Hydrology LIFE (LIFE16/NAT/FI/000583)

Action D4: Monitoring protected bats

Final report: Restoration of boreal wetlands increases bat activity but not species richness

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Summary

The presence of water promotes insect life and provides drinking water for wildlife. Wetlands are therefore assumed to have a positive influence on bats. We survey the literature on the relationship between bats and find evidence that especially abundance (but not necessarily the presence) of bat species are indeed higher in wetlands. However, much of the research on bats and wetlands has been done in constructed wetlands (created in e.g. formerly agricultural fields), with a geographical emphasis on eastern USA and central Europe. Overall, there is relatively little known about the effects of wetland restoration on bats, especially in the boreal zone.

As part of the Hydrology LIFE project, 21 sites in wetlands were acoustically monitored for bats. We conducted a Before-After Control Impact (BACI) study. Using acoustic survey techniques we collected information on bats both before and after restoration, with 7 of the 21 wetlands acting as control sites and 14 as impact (i.e. restored) sites. Acoustic surveys were conducted in May – September in the years 2018, 2019 (before restoration) and in 2021 and 2022 (after restoration), although the analysis took into account the realised timing of the restoration. Species detection for each night was assessed by automated analysis of audio recordings. Main species detected in all sites, and the focus of statistical analyses, were the Northern bat (*Eptesicus nilssonii*) and the *Myotis* species group (four *Myotis* species, *M. brandtii*, *M. daubentonii*, *M. mystacinus*, *M. nattereri*, that were grouped). In addition, we detected Nathusius' pipistrelle (*Pipistrellus nathusii*) although mainly at one site, and had low abundance detection of long-eared bats (*Plecotus auritus*) and individual recordings of noctule bats (*Nyctalus noctula*).

The analyses showed that wetland restoration increased the abundance of Northern bats and the *Myotis* species group, but not the presence of these species. Thus, the restoration primarily increased the usage of wetlands as a feeding site for bats. Our findings are in line with previously published studies. Nevertheless, as our study is a BACI study, the findings provide strong evidence that the restoration activity was the cause of the observed increase in bat activity. We conclude with some recommendations on how to take into account bats when planning wetland restoration.

1. Background

Wetlands are one of the most threatened types of ecosystems, while also being one of the most important ones (Hu et al., 2017; Xu et al., 2019). They, among other things, host a rich biodiversity, are part of the water cycle, provide ecosystemic services to humans, and therefore play an essential role against global climate change (Ramsar Convention Bureau, 2001; Erwin, 2009). But they also face destruction and degradation, through drainage, pollution, or eutrophication for instance, that impede their various roles and capacities (Xu et al., 2019). To that effect, the conservation of wetlands seems critical. But as more than 33 % of them has been lost already (Hu et al., 2017), more actions, such as restoration and construction, are needed to preserve these ecosystems and the roles they play.

One of the roles of wetlands is to provide services to bats: permanent water in wetlands favours the development and abundance of multiple insect species, on which numerous bat species feed, and of other prey such as fish (Salvarina, 2016). Wetlands are also a source of drinking water for bats, and can offer roosting opportunities for some species through the presence of decaying trees (Salvarina, 2016). The importance of wetlands for bats is not only restricted to the temperate climate: from the Amazon to arid environments, presence of water is crucial for bats (Flaquer, 2009; Bader, 2015; Blakey, 2018; Torrent et al., 2018).

Therefore, wetlands are considered of great importance to all bats, and usually host an important diversity of species there (Salvarina, 2016; Mas et al., 2021). The destruction of wetlands, and the deterioration of their quality, will impact bats. Heavy metal pollution, pesticides, eutrophication, light pollution, habitat loss and fragmentation, are only a few threats that have been reported to negatively impact the richness and activity of bat communities in wetlands (Lookingbill et al., 2010; Korine et al., 2015, 2016; Clarke-Wood et al., 2016; Straka et al., 2016).

Thus, global conservation of bats is affected by the conservation of wetlands, and related efforts of construction and restoration of these ecosystems. Despite their importance to bats, studies on how the restoration of wetlands is affecting the diversity or abundance of bats are quite scarce in the literature (fig. 1). Moreover, they are mostly confined to the monitoring of bats after the restoration work, without any possible comparison to presence and activity of bats prior to action (see Menzel et al., 2005 as an exception). Irrespective of this, most research has been conducted on wetlands previously replaced by woodlands, and shows that once the ditches are plugged and trees felled, restored wetlands host more diverse bat communities than other habitats (Menzel et al., 2005; Allagas et al., 2020; Beranek et al., 2021; Li et al., 2021; Snyder et al., 2022). With restoration actions, the water level rose and the presence of water became a permanent feature, habitats were opened, leading to a greater availability of food and roost. Compared to restored wetlands, more research has

been conducted on constructed wetlands, i.e. wetlands built on sites where no wetland has been recorded in the past, and including water bodies built for other purposes, such as retention ponds (fig. 1). High bat activity has also been recorded at these sites, showing that they could also have an important role in bat conservation.



Figure 1: location of studies monitoring bat activity in restored, constructed or drained wetlands. Studies on actual restoration of wetlands are very limited (green dots), most work having been carried on constructed wetlands (orange dots).

Wetlands are a prominent ecosystem in Finland, covering about 15 % of the country's total area (Corine Land Cover data). These ecosystems have been put under enormous pressure in the past, through exploitation of peat and drainage for transformation into arable lands or commercial tree plantations (Strack, 2008; Norstedt et al., 2021). Consequently, research on wetland restoration and drainage in the country is substantial, with a focus on hydrology more than biodiversity (Bring et al., 2022).

In order to start filling the gap of knowledge regarding wetland restoration and bats in Finland and more broadly in the boreal zone, we assessed the effect of restoration on bat presence and activity in several wetlands of Southwestern Finland. Using a Before After Control Impact -sampling scheme, we monitored bat acoustic activity at control and restored sites during several years, between 2018 and 2022. Based on literature on wetland restoration, we expected the presence and activity of bats to increase once ditches were plugged and trees felled, creating better foraging and roosting conditions for all species.

2. Material and methods

2.1. Sampling design

We monitored bat acoustic activity with passive recorders and using a Before After Control Impact (BACI) design (Green, 1979), meaning that monitoring took place before and after the restoration work at both restoration and control sites. This design allows to discriminate the actual impact of the restoration from spatial and temporal variation in bat activity.

The original plan was to carry out most of the restoration work in 2020. Therefore, the monitoring was designed to cover years 2018–2019 ("Before" years) and 2021–2022 ("After" years), while 2020 was left without monitoring. However, because of practical and logistical reasons, on different sites the restoration was conducted over different years. This resulted in some sites having more "Before" years than "After" years and vice versa.

2.2. Study sites

There were 21 monitoring sites, of which 14 were restoration sites and 7 control sites. The 21 sites were spatially grouped in 10 areas (fig. 2; Table 1). However, not all areas had a control site due to the limited number of detectors available. Control sites were mainly in large national parks, where they were chosen among similar habitats as the restoration sites, however 3 out of the 7 controls were in the Pinkjärvi area due to the postponing of restoration.

Table 1. Description of the study sites. Site refers to the audio-detector for bats. Some sites were close to each other within the same area, but not all areas had multiple sites. For each site, it is denoted under "Impact" whether there was a wetland restoration (R) or not (C). A description of the habitat at each site was scored in classes describing the tree cover (score 1-3), soil productivity (score 1-3) and whether there was open water in the proximity (yes or no). For sites located at a restored wetland the first year during which restoration actions were considered to have an impact on bats (considering the data collecting period May-September) is provided. The impact was either because the restoration has started or was finished. Note that in 2020 no data on bats was collected and wetlands restored in 2020 thus in effect first affected bats in 2021.

Area	Site	Impact	Lon	Lat	Tree cover	Soil productivity	Open water	Restoration time
Finnträsk	FIN	R	24.54	60.13	3	3	Yes	2020
Kalkkilammi	KAL	R	24.65	60.55	2	3	Yes	2021

Kylmässuo	KYL	R	23.06	60.24	2	2	No	2019
Kylmässuo	KYL_K	С	23.06	60.23	3	3	No	
Maisaarensu o	MAI	R	22.64	60.92	3	2	No	2021
Nuuksio	NUU1	R	24.52	60.33	3	3	No	2020
Nuuksio	NUU2	R	24.54	60.34	2	2	Yes	2020
Nuuksio	NUU3	R	24.55	60.33	3	3	No	2021
Nuuksio	VEI	R	24.47	60.27	3	2	Yes	2022
Nuuksio	NUU_ K	С	24.55	60.34	1	1	Yes	
Pinkjärvi- Lastensuo	LAS	R	21.83	61.29	3	2	Yes	2020
Pinkjärvi- Lastensuo	PIN1	С	21.73	61.29	3	3	No	
Pinkjärvi- Lastensuo	PIN2	С	21.76	61.29	2	3	No	
Pinkjärvi- Lastensuo	PIN_K	С	21.75	61.30	2	2	Yes	
Sipoonkorpi	SIP1	R	25.17	60.29	3	3	No	2020
Sipoonkorpi	SIP2	R	25.15	60.31	3	3	Yes	2020
Sipoonkorpi	SIP_K	С	25.16	60.31	2	3	No	
Stormossen	STO	R	22.52	60.06	1	2	No	2019
Vajosuo	VAJ1	R	22.34	60.69	3	1	No	2021
Vajosuo	VAJ2	С	22.36	60.68	1	1	No	2021
Yrttikorpi	YRT	R	23.64	60.50	2	3	Yes	2021

The sites were chosen to represent different types of restored peatlands. Only one detector was installed in each site. In the big national parks, Nuuksio and Sipoonkorpi, there were 2–4 sites within each park, otherwise there was one monitoring site per protected area. Because of the role of woodlands for several species of bats during the boreal summer, we set most of our detectors in such habitats, while a few were located in open and semi-open areas (Vasko et al., 2020; Wermundsen & Siivonen, 2008). To reflect these differences at our sites, we quantified tree cover in the area surrounding the detectors by estimating the rough proportion covered by tree canopy there (Vasko et al., 2020). We also assessed soil productivity at our sites, using Ellenberg indicator values, as a way to predict insect abundance (Diekmann, 2003; Vasko et al., 2020). Finally, we measured distance to the closest open water bodies, because of its importance to all bat species, either for drinking or foraging (Vasko et al., 2020; Wermundsen & Siivonen, 2008).

For each site, restoration done between January and September is considered to affect bats the same year, and the bat recordings of this year can be treated as "after" restoration. Restoration done between October and December is considered to affect bats only the year after, and only the recordings from the next monitoring period will be treated as "after" restoration. For instance, bat activity of 2020 will be considered "after" the restoration is the restoration happened between January and September 2020.



Figure 2: Bat monitoring area in SW Finland. Some cities are indicated with a blue diamond. Areas are indicated with a red dot and their name. Each area had one or more sites. See Table 1 for an overview.

2.3. Acoustic monitoring

We used ultrasonic passive recorders (SongMeter SM4) to record bat echolocation calls at monitoring sites. The devices were programmed to record every night, from dusk until dawn, between May 1st and September 30th. Batteries and memory cards were changed once per month. The detectors were placed 5-15 metres from ditches to avoid the units being damaged during ditch clogging. Microphones were placed 1,5–2 metres above the ground level.

In one detector/microphone pair there were more severe problems causing noise files to dominate the recordings rendering the data for the entire season useless. This happened twice, and was not noticed before analysing the data after the season (Maisaarensuo in 2019 and Vajosuo 2 in 2022).

2.4. Acoustic calls analyses

We analysed the data using SonoChiro (Biotope), a programme which automatically classifies recordings into species classes and provides an index of reliability for the classification. Because the northern bat (*Eptesicus nilssonii*) and *Myotis spp*. are very common in SW Finland, observations of those groups were not manually verified. Four *Myotis* species (*M. brandtii, M. daubentonii, M. mystacinus, M. nattereri*) occurring in the data were grouped into *Myotis spp*. because the programme can not reliably distinguish between the species.

2.5. Statistical analyses

We focused on two metrics to quantify bats: (1) Presence; for each month the number of nights with more than 0 detection of a species group was computed. The probability of presence is the ratio of number of nights detected divided by the number of nights the detector was operational for each month. (2) Activity; the number of minutes (defined by the time stamp) with at least one detection of a species per night was computed. We refer to these minutes as active minutes. Activity is expressed as the average number of active minutes per night that was recorded per month. We focused on monthly metrics to take into account seasonal variation. In addition, there were technical problems causing some of the detectors to not record full time between visits (e.g., microphone breaking,

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running out of space on memory cards). Therefore, analysis of monthly metrics of presence and activity took into account the actual numbers of recording nights.

Both presence and activity of a species group was analysed using Generalized Linear Mixed Model (GLMM). For presence, a GLMM with binomial errors and logit link was used. As fixed effects, we included month (as a factor), year (as a factor), whether the data was from before or after restoration (Before or After), the restoration action (Control or Impact), tree cover (as factor), distance to water (less than 1 km away = Yes, more than 1 km away = No) soil productivity (as factor) and the interaction between the Before-After categorisation of each site and the Impact (restored or control). Categorization of a site as before or after was for control sites assumed to follow the intended study design where recordings made before 2020 were "before" and recordings after 2020 "after". Categorization of a site as before or after was for impacted sites assumed to follow the realised timing of the restoration action (Table 1). As we used a BACI design, the critical aspect is whether the interaction between "before-after" and "control-impact" shows statistical significance (REF). For activity, a GLMM with negative binomial errors and log link was used. As fixed effects we included the same effects as for presence and additionally the number of nights recording per month was included after standardising it to zero mean and unit standard deviation. In all models we included area and site as random effects to account for spatial non-independence (area) and repeated measures (site). All GLMMs were implemented in the R package glmmTMB (Brooks et al. 2017) in the program R (R Core Team 2023).

3. Results

3.1. Data collected

The *Myotis spp.* group and *E. nilssonii* were the most common species groups at the sites studied. *Myotis spp.* and *E. nilssonii* we recorded over 85 % (8 919/10 441) and 69 % (7 188/10 441) respectively, of all nights recorded (table 2). Both species groups were also very active as enumerated by the number of active minutes (table 2). In addition, Nathusius' pipistrelle (*Pipistrellus nathusii*) was recorded, although mainly at a single site. There were a few hundred recordings of long-eared bats (*Plecotus auritus*) and individual recordings of noctule bats (*Nyctalus noctula*). For statistical analyses we focus on the two most common species groups.

Table 2. Descriptive statistics of the presence and activity of the two most commonly detected species groups. For each year, the number (N) of sites and number (N) of nights recorded in May – September in all sites are denoted together with the number of nights during which one or more Myotis spp. and *E. nilssonii were detected, as well as the total number of active minutes for each species group.* Whether a bat species group was detected during a night is used as a measure of presence. An active minute for each minute of recording scores whether one or more calls of the bat species group was detected and is used as a measure of activity. Note that recordings were not obtained in one site in 2019 and 2022.

year	N sites	N nights recorded	N nights with <i>Myotis</i> <i>spp.</i>	Active minutes <i>Myotis spp.</i>	N nights with <i>E.</i> <i>nilssonii</i>	Active minutes E. nilssonii
2018	21	2 534	2 119	44 714	1 634	16 324
2019	20	2 778	2 208	38 139	1 760	20 793
2021	21	2 270	2 007	68 996	1 777	34 090
2022	20	2 849	2 585	108 740	2 017	41 536
All years		10 441	8 919	260 589	7 188	112 743

The restoration of wetlands was planned to take place in 2020, and mostly progressed according to schedule (table 3). Two sites with recordings where wetlands were restored already in 2019 and three sites with recordings where wetlands were not yet restored in 2021 (table 3) were exceptions. All fourteen wetlands were restored by 2022.

Table 3. The number of sites with bat recordings categorised as before or after for both control sites and sites impacted by the restoration action. The before – after categorization of control sites were assumed to follow the design where restoration was aimed to take place in 2020, but for the impacted sites the categorization was based on realised restoration taken place before or during the May -September annual period of recording bats. For details on each site, see Table 1. Note the total number of sites with recordings varied across the years, see Table 2.

year	Control		Impact	
	Before	After	Before	After
2018	7	-	14	-
2019	7	-	11	2
2021	-	7	1	13
2022	-	6	-	14

3.2. Is the presence of bats affected by wetland restoration?

The presence of *Myotis spp.* and *E. nilssonii* was high both during the period before and after restoration in both control and impacted sites (fig 3). There was no evidence that wetland restoration changed the presence of these bat species groups (tables 4 and 5). For *Myotis spp.*, presence was only affected by seasonality (month in table 4; fig 4a). For *E. nilssonii*, there were in addition to monthly differences (table 5; fig 4a) also significant differences in presence across years, with higher probability for *E. nilssonii* presence with intermediate tree cover and with open water nearby (table 5).



Figure 3: The mean presence, expressed as the proportion of recording nights with one or more recordings, plotted for (a) Myotis spp. and (b) E. nilssonii in both control and impacted sites before (in black) and after (in grey) the restoration action. Within the context of the BACI design of this study, "Impact" sites are located in wetlands that were restored, whereas no restoration action was undertaken in "Control" sites. Standard error is denoted by the line around the mean. See Table 2 for the number of sites. Plotted here are the raw data.



Figure 4: The average presence (a) and activity (b) of Myotis spp. bats (in blue) and E. nilssonii (in black) for each month of the annual study period. Months are denoted by numbers such that 5 is May and 9 is September. Plotted are data averages, see Tables 4 and 5 for model output.

Table 4. Results of a Generalised Linear Mixed Model with binomial errors and logit link on the proportion of monthly recording nights during which Myotis spp. was present. For factorial variables, the base level is denoted between brackets, and the level contrasting to the base level is denoted. The effect size (Estimate) and its standard error (SE) are provided together with a Wald test (chi square, degrees of freedom (d.f.) and P value) for the variable. Random effects included are site and area, with variances 0.021 and 0.013 respectively. Significant variables are printed in bold.

Variable (base level)	Contrast	Estimate	SE	Chisq	d.f.	Р
Intercept		-0.64	0.20			
Month (May)	June	0.11	0.05	42.03	4	<0.001
	July	0.17	0.05			
	August	0.22	0.05			
	September	-0.03	0.05			
Year (2018)	2019	-0.07	0.04	3.18	3	0.37
	2021	0.00	0.08			
	2022	-0.01	0.08			
Before-After (before)	after	0.05	0.09	0.21	1	0.64

Restoration action (Control)	Impact	-0.03	0.11	0.08	1	0.79
Tree cover (low)	intermediate	0.00	0.20	1.54	2	0.46
	high	-0.11	0.19			
Soil productivity (low)	intermediate	0.35	0.29	4.18	2	0.12
	high	0.48	0.28			
Open water (No)	Yes	0.07	0.09	0.68	1	0.41
B-A x Impact		0.00	0.06	0.01	1	0.98

Table 5. Results of a Generalised Linear Mixed Model with binomial errors and logit link on the proportion of monthly recording nights during which E. nilssonii was present. For factorial variables, the base level is denoted between brackets, and the level contrasting to the base level is denoted. The effect size (Estimate) and its standard error (SE) are provided together with a Wald test (chi square, degrees of freedom (d.f.) and P value) for the variable. Random effects included are site and area, with variances 0.0064 and 0.052 respectively. Significant variables are printed in bold.

Variable (base level)	Contrast	Estimate	SE	Chisq	d.f.	Р
Intercept		-0.76	0.15			
Month (May)	June	0.45	0.05	368.77	4	<0.001
	July	0.63	0.05			
	August	0.55	0.05			
	September	-0.26	0.06			
Year (2018)	2019	-0.08	0.05	5.76	3	0.12
	2021	0.07	0.10			
	2022	0.05	0.10			
Before-After (before)	after	-0.01	0.11	0.11	1	0.74
Restoration action (Control) Impact	0.01	0.10	0.13	1	0.72
Tree cover (low)	intermediate	0.20	0.17	6.93	2	0.03
	high	0.01	0.18			
Soil productivity (low)	intermediate	-0.21	0.18	2.21	2	0.33
	high	-0.28	0.19			
Open water (No)	Yes	0.22	0.08	7.65	1	0.006
B-A x Impact		0.04	0.07	0.26	1	0.61

3.3. Is the activity of bats affected by wetland restoration?

In both species groups, activity varied across months (fig. 4b) and across years (tables 6 and 7). Higher soil productivity increased the activity of *Myotis spp.* (table 6) and the presence of openings increased the activity of *E. nilssonii* (table 7). The activity of both bat species groups was higher during the period after restoration than before in both control and impact sites (fig. 5), although it should be noted that this increase was statistically attributed to the higher activity in the years 2021 and 2022 (tables 6 and 7). Activity increased relatively most in impacted (i.e. restored) sites compared to non-restored (i.e. control) sites (fig. 5; interaction in tables 6 and 7). Thus, there was a positive effect of restoration action on activity in both bat species groups.



Figure 5: The mean active minutes per night plotted for (a) Myotis spp. and (b) E. nilssonii in both control and impacted sites before (in black) and after (in grey) the restoration action. Within the context of the BACI design of this study, "Impact" sites are located in wetlands that were restored, whereas no restoration action was undertaken in "Control" sites. See table 2 for the number of sites. Plotted here are the raw data.

Table 6. Results of a Generalised Linear Mixed Model with negative binomial errors and logarithmic link on the number of monthly active minutes for Myotis spp. For factorial variables, the base level is denoted between brackets, and the level contrasting to the base level is denoted. The effect size (Estimate) and its standard error (SE) are provided together with a Wald test (chi square, degrees of freedom (d.f.) and P value) for the variable. The number of nights recording per month was scaled to zero mean and unit standard deviation. Random effects included are site and area, with variances 0.81 and 0.18 respectively. Negative binomial dispersion was inferred to be 1.83. Significant variables are printed in bold.

Variable (base level)	Contrast	Estimat e	SE	Chisq	d.f.	Ρ
Intercept		4.36	0.74			
N nights recording		0.49	0.06	76.0	1	<0.001
Month (May)	June	0.16	0.13	24.3	4	<0.001
	July	0.30	0.13			
	August	0.46	0.14			
	September	-0.18	0.13			
Year (2018)	2019	-0.40	0.12	22.4	3	<0.001
	2021	0.37	0.25			
	2022	0.36	0.27			
Before-After (before)	after	-0.25	0.26	1.2	1	0.27
Restoration action (Control)	Impact	-0.26	0.59	0.06	1	0.80
Tree cover (low)	intermediate	-0.20	0.91	0.9	2	0.64
	high	-0.59	0.87			
Soil productivity (low)	intermediate	0.99	0.96	8.2	2	0.017
	high	2.15	0.93			
Open water (No)	Yes	0.29	0.47	0.4	1	0.53
B-A x Impact		0.72	0.17	17.4	1	<0.001

Table 7. Results of a Generalised Linear Mixed Model with negative binomial errors and logarithmic link on the number of monthly active minutes for E. nilssonii. For factorial variables, the base level is denoted between brackets, and the level contrasting to the base level is denoted. The effect size (Estimate) and its standard error (SE) are provided together with a Wald test (chi square, degrees of freedom (d.f.) and P value) for the variable. The number of nights recording per month was scaled to zero mean and unit standard deviation. Random effects included are site and area, with variances 0.12 and 0.73 respectively. Negative binomial dispersion was inferred to be 1.82. Significant variables are printed in bold.

Variable (base level)	Effect/Contrast	Estimate	SE	Chisq	d.f.	Ρ
Intercept		4.50	0.52			
N nights recording		0.36	0.05	46.17	1	<0.001
Month (May)	June	1.24	0.13	371.50	4	<0.001
	July	1.69	0.13			
	August	1.02	0.14			
	September	-0.77	0.14			
Year (2018)	2019	-0.19	0.12	3.80	3	0.28
	2021	0.06	0.25			
	2022	0.07	0.25			
Before-After (before)	after	0.03	0.26	2.33	1	0.13
Restoration action (Control)	Impact	0.17	0.35	1.74	1	0.19
Tree cover (low)	intermediate	0.44	0.57	3.68	2	0.16
	high	-0.06	0.57			
Soil productivity (low)	intermediate	-1.46	0.71	5.26	2	0.07
	high	-1.57	0.69			
Open water	Yes	1.09	0.28	14.87	1	<0.001
B-A x Impact		0.44	0.17	6.26	1	0.01

4. Discussion

4.1. Global presence of bats at our sites

Our four-year monitoring of bat acoustic activity provided an important set of data that was mostly comprised of *Myotis spp.* calls, but with site-specific variations (Table 2). The abundance of *Myotis spp.* calls is not surprising, as our sites were dominated by forests and wetlands, which are habitats preferred by the four *Myotis* species present in Southwestern Finland (Vasko et al., 2020; Wermundsen & Siivonen, 2008). Among these four is *Myotis daubentonii*, that will forage over water and roost in trees most of the time (Tidenberg et al., 2019; Wermundsen & Siivonen, 2008). *Myotis brandtii* and *Myotis mystacinus* are also found in Finland and forage in wetlands and forests, but also use anthropic structures for roosting as well as trees (Tidenberg et al., 2019; Wermundsen & Siivonen, 2008). The latter species, *Myotis nattereri*, is a forest specialist that roosts in anthropic structures as well as in trees (Parsons & Jones, 2003; Smith & Racey, 2005; Swift, 1997; Tillon & Aulagnier, 2014).

We also often recorded *E. nilssonii*, which is the most common species of Finland occurring in more open landscapes (Tidenberg et al., 2019). It forages along forest paths and edges as well as over calm waters and peatlands, so it was expected to observe the species both before and after restoration work at our sites (Wermundsen & Siivonen, 2008). The monthly variation of the species' activity (fig. 4) is supported by literature and corresponds with variation of night length and darkness (Gaultier et al., 2023; Rydell, 1991; 1992; Vasko et al., 2020). *Eptesicus nilssonii* usually switches to more secluded habitats such as forests during the summer because of the permanent twilight that occurs at this time of the year.

One additional species recorded in significant numbers, but mostly in one site (Finnträsk) is *P. nathusii*. The species is mostly migrating in Finland, rarely breeding, so its presence in the country is usually restricted in time. However, our results indicate a more important presence in June and July than later in the season. That could indicate that the species is breeding in the region more than just passing through, as has also been reported for nearby sites (Tidenberg et al., 2019).

The recordings also indicate the presence of *Plecotus auritus*, a forest specialist common and breeding in Finland, but under-represented in acoustic data due to its low amplitude echolocation calls (Tidenberg et al., 2019). Lastly, the rare (for Finland) *Nyctalus noctula* was also recorded. The species is an open-space forager that hunts over very diverse habitats but will roost almost exclusively in trees (Dietz et al., 2009). However, breeding in the country is uncertain as only a couple of observations have been reported (Tidenberg et al., 2019).

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4.2 Effects of restoration at our sites

Our results indicate an overall higher acoustic activity of bats at restored sites when compared to control and pre-restoration sites (fig 5), which is consistent with similar studies on restored wetlands (Menzel et al., 2005; Allagas et al., 2020). The restoration work at these sites included the clogging of drainage ditches, a typical action for wetland restoration that facilitates water stagnation and a general rise of the water level. The permanent presence of water favours the abundance of many insect species, with many among them being found in the diet of Finnish bats. For instance, the trawling bat *Myotis daubentonii* concentrates on Chironomidae, very common in the boreal region, while *E. nilssonii* is a Nematocera specialist, both insect groups being linked to aquatic environments for their development (Rydell, 1986; Vesterinen et al., 2016; 2018). Therefore, aforementioned bat species, amongst others, will find wetlands abundant in prey that fit their diet and foraging techniques (Rydell, 1986). Moreover, as the rise in water level is recent, aquatic vegetation is still scarce at the restored sites, facilitating the actual availability of prey that cannot hide from bats (Beranek et al., 2021). The permanent presence of water all bat species for their drinking needs, whether they are using the wetlands as foraging sites or not.

The second action conducted for restoration at our sites was the felling of trees, as in all locations, woodlands for silviculture previously dominated. Felling trees led to the opening of our sites, which favours edge-space species such as *E. nilssonii*, but can repel forest species, for example *Myotis nattereri*, if the habitats are too open. We did not here analyse how site-specific restoration affects the bat fauna, but it is likely that details of how the restoration is performed has consequences for species composition. For instance, substantial tree felling was carried out in Lastensuo in 2020, favouring mostly *E. nilssonii*, which showed a significant increase in activity in 2021 and 2022. On the contrary, there was no tree felling in Nuuksio 1, with the site remaining close, and we could only see an augmentation in activity of *Myotis*.

There are no clear numbers on the suitable proportions of open and close habitats for different bat species, but the more it will tend to a homogeneous landscape, the less rich the bat community is predicted to be (Hayes & Loeb, 2007). From that perspective, restoration of wetlands creates important heterogeneity in the landscape. Moreover, we believe that forest habitats are important for all bat species in Finland, either for their foraging or roosting. Therefore, restoring wetlands in an open landscape could be less favourable for Nordic bats. Trees left untouched in restored locations will probably decay in the next few years due to the permanent water, improving roosting opportunities for bat species that roost under bark or in tree crevices, such as *Myotis brandtii* (Dietz et al., 2009;

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Tillon & Aulagnier, 2014). The opportunities for roosting are especially important if surrounding habitats are not suitable for roosting (due to e.g. an absence of old trees or buildings).

4.3 Recommendations for current and future restoration work

Based on our results and literature, we can affirm that restoration of our wetlands was overall effective, with higher bat activity than at the other sites. To ensure the long-term success of these and further restorations, we recommend the monitoring of additional parameters that could affect the presence and activity of bats in wetlands.

The first of these parameters is the presence of aquatic vegetation. Probably the main attraction for trawling bats, such as *M. daubentonii*, to wetlands is the abundance and availability of insects. If the surface of water is covered by vegetation (reeds for instance), it would offer cover for insects and therefore decrease the foraging success of bats (Beranek et al., 2021). Water bodies should also be monitored for eutrophication at current and future restored wetlands, as it is positively associated with the increase of aquatic vegetation biomass (Partanen, 2007).

Secondly, when restoring wetlands with bats as targeted species, we recommend considering speciesspecific needs, especially in terms of habitat and landscape composition. As stated before, different species have different preferences regarding foraging and roosting habitats, and the surroundings of wetlands should reflect these preferences. This could be seen at some sites, with *Myotis* species avoiding restored ones that were too open with regards to structure. However, because it is impossible to include the needs of all the 13 species present in the country, objectives must be defined on which species or guilds to target the restoration efforts (Lookingbill et al., 2010). First, only a part of these 13 species will use wetlands as foraging sites (*E. nilssonii, Myotis daubentonii*, for example), then among these species, roosting preferences will differ. For instance, *Myotis daubentonii* will prefer trees, while *E. nilssonii* will favour buildings. Therefore, it seems essential to integrate restoration efforts in a broader, landscape-scale planning, where proximity and connectivity to needed habitats exist for targeted species (Lookingbill et al., 2010), along conservation efforts of these habitats, to ensure the long term presence of targeted species at restored sites.

5. Conclusions

We monitored bat acoustic activity at an ensemble of sites that included sites that were restored and control sites. This monitoring took place both before and after the restoration work, allowing us to disentangle the effects of restoration work from spatial and temporal variation in bat presence and activity. In general, this so-called Before-After Control Impact (BACI) design provides strong evidence that the impact (restoration in this study) indeed is the cause of observed differences. Our literature overview shows there are relatively few studies on the impact of wetland restoration on bats and this study thereby provided much-needed experimental evidence supporting its positive effect on bat abundance.

Restoration had a clear positive effect on bats across our sites, with some exceptions, sometimes siteor species-specific. These exceptions were likely due to variations in hydrology, the surface area of felled trees or the surrounding habitats of our restored sites. Most importantly, restoration did not have a negative effect on bats at any of our sites.

We attribute the increase of bat activity at most restored sites to a higher abundance of insects that was made possible by the return of permanent water at restored sites. The felling of trees that opened the sites also favoured the presence of certain species such as *E. nilssonii*.

To allow these restoration efforts to be successful in the long term, we recommend the monitoring of water quality and aquatic vegetation at the restored sites, to maintain adequate foraging grounds for bats. We also believe that habitats surrounding restored sites have an important role to play to ensure the presence of bats, and therefore, their conservation and connectivity to restored wetlands should be considered.

These recommendations should also be studied for the planning of future wetland restoration. To this, we add the importance of defining objectives in terms of bat conservation, especially the need of targeting only a few species. There are 13 species of bats in Finland, all with different preferences regarding foraging sites, winter and summer roosting habitats, diets, etc. For that reason, it is better to focus the efforts of a restoration project on only some of these species to facilitate its planning and maximise its chance of success.

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6. References

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