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The impacts of beaver-modified habitats on small mammal populations in Southern Finland in the context of ecological succession

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A thesis presented for the award of the Master's degree in Organismal Biology and Ecology

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Abstract

Beavers are widely known as ecological engineers, shaping their environment and facilitating many other species, both plant and animal, to thrive. By physically modifying their environment, they induce biological changes and create heterogeneity within the ecosystem. The beaver's impact remains visible even after it has left the dam. Once the flooding has subsided, the site becomes an open meadow, giving way to ecological succession. Several studies have been carried out on the impact of beavers on small mammal populations during their presence. However, very few studies have been carried out on the impact of the habitat modified by beavers on these species in the context of ecological succession. This study was carried out in the Evo Recreation Park in southern Finland. More specifically, three categories of study sites were considered. Five unimpacted control sites, five sites in the early stages of ecological succession and five sites in a more advanced state of ecological succession since the departure of the beavers. At each site, small mammals were counted using snap traps, along with vegetation and dead wood. No significant differences were found between the different stages of succession. Despite the non-significant results of the study, certain trends could be identified. The results suggest that sites recently impacted by beavers support a greater diversity of plant species and small mammals and are slightly more favourable sites for species such as the bank vole (*Myodes glareolus*) and the field vole (*Microtus agrestis*). However, it seemed that sites in a more advanced state of succession are less favourable to the species present, as their physical condition was found to be poorer. These results are in line with the literature. On the one hand, the abundance of small mammals decreases with the advancement of ecological succession and, on the other hand, the positive impacts of the beaver are mainly noticeable at the landscape scale rather than at the patch scale. Beavers have little or no impact on alpha diversity, but they do have a significant positive impact on gamma diversity over time and space, since they increase landscape connectivity and heterogeneity, thereby facilitating the movement of many species. This study suggests a broader and longer-term study of small mammal populations impacted by beavers. More generally, the beaver is a very important conservation tool for freshwater habitats that are heavily impacted by humans, as well as for all the living species associated with them.

Résumé

Les castors sont largement connus comme étant des ingénieurs écologiques façonnant leur environnement et permettant ainsi la facilitation de nombreuses autres espèces, tant végétales qu'animales. En effet, en modifiant son environnement de manière physique, ils induisent des changements biologiques et crée de l'hétérogénéité au sein de l'écosystème. Les impacts du castor restent visibles même après son départ du barrage. En effet, une fois l'inondation partie, le site devient alors une prairie ouverte laissant alors place à la succession écologique. Plusieurs études ont été réalisées sur l'impact des castors sur les populations de petits mammifères lors de leur présence. Cependant très peu d'études ont été effectuées sur l'impact de l'habitat modifié par les castors sur les petits mammifères dans le cadre de la succession écologique. La présente étude a été menée au sein du Park récréatif d'Evo en Finlande du sud et avait pour but d'étudier les populations de petits mammifères dans les stades de succession au sein d'habitats modifiés par le castor. Plus précisément, trois catégories de sites d'étude ont été prises en compte. Cinq sites contrôles non impactés, cinq sites en début de succession écologique et cinq sites en état plus avancé de succession écologique depuis le départ des castors. Sur chacun des sites, un recensement de petits mammifères à l'aide de snap-traps a été effectué ainsi qu'un recensement de la végétation et le comptage de bois morts présents sur les sites. Aucune différence significative n'a été trouvée entre les différents stades de succession. Malgré les résultats non significatifs de l'étude, certaines tendances ont pu être mises en avant. Les résultats suggèrent que les sites récemment impactés par les castors permettent la mise en place d'une plus grande diversité d'espèces végétales et de petits mammifères et seraient des sites légèrement plus favorables à des espèces telles que le campagnol roussâtre (*Myodes glareolus*) et le campagnol des champs (*Microtus agrestis*). Il semblerait cependant que les sites étant dans un état de succession plus avancé ne sont pas favorables aux espèces présentes car leur condition physique y a été retrouvé plus pauvre. Ces résultats sont en accord avec la littérature. Effet, d'une part, l'abondance des petits mammifères décroit avec l'avancement de la succession écologique et, d'autre part, les impacts positifs du castor sont principalement remarquables à l'échelle du paysage plutôt qu'à l'échelle du patch. Le castor ne modifie pas ou très peu la diversité alpha mais a un large impact positif dans le temps et dans l'espace sur la diversité gamma puisqu'il permet la connectivité et l'hétérogénéité du paysage, permettant ainsi la facilitation de nombreuses espèces. Cette étude suggère une étude plus large et plus longue dans le temps des populations de petits mammifères impactées par le castor. Plus généralement, le castor est un moyen de conservation très important pour les habitats d'eaux douces largement impactés par les êtres-humains mais également pour toutes les espèces vivantes y étant associées.

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Introduction

1. Wetland situation worldwide and in Finland

Freshwater is undoubtedly linked to the most fundamental aspects of life. Coastal and riverine ecosystems are among the most important carbon stocks, with most of it stored in wetlands (Liu et al. 2020). Wetlands act as an ecotone between terrestrial and aquatic ecosystems (Liu et al. 2020) and therefore include mangroves, peatlands, swamps, deltas, floodplains, flooded forests, rice fields or coral reefs. Despite covering 1.1% of the Earth surface, wetlands are considered to be among the most valuable ecosystems in the biosphere since they provide more than a quarter of ecosystem services (Nummi and Holopainen 2020; Costanza et al. 2014; Kingsford, Basset, and Jackson 2016). In particular, they are significant carbon stores. Indeed, they store between 20% and 30% of global soil carbon (Liu et al. 2020; Lal 2008). They also have various ecological roles that benefit humans such as flood protection, water quality insurance and food chain support (Verhoeven and Setter 2010). They are, however, very sensitive to natural or anthropogenic interventions such as climate change, rising water levels, dam construction or land use (Liu et al. 2020).

Although they cover only a small part (<1%) of the Earth's surface, freshwaters are home to a great part of biodiversity, with about 12% of the world's known species (Collen et al. 2014; Gleick 1998). Despite their importance from a societal, economic, and ecological perspective, the quality and quantity of freshwaters are in global decline (Dudgeon et al. 2006) and despite interventions to restore them by various actions, this is not sufficient to reverse the trend and is often found to be costly (Law et al. 2017).

Yet unfortunately, wetlands are overexploited, polluted, and degraded by human activities such as hydropower development pressures, flow alterations, habitat degradation and destruction, agriculture and threatened by climate change (Dudgeon et al. 2006). Despite being among the most productive and diverse ecosystems in terms of species and despite their high conservation value (Lal 2008; Liu et al. 2020; Verhoeven and Setter 2010; Nummi and Holopainen 2020), wetlands are in massive decline globally. Indeed, more than 50% of the world's wetland area was lost during the 20th century and in Europe, 60-90% of the wetland area was lost during the 20th century (Čížková et al. 2013; Nummi and Holopainen 2020).

Although they cover only a small part (<1%) of the Earth's surface, freshwaters are home to a great part of biodiversity, with about 12% of the world's known species (Collen et al. 2014; Gleick 1998). Despite their importance from a societal, economic, and ecological perspective, the quality and quantity of freshwaters are in global decline (Dudgeon et al. 2006). Numerous conservation attempts are done but these ecosystems continue to be lost drastically and climate change is expected to worsen the situation (Finlayson 2013). The main cause of their loss is often cited as being land use and alteration (LUCC – Land Use and Cover Change) and this use causes and has caused considerable carbon loss, such as in the Yellow River Delta where 50% of the stored carbon was lost between 1990 and 2015 due to LUCC (Liu et al. 2020; Li et al. 2018).

In Finland, peatlands are a main part of the wetlands (approximately 30% of Finland's surface) and constitute an ecological wealth for the country (Nummi and Holopainen 2020). They cover an area of 60,000 km² and constitute a considerable carbon stock (Simola, Pitkänen, and Turunen 2012). And, unfortunately, many of these areas are drained for agricultural purposes (Nummi and Holopainen 2020). In Finland, due to climate change, it is expected that spring flooding from melting ice will gradually decrease and negatively impact peatlands (Nummi and Holopainen 2020). Beyond the important ecological aspect of the considerable biodiversity resource, peatlands also constitute important societal and economic values (water storage and carbon sequestration) and should therefore receive special attention.

In order to avoid costly and artificial human interventions, natural and ecological solutions can be considered to restore wetlands in general (Davidson and Davidson 2014). Beavers, as ecological engineers, have already proven their worth. Indeed, they have known and useful effects on hydromorphology through the construction of their dams as they recreate wetlands in a way. A study showed a drastic increase in abundance (148%), species richness (46%) and habitat heterogeneity (71%) in terms of plants after 12 years of beaver and dam presence (Law et al. 2017). With the decline and degradation of wetlands in Finland, it seems therefore interesting to know the ecological value of the beaver's return and to study its effects in terms of conservation as well as to use it as a passive management approach to transform habitats impacted by agriculture and other land uses into heterogeneous habitats and wetlands (Law et al. 2017; Nummi and Holopainen 2020).

2. Beaver's status in Europe and Finland

There are two known species still alive today: *Castor fiber*, from Eurasia and *Castor canadensis*, from America, that are quite distinct genetically even though they look physically similar and adopt the same general living and dam-building behaviour (Danilov and Fyodorov 2015).

Beavers have a rather complicated history given that they almost disappeared from Europe and America due to over-hunting and habitat loss in the early 20th century (Nummi et al. 2019; Law et al. 2017), to the point where only 1200 individuals of the species *Castor fiber* remained in only eight populations across Eurasia (Halley, Rosell, and Saveljev 2012). Since then, both species have been reintroduced both in Europe and America and their population has recovered relatively well in America since the 1950s as they have now recolonised almost all their territories and have a population of about 30 million individuals (Nummi et al. 2019). In Europe, following a protection status established in the 20th century (Halley and Rosell 2002), they have been gradually reintroduced. Their population continues to slowly disperse with an estimated population of 1.5 million individuals (Brazier et al. 2021) and the densest stocks are being found in Eastern and Northern Europe (Halley, Rosell, and Saveljev 2012). In Finland, the Eurasian beaver went extinct in 1868 and both the Eurasian (*Castor fiber)* and the North American beaver (*Castor canadensis*) have been reintroduced in the 1950's (Parker et al. 2012). In Evo Recreational Park, where this study takes place, the North American beaver (*Castor canadensis*) is the only beaver species currently present. This reintroduction, protection and interest in the species have been motivated and helped by social and political interest in society and the desire to restore degraded environments such as wetlands (Law et al. 2017).

3. Concepts of ecological engineering, facilitation, and heterogeneity

Natural disturbances, whether abiotic (forest fires, wind) or biotic (insects, fungi, large herbivores, or beavers) are very important for the health of an ecosystem as they ensure habitat regeneration and allow for habitat heterogeneity and a succession of different ecological phases which are essential parts of the habitat dynamics for the survival of several species (Nummi and Kuuluvainen, 2013; Wright, Jones, and Flecker 2002; Nummi et al. 2019;

Willby et al. 2018). As a natural disruption agent, the beaver has this role, although it has been somewhat forgotten due to its mass extinction in Europe and America. One of the interesting aspects is that, in contrast to forest fires, it is active in wet and nutrient-rich areas with high species diversity, as shown in Figure 1 (Nummi and Kuuluvainen 2013). In Finland, for example, natural forest fires are not frequent enough (Vanha-Majamaa et al. 2007) because the habitat is too wet and the wind also has little impact (Nummi and Kuuluvainen 2013) leading to similar continuous forest habitats. The beaver thus plays an essential role in boreal landscapes as it ensures habitat heterogeneity by creating habitats that would not exist without its presence, thus providing necessary habitats for wetland-dependent species (Brazier et al. 2021; Nummi and Kuuluvainen 2013).

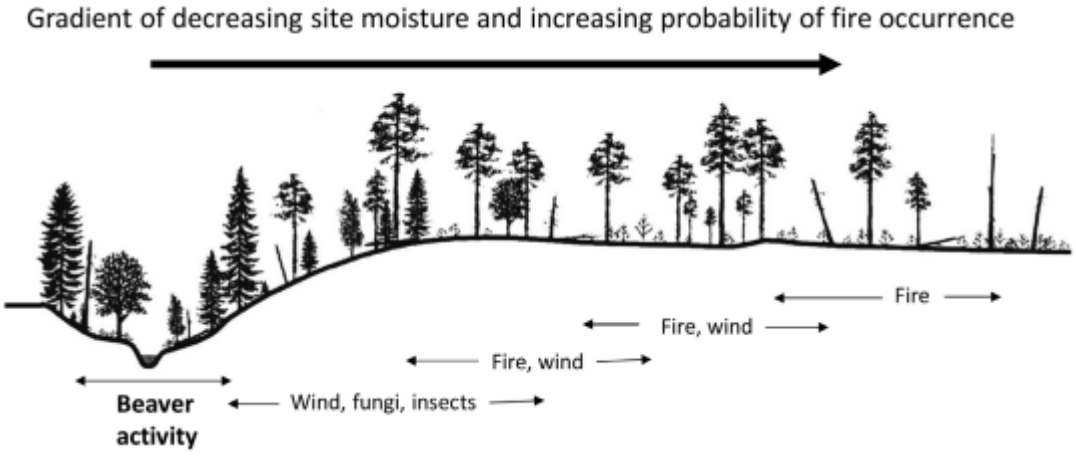


Figure 1: Schematic presentation of the probability of occurrence of different disturbance factors along the topography-related site moisture gradient in boreal forest landscape (Nummi and Kuuluvainen 2013). The beaver has impacts where the fires are not expected to occur.

Beavers are rodents living in family groups in forest habitat. Their role of natural disruptor is explained by their way of living as they build lodges and cut trees in order to construct their dams, leading to a complete habitat modification from terrestrial to aquatic habitat as water rises. Also, when damming flowing waters, they turn lotic aquatic systems to lentic. The time they will stay at one place depends on the habitat productivity. In areas with little organic matter, so-called oligotrophic areas, they will tend to stay for less than 3 years (Hyvönen and Nummi 2008) and will leave after consuming the resources and may return a few decades later when the resources have recovered, whereas in rich and productive areas they may stay for several decades (Nummi and Kuuluvainen, 2013).

Beavers then modify their habitat to meet their ecological needs and resources (Brazier et al. 2021). This makes them play two important roles in addition to the disruptor one: an ecological engineering role and an herbivore role, making their presence useful for certain parts of the ecosystem and the organisms that will benefit from it. In fact, they allow to maintain a certain complexity of the environment by preventing the different levels and habitats of the ecosystem from having a rather simple structure, not being ideal ecologically speaking (Brown et al. 2018). Their role as engineers is mainly seen in the construction of dams, thus inducing a shift from terrestrial to aquatic habitats. While their role as herbivores is seen in the change in tree species composition (by, for instance, consuming deciduous species) and in the modification of forest cover, since by cutting trees they create openings in the forest but also by leading to the death of conifer trees due to the flooding (Nummi and Kuuluvainen 2013).

Ecosystem engineers are defined as organisms that provide facilitation to other species by altering the habitat and consequently the resources available to other species (Nummi et al. 2019). Ecological facilitation is then an interaction situation where a species makes its habitat more favourable to other organisms in different ways such as structural modifications or improvements, thus allowing an improvement of the resources available to other species in the ecosystem (Nummi et al. 2019). Facilitation is therefore particularly important in harsh and stressful environments. This habitat facilitation created by beavers is also helped by patch-level and landscape-level habitat heterogeneity through the disturbance created by dam construction (Wright, Jones, and Flecker 2002; Nummi et al. 2019; Willby et al. 2018).

In conclusion, these different explained roles of the beaver are leading to the facilitation and heterogeneity of the habitat benefiting to other species. Indeed a study shows that the overall effect of ecological engineers on diversity is characterised by a 25% increase in overall species richness and, in addition, the effects are stronger when engineers create new micro-habitats and habitats rather than just modifying them (Romero et al. 2015). For example, the cutting of trees by beavers creates forest openings that allow light to pass through to lower vegetation and make way for plant species that are disadvantaged by competition for light. This allows a higher diversity and abundance of plants (Law et al. 2017) and also creates richer habitats for insects, birds, bats and amphibians (Dalbeck 2020; Stringer and Gaywood 2016; Willby et al. 2018; Nummi et al. 2011).

Without the presence of beavers, riparian landscapes can become unnatural (Naiman, Johnston, and Kelley 1988) and the loss of beavers can lead to the drying out of wetlands. This can lead to the emigration or loss of species within the ecosystem. The loss of beaver can also create some abiotic problems such as loss of water supply, which can also lead to problems during droughts, faster flowing waters containing less woody debris and carbon that are nevertheless essential for many aquatic habitats and on which certain levels of the food chain depend (Brazier et al. 2021).

As already mentioned, to create their dams, beavers graze and fell trees. The dams are then constructed from felled wood, stones and mud and are placed perpendicular to the direction of the river flow (Rosell et al. 2005). The construction of the dam induces a rise and stabilisation of the water level. This flooding provides many benefits such as reduced exposure to terrestrial predators and improved access to resources in flooded areas (Rosell et al. 2005).It also has important effects on aquatic and terrestrial biotopes such as the diversity of different species communities as well as abiotic conditions such as geomorphology, river hydrology or sediments and carbon storage (Brazier et al. 2021), which will be developed in the two following sections.

4. Impact of the beaver presence on the ecosystem

4.1. Abiotic factors

4.1.1. Geomorphology

Considered as primary agents of zoo-geomorphological processes (Brazier et al. 2021), beavers, for the construction of their dams as well as for the quality of their life, will build lodges up to three metres in size (Danilov and Fyodorov 2015) and dig galleries and channels allowing them to transport felled wood, construction materials but also their food (Brazier et al. 2021). This work leads them to release sediments into the water (de Visscher et al. 2014). Firstly, this change in soil structure creates weakened and potentially erodible areas that are susceptible to collapse (Harvey et al. 2019). And, secondly, the channels formed contribute strongly to the dynamism and hydrogeomorphology of the plains as they allow a better landscape connectivity (Hood and Larson 2015; Gorczyca et al. 2018; Pollock et al. 2014). In addition to this, the woody debris generated by the construction of the dam is an additional key to the geomorphological complexity of the habitat (Brazier et al. 2021). Indeed, they not

only provide a good ratio between small and large wood, thus maintaining the stability of the riverbed and banks (Gurnell et al. 2002), but also play an essential role in the life cycle of several species. Finally, the construction of dams allows to maintain the structure and balance of the latter in healthy ecosystems. In degraded ecosystems (being what is most frequently found), it can play a restorative role thanks to the connectivity of the plains (Macfarlane et al. 2017). Figure 2 (Brazier et al. 2021) illustrates that beavers have a positive long-term impact on the geomorphology of the habitat. Indeed, the succession of presence/non-presence of beavers and therefore of a succession of geomorphological modifications on the site allows, in the long term, to create a more diversified habitat, with a better and more heterogeneous hydro-geomorphological structure. This can then lead to the restauration of ecosystems.

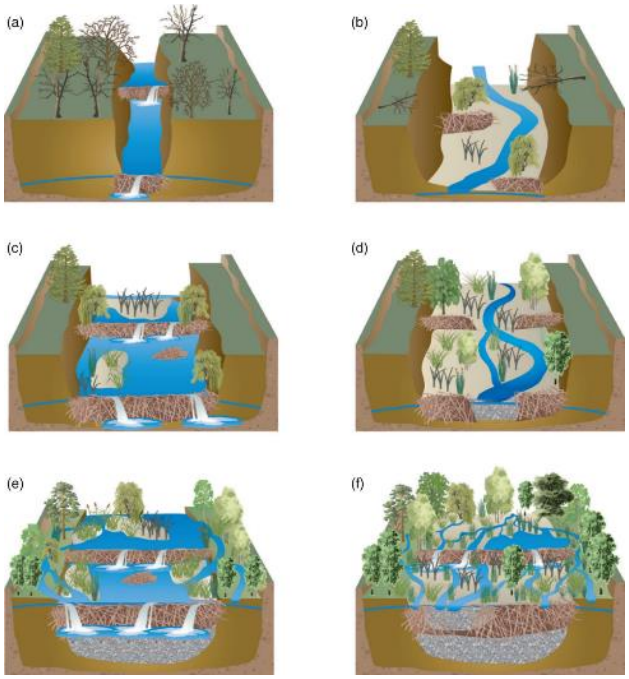


Figure 2: **The influence of beaver activity on the geomorphology of incised streams:** (a) low-flow damming of confined channels with high-flow blowouts causes overtopping, bank widening, and excavation of the channel bed; (b) sediment becomes more mobile and the channel reconfigures with vegetation establishment; (c) channel widening reduces high-flow peak stream power and this provides suitable conditions for wider, more stable dams; (d) sediment accumulates in ponds and raises the height of the channel with dams overtopped and small blow-outs occurring where dams are abandoned; (e) process repeats until dams are rebuilt, channel widens and the water table rises sufficiently to reconnect river channel to the floodplain; and (f) high heterogeneity occurs with vegetation and sediment communities establishing themselves, multi-threaded channels and ponds increase reserves of surface water and dams and dead wood reduce flows and provide wetland habitats (reprinted from Brazier et al. 2021).

4.1.2. Hydrology and water quality

The dams formed will create ponds filled with sediment, nutrients, plants and wildlife. These ponds will then take on the role of essential water storage during droughts as water can be released at low velocity on a continuous basis (Hood and Bayley 2008). This reduction in water flow and the physical separation of flow by the dam reduces longitudinal connectivity while increasing lateral connectivity and pushing the banks (Brazier et al. 2021). However, it stabilises the flow of the stream and above all participates in groundwater recharge and increases water levels and storage through ponds and channels (Brazier et al. 2021).

This change in flow will also imply a modification of sediments and nutrients, which in turn impact water quality. The reduction in upstream/downstream connectivity of the dam causes a change from lotic systems, characteristic of moving freshwater, to lentic systems, characteristic of stagnant freshwater (Hering et al. 2001). The woody debris accumulated at the bottom of the water due to beaver occupation will decompose and release nutrients that will allow the initiation of a host of new food chains, starting with decomposer invertebrates to consumers higher up the chain. Nutrients temporarily immobilised in the pond can be used by aquatic plants, phytoplankton, zooplankton and can also supply vegetation with nitrogen, phosphorus or carbon (Rosell et al. 2005).

4.2. Biotic factors

All these processes and impacts on abiotic factors such as inundation, lateral connectivity and structural heterogeneity create mosaics of diverse habitats, increase the availability of resources or shelters and thus favour niche colonisation. This results in more species rich and biodiverse freshwater and wetland ecosystems (Brazier et al. 2021). The following section therefore focuses on the effects of the beaver's presence on the various types of organisms in the environment.

Firstly, for an ecological engineer to increase the species richness of a landscape, two conditions must be met. Firstly, the engineer must create a patch that includes a combination of sufficient conditions not present elsewhere in the landscape. And secondly, the species that can live in the patch created by the engineer are not found elsewhere in the landscape, where the habitat has not been altered (Wright, Jones, and Flecker 2002).

4.2.1. Plants

The presence of beavers will impact vegetation directly and indirectly over time and space (Rosell et al. 2005). Two factors will change the structure and composition of the forest. Firstly, certain areas and certain trees and plants will end up with their roots in the water because of rising water levels. Secondly, beavers will affect specific plant species through foraging but also for the construction of dams, as beavers are the only ones able to put mature trees on the ground as opposed to elk or other herbivores (Nummi and Kuuluvainen 2013).

Flooding will gradually lead to the death of non-water-tolerant plants to make way for more tolerant or aquatic plants (Nummi and Kuuluvainen 2013). For example, conifers are more likely to die due to flooding than deciduous plants that can survive for some time (Hyvönen and Nummi 2008). The loss of these trees will result in less tree cover, an effect which, reinforced by the herbivory of beavers, will allow more light to enter the area, leaving room for plants competing for light and for plants specific to the wetland area (Brazier et al. 2021).

At the patch scale, aquatic plants may decrease in biomass due to beaver herbivory but also alter or decrease in the diversity of species composition (J. D. Parker, Caudill, and Hay 2007). At the landscape scale, however, there is a difference in composition and a clear improvement in species richness can be observed. The study by Law et al. (2017) showed that species richness was significantly higher after 10-12 years of beaver settlement. Species richness increased by 46% per site and heterogeneity increased by 71%. They also showed a drastic change in the species composition of the sites (Figure 3) and that sites occupied for 10-12 years had a greater amount of indicator species than newer sites (Law et al. 2017).

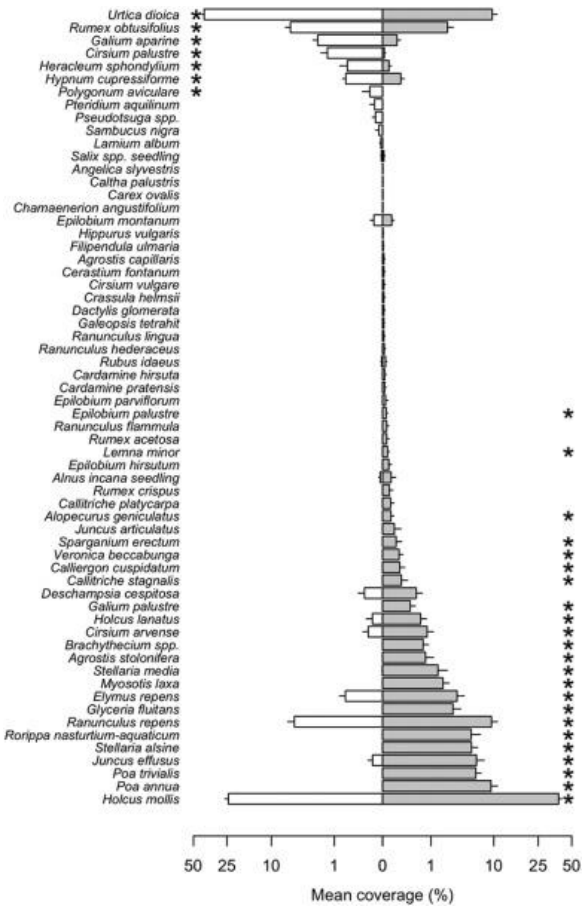


Figure 3: **Change in mean coverage of a series of plant species** between 1-2 years (white bars) and 10-12 years (grey bars) in a beaver-occupied site (Law et al. 2017). The figure shows a shift in the abundance of terrestrial plants for aquatic plants.

Finally, the impact of engineers can show an increase (Martinsen, Cushman, and Whitham 1990) but also a decrease in species richness (Parker, Caudill, and Hay 2007). It is therefore difficult to predict what impacts the presence of beavers will have on an ecosystem, as this also depends on the patch and the biodiversity that was present in the beginning. However, it can be assumed that as beavers increase habitat heterogeneity, they will tend to increase species richness at the landscape scale as they provide habitat types for species that would otherwise be excluded from the landscape (Wright, Jones, and Flecker 2002).

4.2.2. Animals

The change in habitat heterogeneity coupled with a change in plant species composition induced by the presence of the beaver leads to a facilitation of habitat for other species and this facilitation will be even more important in low productivity habitats (Nummi et al. 2019). As a result, it has been shown that many other species benefit from the presence of beavers

and that the creation of new habitats favourable to these species is scale dependent (Johnston 2017).

Firstly, by changing the community structure of invertebrates, favouring lentic taxa (McDowell and Naiman 1986), the ponds created by beaver will attract other animal taxa. For instance, several studies (Cunningham, Calhoun, and Glanz 2007; Dalbeck 2020) have shown the positive impact of beavers on amphibians as they provide them with favourable conditions for breeding and egg-laying as well as shelter and food. These studies also explain the importance of beavers in creating interconnected aquatic networks which facilitate the presence of a greater diversity of amphibians. In addition, it has been shown that the beaver-modified habitat attract more bats than the non-beaver habitats (Nummi et al. 2011; Ciechanowski et al. 2011). Secondly, the study by Snodgrass et al (1998) found that fish species richness increased significantly in the 9 to 17 years of beaver occupation of a pond but that this increase was dependent on the age of the pond as well as the state of drainage upstream of it. After this period of strong increase in species richness, it tends to stabilise or decrease (Snodgrass and Meffe 1998).

Birds are probably among the animals that benefit most from the presence of beavers, as a range of waterfowl can move in. Nummi and Holopainen (2014) observed that bird broods had better survival rates in beaver-inhabited areas and that this was due to an increase in invertebrate abundance in the habitat, facilitated by the presence of the beaver, which is normally a limiting resource (Nummi and Holopainen 2014). In the same study, it could be observed that the number of waterbirds per year per site increased significantly during beaver occupation compared to before. This increase occurred mainly during the first two years of occupation before it stabilised. The abundance of seven bird species increased but this was significant for two particular species: Green Sandpiper (*Tringa ochropus*) and Common teal (*Anas crecca*) (Figure 4) (Nummi and Holopainen 2014).

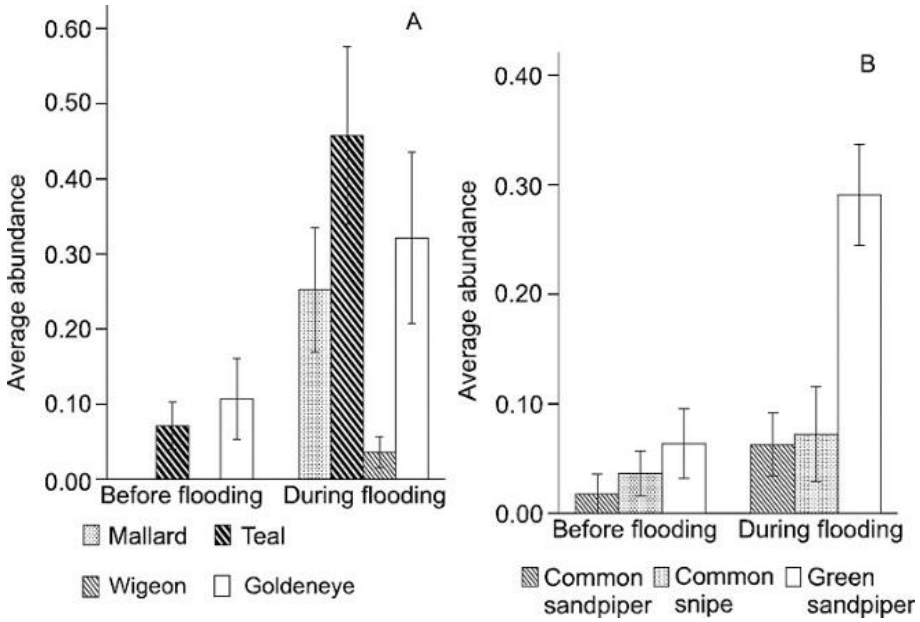


Figure 4: **Average abundance of (A) ducks and (B) waders per survey for 14 beaver ponds before and during beaver occupancy** (Nummi and Holopainen 2014).

The habitat heterogeneity created by the beaver favours a range of bird species such as swans, waterfowl, herons, or ospreys that need the dead wood generated by the beaver to build their nest (Johnston 2017). Woodpeckers or other species requiring nesting cavities benefit from the dead trees due to beaver activity to build their nesting cavities, as do passerines which require grassier and bushier (Johnston 2017) habitat. In Voyageurs National Park (Minnesota, USA), it has been observed that 30% of the park's bird species (77 species) have been observed in beaver meadows and ponds, occupying specific areas such as the emergent zone, littoral zone, shrub zone or dead wood (Johnston 2017).

Several studies show that the species richness and abundance of mammals is also positively impacted by the presence of beaver (Nummi et al. 2019; Johnston 2017; Street et al. 2016; Fedyń et al. 2022). Ponds created by beavers provide many benefits to different mammal species; refuge from predators or on the contrary, hunting area for some, feeding area, insect avoidance or even cooling (Johnston 2017). A study conducted in Poland during winter showed a 25% increase in the species richness and activity of terrestrial mammals at sites occupied by beavers compared to non-beaver occupied sites (Figure 5) (Fedyń et al. 2022). It was also noted that this increased species richness was reflected in areas further away than the beaver sites.

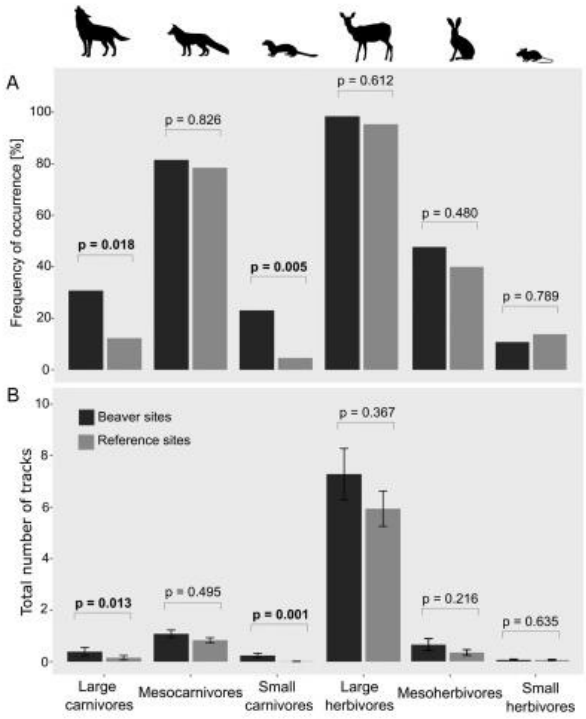


Figure 5: **Frequency of occurrence of ecological groups (A) and the number of tracks per 100 m of all species belonging to an ecological group (B)** recorded on Eurasian beaver *Castor fiber* sites (black bars) and paired reference sites (grey bars) during winter in Poland (Central Europe) (Fedyń et al. 2022).

Similar results were observed by Nummi et al. (2019) with an increase in abundance and species richness of mammals such as moose (*Alces alces*), Eurasian otter (*Lutra lutra*), pine marten (*Martes martes*) and least weasel (*Mustela nivalis*) (Nummi et al. 2019). In Voyageurs National Park, 35 mammal species, or 61% of the park's mammal species, actively use beaver-modified areas. Four species of insectivores, seven species of chiropterans, one lagomorph, 13 carnivores and two artiodactyls have been found (Johnston 2017). Moose and deer particularly benefit from beaver ponds for several reasons mentioned above (escape from predators by swimming, refreshment, feeding, social meeting area) and are animals that particularly require habitat heterogeneity to meet their needs (Street et al. 2016; Johnston 2017). One study confirms the elk's need for beavers by showing that areas modified by beavers are two to four times richer in food biomass for them than simple lakes or ponds (Morris 2014). Wolves, for example, will tend to use these areas as hunting grounds or as a place to establish their burrows, such as in a hole left by a beaver (Johnston 2017). Smaller aquatic or semi-aquatic mammals such as muskrats (*Ondatra zibethicus*), river otters (*Lontra canadensis*) or minks (*Neovison vison*) find a place with stable water levels, many resources,

and places to establish their burrows (Tumlison, Karnes, and King 1982; Johnston 2017; Sundell, Liao, and Nummi 2021).

In conclusion to this section, beavers provide an incredible interface between the terrestrial and aquatic world (Johnston 2017). Through their role as facilitators of communities, they also play the role of keystone species, i.e. the central place in the arch without which the system would collapse (Johnston 2017). It is also interesting to note the importance of the temporal dimension, in addition to the spatial one. In fact, birds see their species richness increase in the first two years of the beaver's presence, while for fish this occurs within 9 to 17 years and for plants, the peak point of species richness is between 11 to 40 years of occupation of a site by a beaver. The positive impact of the beaver therefore extends both spatially and temporally. In a world where wetlands and their associated species are in drastic decline (Amezaga, Santamaría, and Green 2002), even in protected areas (McMenamin, Hadly, and Wright 2008), the usefulness of the beaver in conservation, both from the point of view of habitat and associated species, can no longer be overlooked.

5. Ecological succession following the beaver's presence

As said before, beavers will occupy a site from three years to several decades and it regularly happens that a site is later re-colonized by beavers (Kivinen, Nummi, and Kumpula 2020; Nummi et al. 2019). However, the positive effects of beaver presence do not stop once they have left. When a beaver family leaves a site, the habitat will revert from an aquatic to a terrestrial state, resulting in a lowering of the water level and a drying out of the flooded area. This new terrestrial state becomes 'bare' and ecological succession follows. Ecological succession occurs after a disturbance, i.e. an abrupt loss of biomass, and is defined as a sequential replacement of species (Prach and Walker 2011). Succession can then include changes in communities that are defined by their dominant species, in ecosystems, and finally, structural changes (Prach and Walker 2011). Prach and Walker (2011) explain that there are three components to succession. The first one is the mechanisms that include dispersal and establishment of species, competition, and facilitation. The second component is the different stages of succession. These are generally, one after the other, the pioneer stage, the initial stage, the early stage, the middle stage, and the late stage of succession leading to the climax. Finally, there are different trajectories to ecological succession. They can be convergent, divergent, parallel, circular, or can form complex networks of different successional paths that

will be explained later. Even though it is possible to predict the type of species that will occur through ecological succession depending on the environmental conditions, it is rarely predictable in details and different pathways can occur (Prach and Walker 2011).

Once the beaver family has left, the flooded area will be drained – as the dam is gradually broken without maintenance by beavers – and turned into grassland as the riparian areas are then exposed and colonized by plants, grass or shrubs and in case the beavers do not return to colonise the area, a forest should possibly then established (Kivinen, Nummi, and Kumpula 2020). On the other hand, if a new beaver colony is established, then the ecological succession will be reset and will have to be started again. Recolonization of sites has many benefits for the ecosystem. For example, by reducing the distances between amphibian feeding and breeding grounds, they create high landscape connectivity and thus better species richness (Cunningham, Calhoun, and Glanz 2007). In addition, the repeated recolonization of sites allows for a continuity of deadwood important for many species (Kivinen, Nummi, and Kumpula 2020).

Numerous studies have been carried out on ecological succession from a plant point of view. Soil conditions are modified by the presence of the beaver, so that the soil after the dewatering of the floodplain is rich in nutrients, carbon and nitrogen, due to the anoxic conditions that were present during the flood (Terwilliger and Pastor 1999; Naiman et al. 1994). This accumulation has long-term effects on soil structure and function, even after drainage, and may result in the presence of nutrient-rich habitat patches in place of normally nutrient-poor forests (Anderson et al. 2009). The first stage following flooding is the formation of a nutrient-rich meadow (Nummi et al. 2019). This phase then includes pioneer species, persistent grass species, shade-intolerant species, small shrubs (McMaster and McMaster 2001; Terwilliger and Pastor 1999). Beaver meadows allow the creation of open habitat patches in forested environments and can last up to 70 years before the next phase arrives (Anderson et al. 2009; Terwilliger and Pastor 1999) and woody plants take hold. From this rather low-lying grassland stage, several successional paths can be taken (McMaster and McMaster 2001; Anderson et al. 2009) and the direction towards one or the other possibility is influenced by various site-specific factors such as pre-existing vegetation, hydrology, geomorphology, herbivory, topography or potential recolonisation by beavers. This will add

different successions depending on the frequency, extent and duration of beaver re-flooding (Naiman, Johnston, and Kelley 1988; Anderson et al. 2009; McMaster and McMaster 2001).

The fact that beavers leave a flooded site and return later, sometimes several times in a row, allows a constant evolution of a mosaic of flooded and non-flooded sites and of sites at different stages of ecological succession, thus creating a continuum of wet and dry patches in the forest, but above all a spatial and temporal heterogeneity. This spatial and temporal heterogeneity will inevitably facilitate the presence of different organisms and species at different times and places, both within a flooded patch and within a patch in the process of ecological succession. The beaver provides site connectivity, and its presence can positively influence habitat patches for decades, even after its departure. It is therefore understandable that the presence of the beaver and the effects it generates are of high importance from the point of view of the restoration and conservation of habitats, wetlands, and associated species. However, very few studies have been carried out on the quantitative facilitation of small mammals because of beaver-induced ecological succession. However, as the trophic level of primary producers changes within the habitat, as shown in the introduction, it would be expected to see a change in the composition, species richness and abundance of other species in the food chain.

6. Small mammals ecology and potential impact from the beaver's occupancy

Small mammals are common and numerous and therefore play an important role in the ecosystem as they are critical to its formation and stability. Their abundance impacts the size of predator populations and may indicate disturbances in ecosystem integrity and therefore they are often used as ecological indicators. In addition, their abundance and species composition is primarily influenced by their habitat and they will therefore be among the first to respond to habitat change (Yakimova and Gaidysh 2021).

Järvinen (1978) identified a total of 21 species of small mammals throughout Finland considering the families *Soricidae*, *Talpidae*, *Glinidae*, *Microtidae*, *Muridae* and *Zapodidae* (Järvinen 1978). Figure 6 illustrates the specific distribution of species. The sampling areas were 100 km x 100 km and the figure represents the number of species recorded in each of

these sampling squares. This study shows that southern Finland is the area with, on average, the highest species richness, and this is where the sampling of this thesis took place.

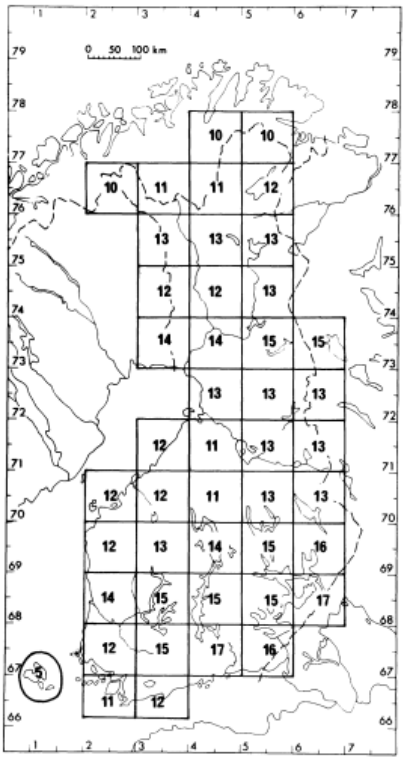


Figure 6: Number of small mammals species in 100 x 100km squares in Finland (Järvinen 1978).

The ecology of small mammals as well as their way of life are variable according to the species, but these will be detailed in the material and methods section within the paragraph devoted to the species studied during this thesis. However, it should be noted that populations fluctuate strongly between years, but also seasonally. Seasonal fluctuations are generated by breeding and non-breeding seasons leading to a general drop of population size during winter and peak in August towards the end of breeding season, as for the bank vole (*Myodes glareolus*), illustrated in Figure 7 (Mazurkiewicz 1994).

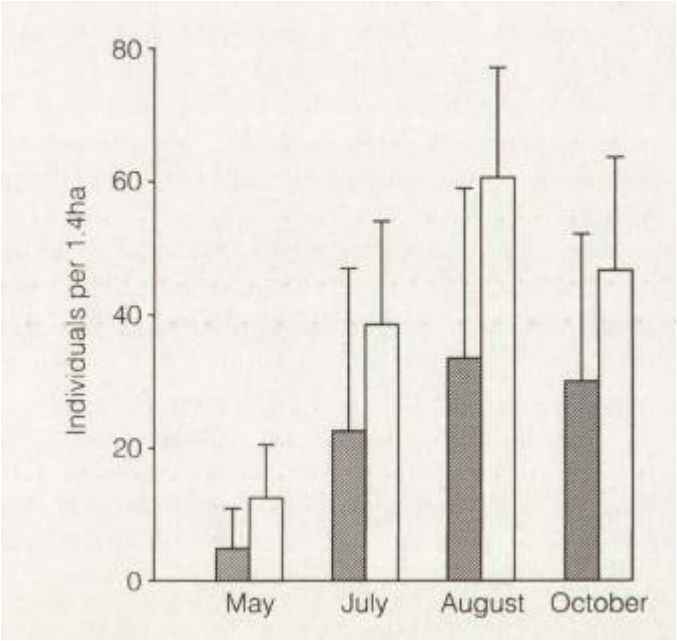


Figure 7: Seasonal changes in the bank vole density (mean and SD) in habitats poor (grey bars) and rich (white bars) in understorey (Reprinted from Mazurkiewicz 1994).

Several studies have shown that the presence of beavers positively impacts small mammals (Bashinskiy 2020; Samas and Ulevičius 2015; Ulevičius and Janulaitis 2007). In particular, Samas and Ulevicius 2015, was able to show significantly higher abundance and species richness of small mammals on beaver lodges. This is explained by the fact that lodges provide warm, stable shelter, especially important during winter. In addition, as mentioned earlier, beavers, while foraging, create openings in the habitat that are also beneficial to some small mammals.

However, few studies have been conducted on the impact of beaver-modified habitats on small mammals once the beavers have left. Sundell et al. 2021, conducted a study on the species composition and abundance of small mammals within ten sites that had been modified by beavers and ten sites that had never been impacted (Sundell, Liao, and Nummi 2021). They found no difference in species richness or abundance but were able to discuss a difference in species composition within sites. Field voles (*Microtus agrestis*), being grass eaters, and invertebrates-eating shrews were found mainly in beaver modified habitats while forest-dwelling lemmings and yellow-necked mice were only found in *control* sites. They concluded that at the local scale, beaver-modified habitats did not have a significant influence on small mammal populations in terms of diversity and abundance, but that there may be an

influence at the landscape scale since the beaver, as mentioned above, provides heterogeneity and facilitation within the landscape, thereby increasing overall diversity.

Thesis objectives and predictions

Knowing that small mammals are indicator species for ecosystem stability and will be among the first to respond to habitat modification (Yakimova and Gaidysh 2021), it is interesting to understand how their populations behave in beaver-modified habitats. Indeed, it has been shown that within homogeneous habitats the rodent fauna is stable due to habitat stability. However, in areas affected by past or present disturbance factors (e.g. human activities), a higher diversity can be observed due to a greater variety of habitats and thus living conditions (Yakimova and Gaidysh 2021). Knowing that beavers cause habitat disturbances that create facilitation, we can expect to observe higher small mammal diversity at areas vacated by beavers. However, the study by Sundell et al. (2021) also studied the populations of small mammals within sites impacted and non-impacted by beavers but without taking into account the different stages of succession. They also expected this type of result, but it was not observed. The present study provides an additional perspective to the Sundell et al. (2021) study by considering the time since beaver departure, allowing for comparison of different ecological successional stages after beaver occupation.

The objective of this thesis is thus to conduct a quantitative study on the spatio-temporal change of small mammal populations in habitats that have been previously occupied and flooded by beavers and are in different phases of ecological succession. It will thus allow to highlight the potential variations in populations through time and habitat succession. The study was carried out in Southern Finland, in a boreal forest landscape and was conducted at the Lammi Biological Station associated with the University of Helsinki. The study was conducted with the aim of potentially providing further evidence of the beaver's ecological value, its value for habitat restoration and conservation of associated species through its role as an ecological engineer, natural disruption agent and facilitator.

To carry this study, the aim was to investigate firstly through a characterization of the sites in the study area via a census of the vegetation and secondly through a census of the small mammal species present on the sites. Morphological characteristics of individuals were also collected in the laboratory in order to potentially determine the population structure of

small mammals within sites impacted by beavers or not. In this study, it was expected to observe different mammal species at the different sites, and therefore at the different successional phases. These species were expected to be either indirectly or directly related to the vegetation composition and habitat structure. For example, we expected an increase in the abundance of meadows specialist species in the early successional stages, of shrub specialist species at the middle stage, and of forest specialist species in the *control* sites. Finally, it was expected to observe a higher species richness and abundance on sites that have been modified by the presence of beavers than on *control* sites. Regarding the quality of the populations, we expected to observe a difference in the age and physical condition of the individuals within the different categories of sites (related to the different stages of ecological succession). We expected this difference in the condition of individuals to illustrate the quality of the sites. Good quality sites would be occupied by older individuals with better fitness and conversely, individuals with poorer fitness and younger individuals would be found in sites of lower quality.

Table 1: Null hypotheses and expectations of the main objectives of this master's thesis.

Null hypotheses	Expectations	Reason of expectation
There is no difference in vegetation composition between the different successional stages in beaver-modified habitats.	The vegetation composition will vary between the different stages of succession.	Due to the beaver actions and the new open area created, it facilitates new species to settle.
There will be no differences in abundance and species richness of small mammals in the different successional stages of beaver-modified habitats.	Different species of small mammals will be found in the different stages of succession ns will be found in different abundances.	The different successional stages provide different habitat types. Forest specialists should be found in *control sites*, meadow specialists should be found in the early successional stages and shrubs specialists should be found in the later stages of succession.
The physical condition of small mammals will remain similar in the different successional stages of beaver-modified habitats.	Small mammals will show different levels of physical conditions between the different successional stages.	To illustrates that depending on the stage of succession of habitats created by beaver, certain stages are more suitable to certain species than others.

Material and methods

1. Site choice and study area

The study was conducted at 15 different sites. All sites are located in Evo Recreational Park in Finland. Evo is located in the municipality of Hämeenlinna, in the Häme region of Southern Finland. The Evo Park is particularly known for its abundant biodiversity (beavers, moose, lynxes, flying squirrels, many species of birds and mushrooms, among many others can be observed there) and is considered to be of great scientific interest. In fact, the Biological Station of the University of Helsinki located in Lammi, where this study took place, has already applied to have Evo Park classified as a park of scientific interest. Numerous ecological research is carried out there every year.

Figure 8 : Finland and Evo location. Modified from *www.alamy.com*.

The selection of sites of interest was made by J. Sundell and P. Nummi who have known the area for many years and are familiar with the history of beaver occupancy, of which they keep track from since 1970 (Kivinen, Nummi, and Kumpula 2020). To allow a meaningful

comparison of the sites, it was necessary to select sites with similar soil and climate characteristics. The selected sites are all located within Evo Recreational Park and are all characterized by a typical hemi-boreal forest environment. All sites are at a similar elevation to exclude potential elevation bias in the study results. The sites are separated by a maximum distance of 10 kilometres from each other, so it can be assumed that they experience the same climatic and weather conditions.

The 15 sites of interest for this study were separated into three different categories (Tables 2 and 3). The first category includes five "*control*" sites that have never been impacted by beavers. The second category includes five sites called "*new*". These *new* sites are sites that were previously occupied by a beaver colony that left the site less than five years ago. These sites are therefore in an early phase of ecological succession. They are very wet on the ground since the flooding has recently disappeared. The third category of sites are the "*old*" sites. The beavers left these sites five or more years ago. They are more wooded and have vegetation that has grown back to some extent. The soil moisture was rather variable. Sometimes still very wet, sometimes less so.

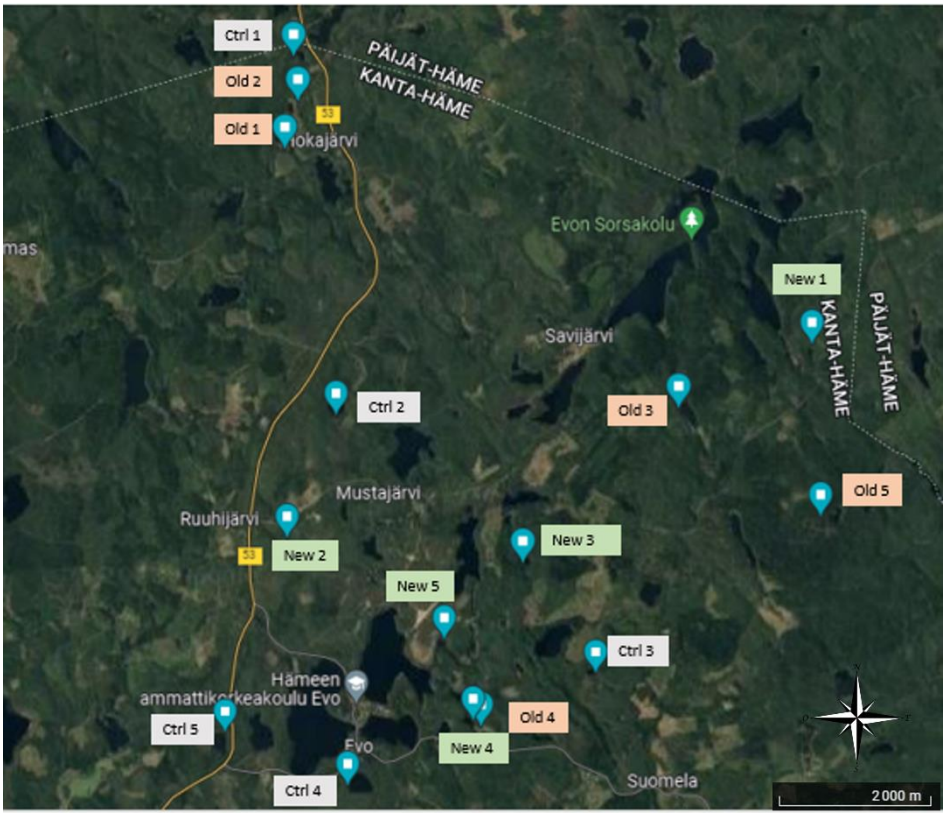


Figure 9: Site location in the Evo area. 15 sites were under analysis, grouped in three categories. The control (ctrl on the figure) have never been occupied by beavers. *New* sites have been left by beavers within the last five

years. O*ld* sites have been left by beaver five years or more ago. Satellite image from www.earth.google.com and modified with PowerPoint on the 21st of January 2023.

In addition, each site was separated into two "study areas". Indeed, each site is near an area of water previously occupied by beavers. More or less close to this water source is a forested area. The *control* sites have very little distance between the water area and the forest, whereas the sites that previously supported beavers have a greater distance between the two areas since some of the forest has been fallen down by rising water and beaver use. As a result of that, each site was separated into two study lines where the surveys that will be detailed later were conducted. The first line, called the shore line, was within five meters of the water's edge and the second line, called the forest line, was within five meters of the forest area (an area not damaged by beavers). This information can be understood with the Figures 10 and 12.

During the study, the *new-5* site that was initially selected was found to be occupied by beavers again, with physical evidence of their presence (typically cut and gnawed trees and rising water levels – Appendix 9) when we visited the site for site surveys. A new *new-5* site was chosen, not far from the original one.

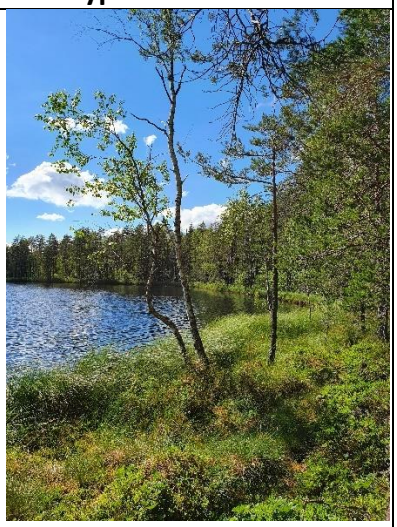
During the course of the study, the Huhmari 2 site (*new-4*) was flooded. Indeed, during the visit for the second session of data collection, we could observe that the water had risen and almost reached the forest edge, flooding the beaver meadow. We first thought it was a recolonization of the beavers, being a common phenomenon, but after analysing the terrain we deduced that it was a flood coming from an upstream lake. However, we decided not to change the site since the first data collection session had already taken place. We therefore moved the collection lines a few meters further so that they would not be in the water. The lines were each moved about three to five meters.

Table 2: Coordinates and altitude of the 15 studied sites.

Site ID	Site name	Latitude	Longitude	Altitude
New-1	Nimetön	61°13’43.6’’N	25°11’34.2’’E	160 m
New-2	Arabianniitty	61°12’41.2’’N	25°05’40.9’’E	136 m
New-3	Vuoripeikonjärvi	61°12’33.1’’N	25°08’19.7’’E	143 m
New-4	Huhmari 2	61°11’42.4’’N	25°07’46.2’’E	131 m

New-5	Tekumi	61°12’08.6’’N	25°07’26.8’’E	130 m
Old-1	Kärppijärvi	61°14’47.0’’N	25°05’39.3’’E	145 m
Old-2	Häntjärvi	61°15’02.2’’N	25°05’48.2’’E	146 m
Old-3	Vähäkeltajärvi	61°13’23.3’’N	25°10’04.5’’E	152 m
Old-4	Huhmari 1	61°11’40.3’’N	25°07’51.8’’E	131 m
Old-5	Viljaskorpi	61°12’48.2’’N	25°11’40.2’’E	171 m
Control-1	Ruuttanjärvi	61°15’17.0’’N	25°05’45.1’’E	149 m
Control-2	Kylökäänjärvi	61°13’21.0’’N	25°06’13.8’’E	145 m
Control-3	Likojärvi	61°11’57.5’’N	25°09’08.7’’E	152 m
Control-4	Iso-Valkjärvi	61°11’21.2’’N	25°06’21.7’’E	134 m
Control-5	Tiponen	61°11’38.3’’N	25°04’59.2’’E	139 m

Table 3: Pictures of what the typical site in each category looked like. *New sites* were characterized by grassy meadows, *old* sites by shrubby meadows and small woody plants and *control sites* by forest habitat.

Typical *new* site	Typical *old* site	Typical contr*ol* site
		

2. Data collection

The data collection was separated into three different parts. The first was the characterization of the habitat (sites) with a census of the vegetation. The second was a census of small mammals in order to study their distribution, abundance and species richness within the different sites. Finally, the collected mammals were analysed by dissection in the lab. In addition, camera traps were installed to get an idea of the larger mammals that could occupy the sites. Unfortunately, due to technical problems, only a few observations could be made but no statistical analysis.

The question of the use of lethal snap-trap was strongly discussed. Indeed, from an ethical and personal standpoint, I questioned this use. However, after discussion with my supervisor Janne Sundell, I made the decision to use these traps, under his advice. In fact they allowed us to collect data on the physical traits of individuals. For example, the sex and the maturity are most of the time impossible to tell from the external look of the species collected. In addition, due to lack of time, field staff, and equipment it turned out to be the easiest use and they produced data that was otherwise impossible to obtain in these conditions. However, this point will be discussed in the perspectives of the thesis.

2.1. Vegetation samples

In order to qualitatively characterize the habitats from a vegetative point of view, a census of the vegetation was carried out (Figure 10). To do this, three 50 cm x 50 cm quadrats were made on each trapping line, on each site. Three quadrats were thus made on the forest line

and three on the shore line. The quadrats were separated with 25 meters. Within these quadrats, all plant species were identified to the species (except for grass, moss, and *Carex sp.*) and were quantitatively estimated according to their percentage of coverage within the quadrat. To proceed to the analysis, the mean of the cover percentage of each species on each site has been calculated from the cover percentage of them in each quadrat of each line. This was in order to have a value for the abundance of each species in each site. These surveys were conducted in mid-July.

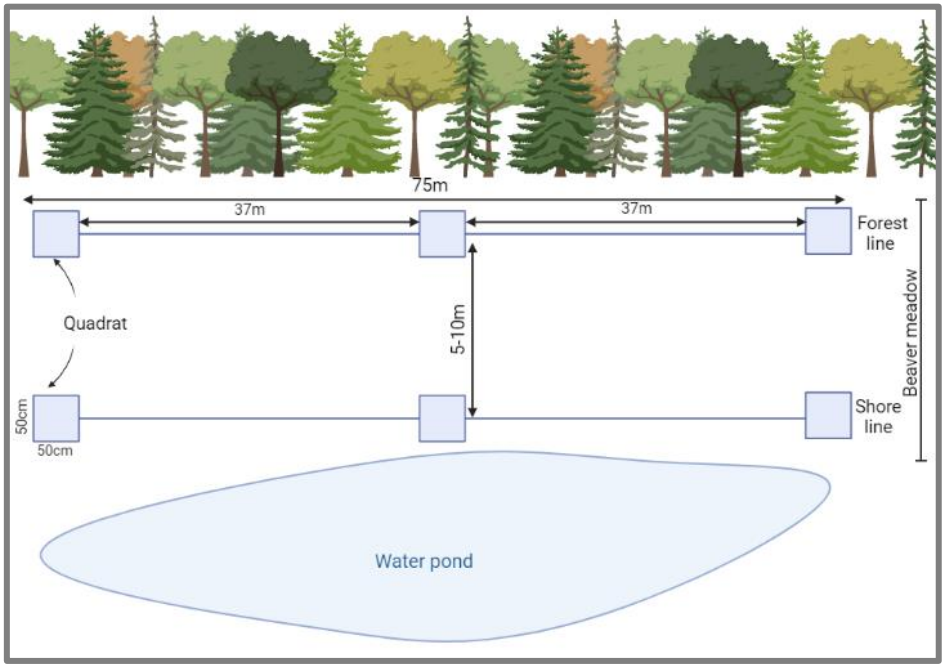


Figure 10: Descriptive diagram of the vegetation sampling method. To make the diagram readable and understandable, the scales have not been respected. The size of the pond is not representative of the reality, it is an abstract distance. Made with *www.biorender.com*.

In addition to this, the overall vegetation cover of the site was also estimated. The two same people estimated the percentage of the cover of the different vegetation layers on the sites. By standing in the centre of the site (halfway between the two circles on Figure 11) we estimated the percentage of the cover of the different vegetation layers: herbaceous (ground), undergrowth and canopy layer. Within the canopy cover, the percentage of conifers and deciduous trees was also estimated. Indeed, conifers are more likely to die due to flooding (Hyvönen and Nummi 2008) while deciduous trees are more likely to be eaten by beaver (Salandre et al. 2017).

Finally, the occupancy of the beaver leaves marks after its passage. Indeed, by cutting trees, it will leave some pieces of dead wood on the sites. A quantification of the dead wood

present was therefore also carried out. To do this, two circles of three meters radius were drawn in the centre of the trapping lines (Figure 11). Within these circles, the number of dead wood lying on the ground and those still standing was counted. This allowed us to determine whether the presence and quantity of dead wood left by beavers has an influence on the presence of small mammals and whether the latter appreciate habitats with more of it.

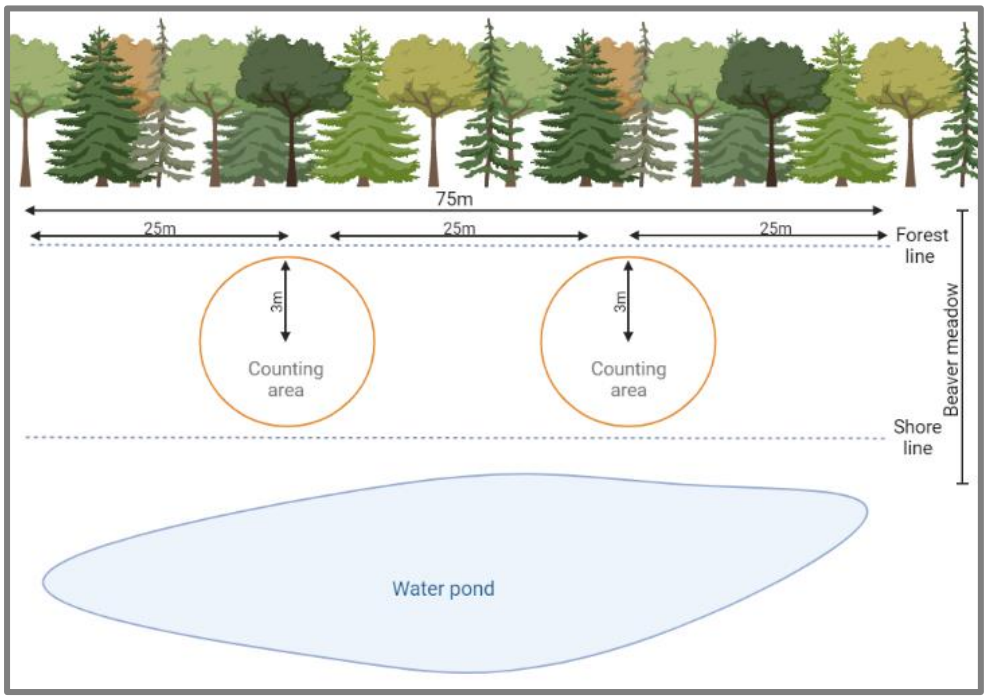


Figure 11: Descriptive diagram of the dead wood sampling method. The pieces of dead wood were counted within the orange circles. To make the diagram readable and understandable, the scales have not been respected. The size of the pond is not representative of the reality, it is an abstract size. Made with *www.biorender.com*.

2.1.1. Collected data

The data collected for the plant species census within the quadrats were stored in an Excel spreadsheet where they were sorted by site, sample line, and quadrats. To perform the necessary analyses on the data, coverage averages for each species were calculated. Thus, there was no longer a distinction between the quadrat number or the sampling line but an average percentage of coverage of each species on each site. Thanks to this, the different biodiversity indices could be calculated and will be explained more precisely in the statistical analysis section (cfr. “3. Statistical analyses”).

The data analysed on sites (percentages of vegetation cover and dead wood count) were simply kept as raw data to average parameters for the three different categories of sites.

2.2. Trapping sessions

To get a census of the population in terms of abundance and species richness as well as data on the sex, age and maturity of the individuals, trapping sessions were carried out using small snap traps. Four sessions were conducted during the first 10 days of July, August, September and October 2022 at each site. The trapping protocol (Figure 12) consisted of placing two trap lines separated by five to ten meters from each other. The first line, shore line, was within three meters of the water's edge (lake or stream) and the second line, forest line, was within three meters of the forest (forest area not damaged by beaver flooding). The two trapping lines were therefore separated by an average of five to ten meters one from the other depending on the size of the area modified by the beavers.

To catch a diversity of small mammal sizes, one of every five small snap traps was a larger rat-trap. A total of 15 traps per line were set. Traps were spaced five meters apart and checked with a tape of specified length. The snap-trap bait consisted of a piece of freshly cut rye bread to attract mammals such as voles and the rat-trap bait consisted of a piece of fresh carrot to attract larger water voles. Here again, the use of snap-traps will be discussed later on.

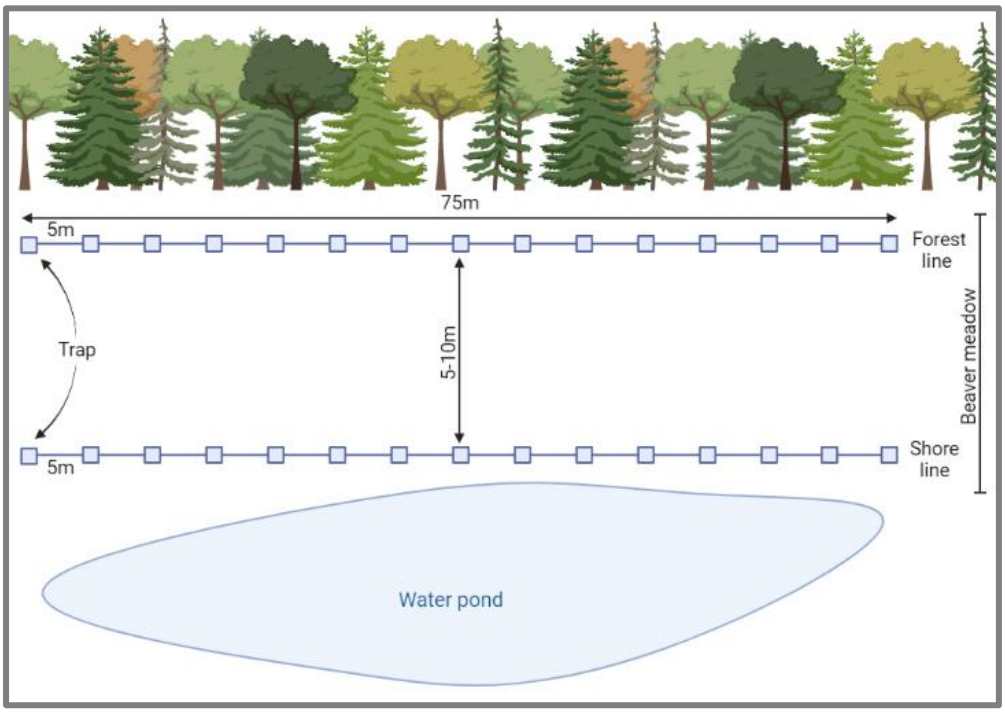


Figure 12: Descriptive diagram of the small mammal sampling method. To make the diagram readable and understandable, the scales have not been respected. The size of the pond is not representative of the reality, it is an abstract distance. Made with *www.biorender.com*.

The traps were set on the first day (three sites per day). On the second day, the traps were checked to collect the individuals caught, change the bait or reposition the traps that had been closed without any catch. The third day was dedicated to collecting the caught individuals and removing the traps from the site. The collected individuals were put in plastic bags and placed in the freezer to be identified and dissected in the laboratory. A rotation of three sites per day allowed the work to be completed in ten days. We then had 60 trap nights per occasion per site which makes 240 trap-nights per site in total at the end of the study. This, multiplied by the 15 sites of interest, we had 3600 trap-nights during the study. In order to avoid biases related to the hours of the day, we made sure that there was an alternation for the hours of visit of the sites. If a site was visited one day in the morning, we made sure that it was then visited in the afternoon. At each trapping session, a change of the location of the trapping lines was done in order to leave enough time to let the population renew itself between two trapping sessions. For example, if the July session was done on the north side of the lake, the August session was done on the south side of the lake. The same protocol was applied to all types of sites (*new*, *old* and *control*).

There were no abiotic measurements taken during this study such as temperature or rainfall. However, we did note on several occasions that rainfall could potentially affect the effectiveness of the traps. Indeed, there were several occasions when traps were empty of bait during our harvests and the trap had not closed. We have suggested several potential explanations for this. The first one is related to a "washing" of the bread by the rain and the second one is the presence of slugs. Sometimes we found slugs eating the bait but they were too light for the trap to close.

2.2.1. Studied species

It is important to note that mammals that can be caught in snap-traps placed on the ground surface, on the litter, are called small mammals (Samas and Ulevičius 2015). Of the fifteen species of small mammals that can be found in this region of Finland (Järvinen and Jarvinen 1978, Figure 7), six different species were found in the present study: three different voles, bank voles (*Myodes glareolus*), water voles (*Arvicola amphibius*) and field voles (*Microtus agrestis*) as well as three different shrews, common shrews (*Sorex araenus*), water shrews (*Neomys fodiens*), and a pygmy shrew (*Sorex minutus*).

The three shrew species studied here are all insectivorous species and the size of their prey is proportional to their body size (Sara Churchfield 1982; Saarikko 1989; Rychlik and Rychlik 1997). Shrews are very territorial species and the size of the territories of individuals varies according to the time of year and the breeding periods (Saarikko 1989). In addition, several different species of shrews can be found in the same habitat because they occupy different ecological niches. Indeed, as the species have different sizes and therefore different preys, they are found in different places in the habitat. For example, common shrews (*Sorex araneus*) being larger in size are more likely to be found in the soil and find their prey in the soil whereas pygmy shrews (*Sorex minutus*) are more likely to be found on the litter, being a smaller species (Saarikko 1989). Generally, larger shrew species (such as common shrews) are found in greater abundance in productive habitats pushing smaller species, such as pygmy shrews, into lower quality habitats (Saarikko 1989). Finally, water shrews (*Neomys fodiens*) are adapted to a semi-aquatic lifestyle and are therefore found near stagnant or flowing water, in marshes or swampy meadows (Rychlik and Rychlik 1997). They feed mainly on aquatic prey and have webbed feet adapted to swimming (Rychlik and Rychlik 1997).

All three species of voles found are herbivorous species and have similar ecology but bank voles (*Myodes glareolus*) will likely eat seeds, fruits, grasses or leaves and field voles (*Microtus agrestis*) herbaceous plants (grasses, sedges) found in meadows or fields. Both species are widely distributed in Europe (Jaarola and Searle 2002). The population sizes of these species fluctuate greatly during the year depending on the breeding season (March/April to October) and the availability of food (Mallorie and Flowerdew 1994). Bank voles are very territorial, especially females during the birthing and offspring care periods (Koskela, Mappes, and Ylonen 1997). Also, bank voles are a eurytopic species, meaning that they are generalists and can easily withstand changes in a large number of factors (Mazurkiewicz 1994). However, the bank voles appreciate habitats with thick vegetation cover and high vegetation to protect them from predators such as birds or other mammals (Mazurkiewicz 1994). Finally, water voles (*Arvicola amphibius*) are a species that forms breeding colonies and lives close to water (Lawton and Woodroffe 1991). They find refuge in the water from their predators and feed on aquatic plants or plants bordering water points (Lawton and Woodroffe 1991).

2.2.2. Laboratory analyses

After having collected the individuals caught in the traps, laboratory analyses were made. First, to identify the species but also to collect various information on them such as their sex, age and maturity, their gestation status or their weight and size. To do this, the individuals were dissected according to an appropriate methodology. To estimate the age of the individuals, different techniques have been used according to the species. The age of all the shrews have been estimated thanks to their teeth colour. Young individuals still have teeth coloured in red while adults have whiter teeth or missing teeth. They also usually have hairless tails and frostbitten legs. Determining the age of common shrews is not very exact as the observation technique can be subjective. When an individual was considered young, it was recorded as immature unless the genitals were clearly visible. We had then binary data for the age of shrews in contrary of other species. The reproductive organs are very small when the individual is immature and sex determination can therefore be difficult.

On the other hand, two techniques were used to determine the age of voles. The age of bank voles was also determined with their teeth. A row of three molars was removed and the upper middle molar was extracted and cleaned before binocular analysis. Depending on the depth of the tooth gutter, the age could be determined in months from one month to 16 months. The teeth of bank voles do not grow constantly, but they wear and the size of crown is getting proportionally smaller than the roots. The age of the field voles was estimated by the analysis of their skin, as their teeth grow constantly and therefore the wearing of teeth cannot be used for age determination. By pulling out the external part of their skin, the internal part could be observed. This method is based on the changes from the juvenile fur to the adult fur. The known change patterns of new fur can be observed under the skin in different pigmentation in areas of growing hair. Depending on the intern pattern of colours, the age could be estimated in weeks, one week to 15 weeks. The maturity of voles was estimated by the size of their reproductive organs.

2.2.3. Collected data

When a mammal was collected in the field, various data about it were entered. The table included one line per individual with the date of collection of the individual, the identification up to the species as well as the site and the line on which it was collected. After the dissection and laboratory analysis of the individuals, different data were added such as the size of the

individual, its sex, its weight with and without intestines, its age and maturity or its gestation status.

These data were used for two different purposes. The first was for the calculation of the different diversity indices that were performed. For this purpose, the data were collected in order to have only one table including the number of individuals per species captured on each site. The rest of the data following the dissection were taken to be able to describe qualitatively the populations within the different sites in the case where the sampling and harvesting were sufficient.

2.3. Camera traps

Although this study focuses on small mammals, it seemed interesting to install camera-traps to have an idea of the species of larger mammals that can be found on the different sites. One camera per site was therefore installed. They were installed close to the shore line to observe what is happening near the water on the sites. The cameras were moved a few times to randomize the shots or when the image was not good. Unfortunately, a technical problem appeared. At the end of the field work sessions, all the SD cards have been emptied on a hard drive to return them to the owner. But by the time the pictures were analysed in more details and the results written down in an excel sheet, the hard drive broke down so most of the pictures were lost. Luckily, pictures taken during the trapping session of October were saved. These cameras were mainly for information purposes and will therefore not be considered in the statistical analyses but will be briefly discussed.

3. Statistical analyses

3.1. Habitat/site characterization

3.1.1. Plant diversity

In order to quantify the diversity of plant species present on the different sites, different diversity indices were calculated to complement each other and to have the most complete view possible of the plant diversity present on the study sites. First, the Shannon index was calculated for each site according to the formula.

$$H = -\sum_{i=1}^{S} pi \ \ln(pi) \qquad (1)$$

Where *S* is the species richness, *i* is one species, and *pi* is the proportion of a species *i* to the total number of individuals *N* in the study area. *Pi* is then calculated by *ni*/*N* where *ni* is the number of individuals of the species *i* and *N* is the total number of individuals within all species. As the Shannon index has shown some limitations in its ability to illustrate the diversity of an environment (Spatharis et al. 2011; Dušek and Popelková 2017), I estimated it was important to add the evenness index and species richness in order to get a complete picture. The evenness, also called Pielou's equitability index, was calculated for each site by the following equation:

$$J = \frac{H}{Hmax} \text{ , with } Hmax = \ln S \qquad (2)$$

Where *S* is, again, the species richness. The species richness of each site was calculated as well as the abundance of each species within each site.

An ANOVA I was carried out on each of the different indices calculated (Shannon index, Evenness, species richness and abundance) in relation to the different categories of sites in order to highlight whether there was a significant difference in these different indices between the three site categories (controlled sites, sites that had been impacted by beavers less than five years ago and those that had been impacted by beavers more than five years ago).

In order to highlight the association of specific plant species with specific site categories, a first FCA (factorial correspondence analysis) was carried out to illustrate the distribution of plant species among the different sites and more particularly between the different site categories (*new*, *old* and *control*). Indeed, the FCA allows the analysis of the association between two categorical variables and thus allows the association between the elements of these two variables to be visualised graphically. In this case, the variables are site category and plant species present.

3.1.2. Vegetation cover

To highlight a potential change in the overall vegetation composition between the sites, the percentage cover of the different vegetative strata was estimated. With these data, the different percentages were grouped by site category and stratum to obtain the average percentage of each stratum (herbaceous, shrubby and arboreal) by site category. The canopy layer was subdivided into two categories: deciduous and coniferous trees. Out of one hundred percent of the canopy stratum, the average percentage of deciduous and coniferous trees within a site was calculated for each category. These results were then illustrated using simple graphs made in RStudio with the packages *ggplot2* and *tidyverse*. Finally, ANOVA I were carried out on the percentage of each vegetation layers in the different categories as well as on the conifers and deciduous cover percentage in the different categories in order to highlight any significant differences between these.

3.1.3. Dead wood

The data collected to estimate the amount of dead wood in the different sites and more specifically the difference between the site categories is count data. Indeed, the number of dead wood was counted at each site. With this counting data, the averages of the number of dead wood pieces found per site per category were calculated. This was done by separating the dead wood found on the ground from the still standing ones in the ground. The results of these averages were illustrated by simple graphs made in RStudio using the packages *ggplot2* and *tidyverse*. Finally, the different amount of dead wood pieces found within the sites was tested with an ANOVA I.

3.2. Characterization of small mammals populations

3.2.1. Diversity, abundance and distribution within the sites

As with the plant diversity analysis, small mammal species diversity was assessed using the Shannon Index (1) and Evenness (2) as well as species richness and abundance. Following this, an ANOVA I was also carried out on these different indices to highlight a potential significant difference in terms of mammalian species diversity between the different site categories. ANOVA I were also carried out on the different abundances of bank voles, field voles and common shrews between the different categories of sites as they were the most abundant species and therefore, the only one's statistical test could be applied on. After that, an FCA was also carried out using RStudio software to graphically highlight the correspondence between the sites and the species found in them, grouped by categories.

3.2.2. Relationship between small mammals presence and the habitat

To analyse the potential relation between the presence of small mammals and the amount of dead wood found within the sites, a first simple linear model was done on the amount of dead wood found and the number of mammals (all species included). Finally, to understand if one specific species was impacted by the presence of dead wood, three simple linear models were fitted between the amount of dead wood and the three most abundant species (bank voles, field voles and common shrews).

In addition, six multiple linear regressions were performed, two on each of the three most abundant species, bank voles, field voles and common shrews. The first model carried out concerned the impact of vegetation cover on small mammals. It therefore involved testing the number of individuals found (count explained variable) and the site category (three-level categorical explanatory variable) in addition to the percentage cover of the ground stratum and finally in addition to the percentage cover of the undergrowth stratum (these last two being count explanatory variables). The second model concerned the impact of the amount of coniferous or deciduous trees on the presence of mammals within the different categories. The model was based on the number of individuals of the species (count explained variable) according to the site category (three-level categorical explanatory variable) in addition to the percentage of conifer cover (count explanatory variable).

3.2.3. *Qualitative characterisation of populations*

The dissection of individuals made it possible to obtain important information for the qualification of populations, such as the sex, age or physical condition of the individuals (weight/size). This information was collected to potentially illustrate the occupation of certain sites by certain types of individuals (according to their age, maturity status, sex or physical condition). The data used were the raw data following dissection. Meaning it included the height in centimetres, the weight without intestines in grams, the sex and the age of each individual collected in the field within the different categories. The following analyses were done only on the three most abundant species (bank voles, field voles and common shrews) as the others were in too low numbers to carry statistical tests. The physical condition of the mammals was calculated for each individual via the formula of the Body Mass Index (BMI) and added to the matrix of the data.

$$BMI = \frac{Mass\ (g)}{Lenght^2(mm)} \quad (3)$$

Firstly, the results have been illustrated with descriptive graphs of the BMI of individuals within the categories according to their sex and the average BMI of individuals within the categories regardless to their sex. ANOVA I was carried out on these data to illustrate the potential significant difference of BMI of the individuals within the categories. Secondly, the number of individuals per age per category was shown in a barplot as well as the average age of individuals within the categories in a dotplot. As well as for the BMI, ANOVA I were carried out on the age of individuals within the categories. Thirdly, the maturity of bank voles and field voles was analysed. Indeed, the maturity of common shrews were noted based on their stage of life, young or adult meaning immature and mature unless their reproductive system was big enough to determine. For each species, a descriptive graph has been done showing the number of mature or immature individuals within the three categories. Then, the percentage of mature individuals found within the sites were calculated to be able to apply an ANOVA I on the number of mature individuals and the categories. Fourthly, the sex ratio of individuals within the categories was tested. After showing the amount of males and females within each categories in a barplot, the percentage of females found in each site was calculated in order to apply an ANOVA I on this percentage and the category of sites.

Finally, to better visualize the importance of these different variables (BMI, age, maturity and sex) in the different species population within the categories, three PCA (Principal Component Analysis) were carried out. One for each of the three species and the different variables mentioned.

Results

1. Habitat/site characterization

1.1. Plant diversity

During the vegetation sampling, 41 different plant species were sampled (Appendix 1). These different species were distributed across the 15 sites, which were grouped into three categories according to beaver occupation.

1.1.1. Plant diversity indices

The mean values of the Shannon index, evenness, abundance, and species richness of plant species in each category of site were calculated by averaging the index values for each site. These values are shown in the Table 4. The Shannon index, evenness, abundance and species richness were, on average, slightly higher within the *new* sites, but the results of the ANOVA I showed these differences to be non-significant (p-value > 0.05) (Figure 13 and Table 5).

Table 4: Mean values of the Shannon index, evenness, abundance, and species richness obtained for the plant species in each category of site.

Site's category	Shannon index	Evenness	Abundance	Species richness
New	1.68848	0.6832050	109.0667	12.5
Old	1.45490	0.6570622	105.6000	9.4
Control	1.55956	0.6748923	122.6667	10.4

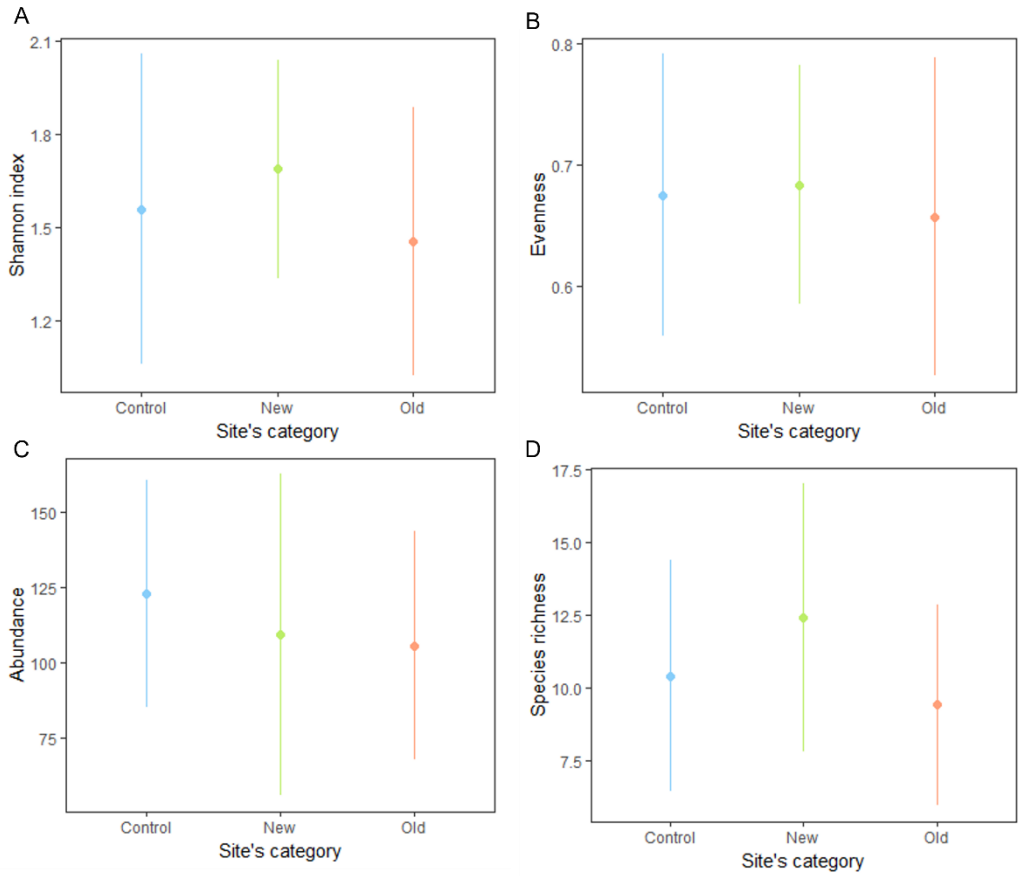


Figure 13: Dot plots of the means of the different diversity indices for plant species in the different sites categories. A: Shannon index. **B**: Evenness. **C**: Abundance. **D**: Species richness. Dots represent the mean values of the indices from the sites of specific categories (control, n*ew* and *old*) and the vertical bars represent their 95% confidence intervals.

Table 5: Results of the ANOVA I tests on the different diversity indices for the vegetation. Df are degrees of freedom, SS are the sum of squares of error, MS are the mean squares of error (SS/Df), Fvalue are the F statistics, Pvalue are the p-values and Sig shows how significant is the p-value (if higher than 0.1 nothing written, if between 0.1 and 0.05 ".", if between 0.05 and 0.01 "*", if between 0.01 and 0.001 "**" and if below 0.001 "***".

Shannon index	Df SS MS Fvalue Pvalue Sig Category 2 0.1368895 0.06844475 0.5675 0.5814 Residuals 12 1.4472303 0.12060252
Evenness	Df SS MS Fvalue Pvalue Sig Category 2 0.001784107 0.0008920534 0.1028 0.9031 Residuals 12 0.104167638 0.0086806365
Abundance	Df SS MS Fvalue Pvalue Sig Category 2 813.7481 406.8741 0.3293 0.7258 Residuals 12 14828.5667 1235.7139
Species richness	Df SS MS Fvalue Pvalue Sig Category 2 23.33333 11.66667 1.0972 0.3651 Residuals 12 127.60000 10.63333

1.1.2. Plants repartition within the sites

The factorial correspondence analysis allows us to visualise the relationships between the plant species recorded and the sites of interest. Two positively linked modalities (plant species or site) are then found close to each other on the graph resulting from the FCA (Figure 14).

Figure 14: Results of the FCA on the vegetation census. A: First two dimensions of the FCA on the site resemblance in accordance with the plant species found. Sites from 1 to 5 correspond to sites from *New-1* to

New-5. Sites from 6 to 10 correspond to sites from *Old-1* to *Old-5*. Sites from 11 to 15 correspond to sites from *Control-1* to *Control-5*. The first principal dimension (= component) represents 24,3% of the variation, while the second dimension represents 17,7% of the variation from the data set. The FCA was carried out with a 95% confidence interval, represented by the ellipses. The ellipses represent the sites grouped by their category (*new*, *old* or *control*). **B: First two dimensions of the FCA on the plant species repartition on the different sites.** The first principal dimension (= component) represents 24,3% of the variation, while the second dimension represents 17,7% of the variation from the data set. The FCA was carried out with a 95% confidence interval.

This first part of the figure (Figure 14A) illustrates the similarity of the sites to each other according to the plant species that were recorded within them. This first FCA (representing 42% of the total variation, by summing the percentages of variation in the first dimension (24.3%) and the second dimension (17.7%)) highlights the fact that all the sites are quite similar to each other since their ellipses overlap. However, we can see that the sites belonging to the *old* category show more differences between them, being more spaced from each other on the graph. What should attract attention here is the ellipse representing the category of *new* sites. Indeed, we can see that these are graphically distinguished from the other two categories, indicating a greater variety within them. This can be explained by the second illustration (Figure 14B) of the FCA representing, this time, the distribution of the different species within the sites. Indeed, we can observe that the stretching of the ellipse corresponding to the sites in the *new* category can be explained by comparing the two graphs. The first graph (Figure 14A) indicates that the site *New-4* is further away from the others. When we compare this with the graph shown in Figure 14B, we can see that four species found at only one site are illustrated in the same place as the site *New-4*. Indeed, I have highlighted the species found at only one site, firstly in pink in Figure 14B and secondly in bold in Table 6. Table 6 also shows that many of the species found at a single site are in fact at sites belonging to the *new* sites category.

Table 6: Plant species found at only one site. The species listed in bold are the species found only in the site *New 4* referring to the explained results.

Species	Site n° - name
Convallaria majalis	*New-3* – Vuoripeikonjärvi
Epilobium palustre	***New-4* – Huhmari 2**
Galium palustre	***New-4* – Huhmari 2**
Scutellaria galericulata	***New-4* – Huhmari 2**
Epilobium parviflorum	***New-4* – Huhmari 2**
Drosera rotundifolia	*New-5* - Tekumi

Halianthus divaricatus	*Old-2* – Häntjärvi
Lysimachia vulgaris	*Old-2* - Häntjärvi
Talinum paniculatum	*Old-3* - Vähäkeltajärvi
Taraxacum officale	*Old-4* - Huhmari 1
Pinus sylvestris	*Old-5* - Viljaskorpi
Linnaea borealis	*Control-3* - Likojärvi
Lysimachia europaea	*Control-3* - Likojärvi
Plantago subulata	*Control-3* - Likojärvi

1.2. Vegetation cover

To possibly show a change in the habitat between sites from a broader vegetation point of view, a quantitative estimation of the different vegetation strata was made. Figure 15 (A) shows a gradual change between the different site categories. Indeed, the canopy and shrub strata gradually decrease from the *control* sites to the *new* sites and are finally the least abundant in the *old* sites. The herbaceous stratum, also called undergrowth, is on the other hand, the lowest in the *control* sites, followed by the *new* sites and finally the highest in the *old* sites. If we look closer on the type of trees composition in the canopy strata, Figure 15 (B) also shows a gradual change in the types of trees present in the different site categories. Conifers disappear over time to be replaced by deciduous trees. There is a shift in the main occupation of the different tree types within the site categories. Sites without beaver occupation are dominated by conifers. Once beavers have impacted the site, deciduous trees tend to increasingly dominate the site. None of the ANOVA I carried out on the different vegetation layers were significant at the 5% threshold (Appendix 5). This is due to the fact that the values in the dataset have a very high variance, with minima and maxima being far apart. Furthermore, the dataset consists of only five replicates per category.

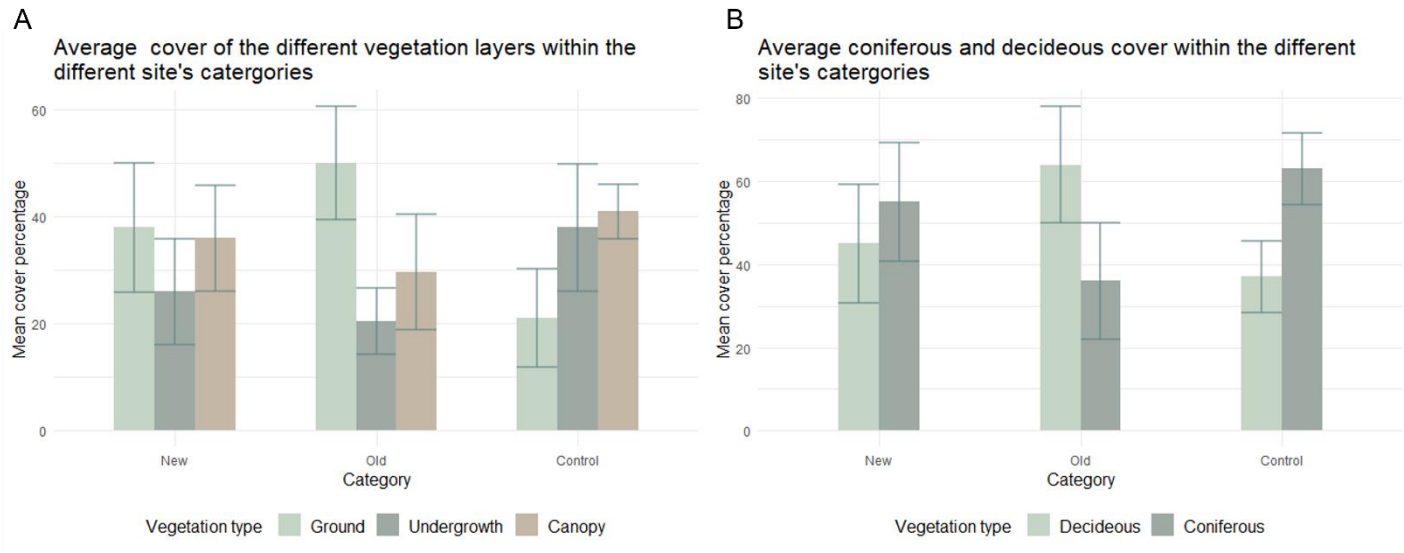


Figure 15: Cover percentage of vegetation within the sites. A: Mean cover percentage of the canopy, undergrowth, and ground vegetation within the different sites categories. B: Mean cover percentage of coniferous and deciduous trees within the different sites categories.

1.3. Dead wood

Here are some counting data of the deadwood pieces counted withing the sites. The figure 17 shows the average of the counted pieces within the different site categories calculated based on the number of pieces found in each site of the different categories. The idea is to make a simple characterisation of the amount of dead wood found on the different categories of sites. The ANOVA I carried out on the amount of dead wood did not show any significant difference between the three stages of ecological succession (Appendix 6). As well as for the vegetation layers, the number of replicates per category is too little and the data variance is large which is probably the reason why the tests were not significant. But if we look at the average of the two types of dead wood (those laying on the ground and those still standing), we can see that the sites with the most deadwood on average are the sites where the beavers left less than five years ago. This is followed by sites from which the beavers left more than five years ago. And finally, the *control* sites had the least amount of dead wood.

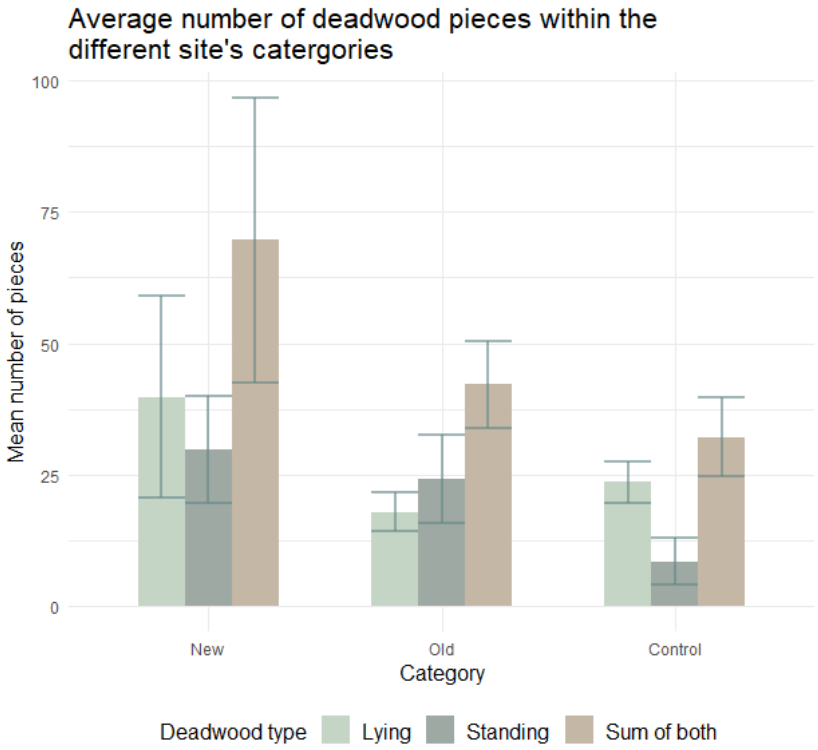


Figure 17: Average number of deadwood pieces counted within the site category. Both lying deadwood and still standing deadwood were counted.

2. Characterization of small mammal populations

2.1. Small mammal diversity indices

During this study, a total of 208 individuals have been collected (all sites and trapping sessions pooled). As with the characterisation of the vegetation of the sites, the different biodiversity characterisation indices were calculated to characterise the small mammal communities within the different sites (Table 7). The statistical analyses (ANOVA I) carried out on these different index values did not reveal any significant differences between them in the different site categories, as illustrated in Figure 18 and Table 8. However, we can discern a certain tendency that the Shannon index, evenness, abundance and species richness of small mammals are on average higher in the *control* category of sites.

Table 7: Mean values of the Shannon index, evenness, abundance, and species richness obtained for the mammal species in each category of site.

Site's category	Shannon index	Evenness	Abundance	Species richness
New	0.85532	0.6825962	14.2	3.6
Old	0.84584	0.7200855	12.8	3.4
Control	1.08926	0.7934560	14.6	4

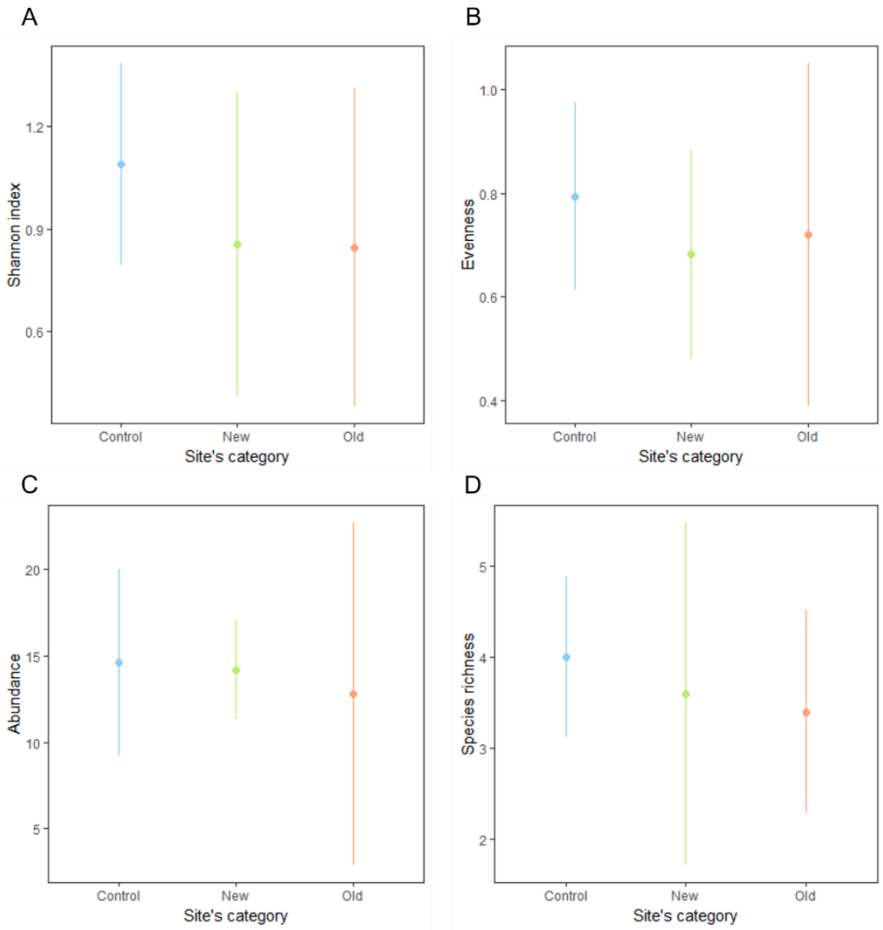


Figure 18: Dot plots of the means of the different diversity indices for small mammals species in the different sites categories. A: Shannon index. **B**: Evenness. **C**: Abundance. **D**: Species richness. Dots represent the mean values of the indices from the sites of specific categories (*control*, *new* and *old*) and the vertical bars represent their 95% confidence intervals.

Table 8: Results of the ANOVA I test on the different diversity indices for the vegetation. Df are degrees of freedom, SS are the sum of squares of error, MS are the mean squares of error (SS/Df), Fvalue are the F statistics, Pvalue are the p-values and Sig shows how significant is the p-value (if higher than 0.1 nothing written, if between 0.1 and 0.05 ".", if between 0.05 and 0.01 "*", if between 0.01 and 0.001 "**" and if below 0.001 "***".

Shannon index	Df SS MS Fvalue Pvalue Sig Category 2 0.1901185 0.09505924 0.8807 0.4396 Residuals 12 1.2951708 0.10793090
Evenness	Df SS MS Fvalue Pvalue Sig Category 2 0.03179758 0.01589879 0.4059 0.6752 Residuals 12 0.46997450 0.03916454
Abundance	Df SS MS Fvalue Pvalue Sig Category 2 0.9333333 0.4666667 0.3889 0.686 Residuals 12 14.4000000 1.2000000
Species richness	Df SS MS Fvalue Pvalue Sig Category 2 8.933333 4.466667 0.1528 0.86 Residuals 12 350.800000 29.233333

2.2. Species distribution within the sites

Table 9 shows the census results for each site grouped into each site category. The highest number of different species was observed within the *new* sites. A total of six different species were recorded within these sites. However, it was in the *control* category that the most individuals were recorded, with a total of 73 individuals recorded, all species combined. Figure 19 shows the number of individuals of each species found in each category.

Table 9: Summarise of small mammals' abundance and species richness in the different site's categories.

Site category	*Number of bank voles*	*Number of field voles*	*Number of water voles*	*Number of common shrews*	*Number of water shrews*	*Number of pygmy shrews*	*Total number of individuals*	*Total number of species*
New	45	7	1	15	2	1	**71**	**6**
Old	36	8	0	14	6	0	**64**	**4**
Control	42	10	2	13	6	0	**73**	**5**

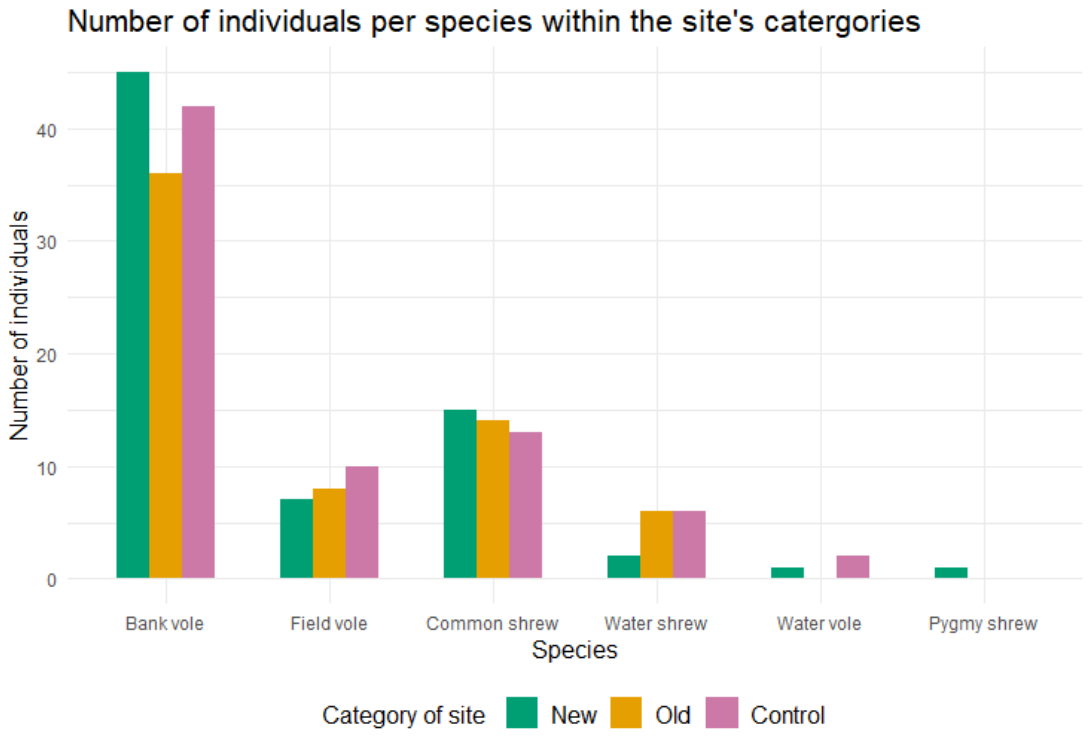


Figure 19: Repartition of the different mammal species found within the different site categories.

Table 10 shows the detailed results of the censuses carried out at the different sites. The site with the highest number of different species was site *New-4*.

Table 10: Detailed results of the census of small mammals in the different sites.

Site	*Number of bank voles*	*Number of field voles*	*Number of water voles*	*Number of common shrews*	*Number of water shrews*	*Number of pygmy shrews*	*Total number of individuals*	*Total number of species*
New-1	10	2	0	2	0	0	**14**	**3**
New-2	4	1	0	7	0	0	**12**	**3**
New-3	11	1	0	0	0	0	**12**	**2**
New-4	11	1	1	2	1	1	**17**	**6**
New-5	9	2	0	4	1	0	**16**	**4**
Old-1	14	1	0	4	1	0	**20**	**4**
Old-2	18	0	0	4	0	0	**22**	**2**
Old-3	2	3	0	3	1	0	**9**	**4**
Old-4	1	1	0	1	0	0	**3**	**3**
Old-5	1	3	0	2	4	0	**10**	**4**
Ctrl-1	8	4	0	4	3	0	**19**	**4**
Ctrl-2	3	1	0	2	2	0	**8**	**4**
Ctrl-3	10	2	1	1	0	0	**14**	**4**
Ctrl-4	11	1	1	4	1	0	**18**	**5**
Ctrl-5	10	2	0	2	0	0	**14**	**3**

As the amount of water shrews, water voles and pygmy shrews collected being too little, statistical tests have been done only on bank voles, field voles and common shrews. Bank voles were found in higher abundance in the *new* sites (Table 9) even though the result of the ANOVA did not show any significant difference of bank vole abundance between the three different sites categories (P-value = 0.8645 and $F_{(2,12)} = 0.1474$). Field voles were found

in higher abundance in *control* sites (Table 9) even though the ANOVA test did not reveal any significant difference between the sites categories (p-value = 0.686 and $F_{(2,12)}$ = 0.3889) but with a sample of 25 individuals, it is too low to strongly confirm the result. Finally, common shrews were more found in the *new* sites (Table 9) but here again, no significant difference was found between the three sites categories (p-value = 0.9447 and $F_{(2,12)}$ = 0.0571). Water shrews were equally found in *old* and *control* sites with 6 individuals found in each against only two individuals in the *new* sites. Only three water voles were found during the study, two in the control sites, one in the *new* sites and one in the *old* sites. Finally, only one pygmy shrew was sampled in a site from the *new* category, making this category the one with the highest species richness.

The FCAs carried out in RStudio show that even though all the categories are quite similar as their ellipses are overlapping and their centre are close to each other, the sites in the *new* category have a slightly different composition from those in the *old* and *control* categories. Indeed, the Figure 20A illustrates the similarity between sites in terms of the different species found within them and their abundance. This FCA represents a total of 72.8% of the total variation, by adding the respective percentages of the two axes (52.2% and 20.6%). The sites in the *new* category are represented by the green ellipse, those in the *old* category are in orange and those in the *control* category are in purple. The position of the ellipses in Figure 20A indicates that the species composition of small mammals in the *new* sites tends to be different from that of the *old* and *control* sites, which are more similar to each other. We can observe that the green ellipse, the one of the *new* sites, is pulled by the *New-4* and *New-2* sites. To better understand this illustration, we can compare it with the graph of the FCA represented in Figure 20B, showing the distribution of mammal species according to their census within the different sites. The species found in Figure 20B at similar positions corresponding to sites *New-2* and *New-4* in Figure 20 are the common shrew (*Sorex araneus*) and pygmy shrew (*Sorex minutus*) respectively. Comparing this observation with Table 8 showing the overall species census within the sites, it can be seen that the pygmy shrew was only recorded once during the study, and this was at site N*ew-4*. On the other hand, the site with the highest number of common shrews was site *New-2*.

In addition to this, it can also be noted that what pulls the ellipse of the *old* category to differ slightly from that of the *control* category in Figure 21 is the water shrew species (*Neomys*

fodiens) which was recorded in greater numbers within *old* site 5 (site number 10 in Figure 20A), although this finding is not strongly marked.

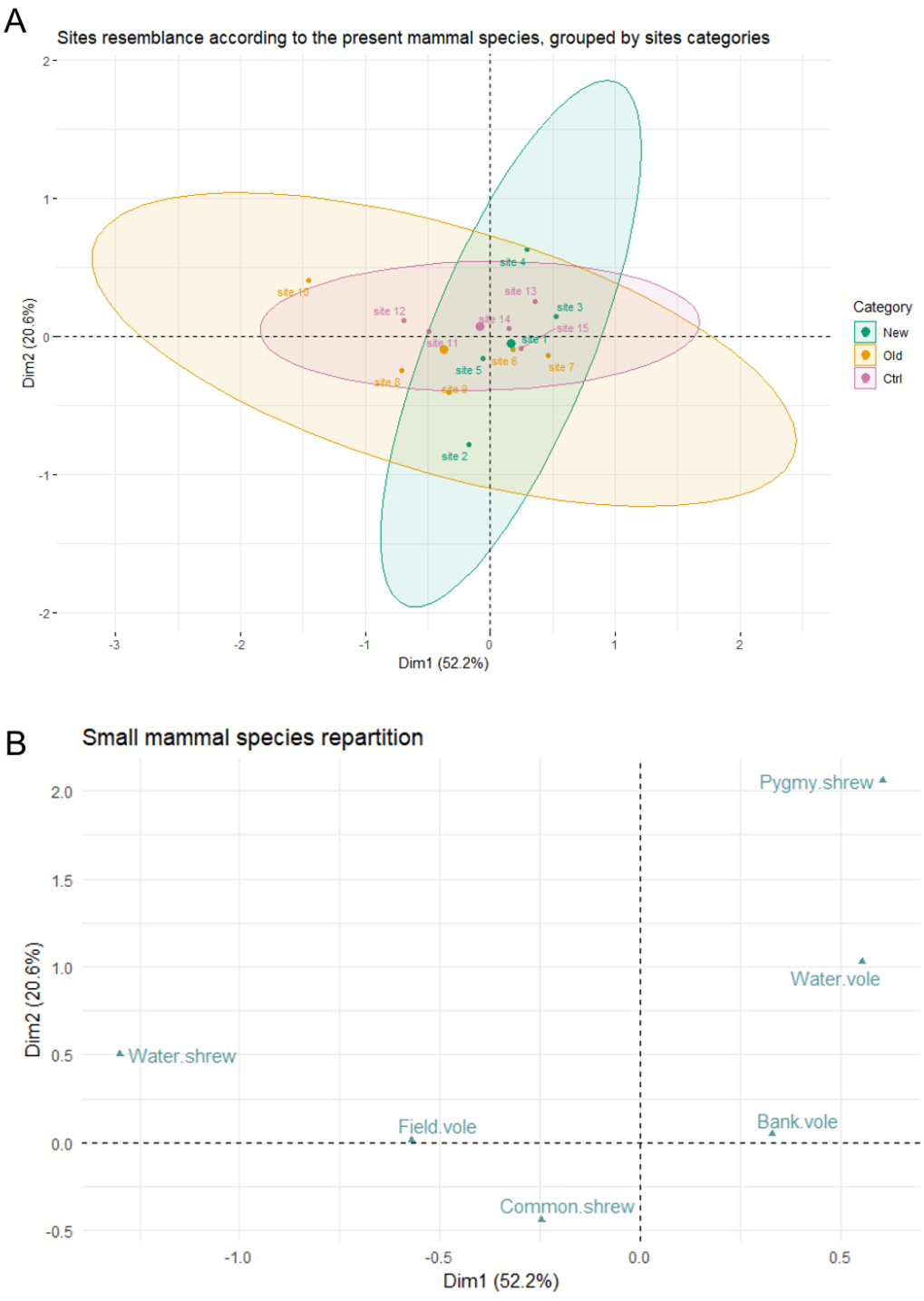


Figure 20: First two dimensions of the FCA on the sites and small mammals found. A: Sites' resemblance in accordance with the small mammals' species found. Sites from 1 to 5 correspond to sites from *New-1* to *New-5*. Sites from 6 to 10 correspond to sites from *Old-1* to *Old-5*. Sites from 11 to 15 correspond to sites from *Control*-1 to *Control*-5. **B:** Small mammals' species repartition on the different sites. The first principal dimension (= component) represents 52,2% of the variation, while the second dimension represents 20,6% of the variation from the data set. The FCA was carried out with a 95% confidence interval, represented by the ellipses. The ellipses represent the sites grouped by their category (*new*, *old* or *control*).

2.2.1. Relationship between small mammals presence and the habitat

To see if the presence of species was linked to the amount of dead wood left on the ground due to beavers, four linear models were fitted on the amount of dead wood lying on the ground within the sites and the abundance mammals' species. Firstly, the model was done with all the species included. Secondly, three different models were done with the bank voles, the field voles, and the common shrews separately. None of these four models showed significant results (Appendix 7).

In addition, to see whether the vegetation cover has an impact on the abundance of small mammals, multiple linear models were fitted on the number of individuals found of each species and the percentage of vegetation cover in each category. Six models were thus made, two for each species with lm(Species ~ Category + Ground + Undergrowth, data) and lm(Species ~ Category + Conifers, data). None of these showed significant results (at the 5% threshold), indicating that the number of individuals found, no matter the species, was not impacted by the amount of ground stratum, the amount of undergrowth, or the type of trees found on the sites, regardless of the category of sites (beaver impacted or not) (Appendix 8).

2.3. Condition of individuals within the sites

For the following analyses, only bank voles, field voles and common shrews were selected as they were the only species with a relatively large sample size.

2.3.1. Bank voles

Figure 21 shows firstly (A) the physical condition of the 118 different bank voles found in the different site categories, sorted by sex. The second part of the figure (B) represents the average BMI of individuals in each site category, calculated based on the average BMI of individuals in each site, all sex included. An ANOVA I was also performed to look for any significant difference in BMI between the different categories. The result of this ANOVA has a p-value of 0.116 ($F_{(2,12)} = 2.589$) confirming that there is no significant difference in the physical condition of the bank voles between the different site categories. However, Graph B in Figure 21 shows that, on average, the bank voles are in slightly poorer condition in the *old* sites than in the *new* or *control* sites.

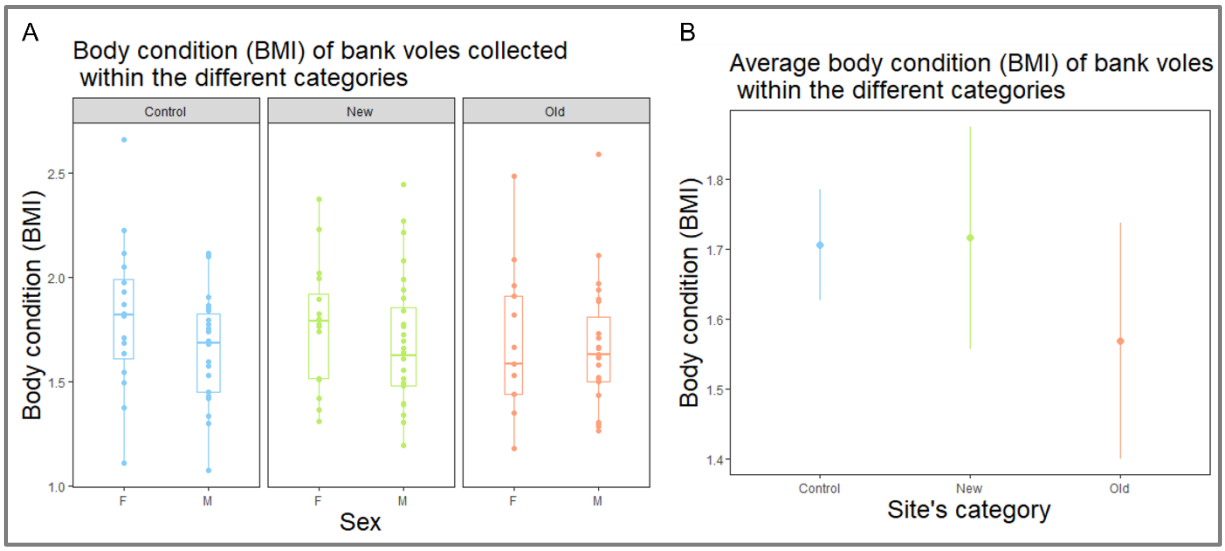


Figure 21: Body condition (Body Mass Index – BMI) of bank voles within the different sites categories. A: Boxplot of the BMI of each individual collected within the different categories, grouped by sex. The box represents the 25 and 75% quantiles. The horizontal bar represents the median and the vertical bars represent the variability of the data. **B**: Dotplot of the average BMI of individuals in each site category, calculated on the basis of the average BMI of individuals in each site, both sexes pooled. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

Figure 22 illustrates, firstly (A), the distribution of the 118 bank voles collected in different age groups (in months) within the different categories. It shows that more individuals of older ages (>7 months) were found in the *new* and *old* sites than in the *control* sites. However, no clear conclusion can be drawn from this graph. To complete this result, graph B of the same figure 22 illustrates the average age of bank voles within the different categories of sites. In this graph, a trend can be observed. Indeed, it seems that the average age increases with the history of the sites. Sites that have been occupied by beavers contain older bank voles than controls and in addition to this, it seems that sites that have been impacted for a longer period of time (>5 years) are occupied by older individuals than sites that have been impacted less than five years ago. However, the ANOVA I performed on the average age of bank voles was not significant. Indeed, with a p-value of 0.1992 ($F_{(2,12)}$ = 1.8514) and five replicates per category, it is only a trend that can be observed.

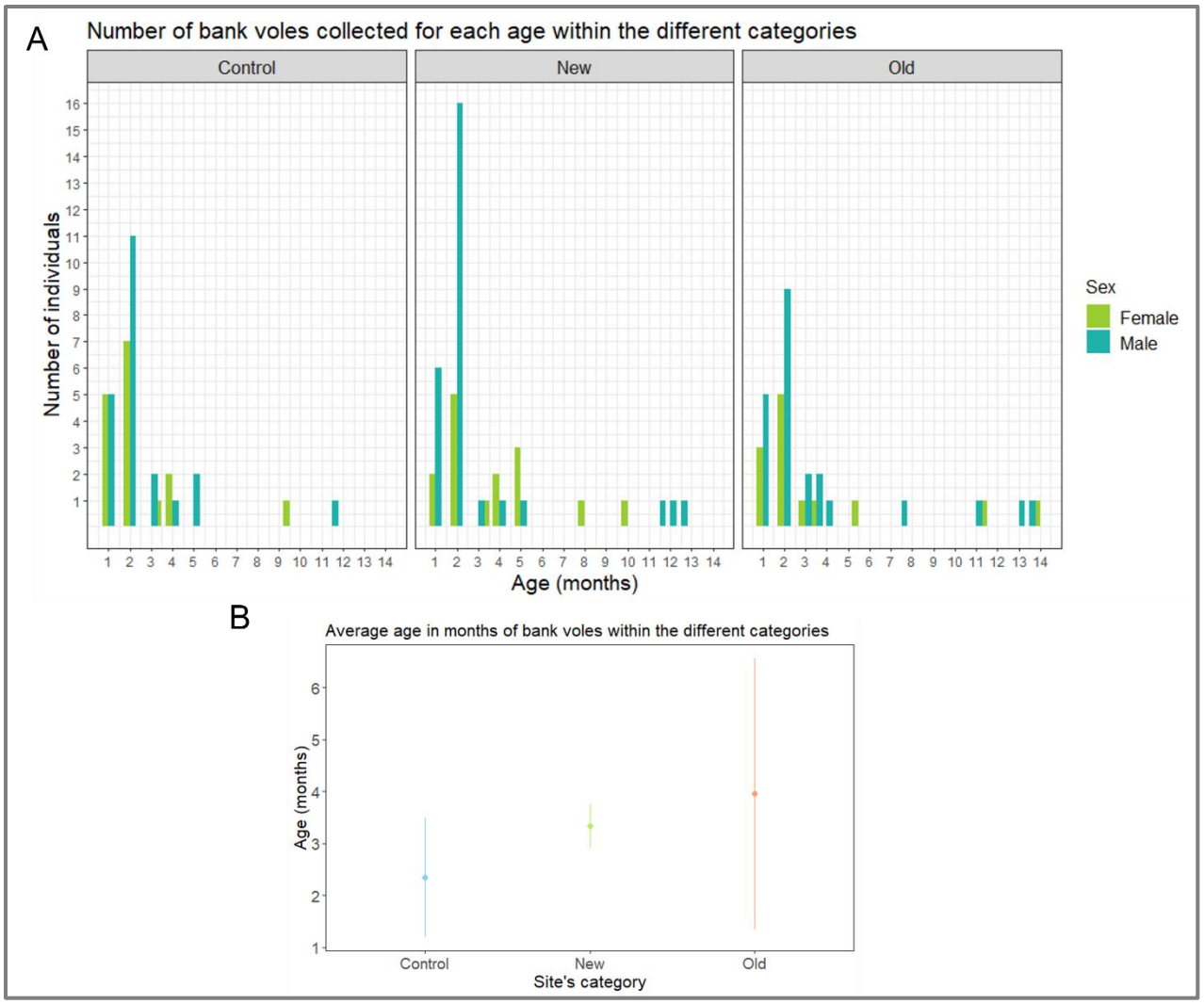


Figure 22: Age repartition and mean age of bank voles within the different sites categories. A: Barplot of the number of bank voles for each age collected within the different categories. **B**: Dotplot of the mean age (in months) of bank voles in each category of site. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

Figure 23A represents the number of mature or immature bank voles found within the different categories depending on the sex. This graph shows that in general, more immature males are found in the different categories while more mature females are found in the *control* and *new* categories. Figure 23B shows the average percentage of mature individuals found in the different site categories, no matter their sex. The ANOVA I test on these did not show any significant results with a p-value of 0.083 ($F_{(2,12)} = 3.098$) but the graph shows a trend where in average, more mature individuals are found in the *control* and *new* categories compared to the *old* category.

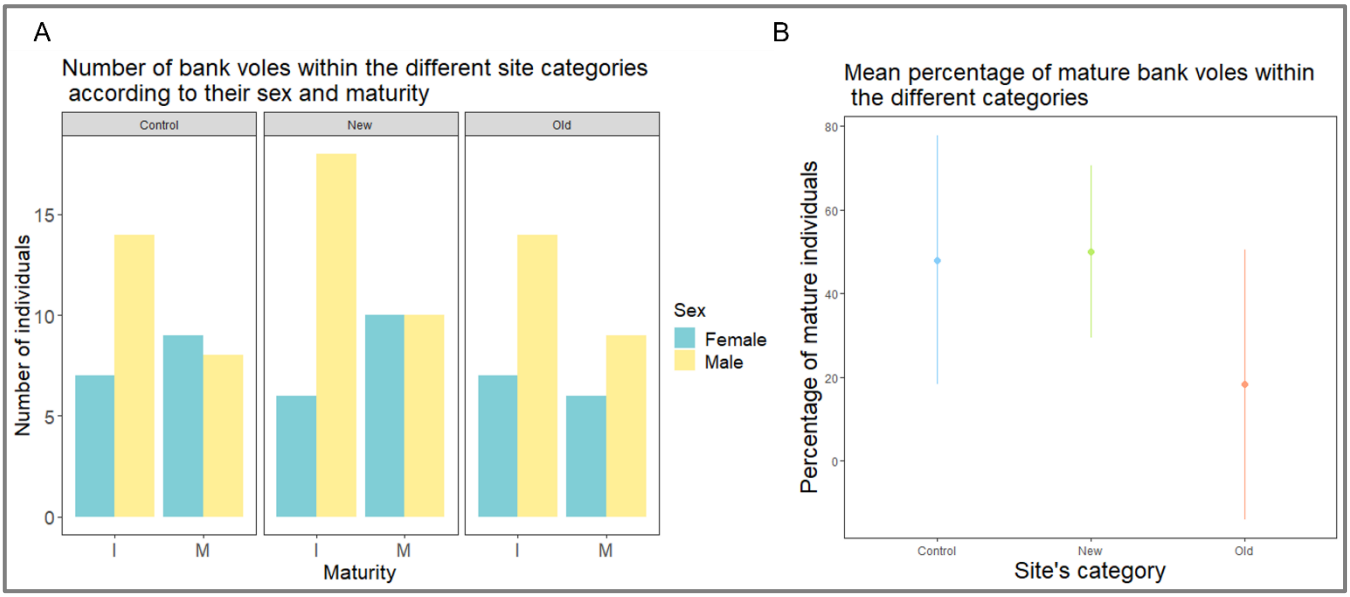


Figure 23: Maturity analysis of bank voles within the site categories. A: Repartition of the mature and immature bank voles within the sites categories according to their sex. "I" means immature individuals and "M" means mature individuals. **B**: Dotplot of the mean percentage of mature bank voles within the different categories. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

The figure 24 shows the amount of male and female bank voles within the three different categories. In general, more males of the bank vole species were found during the study and they were more abundant in each habitat category. To statistically test the sex variable among the different categories, the percentage of females found in each site was calculated. On these data, an ANOVA I was carried on the percentage of females and the category of site. This ANOVA I did not show any significant result (p-value = 0.9877 and $F_{(2,12)} = 0.0124$) meaning that there is no difference in the percentage of females found within the different categories.

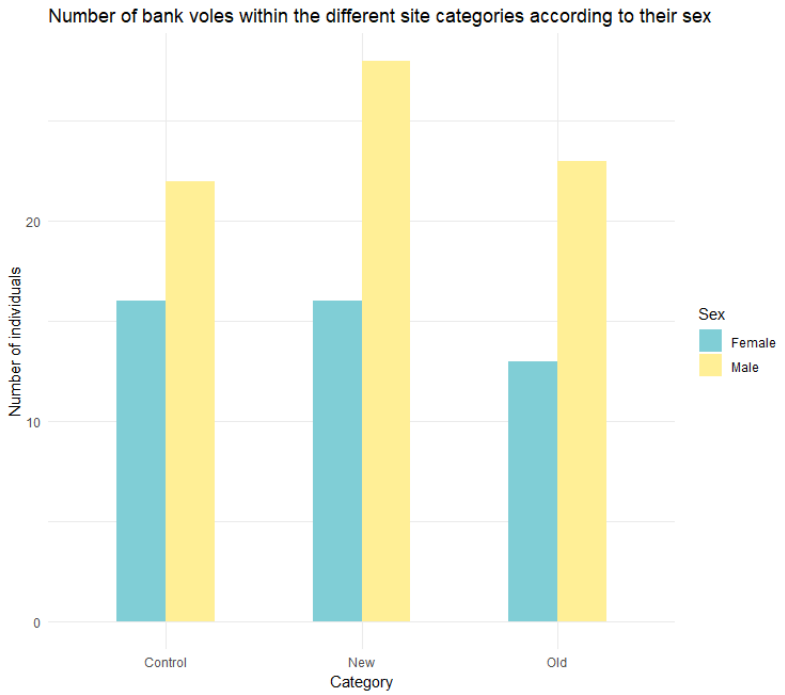


Figure 24: Number of females and males of bank voles found in each category of site.

A PCA was carried out on the different variables characterizing the populations of bank voles within the categories of sites. The results of this PCA are illustrated in Figure 25. The PCA on the individuals characteristics (BMI, age, maturity and sex) represents 71% of the variation being relatively high when summarizing 4 variables into two dimensions. The Figure 25A shows that the maturity and the BMI are correlated to each other whereas they are not with the sex and the age. The Figures 25B and 25C show that the *old* sites tend to have more variance in the characterization of the bank voles populations than the two other categories, which overlap more. Indeed, three of the five *old* sites are characterized by older not mature individuals with a low BMI, while the other sites tend to inhabit individuals with a higher BMI and a higher number of mature individuals.

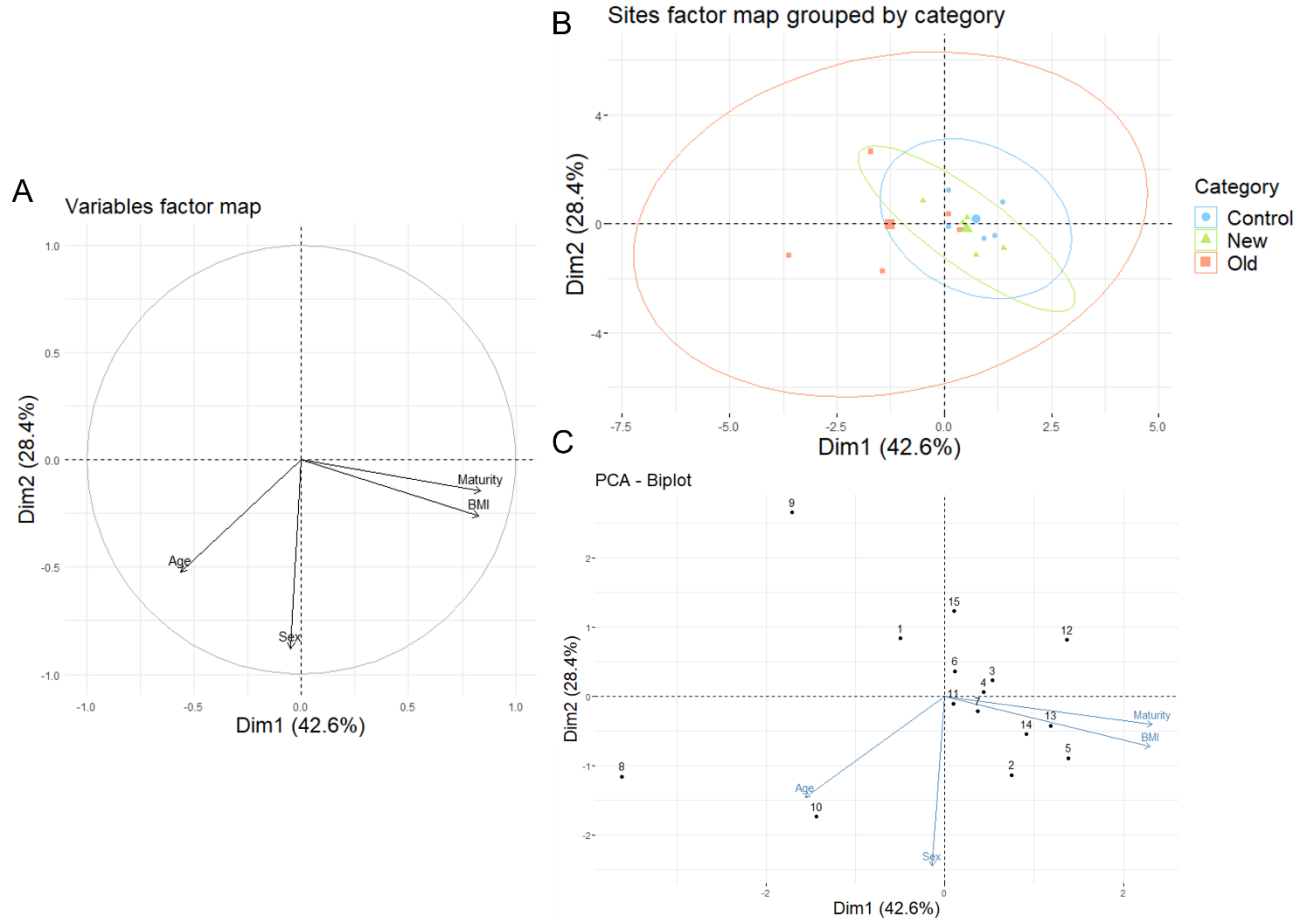


Figure 25: First two dimensions of the PCA on the sites and the bank vole population variables (BMI, age, maturity and sex). A: Factor map of the variables. **B:** Factor map of the sites grouped by category. **C:** Biplot of the PCA. Points from 1 to 5 are for the sites from *New-1* to *New-5*. Points from 6 to 10 are for the sites from *Old-1* to *Old-5*. Points from 11 to 15 are for the sites from *Control*-1 to *Control*-5. The first principal dimension represents 42.6%, while the second represents 28.4% of the variation from the data set. The bigger point inside each group represents the centroid of the fitted ellipse (95% confidence interval). The age represents the mean age of bank voles found in each site. The BMI represents the mean Body Mass index of bank voles found in each site. The sex represents the percentage of females found in each site. The maturity represents the percentage of mature individuals found in each site.

2.3.2. Field voles

Figure 26A represents the physical condition of the individuals of the 25 field voles identified in the 15 sites of the three different categories, sorted by sex. And the Figure 26B illustrates the mean BMI value of field voles within the different categories based on the mean BMI of individuals within the 15 sites. Here too, an ANOVA I was performed. This ANOVA resulted in a p-value of 0.458 ($F_{(2,11)}$ = 0.838) indicating that here again, no significant difference in physical condition can be shown between the different site categories. However, it is important to note that the sample size of only 25 individuals and only five replicates per category, it is very likely too small to draw any conclusions, although Graph B in Figure 26

shows a slight difference in BMI for the field voles in the *new* sites, being on average higher than in the *old* and *control* categories. Indeed, they tend to be in lower body conditions in the *old* sites.

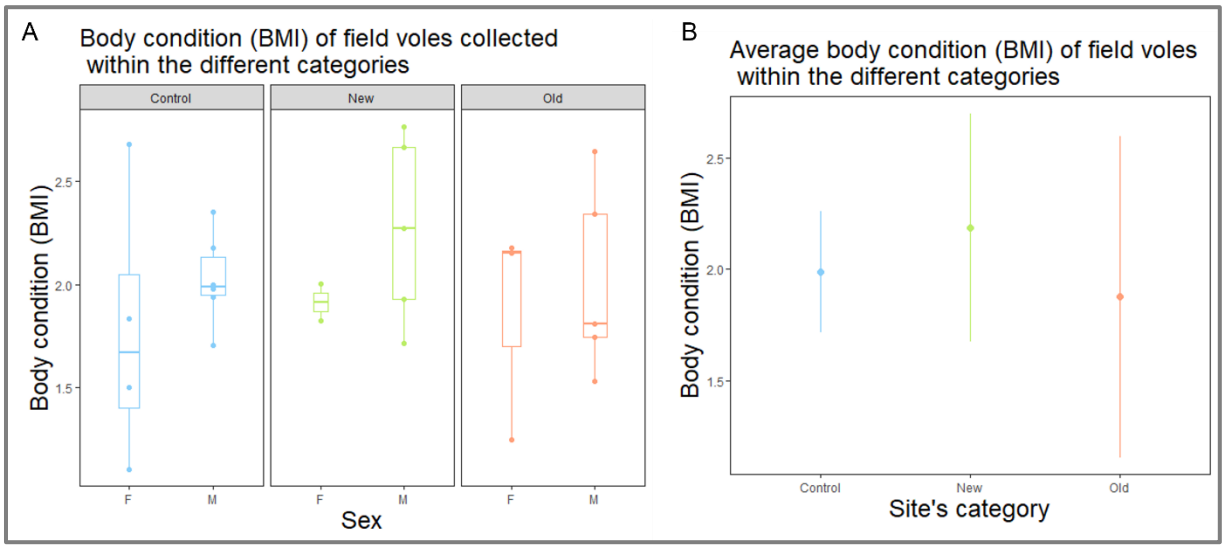


Figure 26: Body condition (Body Mass Index – BMI) of field voles within the different sites categories. A: Boxplot of the BMI of each individual collected within the different categories, grouped by sex. The box represents the 25 and 75% quantiles. The horizontal bar represents the median and the vertical bars represent the variability of the data. **B:** Dotplot of the mean BMI of field voles in each category of site. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

Figure 27 illustrates in A, the repartition of the individuals of different age classes within the three categories and in B, the mean age (in weeks) of field voles in the different categories. Again, it is hard to conclude something precise with the Graph A but it can be noticed that there is a higher number of old (> 7 weeks) individuals found in the *control* and *old* sites. This can be confirmed with the Graph B of the same figure as it shows that the mean age of field voles is higher in the *old* and *control* sites. However, here again, the result of the ANOVA I was not significant with a p-value of 0.661 ($F_{(2,11)} = 0.43$).

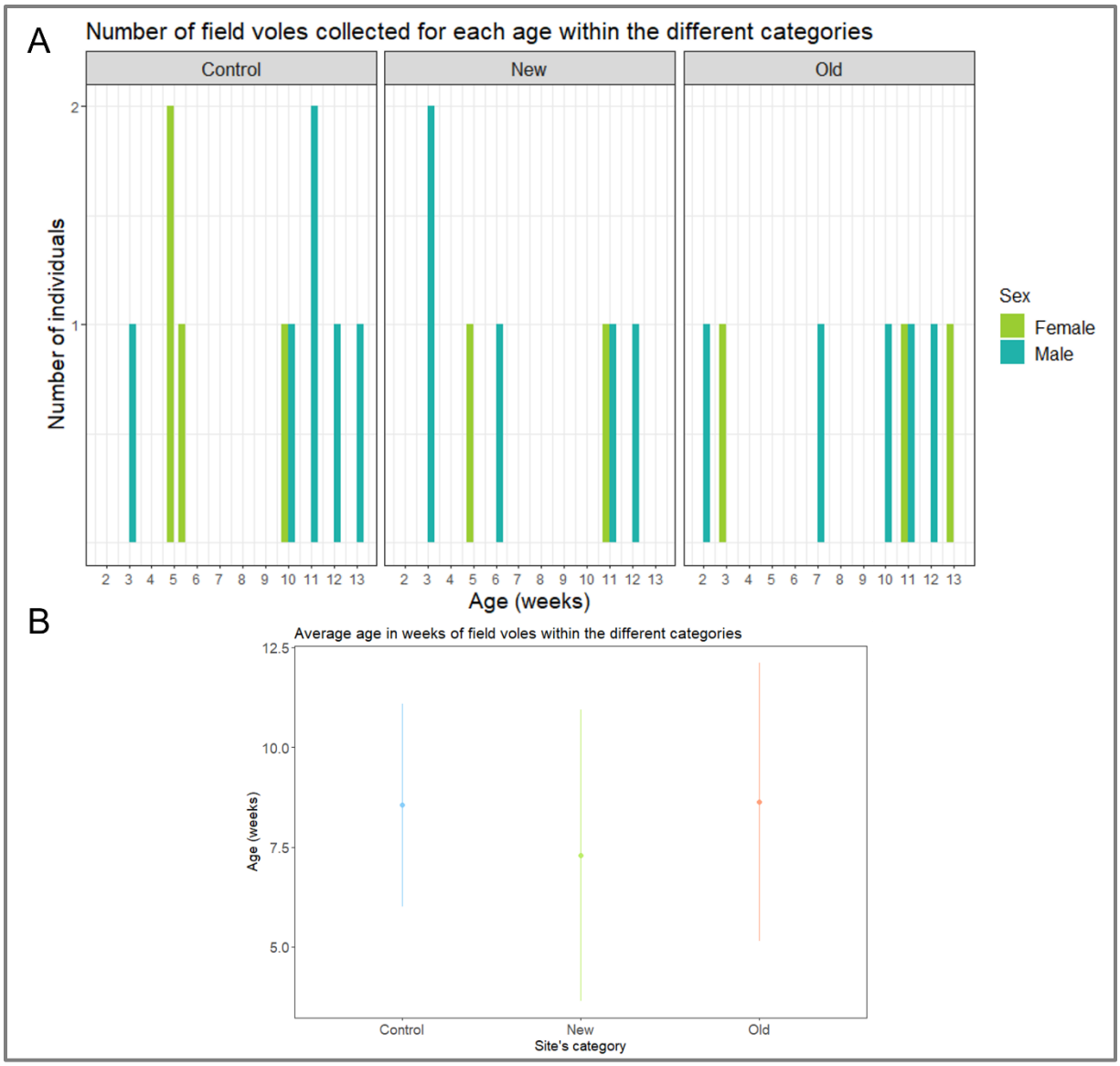


Figure 27: Age repartition and mean age of field voles within the different sites categories. A: Barplot of the number of field voles for each age collected within the different categories. **B**: Dotplot of the mean age (in weeks) of field voles in each category of site. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

Figure 28A illustrates the number of mature or immature field voles within the different categories depending on their sex, showing that more mature males were caught in all categories of sites compared to females. But no matter the sex, more mature individuals were found in each category. The figure 28B shows the average percentage of mature field voles found within the categories no matter their sex. However, the ANOVA I carried out on it did not show any significant result (p-value > 0.05 = 0.243, $F_{(2,11)} = 1.614$) but on the total of 25 individuals found during the study, only three of them were immature. Two of them were found in the *old* sites and one of them in the *new* site.

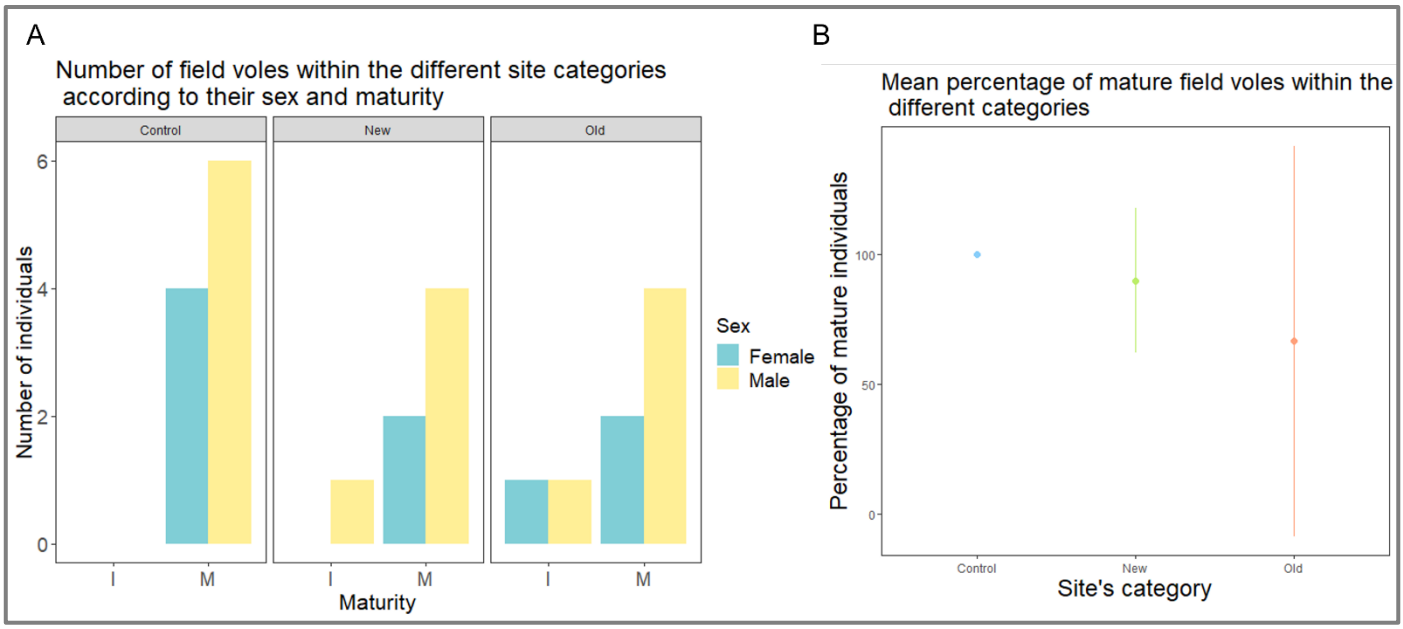


Figure 28: Maturity analysis of field voles within the site categories. A: Repartition of the mature and immature bank voles within the sites categories according to their sex. "I" is for immature individuals and "M" is for mature individuals. **B**: Dotplot of the mean percentage of mature field voles within the different categories. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

The figure 29 shows the amount of male and female field voles within the three different categories. In general, more males of the field vole species were found during the study and they were more abundant in each category. To statistically test the sex variable among the different categories, the percentage of females found in each site was calculated. On these data, an ANOVA I was carried on the percentage of females and the category of site. This ANOVA I did not show any significant result (p-value = 0.497 and $F_{(2,11)} = 0.745$) meaning that there is no difference in the percentage of females found within the different categories.

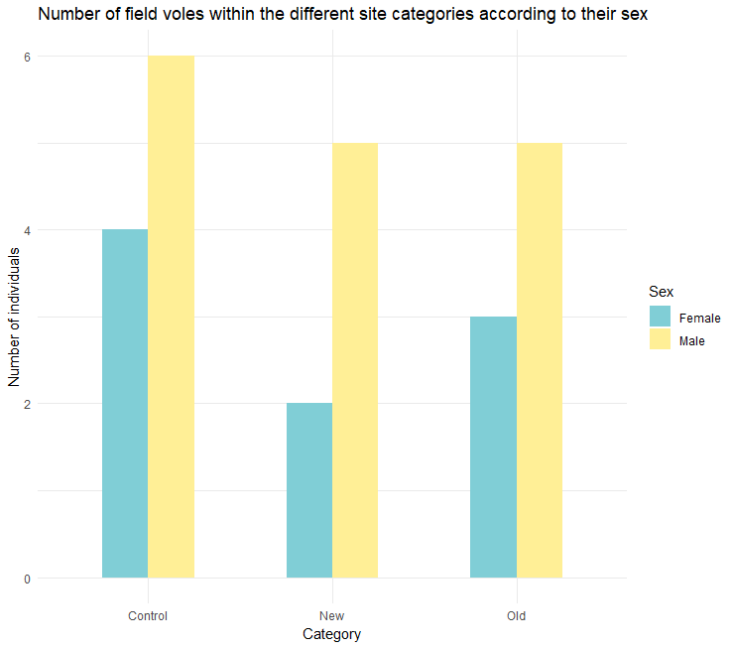


Figure 29: Number of females and males of field voles found in each category of site.

The results of this PCA are illustrated in Figure 30. The PCA on the field voles characteristics (BMI, age, maturity and sex) represents 84.9% of the variation being relatively high when summarizing 4 variables into two dimensions. The Figure 30A shows that the maturity and the BMI are highly correlated to each other. The two are quite correlated to the age but not to the sex of individuals. The Figures 30B and 30C show that the *old* sites tend to have more variance in the characterization of the field voles populations than the two other categories that overlap more. Indeed, two of the five *old* sites pull the orange ellipse showing that some of the *old* sites are characterized by more not mature individuals with a low BMI.

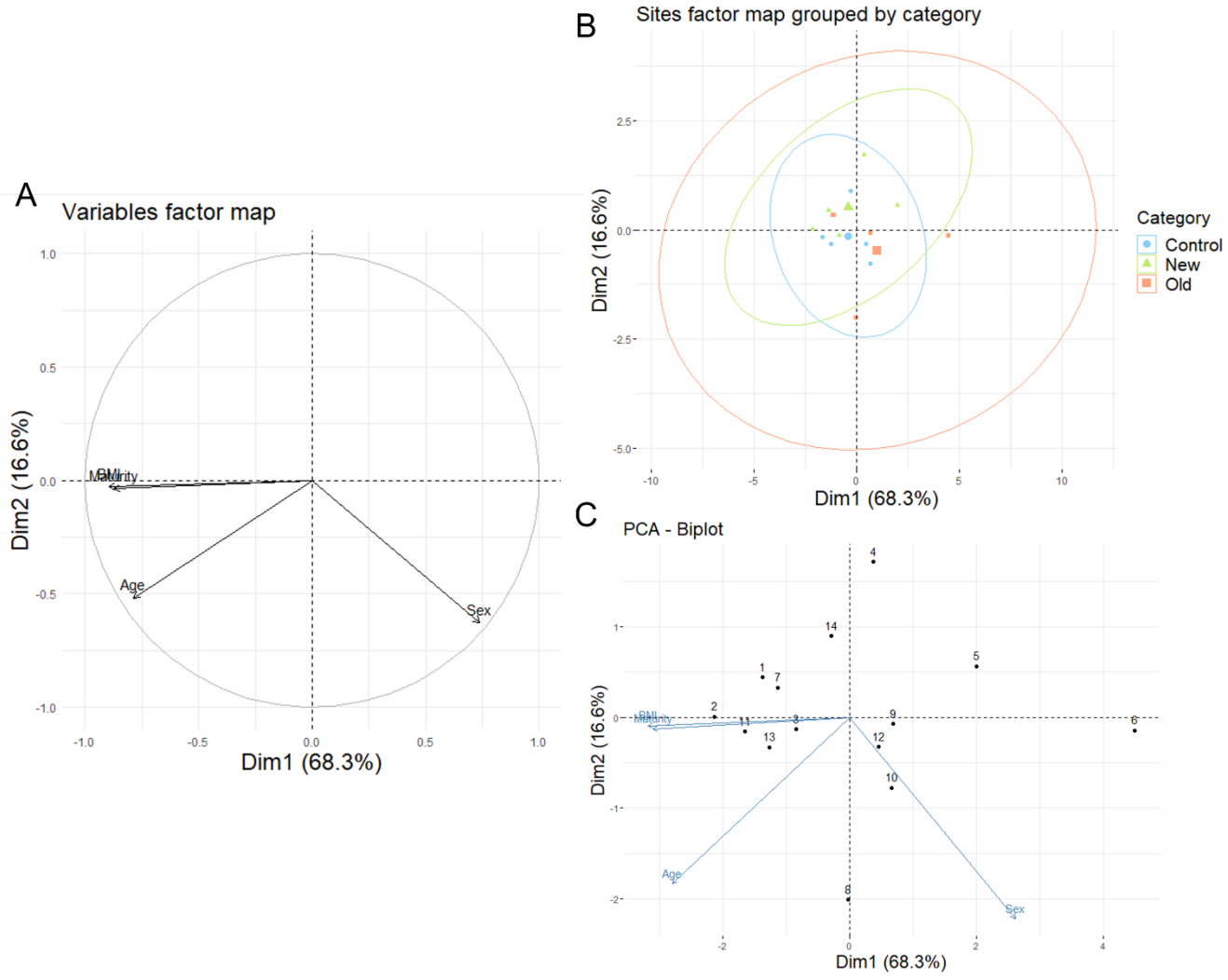


Figure 30: First two dimensions of the PCA on the sites and the field vole population variables (BMI, age, maturity and sex). A: Factor map of the variables. **B:** Factor map of the sites grouped by category. **C:** Biplot of the PCA. Points from 1 to 5 are for the sites from *New-1* to *New-5*. Points from 6 to 10 are for the sites from *Old-1* to *Old-5*. Points from 11 to 15 are for the sites from *Control-1* to *Control-5*. The first principal dimension represents 68.3%, while the second represents 16.6% of the variation from the data set. The bigger point inside each group represents the centroid of the fitted ellipse (95% confidence interval). The age represents the mean age of field voles found in each site. The BMI represents the mean Body Mass index of field voles found in each

site. The sex represents the percentage of females found in each site. The maturity represents the percentage of mature individuals found in each site.

2.3.2. Common shrews

The Figure 31 shows, this time, the BMI of the 41 individuals of common shrews found within the different sites from the three different categories, grouped by sex (A) as well as the average BMI of individuals in each site category, calculated on the basis of the average BMI of individuals in each site, all sex included (B). The ANOVA I done for this species shows a p-value of 0.215 ($F_{(2,11)}$ = 1.772) meaning there is no significant difference in the BMI of common shrews in the different categories. The graph B in Figure 31 shows a slightly higher mean BMI of common shrews in the *control sites* and in the *old* categories.

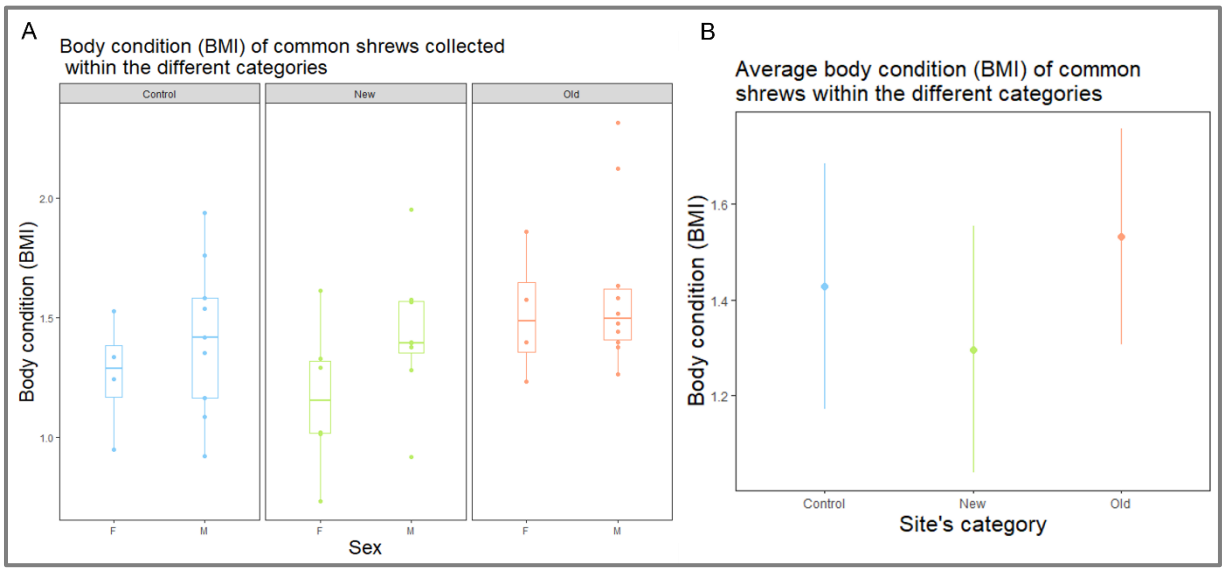


Figure 31: Body condition (Body Mass Index – BMI) of common shrews within the different sites categories. A: Boxplot of the BMI of each individual collected within the different categories, grouped by sex. The box represents the 25 and 75% quantiles. The horizontal bar represents the median and the vertical bars represent the variability of the data. B: Dotplot of the mean BMI of common shrews in each category of site. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

For common shrews, the same analyses for the age as for bank voles and field voles could not be carried out because in this case, the data on the age of common shrews is binary. Indeed, it was not possible to determine the exact age of individuals other than to assign them an adult or juvenile status based on their dentition. In this section, we can consider adult shrews as mature individuals and young ones as immature as there was no precise way to determine their maturity (cf. Material and methods section). To apply statistical tests on these data, the percentage of adult/mature individuals found per site has been calculated. An ANOVA I has then been applied on the percentage of adults in the categories. The result of this ANOVA I was not significant to the 5% threshold, with a P-value of 0.6 ($F_{(2,11)}$ = 0.535) meaning that there is no significant difference in the percentage of adult/mature individuals between the categories. Thus, Figure 32A shows the census of young and adult common shrews in the different categories, grouped by sex. The figure 32B shows the mean percentage of adult/mature individuals found in the different categories.

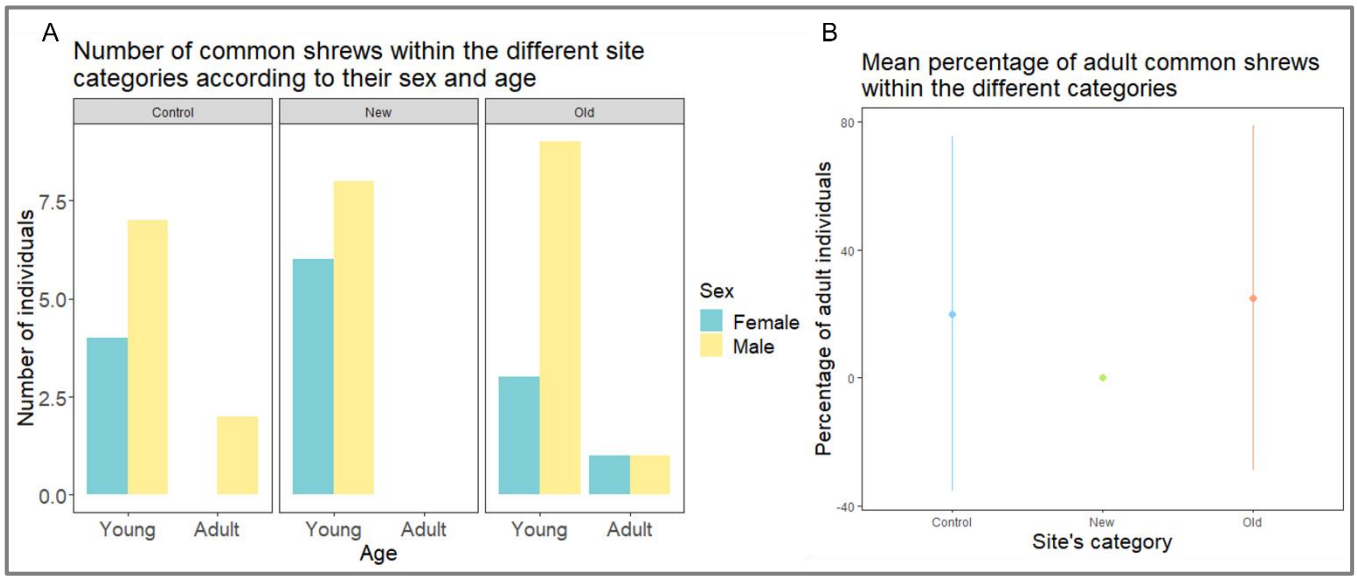


Figure 32: Maturity analysis of common shrews within the site categories. A: Repartition of the adult/mature and young/immature common shrews within the sites categories according to their sex. **B**: Dotplot of the mean percentage of adult/mature common shrews within the different categories. Dots represent the mean values of the and the vertical bars represent their 95% confidence intervals.

The figure 33 shows the amount of male and female common shrews within the three different categories. In general, more males of the common shrew species were found during the study, and they were more abundant in each category. In order to statistically test the sex variable among the different categories, the percentage of females found in each site was calculated. On these data, an ANOVA I was carried on the percentage of females and the category of site. This ANOVA I did not show any significant result (p-value = 0.916 and $F_{(2,11)}$ =

0.089) meaning that there is no difference in the percentage of females found within the different categories.

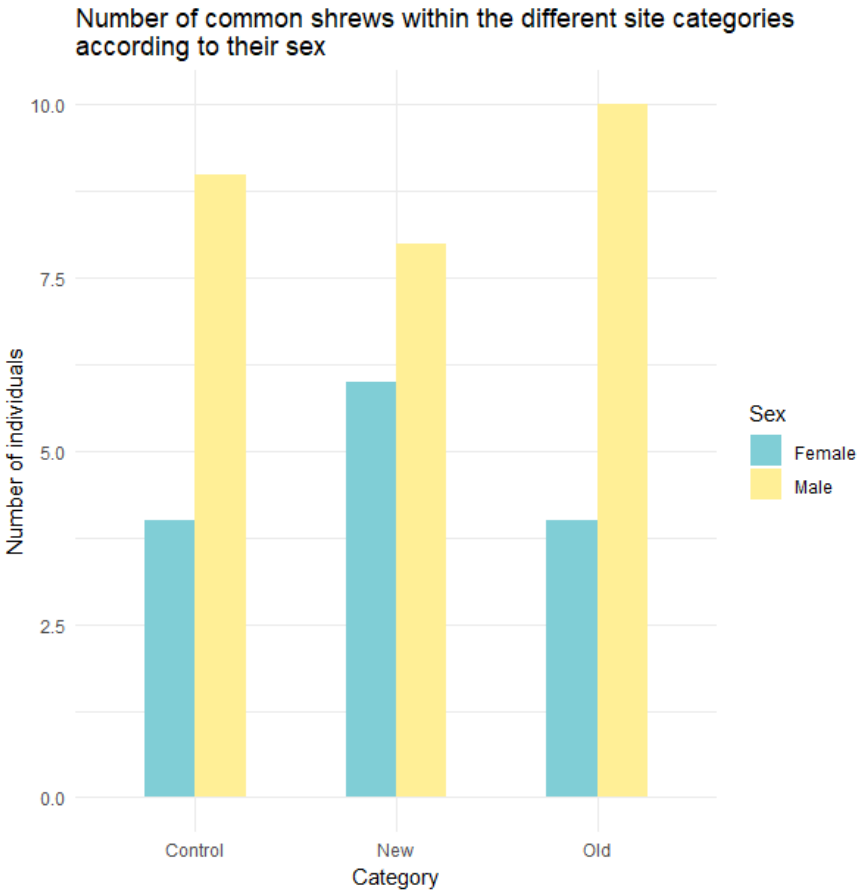


Figure 33: Number of females and males common shrews in the different category of sites.

The results of this PCA are illustrated in Figure 34. The PCA on the common shrews characteristics (BMI, age, maturity and sex) represented in Figure 36 represents 78.9% of the variation being relatively high when summarizing 4 variables into two dimensions. The Figure 34A shows that none of the variables is highly correlated to another one. The Figures 34B and 34C show that all the categories tend to have individuals characterized by different values of the variables as their centroids are around the origin and all the ellipses overlap quite well. However, the *control* sites can be slightly distinguished as they seem to depend more on the age, being either sites with a lot of young individuals or sites with a lot of adult ones(Figure 34B). As a reminder, in the case of common shrews, the age and the maturity represent the same thing. Therefore, only the age has been taken into account in the PCA.

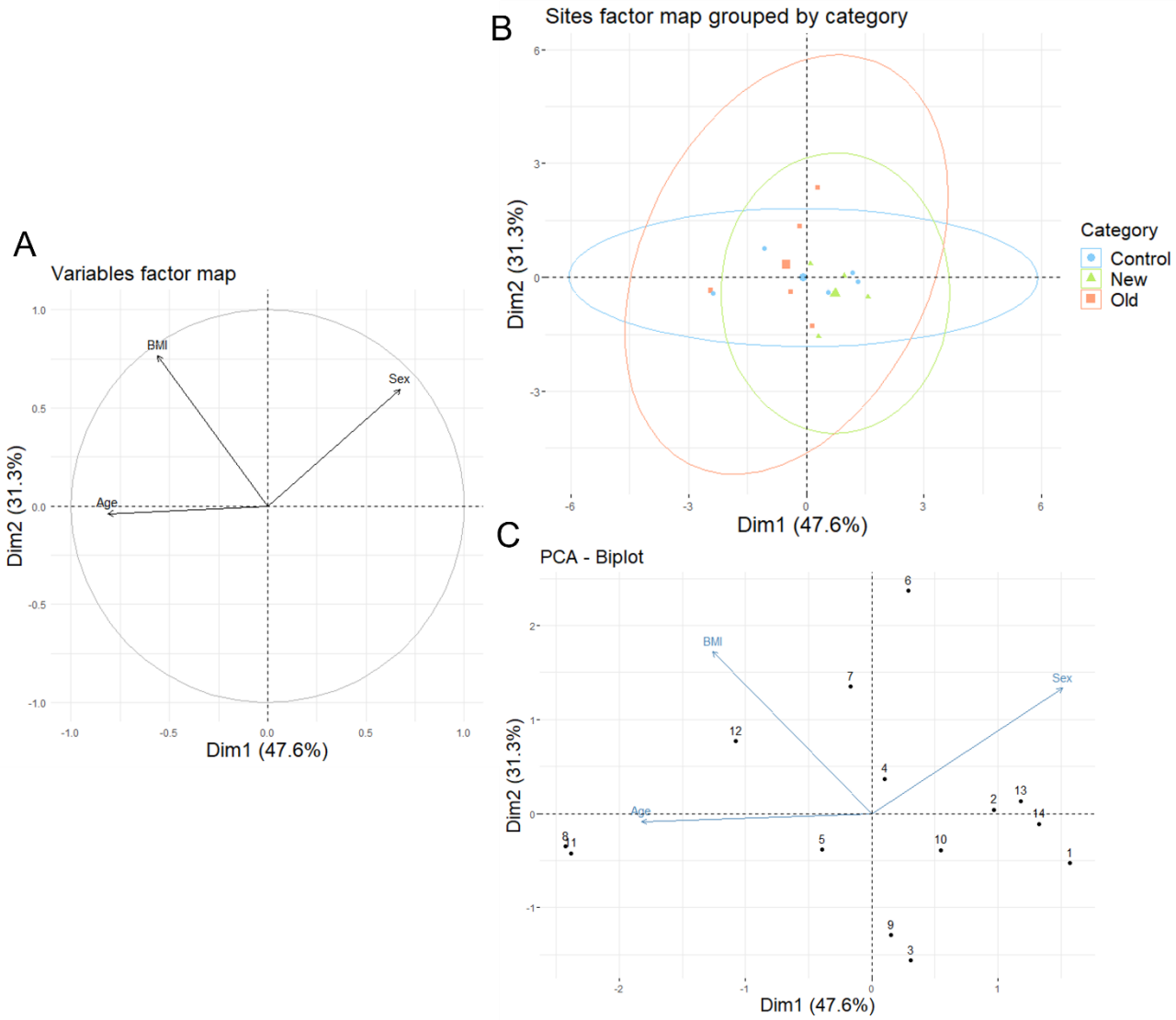


Figure 34: First two dimensions of the PCA on the sites and the common shrews population variables (BMI, age, maturity and sex). A: Factor map of the variables. **B:** Factor map of the sites grouped by category. **C:** Biplot of the PCA. Points from 1 to 5 are for the sites from *New-1* to *New-5*. Points from 6 to 10 are for the sites from *Old-1* to *Old-5*. Points from 11 to 15 are for the sites from *Control-1* to *Control-5*. The first principal dimension represents 47.6%, while the second represents 31.3% of the variation from the data set. The bigger point inside each group represents the centroid of the fitted ellipse (95% confidence interval). The BMI represents the mean Body Mass index of common shrews found in each site. The sex represents the percentage of females found in each site. The age represents the percentage of adult individuals found in each site.

3. Mammals found on camera traps

As explained before, unfortunately, some data from the camera traps were lost due to the breakdown of a hard drive. The saved observation collected are given in the Table 11 below. The given results show that more mammals were found in the beaver-impacted sites than in the non-impacted ones.

Table 11: Results of the mammals found on the camera trap's saved pictures.

Site number	Site name	Species	Date and time	Number of pictures
New-1	Nimeton	*Lepus europaeous* (European hare)	July 2022	1
New-2	Arabianniitty	*Alces alces* (Moose)	6.09.2022	1
New-2	Arabianniitty	*Alces alces* (Moose)	7.09.2022	1
New-2	Arabianniitty	*Vulpes vulpes* (Red fox)	31.10.2022	3
Old-4	Huhmari 1	*Alces alces* (Moose)	July 2022	2
Control-5	Tiponen	*Odocoileus virginianus* (White-tailed dear)	August 2022	3
Control-5	Tiponen	*Odocoileus virginianus* (White-tailed dear)	15.09.2022	3

Discussion

The aim of this study was to investigate the spatio-temporal succession of small mammals at different stages of the ecological succession within habitats previously modified by the presence of beavers. Small mammals are considered to be ecological indicators of the stability of an ecosystem (Yakimova and Gaidysh 2021) and will be among the first to react to a change in their habitat, since some species are highly specialist of some biotopes while others are more generalists. Although very few of the results were significant, several trends were observed and can therefore be carefully discussed.

1. Site characterization with deadwood and vegetation cover

The estimation of the percentage of vegetation cover reveals that the *control* sites have, on average, the highest abundance of conifers, followed by the *new* and then the *old* sites. Conifers are more likely to die from beaver flooding (Levan and Riha 1986) as they are very sensitive to water in their roots. This would explain why there is a decrease in the abundance of conifers in sites impacted by beavers. Where previously forested soils are likely to retain the mycorrhizae essential for most trees (Terwilliger and Pastor 1999), beaver meadows are an exception. Indeed, a study by Wide et al. (1950) showed that ectomycorrhizal fungi are killed due to the prolonged flooding and the anaerobic conditions this creates in addition to beaver activity (Wilde, Youngberg, and Hovind 1950). These ectomycorrhiza are necessary for the recolonization by the conifers, so the beaver meadows are devoid of them (Terwilliger and Pastor 1999). This would explain the evolution over time within the sites. The first conifers were killed by the flooding and those remaining in the *new* sites did not survive the beaver meadow soil, which lacked the ectomycorrhiza necessary for its survival. This would result in *old* sites with a lower abundance of conifers. Another interesting point is that in this same study by Wide et al. (1950), they studied small mammals as vectors for the development of mycorrhizae for the recolonisation of conifers. More specifically, the red-backed vole has the potential to disperse ectomycorrhizal fungal spores into the beaver meadows, but its habitat uses patterns restrict the expression of this potential. However, beavers will eat more deciduous trees (Salandre et al. 2017), which may lower the abundance of deciduous trees on sites during their occupation but they will preferentially eat small diameter trees (< 10 cm), which does not drastically affect the number of deciduous trees present (Hyvönen and Nummi 2008). The empty space left after the flooding creates a great long-term opportunity for

deciduous trees to grow where, previously, the conifers were more abundant (Hyvönen and Nummi 2008). That could then explain why we found more deciduous trees on the *old* sites compared to the *new* sites or *control* sites. All the *old* sites used for the present study had their last occurrence of flooding between six and nine years ago (Appendix 5). To have a better understanding of the recolonization patterns of woody vegetation following beaver occupation, it would be interesting to study sites where the last flooding took place 10 years or more ago.

As expected, the average amount of deadwood pieces on sites is higher in the *new* sites, freshly left by the beavers, followed by the *old* sites as they are the debris from the dead, cut down, and eaten trees by beavers during their occupation. Woody debris is an important structural element of the forest ecosystem and can influence the fauna living there, including small mammals (Bowman et al. 2000; Loeb 1999; Fauteux et al. 2012). They use them for shelter, nesting, travel routes, and foraging. Therefore, it can be expected that the presence of these woody debris influences small mammal populations. Indeed, several studies have shown the relationship between the amount of woody debris found on sites and the abundance of mammals sampled (Bowman et al. 2000; Loeb 1999; Fauteux et al. 2012). These studies were carried out at sites where the woody debris came from forest clearcuts and not from the presence of beavers. In the present study, a simple count of the number of woody debris in two 18.84 meters perimeter zones was carried out at each site. Simple linear models were run to analyze the relationship between the number of woody debris and the abundance of bank voles, field voles, and common shrews found within the sites, being the three species with the largest sample size. However, none of these were significant. It might have been interesting to further analyze the impact of woody debris left by beavers on small mammals. However, a more precise and assiduous method of collecting dead wood would have been necessary, as with the data collected there was no significant difference in the quantity of deadwood found in the different sites categories, impacted or not by beavers. In general, it is important to note that this study had only five replicates of each category of sites, which is not statistically optimal. In addition, even if field voles and common shrews were among the biggest samplings, 25 and 42 individuals are not ideal either to obtain strong statistical results.

The study by Mazurkiewicz et al. (1994) has shown that the abundance of small mammals was not correlated with the species richness of trees, grass or plants but they suggested that the

cover density might influence their abundance. Moreover, the study by (Wikar, Ciechanowski, and Zwolicki 2023) showed the interconnexion of the herbaceous layer with the presence of the dam. As the small mammals were more abundant around the dam, it suggested the importance of this layer for their presence. We expected a relationship between the herbaceous and shrub layers and the presence of small mammals. Unfortunately, our results did not show any significant relationship between these two. Here again, more replicates would have been necessary to show stronger results.

2. Similitudes between vegetation diversity and small mammals' diversity within the beaver-modified sites.

Firstly, indices of vegetation diversity were calculated on each site to characterise the habitat. Sites that have been occupied by beavers less than five years ago (*new* sites) show a species richness, a Shannon Index, and an Evenness slightly higher than in the other site categories. The meadow left behind when beavers leave creates a wide-open space where a high diversity of plant species has the opportunity to develop, starting an ecological succession. On the other side, the *control* sites –the sites that have never been impacted by beavers– showed a higher overall abundance of the different vegetation species than the two other categories, meaning that a higher number of species had their highest abundance in the *control* sites. In this case, the *control* sites were mostly inhabited by several berry species in high abundance. These trends can illustrate the fact that non-disrupted habitats can be described as more stable habitats where sites modified by beaver allow the implementation of different plant species. Previous studies have shown that the overall vegetation diversity increases at the landscape scale due to the beaver impact (Wright, Jones, and Flecker 2002).

Comparing the results of the factorial correspondence analysis of the plant species distribution within the 15 sites (Figures 13 and 14) with the results of the one on the mammal species distribution (Figures 19 and 20) reveals an interesting trend. Indeed, in both cases, *new* sites show a higher variability within them and are slightly different from *control* and *old* sites. What should attract attention here is that in both plant distribution and mammals' distribution, it is the site *New-4* that pulls the ellipse. Firstly, because it is where four different species of plants were exclusively found (*Epilobium palustre, Galium palustre, Scutellaria galericulata* and, *Epilobium parviflorum*), and, more generally, the *new* sites had a higher

number of plant species only found once. *Epilobium palustre*, *Scutellaria galericulata* and *Galium palustre* are plants typically found in habitats such as marshes, swamps, and damp meadows (Kytövuori 1969). *Epilobium palustre* has a role in soil drainage and both herbaceous plants can serve as resources for many species such as insects or small mammals. Finally, *Epilobium parviflorum* is a typical plant of the early stages of ecological successions and although it is best found on dry soils, it can also be found on wet soils such as meadows. Secondly because the *New-4* is the only site where the pygmy shrew (*Sorex minutus*) has been found. In addition to this, the site *New-2* showed the highest abundance in common shrews (*Sorex Araneus*) and more generally, the *new* sites are the sites where all the small mammal species were found. In addition to that, several bigger mammal species were observed with the camera traps in the *New-2* site. Indeed, mooses (*Alces alces*) have been observed twice and a red fox (*Vulpes vulpes*) as well. In addition to that, other bigger mammals were found in sites impacted by beaver, such as the European hare in the *New-1* or more mooses in the *Old-4*. The study of Svanholm Pejstrup et al. (2023) shows that deer can be either positively impacted by the presence of beaver as they promote the presence of deciduous trees or negatively impacted as they can then be in competition for the resources. In that study it seems that deers were more negatively impacted by the presence of beavers (Svanholm Pejstrup, Andersen, and Mayer 2023). The fact that beavers abandon sites after a while provides them with an empty space for different large mammals such as deers to benefit from the higher abundance in deciduous trees without any competition with beavers. In general, based on our results, it would seem that, thanks to the space created by the disappearance of the flooding due to beaver occupation, the sites impacted by beavers and more specially the sites in early stages of succession, offer an open space giving the opportunity to a great diversity of plant and animal species to settle there.

3. Characterization of small mammal populations

The same indices of diversity were calculated for the mammal species. In opposition with our expectations, these showed that the abundance, Shannon Index, Evenness and Species richness are all higher in the *control* sites, even though the statistical tests have not shown any significance in these differences between categories. The fact that the indices were slightly higher in the *control* sites can be, again, explained by the fact that non disturbed habitats are described as more stable habitats (Yakimova and Gaidysh 2021). However, it is

important to note that it is in the *new* sites (recently impacted by beavers) that two of the three most abundant species were found in higher abundance as well as all the species of the study were found. As the overall biodiversity indices, including all species, did not show any clear difference, it seemed important to analyse more in detail the population composition of the different species within the sites. Although statistical tests showed no significant difference between the abundance of the different species (bank voles, field voles and common shrews) in the different stages of ecological succession (*new*, *old* or *control*), some trends can still be observed and discussed. Bank voles were the most common species found in this study, all site categories combined, and they were found in greater numbers in the *new* sites category. Bank voles are a species mainly associated with forest habitats but are very generalist and can therefore be found in a multitude of habitats (Sundell, Liao, and Nummi 2021). In the context of a study of conifer recolonization by small mammals of sites impacted by beaver (Terwilliger and Pastor 1999) showed that bank voles were found to be more abundant in or near forest habitats compared to beaver meadows. However, if their main competitor, the field vole, is not present in the grassy open areas, the bank voles can quite easily take their place and be found within these habitats (Sundell, Liao, and Nummi 2021), which could explain their presence in beaver meadows.

Indeed, in this study, very few field voles were collected (0.69 individuals trapped per 100 trap-nights), which was surprising as we expected to find them in large numbers in habitats impacted by beavers as these are similar to their preferred habitats, i.e. open spaces with a majority of grasses and graminoid plants as their food regime relies on these (S. Churchfield, Hollier, and Brown 1997). Field voles are not the most common species in the area of Evo as it is a mainly forested habitat, which could then explain our small sample. But, surprisingly, Sundell et al. (2021) found the field voles as the second most collected species during their study but just as in the present study, they did not find any significance in the abundance of field voles within the beaver-impacted or non-impacted sites. On the other hand, the study by S. Churchfield, Hollier, and Brown (1997) investigated small mammal populations in an ecological successional framework, but in this case in the context of forest clear-cuts instead of beaver-modified habitats as in this study. However, the different stages of succession remained similar. They found no significant difference in the abundance of field voles at different sites in the different stages of ecological succession, confirming our result.

It is interesting to note that although intrinsic preferences in terms of habitat may be considered fixed, the reality on the ground is not always so. The habitat preference of species will depend on the abiotic and biotic conditions present. So, for example, if a stronger competitor is found in greater density (such as the bank vole) it may push other species towards marginal habitats (Sundell, Church, and Ovaskainen 2012). Even though not statistically significant, we found more field voles in the *control* sites than in the beaver meadows (ten individuals in *control* sites and seven in the *new* sites) but the difference is not strong enough to conclude with our sample size.

Common shrews were slightly more prevalent in both *new* and *old* sites than in *control* sites, although this difference was very slight and not significant. The study of Sundell et al. (2021) confirms this trend as they also found a higher number of common shrews in beaver-modified habitat, but the results of Churchfield et al. (1997) confirms our non-significant difference in the statistical numbers since they did not find either a significant difference in site preference by common shrews between clear-cut grass and graminoid habitats and forested habitats. These kinds of results have also been confirmed by Sundell et al. (2012), where they did not find any difference in habitat use at any density, common shrews being true generalists. However, it would have been expected that they would be more abundant in early successional habitats (*new* sites) since they are insectivorous mammals and could therefore take advantage of the insects attracted by the moisture in beaver-modified habitats (Sundell, Liao, and Nummi 2021). Finally, a few studies were done on the small mammal populations in beaver ponds while they were occupying them (Ulevičius and Janulaitis 2007; Samas and Ulevičius 2015). These studies showed that bank voles and common shrews were significantly more present in beaver sites as they benefited from the beaver lodges (Wikar, Ciechanowski, and Zwolicki 2023).

The only pygmy shrew found in this study was found in a site recently vacated by beavers and thus in an early stage of ecological succession. This habitat is therefore open and mainly composed of herbaceous and graminoid plants. It has been shown that pygmy shrews are generally more likely to be found in grassy than wooded habitats (O'Keeffe and Fairley 1981; Ellenbroek 1980), which may provide an answer as to why the individual was found at this site. However, the collection of a single individual is largely insufficient to conclude anything about the habitat preferences of pygmy shrews at beaver impacted sites. However,

it is notable that pygmy shrews and common shrews are often in sympatry, and each occupy a specific ecological niche (Ellenbroek 1980; Saarikko 1989) and that generally, common shrews use underground galleries while pygmy shrews remain on the ground surface, feeding on smaller insects (Saarikko 1989).

Water voles and water shrews were collected very infrequently (3 water voles, meaning 0.083 individual per 100 trap-nights and 14 water shrews, meaning 0.389 individuals per 100 trap-nights). Water shrews were found in equal numbers within the *old* sites, in a more advanced successional stage and in the *control* sites compared to the *new* sites. Unfortunately, the sampling of this species was too low to be able to give a conclusion on the habitat preference of these species and a greater sampling effort, over a longer period, would be necessary. The same applies to water voles.

The choice of using snap-traps was discussed in order to find the best balance between the effectiveness of the study and its ethics. Indeed, the use of snap-traps was questioned as they are lethal to individuals and the ethical question of what is the coherence of killing animals in the framework of research for ecology and conservation was asked. However, there were only two people to carry out all the fieldwork for two and a half months, whereas the use of live-traps is much more time consuming as they have to be checked twice a day, at sunrise and sunset. Furthermore, when using live-traps, individuals have to be identified and analysed directly in the field, which adds considerable effort. Furthermore, this would not have allowed the collection of data on the age, sex or maturity of the individuals as these could be collected during dissection. Also, the Lammi Biological Station conducts different studies in parallel and a large research group on voles used, as it has done every year for many years, a large majority of the available live-traps, thus leaving not enough for the present study. Finally, the use of snap-traps allowed us to remove the disadvantages associated with the use of live-traps. Indeed, by using snap traps instead, the captured individuals are effectively removed from the population, reducing the chances of recapturing them in subsequent trapping efforts or to get individuals getting used and benefitting from the trap. This allows for a more accurate quantification of the population size and structure, as each captured individual is assumed to represent a unique entity. However, several studies have contrary findings on which trapping method gives the best results in term of quantity of caught animals (Lee 1997; Wikar, Ciechanowski, and Zwolicki 2023). In any case, it has been discussed that there is not an only

good way to trap mammals that are effective for all species (Sundell, Liao, and Nummi 2021). Indeed, the effectiveness of traps depends on the species of interest, the habitat where they are collected and even the seasons (Lee 1997; Williams and Braun 1983). Live-traps and snap-traps are known to better trap small rodents such as bank voles and field voles, while pit-falls are more likely to trap shrews (Wikar, Ciechanowski, and Zwolicki 2023). In the case of this study, the use of snap-traps seemed to be the best decision regarding the different factors we had as snap-traps are from a good use for estimating population density, abundance, or species composition. However, a perspective for the next studies is to use all the three types of traps to avoid any bias due to variation in the relative efficiency of certain traps on specific species. Moreover, live-traps are interesting for studying population dynamics and small mammals behaviour, which could be a good perspective for a longer version of this study in order to have a wider understanding of small mammal spatio-temporal dynamics in successional stages of beaver-modified habitats.

4. Characterization of the individuals within the different populations categories

Although there was no significant difference in the abundance of bank voles, field voles and common shrews in the different stages of ecological succession, it seemed important to study the characteristics of the individuals present on the sites, based on their BMI, age and maturity. Just as we expected to observe greater abundance and greater species richness in sites impacted by beavers, we also expected these same sites to be occupied by individuals in better physical condition (higher Body Mass Index, BMI) and of a more mature age. None of the statistical tests carried out on the average BMI, age or maturity of the different species within the site categories were significant, although different slight trends can be discussed depending on the species.

Surprisingly, bank voles have been observed to tend to have a lower BMI in sites at later stages of succession (*old* sites). In this same category, they tended to be older but not mature individuals, revealing an interesting point as it is usually expected there is a correlation between the age and the maturity of individuals. The fact that individuals tend to be in poorer physical conditions and tend to not be mature in the sites of a later successional stage could indicate an unsuitable habitat for the species. This trend was confirmed by the PCA carried

out. However, having only five site replicates for each category does not allow to have strong and significant statistical results. The fact that the bank voles tend to be in better physical conditions in *new* and *control* categories and that more mature individuals were found in these could be explained by the fact that, on the one hand, the *control* sites correspond to the bank voles preferred forest sites, which provide them with a large number of berry bushes and shelters. And, on the other hand, the *new* sites provide them with a diversity of seeds and grasses that are also of interest to their diet (Wikar, Ciechanowski, and Zwolicki 2023).

As well as for bank voles, field voles tended to have a lower BMI in the late successional stages (*old* sites). The individuals found in these sites were older and most of them were immatures. However, the mean BMI was the highest in the *new* sites even though the difference was not significant. This trend could be explained by the fact that this type of habitat, containing mainly graminoid species, provides them with food and resources suited to their ecological needs. There were no significant differences in the average age of field voles within the different categories. Only three immature individuals were collected out of the 25 field voles. However, it would appear that more males were harvested among the mature individuals, but the sample size was too small to test this statistically. However, one explanation for this could be that, as the study period was a breeding period, females take fewer risks going out and concentrate on caring for their offspring while males tend to be more active and bolder and therefore more frequently sampled than females (Sundell, Church, and Ovaskainen 2012).

A different trend can be observed among common shrews. In fact, the average BMI tended to be higher in the *old* sites, showing that common shrews are in better physical condition within *old* sites. A hypothetical explanation for this could be that the abundance or diversity of invertebrates might be higher in the later stages of succession after the beaver modification of the habitat. Even though it is known that the modification of the habitat by beavers switches the species richness of invertebrates (Nummi and Holopainen 2014; McDowell and Naiman 1986), we do not know studies that looked for differences of these in the context of ecological succession following beavers. Unfortunately, the data collected on the age and maturity of the common shrews do not allow us to draw any conclusions, which is probably due to limitations during dissection. Assessing the age (young/adult) of individuals by the appearance of their teeth is too subjective and only provides crude estimates.

5. Conclusion and perspectives

Our first expectation was confirmed through this study. Indeed, the different stages of succession showed trendy differences (although not significant) between them. Sites impacted by beavers exhibited the expected shift from coniferous to deciduous trees, as well as an abundance of dead wood. Factorial component analyses indicated a slight differentiation between new sites (early succession), which displayed greater species variety compared to *old* sites and *control* sites. *New* sites contained numerous species that appeared only once during the study, supporting previous research on the vegetation changes caused by beavers and the subsequent increase in species richness in the early stages of succession.

Secondly, contrary to expectations, the present study did not demonstrate a clear spatial and temporal change in small mammal populations throughout the succession stages following beaver occupation. In addition, the different species were not found in significantly different abundances within the categories. However, some noteworthy trends emerged from the study, although not statistically significant. Specifically, the *old* sites were found to be less optimal habitats for bank voles and field voles, as indicated by diversity indexes and separate species abundances. Analysis of individual characteristics further revealed that bank voles and field voles in these sites had lower body mass indices (BMI) and were less mature. In contrast, *new* sites displayed greater stability in individual variables, indicating similar conditions or statuses among the individuals. These trends align with other studies demonstrating a decrease in small mammal abundance over time during succession. Additionally, *control* sites exhibited greater stability and slightly higher species abundance, particularly for water voles, water shrews, and field voles, which were among the most frequently encountered species in the study. Conversely, recently vacated sites showed slightly higher abundance of other species, including bank voles, common shrews, and pygmy shrews. Notably, the only pygmy shrew was found in *new* sites, suggesting these locations had the highest species richness. Although the study anticipated finding species specialized in each habitat type (meadow specialists in new sites, shrubland specialists in old sites, and forest specialists in control sites), the collected species were either generalists (such as bank voles and common shrews) found across all sites with no significant difference or specialized species were too scarce for statistical testing. It was surprising that field voles, which typically inhabit graminoid and open

habitats, were not found in greater abundance in beaver-modified sites. However, the ones found in the early successional stages were in average in better physical conditions (BMI).

In conclusion, the patterns of use by small mammals of sites at different stages of ecological succession after the passage of beavers could not be clearly defined in this study, given the very few significant results, even though some trends have been suggested. These few significant results can partly be explained by a limited statistical power due to the relatively small number of replicates (five sites in each category). However, this study is in addition to the study of the general impact of beavers on their environment, and more specifically on small mammals. Few studies of the response of small mammal populations at sites impacted by beavers have produced significant results. However, the study by (Wikar, Ciechanowski, and Zwolicki 2023) provides significant results suggesting the importance of continuing to study small mammal populations under beaver impact. In addition, numerous studies have shown that the presence of beavers increases the abundance of small mammals (Medin 1991; McCaffery and Eby 2016; Frey and Malaney 2009). In the same idea, certain studies have shown that after events such as landslides, fires or clear-cuts, the abundance of small mammals increased in the early stages of succession but tended to decrease with the successional time (Wikar, Ciechanowski, and Zwolicki 2023; Michał and Rafał 2014; Powell and Brooks 1981), suggesting that the same observation could be seen in the beaver-modified habitats.

In order to be able to study more accurately the spatio-temporal evolution of small mammal populations through the ecological succession linked to the presence of the beaver, it would be very interesting to study sites following a complete succession and therefore to have 4 categories. Meaning, firstly, sites that have not initially been impacted by beavers. Secondly, sites occupied by beavers. Thirdly, sites that are in the early stages of ecological succession (less than five years since the beavers left) and finally, sites that are in a more advanced stage of succession (more than five years since the beavers left). Obviously, it is complex to predict the arrival of beavers, but in a park like Evo, where they have been studied for many years, it might be possible to attempt this kind of study over several years. With the same idea in mind, different types of traps would be used to obtain the most accurate results possible as discussed before. In addition, it is well known that the population densities of small mammals fluctuate over the year which might impact their distribution across different types

of habitats (Sundell, Church, and Ovaskainen 2012). Having a study over several years could help understanding better the occupation of beaver-modified sites by small mammals according to their population fluctuations.

Most of the studies published to date have focused on the impact of habitat modified by beavers on bank voles, field voles and common shrews being the species most commonly found in the hemi boreal environment. However, it might be worthwhile taking the studies further and increasing the sampling effort (using optimal traps) in order to collect more data on species such as water voles, water shrews and pygmy shrews and be able to test them statistically. Finally, despite the loss of data from the camera traps, those that were saved suggest that larger mammals make greater use of sites impacted by beavers. The same type of study could therefore be carried out in Evo Park on the impact of beavers on populations of larger mammals in addition to the one by Nummi et al. (2019) and as has already been done in other countries (Johnston 2017; Nummi et al. 2019), adding the perspective of ecological succession. In addition, the presence of larger mammals may be a factor influencing small mammal populations due to predation.

Small mammals are an integral part of the ecosystem and are important for a variety of reasons, such as soil processes. They are also indicators of ecosystem stability. The presence of beavers has already been shown to provide refuge for various endangered species (Wikar, Ciechanowski, and Zwolicki 2023). They can also be a refuge for various species of small mammals dependent on the habitats created by beavers, such as the jumping mouse (*Zapus hudsonicus luteus*), the northern birch mouse (*Sicista betulina*), the water shrew (*Neomys anomalus*), the harvest mouse (*Micromys minutus*) or the water vole (*Arvicola amphibious*) found in open meadows with dense herbaceous vegetation. In addition, the presence of small mammals, as explained above, could be a good vector for the recolonisation of conifers as part of succession (Terwilliger and Pastor 1999).

Overall, by modifying its environment, the beaver will create heterogeneity within the ecosystem and facilitate the development of a large number of plant and animal species. In the case of small mammals, habitat heterogeneity can provide a range of different ecological niches for generalist and specialist species to meet their different ecological needs. Even though this study does not show any significant results but only some trends at the patch scale, habitat modification by beavers certainly provides connectivity between the different

habitats in the landscape, enabling the facilitation of different species, including small mammals. Moreover, we can state that the beaver may not increase the alpha diversity (diversity focusing on the composition and the relative abundance of species in specific habitats) but has undoubtedly an impact on the gamma diversity (Wikar, Ciechanowski, and Zwolicki 2023). The gamma diversity describing a general state on the total number of species present within multiple habitats.

This study adds to the various studies carried out on the impact of beavers on different living organisms, reinforcing the proof of the importance of beavers within the ecosystem through their role as ecological engineers and facilitators. It also reinforces the importance of taking into account the conservation of this key species within hemi-boreal ecosystems in order to preserve the wetlands heavily impacted by humans on which many species depend and benefit as well as humans.

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Appendixes

Appendix 1: Dates of the last occupation of beavers on sites. Source from P. Nummi and J. Sundell follow-up.

Site number	Site name	Year of last occupation
New-1	Nimetön	2018 (4 years ago)
New-2	Arabianniitty	2018 (4 years ago)
New-3	Vuoripeikonjärvi	2018 (4 years ago)
New-4	Huhmari 2	2020 (2 years ago)
New-5	Tekumi	2021 (1 year ago)
Old-1	Kärppijärvi	2013 (9 years ago)
Old-2	Häntjärvi	2013 (9 years ago)
Old-3	Vähäkeltajärvi	2016 (6 years ago)
Old-4	Huhmari 1	2014 (8 years ago)
Old-5	Viljaskorpi	2015 (7 years ago)

Appendix 2: Vegetation census within the different sites. The values represent the mean percentage cover of the species within one quadrat of 50cmx50cm.

Species	*New-1*	*New-2*	*New-3*	*New-4*	*New-5*
Moss	37,5	60,8333333	65,8333333	6,33333333	85
Grass	14	20	0	2,83333333	0,5
Carex sp.	0	1,66666667	1,66666667	10	11,66666667
Calla palustris	16,66666667	0	2,5	0	0
Lysimachia thyrsiflora	10	0,5	0	15,833333	0
Rhodondendron tomentosum	1,66666667	0	0	0	11,66666667
Vaccinium oxycoccos	0,5	0	5,5	0	1,83333333
Dryopteris sp.	1,66666667	1	0,83333333	2,5	0
Betula pubenscens	0	31,66666667	4,66666667	1,66666667	0
Rubus sp.	0	0,5	0	0	0
Phragmites australis	0	0,83333333	0	0	0

Comarum palustre	0	2,5	0,5	0	0
Salix sp.	0	3,33333333	0	0	0
Chamaenerion augustifolium	0	0,5	0	0	0
Picea abies	0	0	8,33333333	0,5	0
Vaccinium uliginosum	0	0	5,83333333	0	12,5
Enpetrium negrium	0	0	5,83333333	0	8,33333333
Andromeda polifolia	0	0	2,16666667	0	3,83333333
Rubus chamaemonus	0	0	1,66666667	0	3,83333333
Vaccinium myrtillus	0	0	10	0	8,33333333
Vaccinium vitis-idaea	0	0	2,16666667	0,5	8,33333333
Convallaria majalis	0	0	0,5	0	0
Oxalis acetoselia	0	0	4,16666667	0	0
Maianthemum bifolium	0	0	0,5	0	0
Equisetum sylvaticum	0	0	0	8,33333333	0
Epilobium parviflorum	0	0	0	0,5	0
Scutellaria galericulata	0	0	0	1,66666667	0
Galium palustre	0	0	0	0,5	0
Epilobium palustre	0	0	0	1	0
Malampyrum pratense	0	0	0	0,5	0
Drosera rotundifolia	0	0	0	0	0,5
Calluna vulgaris	0	0	0	0	8,33333333
Lysimachia vulgaris	0	0	0	0	0
Helianthus divaricatus	0	0	0	0	0
Sorbus aucuparia	0	0	0	0	0
Talinum paniculatum	0	0	0	0	0
Taraxacum officale	0	0	0	0	0
Pinus sylvestris	0	0	0	0	0
Plantago subulata	0	0	0	0	0
Lysimachia europaea	0	0	0	0	0
Linnaea borealis	0	0	0	0	0

Species	***Old-1***	***Old-2***	***Old-3***	***Old-4***	***Old-5***
Moss	94,1666667	55,8333333	38,3333333	32,5	37,5
Grass	0	1,33333333	12,1666667	13,3333333	22,5

Carex sp.	35	4,66666667	38,8333333	0	0
Calla palustris	0	0	3,83333333	0	0
Lysimachia thyrsiflora	0	0	1,33333333	5,83333333	0
Rhodondendron tomentosum	0,83333333	0	0	0	0
Vaccinium oxycoccos	0,83333333	0	0	0	0
Dryopteris sp.	0	0	0	0,83333333	0
Betula pubenscens	0	0	0	0	0,5
Rubus sp.	0	0	0	2,5	0
Phragmites australis	0	1,33333333	2,5	0	0
Comarum palustre	0	1,66666667	0	0	15,8333333
Salix sp.	0	4,16666667	0	0	0
Chamaenerion augustifolium	0	0	0	0	5
Picea abies	0	0,5	0,5	3,33333333	0
Vaccinium uliginosum	0	0	0	0	0
Enpetrium negrium	0	0	0	0	0
Andromeda polifolia	0	0	0	0	0
Rubus chamaemonus	1,16666667	0	0	0	0
Vaccinium myrtillus	6,66666667	13,6666667	5	0	5,83333333
Vaccinium vitis-idaea	3,83333333	12,5	4,16666667	0	18,3333333
Convallaria majalis	0	0	0	0	0
Oxalis acetoselia	0	0	0	0	0
Maianthemum bifolium	0	0	0	0	0,83333333
Equisetum sylvaticum	0	0	5,83333333	0	0
Epilobium parviflorum	0	0	0	0	0
Scutellaria galericulata	0	0	0	0	0
Galium palustre	0	0	0	0	0
Epilobium palustre	0	0	0	0	0
Malampyrum pratense	0	0	0,5	0	0
Drosera rotundifolia	0	0	0	0	0
Calluna vulgaris	0	0	0	0	3,33333333
Lysimachia vulgaris	0	0,83333333	0	0	0
Helianthus divaricatus	0	1,66666667	0	0	0
Sorbus aucuparia	0	2,5	0	0	0
Talinum paniculatum	0	0	3,33333333	0	0
Taraxacum officale	0	0	0	0	0
Pinus sylvestris	0	0	0	0	0,5
Plantago subulata	0	0	0	0	0
Lysimachia europaea	0	0	0	0	0
Linnaea borealis	0	0	0	0	0

Species	**Ctrl-1**	**Ctrl-2**	**Ctrl-3**	**Ctrl-4**	**Ctrl-5**
Moss	85,8333333	45	85	81,6666667	29,6666667
Grass	0	1,5	0	1,33333333	0

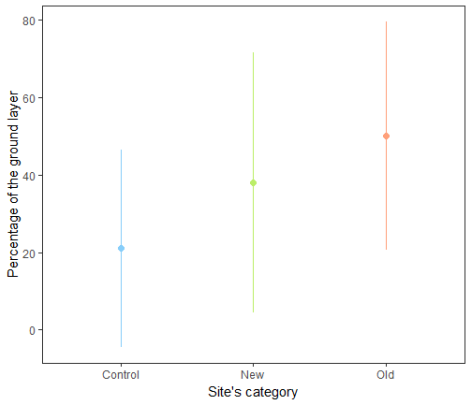
Carex sp.	20	2,5	5,5	4,66666667	5,83333333
Calla palustris	0	9,16666667	0	0	0
Lysimachia thyrsiflora	0	0	0	0	0
Rhodondendron tomentosum	0	2,5	6,66666667	9	10,8333333
Vaccinium oxycoccos	7	0	1	4,16666667	0,5
Dryopteris sp.	0	0	0	0	0
Betula pubenscens	0	0	0	0	0
Rubus sp.	0	0	0	0	0
Phragmites australis	0	0	0	0	0
Comarum palustre	0	0	0	0	0,83333333
Salix sp.	0	0	0	0	0
Chamaenerion augustifolium	0	0	0	0	0
Picea abies	0	0	0	0	0
Vaccinium uliginosum	0	3,33333333	5	5	2,5
Enpetrium negrium	0	0	0	3,33333333	9,5
Andromeda polifolia	0	0	1,66666667	2,16666667	1,33333333
Rubus chamaemonus	0	0	3,33333333	3,33333333	6,66666667
Vaccinium myrtillus	3,66666667	10,8333333	17,1666667	15	15,5
Vaccinium vitis-idaea	5,33333333	6,33333333	19,6666667	15	17,8333333
Convallaria majalis	0	0	0	0	0
Oxalis acetoselia	0	0	0	0	0
Maianthemum bifolium	0	0,5	0	0	0
Equisetum sylvaticum	0	0	0	0	0
Epilobium parviflorum	0	0	0	0	0
Scutellaria galericulata	0	0	0	0	0
Galium palustre	0	0	0	0	0
Epilobium palustre	0	0	0	0	0
Malampyrum pratense	0	0,5	0	0	0
Drosera rotundifolia	0	0	0	0	0
Calluna vulgaris	0	0	0	6,66666667	4,16666667
Lysimachia vulgaris	0	0	0	0	0
Helianthus divaricatus	0	0	0	0	0
Sorbus aucuparia	0	0	1,66666667	0	0
Talinum paniculatum	0	0	0	0	0
Taraxacum officale	0	0	0	0	0
Pinus sylvestris	0	0	0	0	0
Plantago subulata	0	0	4,16666667	0	0
Lysimachia europaea	0	0	0,83333333	0	0
Linnaea borealis	0	0	1,16666667	0	0

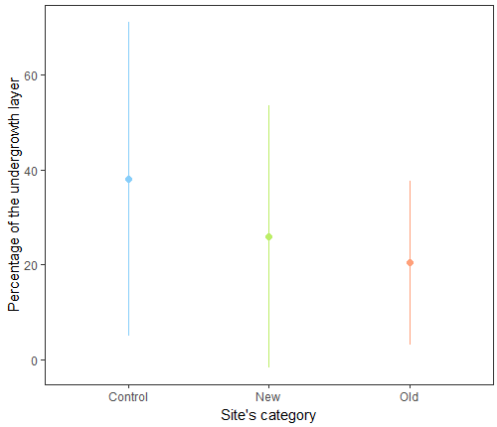
Appendix 3: Results of diversity indices in each site, for mammal census and vegetation census

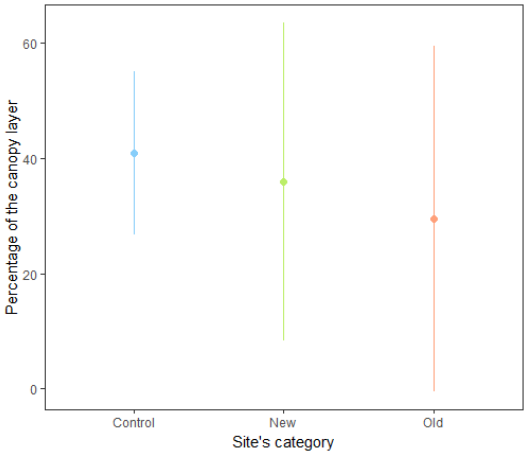
	Vegetation				Mammals			
	Shannon	***Evenness***	***Abundance***	***Sp.Richness***	***Shannon***	***Evenness***	***Abundance***	***Sp.Richness***
New-1	1,4295	0,7346	82	7	0.7968	0.7253	14	3
New- 2	1,3673	0,5702	123,33	11	0.8869	0.8073	12	3
New- 3	1,8292	0,6456	122,67	17	0.286	0.4126	12	2
New- 4	2,0399	0,7730	52,67	14	1.2024	0.6711	17	6
New- 5	1,7765	0,6926	164,67	13	1.1045	0.7967	16	4
Old-1	0,9586	0,4926	142,5	7	0.8711	0.6284	20	4
Old-2	1,5394	0,6195	100,67	12	0.4744	0.6844	22	2
Old-3	1,7676	0,7113	116,33	12	1.3117	0.9462	9	4
Old-4	1,2527	0,6992	58,33	6	1.0985	0.9999	3	3
Old-5	1,7562	0,7627	110,167	10	0.4735	0.3416	10	4
Ctrl-1	0,9499	0,5902	121,83	5	1.3115	0.9491	19	4
Ctrl-2	1,5168	06587	82,167	10	1.3209	0.9528	8	4
Ctrl-3	1,5826	0,6170	152,83	13	0.8982	0.6479	14	4
Ctrl-4	1,6859	0,6785	151,83	12	1.1189	0.6952	19	5
Ctrl-5	2,0626	0,8301	105,167	12	0.7968	0.7253	14	3

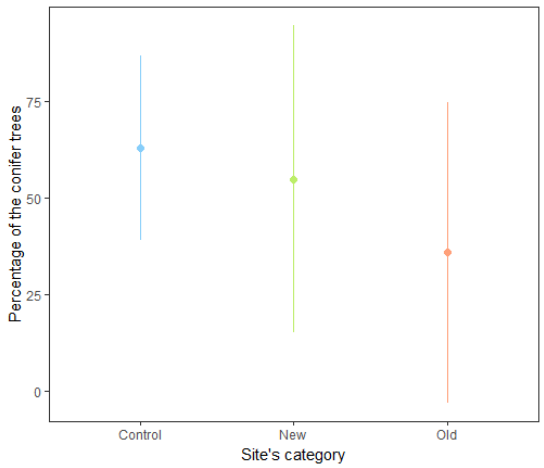
Appendix 4 : Combination of the two FCA of the vegetation survey. Distribution of the plant species within the sites.

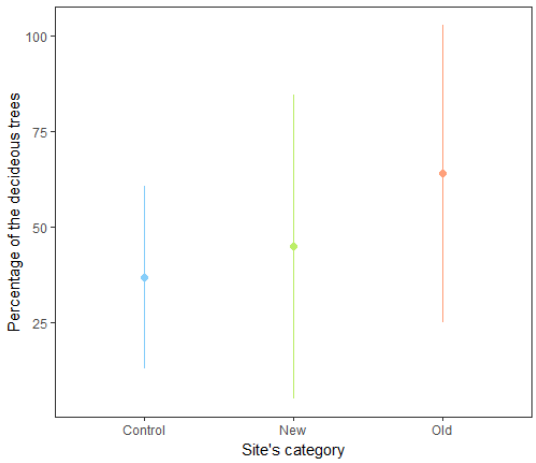
<u>Appendix 5</u> : Results of the anovas carried on the average cover of the different types of vegetation within the categories of sites.

Anova of the average cover of the ground layer in the sites of the different categories	`> EMSanova(Ground~Category, data = ground, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 2123.333 1061.6667 1.8599 0.1979 Error+5Category`
	`Residuals 12 6850.000 570.8333 Error`
	 

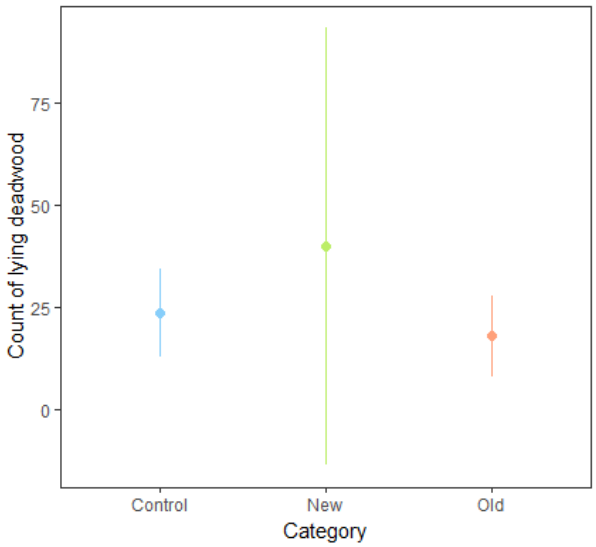
Anova of the average cover of the undergrowth layer in the sites of the different categories	`> EMSanova(Undergrowth~Category, data = undergrowth, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 808.5333 404.2667 0.872 0.443 Error+5Category`
	`Residuals 12 5563.2000 463.6000 Error`
	 

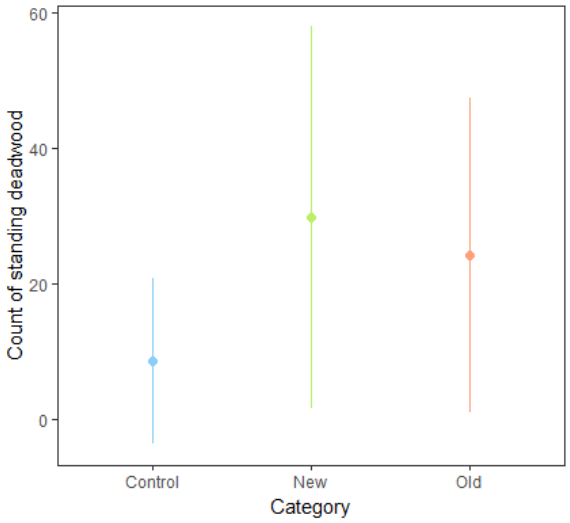
Anova of the average cover of the canopy layer in the sites of the different categories	`> EMSanova(Canopy~Category, data = canopy, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 326.5333 163.2667 0.4062 0.675 Error+5Category`
	`Residuals 12 4823.2000 401.9333 Error`
	 

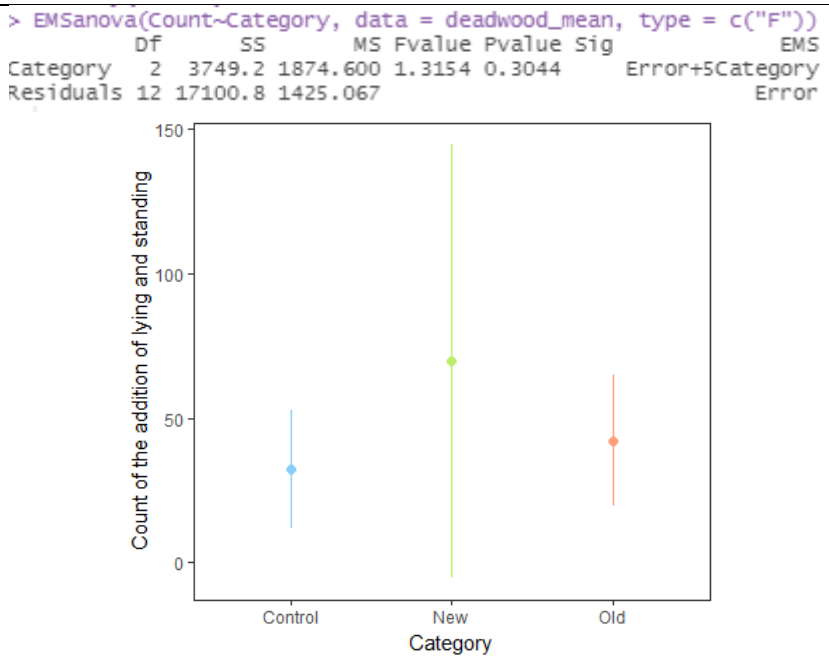
Anova of the average cover of coniferous in the sites of the different categories	`> EMSanova(Coniferous~Category, data = conifers, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 1923.333 961.6667 1.2147 0.3308 Error+5Category`
	`Residuals 12 9500.000 791.6667 Error`
	 

Anova of the average cover of decideous in the sites of the different categories	`> EMSanova(Decideous~Category, data = decideous, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 1923.333 961.6667 1.2147 0.3308 Error+5Category`
	`Residuals 12 9500.000 791.6667 Error`
	 

<u>Appendix 6</u> : Results of the anovas carried on the average number of deadwood pieces found within the categories of sites.

Anova of the amount of lying deadwood in the sites of the different categories	`> EMSanova(Count~Category, data = deadwood_lying, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 1281.733 640.8667 0.9656 0.4085 Error+5Category`
	`Residuals 12 7964.000 663.6667 Error`
	 

Anova of the amount of standing deadwood in the sites of the different categories	`> EMSanova(Count~Category, data = deadwood_standing, type = c("F"))`
	`Df SS MS Fvalue Pvalue Sig EMS`
	`Category 2 1206.933 603.4667 1.8805 0.1948 Error+5Category`
	`Residuals 12 3850.800 320.9000 Error`
	 

Anova of the amount of both lying and standing deadwood in the sites of the different categories	

<u>Appendix 7</u>: Results of the linear models on the amount of lying dead wood with the different small mammal's species within the different categories. Df are degrees of freedom, SS are the sum of squares of error, MS are the mean squares of error (SS/Df), Fvalue are the F statistics, Pvalue are the p-values and Sig shows how significant is the p-value (if higher than 0.1 nothing written, if between 0.1 and 0.05 ".", if between 0.05 and 0.01 "*", if between 0.01 and 0.001 "**" and if below 0.001 "***". Only the lying dead wood was considered as they were expected to impact more the small mammals.

All mammals species ~ Dead wood	Analysis of Variance Table Response: Sum Df Sum Sq Mean Sq F value Pr(>F) Lying_deadwood 1 39.7 39.698 0.4983 0.4949 Residuals 11 876.3 79.664
Bank voles ~ Dead wood	Analysis of Variance Table Response: Bank.vole Df Sum Sq Mean Sq F value Pr(>F) Lying_deadwood 1 4.44 4.4395 0.1668 0.6896 Residuals 13 345.96 26.6123
Field voles ~ Dead wood	Analysis of Variance Table Response: Field.vole Df Sum Sq Mean Sq F value Pr(>F) Lying_deadwood 1 0.0325 0.0325 0.0276 0.8706 Residuals 13 15.3008 1.1770
Common shrews ~ Dead wood	Analysis of Variance Table Response: Common.shrew Df Sum Sq Mean Sq F value Pr(>F) Lying_deadwood 1 0.108 0.1080 0.0332 0.8582 Residuals 13 42.292 3.2532

<u>Appendix 8</u>: Results of the linear models of the cover percentage of the different vegetation layers with the different small mammals species within the different categories. Df are

degrees of freedom, SS are the sum of squares of error, MS are the mean squares of error (SS/Df), Fvalue are the F statistics, Pvalue are the p-values and Sig shows how significant is the p-value (if higher than 0.1 nothing written, if between 0.1 and 0.05 ".", if between 0.05 and 0.01 "*", if between 0.01 and 0.001 "**" and if below 0.001 "***". As the total of the percentage of the ground, undergrowth and canopy layers equals 100%, only the ground and undergrowth layers have been considered in the models as they were expected to impact more the small mammals. The same applied to coniferous and deciduous trees so only deciduous trees were considered.

All mammals species ~ Category + ground	Analysis of Variance Table Response: Sum Df Sum Sq Mean Sq F value Pr(>F) Category 2 69.364 34.682 7.6505 0.1156 Ground 9 299.283 33.254 7.3354 0.1257 Residuals 2 9.067 4.533
All mammals species ~ Category + undergrowth	Analysis of Variance Table Response: Sum Df Sum Sq Mean Sq F value Pr(>F) Category 2 36.45 18.225 0.4486 0.6903 Undergrowth 8 450.30 56.287 1.3855 0.4850 Residuals 2 81.25 40.625
All mammals species ~ Category + Coniferous	Analysis of Variance Table Response: Sum Df Sum Sq Mean Sq F value Pr(>F) Category 2 7.71 3.857 0.0774 0.9260 Coniferous 1 7.91 7.907 0.1587 0.6987 Residuals 10 498.09 49.809
Bank voles ~ Category + ground + undergrowth	Analysis of Variance Table Response: Bank_voles Df Sum Sq Mean Sq F value Pr(>F) Category 2 8.400 4.200 0.1575 0.8563 Ground 1 27.879 27.879 1.0457 0.3306 Undergrowth 1 47.514 47.514 1.7822 0.2115 Residuals 10 266.607 26.661
Bank voles ~ Category + Coniferous	Analysis of Variance Table Response: Bank_voles Df Sum Sq Mean Sq F value Pr(>F) Category 2 8.400 4.200 0.1488 0.8634 Coniferous 1 31.611 31.611 1.1203 0.3125 Residuals 11 310.389 28.217
Field voles ~ Category + ground + undergrowth	Analysis of Variance Table Response: Field_voles Df Sum Sq Mean Sq F value Pr(>F) Category 2 0.9333 0.46667 0.3964 0.6828 Ground 1 2.6213 2.62131 2.2268 0.1665 Undergrowth 1 0.0071 0.00711 0.0060 0.9396 Residuals 10 11.7716 1.17716
Field voles ~ Category + Coniferous	Analysis of Variance Table Response: Bank_voles Df Sum Sq Mean Sq F value Pr(>F) Category 2 8.400 4.200 0.1488 0.8634 Coniferous 1 31.611 31.611 1.1203 0.3125 Residuals 11 310.389 28.217
Common shrews ~ Category + ground + undergrowth	Analysis of Variance Table Response: Common_shrew Df Sum Sq Mean Sq F value Pr(>F) Category 2 0.400 0.2000 0.0507 0.9508 Ground 1 0.778 0.7780 0.1973 0.6663 Undergrowth 1 1.801 1.8014 0.4570 0.5144 Residuals 10 39.421 3.9421

Common shrews ~ Category + Coniferous	Analysis of Variance Table Response: Common_shrew Df Sum Sq Mean Sq F value Pr(>F) Category 2 0.400 0.2000 0.0561 0.9457 Coniferous 1 2.797 2.7967 0.7847 0.3947 Residuals 11 39.203 3.5639

<u>Appendix 9:</u> Additional pictures of field work.

Typical channel dug by beavers that contributes to the dynamism and hydrogeomorphology of the plains as they allow a better landscape connectivity *(Cfr. 4.1.1. Geomorphology p.6)*	**Remains of an unused beaver dam**
	
Fresh and old cuts by beavers	**Set camera trap**

Beaver sighting in another place than the studied sites	The best field mate and me, happy in beautiful Evo