Science of the Total Environment 951 (2024) 175661

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Re-establishing historic ecosystem links through targeted species reintroduction: Beaver-mediated wetlands support increased bat activity

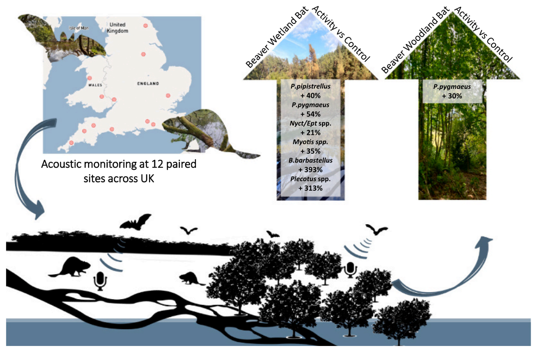
Jack Hooker [a,*], Thomas Foxley [a,b], Emma.L. Stone [b], Paul.R. Lintott [a]

[a] *Department of Applied Sciences, University of the West of England, Bristol, England BS16 1QY, UK*
[b] *Milner Centre for Ecology and Evolution, University of Bath, Claverton Down, Bath BA2 2AY, UK*

HIGHLIGHTS

- As the human population grows, the pressure on global wetlands will escalate.
- Beavers offer a nature-based solution for restoring degraded wetland systems.
- The management of wetlands is critical for the conservation of bat populations.
- Significant increase in activity in beaver-modified habitats for multiple bat species
- The reintroduction of keystone species can re-establish links between aquatic and terrestrial food webs

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:
Ecosystem resilience
Ecosystem services
Nature-based solutions
Species reintroduction
Wetland restoration
Rewilding

ABSTRACT

Despite the global significance of wetlands, conservation strategies often fall short in preserving these ecosystems due to failures in incorporating processes that sustain the ecosystem functioning, hydrological dynamics, ecological processes, and biodiversity of wetlands. Nature-based solutions, such as the reintroduction of beavers, have emerged as effective tools for promoting wetland restoration. Whilst the impact of beavers on wetland restoration is well known, their broader influence on ecosystem health, particularly in modifying habitats for other species, remains inadequately understood. Here we assess the impact that habitat modification through the reintroduction of beavers has on bat populations. There were significantly greater activity levels within beaver-modified wetland habitats for multiple bat species, including higher activity levels of 393 % for *Barbastella barbastellus* and 313 % for *Plecotus* spp.. Additionally, we observed positive effects on bat populations in the woodland habitat surrounding beaver-modified wetland for certain taxa. In the face of escalating challenges posed by climate change and habitat loss, addressing biodiversity loss necessitates a shift toward ecosystem-centric mitigation measures. Our study demonstrates that the reintroduction of keystone species like beavers can re-establish historical facilitative links between aquatic and terrestrial food webs, highlighting the importance of such interventions in fostering the resilience and sustainability of entire ecosystems.

* Corresponding author.
E-mail address: Jack.Hooker@uwe.ac.uk (J. Hooker).

https://doi.org/10.1016/j.scitotenv.2024.175661
Received 1 May 2024; Received in revised form 21 July 2024; Accepted 18 August 2024
Available online 21 August 2024

1. Introduction

Global ecosystems are undergoing unprecedented transformation due to anthropogenic activities linked to food and fiber production, as well as the utilization of carbon-based resources for energy generation (Hong et al., 2021; Winkler et al., 2021). As the human population continues to grow and shift toward urban living, these environmental challenges are poised to escalate, placing greater demands on the global terrestrial surface (Kareiva et al., 2007; Li et al., 2022). Wetlands (areas of land that are permanently or seasonally inundated with water), recognised as crucial components of functionally connected landscapes (Keddy et al., 2009; He et al., 2019), face escalating anthropogenic pressures that modify or replace entire habitats (Reis et al., 2017). The long-term loss of natural wetlands over the last century averages between 54 % and 57 %, reaching up to 90 % in some geographic regions (Junk et al., 2013). Despite their global and regional significance, conventional measures aimed at wetland protection, such as the 1971 Ramsar Convention, have proven insufficient in mitigating anthropogenic pressures on these habitats (Reis et al., 2017). There is therefore a critical need to determine effective approaches to protect wetlands, particularly with the growing need to incorporate nature-based solutions into these strategies.

In regions where wetland ecosystems have suffered terminal damage, the restoration or reconstruction of these habitats through ecological technology and engineering interventions, such as water diversion projects and the plugging of land drains, may represent the only viable option to reverse degraded or disappeared wetland habitats (Xu et al., 2019). Freshwater ecosystems can be at least partially restored through human intervention, such as re-meandering or the addition of large woody material to rivers, pond creation, reversing peatland drainage networks, reducing nutrient pressure or restoring riparian buffer zones to reduce diffuse nutrient loading (Phillips et al., 2005; Williams et al., 2010; Krause et al., 2008; González and Rochefort, 2014; Palmer et al., 2014). However, despite a growing base of case studies and empirical evidence, human efforts to return freshwater ecosystems to a favourable natural condition are often frustrated by inadequate knowledge of historical baseline conditions, a lack of biodiversity response and confounding stressors (Palmer et al., 2014; Moss, 2015). Consequently, despite substantial investments in planning, execution and monitoring, many restoration projects often fall short of achieving their intended objectives (Xu et al., 2019).

An important nature-based solution for restoring ecologically degraded freshwater wetland systems is to re-establish species that are famed for their ecosystem engineering activities. The beaver's (Castoridae spp.) ability to modify freshwater ecosystems as a primary agent of zoogeomorphic processes has no equivalent in the animal kingdom (Westbrook et al., 2011; Johnson et al., 2020; Brazier et al., 2021). The capacity of beavers to restore ecosystem function, habitat dynamics and heterogeneity to degraded habitats has created a rapidly developing interest in their use as restorative agents in both dryland and temperate environments, and the reintroduction of beavers across their former range is regarded as a critical component for restoration of freshwater ecosystems (Halley et al., 2021; Burchsted et al., 2014; Pollock et al., 2014; Gibson et al., 2015).

In the northern hemisphere, beavers were hunted to near-extinction and in countries like Great Britain, the European Beaver (*Castor fiber*) was extirpated from the landscape ~400 years ago (Kitchener and Conroy, 1997). As a result, our collective memory of what beaver-inhabited freshwater ecosystems were like has been lost and similarly, our understanding of how other species co-existed with beavers, many of which may be dependent on beaver ponds, is restricted. Recent beaver reintroductions have therefore provided the opportunity to assess their role in creating ecosystems and shaping the composition of species that inhabit them and the surrounding landscape.

The primary focus on beaver restoration-oriented studies has been on their hydrological and geomorphic effects on the landscape. Despite biodiversity response being a key indicator of restoration effectiveness, it is only relatively recently that the ecological benefits of beaver occupancy have been demonstrated for a variety of organisms spanning trophic levels (e.g. waterbirds, Nummi and Holopainen, 2014; reptiles, Metts et al., 2001; invertebrates, Willby et al., 2018; amphibians, Dalbeck, 2020 and fish, Smith and Mather, 2013). Bats, like other terrestrial consumers, depend on freshwater ecosystems such as wetlands for drinking water, with some species also relying heavily on these habitats as a foraging resource (Adams and Hayes, 2008; Salvarina, 2016). Several species of bat preferentially forage within wetlands (Dietz and Kiefer, 2016) and wetland cover positively impacts bat assemblage richness, diversity, and foraging activity compared with other habitats (e.g. Fukui et al., 2006; Flaquer et al., 2009; Lookingbill et al., 2010; Salsamendi et al., 2012; Šuba et al., 2012; Ciechanowski, 2015; Straka et al., 2016; Blakey et al., 2017). The importance of wetlands also extends to urban environments, where they support higher bat activity and species richness than non-wetland habitats (Straka et al., 2016; Ancillotto et al., 2019). In the UK, bat populations have declined considerably over the last century and the Red List for British Mammals places 4 out of the 11 British mammals at imminent risk of national extinction as bats (Mathews and Harrower, 2020). Due to their importance as foraging and drinking sites, the management of wetland networks may be critical for the conservation of bat populations (Lookingbill et al., 2010).

In addition to the changes in wetland habitat seen in beaver-modified landscapes, the activities of beavers may also lead to benefits for adjacent habitats, such as woodland, because of their selective thinning of woody vegetation, increased soil moisture and shallow inundation of riparian woodland (Haarberg and Rosell, 2006). Not only can this create deadwood roosting habitats for bat species but also alters tree abundance and light availability, changing the woodland structure and allowing a diverse assemblage of plant communities to proliferate (Law et al., 2017). This in turn could lead to an increase in invertebrate species richness and prey availability for bats, whilst the reduction in closed canopy and woodland clutter (i.e. obstacles) may increase the habitat suitability for aerial hawking bat species who preferentially hunt in vegetation gaps (Zwolicki, 2005; Lloyd et al., 2006).

As habitat use by bats in freshwater ecosystems is linked to the spatial structure of riparian vegetation, physical characteristics of the water flow and quality (Vaughan et al., 1997; Rydell et al., 1999; Warren et al., 2000; Downs and Racey, 2006; Kalcounis-Rueppell et al., 2007; Biscardi et al., 2007), beaver-modified landscapes may have the potential to increase optimal foraging habitat for several bat species. Furthermore, as bats represent a mammal group with high trophic diversity that show clear reactions to environmental alterations (Jones et al., 2009; Russo et al., 2021), their response to landscape changes may be an effective indicator of biodiversity restoration in beaver-modified habitats. Indeed, a limited number of studies have found increased bat activity of certain species in areas where beavers have been reintroduced. However, these studies were limited to study sites in the same local area with no clear delineation between control and treatment sites i.e. beavers were able to travel easily between waterbodies (<300 m, Nummi et al., 2011) or surveys were conducted on the same watercourses (<1.7 km) with transects divided into beaver-modified or unmodified sections (Ciechanowski et al., 2011).

To our knowledge, no study has investigated the effects of targeted species reintroduction on bat activity or assessed the importance of beaver-modified woodland and wetland habitats relative to control sites. Here we conducted a paired observational study to investigate changes in bat activity at enclosed beaver (*Castor fiber*) reintroduction projects across England and Wales. In the absence of suitable baseline bat data for each beaver reintroduction site, we chose independent control locations that were of comparable habitat to those present prior to the release of beavers. We compared activity levels of eight bat species/groups (*Pipistrellus pygmaeus*, *Pipistrellus pipistrellus*, *Myotis* spp., *Nyctalus/Eptesicus* spp., *B. barbastellus*, *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros* and *Plecotus* spp.) in beaver reintroduction enclosures and paired control locations, with activity levels recorded in separate woodland and wetland habitats.

We hypothesised that bats would respond positively to localised reintroduction of beavers according to species-specific differences in foraging strategy and habitat preference. We predicted that activity would be higher in beaver enclosures compared to paired control sites for all species due to the increased heterogeneity of woodland and wetland habitat. This includes improved spatial structure of riparian vegetation, physical characteristics of the current and water quality as well as increases in abundance and diversity of invertebrate biomass (Salvarina, 2016; Puttock et al., 2017; Russo et al., 2021). Furthermore, we predicted that increases in activity would be most prevalent in wetland habitats due to the transformative nature of beavers engineering capabilities on watercourses. However, we do not predict there to be negative impacts on bat assemblages resulting from large scale clearance of woodland, due to beavers discriminate and targeted approach to tree felling.

2. Materials and methods

Passive acoustic monitoring was conducted at 12 beaver reintroduction project sites across England and Wales between June and September 2022 representing the period of peak activity for UK bat species (Fig. 1). This study was carried out under ethical approval by the University of the West of England Animal Welfare and Ethics Sub Committee (licence no: 210716: AWESC: R214) under strict recommendations and guidance from government licensing departments Natural England and Natural Resource Wales. Each monitoring period lasted for 7 nights (with the exception of one site that was monitored for 6 nights due to equipment failure) and comprised two full spectrum ultrasonic detectors deployed at wetland and woodland habitats within the beaver reintroduction enclosure. A further two detectors were deployed in paired control locations outside of the beaver enclosure (four detectors in total per site).

We determined the location of control detectors based on habitat suitability, choosing locations that were comparable to beaver enclosure locations prior to species introduction and subsequent change in habitat management (Table 1). For example, if a beaver enclosure was situated around a pre-formed lake or pond then a similar waterbody was used for the control site. In the case where beaver enclosures were situated along streams, control sites were located further along the same stream upstream of the beaver enclosure. We located the control detector as far away from the beaver enclosures as possible, while still being within the boundary of land managed by the same landowner (mean distance,

Fig. 1. Location of study sites surveyed across England and Wales, UK including photographs of example field site recording positions. Reproduced from OS map data by permission of the Ordnance Survey © Crown copyright 2023.

Table 1
Summary of landscape metrics—the mean and SD for habitat area cover within a radius of 2500 m of the paired beaver enclosure and control locations across 12 reintroduction project sites. Spatial analysis of landscape variables was undertaken in QGIS using habitat data extracted from UK CEH Land Cover Map 2021 (Marston et al., 2022).

UKCEH Aggregate Land Cover	Beaver Wetland m^2	Control Wetland m^2	Beaver Woodland m^2	Control Woodland m^2
Broadleaf woodland	367 (289)	383 (308)	369 (291)	380 (310)
Coniferous woodland	132 (219)	129 (206)	131 (219)	126 (199)
Arable	403 (519)	398 (512)	407 (523)	402 (513)
Improved grassland	812 (437)	823 (466)	802 (443)	822 (467)
Semi-natural grassland	53.1 (121)	39.9 (76.5)	55.4 (128)	42.5 (83.6)
Mountain, heath and bog	21 (35.1)	18.9 (31.1)	21.2 (35.4)	18.3 (29.8)
Saltwater	0.25 (0.87)	0.26 (0.89)	0.34 (1.16)	0.20 (0.69)
Freshwater	35.8 (79.1)	34.8 (78.5)	36.2 (79.8)	34.1 (77.8)
Coastal	21.3 (73.9)	21.3 (73.9)	22.3 (77.2)	20.2 (70.1)
Built-up areas and gardens	115 (151)	114 (139)	116 (159)	115 (145)

wetland pairs 528.75 m, SD 259.16, woodland pairs 589.92 m, SD 199.92). As there were no significant differences in landscape cover between paired habitats within site locations, these variables were excluded from further analyses to achieve model simplification. An exception to this were differences recorded in UKCEH aggregate land cover category LC8 which represents freshwater habitats and were therefore anticipated to be distinct from control sites due to the damming and flooding activity of beavers (see supplementary material for statistical analyses of landscape variables for paired locations).

Beaver reintroduction sites comprised fenced off enclosures of various sizes (mean 11.15 ha, SD 15.96 ha) based around a pre-existing water source i.e. a stream, lake or pond in a variety of different landscape settings including broadleaved and coniferous woodland, culm grassland, former agricultural land and wildlife reserves operated by various non-governmental organisations (NGOs). Beaver enclosures were only chosen as study sites if the beavers had been present for a minimum of 6 months to ensure sufficient time for beavers to make changes to habitat composition and structure (mean duration 39.33 months, SD 39.45 months).

Field work was conducted in suitable conditions in accordance with Bat Conservation Trust guidance (2016; i.e. sunset temperature 10 °C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using in-built thermometers within the bat detectors and mean nightly wind speed (mph), mean nightly humidity (%) and total nightly rainfall (mm) were obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 8 km of each site (mean distance 2.83 km, SD 1.87 km). As sites were surveyed continuously for 7 nights each, there may have been occasions where these conditions were not met, however our experimental design ensured paired sites were surveyed on the same nights and would therefore experience the same local weather conditions, controlling for any pairwise effects of weather and date.

Bat activity was recorded for 30 min before sunset to 30 min after sunrise using Anabat Swift full spectrum bat detectors (Titley Scientific, Brendale, QLD, Australia; triggered .wav recording; sample rate 500 kHz; minimum frequency 10 kHz; maximum frequency 250 kHz; minimum event time 2 ms) positioned either at the edge of wetland habitat or within woodland understory using omnidirectional microphones. Automated species identification was necessary as manual classification would have been prohibitively time consuming. We used BatClassify (Scott, 2012) to classify bat calls by species or species groups and consistent with recommendations (López-Baucells et al., 2019; Russo and Voigt, 2016; Rydell et al., 2017) classifications were manually verified using Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) using call parameters as described in Russ (2012) and following Barré et al. (2019) to quantify classification error rates (see supplementary material for detail of error rate modelling approach).

Rather than providing positive and negative classifications for recordings, error rate modelling returns a probability of a correct classification (by species). Following Barré et al. (2019) we removed acoustic data with a maximum error rate tolerance (MERT) of 0.5 (i.e. 50 % correct classification probability). Number of bat passes per night per detector location was used as an index of relative bat activity and calls were grouped into eight species/species groups: *P.pipistrellus*, *P. pygmaeus*, *Myotis* spp., *Nyctalus/Eptesicus* spp., *R. ferrumequinum, R. hipposideros, B. barbastellus* and *Plecotus* spp. Call identifications were grouped together in a genus-wide category for *Myotis* spp. and *Plecotus* spp. due to similarities in call structure between species within the same genus preventing robust manual verification (Schnitzler and Kalko, 2001). In addition, *Nyctalus* spp. and *Eptesicus* spp. are automatically grouped together by BatClassify. *Pipistrellus nathusii* is not classified by BatClassify so were grouped with *P. pipistrellus*. All analyses were performed in R v.4.0.4 (R Core Team, 2022) using the significance level $P < 0.05$. Relationships between beaver-modified habitats and bat activity were assessed by comparing the number of bat passes recorded per night in wetland and woodland habitats present within beaver reintroduction enclosures with paired control locations. We analysed log transformed bat pass count data with generalized linear mixed effect models (GLMMs), with a Poisson distribution using the *glmmTMB* R Package (v1.0.1; Brooks et al., 2017). We fitted the number of bat passes per species/species group per night as the dependent variable, detector location (a factor with two levels: beaver-modified and control) as a fixed effect and site as a random effect. We present effect sizes and standard errors for final models and post-hoc contrast test results in the text as *z*-statistics and *P*-values obtained using the *emmeans* package (v1.4–1; Lenth et al., 2023). We validated final models by simulation using the R package *DHARMa* (v.0.2.0; Hartig, 2024) using residual plots to check for overdispersion, heteroscedasticity and zero inflation.

3. Results

A total of 144,548 bat passes belonging to eight species/species groups were recorded during the 83 nights of monitoring using a MERT of 0.5 in automated identification. The majority of echolocation recordings belonged to *P. pygmaeus* (63,965 passes; 44.3 %) and *P. pipistrellus* (52,687 passes; 36.5 %), followed by *Myotis* spp. (16,018 passes; 11.1 %), *Nyctalus/Eptesicus* spp. (10,531 passes; 7.3 %) with *B. barbastellus*, *Rhinolophus* spp. and *Plecotus* spp. <1 % of species recorded.

We found statistically significant effects of paired detector location on bat activity within wetland and woodland habitats for *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp., *Myotis* spp., *B. barbastellus* and *Plecotus* spp. *Pipistrellus pipistrellus* activity was an average of 40 % higher in beaver-modified wetland habitats compared to paired wetland control locations ($P < 0.001$; Table 2; Fig. 2), with marginally significant differences in bat activity also recorded between beaver-modified woodland and paired control locations ($P = 0.06$ Table 2; Fig. 2). *Pipistrellus pygmaeus* activity was an average of 54 % higher in beaver-modified wetland habitats compared to paired control locations ($P < 0.001$; Table 2; Fig. 2), with significantly higher level of bat activity also recorded between beaver-modified woodland and paired control locations ($P < 0.001$; Table 2; Fig. 2). *Nyctalus/Eptesicus* spp. activity recorded in beaver-modified wetland habitats was significantly higher than paired control locations representing a 21 % higher activity level (*P* 0.05; Table 2; Fig. 2) although no significant differences in activity levels were found between beaver-modified woodland habitat and paired control locations(*P* 0.69; Table 2; Fig. 2). *Myotis* spp. activity was an average of 35 % higher in beaver-modified wetland habitats compared

Table 2
Parameter estimates and standard errors (± s.e), *z*- and *P*- values for fixed effects included in generalized linear mixed models and *post-hoc* comparisons relating bat activity to paired detector location (beaver vs control wetland, beaver vs control woodland) including variance and standard deviation (Std Dev.) of random effect terms.

	Bat Activity (passes)		
P.pipistrellus			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	−0.34 (±0.08)	4.35	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.17 (±0.09)	1.90	0.06
Random Effects	Variance	Std Dev.	
Site (N = 12)	0.10	0.33	
P.pygmaeus			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	0.43 (±0.08)	5.56	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.26 (±0.09)	2.75	<0.01**
Random Effects	Variance	Std Dev.	
Site (N = 12)	0.15	0.38	
Nyctalus/Eptesicus spp.			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.10)	1.94	0.05*
Location (Beaver Woodland vs Control Woodland)	−0.04 (±0.11)	−0.40	0.69
Random Effects	Variance	Std Dev.	
Site (N = 12)	0.29	0.54	
Myotis spp.			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	0.30 (±0.09)	3.46	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.12 (±0.10)	−0.40	0.27
Random Effects	Variance	Std Dev.	
Site (N = 12)	0.07	0.26	
B. barbastellus			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	1.60 (±0.31)	5.09	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.28 (±0.28)	0.98	0.33
Random Effects	Variance	Std Dev.	
Site (N = 12)	1.77	1.33	
***Plecotus* spp.**			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	1.42 (±0.29)	4.96	<0.001***
Location (Beaver Woodland vs Control Woodland)	0.23 (±0.48)	0.47	0.64
Random Effects	Variance	Std Dev.	
Site (N = 12)	0.56	0.75	

Table 2 (*continued*)

	Bat Activity (passes)		
P.pipistrellus			
Fixed Effects	Estimate (± s.e)	z- value	P value
R. ferrumequinum			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	0.19 (±0.55)	0.35	0.73
Location (Beaver Woodland vs Control Woodland)	0.71 (±0.62)	0.47	0.25
Random Effects	Variance	Std Dev.	
Site (N = 12)	68.28	8.26	
R. hipposideros			
Fixed Effects	Estimate (± s.e)	z- value	P value
Location (Beaver Wetland vs Control Wetland)	0.02 (±0.26)	0.08	0.94
Location (Beaver Woodland vs Control Woodland)	−0.01 (±0.62)	−0.02	0.98
Random Effects	Variance	Std Dev.	
Site (N = 12)	25.53	5.05	

to paired control locations ($P < 0.001$; Table 2; Fig. 2), however no significant differences in bat activity were recorded between beaver-modified woodland and paired control locations (*P* 0.27; Table 2; Fig. 2). *Barbastella barbastellus* activity was an average of 393 % higher in beaver-modified wetland habitats compared to paired control locations ($P < 0.001$; Table 2; Fig. 2), however no significant differences in bat activity were recorded between beaver-modified woodland and paired control locations (*P* 0.33; Table 2; Fig. 2). *Plecotus* spp. activity recorded in beaver-modified wetland habitats was significantly higher than paired control locations representing a 313 % greater activity level ($P < 0.001$; Table 2; Fig. 2) although no significant differences activity levels were found between beaver-modified woodland habitat and paired control locations(*P* 0.64; Table 2; Fig. 2). Lastly we found no statistically significant effects of paired detector location on *Rhinolophus* spp. activity in either of the wetland or woodland habitats (*R. ferrumequinum* $P = 0.73$; $P = 0.25$, *R. hipposideros* $P = 0.94$; $P = 0.98$ respectively; Table 2; Fig. 2).

4. Discussion

As countries grapple with the dual threats of climate and biodiversity breakdown, these results are of particular significance as the reintroduction of native fauna is an important nature-based solution for restoring and rewilding areas that have been subject to centuries of anthropogenic pressures and resulting extinction events. Here we show that the release of European beavers (*Castor fiber*) into enclosures at sites across England and Wales had a significant effect on the overall activity of local bat assemblages compared to control locations of comparable habitat unimpacted by beavers. We also highlight species-specific responses in activity dependant on the habitat surveyed within the reintroduction enclosures. Our results demonstrate that targeted species reintroductions could be an effective strategy in rewilding degraded landscapes for a variety of species as well as re-establishing historic links between aquatic and terrestrial ecosystems (Fig. 2; Fig. 3).

We found that the presence of beavers in waterbodies at reintroduction enclosures resulted in a higher level of bat activity recorded over wetland habitats compared to paired controls for the majority of species/species groups studied. We also found no negative impacts on bat activity in woodland habitats resulting from the presence of beavers and

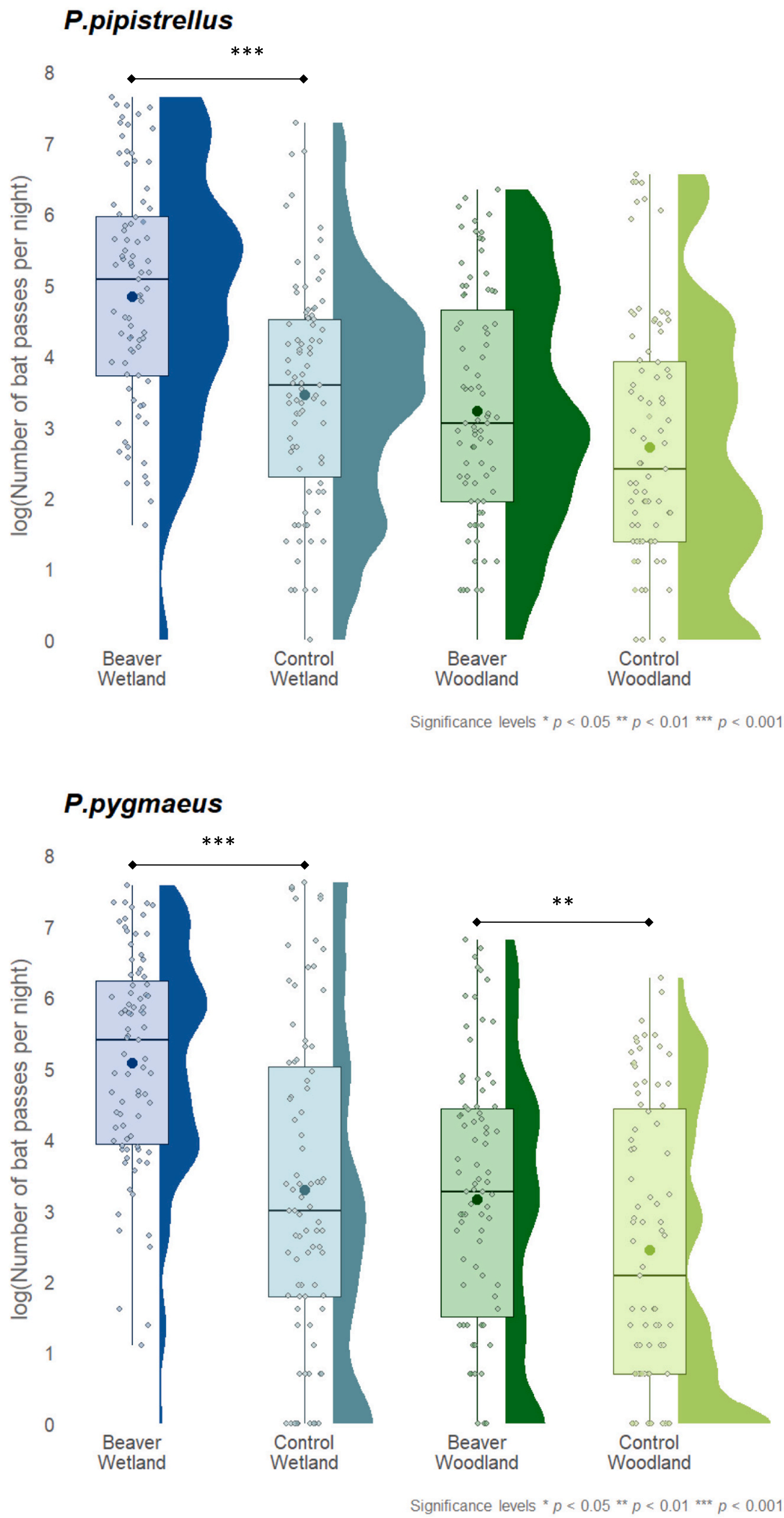


Fig. 2. Raincloud plots displaying data distribution, probability density and summary statistics of nightly bat activity by *P. pipistrellus, P. pygmaeus*, Nyctalus/ Eptesicus spp. and *Myotis* spp. at beaver-modified wetland and woodland habitats compared to paired control locations. Data is presented as log(Number of bat passes per night) with significant within-subject differences during post hoc tests highlighted. Individual dark points indicate mean values across sites ($N = 12$).

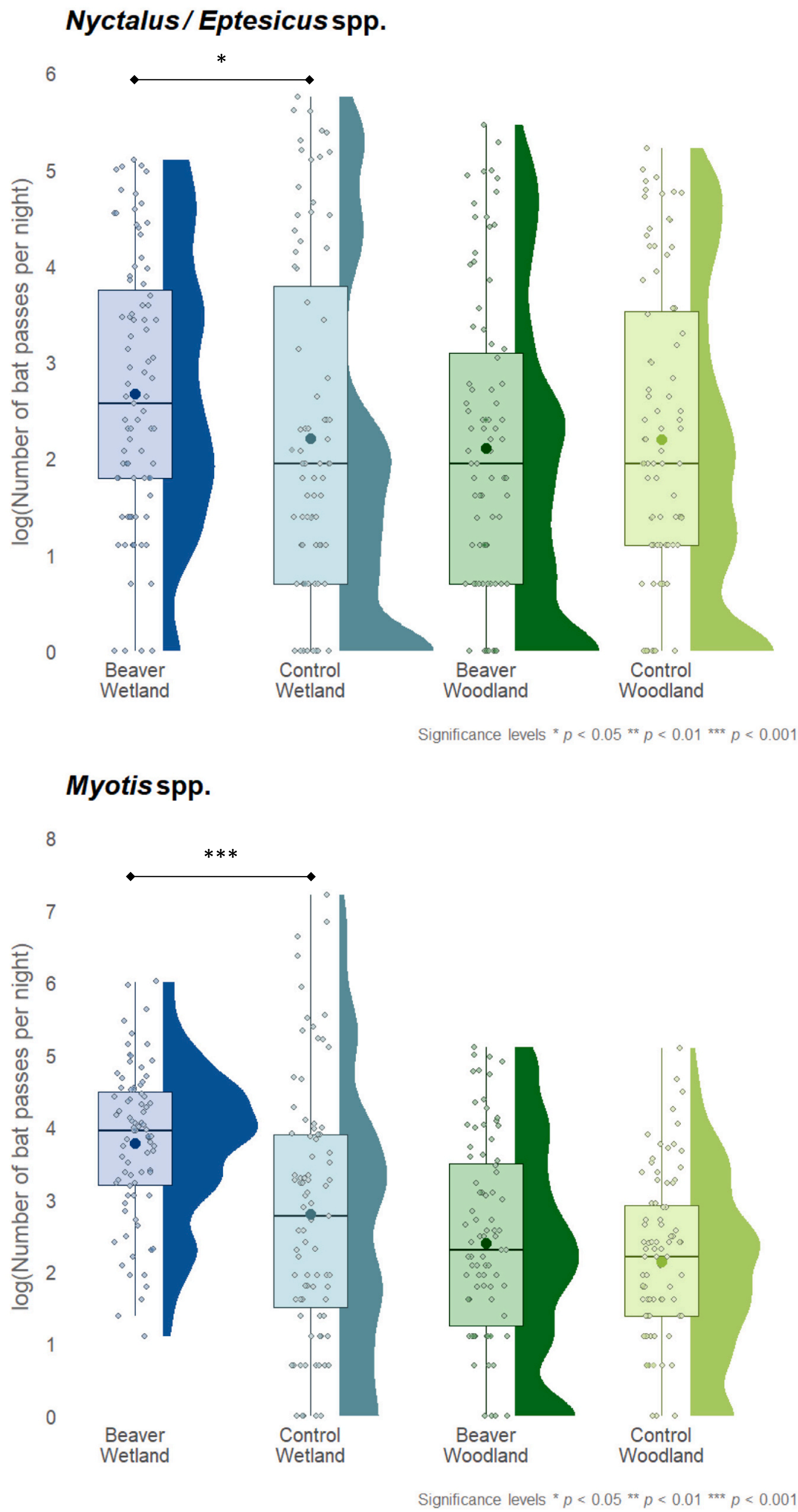


Fig. 2. (*continued*).

indeed found a significant or marginally significant higher level of activity for *Pipistrellus* spp. These findings support our hypotheses and demonstrate that bats respond positively to localised reintroduction of beavers.

As a keystone species, beavers significantly modify the structure, hydrology, geomorphology and biotic community composition of their

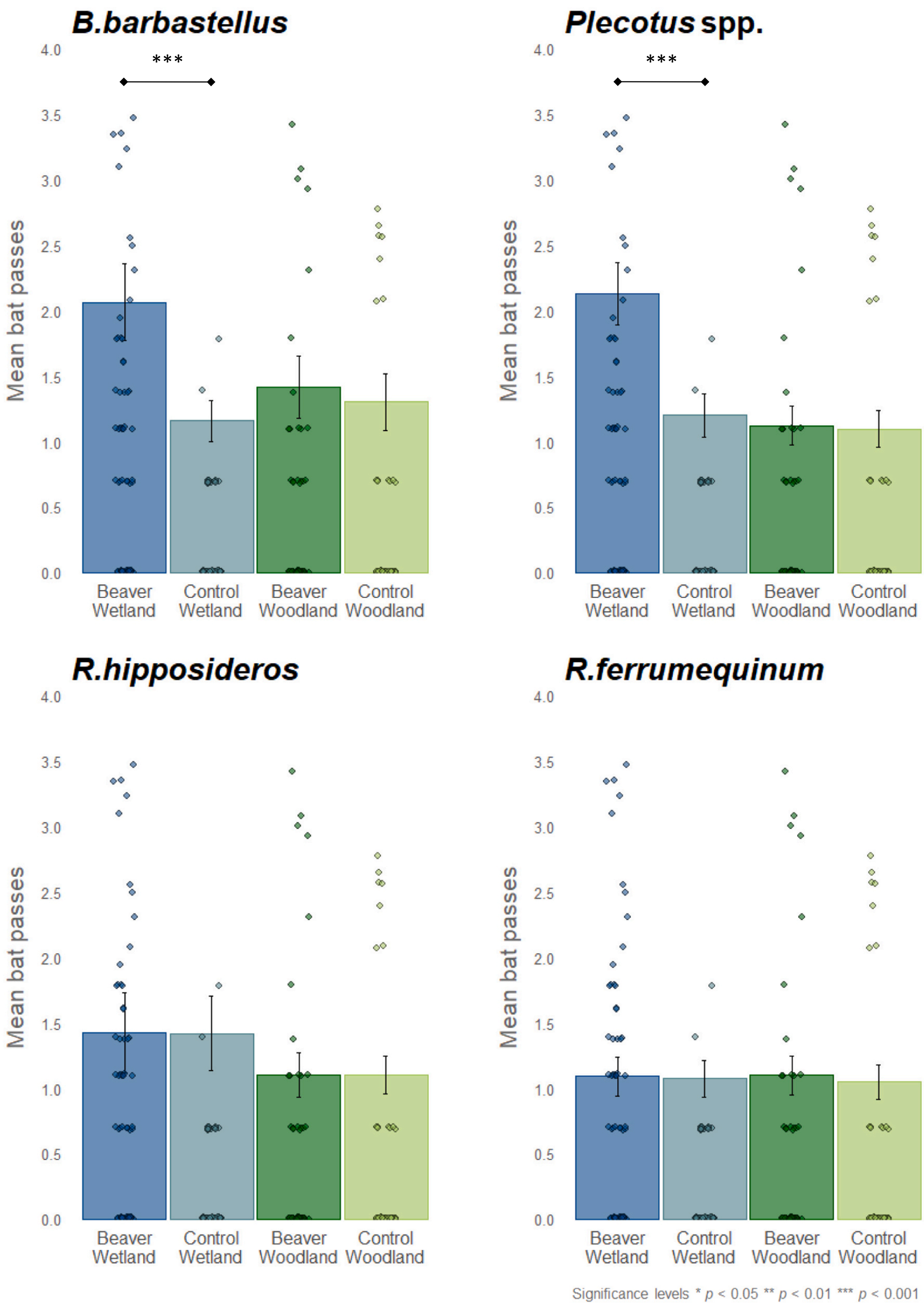


Fig. 3. Bat activity (mean bat passes) by *B. barbastellus, Plecotus* spp., *R. hipposideros* and *R. ferrumequinum* at beaver-modified wetland and woodland habitats compared to paired control locations. Data is presented as mean ± SEM with significant within-subject differences during post hoc tests and individual data points highlighted.

local environment, affecting almost all elements of the aquatic and terrestrial interface which they inhabit (Brazier et al., 2021). Beavers engineer ecosystems in various ways, but most fundamentally through the construction of dams. These dams are constructed from felled wood, stones and mud placed perpendicular to water flow, creating ponds full of sediment and nutrients which slow the flow of water, reducing peaks flows downstream, storing and gently releasing water in times of drought (Hood and Bayley, 2008; Puttock et al., 2017). By creating depositional pond environments and excavating canals, beaver dams have pronounced effects on both aquatic and terrestrial biota and their trophic interactions, as well as enhancing wetland connectivity, and geomorphic dynamism (Correll et al., 2000; Pollock et al., 2014; Gorczyca et al., 2018). In this study, we demonstrate that the modification of wetland habitats by European beaver can have a dramatic positive impact on the surrounding ecosystem and re-establish historic facilitative links between aquatic and terrestrial food webs. Our results indicate that the resulting landscape modifications following beaver reintroductions also lead to improvements in habitats. Furthermore, as bats display sensitivity to alterations in the environment, their heightened activity in beaver-modified habitats may be an effective indicator of biodiversity restoration when rewilding degraded landscapes (Jones et al., 2009; Russo et al., 2021).

We recorded increased activity over wetland habitats for *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp., *Myotis* spp., which comprise the most common species/species groups of bats in the UK and are therefore amongst the largest consumers of insect biomass. Increased activity of *P. pipistrellus, P. pygmaeus*, *Nyctalus/Eptesicus* spp. in wetland habitats aligns with our predictions, as these species are all known to prefer waterbodies or riparian zones, highlighting the regenerative impact the beavers have had on the quality and extent of wetland habitats (Rachwald, 1992; Rydell et al., 1994; Vaughan et al., 1997; Mickevičienė and Mickevičius, 2001; Russ and Montgomery, 2002; Downs and Racey, 2006; Kaňuch et al., 2008; Nummi et al., 2011; Ciechanowski et al., 2011). Furthermore, despite *Myotis* species being grouped together in our analysis due to the similarities in echolocation call structure between species within the same genus (Schnitzler and Kalko, 2001), it is likely that the majority of the calls were of *M. daubentonii* given that this species is widespread throughout the study area and are also strongly associated with riparian habitats (Warren et al., 2000; Russo et al., 2024). As the positive impact on bat activity by localised reintroduction of beavers' ranges across bat species/species groups, it is likely that the drivers behind these increases represent a multi-faceted response according to species-specific differences in foraging strategy and habitat preference.

When beavers flood former terrestrial ecosystems they extend the riparian zone and increase the heterogeneity of stream depth, flow velocity, and benthic habitats such as silty substrates as well as submerged and emergent vegetation (Clifford et al., 1993; France, 1997; Rolauffs et al., 2001). These alterations in turn support increased invertebrate abundance, biomass and/or density and support more lentic species including bats' main aquatic prey, Diptera (especially the family Chironomidae) and Trichoptera (Collen and Gibson, 2000; Rosell et al., 2005; Salvarina, 2016; Osipov et al., 2018; Willby et al., 2018) which can improve the habitat quality and foraging opportunities for bats (Benke et al., 1999; Bush and Wissinger, 2016; Law et al., 2019). This change in invertebrate communities may be particularly important for bat species that favour certain prey species, for example *B. barbastellus* and *Plecotus* spp., are considered to be moth predators and wetlands with beavers have been shown to harbour significantly higher moth diversity (Andersen et al., 2023).

Despite the significant benefits brought about by beaver reintroductions, there is potential for beavers to cause an overall decrease in diversity of animal assemblages or population sizes of particular species. Modification of habitat conditions by beavers can result in ponds that are dominated by unique invertebrate assemblages that thrive in the typically homogeneous benthic habitats that result from increased fine sediment deposition (Descloux et al., 2014; Pulley et al., 2019). However, these impacts would likely only arise as a consequence of limiting beavers to defined areas. At broader scales in which beavers are not confined to enclosures, spatial and temporal variation in successional stages increases the taxonomic, trophic, and/or β-diversity of aquatic invertebrate communities compared to environments lacking beaver modification (Margolis et al., 2001; Law et al., 2016; Bush et al., 2019). Encouraging the wider dispersal of beavers throughout the landscape would further increase the positive impacts of beaver reintroductions on food web dynamics supporting a range of both lotic and lentic invertebrate prey species for bats as well as avoiding the potential creation of homogenous habitats (Law et al., 2016; Bush et al., 2019; Pollock et al., 2014; Willby et al., 2018; Brazier et al., 2021). A similar response was also reported by Ciechanowski et al. (2011) who found that the number of bat passes was significantly higher in the stream sections modified by beavers than in the unmodified sections for *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*, and *N. noctula.* Whilst the experimental design of this study did not quantify levels of beaver modification between study and control sites or indeed control for beavers being able to freely move between the two, their findings do suggest that activity of some species was concentrated in areas where habitat modifications by beaver were most evident.

In addition to the more obvious benefits that result from the beaver presence in waterbodies, such as increased foraging opportunities, the change in hydrological conditions can have direct species-specific benefits for bats. Trawling bat species such as *M. daubentonii* benefit from an acoustic mirror effect when waterbodies transition from shallow and narrow streams with a broken water surface to still beaver ponds (Siemers et al., 2005). This aids surface-based prey detection as acoustically smooth backgrounds such a beaver pond surfaces facilitate echolocation calls that receive no or very low background echo (Siemers et al., 2001, 2005). Indeed, previous observational and playback experiments have found that noise from fast-flowing water could interfere with foraging efficiency in bats that forage close to water surfaces indicating a direct benefit of beaver presence for these species (Frenckell and Barclay, 1987; Mackey and Barclay, 1989; Rydell et al., 1999; Schaub et al., 2008). In our study, the positive response in wetland habitats by bats with different foraging strategies, habitat and prey preferences suggests that the mechanisms behind the increase in activity in beaver-modified landscapes is context and species-dependent, relying on an interplay of factors that improve the quality and extent of habitat available to bats.

In addition to the increase in activity levels of bat species with an affinity to water, we also recorded significantly increased levels of activity for species that are woodland specialists such as the *B. barbastellus* (+393 %) and *Plecotus* spp. (+313 %) in beaver-modified wetland habitats compared to paired control locations. Whilst we did not find any significant differences in activity level of these species in woodland habitats, our results suggest an overall improvement in habitat quality within the reintroduction enclosures. The narrow ecological niche of *B. barbastellus* is largely defined by a preference for roosting in features of old or dead tree trunks, such as under loose bark or within crevices, resulting in populations that are highly dependent on mature broadleaved woodlands (Sierro and Arlettaz, 1997; Russo et al., 2004). However, in lieu of the creation of deadwood habitats via age-related senescence, beavers can create copious amounts of this habitat by raising water levels, with the subsequent inundation causing extensive die-off of trees within woodlands in the flood zone (Thompson et al., 2016). This formation of new deadwood on a short rotation cycle in beaver-created flood sites, coupled with *B. barbastellus'* preference for trees in close proximity to water, may constitute an important habitat creation process for this rare bat species, although more research is required to evaluate the impact of beaver-created flooding on roost availability (Thompson et al., 2016; Carr et al., 2018). A similar rationale may also be a driver behind the increase in *Plecotus* spp. activity recorded within beaver enclosures. As *P. auritus* (the most likely species present within our study area) will roost within trees in natural habitats (Ancillotto and Russo, 2020) the formation of new deadwood by beaver flooding is likely to benefit this species. However, unlike *B. barbastellus, P. auritus* regularly adopt a gleaning foraging strategy and rely more heavily on passive listening to prey-generated sounds, increasing the threat from noise disturbance through mechanisms such as acoustic masking (Luo et al., 2015; Dietz and Kiefer, 2016). Previous studies have found that natural noise sources can cause difficulties for gleaning bat species and therefore the transition from turbulent shallow and narrow streams to still beaver ponds may constitute an improvement in the soundscape for these species (Schaub et al., 2008; Gomes et al., 2021). However, this result should be interpreted with caution as these species have very soft echolocation calls that are often not detected even when bats are present (Dekker et al., 2022).

The results from the current study suggest that beaver reintroduction also has a beneficial effect on bat activity in woodland habitats for some species, with a significant or marginally significant increase in activity recorded for *Pipistrellus* spp. Importantly, given the potential conflicts that arise from tree-cutting by beavers including the potential decrease in tree cover adjacent to beaver habitat (Campbell-Palmer et al., 2016), no negative impacts on bat activity were recorded in woodland habitats for any of the bat species recorded. Whilst beavers do remove cut trees for foraging, building, and as means to wear down their continually growing teeth (Baker and Hill, 2003; Johnston, 2017), they discriminately select trees based on species, size and location as opposed to clearing large areas (Haarberg and Rosell, 2006). This selective thinning of woody plants decreases canopy cover, increasing the amount of sunlight available to understory vegetation and therefore diversifying the spatial structure and species composition of plant communities (Rosell et al., 2005; Zwolicki, 2005; Law et al., 2017). Forest and woodland structure are an important influence on activity patterns of bats and increased levels of forest-associated clutter are a serious limitation for aerial hawking species such as *Pipistrellus* spp. Previous studies have shown that most aerial hawking bats avoid internal parts of dense, intact stands with their activity being negatively correlated with the area of closed canopy and density of trees (Rachwald, 1992; Erickson and West, 2003; Kusch et al., 2004; Lloyd et al., 2006; Fuentes-Montemayor et al., 2013; Froidevaux et al., 2021). In managed forests that are subject to commercial logging, aerial hawkers use either stream corridors or artificial areas of low clutter, which include thinned stands, clear-cuts and trails (Patriquin and Barclay, 2003; Lloyd et al., 2006), whilst in unmanaged forests, the same group of bats have to use canopy gaps created by natural processes such as tree senescence, windthrows or outbreaks of phytophagous insects, fungi or disease (Weiskittel and Hix, 2003; Worrall et al., 2005; Jochner-Oette et al., 2021). The selective cutting of trees by beavers may therefore have a similar function in wooded areas in which they inhabit.

Wetlands are highly productive and biodiverse ecosystems that provide essential regulation, provision and support for critical ecosystem services as well as social and cultural services. Yet despite this, most wetland habitats face numerous and mounting anthropogenic pressures resulting in a vast decline of both area and ecological condition, with international legislation and conventions aimed at recognising the importance of wetlands and promoting their conservation largely failing to mitigate anthropogenic pressures on these habitats. There is a growing understanding that the actions required to protect and restore wetland ecosystems will require nature-based solutions. The capacity of beavers to restore ecosystem function, habitat dynamics and heterogeneity in degraded landscapes has created a rapidly developing interest in their use as restorative agents, with their reintroduction now regarded as a critical component for restoration of freshwater ecosystems. We demonstrate that rewilding areas using beavers can provide a natural and long-term solution to restoring degraded landscapes which not only modifies the structural composition and functional connectivity of a landscape but also increases the species activity found within it. We found that based on a comparison of paired beaver-mediated and control habitats the reintroduction of beavers to wetland habitats is likely to result in significant increases in bat activity for the majority of species recorded, with significant benefits also described for aerial-hawking species in woodland habitats. The greater activity across a range of bat species/species groups that have different foraging strategies, habitat and prey preferences suggests the positive impacts of beavers on a landscape represent a dynamic and multifaceted solution to restore degraded wetland ecosystems.

In order to fully capitalise on the environmental goods and services that beavers can provide, reintroductions need to be facilitated holistically with appropriate management regimes and support for those people or industries that experience negative impacts arising from their activities. Adopting evidence-based management strategies can ensure that successful reintroductions of beavers not only maximize the biodiversity opportunities but also provides genuine 'nature-based solutions' for the many issues facing our wetland ecosystems, all whilst minimising any human-wildlife conflicts that may arise.

CRediT authorship contribution statement

Jack Hooker: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas Foxley:** Formal analysis. **Emma.L. Stone:** Supervision. **Paul.R. Lintott:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

We wish to thank all those organisations and landowners who provided advice and access on the location and suitability of beaver reintroduction project sites and paired woodland and wetland habitats for surveying. These include Cornwall Beaver Project, Eti and Dorette Engi, Devon Wildlife Trust, Dorset Wildlife Trust, Knepp Estate, National Trust, Spain's Hall Estate, Forestry Commission England, North Wales Wildlife Trust, Colin Preece, Nottinghamshire Wildlife Trust.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175661.

References

Adams, R.A., Hayes, M.A., 2008. Water availability and successful lactation by bats as related to climate change in arid regions of Western North America. J. Anim. Ecol. 77 (6), 1115–1121.

Ancillotto, L., Russo, D., 2020. Brown long-eared bat Plecotus auritus (Linnaeus, 1758). In: Hackländer, K., Zachos, F.E. (Eds.), Handbook of the Mammals of Europe. Springer International Publishing (Handbook of the Mammals of Europe), Cham, pp. 1–18. Available at: https://doi.org/10.1007/978-3-319-65038-8_72-1.

Ancillotto, L., et al., 2019. The importance of ponds for the conservation of bats in urban landscapes. Landsc. Urban Plan. 190, 103607. Available at: https://doi.org/10.1016/j.landurbplan.2019.103607.

Andersen, L.H., et al., 2023. Can reintroduction of beavers improve insect biodiversity? J. Environ. Manag. 337, 117719. Available at: https://doi.org/10.1016/j.jenvman.2023.117719.

Baker, B.W., Hill, E.P., 2003. *Beaver (Castor canadensis)*, pp. 288–310. Available at: https://pubs.usgs.gov/publication/87287. (Accessed 11 January 2024).

Barré, K., et al., 2019. Accounting for automated identification errors in acoustic surveys. In: Zamora-Gutierrez, V. (Ed.), Methods in Ecology and Evolution, 10(8), pp. 1171–1188. https://doi.org/10.1111/2041-210X.13198.

Benke, A.C., Ward, G.M., Richardson, T.D., 1999. Beaver-impounded wetlands of the southeastern coastal plain: Habitat-specific composition and dynamics of invertebrates. In: Batzer, D.P., Rader, R.B., Wissinger, S.A. (Eds.), Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley and Sons, pp. 217–245.

Biscardi, S., et al., 2007. Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. J. Zool. 273 (4), 372–381. Available at: https://doi.org/10.1111/j.1469-7998.2007.00337.x.

Blakey, R.V., et al., 2017. Floodplain habitat is disproportionately important for bats in a large river basin. Biol. Conserv. 215, 1–10. Available at: https://doi.org/10.1016/j.biocon.2017.08.030.

Brazier, R.E., et al., 2021. Beaver: nature's ecosystem engineers. WIREs Water 8 (1). https://doi.org/10.1002/wat2.1494.

Brooks, M.E., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9 (2), 378–400.

Burchsted, D., Daniels, M., Wohl, E.E., 2014. Introduction to the special issue on discontinuity of fluvial systems. Geomorphology 205, 1–4. Available at: https://doi.org/10.1016/j.geomorph.2013.04.004.

Bush, B.M., Wissinger, S.A., 2016. Invertebrates in beaver-created wetlands and ponds. In: Batzer, D., Boix, D. (Eds.), Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology. Springer International Publishing, Cham, pp. 411–449. Available at: https://doi.org/10.1007/978-3-319-24978-0_12.

Bush, B.M., et al., 2019. Beaver-created successional gradients increase β-diversity of invertebrates by turnover in stream-wetland complexes. Freshw. Biol. 64 (7), 1265–1274. Available at: https://doi.org/10.1111/fwb.13302.

Campbell-Palmer, R., et al., 2016. The Eurasian Beaver Handbook: Ecology and Management of Castor Fiber.

Carr, A., et al., 2018. Ground-based and LiDAR-derived measurements reveal scale-dependent selection of roost characteristics by the rare tree-dwelling bat Barbastella barbastellus. For. Ecol. Manag. 417, 237–246. Available at: https://doi.org/10.1016/j.foreco.2018.02.041.

Ciechanowski, M., 2015. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern Poland. Eur. J. Wildl. Res. 61 (3), 415–428. Available at: https://doi.org/10.1007/s10344-015-0911-y.

Ciechanowski, M., et al., 2011. Reintroduction of beavers Castor fiber may improve habitat quality for vespertilionid bats foraging in small river valleys. Eur. J. Wildl. Res. 57 (4), 737–747. Available at: https://doi.org/10.1007/s10344-010-0481-y.

Clifford, H.F., Wiley, G.M., Casey, R.J., 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. Can. J. Zool. 71 (7), 1439–1447. Available at: https://doi.org/10.1139/z93-199.

Collen, P., Gibson, R.J., 2000. The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Rev. Fish Biol. Fish. 10 (4), 439–461. Available at: https://doi.org/10.1023/A:1012262217012.

Correll, D.L., Jordan, T.E., Weller, D.E., 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. Biogeochemistry 49 (3), 217–239. Available at: https://doi.org/10.1023/A:1006330501887.

Dalbeck, L., 2020. A review of the influence of beaver Castor fiber on amphibian assemblages in the floodplains of European temperate streams and rivers. Herpetol. J. (Volume 30, Number 3), 135–146. Available at: 10.33256/hj30.3.135146.

Dekker, J., et al., 2022. Differences in acoustic detectibility of bat species hamper Environmental Impact Assessment studies. Eur. J. Wildl. Res. 68 (2), 14. Available at: https://doi.org/10.1007/s10344-022-01562-1.

Descloux, S., Datry, T., Usseglio-Polatera, P., 2014. Trait-based structure of invertebrates along a gradient of sediment colmation: benthos versus hyporheos responses. Sci. Total Environ. 466–467, 265–276. Available at: https://doi.org/10.1016/j.scitotenv.2013.06.082.

Dietz, C., Kiefer, A., 2016. Bats of Britain and Europe.

Downs, N.C., Racey, P.A., 2006. The use by bats of habitat features in mixed farmland in Scotland. Acta Chiropterol. 8 (1), 169–185. https://doi.org/10.3161/1733-5329(2006)8[169:TUBBOH]2.0.CO;2.

Erickson, J.L., West, S.D., 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biol. Conserv. 109 (1), 95–102. Available at: https://doi.org/10.1016/S0006-3207(02)00141-6.

Flaquer, C., et al., 2009. Habitat selection in Nathusius' pipistrelle (*Pipistrellus nathusii*): the importance of wetlands. Acta Chiropterol. 11 (1), 149–155. Available at: https://doi.org/10.3161/150811009X465767.

France, R.L., 1997. The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. Can. J. Zool. 75 (7), 1009–1013. Available at: https://doi.org/10.1139/z97-121.

Frenckell, B. von, Barclay, R.M.R., 1987. Bat activity over calm and turbulent water. Can. J. Zool. 65 (2), 219–222. Available at: https://doi.org/10.1139/z87-035.

Froidevaux, J.S.P., et al., 2021. Bat responses to changes in forest composition and prey abundance depend on landscape matrix and stand structure. Sci. Rep. 11 (1), 10586. Available at: https://doi.org/10.1038/s41598-021-89660-z.

Fuentes-Montemayor, E., et al., 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. Agric. Ecosyst. Environ. 172, 6–15. Available at: https://doi.org/10.1016/j.agee.2013.03.019.

Fukui, D., et al., 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. J. Anim. Ecol. 75 (6), 1252–1258. Available at: https://doi.org/10.1111/j.1365-2656.2006.01146.x.

Gibson, P.P., Olden, J.D., O'Neill, M.W., 2015. Beaver dams shift desert fish assemblages toward dominance by non-native species (Verde River, Arizona, USA). Ecol. Freshw. Fish 24 (3), 355–372. Available at: https://doi.org/10.1111/eff.12150.

Gomes, D.G.E., et al., 2021. Phantom rivers filter birds and bats by acoustic niche. Nat. Commun. 12 (1), 3029. Available at: https://doi.org/10.1038/s41467-021-22390-y.

González, E., Rochefort, L., 2014. Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. Ecol. Eng. 68, 279–290. Available at: https://doi.org/10.1016/j.ecoleng.2014.03.051.

Gorczyca, E., et al., 2018. Can beaver impact promote river renaturalization? The example of the Raba River, southern Poland. Sci. Total Environ. 615, 1048–1060. Available at: https://doi.org/10.1016/j.scitotenv.2017.09.245.

Haarberg, O., Rosell, F., 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. J. Zool. 270 (2), 201–208. Available at: https://doi.org/10.1111/j.1469-7998.2006.00142.x.

Halley, D.J., Saveljev, A.P., Rosell, F., 2021. Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia. Mammal Rev. 51 (1), 1–24. Available at: https://doi.org/10.1111/mam.12216.

Hartig, F., 2024. florianhartig/DHARMa. Available at: https://github.com/florianhartig/DHARMa.

He, F., Zarfl, C., Bremerich, V., David, J.N., Hogan, Z., Kalinkat, G., Tockner, K., Jähnig, S.C., 2019. The global decline of freshwater megafauna. Glob. Chang. Biol. 25 (11), 3883–3892.

Hong, C., et al., 2021. Global and regional drivers of land-use emissions in 1961–2017. Nature 589 (7843), 554–561. Available at: https://doi.org/10.1038/s41586-020-03138-y.

Hood, G.A., Bayley, S.E., 2008. Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biol. Conserv. 141 (2), 556–567. Available at: https://doi.org/10.1016/j.biocon.2007.12.003.

Jochner-Oette, S., et al., 2021. Influence of forest stand structure and competing understory vegetation on ash regeneration—potential effects of ash dieback. Forests 12 (2), 128. Available at: https://doi.org/10.3390/f12020128.

Johnson, M.F., et al., 2020. Biomic river restoration: a new focus for river management. River Res. Appl. 36 (1), 3–12. Available at: https://doi.org/10.1002/rra.3529.

Johnston, C.A., 2017. Beavers: Boreal Ecosystem Engineers. Springer.

Jones, G., et al., 2009. Carpe noctem: the importance of bats as bioindicators. Endanger. Species Res. 8, 93–115. Available at: https://doi.org/10.3354/esr00182.

Junk, W.J., et al., 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. Aquat. Sci. 75 (1), 151–167. Available at: https://doi.org/10.1007/s00027-012-0278-z.

Kalcounis-Rueppell, M., et al., 2007. Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. Biol. Conserv. 138, 120–130. Available at: https://doi.org/10.1016/j.biocon.2007.04.009.

Kaňuch, P., et al., 2008. Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). Mamm. Biol. 73 (2), 147–155. Available at: https://doi.org/10.1016/j.mambio.2006.12.001.

Kareiva, P., et al., 2007. Domesticated nature: shaping landscapes and ecosystems for human welfare. Science 316 (5833), 1866–1869. Available at: https://doi.org/10.1126/science.1140170.

Keddy, P.A., et al., 2009. Wet and wonderful: the world's largest wetlands are conservation priorities. BioScience 59 (1), 39–51. Available at: https://doi.org/10.1525/bio.2009.59.1.8.

Kitchener, A.c., Conroy, J.w.h., 1997. The history of the Eurasian Beaver Castor fiber in Scotland. Mammal Rev. 27 (2), 95–108. Available at: https://doi.org/10.1111/j.1365-2907.1997.tb00374.x.

Krause, S., et al., 2008. Assessing the impact of changes in landuse and management practices on the diffuse pollution and retention of nitrate in a riparian floodplain. Sci. Total Environ. 389 (1), 149–164. Available at: https://doi.org/10.1016/j.scitotenv.2007.08.057.

Kusch, J., et al., 2004. Foraging Habitat Preferences of Bats in Relation to Food Supply and Spatial Vegetation Structures in a Western European Low Mountain Range Forest.

Law, A., McLean, F., Willby, N.J., 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. Freshw. Biol. 61 (4), 486–499. Available at: https://doi.org/10.1111/fwb.12721.

Law, A., et al., 2017. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. Sci. Total Environ. 605–606, 1021–1030. Available at: https://doi.org/10.1016/j.scitotenv.2017.06.173.

Law, A., et al., 2019. Are beavers a solution to the freshwater biodiversity crisis? Divers. Distrib. 25 (11), 1763–1772. Available at: https://doi.org/10.1111/ddi.12978.

Lenth, R.V., et al., 2023. emmeans: Estimated Marginal Means, aka Least-Squares Means. Available at: https://cran.r-project.org/web/packages/emmeans/index.html (Accessed: 11 January 2024).

Li, G., et al., 2022. Global impacts of future urban expansion on terrestrial vertebrate diversity. Nat. Commun. 13 (1), 1628. Available at: https://doi.org/10.1038/s41467-022-29324-2.

Lloyd, A., Law, B., Goldingay, R., 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. Biol. Conserv. 129 (2), 207–220. Available at: https://doi.org/10.1016/j.biocon.2005.10.035.

Lookingbill, T.R., et al., 2010. Influence of wetland networks on bat activity in mixed-use landscapes. Biol. Conserv. 143 (4), 974–983. Available at: https://doi.org/10.1016/j.biocon.2010.01.011.

López-Baucells, A., et al., 2019. Stronger together: combining automated classifiers with manual post-validation optimizes the workload vs reliability trade-off of species identification in bat acoustic surveys. Eco. Inform. 49, 45–53. Available at: https://doi.org/10.1016/j.ecoinf.2018.11.004.

Luo, J., Siemers, B.M., Koselj, K., 2015. How anthropogenic noise affects foraging. Glob. Chang. Biol. 21 (9), 3278–3289. Available at: https://doi.org/10.1111/gcb.12997.

Mackey, R.L., Barclay, R.M.R., 1989. The influence of physical clutter and noise on the activity of bats over water. Can. J. Zool. 67 (5), 1167–1170. Available at: https://doi.org/10.1139/z89-168.

Margolis, B.E., Castro, M.S., Raesly, R.L., 2001. The impact of beaver impoundments on the water chemistry of two Appalachian streams. Can. J. Fish. Aquat. Sci. 58 (11), 2271–2283. Available at: https://doi.org/10.1139/f01-166.

Marston, C., et al., 2022. Land Cover Map 2021 (10m classified pixels, GB). NERC EDS Environmental Information Data Centre. Available at: https://doi.org/10.5285/A22BAA7C-5809-4A02-87E0-3CF87D4E223A.

Mathews, F., Harrower, C., 2020. IUCN-compliant Red List for Britain's Terrestrial Mammals. Assessment by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage (ISBN 978-1-78354-734-0).

Metts, B.S., Lanham, J.D., Russell, K.R., 2001. Evaluation of Herpetofaunal communities on upland streams and beaver-impounded streams in the Upper Piedmont of South Carolina. Am. Midl. Nat. 145 (1), 54–65. https://doi.org/10.1674/0003-0031(2001)145[0054:EOHCOU]2.0.CO;2.

Mickevičienė, I., Mickevičius, E., 2001. The importance of various habitat types to bats (Chiroptera: Verspertilionidae) in Lithuania during the summer period. Acta Zool. Lituan. 11 (1), 3–14. Available at: https://doi.org/10.1080/13921657.2001.10512353.

Moss, B., 2015. Mammals, freshwater reference states, and the mitigation of climate change. Freshw. Biol. 60 (9), 1964–1976. Available at: https://doi.org/10.1111/fwb.12614.

Nummi, P., Holopainen, S., 2014. Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. Aquat. Conserv. Mar. Freshwat. Ecosyst. 24 (5), 623–633. Available at: https://doi.org/10.1002/aqc.2437.

Nummi, P., et al., 2011. Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. Biodivers. Conserv. 20 (4), 851–859. Available at: https://doi.org/10.1007/s10531-010-9986-7.

Osipov, V.V., Bashinskiy, I.V., Podshivalina, V.N., 2018. Influence of the activity of the Eurasian Beaver *Castor fiber* (Castoridae, Mammalia) on the ecosystem biodiversity of small rivers in the forest–steppe zone. Biol. Bull. 45 (10), 1139–1148. Available at: https://doi.org/10.1134/S1062359018100205.

Palmer, M.A., Hondula, K.L., Koch, B.J., 2014. Ecological restoration of streams and rivers: shifting strategies and shifting goals. Annu. Rev. Ecol. Evol. Syst. 45 (1), 247–269. Available at: https://doi.org/10.1146/annurev-ecolsys-120213-091935.

Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. J. Appl. Ecol. 40 (4), 646–657. Available at: https://doi.org/10.1046/j.1365-2664.2003.00831.x.

Phillips, G., et al., 2005. The recovery of a very shallow eutrophic lake, 20 years after the control of effluent derived phosphorus. Freshw. Biol. 50 (10), 1628–1638. Available at: https://doi.org/10.1111/j.1365-2427.2005.01434.x.

Pollock, M.M., et al., 2014. Using beaver dams to restore incised stream ecosystems. BioScience 64 (4), 279–290. Available at: https://doi.org/10.1093/biosci/biu036.

Pulley, S., et al., 2019. The sources and dynamics of fine-grained sediment degrading the Freshwater Pearl Mussel (Margaritifera margaritifera) beds of the River Torridge, Devon, UK. Sci. Total Environ. 657, 420–434. Available at: https://doi.org/10.1016/j.scitotenv.2018.11.401.

Puttock, A., et al., 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. Sci. Total Environ. 576, 430–443. Available at: https://doi.org/10.1016/j.scitotenv.2016.10.122.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rachwald, A., 1992. Habitat preference and activity of the noctule bat Nyctalus noctula in the Białowieża Primeval Forest. *http://katalog.pan.pl/webpac-bin/223bzbsPL/wgbroker.exe?new+-access+top+search+open+NR+ee95400552* (10.4098/AT.arch.92-42).

Reis, V., et al., 2017. A global assessment of inland wetland conservation status. BioScience 67 (6), 523–533. Available at: https://doi.org/10.1093/biosci/bix045.

Rolauffs, P., Hering, D., Lohse, S., 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. Hydrobiologia 459 (1), 201–212. Available at: https://doi.org/10.1023/A:1012507613952.

Rosell, F., et al., 2005. Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Rev. 35 (3–4), 248–276. Available at: https://doi.org/10.1111/j.1365-2907.2005.00067.x.

Russ, R., 2012. British Bat Calls: A Guide to Species Identification. Pelagic Publishing, Exeter, UK.

Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: implications for conservation. Biol. Conserv. 108 (1), 49–58. Available at: https://doi.org/10.1016/S0006-3207(02)00089-7.

Russo, D., Voigt, C.C., 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. Ecol. Indic. 66, 598–602. Available at: https://doi.org/10.1016/j.ecolind.2016.02.036.

Russo, D., et al., 2004. Roost selection by barbastelle bats (Barbastella barbastellus, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. Biol. Conserv. 117 (1), 73–81. Available at: https://doi.org/10.1016/S0006-3207(03)00266-0.

Russo, D., et al., 2021. Do we need to use bats as bioindicators? Biology 10 (8), 693. Available at: https://doi.org/10.3390/biology10080693.

Russo, D., et al., 2024. Higher and bigger: how riparian bats react to climate change. Sci. Total Environ. 913, 169733. Available at: https://doi.org/10.1016/j.scitotenv.2023.169733.

Rydell, J., et al., 1994. Habitat use by bats along rivers in north east Scotland. Folia Zool.-Praha 43, 417.

Rydell, J., Miller, L.A., Jensen, M.E., 1999. Echolocation constraints of Daubenton's Bat foraging over water. Funct. Ecol. 13 (2), 247–255. Available at: https://doi.org/10.1046/j.1365-2435.1999.00304.x.

Rydell, J., et al., 2017. Testing the performances of automated identification of bat echolocation calls: a request for prudence. Ecol. Indic. 78, 416–420. Available at: https://doi.org/10.1016/j.ecolind.2017.03.023.

Salsamendi, E., et al., 2012. Foraging ecology in Mehely's horseshoe bats: influence of habitat structure and water availability. Acta Chiropterol. 14 (1), 121–132. Available at: https://doi.org/10.3161/150811012X654330.

Salvarina, I., 2016. Bats and aquatic habitats: a review of habitat use and anthropogenic impacts: review of bats' use of aquatic habitats. Mammal Rev. 46 (2), 131–143. Available at: https://doi.org/10.1111/mam.12059.

Schaub, A., Ostwald, J., Siemers, B.M., 2008. Foraging bats avoid noise. J. Exp. Biol. 211 (19), 3174–3180. Available at: https://doi.org/10.1242/jeb.022863.

Schnitzler, H.-U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. BioScience 51 (7), 557. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2.

Scott, C., 2012. chrisscott / batclassify — Bitbucket. Available at: https://bitbucket.org/chrisscott/batclassify/src/master/ (Accessed: 11 January 2024).

Siemers, B.M., Stilz, P., Schnitzler, H.U., 2001. The acoustic advantage of hunting at low heights above water: behavioural experiments on the European "trawling" bats Myotis capaccinii, M. dasycneme and M. daubentonii. J. Exp. Biol. 204 (Pt 22), 3843–3854. Available at: https://doi.org/10.1242/jeb.204.22.3843.

Siemers, B.M., Baur, E., Schnitzler, H.-U., 2005. Acoustic mirror effect increases prey detection distance in trawling bats. Naturwissenschaften 92 (6), 272–276. Available at: https://doi.org/10.1007/s00114-005-0622-4.

Sierro, A., Arlettaz, R., 1997. Barbastelle bats (Barbastella spp.) specialize in the predation of moths: implications for foraging tactics and conservation. Acta Oecol. 18 (2), 91–106. Available at: https://doi.org/10.1016/S1146-609X(97)80067-7.

Smith, J.M., Mather, M.E., 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. Freshw. Biol. 58 (7), 1523–1538. Available at: https://doi.org/10.1111/fwb.12153.

Straka, T.M., et al., 2016. Urban bat communities are affected by wetland size, quality, and pollution levels. Ecol. Evol. 6 (14), 4761–4774. Available at: https://doi.org/10.1002/ece3.2224.

Šuba, J., Petersons, G., Rydell, J., 2012. Fly-and-forage strategy in the bat Pipistrellus nathusii during autumn migration. Acta Chiropterol. 14 (2), 379–385. Available at: https://doi.org/10.3161/150811012X661693.

Thompson, S., Vehkaoja, M., Nummi, P., 2016. Beaver-created deadwood dynamics in the boreal forest. For. Ecol. Manag. 360, 1–8. Available at: https://doi.org/10.1016/j.foreco.2015.10.019.

Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. Appl. Ecol. 34 (3), 716. Available at: https://doi.org/10.2307/2404918.

Warren, R.D., et al., 2000. The distribution of Daubenton's bats (Myotis daubentonii) and pipistrelle bats (Pipistrellus pipistrellus) (Vespertilionidae) in relation to small-scale variation in riverine habitat. Biol. Conserv. 92 (1), 85–91. Available at: https://doi.org/10.1016/S0006-3207(99)00062-2.

Weiskittel, A., Hix, D., 2003. Canopy Gap Characteristics of an Oak-Beech-Maple Old-Growth Forest in Northeastern Ohio. Available at: https://www.semanticscholar.org/paper/Canopy-Gap-Characteristics-of-an-Oak-Beech-Maple-in-Weiskittel-Hix/ccf4ada55168584b08b7f73a8df8cbb8d7cf3b8d (Accessed: 11 January 2024).

Westbrook, C.J., Cooper, D.J., Baker, B.W., 2011. Beaver assisted river valley formation. River Res. Appl. 27 (2), 247–256. Available at: https://doi.org/10.1002/rra.1359.

Willby, N.J., et al., 2018. Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. Philos. Trans. R. Soc. B 373 (1761), 20170444. Available at: https://doi.org/10.1098/rstb.2017.0444.

Williams, P., Whitfield, M., Biggs, J., 2010. How can we make new ponds biodiverse? A case study monitored over 7 years. In: Oertli, B., et al. (Eds.), Pond Conservation in Europe. Springer Netherlands (Developments in Hydrobiology 210), Dordrecht, pp. 137–148. Available at: https://doi.org/10.1007/978-90-481-9088-1_12.

Winkler, K., et al., 2021. Global land use changes are four times greater than previously estimated. Nat. Commun. 12 (1), 2501. Available at: https://doi.org/10.1038/s41467-021-22702-2.

Worrall, J.J., Lee, T.D., Harrington, T.C., 2005. Forest dynamics and agents that initiate and expand canopy gaps in Picea–Abies forests of Crawford Notch, New Hampshire, USA. J. Ecol. 93 (1), 178–190. Available at: https://doi.org/10.1111/j.1365-2745.2004.00937.x.

Xu, T., et al., 2019. Wetlands of international importance: status, threats, and future protection. Int. J. Environ. Res. Public Health 16 (10), 1818. Available at: https://doi.org/10.3390/ijerph16101818.

Zwolicki, A., 2005. European Beaver Castor fiber - a keystone species for the river valley ecosystems. Ecol. Quest. 6, 106–109.