

FIRE AND FLOOD OCCURRENCE IN THE HABITATS OF THE ENDANGERED BUTTERFLY *COENONYMPHA* *OEDIPPUS* IN SLOVENIA

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Habitat of *Coenonympha oedippus* in 2020, ten months after the fire in Cerje.

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Fire and flood occurrence in the habitats of the endangered butterfly *Coenonympha oedippus* in Slovenia

ABSTRACT: In Slovenia the False ringlet *Coenonympha oedippus* uniquely occurs both on wet (Ljubljana Marsh and surroundings) and dry grasslands (Slovenian Istria, Karst, Gorica Hills). Natural hazards that threaten its habitats include fires and floods; the frequency of their occurrence in the former and existing habitats of *C. oedippus* was determined using the χ^2 -test. We showed that habitats on wet grasslands are less threatened by fire than those on dry grasslands. Among the latter, habitats in the Karst and Slovenian Istria are the most threatened. Habitats of *C. oedippus* are threatened by flooding only in Slovenian Istria and Ljubljana Marsh. Considering the extent of fire and flood risk and fragmentation of *C. oedippus* habitats in Slovenia, we assume that such natural hazards may lead to local extinction of the species.

KEY WORDS: natural hazards, fires, floods, threats, butterfly, False ringlet, *Coenonympha oedippus*, western and central Slovenia

Prisotnost požarov in poplav v življenjskih okoljih ogrožene vrste metulja barjanski okarček (*Coenonympha oedippus*) v Sloveniji

POVZETEK: Barjanski okarček se v Sloveniji edinstveno pojavlja tako na vlažnih (Ljubljansko barje z okolico) kot na suhih travniških (slovenska Istra, Kras, Goriška brda). Med naravnimi nesrečami, ki ogrožajo njegove habitatne krpe, so požari in poplave. Njihovo pogostost pojavljanja v nekdanjih in obstoječih bivališčih barjanskega okarčka smo ugotavljali s χ^2 -testom. Pokazali smo, da so življenjska okolja na vlažnih travniških požarno manj ogrožena kot na suhih travniških. Med slednjimi so najbolj ogrožene habitatne krpe na Krasu in v slovenski Istri. Habitatne krpe barjanskega okarčka so poplavno ogrožene le v slovenski Istri in na Ljubljanskem barju. Glede na stopnjo požarne in poplavne ogroženosti ter razdrobljenosti življenjskih okolij barjanskega okarčka v Sloveniji domnevamo, da lahko tovrstne naravne nesreče povzročijo lokalno izumrtje vrste.

KLJUČNE BESEDE: naravne nesreče, požari, poplave, ogroženost, barjanski okarček, *Coenonympha oedippus*, zahodna in osrednja Slovenija

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1 Introduction

Human activities have an exceptional impact on the distribution of species and their populations. Many butterfly species now live in increasingly degraded environments due to habitat loss and fragmentation (Čelik 2003; Hanski and Gaggiotti 2004; Rakar 2016; Crawford and Keyghobadi 2018; Nowicki et al. 2018; Jeliakov et al. 2019). Habitat fragmentation and isolation reduce connectivity of habitat patches and have a negative effect on species establishment and on the species' genetic pool (Nowicki et al. 2018). The term natural hazard, which includes floods, droughts, fires, landslides, torrential deposition, subsidence, hail, frost, and earthquakes, is used primarily to describe and assess impacts on society (Komac, Zorn and Pavšek 2010), and less often on nature. The synergy of human interventions that degrade or even destroy species' habitats and natural hazards can greatly increase the probability of extinction of small local populations of a species (Hanski 1997).

The False ringlet, *Coenonympha oedippus* (Fabricius 1787) (Nymphalidae: Satyrinae, Figure 1), is one of the 15 most threatened butterfly species in Europe (van Swaay et al. 2010). The species inhabits two different types of habitats: wet grasslands (in most of its range in Europe) and dry grasslands up to later successional stages at the southern limit of its European distribution (Slovenia, Italy, and Croatia; Habeler 1972; Čelik and Rebeušek 1996; Šašič 2010; Čelik 2015b). Populations of the two ecotypes of *C. oedippus* in Slovenia differ morphologically and genetically (Jugovic et al. 2018; Zupan et al. 2021). The remaining populations on wet meadows are found only in central Slovenia in the Ljubljana Marsh (*Ljubljansko barje*). Populations on dry habitats live in Slovenian Istria, in the Karst (*Kras*), in Gorica Hills (*Goriška brda*), and in the southern outskirts of Banjšice and Trnovo Forest plateau (*Trnovski gozd*). Despite the high regional diversity of Slovenia (Perko and Ciglič 2020) and the disjunct geographic distribution of *C. oedippus*, the species is most threatened due to agricultural intensification on the one hand and abandonment of land use on the other (Zupan et al. 2020). The distribution and presence of *C. oedippus* in habitat patches is determined, among other things, by the height of grass litter and the density of the herbaceous vegetation, the adequate representation of host and nectar plants, and the management of grasslands (Čelik 2015a; Čelik et al. 2015; Čelik, Šilc and Vreš 2018; Čelik 2020; 2021; Čelik et al. 2021). Natural hazards have always been part of natural variability (Komac, Zorn and Pavšek 2010). Occasional natural disturbances typical of the species' distribution area do not affect the survival of stable populations. Natural hazards particularly threaten rare species with small populations inhabiting fragmented habitats and specialized species with low dispersal ability (Keyghobadi 2007; Devictor and Julliard 2008). Because of its short generation time, *C. oedippus* responds quickly to unfavourable changes in the environment (Čelik 2007). The habitat of *C. oedippus* in Slovenia is extremely spatially fragmented; its abundance has declined throughout the range in recent years (Verovnik et al. 2009; Čelik and Verovnik 2010; Čelik 2015b; Verovnik et al. 2015). In 2019, only one population was still living in the Ljubljana Marsh (Škofljica - Mostišče); and in 2019–2022, a new population was established in Ig Marsh (*Iški morost*) by rearing *C. oedippus* (Čelik 2020; 2021). Both populations in Ljubljana Marsh are below the probability threshold for long-term survival of the species. *C. oedippus* on wet grasslands is threatened by hydromelioration, agromelioration, agro-chemicalization, frequent mowing, abandonment of land use, and urbanization (Čelik 2015a; 2020; 2021); while populations on dry habitats are threatened primarily by the overgrowing of grasslands into forests and their conversion into intensive grassland and permanent plantations (Zakšek and Verovnik 2020; Zupan et al. 2020). *C. oedippus* is a protected species in Slovenia (Uredba o zavarovanih prostoživečih živalskih vrstah, Uradni list RS št. 46, 2004) and is classified as endangered in the Slovenian Red List of endangered butterflies (Pravilnik o uvrstitvi ogroženih rastlinskih in živalskih vrst v Rdeči seznam, Uradni List RS 2002; 2010). *C. oedippus* is also listed as a Natura 2000 species and must be protected under the Habitats Directive (Council Directive 92/43/EEC, 1992) in and outside special areas of conservation.

The impact of natural hazards on *C. oedippus* in Slovenia has not yet been studied, but its potential impact was detected in 2010 in the area southeast of Ljubljana Marsh in the Duplica Stream Valley near Grosuplje. A heavy hailstorm in 2010, at the time of emergence of the adult butterflies, is the most likely reason for the local extinction of the species. The size of the population in this area was estimated at 400 individuals in 2009 (Verovnik et al. 2009), in 2011 it decreased to about 20 individuals (Verovnik et al. 2011), and in 2014 the species was no longer confirmed in this area (Čelik 2015a).



Figure 1: Male (left) and female (right) of *Coenonympha oedippus*.

The significant effects of natural hazards on changes in species composition and population dynamics are confirmed by studies of other butterfly species (Swengel 2001; Cleary and Genner 2004; Ricouart et al. 2013). In the last twenty years, the lack of precipitation has led to frequent and intense droughts, which increases the risk of fires in the natural environment (Sušnik and Gregorič 2017). Droughts dry out vegetation, reducing the amount of nectar available to butterflies and the nutritional value of the plant parts on which the caterpillars feed. Fires reduce the abundance of invertebrate species in affected areas and result in lower butterfly populations (Fleishman 2000; Huntzinger 2003; Cleary and Genner 2004; Pryke and Samways 2012; Ricouart et al. 2013; Moranz, Fuhlendorf and Engle 2014; Henderson, Meunier and Holoubek 2018). After fire, the species composition changes, and the empty space may first be colonized by non-native species. The recovery time of areas affected by natural hazards is difficult to predict (Jackson and Sax 2009).

In this study, we investigated the occurrence of natural hazards in *C. oedippus* habitats in Slovenia. We compared differences in fire and flood risk between wet and dry habitats and between different geographic regions.

2 Study area and methods

There are differences between geographical areas in terms of knowledge and quality of data on the occupancy of habitat patches of *C. oedippus* in Slovenia: wet habitats are much better studied than dry ones. We included 56 habitat patches from the entire distribution range of *C. oedippus* in Slovenia in the period 2002–2016 in the analysis (Table 1, Figure 2). All occurrence data published before 2012 were verified in the field in 2013–2016 and supplemented with data from fieldwork. Later published data on the distribution of the species (after 2016; Zakšek and Verovnik 2020) were not included (see also Verovnik et al. 2009; Verovnik et al. 2015).

C. oedippus habitat patches were defined as individual meadows, where the species was detected during 2002–2016. The size of the patch was defined on site according to: i) the boundaries surrounding these meadows, and ii) the adequate representation of plant species (host plants for caterpillars). We then drew polygons of habitat patches with ArcGIS 10.4.1. and calculated the areas (in hectares) of each patch (Table 1).

Depending on the type of habitat, we divided habitat patches into wet (seven habitat patches; Ljubljana Marsh with surroundings of Grosuplje) and dry (49 habitat patches; Slovenian Istria, Karst, Gorica Hills, Banjšice, and Trnovo Forest plateau) (Čelik 2003; Čelik and Verovnik 2010). Based on the geographical defined management units for the conservation of *C. oedippus* populations in Slovenia (Zupan et al. 2021), we divided the habitat patches into four groups: Slovenian Istria (25 habitat patches), Karst (13 habitat patch-

es), Gorica Hills (with Trnovo Forest plateau and Banjšice; 11 habitat patches), and the Ljubljana Marsh with the surroundings of Grosuplje (seven habitat patches; Figure 2).

We have reviewed all available data on exceptional natural events in Slovenia that fall under the definition of natural hazards and at the same time have at least an indirect connection with the habitat patches of *C. oedippus*. In karst areas, these events are mainly soil subsidence and sinkholes, slope movements, and flash flooding (inability to drain rainwater) (Parise 2015). Flysch areas are characterized by landslides, with soil erosion occurring more frequently in areas of greater slope where agricultural use and forest clearing are intensive (Zorn and Komac 2009; Ravbar 2010). Floods are the most apparent natural hazard in Ljubljana Marsh (Gašperič 2004). For the entire study area, we also considered the risk of forest fires as a natural hazard, which is greater when there is seasonal water scarcity that causes vegetation to dry out (Turlure et al. 2013).

After reviewing data on natural hazards from the Slovenian Environment Agency (*Agencija Republike Slovenije za okolje: Geoportal* and *Atlas okolja*) and Agricultural Institute of Slovenia (*Kmetijski inštitut Slovenije: eTLA portal*), we included only floods and forest fires in the analysis of threats to species' habitats; for other natural hazards available data were insufficient for a detailed analysis.

2.1 Floods in the distribution area of *Coenonympha oedippus*

Despite the construction of numerous drainage ditches, flooding still occurs regularly in Ljubljana Marsh (Gašperič 2004; Komac, Natek and Zorn 2008). The extent of regular flooding has decreased most in the south-eastern part of this area (Kolbezen 1985). According to the Slovenian Environment Agency data flooding is frequent in autumn and winter, rare in spring, and extremely rare in summer, depending on the distribution and amount of precipitation. Frequent floods affect the central (lowest) parts of Ljubljana Marsh (about 15% of the area). During extremely large floods (karstic or torrential in origin), the floodplain extends from the Ljubljanica River along its tributaries, so that a good half of the area is under water (Gašperič 2004; Komac, Natek and Zorn 2008). The reason for the occurrence of floods is the extremely long retention of water on the surface due to impermeable and poorly permeable layers. The subsidence of the Ljubljana Marsh leads to the formation of depressions where flood waters are retained for a long time (Gams 1990; Zajc 2010). The Duplica Stream drainage basin is a hydrographic system separate from the Ljubljana Marsh.

In Slovenian Istria, the only surface water in close proximity to *C. oedippus* habitats that is occasionally flooded is the Dragonja River with its tributaries. There are no surface waters in the Karst. In the distribution areas of the species in the Gorica Hills, there are watercourses belonging to the catchment areas of the Pevmca Stream, Reka Stream, Idrija Stream, and Soča River.

2.2 Fires in the distribution area of *Coenonympha oedippus*

The Primorska region is the area with the highest fire risk in Slovenia, especially in the hot and dry periods of the summer months (Veble and Brečko Grubar 2016; see also Slovenia Forest Service; *Zavod za gozdove Slovenije*). Fire risk can be high already in early spring, when the intensity of solar radiation increases and there is an excess of dry, dead vegetation, while at the same time human activities in nature are very high (Pečenko 2005). Fires can be caused by traditional agricultural practices (prescribed burning, e.g., in Ljubljana Marsh), carelessness (accidental fire), or simply by the drying of vegetation during the summer months (self-combustion). The bora wind in Primorska further dries out vegetation and dead organic material and, in the event of a fire, accelerates its spread by providing the oxygen necessary for combustion and carrying sparks to new areas (Pečenko 2005). Pine forests and deciduous forests in warm and dry habitats are most susceptible to fire (Prebevšek 1998).

Occasional small fires occur frequently in the Karst (Veble and Brečko Grubar 2016). One of the largest fires occurred in the summer of 1994 in the area between Renče, Opatje selo, and Lokvica, burning 575 ha of pine forest (Zoratti 1995). The second major fire occurred in August 2019, when 85 ha of land burned in Cerje (near Lokvica and Opatje selo) (Komac 2022). The last, largest fire in July 2022 in the Karst burned 3,707 ha of land (Košiček 2022).

Table 1: List of habitat patches with at least one confirmed occurrence of *Coenonympha oedippus* in 2002–2016, and dates of flood events in a period since 1980. Patches located outside Natura 2000 sites are marked with a dash (–).

Geographical area / Habitat patch	Natura 2000 site code and name	Area (ha)	Flood event
Ljubljana Marsh (<i>Ljubljansko barje</i>)		16,03	
1 Škofljica - Mostišče	3000271–Ljubljansko barje	2,69	18.–20. 9. 2010
2 Škofljica - Podvin	3000271–Ljubljansko barje	1,78	18.–20. 9. 2010
3 Grosuplje - Skobčev mlin 1, Duplica	3000141–Duplica	5,01	18.–20. 9. 2010
4 Grosuplje - Skobčev mlin 2, Duplica	3000141–Duplica	0,38	18.–20. 9. 2010
5 Grosuplje - Skobčev mlin 3, Duplica	3000141–Duplica	2,58	18.–20. 9. 2010
6 Želimlje	3000271–Ljubljansko barje	2,68	18.–20. 9. 2010
7 Pijava Gorica - Podblato	3000271–Ljubljansko barje	0,91	
Slovenian Istria (<i>Slovenska Istra</i>)		45,90	
8 Izola - Cetore	–	2,47	
9 Baredi - Repka farm	–	0,63	
10 Parecag - Šorgo farm	–	0,13	
11 Dovin 1	3000212–Slovenska Istra	0,40	
12 Dovin 2	3000212–Slovenska Istra	0,20	
13 Dovin 3	3000212–Slovenska Istra	0,75	18.–20. 9. 2010
14 Abrami	3000212–Slovenska Istra	1,25	
15 Draga	3000212–Slovenska Istra	1,21	
16 Dragonja - Supot	3000212–Slovenska Istra	0,11	18.–20. 9. 2010
17 Čupinje	3000212–Slovenska Istra	0,82	
18 Gradišče - Krkavče	3000212–Slovenska Istra	3,38	
19 Koštabona	3000212–Slovenska Istra	0,11	
20 Jamnjek - Krkavče	3000212–Slovenska Istra	6,14	18.–20. 9. 2010
21 Nova vas nad Dragonjo	3000212–Slovenska Istra	0,51	
22 Padna	3000212–Slovenska Istra	0,54	
23 Petrinjevica	3000212–Slovenska Istra	0,97	18.–20. 9. 2010
24 Planjave	3000212–Slovenska Istra	2,10	
25 Plešivica	3000212–Slovenska Istra	0,17	
26 Solne - Krkavče	3000212–Slovenska Istra	2,15	
27 Sveti Maver	3000212–Slovenska Istra	1,31	
28 Sveti Peter	3000212–Slovenska Istra	1,12	
29 Smokvica - Velika vala	3000276–Kras	0,79	
30 Dolgo Brdo	–	1,14	
31 Upper course of Rakovec Stream	3000276–Kras	0,60	
32 Rovance	–	16,91	
Karst (<i>Kras</i>)		6,51	
33 Opatje selo 1	3000276–Kras	0,14	
34 Opatje selo 2	3000276–Kras	0,07	
35 Opatje selo 3	3000276–Kras	0,20	
36 Opatje selo 4	3000276–Kras	1,21	
37 Opatje selo 5	3000276–Kras	0,59	
38 Opatje selo 6	3000276–Kras	0,24	
39 Opatje selo 7	3000276–Kras	0,17	

40	Opatje selo 8	3000276–Kras	0,60	
41	Opatje selo 9	3000276–Kras	0,80	
42	Brestovica pri Komnu	3000276–Kras	0,18	
43	Vojščica	3000276–Kras	0,66	
44	Gorjansko	3000276–Kras	1,11	
45	Tublje pri Komnu	3000276–Kras	0,55	
	Gorica Hills (<i>Goriška brda</i>)		13,93	
46	Golo Brdo - Idrija Stream Valley	–	2,89	
47	Plave - Strmec	3000379–Vrhoveljska planina	0,42	
48	Senik - Kajenca	–	0,30	
49	Vrhovlje pri Kožbani	–	0,32	
50	Gonjače - Vrhovec	3000290–Goriška brda	4,01	
51	Podsabotin	3000290–Goriška brda	5,83	
52	Solkan	–	0,16	25. 12. 2009, 5. 11. 2012*
	Banjšice and Trnovo Forest plateau (<i>Banjšice and Trnovski gozd</i>)		3,51	
53	Banjšice	3000034–Banjšice	0,15	
54	Ravnica 1	–	1,09	
55	Ravnica 2	–	1,04	
56	Ravnica 3	–	1,22	

*The habitat patch (Euclidean distance of 60 m from the Soča riverbed) was not flooded due to the difference in elevation between the height of the flood and the location of the habitat patch.

2.3 Data selection on the occurrence of fires and floods in *Coenonympha oedippus* habitat patches

Fire risk in *C. oedippus* habitat patches was determined based on the 2011–2020 Forest management plans for forest management areas (*Gozdnogospodarski načrti gozdnogospodarskih območij*), where the Slovenia Forest Service's Forest fire risk map classifies fires into four categories (Table 2). We compared the geographic data (shp layer) of forest fire threat with the layer of *C. oedippus* habitat patches in the ArcGIS 10.4.1 program. The threat to an individual habitat patch from the confirmed occurrence of a species (regardless of threat level) was defined as direct or indirect. A habitat patch is directly threatened if it is itself an open, light fire-prone forest or directly adjacent to a fire-prone forest. A habitat patch is indirectly threatened if the edge of the nearest fire-prone forest is no more than 1000 m (Euclidean distance) from the edge of the habitat patch.

For the statistical analysis of the distance to the nearest fire-prone forest, we used two classes: 0–200 m and 201–1000 m. We chose the upper limit of the first class at 200 m because the vast majority of *C. oedippus* flights are less than 200 m (> 85%, Vereš 2022). We chose the upper limit of the second class at 1000 m because this corresponds to the longest recorded flight length of this species in the Karst (Čelik and Verovnik 2010).

Flood risk data were obtained from documents describing the frequency and extent of flooding. The data on the frequency of flood occurrence, which were obtained from the eTLA portal (provided by Agricultural Institute of Slovenia), were divided into three categories: non-flooded areas, areas with very rare floods, and areas with frequent floods. Data on the flooded area at return periods of ten, one hundred and five hundred years were obtained from the databases *Geoportal* and *Atlas okolja* (provided by Slovenian Environment Agency). We then compared the geographic layer of the extent of floods with different return periods with the layer of habitat patches of *C. oedippus* in the program ArcGIS 10.4.1 and with the location of each habitat patch in the display of flood frequency in the *Atlas okolja*.

Table 2: Analyzed parameters of natural hazards in the distribution area of *Coenonympha oedippus* in Slovenia.

Parameters of natural hazards	Parameter type	Parameter categories	Source
Fires			
Forest fire risk	Ordinal	Level 1 – very high risk, Level 2 – high risk, Level 3 – medium risk, Level 4 – low risk	Slovenia Forest Service
Distance to the nearest fire-prone forest	Ordinal	0–200 m, 201–1000 m	Slovenian Environment Agency (<i>Atlas okolja</i>)
Floods			
Frequency of flood occurrence	Ordinal	non-flooded areas, areas with very rare floods, areas with frequent floods	Agricultural Institute of Slovenia (<i>eTLA</i>)
Flooded area at different return intervals*	Ordinal	return period of 10 years, return period of 100 years, return period of 500 years	Slovenian Environment Agency (<i>Geoport</i> and <i>Atlas okolja</i>)

* We did not compare the parameter »Flooded area at different return intervals« between habitat types/management units, because for this parameter we have data only for Ljubljana Marsh.

We also determined the presence of individual flood events in the species' habitat patches. In this analysis, we included 15 flood events that have occurred since 1980: 6.–15. 11. 2014, 5.–6. 11. 2012, 27.–28. 10. 2012, 18.–20. 9. 2010, 25. 12. 2009, 23. 12. 2009, 3.–4. 8. 2009, 30. 3. 2009, 18.–19. 9. 2007, 5.–8. 10. 1998, 10. 12. 1990, 1.–2. 11. 1990, 5. 8. 1987, 15. 6. 1987, 9. 10. 1980. For data on individual flood events obtained from the *Atlas okolja*, we manually entered the coordinates of each habitat patch into the search engine and verified whether flooding occurred.

If we detected the presence of several different flooding categories in a habitat patch (e.g., very rare and frequent floods; Table 2), we included all categories of the individual habitat patch in the statistical analysis.

2.4. Data analyses

Frequencies of individual fire and flood risk parameters (Table 2) were analysed for each management unit (Slovenian Istria, Karst, Gorica Hills and Ljubljana Marsh) and for both habitat types (wet, dry). To determine whether management units/habitat types differ in terms of flood and fire risk (fire risk of the forests in Slovenia, distance to nearest fire-prone forest, frequency of flood occurrence; Table 2), we used the χ^2 -test for association with the likelihood ratio statistic (LR). Standardized residuals (SR) were used to determine which class of each fire and flood parameter contributed most to the overall difference between management units or between habitat types. SR values $> |2|$ were considered statistically significant ($p < 0.05$). We did not compare the parameter »Flooded area at different return intervals« with the χ^2 -test for association, neither between habitat types nor between management units, because for this parameter data are available only for Ljubljana Marsh.

Using the χ^2 -test for homogeneity of frequencies, we determined the uniformity of occurrence for three parameters of natural hazards (forest fire risk, distance to the nearest fire-prone forest, frequency of flood occurrence; Table 2) in habitat patches for each management unit and habitat type. For the parameter »Distance to the nearest fire-prone forest«, where we compared the homogeneity of frequencies between two classes, we used χ^2 -test with Yates correction.

SPSS ver. 27 was used for the χ^2 -test of association and homogeneity.

Most of the heterogeneity in relief was encompassed within the selected habitat patches in each management unit (Figure 2). We also considered the following parameters when interpreting the results: elevation difference between flooded and non-flooded habitats, distance from flooded habitats/forest fires, and different hydrologic systems.

3 Results

More than half (55.6%) of the surveyed habitat patches are smaller than 1 ha and 75.0% of them are smaller than 1.5 ha. The total area of the studied habitat patches in Slovenian Istria (25 patches) was 45.90 ha, in the Karst (13 patches) 6.51 ha, in Gorica Hills (11 patches) 17.44 ha and in Ljubljana Marsh (seven patches) 16.03 ha. The management units differ in terms of forest fire risk, with Gorica Hills and Ljubljana Marsh contributing the most to the overall difference (Table 3a). Gorica Hills has significantly more habitat patches with high fire risk (level 2: 72.7%) than the other units, while Ljubljana Marsh has more habitat patches with medium fire risk (level 3: 57.1%) and significantly fewer habitat patches with very high fire risk (level 1: 0%) compared to the other three management units. In the most fire-prone parts of Primorska (Karst and Slovenian Istria) more than 90% of habitat patches fall within category of very high fire risk (level 1), which corresponds to 6.38 ha of the species' habitat in the Karst and 41.20 ha in Slovenian Istria (Table 3a, Figure 2).

The two habitat types differ in their fire risk, as the number of habitat patches with very high fire risk (level 1) is significantly lower and with medium fire risk (level 3) is significantly higher in wet habitats (Table 3b). In wet habitats, 57.1% of habitat patches (8.06 ha) have medium fire risk (level 3) and 42.9% of patches (7.97 ha) have high fire risk (level 2). In dry habitats, more than three-quarters (77.6%) of habitat patches have a very high fire risk (level 1).

Habitat patches in management units also differ according to their distance from forest fires (Table 3a). Compared to the other units, there are significantly more habitat patches (20.0%) in Slovenian Istria at a distance of more than 200 m from fire-prone forests. The remaining 80.0% of habitat patches (or 38.01 ha) are located in close proximity (distance > 200 m) to fire-prone forests. In the other three management units, all habitat patches are less than 200 m from fire-prone forests. There is no statistically significant difference between the two habitat types in terms of distance of habitat patches from forest fires (Table 3b).

The frequency of flooding in the habitat patches differs between the four management units (Table 3a) and between the two habitat types (Table 3b). Slovenian Istria and Ljubljana Marsh contribute the most to the differences between management units. Compared to the other management units, the former has more areas with very rare floods (52.0% of habitat patches, corresponding to an area of 18.39 ha), while the latter has more habitat patches at risk of frequent floods (18.2%, corresponding to an area of 4.47 ha). The two habitat types differ in the frequency of flooding, as wet habitat patches are typically more exposed to frequent flooding than dry habitat patches.

The distribution of fire risk in habitat patches is uniform only in Ljubljana Marsh; in Gorica Hills, fire risk level 2 (72.7%) predominates, while in Slovenian Istria and Karst most habitat patches (> 90%) are exposed to the fire risk level 1 (Table 4). Accordingly, the highest fire risk (level 1) also prevails in the dry habitat type. In all management units and in both habitat types, habitat patches located less than 200 meters from fire-prone forests prevail. The frequency of flood occurrence in habitat patches is uniform only in Ljubljana Marsh (all three categories of flood occurrence are present); in Slovenian Istria habitat patches with very rare flood occurrences dominate (52.0%). In the Karst, all patches are located in non-flooded areas, as are the majority (90.9%) of habitat patches in Gorica Hills. Overall, non-flooded habitat patches predominate in the dry habitat type, while habitat patches subject to frequent flooding were not recorded in this habitat type.

A review of the individual flood events shows that the September 18-20, 2010, flood inundated 10 habitat areas, four in Slovenian Istria (with an area of 7.97 ha) and six in Ljubljana Marsh (with an area of 15.12 ha; Table 1). In Gorica Hills, only one habitat patch (Table 1) was located in close proximity to the flood events of December 25, 2009, and November 5, 2012, but even this was not flooded due to the difference in elevation between the flood level and the habitat location.

Analyzing the data describing the extent of floods with return periods of 10, 100 and 500 years in Slovenia, we found that such floods threaten only the habitats of *C. oedippus* in the Ljubljana Marsh. Floods with return periods of 100 and 500 years reach all habitat patches there, floods with a return period of 10 years threaten only habitat patches in Želimiže Valley (2.68 ha) and near Grosuplje (Skobčev mlin 3: 2.58 ha), both of which were inhabited by the species in the past.

Figure 2: Slovenia Forest Service Forest fire risk map and illustration of studied habitat patches of *Coenonympha oedippus* in Slovenia (Note: Due to close geographic proximity of habitat patches, the number of symbols in the figure may differ from the number of habitat patches in Table 1). Habitat patches are classified by management units. D - dry habitats, W - wet habitats. ► p. 66

Table 3. Categories of natural hazard parameters that contribute most to differences between management units (a) and habitat types (b) according to χ^2 -test for association with the likelihood ratio statistic (LR), LR with standardized residuals (SR > |z|, in bold). N - the number of *Coenonympha oedippus* habitat patches, df - degrees of freedom; p - statistical significance.

(a) Management units	Slovenian Istria			Karst			Gorica Hills			Ljubljana Marsh		
	N	%	SR	N	%	SR	N	%	SR	N	%	SR
Parameters of natural hazards ¹												
Forest fire risk ² (LR = 45,96, df = 6, p < 0,001)												
Level 1	23	92,0	1,5	12	92,3	1,1	3	27,3	-1,6	0	0	-2,2
Level 2	2	8,0	-1,7	1	7,7	-1,2	8	72,7	3,2	3	42,9	0,9
Level 3	0	0	-1,3	0	0	-1	0	0	-0,9	4	57,1	4,9
Distance to the nearest fire-prone forest (LR = 8,68, df = 3, p < 0,05)												
0–200 m	20	80,0	-0,6	13	100	0,3	11	100	0,3	7	100	0,2
201–1000 m	5	20,0	1,9	0	0	-1,1	0	0	-1	0	0	-0,8
Frequency of flood occurrence (LR = 24,50, df = 6, p < 0,001)												
areas with frequent floods	0	0	-0,9	0	0	-0,7	0	0	-0,6	2	18,2	2,7
areas with very rare floods	13	52,0	2,2	0	0	-1,9	1	9,1	-1,2	3	27,3	-0,1
non-flooded areas	12	48,0	-1,2	13	100	1,4	10	90,9	0,9	6	54,5	-0,6
(b) Habitat type												
Dry habitats ²												
Parameters of natural hazards ¹												
Forest fire risk ³ (LR = 27,65, df = 2, p < 0,001)												
Level 1	38	77,6	0,8	0	0	0	0	0	0	0	0	-2,2
Level 2	11	22,4	-0,4	0	0	-0,4	3	42,9	0,9	3	42,9	0,9
Level 3	0	0	-1,9	0	0	-1,9	4	57,1	4,9	4	57,1	4,9
Distance to the nearest fire-prone forest (LR = 1,40, df = 1, NS)												
0–200 m	44	89,8	-0,1	0	0	-0,1	7	100	0,2	7	100	0,2
201–1000 m	5	10,2	0,3	0	0	0,3	0	0	-0,8	0	0	-0,8
Frequency of flood occurrence (LR = 7,19, df = 2, p < 0,05)												
areas with frequent floods	0	0	-1,3	0	0	-1,3	2	18,2	2,7	2	18,2	2,7
areas with very rare floods	14	28,6	0	14	28,6	0	3	27,3	-0,1	3	27,3	-0,1
non-flooded areas	35	71,4	0,3	35	71,4	0,3	6	54,5	-0,6	6	54,5	-0,6

¹ The parameter »Flooded area at different return intervals« is commented in the text.² The dry habitat type includes 3 management units: Slovenian Istria, Karst and Gorica Hills.³ The fourth level of fire risk was not represented in the studied habitat patches and is therefore not shown.

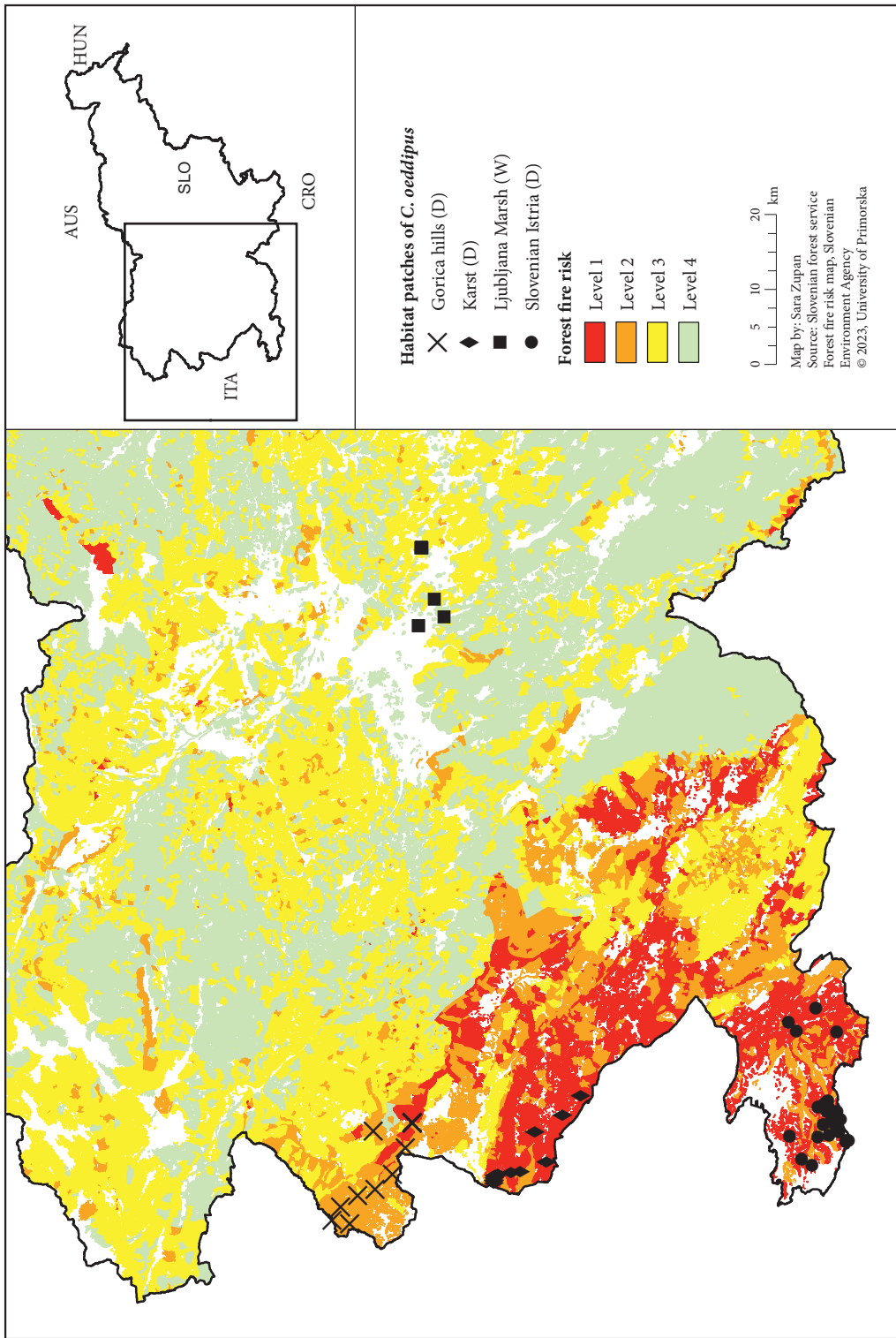
NS – not statistically significant.

Table 4: Representation of habitat patches in each management unit and habitat type for the three considered parameters of natural hazards in the distribution area of *Coenonympha oedippus* in Slovenia, calculated with the χ^2 -test for homogeneity of frequencies. Predominant = the predominant category of the natural hazard parameter and the percentage of habitat patches in this category, p – statistical significance (**** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; NS – not statistically significant).

Management unit / Parameters of natural hazards	Slovenian Istria		Karst		Gorica Hills		Ljubljana Marsh/Wet habitat		Dry habitat ²	
	p	Predominant	p	Predominant	p	Predominant	p	Predominant	p	Predominant
Forest fire risk	***	Level 1 (92,0%)	***	Level 1 (92,3%)	*	Level 2 (72,7%)	NS	Level 3 (57,1%)	***	Level 1 (77,6%)
Distance to the nearest fire-prone forest	**	0–200 m (80,0%)	***	0–200 m (100%)	**	0–200 m (100%)	*	0–200 m (100%)	***	0–200 m (89,8%)
Frequency of flood occurrence	**	very rare floods (52,0%)	***	non-flooded areas (100%)	***	non-flooded areas (90,9%)	NS	non-flooded areas (54,5%)	***	non-flooded areas (71,4%)

¹ Calculated with Yates correction.

² The dry habitat type includes three management units: Slovenian Istria, Karst and Gorica Hills.



4 Discussion

4.1 The fire risk to the habitat of *Coenonympha oedippus*

According to the Slovenia Forest Service forests cover 58.2% of the land area in Slovenia. The risk of forest fires is present in four different levels nationwide. Fire risk in *C. oedippus* habitat patches falls in one of the three highest levels of fire risk. The distance of habitat patches from fire-prone forests is less than 200 m in all management units studied; except for five habitat patches in Slovenian Istria with an area of 7.89 ha. According to the guidelines of the Firefighters Association of Slovenia (*Gasilska zveza Slovenije*; see <https://gasilec.net/>) the speed of fire spread on levelled terrain at a wind speed of 20 km/h is 600 m/h and increases with increasing wind speed. This means that after igniting dry grass at the forest edge, fire can spread extremely quickly to dry grassland, which represents the majority of habitat patches suitable for *C. oedippus* in Slovenia. Fire risk to *C. oedippus* habitat is very high in the management units of Slovenian Istria and Karst, high in Gorica Hills, and medium in Ljubljana Marsh. However, in the latter management unit, prescribed burning of grassland and/or other plant biomass in early spring or autumn increases the fire risk.

In Slovenia populations on wet habitats are genetically unique (Zupan et al. 2021); only two populations currently live in Ljubljana Marsh. One of them was established by reintroducing individuals reared in nurseries in 2019–2022 (Čelik 2020; 2021; 2022). Both populations are vulnerable to extreme natural events. Prescribed burning of grasslands does not directly threaten them because the conservation measures and habitat management of both populations are adapted to the ecological needs of the species and do not allow activities that are harmful to the species. Prescribed fires of plant biomass threaten them indirectly, if the fire spreads to nearby areas and then encroaches on the populations' habitat. The same is true for areas that are being restored with the aim of creating a habitat suitable for the species, which could potentially be inhabited by individuals of both existing populations in the future (Čelik, Šilc and Vereš 2018).

Researchers from Poland, however, advocate burning wet habitats of *C. oedippus* (Sielezniew et al. 2010). There, sporadic fires in early spring, before caterpillars begin feeding after winter dormancy, limit succession in the habitat and maintain grasslands. However, the effects of fires on the abundance of *C. oedippus* were not examined in the above study.

In western Slovenia, forest fires pose a greater direct threat to the species' habitat than in Ljubljana Marsh. In the northwestern part of the Karst, the population of *C. oedippus* is one of the largest on dry habitats (Čelik et al. 2005), the size of which has been monitored since 2009 as part of the national monitoring of selected Natura 2000 species (Verovnik et al. 2009). The fire on Cerje in August 2019 destroyed 46.1% (10.88 ha) of the habitat of this population included in the national monitoring area as of 2019 (Vereš 2022). At the time of the fire, the species was in the stage of young caterpillars which were unable to move away from the burning meadows. The result of the fire was a drastic decline in the population by 56% in 2020 compared to the previous year when the pre-fire size was estimated (Vereš 2022). Only consecutive monitoring years of the local population, which is currently being conducted by researchers from the University of Primorska, will provide a realistic assessment of the consequences of the fire. The process of natural grassland recovery in the Karst after the 2019 fire was interrupted by another fire in July 2022, when 3,707 ha of land burned (Košček 2022). This fire covered almost the entire monitoring area of this population (see Map 1 in Košček 2022). In the north western part of the Karst, *C. oedippus* was also found scattered outside the area burned in the 2022 fire (Verovnik et al. 2009; 2015; Zakšek et al. 2019), increasing the likelihood that one of the once-largest populations in the Karst will be restored by spontaneous immigration from areas not affected by the fire into the burned area as the land naturally regenerates into habitat suitable for *C. oedippus*. Preliminary results of vegetation surveys on Cerje between the last two fires (2019 and 2022), conducted by researchers from Research Centre of the Slovenian Academy of Sciences and Arts, Jovan Hadži Institute of Biology, indicate that autochthonous herbaceous vegetation on some grasslands recovered to suitable habitat in just three years. Fires can have extremely devastating effects on *C. oedippus* throughout the year, as non-mobile (eggs: June–July; pupae: May–June) or low-mobile (caterpillars: June–May) developmental stages are always present in the population (Čelik 2015a; 2015b). If the fire is not too large and does not spread too rapidly during the period of adult emergence (June–July), butterflies that are not trapped in the fire zone may retreat to nearby unburnt areas. If the fire occurs during the last part of the butterfly flight season, fertilized females that predominate in the population, may move

away from the fire area to establish a new generation. In organisms exposed to the threat of fire, there is increased selection pressure on the evolution of strategies to survive such events, but fire survival mechanisms other than escape/retreat have not been extensively studied in animals (Nowicki, Marczyk and Kajzer-Bonk 2015). Also, during large fires, small areas remain unaffected and can serve as refugia for butterflies (Swengel and Swengel 2007). Suitable refugia for the myrmecophilous butterfly species *Phengaris teleius* and *P. nausithous* (Lycaenidae) also include ant nests, where caterpillars and pupae may survive in the event of fire during this developmental phase (Nowicki, Marczyk and Kajzer-Bonk 2015). The authors note that the results should not be generalized to all habitats and species, as this case is a distinctive feature of myrmecophilous butterfly species.

Prescribed burning, sometimes used to limit grasslands succession (Swengel 1996; Robel et al. 1998; Lyet et al. 2009), has been suggested by some authors as a positive management measure (Middleton 2013). However, fire inevitably reduces landscape mosaicity, has variable and often unknown effects in terms of the timing of restoration of suitable habitat for different species (Swengel and Swengel 2007), and could lead to the establishment of non-native species that are often more successful in pioneer habitats than native species (Allen, Steers and Dickens 2011).

4.2 The flood risk to the habitat of *Coenonympha oedippus*

The habitat patches at highest risk of flooding are located in Ljubljana Marsh, followed by the habitat patches in Slovenian Istria in the immediate vicinity of the Dragonja River. The first area is characterized by very rare to frequent flooding, the second only by very rare flooding. The studied habitat patches in Gorica Hills and in the Karst are not at risk of flooding.

Short-term flooding does not usually affect the survival of caterpillars of Nymphalidae butterflies: *Neptis rivularis* (Konvička, Nedved and Fric 2002) and *Coenonympha tullia* (Joy and Pullin 1997; 1999) can survive flooding for up to three days without consequences, but as the duration of flooding increases, the survival rate of *N. rivularis* caterpillars decreases. Caterpillars of *C. tullia* can survive flooding for up to 52 days, but a flood of seven days results in mortality of up to 50% in the further developmental stages of the caterpillars (Joy and Pullin 1997; 1999). Flooding of ant nests hosting caterpillars of *P. teleius* and *P. nausithous* for three weeks had no negative effect on their population size the following year (Kajzer-Bonk et al. 2013). Prolonged flooding (over 28 days) resulted in the death of 65% of *Lycaena dispar* (Lycaenidae) caterpillars; and increased mortality among survivors at the end of overwintering (Nicholls and Pullin 2003). Flooding in the area of *C. oedippus* habitat patches included in this study occurs most frequently in spring and autumn, when the species is in the stage of less mobile young caterpillars. Considering that survival is highly dependent on the duration of flooding, we hypothesize that at least prolonged flooding may have a detrimental effect on the survival of *C. oedippus* caterpillars. Shorter floods do not adversely affect the related butterfly *C. tullia* (Joy and Pullin 1997; 1999; Konvička, Nedved and Fric 2002). Based on the similarity of the habitats of the two species, we can conclude that short floods do not have a negative impact on the studied species (e.g., floods between September 18 and 20, 2010, in Slovenian Istria and Ljubljana Marsh). High soil humidity following an exceptional amount of precipitation can also have a positive effect (Kajzer-Bonk et al. 2013) by reducing the intensity of agricultural use. The persistent soil humidity in Ljubljana Marsh in summer and autumn 2014 made it impossible for farmers to perform regular activities; the wet meadows with one of the last *C. oedippus* populations in this area were not mowed, which resulted in a 2.5-fold increase of the population the following year (Čelik 2015a).

The invertebrates best adapted to flooding are Annelida and some insect larvae (Plum and Filser 2005). For species that do not have specific physiological adaptations retreat, migration from flooded areas, and recolonization are important survival strategies after disturbance ceases (Plum and Filser 2005). Determinants that can significantly affect survival of populations during floods are heterogeneity of (micro)relief, the flood extent, and available suitable habitat outside of flooded area. Diverse micro-relief is important for hibernating caterpillars, which become active at high water levels and retreat to non-flooded plant parts (Joy and Pullin 1997). If topography is heterogeneous, elevated habitat parts may not be inundated and may provide refuge from high water for a part of the population (Nicholls and Pullin 2003); these areas serve as population sources for previously impacted areas (Konvička, Nedved and Fric 2002). A population exposed to flooding can survive if suitable habitat is available within its flight range. The flight ability of *C. oedippus* butterflies in Ljubljana Marsh is low, up to a maximum of 340 m (Čelik and Verovnik 2010),

but they can travel longer distances (up to 1000 m) with the help of the wind (Verovnik et al. 2009; Čelik and Verovnik 2010; Čelik, Vreš and Seliškar 2010). During prolonged flooding, the viability of populations could be further compromised by the lack of suitable habitat outside the flooded area to which the butterflies can retreat. Also, in the Dragonja River Valley (Slovenian Istria) distances between flood-prone habitat patches and other areas are generally greater than the flight ability of *C. oedippus*.

5 Conclusions

This study is the first to address fire and flood risk in *Coenonympha oedippus* habitats. The use of publicly available spatial data combined with data on the exact geographic location of habitat patches contributes to knowledge based on which we can plan better conservation measures. However informative, this approach cannot fully replace field work, which, despite its time-consuming nature, provides invaluable information on the condition of a specific habitat patch. Because of its ecological duality (populations in wet and dry habitats) and fragmented distribution, *C. oedippus* is an extremely intriguing species from an evolutionary and ecological perspective. In Slovenian Istria, Karst and Gorica Hills, the probability of fires in the species' habitats is high, while in Ljubljana Marsh habitats are safer from naturally occurring fires, but more vulnerable to prescribed fires. Thus, the overall natural fire risk is lower in wet habitats than in dry habitats. The opposite is true for flood risk, to which populations in wet grasslands are more exposed. Species living in areas of natural disturbance have adapted to these using different strategies. Widespread species with stable populations recovers quickly after such events, but for endangered species such as *C. oedippus*, natural disturbance can lead to local extinction. With this review study, we have shown that *C. oedippus* habitats in Slovenia are threatened by both floods and fires.

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