0.00 ± 0.028	−0.002	0.00	0.00	0.9812	−0.02 ± 0.018	−0.042	0.01	1.08	0.3292
entire metapopulation	−0.01 ± 0.020	−0.018	0.00	0.14	0.7186	−0.02 ± 0.012	−0.048	0.21	3.36	0.1043
P. alcon										
outside Natura 2000	0.00 ± 0.047	−0.011	0.00	0.01	0.9203	−0.13 ± 0.027	−0.257	0.70	22.23	**0.0015**
inside Natura 2000	0.02 ± 0.026	0.038	0.00	0.39	0.5540	−002 ± 0.014	−0.049	0.14	2.47	0.1550
entire metapopulation	−0.02 ± 0.025	0.037	0.00	0.39	0.5555	−0.02 ± 0.013	−0.053	0.19	3.07	0.1178

prevailed outside N2000, except for *P. alcon* in which the habitat loss also continued within N2000 (Tables 1 & 2; Figs. 1 & 2).

The average yearly loss per patch was significantly higher outside N2000 in the case of *P. teleius* and *P. nausithous* habitats after the establishment of the N2000 sites (Mann-Whitney test: $U_{\text{after}} = 15.5$, $P = 0.0305$), while no difference was found between the same groups of patches before 2011 (Mann-Whitney test: $U_{\text{before}} = 31.5$, $P = 0.4529$; Fig. A.1). There was no difference in average habitat loss in the case of *P. alcon*, regardless of the establishment of the N2000 sites (Mann-Whitney tests: $U_{\text{before}} = 30.5$, $P = 0.4015$; $U_{\text{after}} = 35.0$, $P = 0.6588$).

3.2. Population dynamics

Over of the period of 2003–2020 the numbers of the investigated butterflies declined in all three species (Fig. A.2). Abundances dropped on average by 1% (in *P. teleius*) to 3% (in both *P. nausithous* and *P. alcon*) per year and this negative trend was statistically significant for the two latter species (Fig. A.2).

Before the establishment of the N2000 sites the negative trends were observed for the entire metapopulation of *P. teleius*, and also within patches located inside the current N2000 sites (Table 3, Fig. 3a).

More specifically, the decreasing abundances were revealed in small patches regardless of their location (Table 3). In turn, the populations of *P. nausithous* located outside the current N2000 sites experienced negative trends in small patches, whereas in big patches an opposite trend was found (Table 3). The populations of *P. alcon* did not show any significant trends before the establishment of the N2000 sites.

After the establishment of the N2000 sites the entire metapopulation of *P. teleius* no longer experienced a negative trend (Table 3). For all the three studied species local population declines were detected outside Natura 2000 sites, with marginally non-significant effect in the case of *P. teleius* (Table 3; Fig. 3b, d, f). Additionally, the negative trends outside N2000 sites were visible in small and medium-size patches (Table 3). Inside N2000 local populations were generally stable for all the three species, but with negative trends in small patches (Table 3).

The estimated butterfly loss turned out significantly higher outside the N2000 sites after their establishment only for *P. teleius* (Mann-Whitney test: $U_{\text{after}} = 2.0$, $P < 0.0005$), but not in the other investigated cases (Fig. 4; Fig. A.3).

In still persisting populations, the frequencies of decreasing and increasing ones did not differ inside and outside the current N2000 sites both before their establishment (Fisher test: $P_{teleius} = 0.6492$; $P_{nausithous} = 0.1536$; $P_{alcon} = 0.5952$) and afterwards (Fisher test: $P_{teleius} = 0.3431$; $P_{nausithous} = 0.4192$; $P_{alcon} = 0.4167$) (Table A.1).

The year-to-year changes in the metapopulation size of *P. nausithous* were negatively affected by the mean temperature in autumn (Fig. 5a, Table A.2). Additionally, the metapopulation dynamics of *P. alcon* was negatively dependent on total precipitation in summer (Fig. 5b, Table A.2). No significant effects of weather parameters were detected for *M. teleius*.

4. Discussion

Our study revealed negative trends in both the number of habitat patches and their area available for the three studied butterfly species. Habitats of *P. teleius* and *P. nausithous* shrinked substantially outside the Natura 2000 sites, which encompass relatively few but mostly the largest patches (Table 1). Nevertheless, the protective regime did not prevent the disappearance of small patches: none of them exist anymore within the protected sites (Table 1). Thus our findings indicate that Natura 2000 protection form allows to effectively preserve medium- and big-sized habitat patches, but not the small ones. In the case of *P. alcon*, all its habitat patches are small and gradually disappearing regardless of their location either within or outside the N2000 sites.

Butterfly population declines recorded in our study are concordant with the recent research by Forister et al. (2021), who surveyed 72 sites

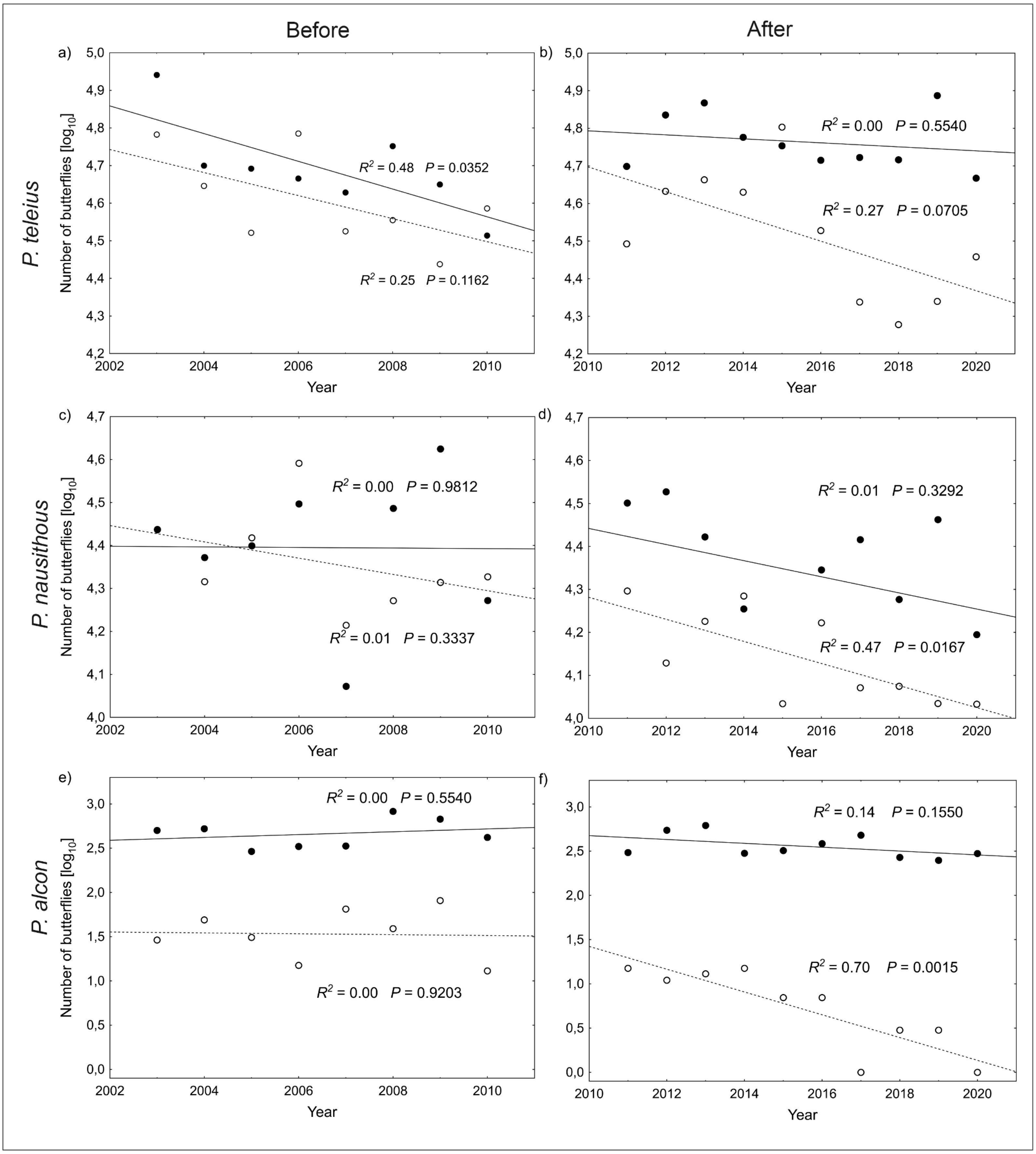

Fig. 3. Year-to-year changes in abundances of the three investigated butterfly species: *P. teleius* (a, b), *P. nausithous* and (c, d) *P. alcon* (e, f) inside (black dots, solid lines) and outside (empty dots, broken lines) Natura 2000. Regression lines with fractions of explained variation (adjusted R^2) and significance (*P*) are depicted. Left and right panels show trends before and after the establishment of the N2000 sites respectively.

in the USA for over two decades, and revealed the mean decline of 1.6 % per year in 50 butterfly species considered. More importantly, our study revealed that the status of protected species alone (i.e. without area protection) is not sufficient to prevent species declines, as the abundances of the focal butterflies decreased significantly outside protected Natura 2000 sites. On the other hand, it appears that local populations within the Natura 2000 network are more stable and spared from the prevailing negative population trends.

Our results are partly consistent with those of Rada et al. (2019) who found that butterfly species richness was significantly higher inside N2000 sites and decreased with increasing distance from them. On the other hand, across 11 years of their study these authors revealed the decline in butterfly species richness by 10% regardless of sampling location. The fact that in our study the declines prevailed outside N2000 sites, while no significant negative trends were detected within them, which possibly reflects generally better grassland biodiversity status in our study region where relatively slow socio-economic transformation in Poland so far might have postponed negative impacts on the most precious semi-natural areas. More importantly, it should be stressed that we considered the N2000 sites specifically created to protect *Phengaris* butterflies, whereas in the study by Rada et al. (2019) butterflies were used as an example for a non-target species group. Hence, the habitats

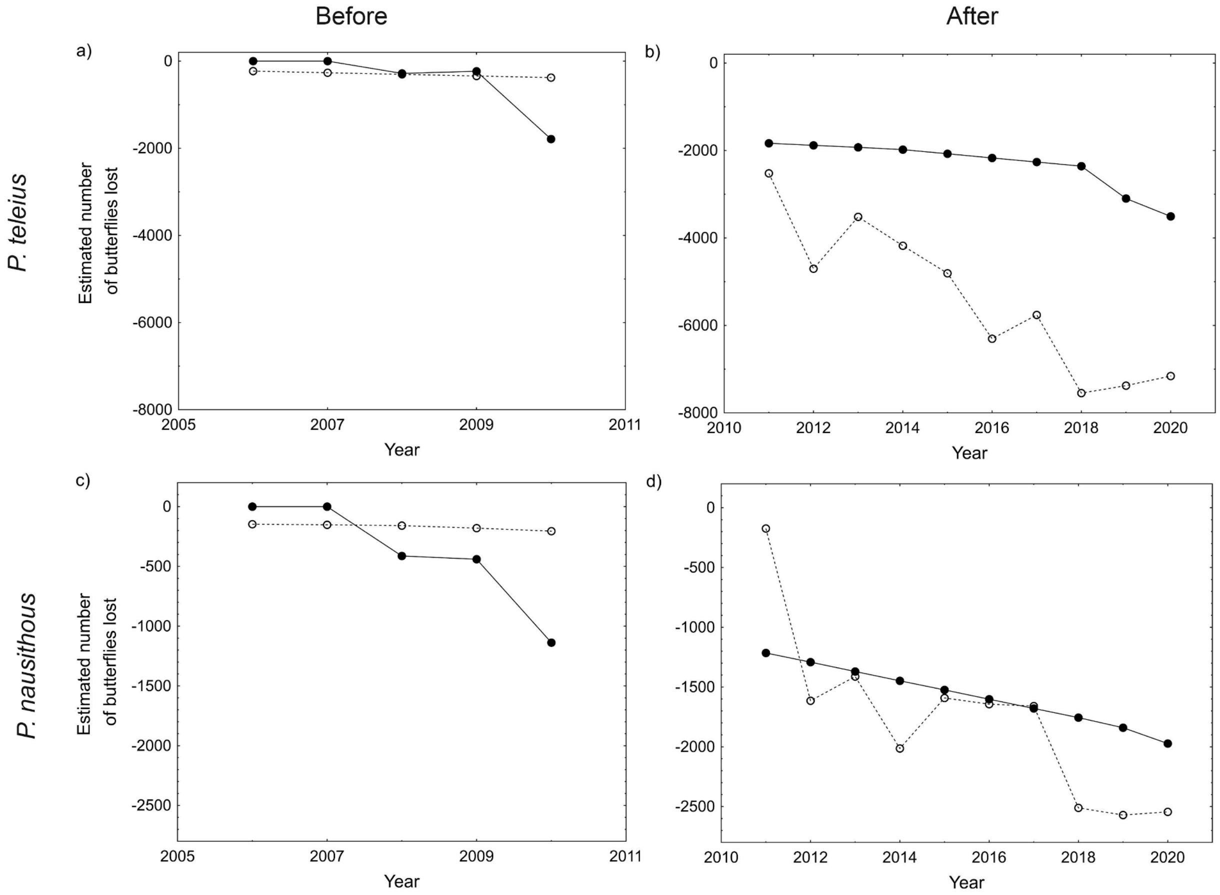

Fig. 4. Estimated butterfly loss per year in the investigated species: *P. teleius* (a, b) and *P. nausithous* (c, d) in habitat patches that vanished inside (black symbols, solid lines) and outside (empty symbols, broken lines) Natura 2000.

and especially management regime of the N2000 sites in the latter study did not necessarily correspond with the requirements of the investigated group.

Undoubtedly, the typically bigger size of the habitat patches within the N2000 sites is an important factor in this respect, but even tiny populations of *P. alcon* occupying very small patches turned more stable inside than outside N2000. After N2000 establishment we found continuation of negative trends in small and medium-sized habitat patches outside N2000 sites. According to metapopulation theory smaller and more isolated patches are more likely to experience local population extinctions and remain vacant, and this was also confirmed empirically for *Phengaris* metapopulations (Nowicki et al., 2007). Moreover, specifically for *Phengaris* butterflies the edge fragments of their patches are the most important, and they are affected by the patch surroundings (Nowicki et al. 2013). Hence, the negative trends outside N2000 sites may be explained by lower share of favourable (semi)natural areas in the matrix, and these trends are more eminent in smaller patches, which are less resistant to the impacts of patch surroundings. In N2000 sites even small patches are surrounded by green areas, which act as buffers preventing anthropogenic pressure (e.g. draining connected with built-up areas) as well as enhance quality and connectivity of habitat patches. The above rationale is consistent with our previous study which revealed that patch surroundings rather than habitat area primarily explained abundance patterns of *Phengaris* butterflies (Kajzer-Bonk et al., 2016a).

Although the value of small populations for species conservation is sometimes questioned (cf. Nowicki et al. 2019), they can support maintaining genetic variability at a metapopulation scale and serve as stepping stones for other subpopulations (Haddad 1999). The persistence of small populations may be assured due to short flight period with synchronous emergence of both sexes, long life expectancy and undisturbed movements of individuals within patch, which increase random mating chances (Nowicki et al., 2019). Nevertheless, in long-term perspective larger and thus less fluctuating populations are bound to be more viable (Nowicki, 2017). In the present study, we recorded that at large and medium-sized patches located inside the N2000 sites *P. teleius* and *P. nausithous* displayed generally stable population trends after the N2000 establishment. One of the possible explanations for such a pattern may be the enhanced habitat quality due to improved management, namely occasional moving of some previously abandoned meadows (authors' unpubl. data).

Our results reveal difficulties in the effective functioning of the N2000 network in urban areas. In particular, there were no differences in the estimated loss of butterflies inside and outside the N2000 sites despite much lower loss of habitats inside the N2000 sites. Indirectly it also indicates higher quality of lost habitats within the N2000 sites. Moreover, establishing the N2000 sites did not spare small habitat patches from vanishing (Table 3). Similarly, Concepción (2021) found that while the N2000 network generally prevents urban sprawl, its protection is not perfect as the N2000 sites still remain under relatively high pressure from urbanized areas and may require specific management tools.

The metapopulation of *P. nausithous* and *P. alcon* turned out more sensitive to weather variability and are thus probably better indicators of changes than *P. teleius*. In turn, the metapopulation of the latter species appears the most stable and resilient to weather patterns. The potential reason for the discrepancy in sensitivity to weather between *P. nausithous* and *P. alcon* vs. *P. teleius* is the difference in their host ant specificity. Within the investigated region *P. nausithous* and *P. alcon* are highly specific in their host use (to *M. rubra* and M. *scabrinodis*,

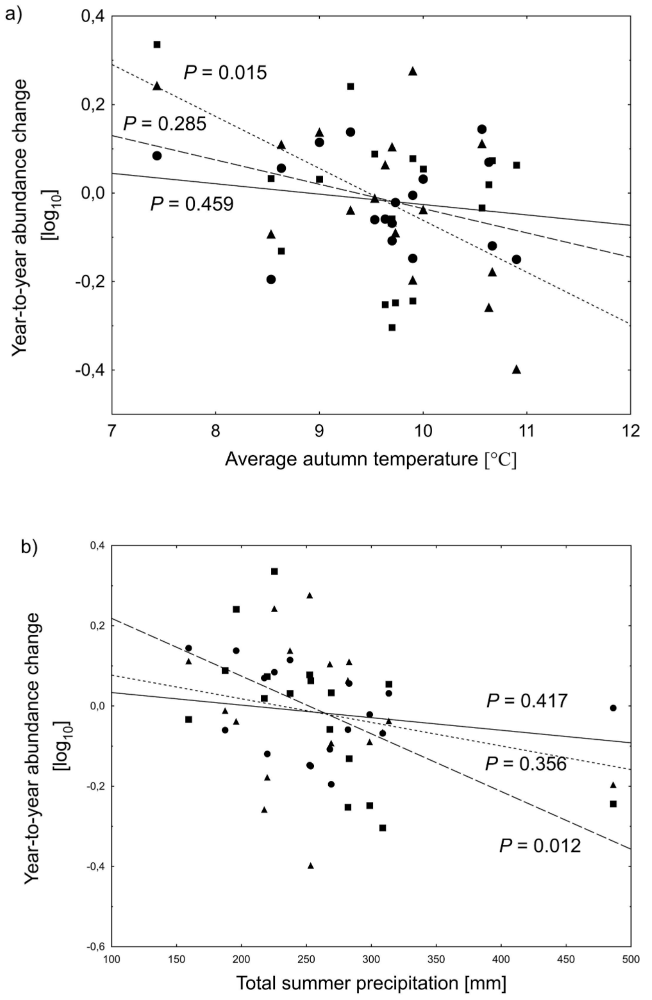

Fig. 5. Relation between average autumn temperature (a) or total summer precipitation (b) and the year-to-year changes in abundance of the three investigated butterfly species: *P. teleius* (dots, solid lines), *P. nausithous* (triangles, dotted lines) and *P. alcon* (squares, broken lines). Linear regression lines with significance (*P*) are depicted.

respectively), whereas *P. teleius* is much more flexible, using several hosts such as *M. scabrinodis*, *M. rubra*, *M. ruginodis*, and *M. rugulosa* (Witek et al., 2008). It is known that *Myrmica* ants are sensitive to environmental changes, which lead to their declines and changes in ant community composition (Kajzer-Bonk et al., 2016b). More specifically, temperature variation may disturb conditions for *Myrmica* brood development (Kipyatkov and Lopatina, 2002), affect forager abundance, or increase competition with other ant species (Diamond et al., 2017).

As large cover of green areas within urbanized landscapes may reduce the negative effects of urban heat islands (Bounoua et al., 2015), the protection of semi-natural meadows within cities may have a double positive impact, both stabilizing local climate as well as supporting the conservation of not only the endangered butterflies, but also of the entire spectrum of meadow biodiversity. However, in urbanistic plans grasslands are often regarded as neglectable component of the landscape (unlike e.g. woodlands), and sacrificed without any prior biodiversity assessment. Apart from being built-up, they are often drained, afforested and managed improperly, either through intensification of agricultural use or complete abandonment; Kajzer-Bonk, 2017).

As heat generation depends primarily on the intensity of development, amount of green areas and urban cover (Clinton and Gong, 2013), the proper spatial planning which promotes compact urban growth and protection of undamaged vegetation fragments is a reasonable solution for mitigating the urban heat impacts. It has been found that the threshold of 65% cover of green areas may neutralize the heating effect of buildings and stabilize temperature at 1.3 °C higher than in urban outskirts (Bounoua et al., 2015). Such an approach has also other crucial benefits due to curbing a range of harmful urbanization effects: habitat loss and fragmentation (Dobbs et al., 2017), spread of invasive species (Sushinsky et al., 2013), decreasing species diversity (Sol et al., 2017) and abundances (Aronson et al., 2014). In addition, green urban areas provide numerous ecosystem services including water storage, air filtration, mitigation of natural disasters (e.g. droughts or floods), soil-forming processes, and pollination (Bolund and Hunhammar, 1999). Maintaining (semi) natural areas in cities is thus crucial for human well-being, improving mental health, cognitive functions, pregnancy outcomes as well as decreasing probability of cardiovascular diseases, type II diabetes and mortality (WHO, 2016). Green areas may also play a vital educational role in raising public awareness on the importance of urban biodiversity for human health and life quality, and the perception of biodiversity as a value in itself. However, not every component of biodiversity is equally popular or considered meaningful. Regardless of the declared general enthusiasm for high species diversity, citizens are often are afraid of wilderness in their direct neighborhood (Skår, 2010) and commonly against insects (Schwarz et al., 2014). This is one of the possible reasons of the ineffective protection of butterflies and insects in general, including non-charismatic species. Moreover, the existing legal tools consider the destruction of protected species populations or their habitats to be of little social harm and enforce low (if any) penalties (GDEP, 2017).

5. Conservation recommendations

Our research carries an important message that the protected areas support halting the decline of precious habitats and their inhabitants. In turn, the species protection alone seems insufficient as revealed by the present study. Hence, whenever possible it is worth to revise the borders of the existing Natura 2000 sites and expand them to cover entire metapopulations of species of conservation concern. Alternatively, in the case it is impossible, other forms of area protection could be established, e.g. small-size grassland reserves for butterflies and other meadow species. Our study also revealed that once habitat loss within protected sites occurs, it is accompanied with a greater loss in their precious species (in our case expressed in the estimated decrease in the focal butterfly numbers), which most likely implies more than average quality, and thus also importance, of such habitat fragments. For effective conservation, the drivers of habitat loss within and outside Natura 2000 sites should first be defined to prevent further negative developments. Subsequently, the efforts should be focused on habitat restoration and protecting as many of the remaining habitat fragments as possible. In the urban setting, apart from sustaining local biodiversity such actions can provide additional benefits in form of reducing the negative effects of the urban heat islands.

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CRediT authorship contribution statement

Joanna Kajzer-Bonk: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Piotr Nowicki:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108518.

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