Boreal Peatland Life-project

The effects of drainage and restoration on mire butterfly abundance and species richness

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Abstract

In Finland peatlands have been extensively drained for forestry, agriculture and peat production, and this drainage has caused significant population declines of mire butterflies. Here we report the effects of drainage and restoration on total abundance and species richness of mire butterflies and other butterfly species and also on abundance of each individual species from a monitoring scheme initiated in the Boreal Peatland Life-project. We found that both abundance and species richness of mire butterfly species were lower in drained sites than in pristine sites confirming that drainage has a negative influence of these species. We also found an encouraging result that the number of mire butterfly species increased already few years after restoration in the restored sites. This project provided evidence that restoration is successful and increases number of mire specialist species in restored mires. The monitoring setups established during Boreal Peatland Life-project form an interesting monitoring opportunity to increase knowledge about the long term effects of restoration and monitoring. Every effort will be made to continue the monitoring to allow us to judge the long term impacts of mire restoration.

Introduction

Habitat loss and fragmentation has been recognized as a major cause of global biodiversity loss (Foley et al. 2005; Fischer et al. 2007). Altogether 60 % of peatlands In Europe (Vasander et al. 2003) and in Finland have been drained for forestry, agriculture and peat production (Vasander 1998, Heikkilä et al. 2002, Rassi et al. 2010). Habitat degradation has been most intensive in Southern and Central Finland, where only 25 % peatlands remain intact (Virkkala et al. 2000). Peatlands are the main habitat type for 223 (4,5%) red-listed species and one habitat type among others for 420 red-listed species in Finland, including plants, invertebrates, and vertebrates (Rassi et al. 2010). Drainage has caused significant population declines of mire butterflies (Marttila 2005, Rassi et al. 2010). Although drainage has been most intense in 1960's and 1970's, the decline of mire butterfly populations have not been observed until past two decades (Marttila 2005, Rassi et al. 2010). This phenomenon is known as extinction debt, meaning there is a time lag after habitat deterioration before populations disappear (Tilman et al. 1994; Hanski 2000, Hanski and Ovaskainen, 2002).

Restoring ecosystems has become internationally important way to slow down the loss of biodiversity and maintain ecosystem services (European Union 2010). Restoration attempts to return an ecosystem to its historic trajectory and it is considered as being the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (SER International 2004). In Finland, the restoration of forest and peatland habitats became an established element of the management of protected areas since the launch of the Forest Biodiversity Programme METSO in 2003. In total 19 000 hectares of peatlands have been restored between 1989-2012 (Aapala et al. 2013).

Most of the Finnish protected peatlands are included in the Natura 2000 network. Even inside Natura 2000 network populations of several mire species will be reduced and eventually become threatened without rapid conservation and restoration effort. The largest LIFE Nature project in Finland, Boreal Peatland Life-project started in January 2010. The project aims at restoring nearly 4 300 hectares of various kind of peatlands. This five year project includes 54 Natura 2000 sites around Finland, with special attention paid to Central Finland. The main aim of the project is to restore the natural hydrology of the mires by filling in and blocking the ditches and by clearing trees to recreate the landscape as it was prior to the ditching. Restoration is concentrated on ecologically highly valuable areas and also some spots outside Natura areas are included into project area (Boreal Peatland Life Project 2013). After restoration spontaneous recolonization of peatland species is likely, because there usually exists some relict populations of the original peatland species. For most species, the restoration will also increase the connectivity and decrease the fragmentation of the Natura 2000 peatland habitats (Boreal Peatland Life Project 2008).

Relatively recently started restoration actions in peatlands have not provided yet much knowledge of the ecological effects of restoration and open questions still remain. Practical restoration projects should be closely linked with monitoring and research whenever possible (Heikkilä & Lindholm 1997). Monitoring enables to correct actions in order to better achieve restoration goals (adaptive management, Walters & Holling 1990). Boreal Peatland Life-project initiated a monitoring scheme that aims at the evaluation of the success of the restoration at many levels. To evaluate the general success of restoration, butterflies are monitored among some other taxa. Here we report the effects of drainage and restoration on total abundance and species richness of mire butterflies and other butterfly species and also on abundance of each individual species.

Material and methods

Study sites

During the first year of Boreal Peatland Life-project, in 2010, data on butterflies (Hesperioidea and Papilionoidea) was collected from 12 study areas (mire complexes). There were 6 transect lines total in each area with 3 different treatments: 1) drained sites that will be restored after the first observation period 2) drained sites that will not be restored and 3) pristine sites. In 2011 data was collected on 2 mires (12 transect lines), where restoration actions had been completed. In 2012 data on 4 mires (restored, previous 2 included) was collected, in 2013 data on 5 mires was collected (previous 4 included) and in 2014 data on 10 mires (previous 5 included). To increase reliability in statistical testing, we included in the analyses data that had been collected in 2003 and in 2007 from 9 mires in Natura-areas. In this older data experimental setups were identical and all pristine sites were included in the Natura 2000 network. In these areas restoration actions were performed between 2003 and 2005. By using this old data, we also got geographically more extensive dataset and thus the results can be better generalised: in older data four study areas were located in Central Finland province and five areas in North Carelia province. In Boreal Peatland Life-project, monitored butterfly mires are mainly in Western Finland. Species colonization of restored habitats is a slow process and thus data of short time period after restoration in Life-mires alone would not have enabled to test the effect of restoration.

Butterfly monitoring and environmental variables

Line transect sampling method developed by Pollard (1977) was used to collect butterfly data. There were 6 transect lines (250 m each) in each study area (21 mires total) with three different treatments (2 lines for each treatment): 1) drained habitat to be restored 2) drained habitat in forestry use and 3) pristine habitat. One mire area in older data had exceptionally four restored transect lines.

Transect counts were not carried out if the temperature was below 13 degrees of Celsius; when it was 13 to 17°C, counts were carried out only in sunny conditions (60 % sunshine minimum). Above 17°C weather conditions might be cloudy, but not rainy. The recorder walked at a uniform pace and recorded butterflies seen within 5 x 5 meters area in the front of the recorder. Stops were made to resolve identification problems, recording being resumed from the point where the walk was interrupted. Monitoring was not carried out if wind rose to six, estimated with Beaufort-scale. Counts were made mainly between 11 a.m. – 4 p.m. Number of visits varied due to weather conditions during field season, thus the number of visits was taken into account in statistical testing. Butterfly monitoring started when *Boloria freija* started flight, usually in the middle of May. Counting was carried out weekly, depending on weather. Number of visits per area varied from 7 to 15.

Butterflies of the superfamilies Hesperioidea and Papilionoidea were observed in this study. Butterflies were categorized into mire butterflies according to Pöyry et al. 2001 (classes 1-3) and into other butterflies. Mire butteflies were *Albulina optilete (2), Boloria aquilonaris (1), Boloria eunomia (1), Boloria euphrosyne (3), Boloria freija (1), Boloria frigga (1), Brenthis ino (3), Coenonympha tullia (2), Colias palaeno (2), Erebia embla (1), Oeneis jutta (1), Pyrgus centaureae (1*). Numbers 1-3 indicate how bonded species is to mire habitats (Pöyry et al. 2001). Species in class 1 are true specialists that occur only in mire habitats. Class 2 includes species that have more than 50 % of all populations in mire habitats. Species in class 3 have less than 50 % of populations in mire habitats, but they are commonly observed in mires. All mire species listed here were observed in Life-project mires. In older data on other Natura mires, *O. jutta* was missing, because it is on flight only in even years. Among other butterfly species was a pair of species, *Plebeijus argus* and *Plebeijus idas,* that were not separated due to identification problems (females of these species are impossible to separate in the field). This pair of blues was very numerous and it should be noted, that this species pair comprise 55 % of all butterfly observations in our data.

Data analysis

We used SPSS (22.0) in all statistical tests. Butterfly data was hierarchically structured because of different areas and different treatments, thus we used mixed model analysis. First we analyzed the effect of treatment and number of visits on butterfly species richness and individual abundance using data collected before restoration. Dependent variable was a number of species or individuals (mire butterfly species or other species). Treatment (drained site to be restored, drained site, pristine site) and number of visits were added into the mixed model as fixed effects. Site was a random effect. Finally, also each butterfly species (individual numbers of species with >10 observations during study) were added one by one into the model as dependent variable.

Next we analyzed the effect of treatment, repeated measure, number of visits and the interaction between repeated measure and treatment (effect of restoration). First we analyzed situation after first observation period after restoration. Then we combined data on first and second observation periods after restoration when this data was available (5 sites, we counted average number of individuals and total species numbers of these two field seasons) and included also these into analyses. We continued by combining data on first, second, and third observation period after restoration (4 sites). Finally also fourth observation period after restoration (2 sites) was included into the analyses with previous data. In these analyses dependent variable was number of individuals or number of species (mire butterfly species or other species). We entered treatment, repeated measure, number of visits and interaction between repeated measure and treatment into the model as fixed effects. Number of visits was a covariate and area was a random effect.

Finally, also each butterfly species (individual numbers of species with >10 observations during study) were added one by one into the model as dependent variable. When analyzing individual species, all observation periods were used.

Data on abundance for mire species and other species was (ln+1)-transformed before the analyses. Also data on abundance of individual species was (ln+1)-transformed. Figures illustrate untransformed numbers.

Results

Numbers of study mires, species and individuals in different sites are listed in appendix 1. List of species observed are in appendix 2 (older data) and in appendix 3 (Boreal Peatland Life-data). Mean number of individuals of each species before and after restoration are in appendix 4.

Species richness of mire butterflies before restoration

Treatment had an effect on mire butterfly species richness, but number of visits had no effect (Table 1). There were more mire species in pristine sites than in drained sites to be restored (Pairwise LSD comparison, MD = 2,524, SE = 0,513, df = 39,889, p < 0,001) or in drained sites that will not be restored (Pairwise LSD comparison, MD = 3,235, SE = 0,513, df = 39,896, p < 0,001) but there was no difference between drained sites to be restored and drained sites (Pairwise LSD comparison, MD = 0,711, SE = 0,513, df = 39,896, p = 0,173) (Figure 1).

Table 1. Mixed model analysis for mire species richness

Source	Numerator df	Denominator df	F	p
Intercept	1	19,070	19,445	< 0,001
Treatment	2	39,893	21,953	< 0,001
Number of visits	1	19,084	0,377	0,546

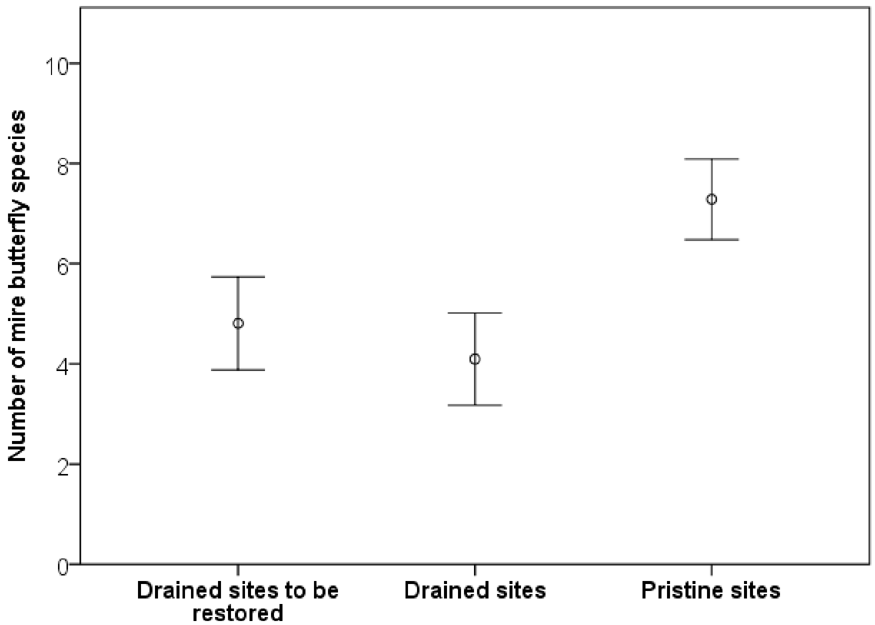

Figure 1. Number of mire butterfly species (error bars show 95% CI of mean)

Abundance of mire butterflies before restoration

Treatment had an effect on mire butterfly abundance, but number of visits had no effect (Table 2). There were more mire butterfly individuals in pristine sites than in drained sites to be restored (Pairwise LSD comparison, MD = 0,664, SE = 0,251, df = 39,916, p = 0,012) or in drained sites that will not be restored (Pairwise LSD comparison, MD = 0,796, SE = 0,251, df = 39,921, p = 0,003) but there was no difference between drained sites to be restored and drained sites that will not be restored (Pairwise LSD comparison, MD = 0,132, SE = 0,251, df = 39,921, p = 0,601) (Figure 2).

Table 2. Mixed model analysis for abundance of mire butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	19,060	43,672	< 0,001
Treatment	2	39,919	5,777	0,006
Number of visits	1	19,071	0,007	0,935

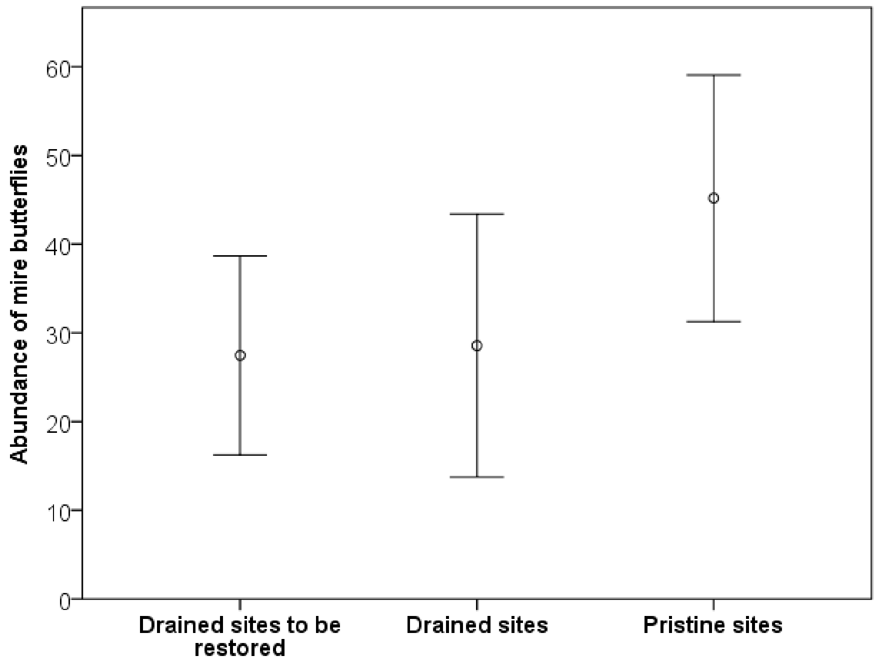

Figure 2. Abundance of mire butterflies (error bars show 95% CI of mean)

Species richness of other butterflies before restoration

Treatment or number of visits had no effect on species richness of other butterflies (Table 3).

Table 3. Mixed model analysis for species richness of other butterflies

Source	Numerator df	Denominator df	F	p
Intercept	1	19,071	50,202	< 0,001
Treatment	2	39,982	0,499	0,611
Number of visits	1	19,078	0,480	0,497

Abundance of other butterflies before restoration

Treatment tended to have an effect on abundance of other butterflies, but number of visits did not have an effect (Table 4). There were more other butterfly individuals in pristine sites than in drained sites that will not be restored (Pairwise LSD comparison, MD = 0,649, SE = 0,268, df = 40,00, p = 0,020) and there tended to be more individuals in drained sites to be restored than in drained sites that will not be restored (Pairwise LSD comparison, MD = 0,466, SE = 0,268, df = 40,00 , p = 0,090). There was no difference between pristine sites and drained sites to be restored (Pairwise LSD comparison, MD = 0,184, SE = 0,268, df = 39,989, p = 0,497) (Figure 3).

Table 4. Mixed model analysis for abundance of other butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	19,270	45,245	< 0,001
Treatment	2	39,996	3,125	0,055
Number of visits	1	19,293	2,895	0,105

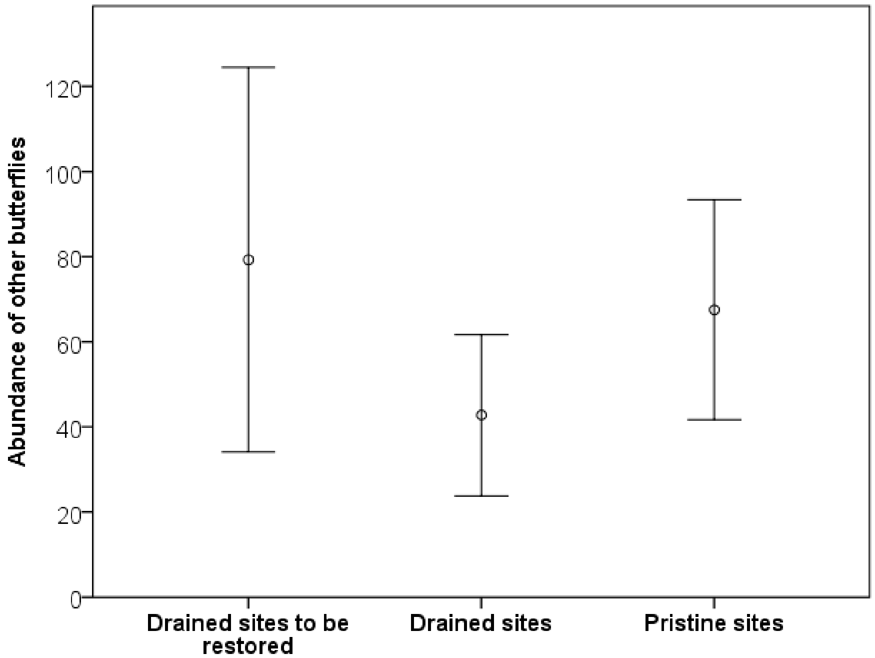

Figure 3. Abundance of other butterflies (error bars show 95% CI of mean)

Abundance of individual species before restoration

Results of the effect of treatment and number of visits on abundance of each species before restoration are in Table 5.

Table 5. The effect of treatment and number of visits on abundance of each species before restoration. Species marked with * are classified as mire butterflies. Class numbers (1-3) indicate how bonded a mire species is to mire habitats (see section "Butterfly monitoring and environmental variables"). - species is more abundant in pristine sites. + species is more abundant in drained sites or drained sites to be restored. For p-values *<0,05, **<0,01, ***<0,001. Difference between treatments is mainly between pristine and drained sites not to be restored. For number of visits df = 1 and 19 and for treatment df = 2 and 40. Only species with >10 observations during study are included in the analyses. Hessian matrix was not positive for species written in red (due to small sample size) and thus results for these species should be interpreted with caution.

Species	Class (1-3)	Number of visits		Treatment		
		F	p	F	p	+/-

*Albulina optilete**	2	0,201	0,659	1,179	0,318	(+)
*Boloria aquilonaris**	1	3,370	0,082	10,424	<0,001***	-
*Boloria eunomia**	1	12,446	0,002**	6,431	0,004**	-
*Boloria euphrosyne**	3	0,379	0,545	1,103	0,342	(+)
*Boloria freija**	1	0,308	0,585	11,622	<0,001***	-
*Boloria frigga**	1	2,296	0,135	5,130	0,009**	-
Boloria selene	-	0,513	0,477	0,471	0,627	(+)
*Brenthis ino**	3	2,760	0,113	1,086	0,347	(+)
Callophrys rubi	-	0,732	0,403	0,748	0,480	(+)
Celastrina argiolus	-	4,014	0,059	6,875	0,003**	+
*Coenonympha tullia**	2	4,360	0,050	30,860	<0,001***	-
*Colias palaeno**	2	6,260	0,022*	0,349	0,708	(-)
*Erebia embla**	1	0,273	0,607	0,738	0,484	(+)
Erebia ligea	-	8,310	0,010*	4,717	0,014*	+
Gonepteryx rhamni	-	4,516	0,047*	1,130	0,333	(+)
*Oeneis jutta**	1	13,346	0,002**	6,711	0,003**	-
Pieris napi	-	0,007	0,935	0,255	0,776	(+)
Plebeius argus/idas	-	2,448	0,134	5,788	0,006**	-
*Pyrgus centaureae**	1	0,151	0,699	1,767	0,180	(-)

Effect of restoration on species richness of mire butterflies (first observation period after restoration)

We found an interaction between repeated measure and treatment (Table 6). Interaction was such that there were more mire butterfly species after restoration in restored sites (Figure 4). Treatment had also an effect on mire butterfly species richness, but number of visits had no effect (Table 6). There were more mire species in pristine sites than in restored (Pairwise LSD comparison, MD = 1,769, SE = 0,419, df = 41,647, p < 0,001) or in drained sites (Pairwise LSD comparison, MD = 3,064, SE = 0,419, df = 41,647, p < 0,001). There was also a difference between restored and drained sites, such that there were more species in restored sites (Pairwise LSD comparison, MD = 1,296, SE = 0,419, df = 41,652, p = 0,004) (Figure 4).

Table 6. Mixed model analysis for mire species richness

Source	Numerator df	Denominator df	F	p
Intercept	1	66,186	36,199	< 0,001
Repeated measure	1	62,905	0,084	0,772
Treatment	2	41,649	26,917	< 0,001
Number of visits	1	70,842	1,514	0,223
Repeated measure*Treatment	2	56,432	3,515	0,036

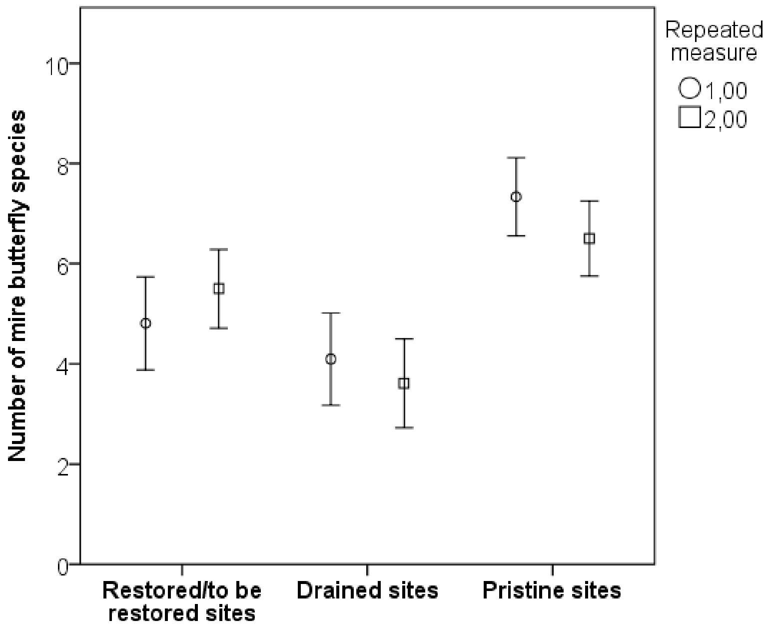

Figure 4. Number of mire butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of mire butterflies (first observation period after restoration)

Treatment had an effect on mire butterfly abundance, but repeated measure, number of visits or interaction between repeated measure and treatment had no effect (Table 7). There were more mire butterfly individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,748, SE = 0,212, df = 41,416, p = 0,001) and there tended to be more mire butterfly individuals in pristine sites than in restored sites (Pairwise LSD comparison, MD = 0,426, SE = 0,212, df = 41,417, p = 0,051) but there were no difference between restored and drained sites (Pairwise LSD comparison, MD = 0,321, SE = 0,212, df = 41,420, p = 0,137) (Figure 5).

Table 7. Mixed model analysis for abundance of mire butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	68,987	86,209	< 0,001
Repeated measure	1	60,476	0,067	0,797
Treatment	2	41,418	6,249	0,004
Number of visits	1	72,318	0,001	0,977
Repeated measure*Treatment	2	54,759	1,895	0,160

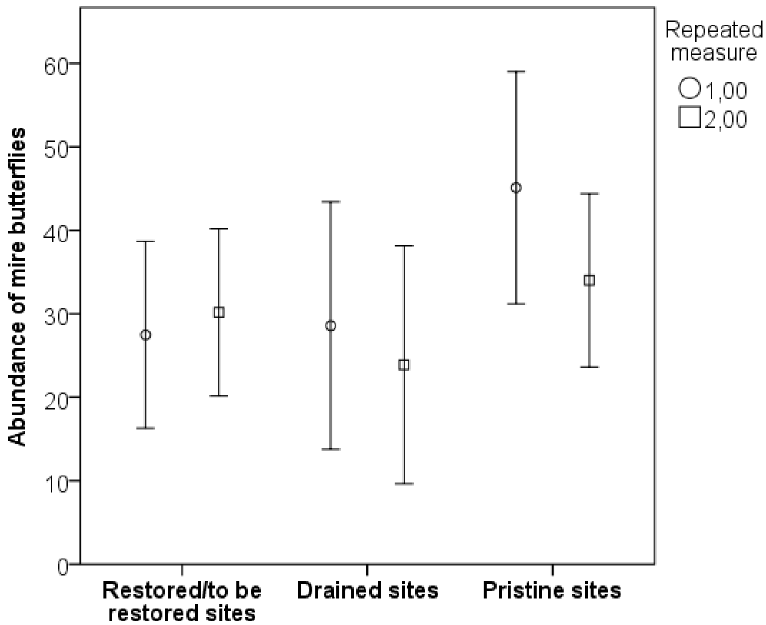

Figure 5. Abundance of mire butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of other butterflies (first observation period after restoration)

When we analyzed all other (generalist) species, repeated measure had an effect on species richness, but treatment, number of visits or the interaction between repeated measure and treatment had no effect (Table 8, figure 6).

The difference between repeated measures was such that there were more other butterfly species on the second observation period than on the first period (Pairwise LSD comparison, MD = 0,577, SE = 0,248, df = 65,302, p = 0,023).

Table 8. Mixed model analysis for richness of other butterfly species

Source	Numerator df	Denominator df	F	p
Intercept	1	50,711	26,465	< 0,001
Repeated measure	1	65,302	5,423	0,023
Treatment	2	40,452	2,019	0,146
Number of visits	1	52,868	0,051	0,822
Repeated measure*Treatment	2	58,620	0,941	0,396

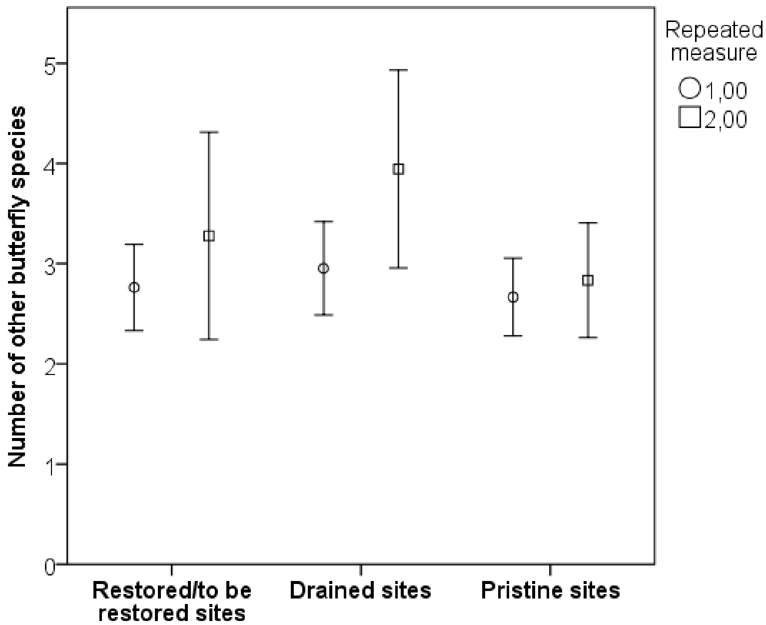

Figure 6. Number of other butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of other butterflies (first observation period after restoration)

Repeated measure had an effect on abundance of other butterflies and treatment tended to have an effect, but number of visits or interaction between repeated measure and treatment had no effect on abundance of other butterflies (Table 9, Figure 7).

The difference between repeated measures were such that there were more other butterfly individuals on the second observation period than on the first period (Pairwise LSD comparison, MD = 0,267, SE = 0,127, df = 55,276, p = 0,040). There were more other butterfly individuals in restored sites than in drained sites (Pairwise LSD comparison, MD = 0,516, SE = 0,225, df = 40,025, p = 0,027) and there tended to be more individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,426, SE = 0,225, df = 40,021, p = 0,066). There were no difference between restored and pristine sites (Pairwise LSD comparison, MD = 0,090, SE = 0,225, df = 40,021, p = 0,691).

Table 9. Mixed model analysis for abundance of other butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	69,910	81,837	< 0,001
Repeated measure	1	55,276	4,446	0,040
Treatment	2	40,022	2,994	0,061
Number of visits	1	65,615	0,034	0,854
Repeated measure*Treatment	2	52,861	2,294	0,111

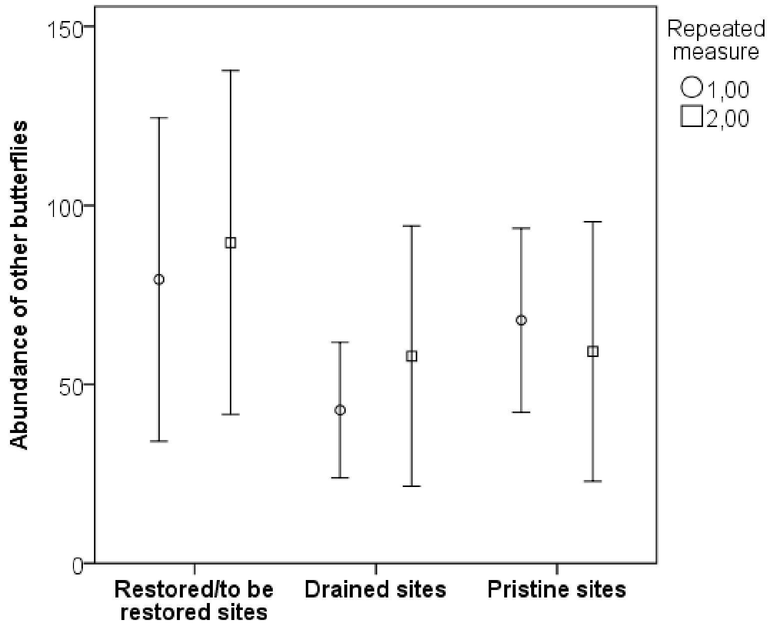

Figure 7. Abundance of other butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of mire butterflies (includes also second observation period after restoration, when this data is available)

We found an interaction between repeated measure and treatment (Table 10). Interaction was such that there were more mire butterfly species after restoration in restored sites (Figure 8). Treatment had also an effect on mire butterfly species richness, but number of visits had no effect (Table 10). There were more mire species in pristine sites than in restored (Pairwise LSD comparison, MD = 1,744, SE = 0,419, df = 41,648, p < 0,001) or in drained sites (Pairwise LSD comparison, MD = 3,094, SE = 0,419, df = 41,642, p <0,001). There was also a difference between restored and drained sites, such that there were more species in restored sites (Pairwise LSD comparison, MD = 1,350, SE = 0,419, df = 41,649, p = 0,002) (Figure 8).

Table 10. Mixed model analysis for mire species richness

Source	Numerator df	Denominator df	F	p
Intercept	1	64,014	34,147	< 0,001
Repeated measure	1	63,532	0,725	0,398
Treatment	2	41,646	27,442	< 0,001
Number of visits	1	68,753	2,305	0,134
Repeated measure*Treatment	2	56,671	3,920	0,025

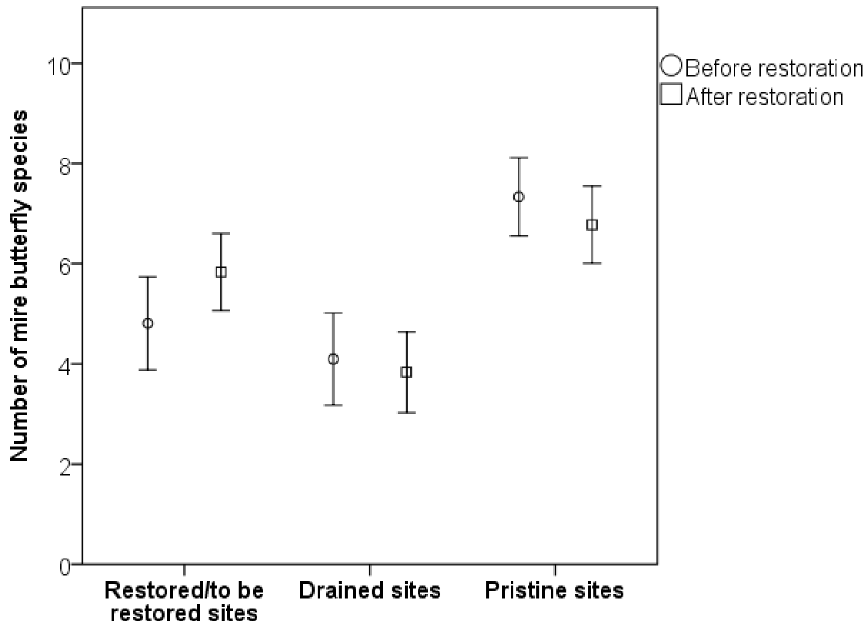

Figure 8. Number of mire butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of mire butterflies (includes also second observation period after restoration, when this data is available)

Treatment had an effect on mire butterfly abundance, but repeated measure, number of visits or interaction between repeated measure and treatment had no effect (Table 11). There were more mire butterfly individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,781, SE = 0,209, df = 41,389, p < 0,001) or in restored sites (Pairwise LSD comparison, MD = 0,475, SE = 0,209, df = 41,394 , p = 0,028) but there were no difference between restored and drained sites (Pairwise LSD comparison, MD = 0,306, SE = 0,209, df = 41,395, p = 0,152) (Figure 9).

Table 11. Mixed model analysis for abundance of mire butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	67,423	90,855	< 0,001
Repeated measure	1	60,905	0,342	0,561
Treatment	2	41,393	7,074	0,002
Number of visits	1	71,710	0,057	0,812
Repeated measure*Treatment	2	54,454	1,378	0,261

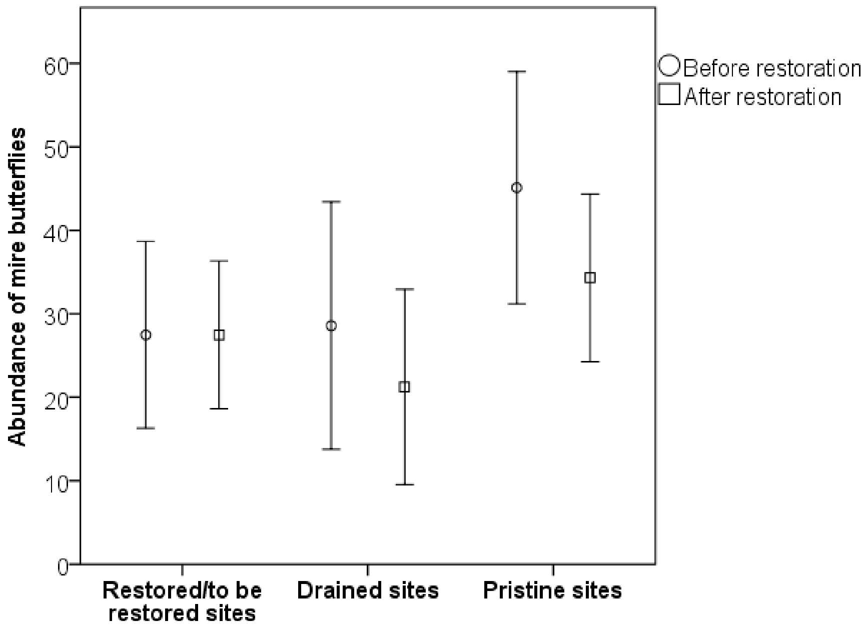

Figure 9. Abundance of mire butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of other butterflies (includes also second observation period after restoration, when this data is available)

When we analyzed all other (generalist) species, repeated measure had an effect on species richness, but treatment, number of visits or the interaction between repeated measure and treatment had no effect (Table 8, figure 10).

The difference between repeated measures was such that there were more other butterfly species after restoration (Pairwise LSD comparison, MD = 0,577, SE = 0,248, df = 65,302, p = 0,023). However, this result does not mean that restoration had an effect because there was no interaction, but simply that during the latter samplings there was in general more species.

Table 12. Mixed model analysis for richness of other butterfly species

Source	Numerator df	Denominator df	F	p
Intercept	1	46,477	24,595	< 0,001
Repeated measure	1	65,738	10,008	0,002
Treatment	2	40,346	2,282	0,115
Number of visits	1	48,112	0,116	0,735
Repeated measure*Treatment	2	59,013	1,007	0,372

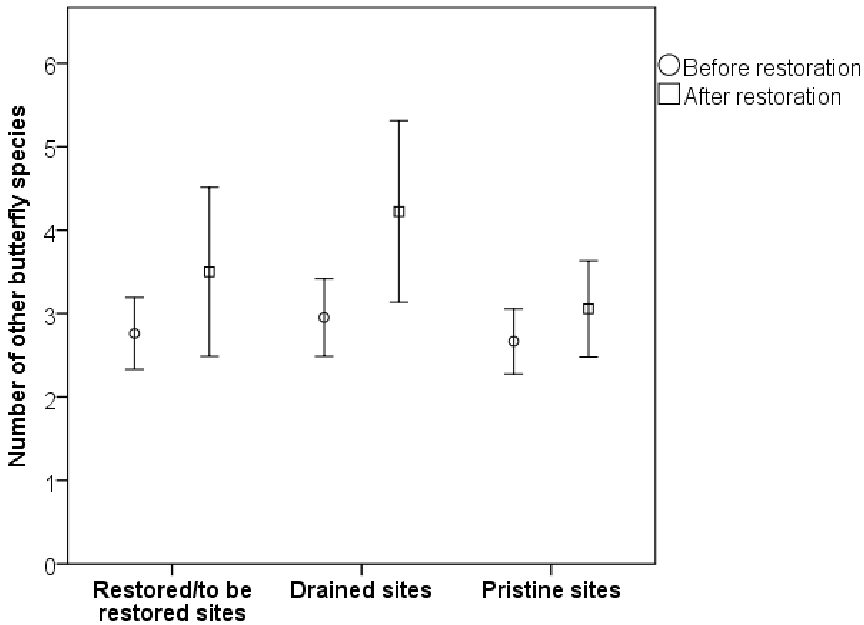

Figure 10. Number of other butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of other butterflies (includes also second observation period after restoration, when this data is available)

Interaction between repeated measure and treatment tended to have an effect on abundance of other butterflies. Interaction was such that there were less other butterfly individuals in pristine sites after restoration. Also treatment tended to have an effect. (Table 13, Figure 11). There were more other butterfly individuals in restored sites than in drained sites (Pairwise LSD comparison, MD = 0,535, SE = 0,223, df = 39,983, p = 0,021) and there tended to be more individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,410, SE = 0,223, df = 39,978, p = 0,073). There were no difference between restored and pristine sites (Pairwise LSD comparison, MD = 0,125, SE = 0,223, df = 39,983, p = 0,577).

Table 13. Mixed model analysis for abundance of other butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	69,690	94,309	< 0,001
Repeated measure	1	55,753	1,990	0,164
Treatment	2	39,981	3,154	0,053
Number of visits	1	67,060	0,115	0,736
Repeated measure*Treatment	2	52,591	3,153	0,051

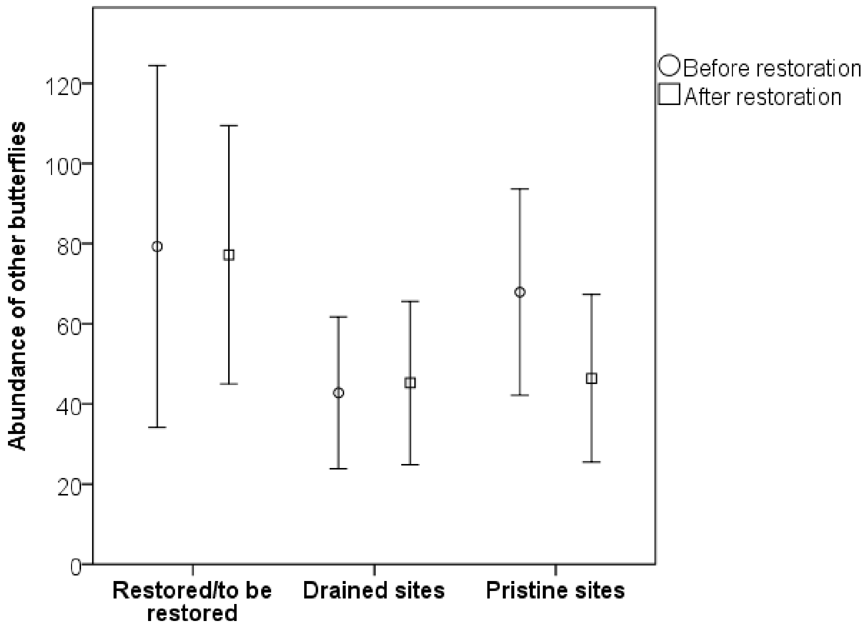

Figure 11. Abundance of other butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of mire butterflies (includes also second and third observation period after restoration, when this data is available)

We found an interaction between repeated measure and treatment (Table 14). Interaction was such that there were more mire butterfly species after restoration in restored sites (Figure 12). Treatment had also an effect on mire butterfly species richness and number of visits tended to have an effect (Table 14). There were more mire species in pristine sites than in restored (Pairwise LSD comparison, MD = 1,770, SE = 0,430, df = 41,671, p < 0,001) or in drained sites (Pairwise LSD comparison, MD = 3,144, SE = 0,430, df = 41,674, p <0,001). There was also a difference between restored and drained sites, such that there were more species in restored sites (Pairwise LSD comparison, MD = 1,375, SE = 0,430, df = 41,682, p = 0,003) (Figure 12).

Table 14. Mixed model analysis for mire species richness

Source	Numerator df	Denominator df	F	p
Intercept	1	64,788	29,604	< 0,001
Repeated measure	1	63,348	1,692	0,198
Treatment	2	41,676	26,896	< 0,001
Number of visits	1	69,448	2,817	0,098
Repeated measure*Treatment	2	56,842	3,572	0,035

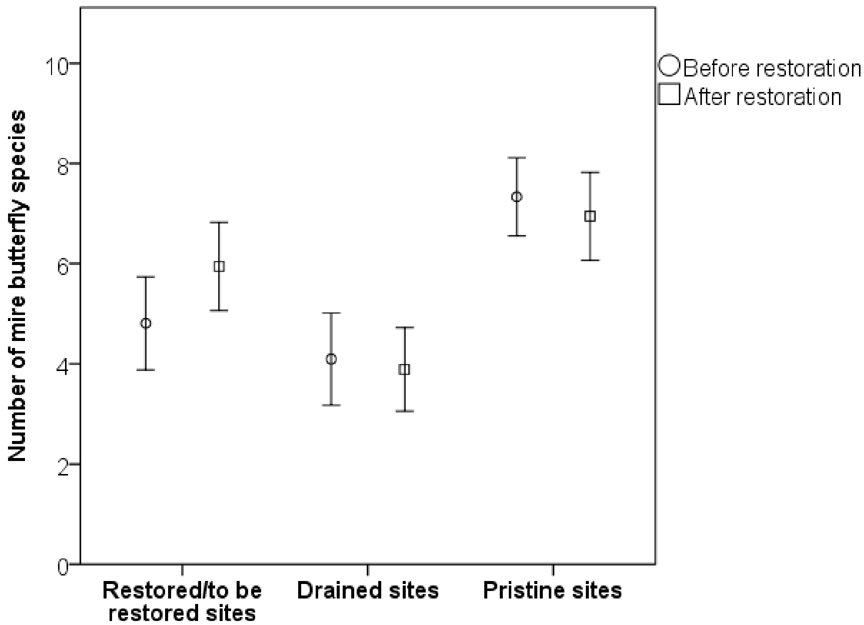

Figure 12. Number of mire butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of mire butterflies (includes also second and third observation period after restoration, when this data is available)

Treatment had an effect on mire butterfly abundance, but repeated measure, number of visits or interaction between repeated measure and treatment had no effect (Table 15). There were more mire butterfly individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,781, SE = 0,209, df = 41,393, p = 0,001) or in restored sites (Pairwise LSD comparison, MD = 0,476, SE = 0,209, df = 41,391, p = 0,028) but there were no difference between restored and drained sites (Pairwise LSD comparison, MD = 0,306, SE = 0,209, df = 41,399, p = 0,151) (Figure 13).

Table 15. Mixed model analysis for abundance of mire butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	67,699	91,523	< 0,001
Repeated measure	1	60,577	0,371	0,545
Treatment	2	41,394	7,082	0,002
Number of visits	1	71,835	0,088	0,767
Repeated measure*Treatment	2	54,322	1,381	0,260

Figure 13. Abundance of mire butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of other butterflies (includes also second and third observation period after restoration, when this data is available)

When we analyzed all other (generalist) species, repeated measure had an effect on species richness, but treatment, number of visits or the interaction between repeated measure and treatment had no effect (Table 16, figure 14).

The difference between repeated measures was such that there were more other butterfly species after restoration than before restoration (Pairwise LSD comparison, MD = 0,953, SE = 0,286, df = 65,762, p = 0,001).

Table 16. Mixed model analysis for richness of other butterfly species

Source	Numerator df	Denominator df	F	p
Intercept	1	49,971	18,353	< 0,001
Repeated measure	1	65,762	11,094	0,001
Treatment	2	40,395	2,262	0,117
Number of visits	1	52,160	0,200	0,657
Repeated measure*Treatment	2	59,058	0,976	0,383

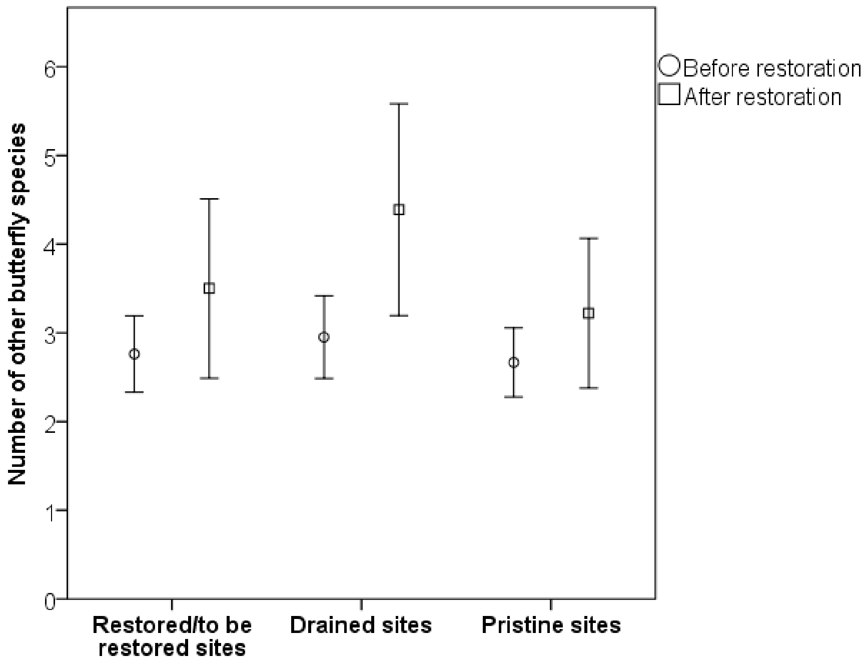

Figure 14. Number of other butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of other butterflies (includes also second and third observation period after restoration, when this data is available)

Interaction between repeated measure and treatment tended to have an effect on abundance of other butterflies. Interaction was such that there were less other butterfly individuals in pristine sites after restoration. Also treatment tended to have an effect. (Table 17, Figure 15). There were more other butterfly individuals in restored sites than in drained sites (Pairwise LSD comparison, MD = 0,535, SE = 0,223, df = 39,988, p = 0,021) and there tended to be more individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,410, SE = 0,223, df =39,982, p = 0,073). There were no difference between restored and pristine sites (Pairwise LSD comparison, MD = 0,125, SE = 0,223, df = 39,980, p = 0,577).

Table 17. Mixed model analysis for abundance of other butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	69,775	93,942	< 0,001
Repeated measure	1	55,649	2,027	0,160
Treatment	2	39,983	3,157	0,053
Number of visits	1	66,928	0,109	0,743
Repeated measure*Treatment	2	52,667	3,147	0,051

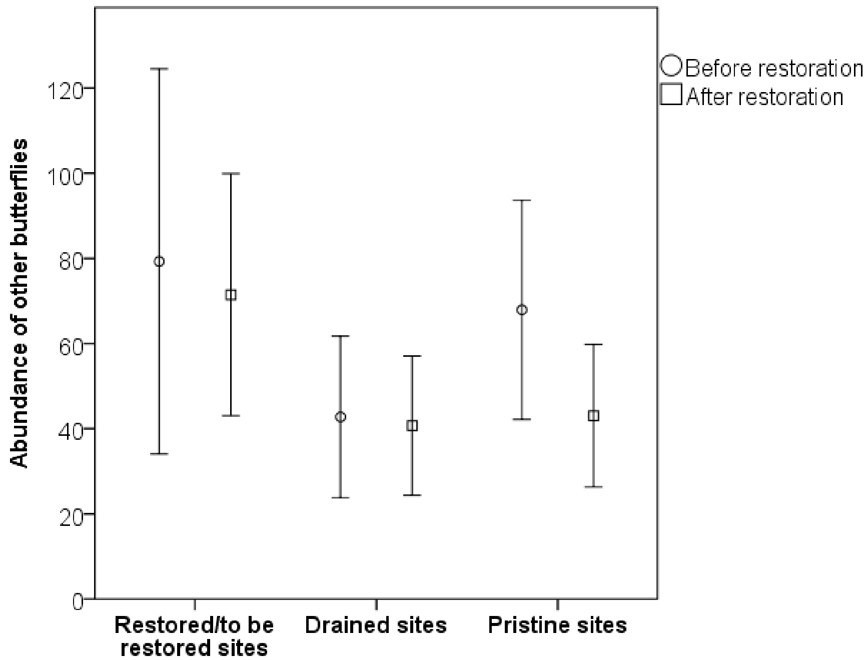

Figure 15. Abundance of other butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of mire butterflies (includes also second, third and fourth observation period after restoration, when this data is available)

We found an interaction between repeated measure and treatment (Table 18). Interaction was such that there were more mire butterfly species after restoration in restored sites (Figure 15). Number of mire species tended to be higher after restoration (Pairwise LSD comparison, MD = 0,497, SE = 0,281, df = 63,045, p = 0,083) and also number of visits tended to have an effect. Treatment had also an effect on mire butterfly species richness. There were more mire species in pristine sites than in restored (Pairwise LSD comparison, MD = 1,715, SE = 0,426, df = 41,662, p < 0,001) or in drained sites (Pairwise LSD comparison, MD = 3,116, SE = 0,426, df = 41,664, p <0,001). There was also a difference between restored and drained sites, such that there were more species in restored sites (Pairwise LSD comparison, MD = 1,401, SE = 0,426, df = 41,674, p = 0,002) (Figure 16).

Table 18. Mixed model analysis for mire species richness

Source	Numerator df	Denominator df	F	p
Intercept	1	66,468	26,928	< 0,001
Repeated measure	1	63,045	3,112	0,083
Treatment	2	41,666	26,867	< 0,001
Number of visits	1	71,107	3,272	0,075
Repeated measure*Treatment	2	56,849	4,011	0,023

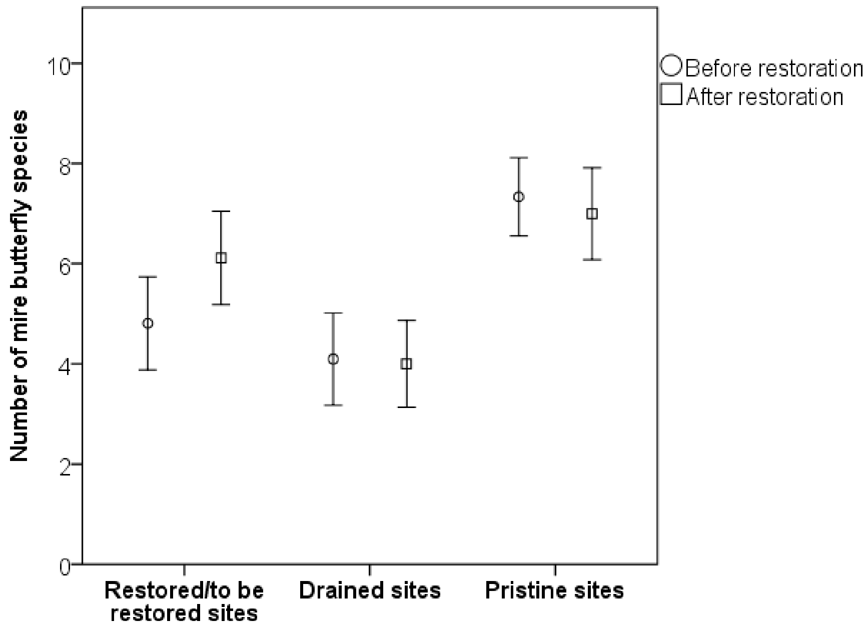

Figure 16. Number of mire butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of mire butterflies (includes also second, third and fourth observation period after restoration, when this data is available)

Treatment had an effect on mire butterfly abundance, but repeated measure, number of visits or interaction between repeated measure and treatment had no effect (Table 19). There were more mire butterfly individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,782, SE = 0,209, df = 41,394, p = 0,001) or in restored sites (Pairwise LSD comparison, MD = 0,475, SE = 0,209, df = 41,392, p = 0,028) but there were no difference between restored and drained sites (Pairwise LSD comparison, MD = 0,306, SE = 0,209, df = 41,401, p = 0,151) (Figure 17).

Table 19. Mixed model analysis for abundance of mire butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	67,549	91,540	< 0,001
Repeated measure	1	60,733	0,379	0,541
Treatment	2	41,396	7,082	0,002
Number of visits	1	71,771	0,097	0,757
Repeated measure*Treatment	2	54,321	1,382	0,260

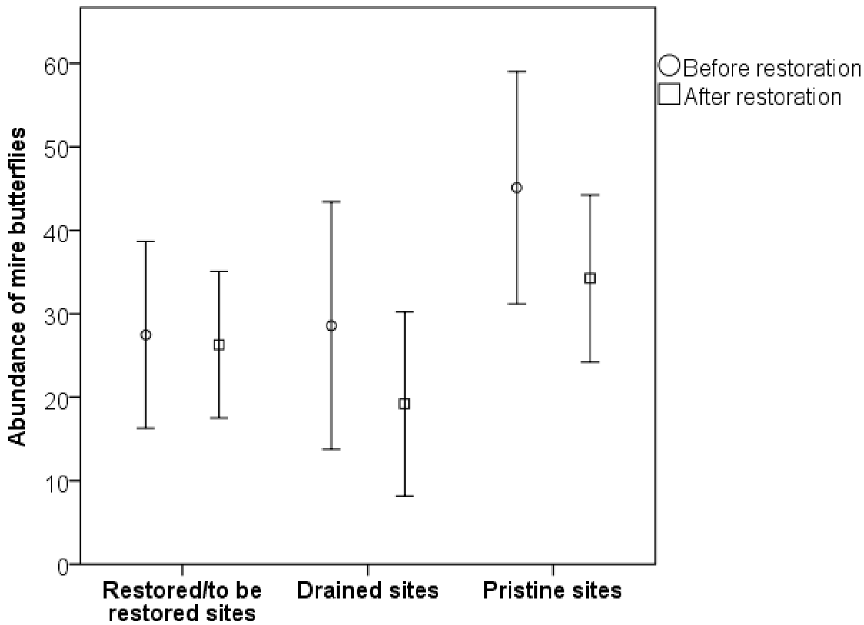

Figure 17. Abundance of mire butterflies (error bars show 95% CI of mean)

Effect of restoration on species richness of other butterflies (includes also second, third and fourth observation period after restoration, when this data is available)

When we analyzed all other (generalist) species, repeated measure had an effect on species richness, but treatment, number of visits or the interaction between repeated measure and treatment had no effect (Table 20, figure 18).

The difference between repeated measures was such that there were more other butterfly species after restoration than before restoration (Pairwise LSD comparison, MD = 0,946, SE = 0,287, df = 65,912, p = 0,002).

Table 20. Mixed model analysis for richness of other butterfly species

Source	Numerator df	Denominator df	F	p
Intercept	1	49,637	18,936	< 0,001
Repeated measure	1	65,912	10,912	0,002
Treatment	2	40,398	2,260	0,117
Number of visits	1	51,785	0,144	0,706
Repeated measure*Treatment	2	59,091	0,975	0,383

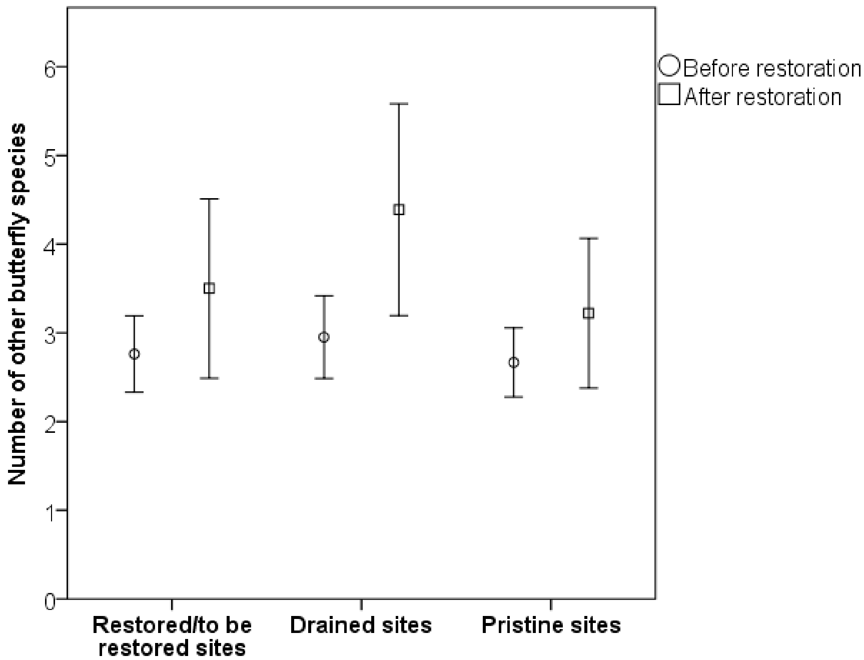

Figure 18. Number of other butterfly species (error bars show 95% CI of mean)

Effect of restoration on abundance of other butterflies (includes also second, third and fourth observation period after restoration, when this data is available)

Interaction between repeated measure and treatment tended to have an effect on abundance of other butterflies. Interaction was such that there were less other butterfly individuals in pristine sites after restoration. Also treatment tended to have an effect (Table 21, Figure 19). There were more other butterfly individuals in restored sites than in drained sites (Pairwise LSD comparison, MD = 0,535, SE = 0,223, df = 39,989, p = 0,021) and there tended to be more individuals in pristine sites than in drained sites (Pairwise LSD comparison, MD = 0,410, SE = 0,223, df = 39,981, p = 0,073). There were no difference between restored and pristine sites (Pairwise LSD comparison, MD = 0,125, SE = 0,223, df = 39,980, p = 0,577).

Table 21. Mixed model analysis for abundance of other butterflies (number of individuals)

Source	Numerator df	Denominator df	F	p
Intercept	1	69,744	94,075	< 0,001
Repeated measure	1	55,755	1,976	0,165
Treatment	2	39,983	3,159	0,053
Number of visits	1	67,068	0,126	0,724
Repeated measure*Treatment	2	52,640	3,147	0,051

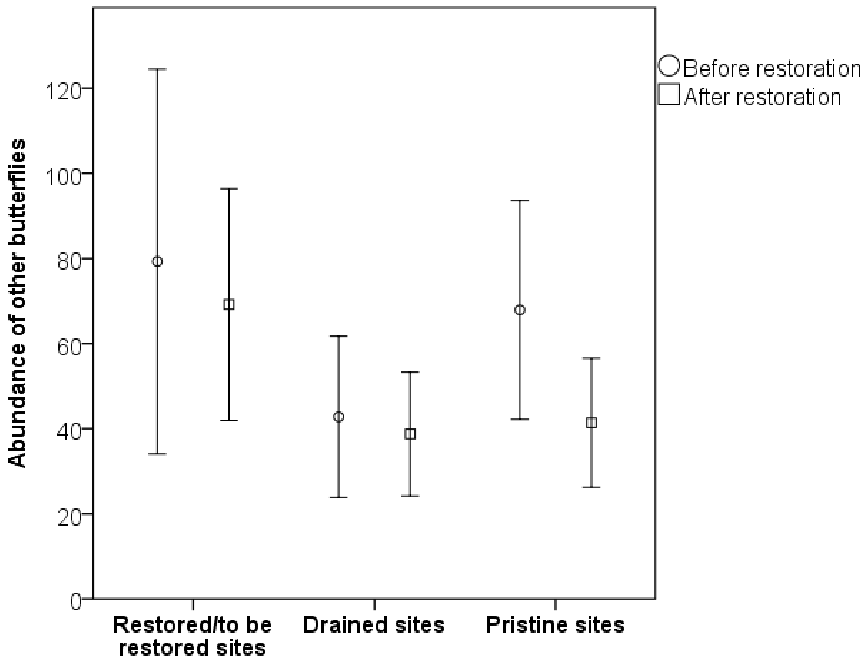

Figure 19. Abundance of other butterflies (error bars show 95% CI of mean)

Effect of restoration on abundance of each species

Results of the effect of restoration on abundance of each species are in table 22. These analyses are conducted with all of the repeated measures included.

Table 22. The effect of restoration on abundance of each species. Species marked with * are classified as mire butterflies. For p-values *<0.05, **<0,01, ***<0,001. Class numbers (1-3) indicate how bonded a mire species is to mire habitats (see section "Butterfly monitoring and environmental variables"). Difference between treatments is mainly between pristine and drained sites (not to be restored). O. jutta is on flight in even years, E. ligea and E.embla mainly in odd years. Hessian matrix was not positive for species written in red (due to small sample size) and thus results for these species should be interpreted with caution.

Species	Class (1-3)	Repeated measure		Number of visits		Treatment		Repeated measure*Treatment	
		F	p	F	p	F	p	F	p
*Albulina optilete**	2	5,684	<0,001 ***	1,261	0,265	0,024	0,976	0,694	0,696
*Boloria aquilonaris**	1	2,657	0,039*	1,845	0,178	22,246	<0,001 ***	1,245	0,285
*Boloria eunomia**	1	0,796	0,530	15,150	<0,001 ***	3,950	0,026*	0,646	0,737
*Boloria euphrosyne**	3	4,563	0,002**	0,121	0,728	0,373	0,691	1,583	0,140
*Boloria freija**	1	0,836	0,505	1,947	0,167	3,370	0,042*	0,614	0,764

*Boloria frigga**	1	1,322	0,268	1,473	0,227	3,212	0,045*	1,108	0,366
Boloria selene	-	1,876	0,120	0,005	0,945	1,242	0,298	0,580	0,792
*Brenthis ino**	3	4,253	0,003	1,698	0,196	1,377	0,263	0,991	0,449
Callophrys rubi	-	1,088	0,366	0,102	0,750	8,006	0,001**	0,829	0,579
Celastrina argiolus	-	3,276	0,014*	1,255	0,266	3,809	0,029*	0,651	0,733
*Coenonympha tullia**	2	1,530	0,198	2,743	0,102	20,725	<0,001***	0,748	0,649
*Colias palaeno**	2	0,295	0,880	21,845	<0,001***	1,371	0,264	0,900	0,520
*Erebia embla**	1	0,263	0,901	3,953	0,050	0,539	0,586	0,254	0,978
Erebia ligea	-	2,327	0,060	12,793	<0,001***	4,144	0,020*	1,278	0,262
Gonepteryx rhamni	-	0,816	0,518	5,557	0,022*	0,118	0,889	0,471	0,873
*Oeneis jutta**	1	4,260	0,004**	11,570	0,001**	5,534	0,007**	1,841	0,082
Pieris napi	-	0,576	0,680	0,188	0,666	2,451	0,094	1,478	0,176
Plebeius argus/idas	-	5,042	0,001**	0,011	0,916	5,361	0,008**	0,568	0,802
*Pyrgus centaureae**	1	0,645	0,632	0,675	0,414	0,355	0,703	0,358	0,940

Discussion

Effect of drainage

It has been stated, that drained sites to be restored were chosen to be restored partly based on natural values of the sites (Boreal Peatland Life Project 2008). We found no difference in mire species richness or abundance between drained sites to be restored and drained sites that will remain in forestry use when all data was analyzed. However, in older dataset (years 2003 and 2007) there was a difference in mire species richness between drained sites to be restored and drained sites that remained in forestry use (Loukola 2008).

In the analyses before restoration and after restoration, we found that both abundance and species richness of mire species were lower in drained sites than in pristine sites. Similar conclusions about the decline of mire butterflies following drainage have also been reached in other studies (Rintala et al. 2000, Hiltula et al. 2005, Pöyry 2001, Uusitalo 2006, Loukola 2008). Mire species decline after drainage has been connected to changes in microclimates and vegetation (Pöyry 2001). However, it has been noted, that physical characteristic of mires are more important for mire butterflies than mere plant species composition (Marttila 2005, Pöyry 2001). Many mire butterfly larvae are polyphagous and live on hummock plants and dwarf shrubs that are less affected by drainage. These plants usually start to decline only when forest becomes too shady, which may take decades (Laine et al. 1995).

In generalist species, drainage did not have an effect on species richness. However, treatment tended to have such an effect that there were more generalist butterfly individuals in pristine sites than in drained sites.

Mire butterfly species most vulnerable to habitat changes are *Pyrgus centaureae, Boloria freija, Boloria frigga* and *Erebia embla* (Pöyry 2001, Uusitalo et al. 2006). All these species are class 1 species (Pöyry et al. 2001), meaning they are tightly specialized to mire habitats. These species disappear soon after drainage and it has been suggested, that the early life stages of these species are very sensitive to microclimatic changes (Pöyry & Loukola 2013). Our results are partly in line with these suggestions, because *B. freija* and *B. frigga* were among species that most suffered from drainage. Lack of significant effect of treatment on *P. centaurea* and *E.embla* may be due to low number of observations and thus weak power of the analyses. Overall, in our study the effect of treatment on individual species seems to be dependent on how dependent a species is from the mire habitats, because 5 out of 7 species most dependent on mire habitats (class 1 species) were mainly observed in pristine sites, whereas treatment had no effect on mire species least dependent on mire habitats (class 3 species), *Brenthis ino* and *Boloria euphrosyne*. Only two species, both generalist butterflies, were more abundant in drained sites than in pristine sites. Generalist butterflies have not strict habitat requirements related to microclimate prevailing in pristine mires (Marttila et al. 1990, Pöyry 2001).

Effect of restoration

When analyzing the effects of restoration, we found that the number of mire species increased in restored sites. When inspecting the effects of treatment, we saw that before restoration, there was no difference in mire species richness between drained sites and drained sites to be restored. After restoration there were more mire species in restored sites than in drained sites. However, abundance (number of individuals) of mire butterflies as a group or tested as individual species did not increase after restoration.

Species colonization of restored habitats is a slow process (species credit, Hanski et al. 2000). Colonization may be hindered by low dispersal ability, because butterfly species living in fragmented landscapes typically disperse at most couple of kilometers (Thomas & Hanski 2004) and species specialized in their habitats are less mobile than species with wider niche breadth (Warren et al. 2001, Komonen et al. 2004). There is no specific information of dispersal behavior of mire butterflies, but according to expert evaluations (Komonen et al 2004.) most specialized mire species have low dispersal ability. In one case study in Seitseminen national park, restoration had no effect on mire butterfly species richness after four years, but after 11 years 4 mire species had returned into area (Turunen 1998). Restoration actions have been conducted quite recently in our study areas and result of increased numbers of mire species this soon after restoration is encouraging.

There were more other butterfly species after restoration than before restoration and abundance of other butterflies tended to decrease in pristine sites after restoration. These species richness results are independent of the treatments (no interactions) and can probably be explained by annual variation in butterfly numbers which is typical in Finland (Marttila 2005).

Conclusions

We found a clear negative effect of drainage on both abundance and species richness of mire butterflies. We also found an encouraging result that the number of mire butterfly species increased already few years after restoration in the restored sites.

Although new ditches are no longer being dug in Finland's peatlands the state of our peatland habitats is still deteriorating due to the impacts of earlier drainage schemes. Many potentially restorable drained peatlands still have relict populations of mire butterflies or they have recolonization sources of endangered butterflies nearby. This project provided evidence that restoration is successful and increases number of mire specialist species in restored mires.

Existing experimental setups of this study form an interesting monitoring opportunity to increase knowledge about the long term effects of restoration and monitoring should be continued to judge the long term impacts of mire restoration in Finland.

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Year	Number of mires	Number of species	Number of individuals	Mire butterfly species	Mire butterfly individuals	Species in restored sites/sites to be restored	Individuals in restored sites/sites to be restored	Species in drained sites	Individuals in drained sites	Species in pristine sites	Individuals in pristine sites
2003	9	21	1909	11	832	18	782	13	358	17	766
2007	9	28	2101	11	912	22	966	17	471	19	664
2010	12	27	4188	12	1292	18	1494	20	1082	21	1612
2011	2	20	1824	9	302	11	682	15	622	14	520
2012	4	15	665	10	210	13	293	8	159	14	213
2013	5	22	1017	10	293	13	403	14	269	15	345
2014	10	21	1910	12	580	16	868	15	363	17	679

Appendix 1. Numbers of study mires, species and individuals in different sites

Species	2003 (9 mires)	2007 (9 mires)
*Albulina optilete**	140	264
Argynnis aglaja	0	1
Aporia crataegi	0	5
*Boloria aquilonaris**	32	65
*Boloria eunomia**	123	84
*Boloria euphrosyne**	171	245
*Boloria freija**	12	2
*Boloria frigga**	19	27
Boloria selene	3	12
*Brenthis ino**	64	67
Callophrys rubi	123	249
Carterocephalus silvicola	0	2
Celastrina argiolus	2	11
*Coenonympha tullia**	58	40
*Colias palaeno**	198	115
*Erebia embla**	7	1
Erebia ligea	22	23
Gonepteryx rhamni	7	11
Lasiommata petropolitana	0	1
Leptidea sinapis	0	1
Mellica athalia	1	6
Nymphalis antiopa	3	1
Papilio machaon	0	3
Pieris napi	4	4
Plebeius argus	911	854
*Pyrgus centaureae**	8	2
Thymelicus lineola	0	1
Vanessa cardui	1	5

Appendix 2. Species observed in 2003 and 2007. Species marked with * are classified as mire species (Pöyry et al., classes 1-3). *O. jutta* is missing because it is on flight in even years.

Species	2010 (12 areas)	2011 (2 areas)	2012 (4 areas)	2013 (5 areas)	2014 (10 areas)
*Albulina optilete**	228	174	48	12	44
Anthocharis cardamines	0	0	0	1	0
Aphantopus hyperantus	0	0	0	4	0
Argynnis aglaja	0	0	0	0	1
*Boloria aquilonaris**	223	31	30	68	217
*Boloria eunomia**	51	6	14	17	39
*Boloria euphrosyne**	202	53	42	34	43
*Boloria freija**	20	0	9	3	5
*Boloria frigga**	2	2	0	6	1
Boloria selene	2	4	2	2	1
*Brenthis ino**	246	22	23	33	62
Callophrys rubi	359	70	165	140	184
Celastrina argiolus	49	13	28	28	22
Coenonympha pamphilus	0	0	0	0	6
*Coenonympha tullia**	51	8	11	28	47
*Colias palaeno**	96	5	13	48	53
*Erebia embla**	9	1	0	1	14
Erebia ligea	4	15	0	15	4
Gonepteryx rhamni	0	0	0	1	0
Lasiommata petropolitana	1	1	0	1	0
Lycaena virgaurea	3	1	0	0	0
Nymphalis antiopa	1	1	0	2	2
Nymphalis c-album	1	0	0	0	0
Nymphalis io	4	0	0	0	0
Nymphalis urticae	4	0	0	0	0
*Oeneis jutta**	162	0	19	0	54
Papilio machaon	1	0	0	0	0
Pieris brassicae	2	1	0	0	0
Pieris napi	5	4	1	5	4
Plebeius argus/idas	2459	1408	259	534	1106
*Pyrgus centaureae**	3	0	1	0	1
Pyrgus malvae	0	0	0	1	0
Thymelicus lineola	1	4	0	0	0

Appendix 3. Species observed in Boreal Peatland Life-project mires during years 2010-2014. Species marked with * are classified as mire species (Pöyry et al., classes 1-3). *O. jutta* is on flight in even years and *E. embla* mainly in odd years.

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Species	2003 before restoration	2007 after restoration	2010 before restoration	2011 after restoration	2012 after restoration	2013 after restoration	2014 after restoration
*Albulina optilete**	4,11	11,56	4,42	36,00	3,50	0,60	1,4
*Boloria aquilonaris**	0,55	2,44	4,42	5,50	1,50	1,20	5,6
*Boloria eunomia**	4,22	1,89	0,42	1,00	0,25	1,80	1,8
*Boloria euphrosyne**	7,88	9,33	4,00	8,50	5,25	1,40	1,5
*Boloria freija**	0,44	0	0,08	0	0,25	0	0,1
*Boloria frigga**	0,11	0,11	0	0	0	0	0
Boloria selene	0,11	0,33	0	0,50	0	0	0,1
*Brenthis ino**	3,67	4,67	8,25	5,50	3,75	3,20	2,5
Callophrys rubi	4,44	12,11	9,33	16,00	16,75	14,20	6,9
Celastrina argiolus	0,11	0,67	0,83	3,00	2,50	2,20	0,2
*Coenonympha tullia**	1,00	1,33	0,75	0	1,00	0,80	0,6
*Colias palaeno**	7,00	6,33	2,08	1,50	1,50	2,80	2,6
*Erebia embla**	0,11	0	0	0	0	0	0,1
Erebia ligea	0,78	0,44	0,33	0	0	1,2	0,3
Gonepteryx rhamni	0,44	0,67	0	0	0	0	0
*Oeneis jutta**	0	0	1,67	0	0,25	0	0,5
Pieris napi	0,44	0	0,08	1,50	0	0,40	0
Plebeius argus/idas	44,89	45,67	87,42	262,00	36,75	50,60	62,5
*Pyrgus centaureae**	0,11	0,11	0,08	0	0	0	0

Appendix 4. Mean number of individuals of each species that were observed at minimum 10 times during the whole study, counted per restored/to be restored site. Number of sites 9 in 2003 and in 2007, 12 in 2010, 2 in 2011, 4 in 2012, 5 in 2013 and 10 in 2014.

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Pristine site in Pyhä-Häkki National Park (Photo: Paula Rantanen, 2010)

Restored site in Pyhä-Häkki (Photo: Niina Sormunen, 2013, restored 2012).

Drained site in Pyhä-Häkki (Photo: Paula Rantanen, 2010)

Restored site in Kiemanneva (Photo: Anna Uusitalo, 2004 restored 2004)

Restored site in Kulhanvuori (Photo: Teemu Rintala, 2003, restored 2003)

Pristine site in Haapakeidas (Photo: Terhi Lensu, 2010)

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Pristine site in Kauhaneva (Photo: Terhi Lensu 2010)

Drained site in Kauhaneva (Photo: Terhi Lensu 2010)

Drained site before restoration in Kauhaneva (Photo: Terhi Lensu 2010)

Pristine site in Kukilankeidas (Photo: Terhi Lensu 2010)

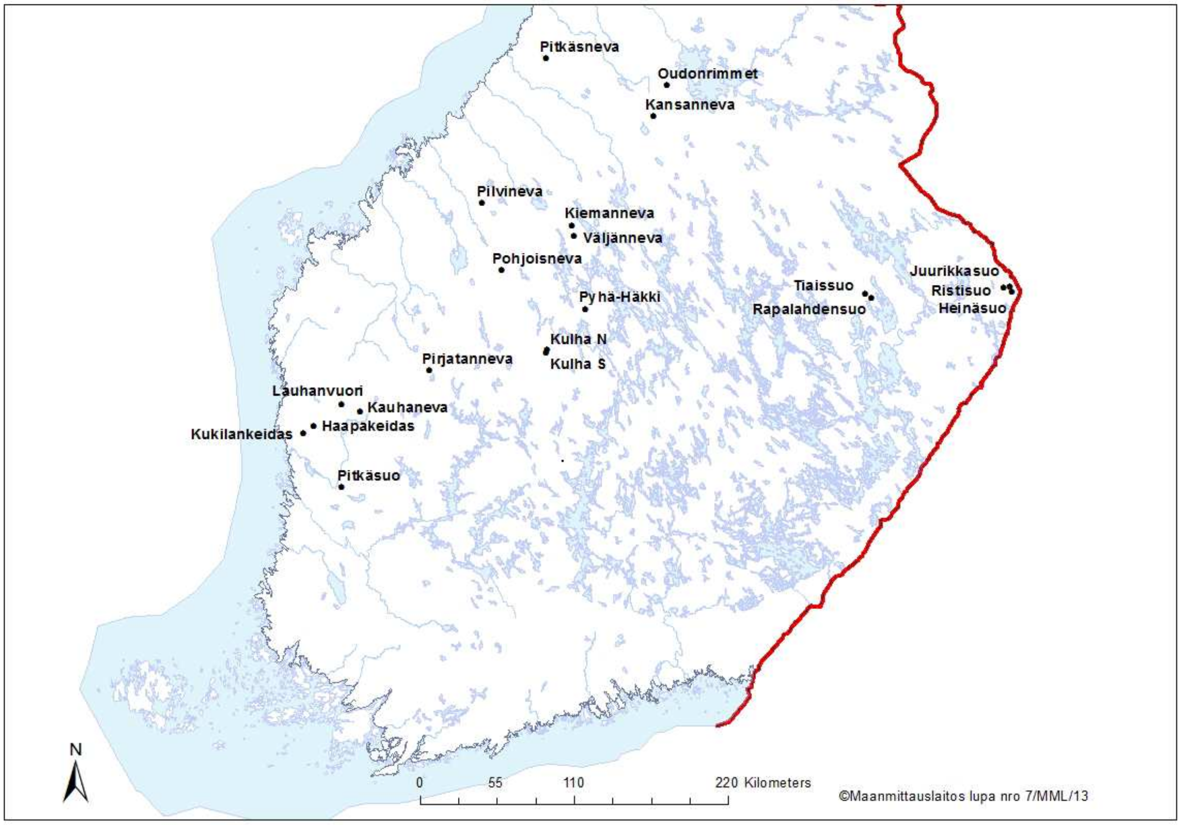

Figure X. Study area locations

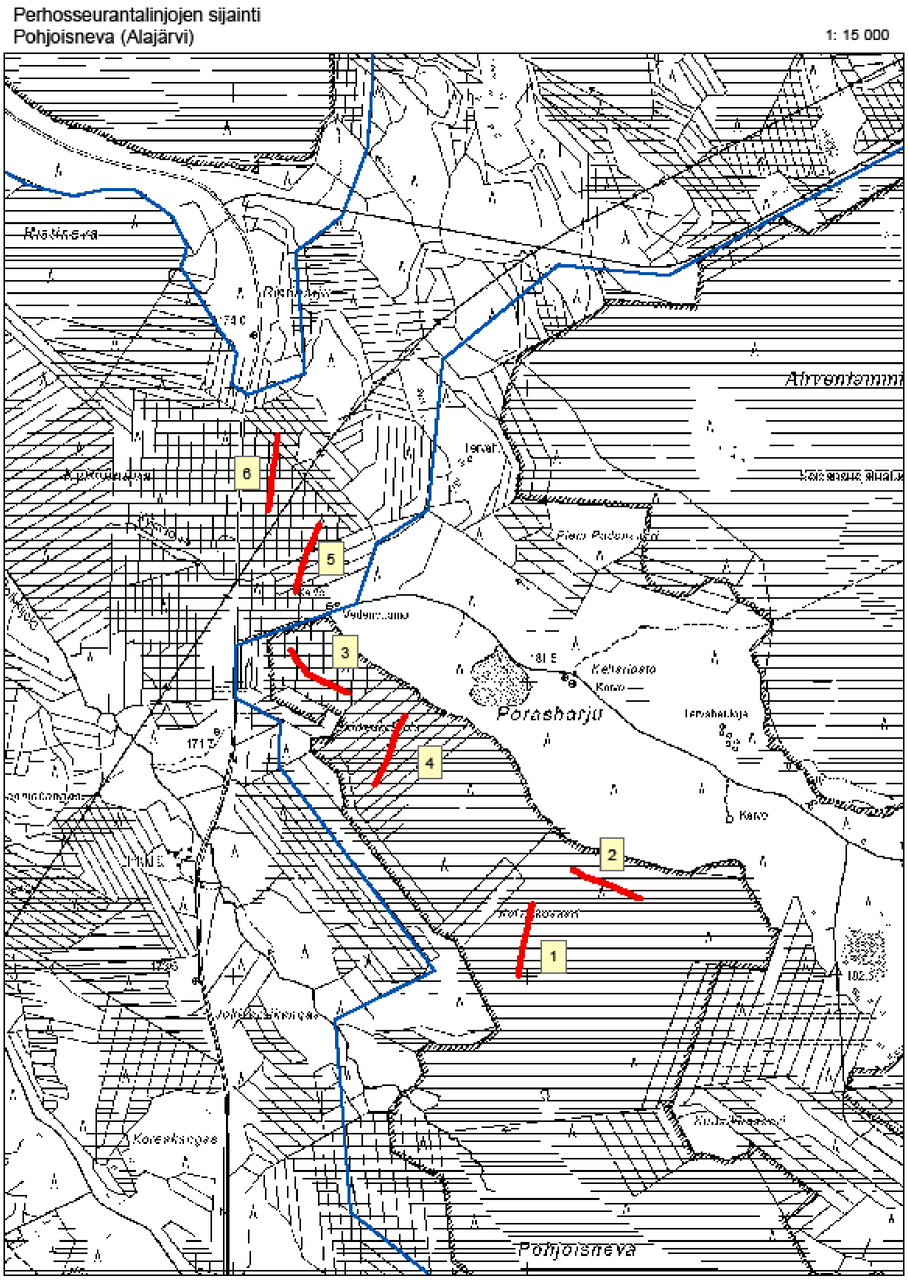

Figure X. Example of a study area with 6 transect lines (1 and 2 = pristine site, 3 and 4 = restored, 5 and 6 = drained site in forestry use)

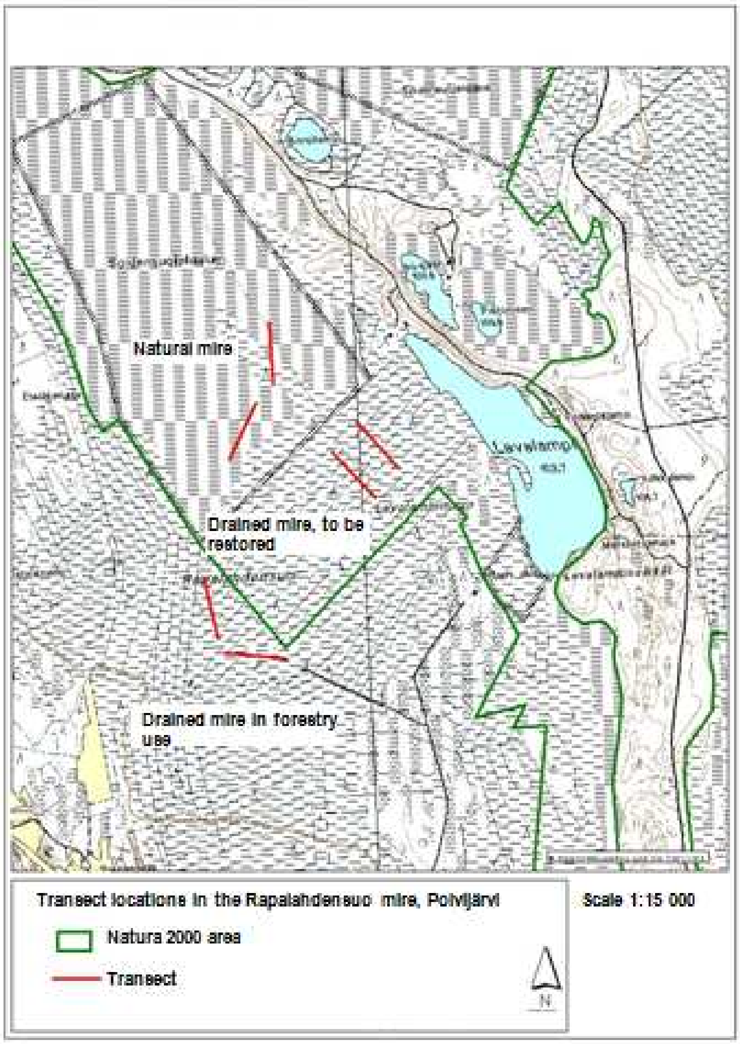

Figure X. Transect locations in one study area.