Direct and indirect impacts of beaver ecosystem engineering have mixed effects on bats across feeding guilds.

ABSTRACT

Research Highlight: Moser, Valentin; Capitani, Leonardo; Zehnder, Luca; Hürbin, Alex; Obrist, Martin; Ecker, Klaus; Boch, Steffen; Minnig, Silvan; Angst, Christof; Pomati, Francesco; Risch, Anita (2025). Habitat heterogeneity and food availability in beaver-engineered streams foster bat richness, activity and feeding. *Journal of Animal Ecology.*

Ecosystem engineers increase habitat heterogeneity, altering abiotic and biotic resources, and are key to effective nature recovery. Reintroductions of Eurasian beavers (*Castor fiber*) in Europe have indirectly benefitted multiple taxonomic groups, aquatic and terrestrial, as their activities result in wetland restoration, and diversification of vegetation composition and structure. Bats have been found to be positively impacted by beaver activity, yet the causal drivers were unknown. In a recent study, Moser et al. (2025) monitored bat species richness, activity and foraging activity at beaver pools and control beaver-free sites in Switzerland, finding significant increases in all three measures. Importantly, this study is the first to show significant positive impacts on bat foraging at beaver engineered sites and increases in species richness included red-listed species of conservation concern. By testing causal links of the impact of direct (increased canopy heterogeneity and standing deadwood density) and indirect (increased arthropod prey abundance) impacts of beaver engineering on bats, the authors found mixed responses at the foraging guild level. Edge-hunting aerial hawkers benefitted most from beaver engineering and increased standing deadwood density was shown to have the strongest impact on bats. This study provides key evidence for the positive outcomes of beaver reintroductions on local biodiversity, highlighting the value of ecosystem engineers for nature recovery strategies.

KEYWORDS

Arthropods; deadwood; canopy-heterogeneity; ecosystem engineers; foraging guilds; cascade; nature recovery; rewilding

MAIN TEXT

Increasing habitat heterogeneity is key for reversing biodiversity declines, improving resilience and ecosystem function. Ecosystem engineers, species that modify or create habitats, altering the availability of biotic and abiotic resources (Jones et al., 1994), often have cascade effects on the species community, locally and at the landscape scale. The direct and indirect effects of ecosystem engineer reintroductions on wider biodiversity can boost nature recovery and conservation strategies, particularly when resources are limited. Beavers (*Castor fiber* and *C. canadensis*) are iconic ecosystem engineers in the northern hemisphere, modifying terrestrial and aquatic freshwater habitats through vegetation foraging and damming watercourses. By creating wetlands, beavers provide important ecosystem services including, water storage and purification, carbon sequestration, and biodiversity provision (Thompson et al., 2021). In Europe, the recovery of Eurasian beaver, *C. fiber,* populations increased habitat heterogeneity, directly increasing standing deadwood (Thompson et al., 2016) and variation in vegetation composition (Willby et al., 2018), indirectly enhancing aquatic and terrestrial biodiversity across trophic levels (Andersen et al., 2024; Bush et al., 2019; Fedyń et al., 2022; Graham & Goodenough, 2024; Hooker et al., 2024; Law et al., 2019). Increases in bat activity and species diversity have been linked to beaver engineering, with direct and indirect mechanisms proposed as drivers (Ciechanowski et al., 2011; Graham & Goodenough, 2024; Hooker et al., 2024). Freshwater ecosystems are vital for bats, providing drinking water, and foraging opportunities for many species (Heim et al., 2018; Vaughan et al., 1997). Most European bats are insectivorous, and their populations are thought to have undergone significant declines over the past century, in part due to habitat loss and fragmentation, roost loss, and a reduction in arthropod prey (Browning et al., 2021). Habitat structure requirements vary between bat species due to traits including wing morphology, echolocation call characteristics, and prey species preferences (Denzinger

& Schnitzler, 2013; Frey-Ehrenbold et al., 2013). Grouping by habitat type only, European bats can be classed as short-range echolocators (SRE), mid-range echolocators (MRE), and long-range echolocators (LRE), which predominantly forage in cluttered, edge, and open habitats, respectively. Differing responses to beaver presence between bat species have been previously observed (Hooker et al., 2024), but these have not been explicitly assessed at the foraging guild level. Beaver reintroductions could offer a cost-effective nature-based solution; however, evidence for the mechanisms through which bats are impacted by beaver presence in the landscape is poor, and impacts on specific bat behaviours are unknown.

A recent study by Moser et al. (2025) has addressed these key gaps by identifying direct and indirect mechanisms driving changes in overall activity, foraging activity (hereafter foraging), and species richness of bats, including at the foraging guild level, at beaver engineered freshwater sites. Importantly, they found increases in nationally red-listed bat species and foraging activity over beaver pools, highlighting beaver engineering as a potential nature-based solution for supporting bat population recovery. By mapping pathways between proposed mechanisms, the authors show direct effects of beaver engineering, increasing canopy heterogeneity and standing deadwood density (hereafter deadwood), and the indirect effect of increased arthropod abundance were mixed between guilds. A paired study design and passive acoustic monitoring were used to collect bat data at beaver engineered pools and control sites along eight streams in Switzerland. Flying arthropod abundance, vegetation composition, and habitat structure were concurrently surveyed. Each stream's beaver pool and control site were in comparable a habitat and separated by 500 m (Moser et al., 2025), well within most bats' nightly dispersal distance (Boughey et al., 2011; Nicholls & A. Racey, 2006). All European bats use echolocation to navigate the landscape and locate arthropod prey, and echolocation call characteristics can be used to identify species or feeding guilds. When homing in on arthropod prey, some insectivorous bats change their echolocation call sequence to feeding buzzes, enabling foraging behaviour to be identified from passive acoustic data (Russ, 2021). Using generalised linear models, Moser et al. (2025) found bat species richness, overall activity and foraging were found to be significantly higher over beaver pools, compared to control sites (Figure 1). Whilst the former two responses have been previously recorded (Ciechanowski et al., 2011; Graham & Goodenough, 2024; Hooker et al., 2024), the 2.3 increase in foraging over beaver pools is an important novel finding. Restoring natural habitats, including riparian habitats, and identifying structural features important for behaviours such as foraging are essential for facilitating bat population recovery.

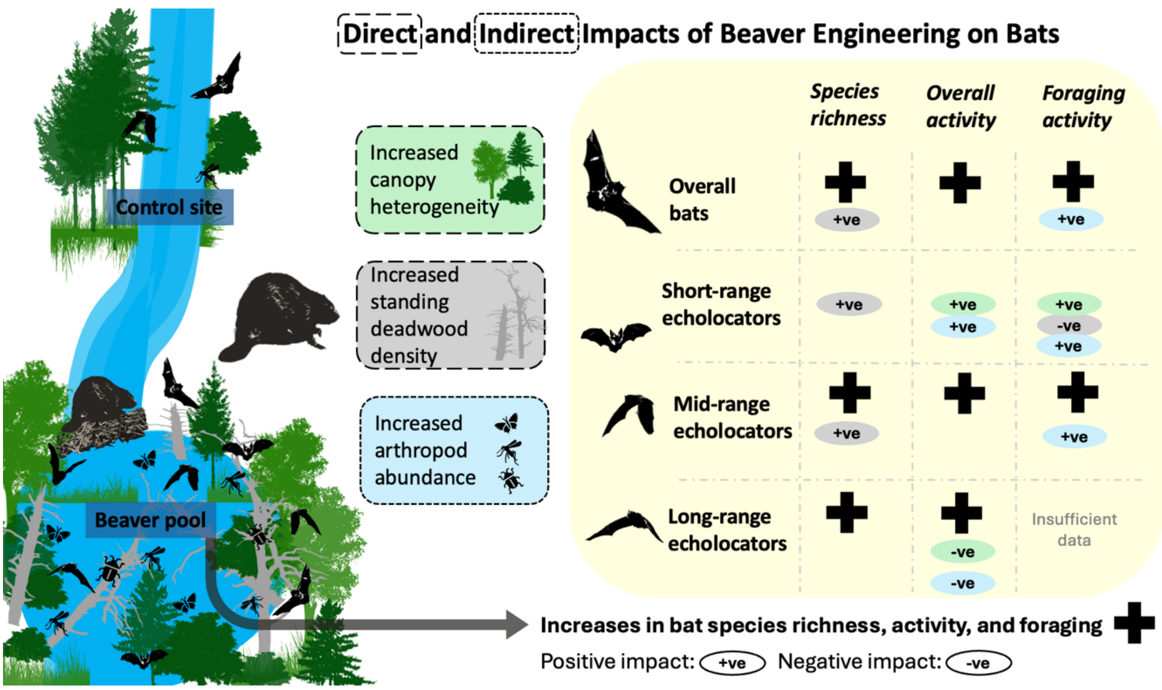

Figure 1: Direct and indirect impacts of beaver engineering on bat species richness, overall activity, and foraging activity as reported by Moser et al. (2025). Solid crosses indicate where overall bat and foraging guild level species richness, overall activity, and foraging activity were significantly positively higher over beaver

pools. Direct impacts of beaver engineering, increased canopy heterogeneity and increased standing deadwood, are shown in green and grey boxes, respectively, outlined by dashed lines. The tested indirect effect of beaver engineering increased arthropod abundance is shown in the blue box with a dotted outline. Coloured ellipsoids indicate where the direct and indirect effects on species richness, overall activity, or foraging activity were positively (+ve) or negatively (-ve) significant.

By testing the mechanisms behind positive impacts of beaver engineering on bats, Moser et al. (2025) show differing responses between foraging guilds, emphasising the need for nuance when considering beavers as agents of nature recovery. Most bat detections were MRE species, with 67% of activity identified as generalist *Pipistrellus pipistrellus*, which likely drove overall bat responses to beaver engineering and direct and indirect effects (Figure 1). Increased deadwood directly, positively impacted MRE richness and arthropod abundance, which positively impacted foraging as an indirect effect of beaver presence (Figure 1) (Moser et al., 2025). Deadwood provides crucial roosting opportunities for many bat species, particularly native woodland specialists (Boonman, 2000; Russo et al., 2007; Tillon et al., 2016), and contributes to habitat complexity, yet SRE foraging was negatively impacted by deadwood (Figure 1). Deadwood density was highest in open areas flooded by beaver engineering, and SRE detections were dominated by *Myotis daubentonii*, which, although a riparian foraging specialist, prefer uncluttered, smooth waterways (Todd & Williamson, 2019). Conversely, significant positive interactions were found between increased canopy heterogeneity and activity and foraging of clutter adapted SRE (Moser et al., 2025), many of which are native woodland specialists (Murphy et al., 2012; Russo et al., 2007), benefitting from increased hunting niches (Jung et al., 2012). The loss or lack of open habitat in beaver engineered systems negatively impacted LRE activity (Moser et al., 2025), and mechanisms behind reported significant increases in richness and activity of species in this guild over beaver pools remains unclear (Figure 1) (Hooker et al., 2024).

Beaver presence was found to directly positively and negatively impact activity, foraging and richness overall and at the guild level, indicating there are drivers untested by Moser et al. (2025). These could include the creation of habitat corridors, changes to invertebrate prey species composition, or reducing water flow rate which aids echolocation (Boughey et al., 2011; Bush et al., 2019; Rydell et al., 1999). Arthropods were collected directly above the water, missing non-flying or high-flying arthropod prey, targeted by SRE gleaners and LRE aerial hawkers, respectively. The arthropod diversity was not reported by Moser et al. (2025), but if it was unchanged by beaver presence (Willby et al., 2018) foraging opportunities would remain limited for some bat species explaining the unexpectedly low strength impact of increased arthropod abundance. Beaver pool successional stage affects arthropod diversity (Bush et al., 2019) and, thus, likely bat responses. Increasing the scale of the study to include beaver pools older than 12 years, and a stratified sample of habitats, would strengthen evidence for the causal impacts of beaver engineering on bats, broadly and at the guild or species level. Moser et al. (2025) were unable to test the impact of landscape composition or anthropogenic impacts due to limited sample size, yet higher bat species diversity and abundance are associated with natural, well-connected landscapes (Boughey et al., 2011; Frey-Ehrenbold et al., 2013; Heim et al., 2018; Nicholls & A. Racey, 2006; Vaughan et al., 1997). Identifying locations where beaver reintroductions have the greatest positive impact on bat communities, such as in intensive agricultural landscapes, would direct successful nature recovery measures.

Moser et al. (2025) provide further evidence for the cascade effects of beaver reintroductions across trophic levels (Bush et al., 2019; Fedyń et al., 2022; Willby et al., 2018). Demonstrating specific behavioural responses to direct and indirect impacts of beaver engineering across bat species emphasises the key role they play in supporting rewilding efforts and biodiversity recovery. Although bats overall benefited, the authors highlight the need for further research to understand species responses to beaver particularly across a larger sample of landcovers and beaver created wetlands successional stages (Bush et al., 2019).

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY

Data have not been archived because this article does not use data.

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