

Eurasian beaver (*Castor fiber*) occupation time drives the structure of plant pollinator communities



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Chosen Journal: Journal of Animal Ecology

Justification

The Journal of Animal Ecology is an established, respected and impactful publication supporting novel, top level, leading research that advances our knowledge on ecological principles. This study fits the scope of the journal well, showing ecosystem engineering by Eurasian beavers indirectly impacts plant pollinator communities and the way they interact. With the potential to advance views on how best to conserve ecosystem services in the face of a climate and ecological emergency, alongside bringing together two areas of research the journal has extensively covered, it's felt that this article will be well received by the journals editors and readers alike.

Abstract

Habitat loss drives declines in biodiversity, threatening the viability of interaction networks that underpin the ecosystem service of pollination. However, recent reintroduction of the ecosystem engineer Eurasian beaver (*Castor fiber*) to the UK has been shown to restore wetlands and reverse declines in biodiversity across different taxonomic groups. Yet, it remains unclear how the ecosystem service of pollination responds to ecosystem engineer driven habitat change. Using plant (insect) pollinator interaction network data collected from transects on sites of beaver presence and absence, it is shown here that the length of beaver occupancy (a proxy for the level of engineering) significantly changes the networks. Specifically, network metrics peaked during medium length beaver occupancy (4-5 years) with significant increases in network richness, generality and pollinator abundance. Long term beaver occupancy sites saw a decrease in network metrics compared to medium length sites, likely due to a reduction in engineering activity. These results indicate that the beavers ability to restore degraded ecosystems and increase their resilience through habitat engineering extends to plant pollination networks, but network improvements are related to the length of beaver occupancy. Therefore, a wider release of beavers in England (currently under government consultation) is suggested, as contiguous wild beaver populations will best support widespread plant pollination network restoration through the creation of a network of habitat patches subject to medium length beaver occupancy and ecosystem engineering.

Keywords: beavers, ecosystem engineering, networks, pollination, richness

1 | Introduction

Habitat loss is the leading cause of biodiversity decline and the emerging species extinction crisis (Hilton-Taylor and Brackett, 2000; Barnosky *et al*, 2011). This is of major concern as the loss of species leads to the loss of ecosystem functions and stability. Initial biodiversity loss can cause cascades of secondary extinctions within an ecosystem (Paine, 1966; Borrvall and Ebenman, 2006; Montoya, Pimm and Sole, 2006) largely magnifying the initial impact (Kehoe, Frago and Sanders, 2021). This is because species rely on each other and on whole ecosystem functionality which in turn requires a suite of co-evolved species within interaction networks (Allesina and Bodini, 2004; Novella-Fernandez *et al*, 2019; Simmons *et al*, 2019). Additionally, fully functioning ecosystems with intact habitat and species assemblages return the greatest ecosystem service benefits. One such benefit dependent on interaction networks is pollination as 75% of crops and 80% of wild plants rely on animal mediated pollination (Hallmann *et al*, 2017; Latty and Dakos, 2019). Traditionally, conservation aimed to counteract habitat and species loss by intensively managing high value natural areas, with management often replicating extirpated species (Walker *et al*, 2004; DeVries *et al*, 2012). Nevertheless, a 76% decline in insect biomass within protected areas demonstrates that this has not worked and suggests a new approach is needed to restore habitats and the species networks within them (Hallmann *et al*, 2017). The use of process led habitat restoration, often through reintroduction of ecosystem engineers shows promise, being inexpensive and continual (Wright and Jones, 2006; Brazier *et al*, 2021). However, despite it known that habitat restoration can save species, it remains unclear how ecosystem engineer driven habitat restoration influences network functionality (Sanders *et al*, 2014).

In bipartite mutualistic plant pollinator networks, study of the number, variety and intricacy of interactions has revealed that one to one species interactions are the exception, not the norm (Olesen *et al*, 2007; Bennett *et al*, 2018; Simmons *et al*, 2019; Gerard *et al*, 2020). Pollination networks tend to demonstrate a specific pattern of generalisation, with a core of generalist species linking the whole network in a nested structure (Resasco, Chacoff and Vazquez, 2021). Consequently, these networks are more stable and persist for the longest, as interaction changes within the network do not necessarily have population level effects (Parra-Tabla and Arceo-Gomez, 2021). An important feature of a nested network structure is that specialist species preferentially interact with generalist species (Ulrich, Almeida-Neto and Gotelli, 2009). This builds redundancy (Bluthgen and Klien, 2011) into the networks, making network function (interactions) more robust to random species loss and environmental fluctuations. Goldstein and Zych (2016) have proven this by experimentally removing a core plant species from networks, finding no significant change or destabilisation in interactions. However, declines in the most species rich taxa (Spiesman and Inouye, 2013) and significant habitat loss pushes networks beyond their limits of adaptation as declines in biodiversity reduce the suite of species with complimentary roles that maintain network function (Olesen *et al*, 2007; Bluthgen and Klien, 2011). This has led to calls for the conservation of interactions over species as functional extinction (the loss of an interaction between species) occurs before species extinction due to declines in species abundance (Valiente-Banuet *et al*, 2015). Although, the efficacy of population reinforcement for plant and pollinator species has been proven (Fisogini *et al*, 2021) anthropogenic recreation of species communities and habitats can struggle

to provide the competition, disturbance regimes and abiotic factors to promote the growth of plants that are highly interconnected core species within the interaction network. Yet, these are the species essential for habitat restoration (Sabatino, Rovere and Meli, 2021). This suggests selective reintroductions of key species is needed to restore networks and thus conserve interactions.

Ecosystem engineers change the physical environment through the manipulation of habitats and control of resources (Jones, Lawton and Shachak, 1994; Sanders *et al*, 2014; Puttock *et al*, 2017). One such species is the Eurasian beaver (*Castor fiber*), capable of changing habitat at a large scale through dam building and cutting down trees (Brazier *et al*, 2021). Recent studies demonstrate the importance of beavers in river re-naturalisation (Gorczyca *et al*, 2018), flood reduction and water purification (Puttock *et al*, 2017; 2018; 2020). Benefits are not limited to abiotic features. Rising water tables from beaver dams creates new wetlands reversing unsustainable freshwater biodiversity decline and a 90% loss of this habitat (Junk *et al*, 2013; Puttock *et al*, 2017; Law *et al*, 2019). Moreover, the increased structural heterogeneity of beaver crafted wetlands drives significant biodiversity increase, frogspawn clumps increasing from 10 to 580 over the first five years of beaver reintroduction, a 321% increase in species richness in beaver wetlands versus non-beaver wetlands and even increasing arthropod community diversity among the same stand of trees after beaver release (Puttock *et al*, 2017; Durben *et al*, 2021; Nummi *et al*, 2021). Higher volumes of deadwood also bring in saproxylic specialist species (Rotheray, 2012; Thompson, Vehkaoja and Nummi, 2016). The positive impacts of this habitat restoration carry over to agriculture and forestry dominant landscapes where beavers are present although it is not clear how this happens in highly fragmented landscapes such as that of the

UK (Law, Mclean and Willby, 2016; Law *et al*, 2019). However, evidence also suggests alpha diversity of aquatic macroinvertebrates declines at sites newly colonised by beavers as the transition from lotic to lentic environments influences community composition (Law, Mclean and Willby, 2016). Furthermore, selective grazing by the beavers could contribute to the decline of rare species (Law, Jones and Willby, 2014; Stringer and Gaywood, 2016). Nonetheless, species (and habitat) diversity increased at the landscape scale in these studies as dynamic habitat mosaics of engineered and un-engineered areas develop from beaver activity (Brazier *et al*, 2016; Law, Mclean and Willby, 2016). These communities are not a subset of the pre-beaver engineered landscape, particularly so for the botanical diversity (Law *et al*, 2019). As such, habitat change and heterogeneity increases from beaver engineering may significantly enhance the diversity, interaction richness and robustness of insect mediated plant pollination networks, yet uncertainty remains around this.

To test whether Eurasian beaver induced habitat engineering will increase plant pollination network diversity, richness and robustness, beaver impact was investigated across sites where beavers were present and absent in sections of the same watercourse. Like many ecosystem engineers, beavers influence the provision of essential ecosystem services through their dams, dredging, burrowing and tree felling (Puttock *et al*, 2017). As engineering influences nodes in ecological networks (Sanders *et al*, 2014) and beaver reintroduction has repeatedly shown substantial biodiversity increases (Law *et al*, 2019; Brazier *et al*, 2021), it is likely that pollinating insect abundance and diversity will increase, changing interactions within the networks at the same time. The benefits of more diverse and species abundant pollinator networks include increased levels of pollination and therefore food provision to human and

natural systems as well as supporting food webs where insects are prey for many species (Puttock *et al*, 2017). Therefore, the ongoing reintroduction of beavers to England (Defra, 2021; Gov.UK, 2021; Heydon *et al*, 2021) provides a great opportunity to study these effects on pollination networks. This could also help to secure the long term future of beavers in England, contributing to cost benefit analyses, by filling a gap in the knowledge created by the absence and subsequent return of the native species to England, after being extirpated 400 years ago (Kitchener and Conroy; 1997).

Specifically, this study aimed to compare plant pollinator visitation networks between different beaver release sites as the reintroductions have taken place at different times. Increasing length of beaver occupancy on a site leads to greater levels of engineering (up to a set point) which have been linked to increased species accumulation and heterogeneity (Law *et al*, 2017). Therefore, it was expected that plant pollinator network metrics such as nestedness, connectance and robustness as well as species richness would increase as the length of beaver occupancy increases. Secondly, network comparison, between sites where beaver had been reintroduced against beaver absent control sites, were planned to identify if the species and network diversity, robustness, abundance and nestedness increased in response to habitat engineering. Higher species abundance and diversity, along with more network interactions and specialist pollinator species were expected where beaver were present as engineering creates a mosaic of habitat patches at different successional stages, providing more niches (Law, Mclean and Willby, 2016). Finally, community composition was investigated to identify change in abundance and species richness of pollinators in relation to the length of beaver occupation and beaver presence or absence at a site.

2 | Methods

2.1 | Study sites

Data was collected by site surveys between May and August 2021 from eleven locations across the South West of England where Eurasian beaver (*Castor fiber*) have been reintroduced or naturally dispersed to. Further background data such as beaver reintroduction dates and enclosure sizes were collected from email communications with the stakeholders (*table 1*). Such information may help to disentangle any influence of beavers on networks from existing site or habitat variation. While the habitats showed wide variation across locations, they can be broadly divided into three main habitat categories: upland sites with fast flowing watercourses and native ancient oak woodlands (with the exception of one forestry site) among agricultural matrices, lowland semi wooded sites among agricultural matrices and urban greenspaces or highly anthropogenically modified watercourses (*figure 1*). All of these sites were developing wetland features regardless of their starting habitat, getting progressively wetter and constantly changing over time as beaver engineering continues (Law *et al*, 2017; Puttock *et al*, 2017). Temporal variation in engineering activities were also widely sampled with beaver release dates for the eleven locations ranging from spring 2011 to autumn 2020. Nine of these releases were from 2016 onwards and five of those from 2019 onwards (*table 1*). Such variation in release dates is apparent by observation alone, with the longer running release sites appearing to contain greater volumes of impounded water, deadwood, relic ponds and sunlight reaching the ground. Management of the engineering activities that drive these changes are minimal, with the occasional removal of dams and installation of tree protection and flow devices

(Brazier *et al*, 2020). This occurred more often at locations where beavers were free-living (four of the locations included in this study). The remaining seven locations have beavers in fenced enclosures, with a mean enclosure size of 6.1 acres. As a result, offspring are removed once old enough, to replicate natural dispersal.

2.2 | Data collection

Each of the eleven locations were surveyed three times for plant pollinator interactions during favourable weather conditions of a minimum 13°C with 60% sunshine (Butterfly Conservation, 2021). Two 50 metre transects were walked at each location, one where beavers were present and the other where beavers were absent (the control). Starting upstream and walking downstream the surveyor would scan for interactions between insects and plants one metre either side of and in front of them (Gibson *et al*, 2011). Therefore, the watercourse would always be one metre away from the surveyor. Flowers from ground level up to the head height of the surveyor were recorded where an interaction took place to ensure flowering shrubs and occasionally trees were not explicitly excluded from the networks. An interaction between an insect pollinator and a plant was defined as any time an insect was in contact with the reproductive organs of the plant (Gibson *et al*, 2011). If an individual insect were to land on multiple plant species within the survey radius, then each plant species would be counted as having had an interaction with that insect species. Plants were identified to species or genus and insects to family, genus or species. Specimens that could not be identified in the field were preserved in 70% ethanol.

The transect location at habitats where beavers were present was decided by identifying the most upstream dam and measuring the next 50 metres downstream,

this representing beaver induced habitat change. Beaver absent transects where no beaver engineering of the watercourse had taken place were then started 200 metres upstream of the beaver present transect to reduce the influence of beaver engineering (such as rising water tables) on plant and insect communities (Law *et al*, 2017). In instances where the watercourse did not permit this separation between transects, such as the very top of headwater streams, the surveyor simply moved as far upstream as possible. Conversely, at locations with free living beavers, stretches of watercourse which had not been subject to or influenced by engineering were harder to find than where beavers were enclosed. Furthermore, being unable to account for any upstream engineering the surveyor had to use the least modified section of watercourse. Control transects were also selected based on habitat similarity (or at least how similar the two sites may have been pre-beaver) to where the beaver present transect had been conducted to limit the influence of habitat variability on the outcome of the networks.

2.3 | Statistical analysis

Data analysis was conducted in R version 4.0.3. Initially, interaction networks were constructed for each beaver present treatment and beaver absent control site using the package “bipartite” (Dormann, Gruber and Fruend, 2008). Following network construction it became apparent that the only urban location in the study needed to be removed from further analyses due to insufficient network data for the beaver present transect, as a result of this enclosure being massively overgrazed by deer. Network metrics were then extracted from the remaining 20 networks (Dormann *et al*, 2009) to enable comparison of the networks using generalised linear models (GLM’s) and linear mixed effect models (LMEM’s). A subset of this data was created, isolating treatment

sites (beaver presence) to look at the effect of length of beaver occupancy on nestedness, robustness, connectance, total network richness, insect (higher level) richness, plant (lower level) richness and links per species. Sites were categorised into recent (1-2 years), medium (4-5 years) and long (7-10 years) beaver occupation. GLM's were run to investigate this with the network metrics as the response variable, each in their own model, and beaver occupancy length as the explanatory variable. Returning to the whole dataset, the same network metrics were then used in the LMEM's to analyse the effects of beaver presence or absence. Each network metric was fitted as a response variable in their own model. The explanatory variable was beaver presence/absence with site fitted as a random factor to account for the variation between locations.

Data on the species abundance and richness for hoverflies, bees and all pollinators were also extracted from the raw data to allow community composition changes under the influence of beaver engineering to be investigated. For this purpose all bee species were grouped together. GLM's were run to determine change in composition in relation to the length of beaver occupancy on a site, while LMEM's were used to find the effect of beaver presence versus absence. Response variables were hoverfly abundance, bee abundance, hoverfly richness, bee richness and total insect richness, while the explanatory variable used in the GLM's was length of beaver occupancy. Response variables were the same for LMEM's, but the explanatory variable was beaver presence/absence and site again fitted as a random effect. All of the GLM's and LMEM's outputs were visually checked to ensure they fitted model assumptions.

Table 1 – Background information for the study locations arranged by beaver release date (most recent first). For habitat type, where beaver are present wetland habitat features as a result of engineering have not been noted but appeared to increase with the length of beaver occupancy.

Location	Beaver arrival date	Enclosure size (acres)	Habitat type (treatment site)	Habitat type (control site)
Poole Farm	November 2020	5.26	Broadleaf woodland and highly modified watercourse in an urban greenspace	Broadleaf woodland and highly modified watercourse in an urban greenspace
Cabilla	July 2020	5	Ancient oak woodland	Ancient oak woodland
Hamatethy	Mid 2020	8.5	Conifer plantation	Conifer plantation
Holnicote Paddocks	January 2020	6.67	Mixed woodland and highly modified watercourse	Mature planted broadleaf woodland
Holnicote Whitemans	December 2019	4.94	Ancient oak woodland	Ancient oak woodland and grazing pasture
Woodland Valley	June 2017	5.4	Planted broadleaf woodland	Broadleaf woodland and planted wildflower meadow
Otterhead Lakes	2017	Free living population	Mixed dry and wet woodland	Mixed dry and wet woodland
Clyst William	May 2016	Free living population	Wet woodland and fen meadow	Broadleaf woodland and grassland
Yettington	2016	Free living population	Wetland	Wet woodland
Percy's	August 2014	Free living population	Broadleaf woodland	Broadleaf woodland
Boldventure	March 2011	6.9	Wet woodland and culm grassland	Mature hedgerow and planted wildflower meadow

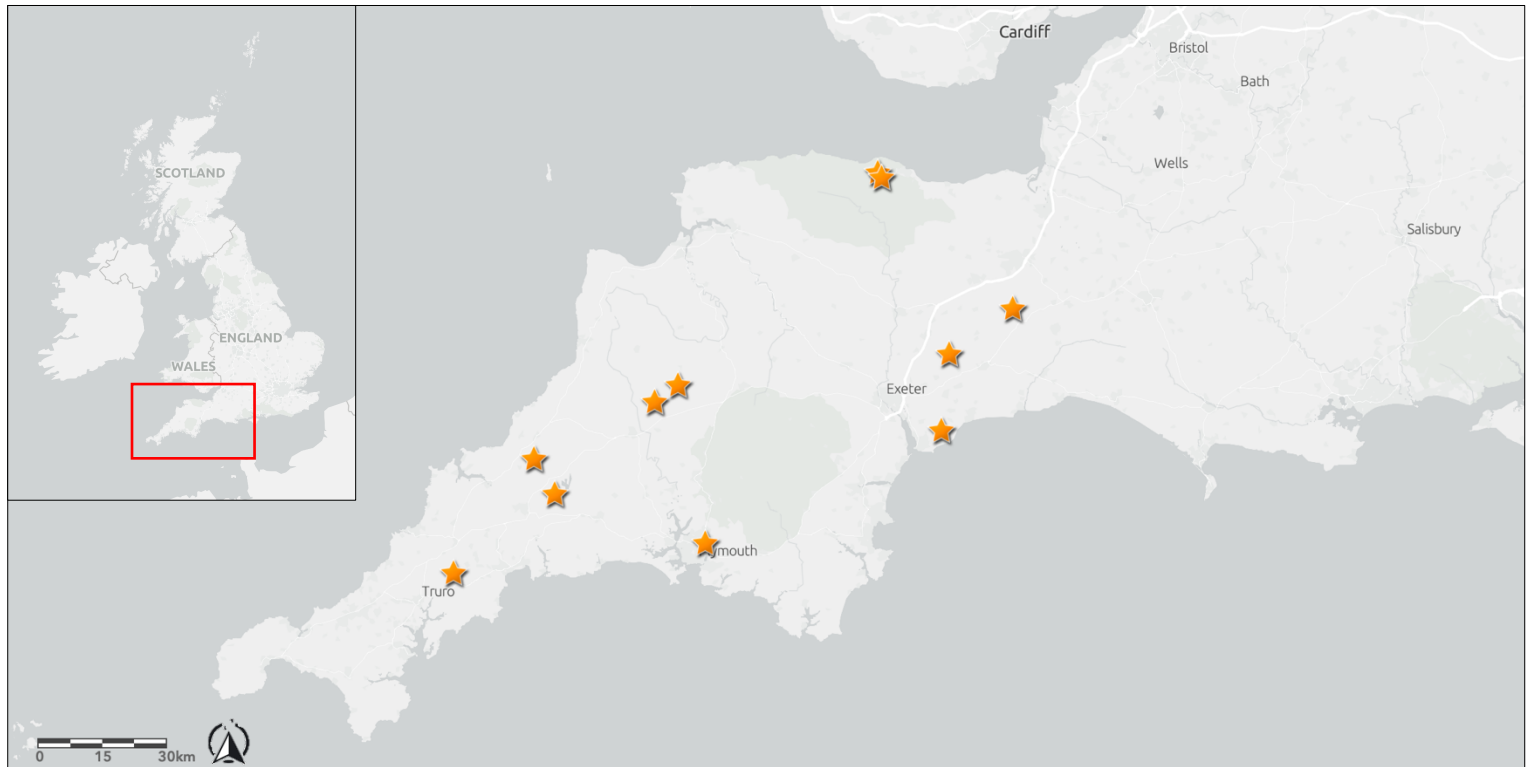
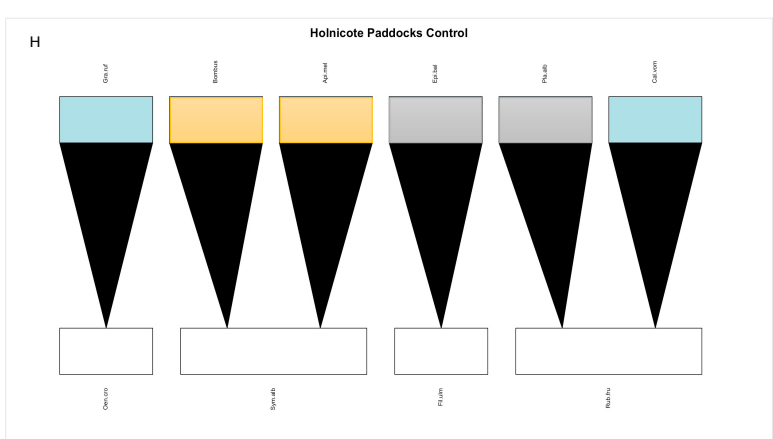
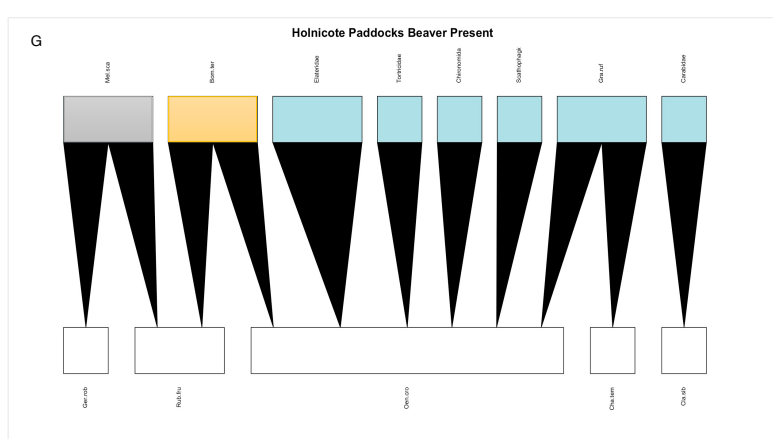
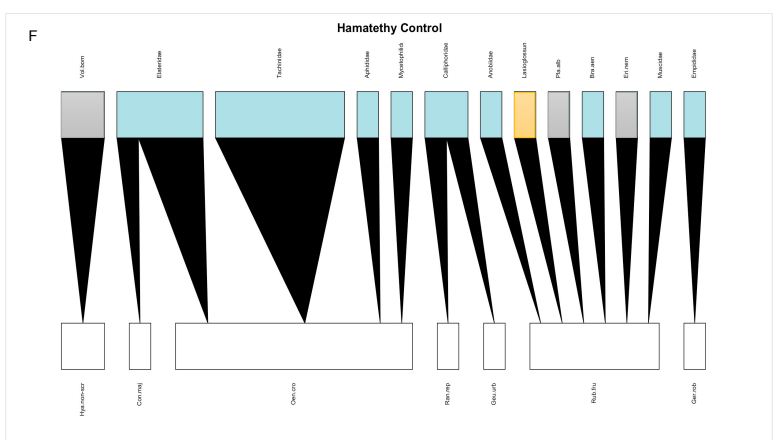
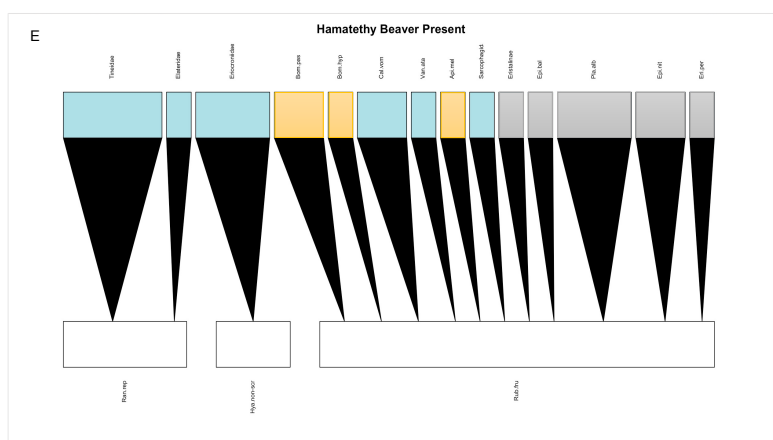
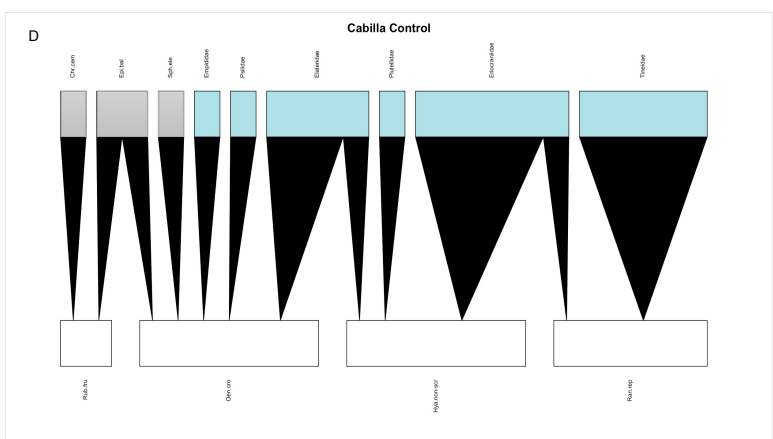
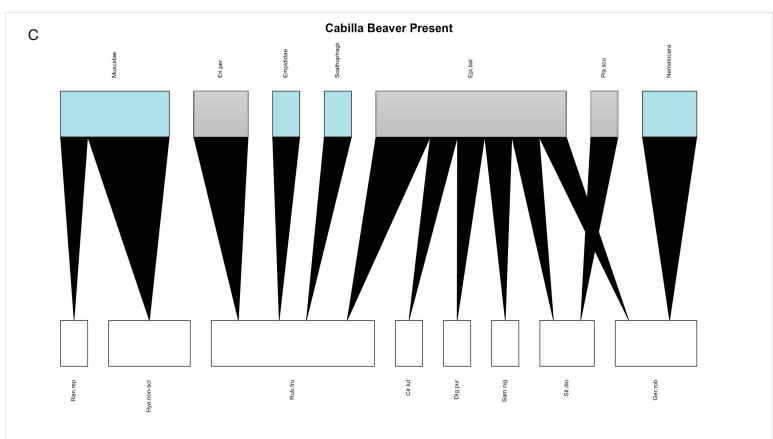
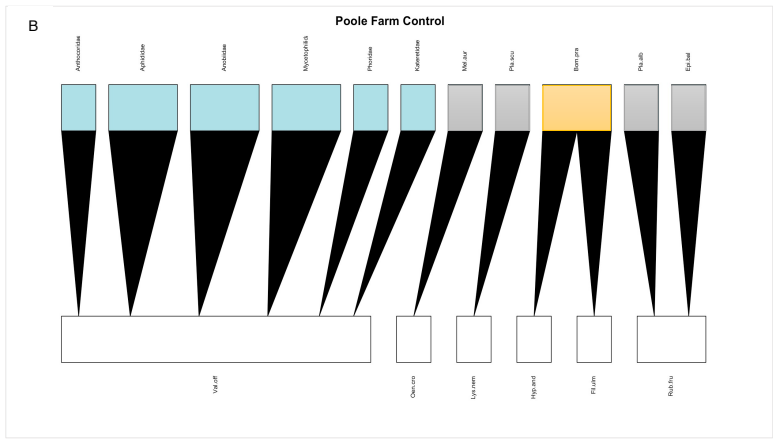
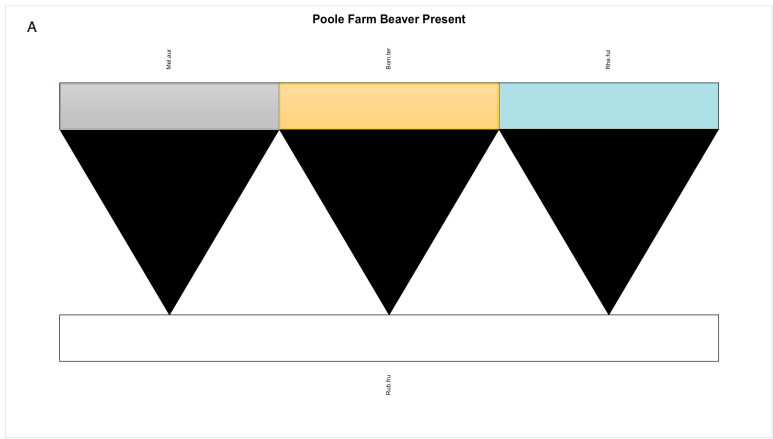


Figure 1 – All eleven study locations across South West England with pictures from five of the different beaver present sites to demonstrate habitat and beaver engineering variability. Made using ArcGIS online (ESRI) 2021, licenced to the University of Exeter.

3 | Results

In total 106 insect species, genera or family and 45 plant species were identified across the eleven locations, with 726 interactions observed. Network structure (*figure 2*) was variable in response to ecosystem engineering. The more species rich networks contained greater species abundance, links per species and number of interactions. These networks also had a greater abundance of generalist pollinator species. Nevertheless, a common feature across all sites was the reliance on a handful of generalist plant species; creeping buttercup (*Ranunculus repens*), hemlock water dropwort (*Oenanthe crocata*) and bramble (*Rubus fruticosus*). These were also some of the most abundant plant species (unpublished data).



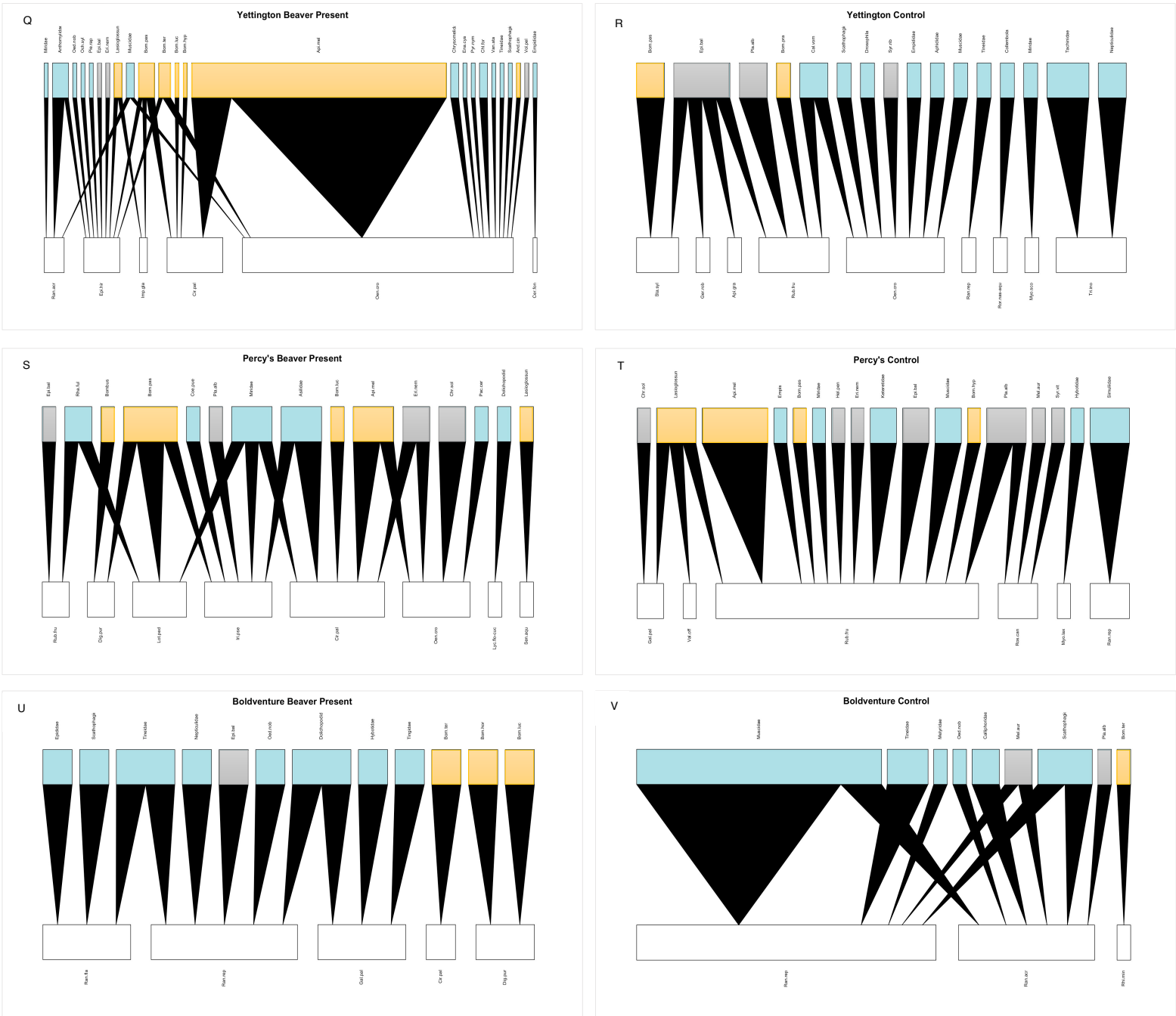


Figure 2 – Bipartite interaction networks for all eleven study locations, showing both the beaver present and beaver absent site networks. The figure is arranged by the length of beaver occupancy (starting with the location that reintroduced beavers most recently) and shows how network complexity in the form of species richness and links per species increases from recent (A to J) to medium (K to R) length beaver occupancy sites and then falls again when moving onto long (S to V) term occupancy sites. Each box (node) in a network represents one species, with a wider box showing greater relative abundance of the species. Coloured nodes are the higher level species (insects), with yellow nodes for bees, grey nodes for hoverflies and blue nodes for all other pollinator species recorded. White nodes represent lower level species (plants) and black triangles show interactions between species. The wider the base of the triangle, the more frequently the interaction (pollination event) was recorded. See appendices 1 and 2 for full species, genus and family names of insects and plants included in these networks.

3.1 | Length of beaver occupation

Network responses to beaver occupation length were variable (*figure 3*). Insect (higher level in the network) species richness peaked at medium length beaver occupancy where it was significantly higher than richness on recent or long sites (*table 2*). Insect richness then declined, meaning long term beaver occupancy sites were not significantly different from recent. This response was mirrored in total network species richness which also saw a significant increase on medium length occupancy sites (*table 2*). However, plant (lower level in the network) species richness, and robustness showed a non-significant increase, while connectance showed a non-significant decline as beaver occupation length increased (*table 2*). Network nestedness saw a near significant change, becoming more nested (closer to 0) when moving from recent to medium length beaver occupancy but then returning to a less nested state on sites with long term beaver occupancy. This pattern appears to be responding to the changes in insect species richness. The same pattern (the greatest number of links per species occurs during medium length beaver occupancy) is seen again with links per species which significantly increased with beaver occupation length ($\chi^2_{(2)} = 8.5099$, $p = 0.0142$).

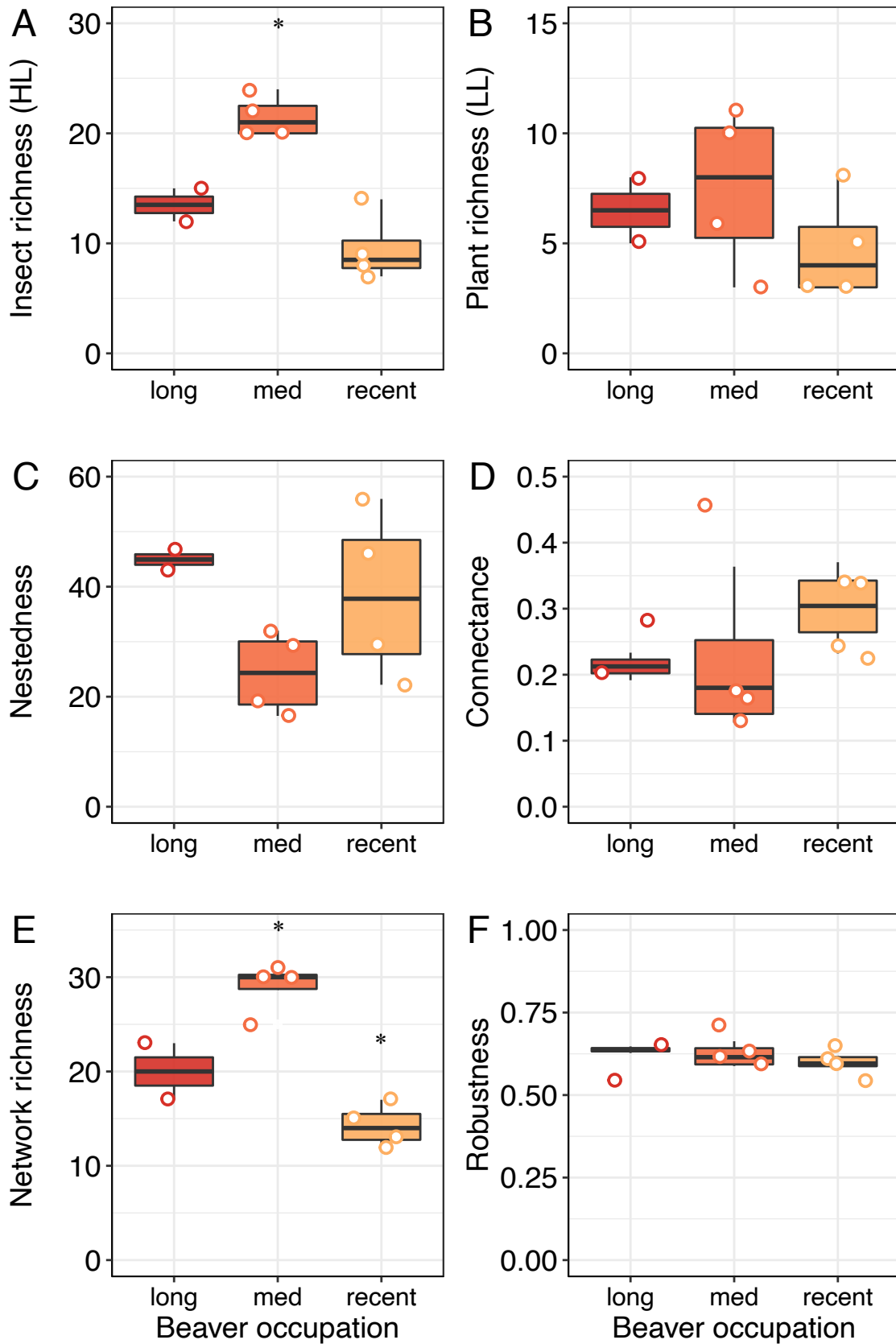


Figure 3 – The influence of the length of beaver occupancy on six network metrics. Beaver occupation refers to the length of time since the beavers initial arrival to a site and was recorded in years, then grouped as; recent (1-2 years), med[ium] (4-5 years) and long (7-10 years). Each circle indicates an individual sites' value for the respective network metric. An * indicates significance.

Table 2 – GLM outputs (test = χ^2) of the overall effect of beaver occupation length on network metrics (An * indicates significance).

Variable	LR Chisq	Df	Pr(>Chisq)
Insect richness (HL)	46.31	2	<0.001*
Plant richness (LL)	1.73	2	0.423
Nestedness	5.49	2	0.064
Connectance	2.91	2	0.234
Network richness	56.17	2	<0.001*
Robustness	1.11	2	0.573

3.2 | Effects of beaver presence and absence

The presence of beavers and their engineering of the landscape was found to create no significant difference in network metrics when compared to the beaver absent control sites (*table 3*). However, sites where beaver are present showed more variation in higher and lower level species richness and nestedness (*figure 4*), suggesting ecosystem engineering may have been having a weak effect on these network metrics. Furthermore, all the metrics bar nestedness and connectance showed very marginal non-significant increases in the presence of beaver engineering. Such a pattern was also seen in the metric links per species ($\chi^2_{(1)} = 0681$, $p = 0.409$), while network nestedness non-significantly decreased in the presence of beavers.

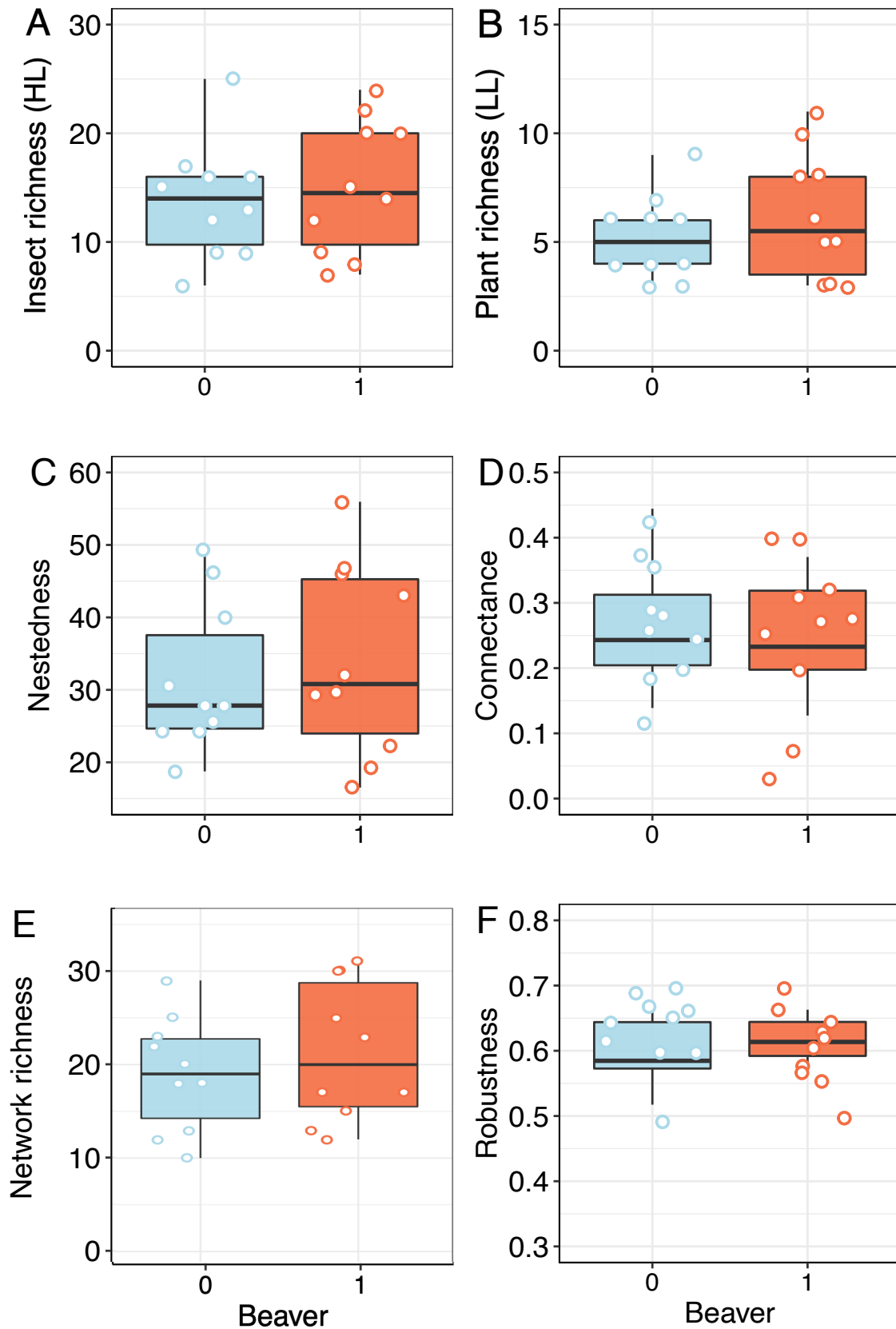


Figure 4 – The influence of beaver presence (1) and absence (0) on six network metrics. Lower values for nestedness show a more nested network. Higher values in the other five network metrics show greater species richness, connectance and robustness. Each circle indicates an individual sites' value for the respective network metric. An * indicates significance.

Table 3 – Linear mixed effect model outputs on the overall effect of beaver presence or absence on network metrics, with site ID fitted as a random effect (An * indicates significance).

Variable	Chisq	DF	Pr(>Chisq)
Insect richness HL	0.90	1	0.342
Plant richness LL	0.81	1	0.368
Nestedness	0.24	1	0.622
Connectance	0.13	1	0.723
Network richness	2.77	1	0.096
Robustness	1.28	1	0.258

3.3 | Community composition

Community composition significantly changed with the length of beaver occupancy at sites. Total pollinator abundance as well as hoverfly and bee abundance was significantly higher on medium length occupancy sites than on recent or long term occupancy sites (*table 4*). Yet, there was no significant difference between recent and long term occupancy sites. Moreover, hoverfly and bee species richness did not significantly increase during any length of beaver occupancy. However, bee species richness was the only community measure to break the pattern where the highest mean values occurred during medium length beaver occupancy (*figure 5*). Although, when comparing the effects of beaver presence and absence there was no significant effect of beaver presence on community composition (*table 5*). Still, non-significant increases in the mean of all measures except total pollinator abundance occurred where beaver were present, alongside an interesting outlier for bee abundance (*figure 6*).

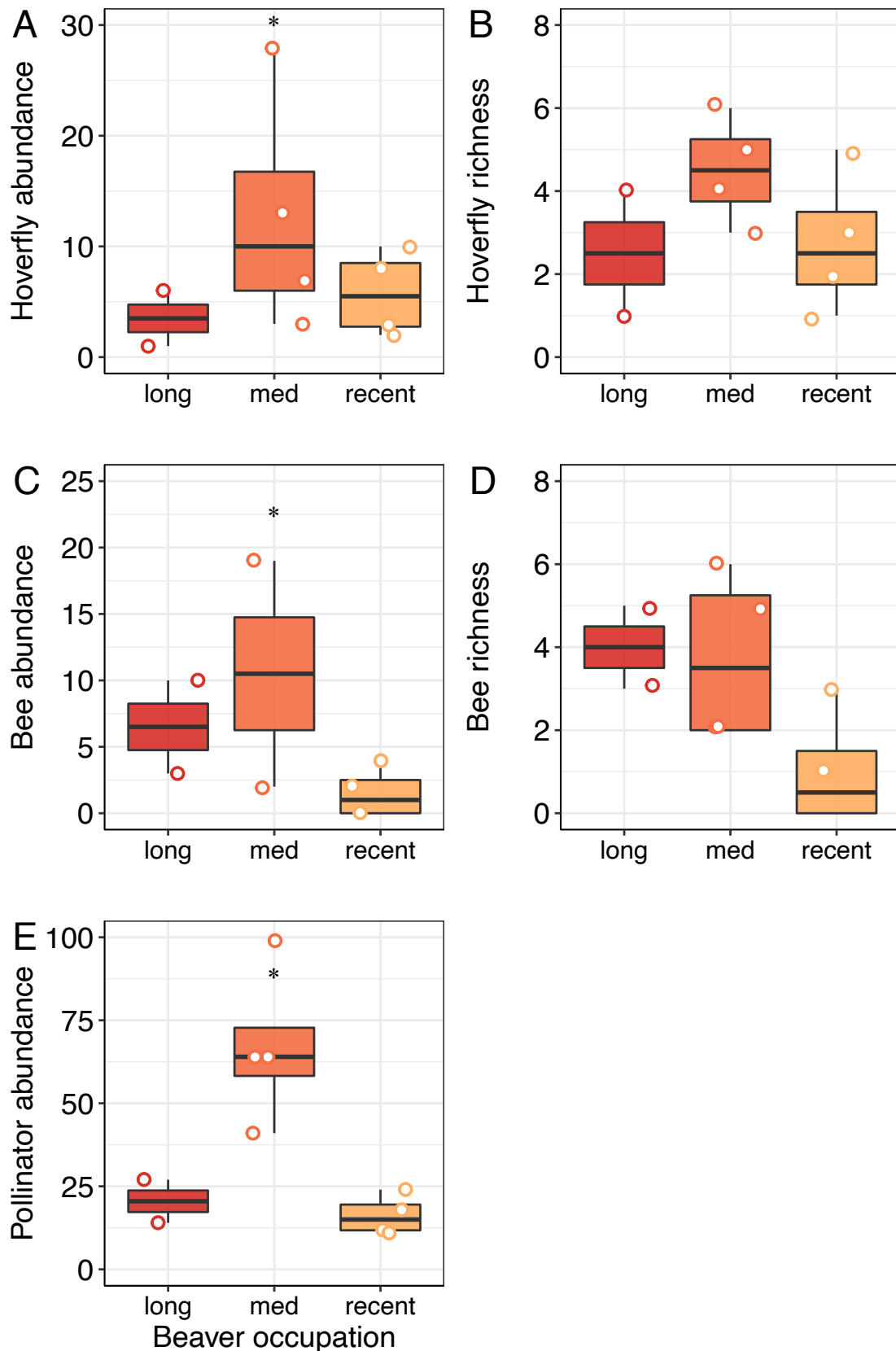


Figure 5 – Community composition changes in response to the length of beaver occupancy. **A.** Abundance of all hoverfly species recorded, **B.** species richness of hoverflies, **C.** abundance of all bee species recorded (bumble, honey and solitary), **D.** species richness of bees and **E.** total abundance of all species of pollinator recorded. Beaver occupancy refers to the length of time since the beavers initial arrival to a site and was recorded in years, then grouped as; recent (1-2 years), med[ium] (4-5 years) and long (7-10 years). Each circle indicates an individual sites' value for the respective variable. An * indicates significance.

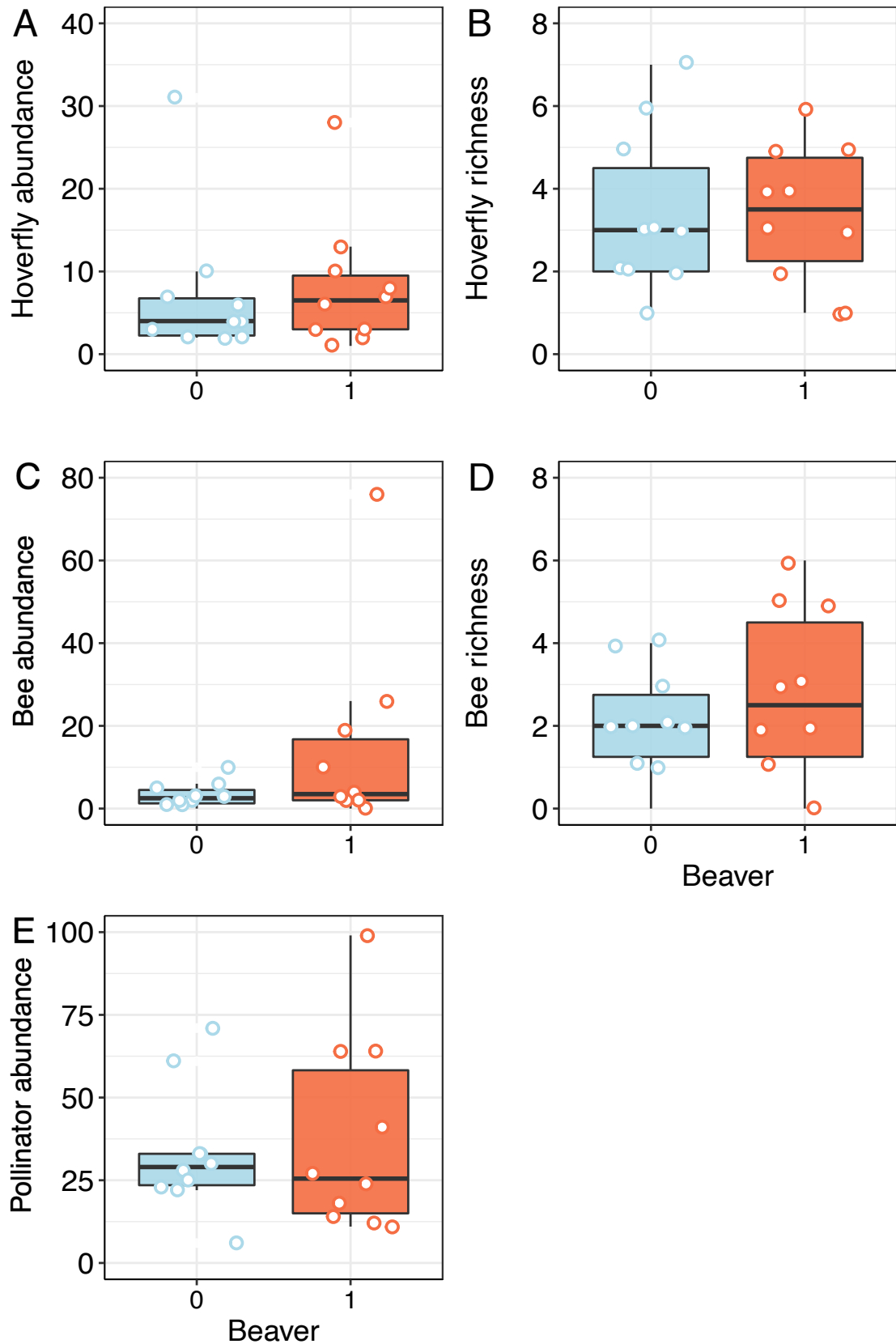


Figure 6 – Community composition changes in response to beaver presence (1) or absence (0). **A.** Abundance of all hoverfly species recorded, **B.** species richness of hoverflies, **C.** abundance of all bee species recorded (bumble, honey and solitary), **D.** species richness of bees and **E.** total abundance of all species of pollinator recorded. Each circle indicates an individual sites' value for the respective variable. An * indicates significance.

Table 4 - GLM outputs (test = χ^2) of the overall effect of beaver occupation length on community structure (An * indicates significance).

Variable	LR Chisq	Df	Pr(>Chisq)
Hoverfly abundance	18.76	2	<0.001*
Hoverfly richness	3.13	2	0.210
Bee abundance	9.10	2	0.011 *
Bee richness	5.82	2	0.055
Total insect abundance	29.73	2	<0.001*

Table 5 – Linear mixed effect model outputs on the overall effect of beaver presence or absence on community composition, with site ID fitted as a random effect (An * indicates significance).

Variable	LR Chisq	Df	Pr(>Chisq)
Hoverfly abundance	0.56	1	0.456
Hoverfly richness	0	1	1
Bee abundance	2.19	1	0.139
Bee richness	1.10	1	0.294
Total insect abundance	0.25	1	0.619

4 | Discussion

Ecosystem engineering by Eurasian beavers had a surprisingly small effect on plant pollinator networks when comparing the effect of beaver presence to absence, with variation in network metrics tending to non-significantly increase with beaver presence. Similarly, beaver presence versus absence had no significant effect on community composition. By contrast, length of beaver occupation had a non-linear effect on pollinator abundance, with generalist pollinators (hoverflies and bees (Osborne *et al*, 2008; Lucas *et al*, 2018)) significantly increasing on medium length occupancy sites. Finally, despite the findings for beaver presence versus absence, the network metrics insect richness and network richness significantly changed in response to length of beaver occupancy and thus engineering. Evidence was found to suggest that medium length beaver occupancy (4-5 years) increased network nestedness and richness the most.

The results for network metrics at beaver present versus absent sites suggests that beaver engineering is having an effect on the networks, yet this was not enough to be significant. It is possible that beaver absent (control) transects were located too close to the beaver present transects, limiting these results. The significant increase in pollinator abundance with length of beaver occupancy found here would support theory for a positive spill over effect whereby beaver present sites are acting as source populations, thus homogenising treatment and control transects (Nummi *et al*, 2021). Furthermore, hoverfly species including the marmalade hoverfly (*Episyrphus balteatus*) can migrate across the English channel (Wotton *et al*, 2019), while the buff tailed bumblebee (*Bombus terrestris*) can travel 1.5km (Osborne *et al*, 2008).

Subsequently, both species, which were commonly recorded in this study, could have flown the 200 metres between treatment and control sites used here. Therefore, increasing the distance between the transects could solve this. Additionally, having two control transects per treatment transect, at different distances upstream, could determine whether distance influences networks, and the strength of the effects. That said, network studies commonly struggle to capture the full range of complexity within networks due to insufficient comprehension of how temporal variation effects network structure (Schwarz *et al*, 2020). Similarly, this study found the temporal variation of seasonality difficult to address, with only three repeats done for each transect during summer 2021. Furthermore, the inability to control for, pre-beaver communities and networks, existing non-beaver related conservation of habitats on control sites, and the reality that control sites for free living beaver populations were not entirely free of the influence of engineering could all explain why engineering had no significant effect on the networks when comparing beaver presence and absence (Colom, Traveset and Stefanescu, 2021).

Discounting potential methodological flaws, for networks not to respond significantly to beaver engineering compared to beaver absent control sites is surprising given typical engineering activities (Brazier *et al*, 2021) had occurred across all of the sites, albeit at different levels. However, network response to engineering was not entirely absent with mean insect and plant species richness, network richness and robustness marginally increasing, while connectance marginally decreased. Habitat fragmentation is proposed as one explanation for this as new species colonisations of the beaver sites would be restricted (Hagen *et al*, 2012; Spiesman and Inouye, 2013; Hallmann *et al*, 2017). With species richness and abundance the architects of network structure

(Spiesman and Inouye, 2013) a lack of new colonisations limits the species community and therefore network richness, connectance and robustness to the species and interactions already present before beaver arrival. Consequently, any change in the networks due to ecosystem engineering is constrained by the limited change available (abundance and range) to the existing number of species. Furthermore, clonally reproducing plants already on beaver sites fill gaps created from engineering quicker than new species colonise them (Law, Jones and Willby, 2014). As such, the beaver present and absent communities, and therefore networks, remain homogeneous. However, increased species richness has been found on highly fragment sites in the UK where beaver are present (Law *et al*, 2017; Brazier *et al*, 2021), including on sites studied here (Brazier *et al*, 2020), yet how new species reach and colonise these sites remains unclear (Law, Mclean and Willby, 2016). Indeed, beaver wetlands contain unique species assemblages (including insects) that are not a subset of those found in the surrounding freshwater environment (Law, Mclean and Willby, 2016). Tree felling and coppicing facilitate these species rich assemblages (Thompson, Vehkaoja, and Nummi, 2016; Durben *et al*, 2021) by increasing sunlight reaching ground level, supporting plant growth from relic seed banks, activated by canal digging and damming (Ray, Rebertus and Ray, 2001). Hence, food and basking resources for insects increase in restored wetlands. Furthermore, the disturbance and habitat change introduced by engineering can see the loss of one guild of species and their gradual replacement by another guild as abiotic conditions change locally (Law, Mclean and Willby, 2016). Thus, greater differences in species composition are created between beaver present and absent sites while also increasing alpha diversity at a landscape scale. Yet, this did not translated into significant network changes as networks are still

rewiring interactions following new species arrival, species loss and habitat disturbance (Sanders *et al*, 2014; Cariveau, Bruninga-Socolar and Paradeee, 2020). This means some species recorded here may be functionally extinct (Valiente-Banuet *et al*, 2015), or network metrics are not truly reflecting network change as newly colonising species were present at such low levels they were unrecorded. It is more likely for specialist species to occur at these low levels (Phillips *et al*, 2020), despite engineering restoring habitat, reversing fragmentation and increasing floral and non-floral resource provisions (Cariveau, Bruninga-Socolar and Paradeee, 2020). Moreover, species including *Eristalis* hoverflies (recorded here) become less specialised as spring transitions into summer, so the summer survey season used here will have likely missed interactions between species (Lucas *et al*, 2018). This may also explain the increased generality (shown by links per species) and lower nestedness seen here, especially as community composition shows increased abundance of generalist pollinators (hoverflies and bees).

For species abundance and richness to increase with the length of beaver occupancy on a site is a fairly typical finding (Stringer and Gaywood, 2016; Law *et al*, 2019; Brazier *et al*, 2021; Durben *et al*, 2021; Nummi *et al*, 2021) but for them to peak at medium length beaver occupancy was unexpected. Even so, the more unique feature of this study is the minimal, non-significant change in community composition where beaver are present compared to absent. This lack of change may be the product of grouping all beaver present sites into one group, not accounting for the length of beaver occupancy, thus lowering the overall mean while increasing variation. If instead comparison is drawn between the length of beaver occupation and the beaver absent control sites, it can be seen that over time, engineering drives very apparent changes

in community composition. With older beaver ponds speeding up the colonisation of new ones located nearby (Law, Mclean and Willby, 2016) and high recruitment yet little loss of macrophyte species on beaver wetlands over time (Law, Jones and Willby, 2014), younger beaver wetlands with less engineering will have lower species abundance and richness. Such a finding explains the increases seen at medium length beaver occupancy sites, but this rule would also be expected to carry over to longer durations of beaver presence (Law *et al*, 2017). With the exception of bee richness, this was not the case. However, constant succession on these highly dynamic beaver wetlands drives fluctuations in species abundance and niche availability (Rosell *et al*, 2005; Law *et al*, 2017). This was seen in a mass bloom of hemlock water dropwort on one medium length site that led to 54 interactions with honey bees. Nothing similar was seen on long term or recent sites, possibly caused by different plant communities and abundances, although this is not clear. Furthermore, the ephemeral nature of engineering features, such as freshly felled or standing deadwood and dams can see these features decrease, become redundant or relic, leading to localised species decline and loss (Thompson, Vehkaoja, and Nummi, 2016), especially if beavers have abandoned these areas. Together, these suggest an explanation for lower abundance and richness on long term beaver sites. Therefore, the enclosure of beavers will not provide significant long term benefit to plant pollinator networks as enclosure prevents restoration of a mosaic of habitats (Fantinato, Del Vecchio and Buffa, 2019) at different stages of engineering, most importantly medium length engineering, from spreading across the landscape. Furthermore, after about seven years of engineering, a lack of habitat amelioration sees the productivity of older sites drop (Nummi *et al*, 2021). Consequently, an agricultural matrix surrounding an aging fragmented beaver wetland

will exacerbate declines in richness and abundance as the agricultural landscape is unlikely to support strong metapopulations of more specialised species (Redhead *et al*, 2018; Nummi *et al*, 2021). Resources used by *Eristalis* hoverfly larvae include freshly dead or snagged wood and nutrient enriched water (Lucas *et al*, 2018). These are less common in the wider landscape, but are provided by engineering. Indeed, broken dams and relic ponds were seen on both of the long term sites and one medium length site, resulting in an absence of insects around the remaining expanse of bare ground, or a monoculture of the fastest colonising plant. The beavers can then exacerbate species declines further through uneven pressures from central place foraging and selective foraging (Law, Jones and Willby, 2014; Stringer and Gaywood, 2016), potentially making it harder for specialist species to survive in the remaining habitat (Hagen *et al*, 2012). This would explain significant increases of hoverfly and bee species abundance (generalists) during medium length beaver occupancy. In fact, disturbance could also account for low levels of abundance and richness on recent beaver sites, where levels of disturbance are high as engineering causes habitat change, which can drive species loss (Law, Mclean and Willby, 2016). Hence, mid-length beaver occupancy appears to be the intermediary zone with optimal conditions for generalists and specialists, so the strongest networks should be expected here.

A key prediction of the increasing length of beaver occupancy was for network richness, robustness and connectance to increase. This study found partial support, with network richness and insect richness on medium length beaver occupancy sites significantly higher. Indeed, increasing species richness over time is representative of successful habitat restoration. Moreover, the recovery of higher level species is particularly sensitive to this temporal gradient (Kaiser-Bunbury *et al*, 2017).

Consequently, expectation was for long term beaver sites to have had even higher richness than medium sites, but this was not the case, as stated previously. However, it is likely that poorer weather for the oldest site meant that the interactions surveyed were probably not representative. Despite that, a net increase in richness on long term beaver sites over recent sites was still present. This is because, although networks respond to habitat restoration as early as the first flowering season after restoration (Kaiser-Bunbury *et al*, 2017), these early communities on beaver wetlands do not fully represent the potential of restoration, which is seen after ten to twelve years (Law *et al*, 2017). Furthermore, multiple generations of beavers can occupy the same site, suggesting that ten years is not representative of network response to long term occupancy (Thompson, Vehkaoja and Nummi, 2016). However, richness is maintained on multi-generational wetlands in mosaics of beaver occupancy and abandonment on sub-sections of a territory, due to feedback from engineering onto the engineer (Jones *et al*, 2010; Thompson, Vehkaoja and Nummi, 2016). Average patch occupancy is three years, not dissimilar from the medium length sites in this study. Thus, it is probable that medium length occupancy sites support the most species rich networks within a wider long term occupancy site through waves of engineering creating fresh resource availability and heterogeneity. If this is the case, the enclosure of beavers and their engineering to 200 metres of watercourse for ten years is a long time, and would account for network declines seen (Cariveau, Bruninga-Socular and Pardee, 2020).

Another result of increased species richness and abundance on beaver wetlands seen here, which is due to ecosystem engineering creating a highly complex, dynamic mosaic of habitats (Nummi *et al*, 2021) is the near significant increase in nestedness

on medium length sites. Interestingly, light at ground level on beaver present sites increased with site age, suggesting species richness and nestedness respond best to a patchwork of sun and shade, likely determined by plant species preferences. Although, grazing, dams and canals distributing water also lead to greater floral diversity (Law *et al*, 2019; Brazier *et al*, 2021). The specialisation of solitary bees has been found to increase with higher floral diversity, yet honey and bumblebees do not (Ebeling, Klein and Tscharrntke, 2011). Furthermore, only two solitary bee species were recorded and plant richness did not significantly increase. Together, these will have limited the change in nestedness. Alongside this, greater floral diversity leads to the proposal that pollen availability and quality increased, raising pollination rates and competition. More competition can make it harder for specialist species to colonise a site so limiting change in network nestedness. Not only that but competition can also limit network interactions affecting nestedness and connectance (Cariveau, Bruninga-Socolar and Pardee, 2020). Indeed, recent beaver sites with less engineering and species richness had higher network connectance, likely due to a core of generalist species (Spiesman and Inouye, 2013). However, these more connected networks had lower generalism (shown by links per species) than medium length beaver sites, indicating the presence of a trade off, which was unexpected. Yet, generalist species are more resistant to climate change ergo, so is a more generalist network (Cariveau, Bruninga-Socolar and Pardee, 2020; Maia *et al*, 2021). Alongside this, networks were also non-significantly more robust as length of beaver occupancy increased, because species richness increases led to higher redundancy. Again, hoverfly increases will have contributed to this as their generalism increases network redundancy and their abundance stabilises pollination rates (Lucas *et al*, 2018). Together, these suggest

beaver habitat restoration could play a crucially important role in helping sustain and strengthen a vital ecosystem service (pollination), which makes up for declines in connectance. Therefore, further release of beavers would be beneficial, especially now as wild populations in England are being genuinely considered (Defra, 2021).

5 | Conclusion

This study illustrates that the passage of time has a central role in determining the influence ecosystem engineering has on plant pollinator networks. Significant increases in the two key architects of plant pollinator networks, species richness and abundance (Spiesman and Inouye, 2013; Kaiser-Bunbury *et al*, 2014), indicates the potential change in networks driven by ecosystem engineer induced habitat change is likely far greater than that seen here. Of particular interest are the patterns and determining variables leading to medium length beaver occupancy sites having the greatest benefits for network richness, nestedness and species abundance, and the trade off that occurs between network connectance and generality. It is likely that these patterns are influenced by the rise and fall in disturbance and productivity from habitat engineering and succession of sites affecting resource availability, but habitat fragmentation or methodological shortcomings of survey technique could also be responsible. Hence, continuing this study by surveying in spring and summer over multiple years should be a priority, to identify whether changes in network metrics (over length of beaver occupancy and between beaver present and absent sites) were limited by environmental conditions and short survey windows (Schwarz *et al*, 2020), particularly for long term sites. Nevertheless, the current findings suggest a need to

remove enclosure fences and permit (larger) free living populations of beavers in England (Defra, 2021) in order to provide enough habitat patches subject to medium length engineering. In amongst a landscape scale mosaic of habitats, these mid length patches provide the most support to the vital ecosystem service of pollination, reverse species richness declines and increase network resilience to climate and ecological perturbations (due to higher generalism). Therefore, early evidence for the benefit of ecosystem engineering on plant pollinator networks is presented here, indicating how Eurasian beaver induced habitat restoration can help restore and conserve the ecosystem service of pollination, in turn supporting biodiversity and human health.

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Appendix

Appendix 1 – Pollinator species list

Abbreviation	Latin Name	Common Name
Agromyzidae	Agromyzidae	Leaf Miner Flies
And.cin	Andrena cineraria	Ashy mining bee
Anobiidae	Anobiidae	Death Watch Beetles
Anthocoridae	Anthocoridae	Flower Bugs
Anthomyiidae	Anthomyiidae	Flies
Api.mel	Apis mellifera	Honey Bee
Aphididae	Aphididae	Aphids
Asilidae	Asilidae	Robber Flies
Bombus	Bombus (unidentified spp.)	Bumblebee
Bom.hor	Bombus hortorum	Garden Bumblebee
Bom.hyp	Bombus hypnorum	Tree Bumblebee
Bom.lap	Bombus lapidarius	Red-tailed Bumblebee
Bom.luc	Bombus lucorum	White-tailed Bumblebee
Bom.pas	Bombus pascuorum	Common Carder Bee
Bom.pra	Bombus pratorum	Early Bumblebee
Bom.ter	Bombus terrestris	Buff-tailed Bumblebee
Brachonidae	Brachonidae	Braconid Parasitoid Wasps
Bra.aen	Brassicogethes aeneus	Common Pollen Beetle
Cal.vom	Calliphora vomitoria	Bluebottle
Calliphoridae	Calliphoridae	Blow Flies
Carabidae	Carabidae	Ground Beetles
Chaoboridae	Chaoboridae	Phantom Midges
Chironomidae	Chironomidae	Non-biting Midges
Chl.for	Chloromyia formosa	Broad Centurion Fly
Chr.cem	Chrysogaster cemiteriorum	Hoverfly
Chr.sol	Chrysogaster solstitialis	Hoverfly
Chrysomelidae	Chrysomelidae	Leaf Beetles
Coe.pue	Coenagrion puella	Azure Damselfly
Collembola	Collembola	Springtails
Curculionidae	Curculionidae	True weevils
Dolichopodidae	Dolichopodidae	Long-legged Flies
Drosophila	Drosophila	Fruit Flies
Elateridae	Elateridae	Click Beetles
Empididae	Empididae	Dagger Flies
Empis	Empis	Dance Flies
Ena.cya	Enallagma cyathigerum	Common blue damselfly
Epi.nit	Epistrophe nitidicollis	Hoverfly
Epi.bal	Episyrphus balteatus	Marmalade hoverfly
Eriocraniidae	Eriocraniidae	Sparkling archaic sun moths
Eristalinae	Eristalinae	Hoverfly
Eri.nem	Eristalis nemorum	Hoverfly
Eri.per	Eristalis pertinax	Hoverfly
Eupeodes	Eupeodes	Hoverfly
Gra.ruf	Grammoptera ruficornis	Longhorn Beetle

Gry.sty	Grypocoris stysi	Mirid Bug
Hel.pen	Helophilus pendulus	The Footballer Hoverfly
Hybotidae	Hybotidae	Dance Flies
Ichneumonidae	Ichneumonidae	Ichneumon parasitoid wasps
Kateretidae	Kateretidae	Short-winged Flower Beetles
Lag.hir	Lagria hirta	Darkling Beetle
Lasioglossum	Lasioglossum	Sweet Bees
Lauxaniidae	Lauxaniidae	Flies
Lej.met	Lejogaster metallina	Green Marsh Hoverfly
Luc.cae	Lucilia caesar	Greenbottle
Man.jur	Maniola jurtina	Meadow Brown Butterfly
Mel.sca	Melanostoma scalare	Hoverfly
Mel.aur	Meliscaeva auricollis	Hoverfly
Melyridae	Melyridae	Soft-winged Flower Beetles
Miridae	Miridae	Mirid Bugs
Mis.vat	Misumena vatia	Crab Spider
Muscidae	Muscidae	House Flies
Mya.flo	Myathropa florea	Hoverfly
Mycetophilidae	Mycetophilidae	Fungus gnats
Myr.rub	Myrmica rubra	Common Red Ant
Nematocera	Nematocera	Elongated Flies
Neoascia	Neoascia (unidentified spp.)	Hoverfly
Neo.ten	Neoascia tenur	Bridged Clubtail Hoverfly
Nepticulidae	Nepticulidae	Pigmy Moths
Och.syl	Ochlodes sylvanus	Large Skipper Butterfly
Oed.nob	Oedemera nobilis	Thick legged flower beetle
Pac.atr	Pachygaster atra	Dark-winged Black Soldierfly
Pac.cer	Pachytodes cerambyciformes	Speckled Longhorn Beetle
Per.ful	Pericoma fuliginosa	Owl Midge
Pha.ruf	Phaonia rufiventris	House Flies
Phoridae	Phoridae	Hump-backed Flies
Pie.rap	Pieris rapae	Small White Butterfly
Piophilidae	Piophilidae	Flies
Pip.vid	Pipizella viduata	Hoverfly
Pipunculidae	Pipunculidae	Big-headed Flies
Pla.alb	Platycheirus albimanus	White-footed Hoverfly
Pla.scu	Platycheirus scutatus	Hoverfly
Plutellidae	Plutellidae	Diamondback moths
Pra.phe	Prasocuris phellandrii	Leaf Beetles
Psilidae	Psilidae	Rust Flies
Pyr.nym	Pyrrhosoma nymphula	Large red damselfly
Rhagionidae	Rhagionidae	Snipe Flies
Rha.ful	Rhagonycha fulva	Common red soldier beetle
Rut.mac	Rutpela maculata	Spotted Longhorn Beetle
Sap.opa	Sapromyza opaca	Flies
Sarcophagidae	Sarcophagidae	Flesh Fly
Sca.pyr	Scaeva pyrastris	Pied Hoverfly
Scathophagidae	Scathophagidae	Dung Flies

Simuliidae	Simuliidae	Black Flies
Sph.ele	Sphegina elegans	Hoverfly
Straphylinidae	Straphylinidae	Rove Beetles
Syr.rib	Syrphus ribesii	Hoverfly
Syr.vit	Syrphus vitripennis	Hoverfly
Tachinidae	Tachinidae	Tachinid Flies
Therevidae	Therevidae	Stiletto Flies
Tineidae	Tineidae	<u>Clothes Moths</u>
Tingidae	Tingidae	Lace Bugs
Tortricidae	Tortricidae	Tortrix Moths
Van.ata	Vanessa atalanta	Red Admiral Butterfly
Vol.bom	Volucella bombylans	Bumblebee Hoverfly
Vol.pel	Volucella pellucens	Pellucid Hoverfly

Appendix 2 – Plant species list

Abbreviation	Latin Name	Common Name
Aeg.pod	Aegopodium podagraria	Ground Elder
Api.gra	Apium graveolens	Wild Celery
Cen.nig	Centaurea nigra	Common/Black Knapweed
Cer.fon	Cerastium fontanum	Common Mouse-ear
Cha.tem	Chaerophyllum temulum	Rough Chervil
Cic.int	Cichorium intybus	Chicory
Cir.lut	Circaea lutetiana	Enchanter's Nightshade
Cir.arv	Cirsium arvense	Creeping Thistle
Cir.pal	Cirsium palustre	Marsh Thistle
Cir.vul	Cirsium vulgare	Spear Thistle
Clasib	Claytonia sibirica	Pink Purslane
Dig.pur	Digitalis purpurea	Foxglove
Epi.hir	Epilobium hirsutum	Great willowherb
Fil.ulm	Filipendula ulmaria	Meadowsweet
Gal.pal	Galium palustre	Common Marsh Bedstraw
Ger.rob	Geranium robertianum	Herb Robert
Her.sph	Heracleum sphondylium	Hogweed
Hya.non-scr	Hyacinthoides non-scripta	English Bluebell
Hyp.and	Hypericum androsaemum	Tutsan
Imp.gla	Impatiens glandulifera	Himalayan Balsam
Iri.pse	Iris pseudacorus	Yellow Flag Iris
Lot.ped	Lotus pedunculatus	Greater Birds Foot Trefoil
Lyc.flo-cuc	Lychnis flos-cuculi	Ragged-robin
Lys.nem	Lysimachia nemorum	Yellow Pimpernel
Myo.lax	Myosotis laxa	Tufted Forget-me-not
Myo.sco	Myosotis scorpioides	Water Forget-me-not
Myo.sec	Myosotis secunda	Creeping Forget-me-not
Oen.cro	Oenanthe crocata	Hemlock Water Dropwort
Ran.acr	Ranunculus acris	Meadow Buttercup
Ran.flu	Ranunculus flammula	Lesser Spearwort
Ran.rep	Ranunculus repens	Creeping Buttercup
Rhi.min	Rhinanthus minor	Yellow Rattle

Ror.nas-aqu	Rorippa nasturtium-aquaticum	Water Cress
Ros.can	Rosa canina	Dog Rose
Rub.fru	Rubus fruticosus	Bramble
Sam.nig	Sambucus nigra	Elder
San.eur	Sanicula europaea	Sanicle
Sen.aqu	Senecio aquaticus	Marsh Ragwort
Sil.dio	Silene dioica	Red Campion
Sol.dul	Solanum dulcamara	Bittersweet Nightshade
Sta.syl	Stachys sylvatica	Hedge Woundwort
Ste.gra	Stellaria graminea	Lesser Stitchwort
Sym.alb	Symphoricarpos albus	Snowberry
Tri.ino	Tripleurospermum inodorum	Scentless Mayweed
Val.off	Valeriana officinalis	Common Valerian

References

- ALLESINA, S. & BODINI, A. 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. *Journal of Theoretical Biology*, 230, 351-358.
- BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O. U., SWARTZ, B., QUENTAL, T. B., MARSHALL, C., MCGUIRE, J. L., LINDSEY, E. L., MAGUIRE, K. C., MERSEY, B. & FERRER, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51-57.
- BENNETT, J. M., THOMPSON, A., GOIA, I., FELDMANN, R., STEFAN, V., BOGDAN, A., RAKOSY, D., BELOIU, M., BIRO, I. B., BLUEMEL, S., FILIP, M., MADAJ, A. M., MARTIN, A., PASSONNEAU, S., KALISCH, D. P., SCHERER, G. & KNIGHT, T. M. 2018. A review of European studies on pollination networks and pollen limitation, and a case study designed to fill in a gap. *Aob Plants*, 10, 10.
- BLUTHGEN, N. & KLEIN, A. M. 2011. Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic and Applied Ecology*, 12, 282-291.
- BORRVALL, C. & EBENMAN, B. 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. *Ecology Letters*, 9, 435-442.
- BRAZIER, R. E., ELLIOTT, M., ANDISON, E., AUSTER, R.E., BRIDGEWATER, S., BURGESS, P., CHANT, J., GRAHAM, H., KNOTT, E., PUTTOCK, A.K., SANSUM, P., VOWLES, A. 2020. River Otter Beaver Trial: Science and Evidence Report.
- BRAZIER, R. E., PUTTOCK, A., GRAHAM, H. A., AUSTER, R. E., DAVIES, K. H. & BROWN, C. M. L. 2021. Beaver: Nature's ecosystem engineers. *Wiley Interdisciplinary Reviews-Water*, 8.
- BRAZIER, R. P., ALAN. GRAHAM, HUGH. ANDERSON, K AREN. CUNLIFFE, ANDREW AND ELLIOTT, MARK. 2016. Quantifying the multiple, environmental benefits of reintroducing the Eurasian Beaver. Geophysical Research Abstracts.
- CARIVEAU, D. P., BRUNINGA-SOCOLAR, B. & PARDEE, G. L. 2020. A review of the challenges and opportunities for restoring animal-mediated pollination of native plants. *Emerging Topics in Life Sciences*, 4, 99-109.
- COLOM, P., TRAVESET, A. & STEFANESCU, C. 2021. Long-term effects of abandonment and restoration of Mediterranean meadows on butterfly-plant interactions. *Journal of Insect Conservation*, 25, 383-393.
- CONSERVATION, B. 2021. Wider Countryside Butterfly Survey.
- DEFRA 2021. Approach to beaver reintroduction and management in England: Consultation document. Retrieved on 02/09/2021 from https://consult.defra.gov.uk/natural-environment-policy/beaver-reintroduction-and-management/supporting_documents/Consultation%20on%20beaver%20reintroduction%20and%20management_accessible.pdf.
- DEVRIES, P., FETHERSTON, K. L., VITALE, A. & MADSEN, S. 2012. Emulating Riverine Landscape Controls of Beaver in Stream Restoration. *Fisheries*, 37, 246-255.
- DORMANN, C. F., FRUEND, J., BLUETHGEN, N. & GRUBER B. 2009. Indices, graphs and null models: analysing bipartite ecological networks. . The Open Ecology Journal,.

- DORMANN, C. F., GRUBER B. & FRUEND, J. 2008. Introducing the bipartite Package: Analysing Ecological Networks. . R news.
- DURBEN, R. M., WALKER, F. M., HOLESKI, L., KEITH, A. R., KOVACS, Z., HURTEAU, S. R., LINDROTH, R. L., SHUSTER, S. M. & WHITHAM, T. G. 2021. Beavers, Bugs and Chemistry: A Mammalian Herbivore Changes Chemistry Composition and Arthropod Communities in Foundation Tree Species. *Forests*, 12.
- EBELING, A., KLEIN, A. M. & TSCHARNTKE, T. 2011. Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic and Applied Ecology*, 12, 300-309.
- FANTINATO, E., DEL VECCHIO, S. & BUFFA, G. 2019. The co-occurrence of different grassland communities increases the stability of pollination networks. *Flora*, 255, 11-17.
- FISOJNI, A., MASSOL, F., DE MANINCOR, N., QUARANTA, M., BOGO, G., BORTOLOTTI, L. & GALLONI, M. 2021. Network analysis highlights increased generalisation and evenness of plant-pollinator interactions after conservation measures. *Acta Oecologica-International Journal of Ecology*, 110.
- GERARD, M., VANDERPLANCK, M., WOOD, T. & MICHEZ, D. 2020. Global warming and plant-pollinator mismatches. *Emerging Topics in Life Sciences*, 4, 77-86.
- GIBSON, R. H., KNOTT, B., EBERLEIN, T. & MEMMOTT, J. 2011. Sampling method influences the structure of plant-pollinator networks. *Oikos*, 120, 822-831.
- GOLDSTEIN, J. & ZYCH, M. 2016. What if we lose a hub? Experimental testing of pollination network resilience to removal of keystone floral resources. *Arthropod-Plant Interactions*, 10, 263-271.
- GORCZYCA, E., KRZEMIEN, K., SOBUCKI, M. & JARZYNA, K. 2018. Can beaver impact promote river renaturalisation? The example of the Raba River, southern Poland. *Science of the Total Environment*, 615, 1048-1060.
- GOV.UK. 2021. Landmark consultation launched on the reintroduction of beavers in England. Retrieved on 02/09/21 from <https://www.gov.uk/government/news/landmark-consultation-launched-on-the-reintroduction-of-beavers-in-england>
- HAGEN, M., KISSLING, W. D., RASMUSSEN, C., DE AGUIAR, M. A. M., BROWN, L. E., CARSTENSEN, D. W., ALVES-DOS-SANTOS, I., DUPONT, Y. L., EDWARDS, F. K., GENINI, J., GUIMARAES, P. R., JENKINS, G. B., JORDANO, P., KAISER-BUNBURY, C. N., LEDGER, M. E., MAIA, K. P., MARQUITTI, F. M. D., MCLAUGHLIN, O., MORELLATO, L. P. C., O'GORMAN, E. J., TROJELSGAARD, K., TYLIANAKIS, J. M., VIDAL, M. M., WOODWARD, G. & OLESEN, J. M. 2012. Biodiversity, Species Interactions and Ecological Networks in a Fragmented World. *Advances in Ecological Research, Vol 46: Global Change in Multispecies Systems, Pt 1*, 46, 89-210.
- HALLMANN, C. A., SORG, M., JONGEJANS, E., SIEPEL, H., HOFLAND, N., SCHWAN, H., STENMANS, W., MULLER, A., SUMSER, H., HORREN, T., GOULSON, D. & DE KROON, H. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *Plos One*, 12, 21.
- HEYDON M.J. , P., D. , GRAY, S. , WAGSTAFF, G. , ASHTON, M.E.M. & ANDISON, E. 2021. Beaver reintroductions in England: 2000 – 2021. . JP036. Natural England, York.
- HILTON-TAYLOR C. & BRACKETT, D. 2000. IUCN Red List of Threatened Species . World Conserv. Union, Gland Switzerland: IUCN.
- JONES, C. G., GUTIERREZ, J. L., BYERS, J. E., CROOKS, J. A., LAMBRINOS, J. G. & TALLEY, T. S. 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos*, 119, 1862–1869
- JONES, C. G., LAWTON, J. H. & SHACHAK, M. 1994. Organisms as ecosystem engineers. *Oikos*, 69, 373-386.
- JUNK, W. J., AN, S. Q., FINLAYSON, C. M., GOPAL, B., KVET, J., MITCHELL, S. A., MITSCH, W. J. & ROBERTS, R. D. 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquatic Sciences*, 75, 151-167.
- KAISER-BUNBURY, C. N., MOUGAL, J., WHITTINGTON, A. E., VALENTIN, T., GABRIEL, R., OLESEN, J. M. & BLUTHGEN, N. 2017. Ecosystem restoration strengthens pollination network resilience and function. *Nature*, 542, 223-227.
- KAISER-BUNBURY, C. N., VAZQUEZ, D. P., STANG, M. & GHAZOUL, J. 2014. Determinants of the microstructure of plant-pollinator networks. *Ecology*, 95, 3314-3324.
- KEHOE, R., FRAGO, E. & SANDERS, D. 2021. Cascading extinctions as a hidden driver of insect decline. *Ecological Entomology*, 46, 743-756.
- KITCHENER, A. C. A. C., J. W. H. 1997. The history of the Eurasian Beaver *Castor fiber* in Scotland. *Mammal Review*.
- LATTY, T. & DAKOS, V. 2019. The risk of threshold responses, tipping points, and cascading failures in pollination systems. *Biodiversity and Conservation*, 28, 3389-3406.

- LAW, A., GAYWOOD, M. J., JONES, K. C., RAMSAY, P. & WILLBY, N. J. 2017. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Science of the Total Environment*, 605, 1021-1030.
- LAW, A., JONES, K. C. & WILLBY, N. J. 2014. Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. *Aquatic Botany*, 116, 27-34.
- LAW, A., LEVANONI, O., FOSTER, G., ECKE, F. & WILLBY, N. J. 2019. Are beavers a solution to the freshwater biodiversity crisis? *Diversity and Distributions*, 25, 1763-1772.
- LAW, A., MCLEAN, F. & WILLBY, N. J. 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology*, 61, 486-499.
- LUCAS, A., BODGER, O., BROSI, B. J., FORD, C. R., FORMAN, D. W., GREIG, C., HEGARTY, M., NEYLAND, P. J. & DE VERE, N. 2018. Generalisation and specialisation in hoverfly (Syrphidae) grassland pollen transport networks revealed by DNA metabarcoding. *Journal of Animal Ecology*, 87, 1008-1021.
- MAIA, K. P., MARQUITTI, F. M. D., VAUGHAN, I. P., MEMMOTT, J. & RAIMUNDO, R. L. G. 2021. Interaction generalisation and demographic feedbacks drive the resilience of plant-insect networks to extinctions. *Journal of Animal Ecology*, 90, 2109-2121.
- MONTOYA, J. M., PIMM, S. L. & SOLE, R. V. 2006. Ecological networks and their fragility. *Nature*, 442, 259-264.
- NOVELLA-FERNANDEZ, R., RODRIGO, A., ARNAN, X. & BOSCH, J. 2019. Interaction strength in plant-pollinator networks: Are we using the right measure? *Plos One*, 14, 15.
- NUMMI, P., LIAO, W. F., VAN DER SCHEER, J. & LOEHR, J. 2021. Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation*, 30, 2655-2670.
- OLESEN, J. M., BASCOMPTE, J., DUPONT, Y. L. & JORDANO, P. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19891-19896.
- OSBORNE, J. L., MARTIN, A. P., CARRECK, N. L., SWAIN, J. L., KNIGHT, M. E., GOULSON, D., HALE, R. J. & SANDERSON, R. A. 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, 77, 406-415.
- PAINE, R. T. 1966. FOOD WEB COMPLEXITY AND SPECIES DIVERSITY. *American Naturalist*, 100, 65-+.
- PARRA-TABLA, V. & ARCEO-GOMEZ, G. 2021. Impacts of plant invasions in native plant-pollinator networks. *New Phytologist*, 230, 2117-2128.
- PHILLIPS, R. D., PEAKALL, R., VAN DER NIET, T. & JOHNSON, S. D. 2020. Niche Perspectives on Plant-Pollinator Interactions. *Trends in Plant Science*, 25, 779-793.
- PUTTOCK, A., GRAHAM, H. A., ASHE, J., LUSCOMBE, D. J. & BRAZIER, R. E. 2020. Beaver dams attenuate flow: A multi-site study. *Hydrological Processes*, 35.
- PUTTOCK, A., GRAHAM, H. A., CARLESS, D. & BRAZIER, R. E. 2018. Sediment and nutrient storage in a beaver engineered wetland. *Earth Surface Processes and Landforms*, 43, 2358-2370.
- PUTTOCK, A., GRAHAM, H. A., CUNLIFFE, A. M., ELLIOTT, M. & BRAZIER, R. E. 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of the Total Environment*, 576, 430-443.
- RAY, A. M., REBERTUS, A. J. & RAY, H. L. 2001. Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 79, 487-499.
- RESASCO, J., CHACOFF, N. P. & VAZQUEZ, D. P. 2021. Plant-pollinator interactions between generalists persist over time and space. *Ecology*, 102.
- ROSELL, F., BOZSER, O., COLLEN, P. & PARKER, H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35, 248-276.
- ROTHERAY, E. L. 2012. The ecology and conservation of endangered saproxylic hoverflies (Diptera, Syrphidae) in Scotland. University of Stirling
- SABATINO, M., ROVERE, A. & MELI, P. 2021. Restoring pollination is not only about pollinators: Combining ecological and practical information to identify priority plant species for restoration of the Pampa grasslands of Argentina. *Journal for Nature Conservation*, 61.
- SANDERS, D., JONES, C. G., THEBAULT, E., BOUMA, T. J., VAN DER HEIDE, T., VAN BELZEN, J. & BAROT, S. 2014. Integrating ecosystem engineering and food webs. *Oikos*, 123, 513-524.
- SCHWARZ, B., VAZQUEZ, D. P., CARADONNA, P. J., KNIGHT, T. M., BENADI, G., DORMANN, C. F., GAUZENS, B., MOTIVANS, E., RESASCO, J., BLUTHGEN, N., BURKLE, L. A., FANG, Q., KAISER-BUNBURY, C. N., ALARCON, R., BAIN, J. A., CHACOFF, N. P., HUANG, S. Q., LEBUHN, G., MACLEOD, M., PETANIDOU, T., RASMUSSEN, C., SIMANONOK, M. P., THOMPSON, A. H. & FRUND, J. 2020. Temporal scale-dependence of plant-pollinator networks. *Oikos*, 129, 1289-1302.

- SIMMONS, B. I., CIRTWILL, A. R., BAKER, N. J., WAUCHOPE, H. S., DICKS, L. V., STOUFFER, D. B. & SUTHERLAND, W. J. 2019. Motifs in bipartite ecological networks: uncovering indirect interactions. *Oikos*, 128, 154-170.
- SPIESMAN, B. J. & INOUE, B. D. 2013. Habitat loss alters the architecture of plant-pollinator interaction networks. *Ecology*, 94, 2688-2696.
- STRINGER, A. P. & GAYWOOD, M. J. 2016. The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, 46, 270-283.
- THOMPSON, S., VEHKAOJA, M. & NUMMI, P. 2016. Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management*, 360, 1-8.
- ULRICH, W., ALMEIDA, M. & GOTELLI, N. J. 2009. A consumer's guide to nestedness analysis. *Oikos*, 118, 3-17.
- VALIENTE-BANUET, A., AIZEN, M. A., ALCANTARA, J. M., ARROYO, J., COCUCCHI, A., GALETTI, M., GARCIA, M. B., GARCIA, D., GOMEZ, J. M., JORDANO, P., MEDEL, R., NAVARRO, L., OBESO, J. R., OVIEDO, R., RAMIREZ, N., REY, P. J., TRAVESET, A., VERDU, M. & ZAMORA, R. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, 29, 299-307.
- WALKER, K. J., STEVENS, P. A., STEVENS, D. P., MOUNTFORD, J. O., MANCHESTER, S. J. & PYWELL, R. F. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation*, 119, 1-18.
- WOTTON, K. R., GAO, B. Y., MENZ, M. H. M., MORRIS, R. K. A., BALL, S. G., LIM, K. S., REYNOLDS, D. R., HU, G. & CHAPMAN, J. W. 2019. Mass Seasonal Migrations of Hoverflies Provide Extensive Pollination and Crop Protection Services. *Current Biology*, 29, 2167-+.
- WRIGHT, J. P. & JONES, C. G. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *Bioscience*, 56, 203-209.