

Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
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Veteran oaks, biodiversity and ecosystem functioning in southern Norway

Biologisk mangfold og
økosystemfunksjoner i gamle eiker

Ross Wetherbee

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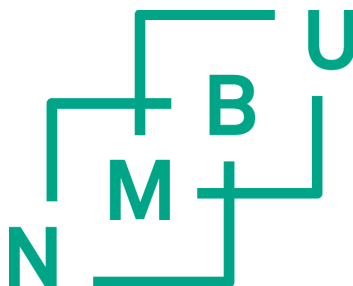
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Acknowledgements

Since I was a child, I loved animals. The incredible diversity of shapes, sizes, colors and lifestyles captured my imagination. And no group of animals epitomizes this vast array of diversity better than beetles! To the disinterested eye, these seemingly insignificant little creatures mostly go unnoticed, but once you start looking, an incredible and bizarre world is revealed. But this world is dependent on another, one whose clock is operating on a much longer time scale - the world of the veteran oak. Slow and steady, as the eons unfold, they remain tethered to a place. How magnificent the intersection of these two worlds! And yet, these worlds and ours are not independent, but instead are deeply interwoven into the fabric of our existence. It has been a great pleasure to study this magnificent intersection of life.

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Ross Wetherbee

Norderås, April 2nd, 2021

A handwritten signature in black ink, appearing to read "Ross Wetherbee". The signature is fluid and cursive, with the first name "Ross" written in a larger, more prominent script than the last name "Wetherbee".

Contents

Acknowledgments	v
Contents	ix
List of papers	xi
List of datasets	xii
Summary	xiii
Sammendrag	xv
Synopsis	1
Introduction	3
Methods	12
Main results	23
Discussion	27
Conclusion	34
References	35

List of papers

Paper 1

Wetherbee, R., Birkemoe, T., Skarpaas, O., and Sverdrup-Thygeson, A. (2020) Hollow oaks and beetle functional diversity: significance of surroundings extends beyond taxonomy. *Ecology and Evolution* 10:819-831.

Paper 2

Wetherbee, R., Birkemoe, T., and Sverdrup-Thygeson, A. (2020) Veteran trees are a source of natural enemies. *Scientific Reports* 10:18485.

Paper 3

Wetherbee, R., Birkemoe, T., Burner, R. C., Sverdrup-Thygeson, A. (2021) Veteran trees have divergent effects on beetle diversity and wood decomposition. *PLOS ONE* 16(3): e0248756. <https://doi.org/10.1371/journal.pone.0248756>

Paper 4

Wetherbee, R., Birkemoe, T., Asplund, J., Renco, M., and Sverdrup-Thygeson, A. It takes a community to maintain a tree hollow: macrofauna increase decomposition, enhance wood mould production and structure lower trophic levels. *Manuscript*

List of datasets

Wetherbee, R., Birkemoe, T., Sverdrup-Thygeson, A., Ligaard, S., Tourani, M. (2020) Beetles from old forest (*Quercus* sp.) at Larvik. In: Sciences NUoL, GBIF. editor. Occurrence dataset. <https://doi.org/10.15468/5bxyph>

Wetherbee, R., Birkemoe, T., Sverdrup-Thygeson, A., Ligaard S., Marthinsen, G. Beetle larvae from mesocosm experiment in southern Norway. In: BOLD Systems. *Unpublished*.

Summary

Veteran trees are keystone structures in landscapes, hotspots for biodiversity and have high cultural value. They are also declining globally, and this threatens the species that are dependent on them, and the ecosystem functions they promote. Ecosystem functions are the physicochemical and biological processes that occur within ecosystems that maintain life. A key link between biodiversity and ecosystem functioning is the traits of the species. This diversity of traits is also known as functional diversity, and high levels of functional diversity in a community promote multiple ecosystem processes and make these processes more resilient to change. There is a large amount of evidence to support the conclusion that biodiversity influences ecosystem functioning, but few studies address this related to invertebrate diversity in veteran trees.

My research has explored the multifaceted predictors of taxonomic and functional diversity of veteran oaks invertebrate communities, and measured the contribution of these communities to ecosystem functioning. In Paper 1, I considered three possible ecosystem functions promoted by veteran oak beetle communities (decomposition, predation and pollination), and explored how the veteran oaks and their landscape contexts influence this diversity (both taxonomic and functional). In the two corresponding papers (Papers 2 and 3), I focused more closely on predation and decomposition (respectively), and examined the differences in these processes and beetle communities involved in them between veteran and young oaks. Lastly, in Paper 4 I used a mesocosm experiment to explore how community complexity influences biotic interactions and decomposition in tree hollows. All my research was conducted around veteran oaks in southern Norway.

In Paper 1, I found that the features of veteran trees (e.g.: senescence, circumference and regrowth) and the landscape that they were in had different influences on species richness and functional diversity within the different groups of decomposers, predatory and flower visiting beetles. In Paper 2, I found that there were more species of predatory beetles with greater functional diversity around veteran oaks than young oaks, and this corresponded with greater invertebrate predation rates. In Paper 3, I found a similar effect on the wood decomposing beetles, with a greater number of species and higher functional diversity around veteran trees than young trees. However, I found the opposite effect on decomposition of the small diameter wood, with slower rates around the veteran trees. In Paper 4, I found that community complexity increased decomposition rates and wood mold production in tree hollows, and that macrofauna influenced the decomposition pathway and nematode community structure and maturity.

The findings from my research support the concept that veteran trees are important for biodiversity, and indicate that veteran trees and their communities influence ecosystem functions, such as invertebrate predation and decomposition. They also highlight the importance of community complexity and habitat heterogeneity for promoting biodiversity and ecosystem functioning. Results

from my work indicate that there is the potential for synergies between the conservation of veteran trees and sustainable agriculture and forestry. Protecting and valuing veteran trees and their communities, and reintegrating them into land use practices, is an essential step towards a more sustainable system of management, and has the possibility of enhancing the wellbeing of people while promoting biodiversity.

Sammendrag

Gamle trær er nøkkelstrukturer i landskapet, de er viktige for biologisk mangfold og de har høy kulturell verdi. De minker globalt, og dette truer artene som er avhengige av dem samt de økosystemfunksjonene disse trærne fremmer. Økosystemfunksjoner er de fysiske-kjemiske og biologiske prosessene som forekommer i økosystemer og som støtter opp om liv. Artenes egenskaper utgjør en sentral kobling mellom biologisk mangfold og økosystemfunksjoner. Dette mangfoldet av egenskaper er også kjent som funksjonelt mangfold, og høye nivåer av funksjonelt mangfold i et samfunn fremmer flere økosystemprosesser og gjør disse prosessene mer motstandsdyktige mot endring. Mye forskning peker på at biologisk mangfold påvirker økosystemfunksjon, men få studier tar for seg dette i sammenheng med mangfold av insekter i gamle trær. Forskningen min har utforsket de flersidige driverne for taksonomisk og funksjonelt mangfold i insektmiljøer som forekommer i gamle eiketrær, og målt bidragene fra disse til økosystemfunksjoner.

Resultatene fra forskningen min støtter oppfatningen om at gamle trær er viktige for biologisk mangfold, og peker på at gamle trær og samfunnene deres bidrar til viktige økosystemfunksjoner, eksempelvis predasjon av insekter og nedbrytning av organisk materiale. Resultatene fremhever også viktigheten av samfunnskompleksitet og habitatsmangfold for å fremme biologisk mangfold og viktige økosystemfunksjoner. Forskningen min viser dessuten at det finnes mulige synergier mellom bevaring av gamle trær og bærekraftig jordbruk. Å beskytte og verdsette gamle trær og lokalsamfunnene deres, samt integrere disse på nytt i landbrukspraksis, er et viktig skritt mot et mer bærekraftig forvaltningssystem som har mulighet for å forbedre folks velvære samtidig som det fremmer biologisk mangfold.

Synopsis

Introduction

In the past 50 years there has been a dramatic loss in global biodiversity, and this decline is predicted to continue or to accelerate (Reid et al. 2005, IPBES 2018). The primary causes of biodiversity loss are related to human activities, such as the overexploitation of the natural environment, pollution, the destruction of habitat and climate change (Dirzo and Raven 2003, Hooper et al. 2005, Virah-Sawmy et al. 2014, Bernhardt et al. 2017). This is of major concern because biodiversity regulates energy fluxes and matter, including carbon uptake, nutrient cycling and oxygen production (Reiss et al. 2009). The combination of these processes, their properties and their maintenance make up what has been termed ecosystem functions (Naeem and Wright 2003, Reiss et al. 2009). All societies are dependent on ecosystem functions to support human existence and wellbeing (Box 1), and research clearly indicates that loss of biodiversity results in a reduction of these processes (Cardinale et al. 2012, Kadykalo et al. 2019). Therefore, the ongoing global loss of biodiversity is of major concern for ecosystems and humans alike (Cardinale et al. 2012, IPBES 2018).

Of special concern is the decline of insects, as a large body of recent research has found evidence of insects declining in abundances, biomass, species richness and range sizes (Sánchez-Bayo and Wyckhuys 2019, Wagner 2020). These declines include both specialist and generalist species, and evidence indicates that over 40% of insect species are threatened with extinction (Sánchez-Bayo and Wyckhuys 2019). While there are exceptions and most reports come from western and northern Europe, a growing body of literature suggests that this is a global trend (Sánchez-Bayo and Wyckhuys 2019, Wagner 2020, Wagner et al. 2021). The global insect decline is likely to have large impacts because insects make up much of the animal biomass, and link primary producers and consumers (Wagner 2020). They also play important roles in many ecosystem processes, such as pollination, regulation of pests, nutrient cycling and soil formation (Wagner et al. 2021). There are many causes of global insect decline, but habitat loss has been highlighted as one of the most important (Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021).

Box 1: Ecosystem services and nature's contribution to people

Nature's contribution to people (NCP), introduced by IPBES (2018), has been suggested as a framework to help societies better understand and relate to the ecosystems on which they depend, and is defined as all the contributions, both positive and negative, of living nature to people's quality of life (Diaz et al. 2018). NCP in conception, is intended to replace the previous terminology of ecosystem services (ES), which can be defined as the benefits that humans obtain from ecosystems (Seppelt et al. 2011). ES has been critiqued for being anthropocentric, promoting an exploitative human–nature relationship and commodification of nature, attempting to place economic value on nature, conflicting with biodiversity conservation objectives, having vague definitions, and implying that all outcomes of ecosystem processes are desirable (Schröter et al. 2014). Additional critiques include ignoring other ways of viewing nature, such as Indigenous ontologies, and other sources of knowledge, such as traditional ecological knowledge and critical feedbacks between Indigenous and local people and nature (Comberti et al. 2015). However, a citation report from Web of Science indicates that the terminology NCP is not taking off quickly, while ES remains commonly used. A recent study found that researchers using qualitative methods are more likely to use the term NCP, whereas researchers using quantitative methods were predominantly inclined to use ES (Pires et al. 2020). The reason for this may be that the framework of ES is both broadly understandable and applicable, and is deeply embedded in the current scientific paradigm. Furthermore, there is broad overlap between the frameworks (Kadykalo et al. 2019), and there are certain difficulties with applying the new elements of NCP. For instance, it is not clear how to integrate other views of nature or sources of knowledge into quantitative scientific research, and how different views and knowledge sources should be deemed creditable. Also, recent work has highlighted that there is a perceived lack of relevant data and methodologies for NCP assessments (Keller et al. 2018). At this point NCP clearly needs development, and in its current state it seems unlikely to replace ES. Nevertheless, NCP may represent a step in the right direction of developing a framework that is more inclusive and less laden with terminology focused on the exploitation of natural resources.

One critical habitat for many insects is large, old trees (Stokland et al. 2012). Some trees can have life spans that extend hundreds or even thousands of years (Lindenmayer et al. 2012), and these long-lived individuals are also declining globally as a result of human activities, such as intensification of land use, the abandonment of traditional management and climate change (Siitonen and Ranius 2015, Lindenmayer and Laurance 2016). In addition to providing critical habitat for a diverse set of species, large, old trees are involved in a wide range of ecosystem processes, such as altering local climates, contributing to nutrients cycling and hydrological regimes (Lindenmayer and Laurance 2016). The size and the age of trees affect the quantity and quality of microhabitat associated with them (Siitonen and Ranius 2015). When trees reach extreme ages, they become keystone structures in landscapes (Müller et al. 2013, Parmain and Bouget 2018) and contribute to both biodiversity and human well-being (Lindenmayer et al. 2014). There are several terms for these large, old trees, but for this work I have chosen to use the term veteran (Box 2).

Box 2: A tree by any other name



Trees that reach old age interact with many generations of people through their lives, and consequently are given different names. In my work, I have decided to call these old trees ‘veteran’. Although other terms such as hollow, monumental or ancient have also been used, in my view these terms only capture a single element of old, ecologically and culturally valuable trees. The word veteran, on the other hand, is derived from the Latin *vetus*, meaning old. In modern English, veteran is defined as one who has had a long service or experience in a particular occupation or field. In this terminology, both age and service (or function) are emphasized, as well as an implicit appreciation for the contribution of the individual. This latter point is especially important, because the ecological and cultural value of an individual old tree can be immense (Lindenmayer et al. 2014). This is why I have chosen to use the terminology veteran trees. Nevertheless, with good management many of the so-called veteran trees that I have studied in this work will live on, long after I am gone, and likely take on other names.

Veteran oaks (*Quercus* spp.) are especially important for insect biodiversity in northern European forests (Siitonen and Ranius 2015), and many of the insects associated with these trees are saproxylic, meaning that they are dependent on dead wood at some stage in their life cycles (Stokland et al. 2012). The vast amount of biodiversity in dead wood is a well-documented phenomenon, and described even in early research (Silvestri 1913, Stokland et al. 2012). The reasons why there are many species associated with dead wood are multifaceted and complex, but in short, dead wood is abundant, full of energy, diverse and breaks down slowly (Stokland et al. 2012). The abundance of woody material is difficult to overstate. Trees produce the highest amount of terrestrial biomass and more than 73 billion tons of carbon is stored in naturally occurring dead wood, globally (Pan et al. 2011). In order to visualize the high amount of energy trapped in dead wood, one only need to consider the amount of heat that is produced by a campfire. There is a direct relationship between that heat and the amount of energy in wood. Furthermore, there are many species of woody plants, and wood breaks down slowly due to the presence of decay resistant compounds and the recalcitrant nature of its structure (Ulyshen 2016). In northern systems it takes 50 to 100 years for a log to fully break down, and this process can take much longer depending on the species, size of the log and its vertical position (Stokland et al. 2012). This results in the decomposition process following many different paths and providing a plethora of microhabitats along the way (Stokland et al. 2012).

Tree hollows and other microhabitats

The hollow of veteran trees is an especially important microhabitat, because it provides a stable, nutrient rich environment that hosts many specialized invertebrates (Bütler et al. 2013, Siitonen and Ranius 2015). In northern Europe, oaks typically begin to develop hollows when they are more than two hundred years old (Ranius et al. 2009). This development begins when the tree is damaged and the sapwood and heartwood is exposed (Stokland et al. 2012). Trees may continue to live for many hundreds of years after the hollow initially develops, and during this time, the hollow continues to increase in size and structural complexity (Ranius et al. 2009). The partially degraded organic material that gathers inside of tree hollows is known as wood mould. Wood mould is nitrogen-rich and a key feature of tree hollows (Micó et al. 2015). In fact, the amount of wood mould that a veteran tree contains is positively related to the number of insects associated with the tree (Ranius et al. 2009, Landvik et al. 2016).

While some work has been done on biotic interactions in tree hollows, it has primarily been focused on beetles, and it is assumed that they are the most important insects for wood mould production (Sanchez-Galvan et al. 2014, Micó 2018, Sánchez-Galván et al. 2018). In contrast, there has been basically no research done on smaller organisms (Stokland et al. 2012). Tree hollows are in many ways analogous to soil systems, in that they are composed of a resource base that primarily consist of

decomposing plant matter and three major groups of organisms: microbes (bacteria and fungi), mesofauna (0.1 – 2.0 mm, springtails, mites and nematodes) and macrofauna (> 5.0 mm, insects and other large invertebrates) (Wardle et al. 1998, Neher 2001, David 2014). The microbes are considered to be the primary decomposer group (Gessner et al. 2010), and bacteria-dominated energy channels have faster turnover rates than those that are dominated by fungi (Bell et al. 2009). Within the mesofauna, nematodes are generally considered to be the most important for decomposition rates and nutrients cycling (Neher 2001, Ferris 2010). They are also extraordinarily abundant and diverse (Ferris et al. 2001), and are easily classified into functional groups. This makes them excellent indicators of microbial communities, food web structure and energy channels (Ferris 2010). Macrofauna are involved in many soil processes related to decomposition and nutrient release, but their exact role in these processes remains poorly understood (David 2014, Menta and Remelli 2020). This is especially the case in tree hollows, and very little is known about how community diversity influences decomposition rates and wood mould formation or what role different groups of organisms play in structuring these vital habitats.

Additional microhabitats associated with veteran trees are dead branches, large root systems that provide a source of subterranean dead wood, fungal fruiting bodies and coarse bark (Stokland et al. 2012, Bütler et al. 2013). The surroundings of veteran trees also influence the microhabitats and insect communities. The most obvious example of this is the distinction between veteran trees in forests and in open landscapes. This difference influences the tree's size, shape, maximum age and microhabitats (Stokland et al. 2012, Parmain and Bouget 2018), and also, the insect communities (Sverdrup-Thygeson et al. 2010, Sverdrup-Thygeson et al. 2017). Other aspects of the surroundings that influence insect communities are regrowth around the tree, sun exposure and temperature, isolation from other veteran trees and the stand maturity (Ranius and Jansson 2000, Ranius et al. 2009, Sverdrup-Thygeson et al. 2010, Gough et al. 2014, Gossner et al. 2016, Pilskog et al. 2016).

Habitat-heterogeneity

Two possible hypotheses have been suggested to explain why there is high levels of diversity around veteran trees (Müller et al. 2013) and dead wood in general (Seibold et al. 2016b). The first is the habitat heterogeneity hypothesis, which predicts that high diversity of microhabitats should promote overall species richness and functional diversity (Tews et al. 2004). The second is the resource hypothesis, which predicts that species diversity will increase with substrate density (i.e.: the amount of deadwood) (Srivastava and Lawton 1998, Blakely and Didham 2010). Aspects of dead wood that influence insect diversity include features of the dead wood, such as the diameter, decay stage, vertical position and tree species (Grove 2002, Heilmann-Clausen and Christensen 2004, Müller et al. 2015, Seibold et al. 2018), as well as what caused the wood to die, fire being especially important for many specialized species

(Stokland et al. 2012). Insect diversity is also influenced by the canopy cover (Bässler et al. 2010, Seibold et al. 2016a) and canopy openness has been found to influence the relationship between habitat heterogeneity and beetle species richness (Seibold et al. 2016b). Additionally, the amount and access to dead wood in the landscape has been shown to influence beetle diversity (Sverdrup-Thygeson et al. 2014).

Biodiversity and ecosystem functioning

A large amount of research has found a link between biodiversity and ecosystem functioning (Reiss et al. 2009). However, few studies have considered this link in communities associated with dead wood (Ulyshen 2013), and to my knowledge, no studies have addressed this in the context of insect diversity in veteran trees. Additionally, the link between biodiversity and ecosystem functioning is not straightforward, and a community's contribution to ecosystem functioning is more closely related to diversity in relevant functional traits than to the number of species within the community (Heemsbergen et al. 2004, Lefcheck and Duffy 2015, Moretti et al. 2017). This diversity in traits is also known as functional diversity (Box 3), and high levels of functional diversity in a community promotes multiple ecosystem processes and make these processes more resilient to change (Grime et al. 1997, Diaz and Cabido 2001, Folke et al. 2004, Reiss et al. 2009, Tilman et al. 2014). Veteran trees are, in a sense, 'islands' of high biodiversity as they are surrounded by other trees that support less species-rich communities (Müller et al. 2013). Thus, research related to the influence of veteran trees and their associated biodiversity on ecosystem functioning has a two-fold advantage, in that it can elucidate the relationship between biodiversity and ecosystem function and simultaneously provide incentives to protect these valuable organisms.

Decomposition of wood

Veteran trees and their communities may be influencing decomposition, due to the large diversity of organisms involved in this process associated with veteran trees. However, the relationship between biodiversity and decomposition is complex, with many interactions among diverse organisms (Hättenschwiler et al. 2005, Gessner et al. 2010). As I discussed previously, there are high volumes of dead wood that contain larger amounts of resources, and for this reason wood decomposition is important for nutrients and carbon cycling (Pan et al. 2011). Although fungi and bacteria are the primary organisms involved in decomposition (Gessner et al. 2010), insects play an important role in the process as well (Ulyshen 2016). In northern ecosystems where termites are absent, beetles are likely the insects that contribute the most to wood decomposition (Stokland et al. 2012, Ulyshen et al. 2014).

Box 3: Functional diversity



“endless forms most beautiful and most wonderful”

- Charles Darwin

Functional diversity refers to the components of biodiversity that influence how an ecosystem functions (Tilman 2001). Functional diversity is comprised of functional traits, which are phenotypic aspects of an organism's morphology, physiology, phenology or behavior with an effect on ecosystem processes (McGill et al. 2006, Diaz et al. 2013). For instance, body size is an important trait for insects as it is linked to other life-history traits such as life span and dispersal ability, and it influences the amount and composition of resources used by the organism (Moretti et al. 2017). The large species *Trypocopris vernalis* (C) uses their size to excavate burrows and maneuver dung of large mammals, while the relatively small cerambycid, *Pogonocherus hispidulus* (F), is able to inhabit small diameter wood. Other traits such as eye size have been linked to prey recognition as well as hunting strategy (Fountain-Jones et al. 2015), and this can be seen in the image of *Pyrochroa coccinea* (E), which hunts in the open, compared to *Silpha atrata* (B) which has small eyes and typically hunts for snails under logs. Body shape may influence how the species interacts with floral architecture (Patt et al. 1997) as can be seen in the images of *Anastrangalia reyi* (A), *Gaurotes virginea* (D), and *P. coccinea* (E). High levels of Functional diversity in a community promotes multiple ecosystem processes and make these processes more resilient to change, but a shortage of information on traits and their exact relationships to ecosystem functions remains a fundamental challenge (Wong et al. 2019).

Beetles increase decomposition of wood in several ways. Some beetles directly consume dead wood and the fungi living within it (Edmonds and Eglitis 1989, Cornwell et al. 2009, Angers et al. 2011, Ulyshen et al. 2016). Beetles that bore into the wood, as called xylophagous (Graham 1925), create tunnels that facilitate colonization by other organisms, improve aeration and increase fragmentation of the wood (Ulyshen 2016). Beetles also interact with the bark and this can both increase decomposition by allowing more organisms to access the wood, and slow down the process by causing the wood to dry out (Ulyshen et al. 2016). Additionally, beetles may act as dispersers of fungal spores to dead wood (Dowding 1984, Swift and Boddy 1984, Ulyshen 2016, Jacobsen et al. 2017, Jacobsen et al. 2018). Some beetles have an extremely tight association with certain fungi and in some cases actively cultivate it, and even have a specialized organ, the mycangium, for transporting fungi, while others may disperse fungi less intentionally (Birkemoe et al. 2018). It is likely that the diversity of organisms associated with veteran trees has some effect on decomposition of wood, yet this remains largely unexplored.

Predation

Another important ecosystem process that veteran trees and their communities may be influencing is predation. Invertebrate pests cause considerable negative impacts on society, such as the destruction of crops and forests, and this is predicted to increase with climate change (Porter et al. 1991, Deutsch et al. 2018). The pervasive method of using pesticides to control invertebrate pests has many interrelated costs for local people, future generations and biological communities, which include reducing human health and contributing to biodiversity loss (Pimentel et al. 1992, Wilson and Tisdell 2001, Horrigan et al. 2002, Popp et al. 2013). Promoting predation by natural enemies of invertebrate pests is a viable alternate, and can be beneficial for people and ecosystems (Barbosa 1998). Evidence suggests that predation rates are higher when the communities of natural enemies has complementary traits (Greenop et al. 2018, Snyder 2019). Traits are considered to be complementary when they result in predators attacking different pest species, being active at different times (both throughout the season and the diurnal cycle) and having different hunting behaviors (Snyder 2019). Additionally, research has shown that landscape complexity is critical for predation by natural enemies because higher levels of habitat heterogeneity increases the ability of multiple enemies to coexist (Perez-Alvarez et al. 2019, Snyder 2019). As previously mentioned, veteran trees increase the structural complexity of the landscape, and they are also a potential source of diverse predators. However, it remains unknown to what extent the presence of veteran trees influences predation by natural enemies.

Project aims and research questions

In this project I have explored the multifaceted drivers of diversity (taxonomic and functional) within veteran oak beetle communities, and measured the communities' contribution to ecosystem functioning. In Paper 1, I addressed the question: how are the veteran oaks and their landscape contexts influencing diversity within three functional groups of beetles: decomposers, predators and flower visitors? In Paper 2, I focused more closely on invertebrate predation and addressed the question: do veteran oaks have a greater diversity of predatory beetles than young oaks, and does this correspond with higher predation rates? In Paper 3, I used a similar approach as Paper 2 to focus on wood decomposition and addressed the question: do veteran oaks have a greater diversity of wood-decomposing beetles than young oaks, and how does this relate to decomposition of small diameter wood in early decay? Lastly, in Paper 4, I used a mesocosm experiment to explore biotic interactions and decomposition in tree hollows and addressed the question: how does community complexity in tree hollows influence decomposition rates, trophic structuring and wood mould production? All my research was conducted in southern Norway and focused on veteran oaks. Paper 1 was based on a pre-existing dataset of beetles captured around 61 veteran oaks between 2004 and 2014. My field experiments in Papers 2, 3 and 4 were conducted around a set of 20 veteran oaks, and Papers 2 and 3 also included an additional 20 young oaks. Sampling was conducted in 2017 and 2018 for Papers 2 and 3, while sampling for Paper 4 was carried out from 2017 to 2019.

Methods

Study system

Oak (*Quercus*) is a large genus of temperate, mostly deciduous trees with broad distribution primarily in the northern hemisphere. The two species that occur in Norway are *Quercus robur*, commonly known as the pedunculate or English oak, and *Q. petraea*, commonly known as the sessile or Cornish oak. *Q. robur* is more common in Norway and the two species are known to hybridize (Jensen et al. 2009). In Norway oaks are distributed as far north as Ålesund and all the way south to the southern Swedish border. They are more common in the southeast where their distribution moves inland, while in the west they are distributed along the coast. In this work, I have defined a veteran oak based on the Norwegian national management regulations, as a tree of at least 95cm in circumference with a visible cavity in the trunk (Lovdata 2011). In Papers 2 and 3, I also included young oaks, which is defined as an oak with a circumference of less than 150 cm and no visible hollow.

In Europe, oaks survived the last glacial maximum in the Mediterranean region and recolonized Norway approximately 7000 years ago (Brewer et al. 2002). Records indicate that oak began to be exported from Norway to central Europe approximately 1000 years ago (Vogt 1886, SSB 1977). Oak exports progressively intensified through the 14th and 15th century as it increased in value due to its use in ship building (Vogt 1886, Vevstad 1998, Daly 2007, Moore 2010). Nevertheless, oak was a dominant tree species in southern Norway with large coastal and inland oak forests (Pilskog 2016). This rapidly changed with the introduction of the waterwheel-driven gate saw to Norway in the 1500's (Vevstad 1998, Moore 2010). Within one hundred years of the introduction of this new technology, large oaks became rare in accessible places along the coast (Pilskog 2016), and the coastal oak forests in southern Norway had become depleted by the mid-1600's (Moore 2010). This led to logging in the inland forests, which intensified in the 1800's and continued until the mid-1900's.

In the 1900's, oaks became scarce in Norway and a less valuable export since it was no longer used in ship building, while the demand for pine and spruce intensified (Vevstad 1998). This led to the development of pine and spruce production forests that dominate southern Norway today. Recently, the Norwegian government has recognized the importance of veteran oaks for biodiversity, and put some protective measures in place and provides financial support for the care and maintenance of selected trees (Regjeringen 2017). These regulations are far from strict and only apply to state owned land and official permitting processes, and the forestry sector follows its own set of regulations regarding veteran trees (MiS 2017). Estimates indicate that there are approximately 60,000 veteran oaks in Norway (Sverdrup-Thygeson et al. 2018).

Veteran oaks typically occur either in forests or open landscapes (Figure 1), and, as discussed in the introduction, this dichotomy in surroundings has a major influence on the insect communities.

Veteran oaks in forests are primarily found in areas that are difficult to log, such as on rocky hill tops or in steep terrain and are often surrounded by managed forests. Veteran oaks in open landscapes, on the other hand, are typically found in parks, near historical buildings, such as churches and old farms, or in agricultural areas, and are surrounded by a matrix of fields and patches of trees (Skarpaas et al. 2017).



Figure 1: Veteran oaks in Norway are either found in forests (left), or in open landscapes (right). This difference results in different tree forms. In forests trees are tall and strait with few large branches, while in open landscapes trees are open with large low branches. Veteran oaks in forests tend to be on rocky hilltops and steep slopes that are difficult to access and surrounded by managed forests, while veteran oaks in open landscapes are typically found in parks, near historical building such as churches and old farms or in agricultural areas, and are surrounded by fields and small patches of trees.

Study sites

All study sites were in southern Norway within the main distribution of oaks (Figure 2). Paper 1 was based on a pre-existing dataset of beetles trapped around 61 veteran oaks that were located within 27 sites. Sites were originally selected based on forest inventories of veteran oaks from the forestry sector and the municipalities. For Papers 2, 3 and 4, I used 20 veteran oaks that were selected from the database of veteran oaks in Norway (ARKO 2011). The veteran trees in Paper 1 were located between the southern tip of Norway, near Kristiansand, to approximately 15 km north of Oslo, while the veteran trees in Papers 2, 3 and 4 were within a 30 km radius of the city of Larvik. The forest around Larvik is primarily spruce (45 %), deciduous tree (35 %) and pine (15 %) with only 2 % of the production forest being oak (Pilskog 2016). In all studies, I included veteran oaks from both forests and open landscapes to cover the typical Norwegian landscapes in which veteran oaks occur.

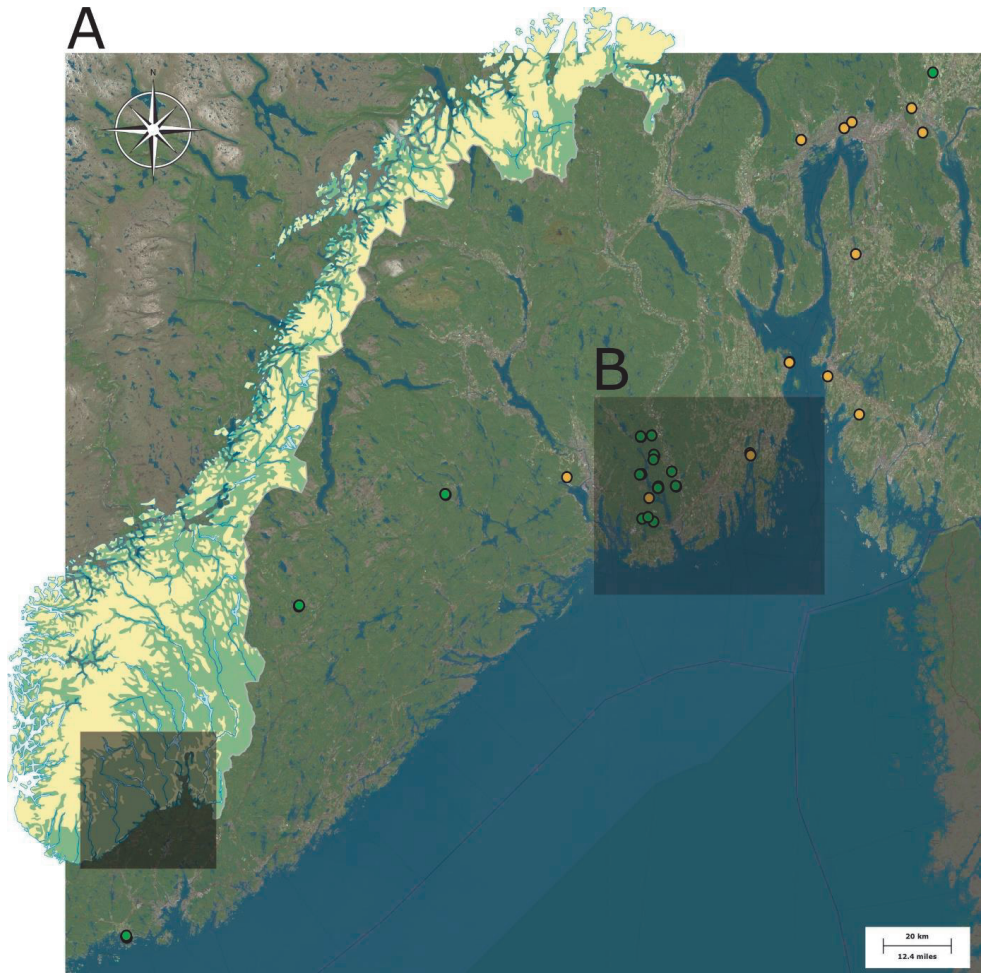


Figure 2: Maps of the study sites. Paper 1 was based on a preexisting dataset that was collected around 61 veteran oaks between 2004 to 2011 (A). Papers 2-4 were based on field experiments conducted around 20 veteran oaks from 2017 to 2019 (B). Green points are veteran oaks in forests and yellow points are veteran oaks in open landscapes. Forest cover is marked in dark green on the map of Norway.

Study design

In my research, I have used a series of field experiments and a large pre-existing dataset to explore veteran oaks invertebrate diversity and measure its contribution to ecosystem functioning (Table 1). For Paper 1, beetles were trapped intermittently between 2004 and 2011 as part of a long-term study of veteran oaks and the National Program for Surveying and Monitoring Biodiversity in Norway (ARKO 2011). Beetle species were subsequently divided into the three functional groups that were not mutually exclusive: decomposers, predators and flower-visitors. Important traits related to each of these ecosystem functions were identified based on previous studies (Gossner et al. 2013, Seibold et al. 2015,

Pilskog et al. 2016, Sverdrup-Thygeson et al. 2017), protocols for selecting insect functional traits (Fountain-Jones et al. 2015, Moretti et al. 2017) or calculated from available material. Additionally, variables that described the trees and their surroundings were either collected at the time of sampling or calculated (see section below for details). These variables were subsequently used to predict beetle diversity within each of the functional groups.

Table 1: Overview of the topics and methods in the papers.

Paper	Ecosystem function	Measure of ecosystem function	Measure of communities	Functional groups	Number of trees	Years
1	Decomposition, predation and pollination	Only accessed through the beetle functional diversity	Two flight intercept traps	Beetles that were decomposers, predators and flower visitors	61 veteran	2004-11
2	Predation	Attack marks on artificial caterpillars	One flight intercept trap	Predatory beetles	40 (20 veteran and 20 young)	2017&18
3	Decomposition of small diameter wood	Density and weight loss of wood bundles	One flight intercept trap and bundles of wood	Wood-decomposing beetles	40 (20 veteran and 20 young)	2017&18
4	Litter decomposition	Weight loss of material in the boxes (leaves, sawdust and wood mould) and nutrients in wood mould	Large wooden boxes	Macrofauna and mesofauna	20 veteran	2017-19

The experimental design for Papers 2 and 3 were similar (Figure 3). I matched each of the 20 veteran trees with a young oak that was within 200 m and had similar immediate surroundings (e.g. openness, sun exposure and surrounding tree species), and sampled the communities with a flight intercept trap hanging from the canopy of every tree (N = 40). For Paper 2, I also placed artificial caterpillars made of plasticine around the trees to measure predation rates. Beetle communities were measured in 2017 and 2018, while the artificial caterpillars were only deployed in 2018. For Paper 3, I placed bundles of recently cut small diameter oak branches (50 cm long and 1-3 cm in diameter) around the trees to measure colonization and wood decomposition rates. Bundles were transported to the field sites in May 2017 and retrieved in October 2018.

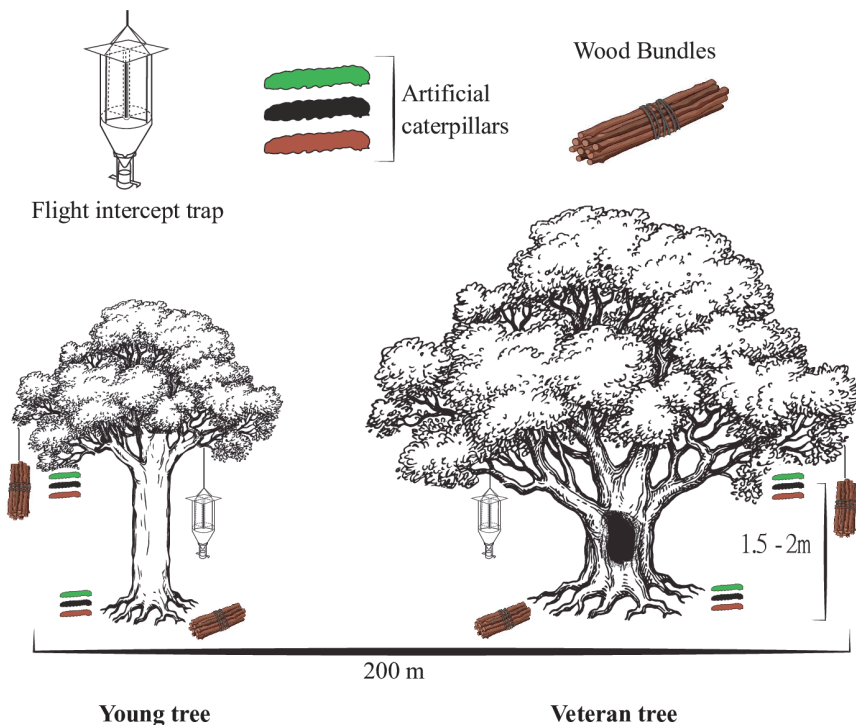


Figure 3: Figure of the study design for Papers 2 and 3 that I used to measure the contribution of veteran oak invertebrate communities to predation by natural enemies (Paper 2), and wood decomposition rates (Paper 3). I measured beetle diversity with flight intercept traps, predation rates with attack marks left on artificial caterpillars and decomposition rates of bundles of small diameter wood around 20 pairs of young and veteran oaks in southern Norway. The artificial caterpillars were made from plasticine in three colors to mimic lepidoptera larvae found in Scandinavian forests. The bundles of wood consisted of 6 recent cut oak branches that were 1-3 cm in diameter. The flight intercept traps were active through the summer of 2017 and 2018, while the artificial caterpillars were deployed throughout the summer of 2018, and the bundles were placed out in the spring of 2017 and collected in fall of 2018.

In Paper 4, I used a mesocosm experiment to test how community complexity affects decomposition rates, wood mould creation and trophic structuring in tree hollows. Wooden boxes (50 x 30 x 30 cm) designed to simulate a tree hollow were made of oak and filled with material that was similar to what is found in tree hollows (wood mould taken from a dead hollow oak, oak leaf litter and sawdust). Additionally, the boxes were started with one of three treatments along a community complexity gradient: i) a complex community of macrofauna and mesofauna, ii) a simple community of mesofauna, iii) and only the defaunated material. In May 2017, a box with each of the treatments was hung on all 20 veteran trees (N = 60) and left in the field for 3 seasons. In October 2019, the boxes were retrieved and transported to the lab for further processing (Figure 4).



Figure 4: For Paper 4, large wooden boxes (50 x 30 x 30 cm) were constructed from oak boards and filled with material to imitate tree hollows (wood mould, oak leaf litter, and oak sawdust). The boxes were started with one of three treatments: complex community with macrofauna and mesofauna, simple community without the macrofauna, and only the defaunated material. In the simple community treatment, macrofauna were removed by hand, and in the defaunated treatment the material was treated with liquid nitrogen to kill all fauna (A). The boxes were then transported into the field (B) and one box from each treatment was hung from each of the 20 veteran oaks (C). The boxes remained in the field for three seasons, after which they were collected and transported back to the lab (D). The boxes were subsequently placed in a cooler room (5° C) for three months, to break possible diapauses, and were then moved to a warm room (15° C) with controlled light set on a 12-hour light/dark cycle. During this extraction process, a funnel leading to a collection vial with 98% ethanol was placed over the entrance hole of each box to collect dispersing invertebrates (E). After three months of this extraction process, the boxes were opened and the remaining invertebrates were captured by hand, and each layer of organic material (leaves, sawdust and wood mould) was weighted.

Measurement and identification of communities

Papers 1, 2 and 3 all used the same type of flight intercept traps: 20 x 40 cm windows with a funnel below leading to a vial containing ethylene glycol, water (4:1 mixture) and a drop of detergent used as a surfactant. For Paper 1, sampling was carried out with two traps per tree, one hanging in the canopy and one directly in front of the hollow. For Papers 2 and 3, sampling was carried out with a single trap hanging in the canopy (Figure 3). In all studies, the traps were active throughout the summer and emptied once a month from May to August. All beetles were identified to the species level following the taxonomy of The Norwegian Biodiversity Information Centre (NBIC 2018) by an expert. For Paper 2, all predatory beetles were selected for further analysis, and for Paper 3 all beetles involved in wood decomposition were selected. Trait information for all studies was collected from literature or calculated from available material, after which functional diversity was calculated for each of the groups of beetles.

For Paper 3, all branches originated from three living oaks and were collected early in May 2017. The branches were transported back to the lab where they were randomly mixed, sorted into

bundles and weighed. The bundles were then transported to the field sites between the 16th and the 25th of May 2017. One bundle was placed at the base of each tree, and one was hung from the canopy (Figure 3). The bundles remained in the field for two seasons and were retrieved in the middle of August 2018. Upon collection, the bundles were placed directly into rearing chambers in the field. Rearing chambers consisted of non-transparent cardboard barrels (50 cm diameter and 150 cm length) with a plastic lid and a transparent collection vial mounted on it. The bundles were then reared for one year in an open-air building at ambient temperatures (September 2018 to October 2019). The collection vials were emptied regularly and at the end of rearing all invertebrates found inside the barrels were collected. Beetles extracted from the bundles were identified to species in the same manner as the beetles collected in the flight intercept traps, and all other invertebrates collected during the extractions were identified to order.

For Paper 4, the boxes were placed in a cooler room (5° C) for three months after they were retrieved from the field so that the invertebrates would enter diapause. They were then moved to a warm room (15° C), and extracted for dispersing adult invertebrates for three months. Once the extractions were complete, the material inside the boxes was sorted for invertebrates. Additionally, 100 g samples from the wood mould were taken for nematode extractions. All adult beetles collected in the extraction traps and during the material sort were identified to species. Additionally, the beetle larvae were sorted into morpho groups within each box. One larva was selected from each group and sent for DNA barcoding in collaboration with NorBOLD. All other macrofauna were only identified to order. Nematodes were extracted by combination of sieving, decanting and funnel method (Renčo et al. 2012). After extractions, the nematodes in the water suspension were heat-killed, fixed in FAA and counted under a stereomicroscope (LEICA S8APO, Germany, magnification up to 80×). When abundance was over 200, at least 100 randomly selected nematodes were identified, and abundance of all genera were expressed to total nematode abundance at the end of identification. All individuals from the sample were identified if total abundance was under 200.

Measurement of ecosystem functions

Ecosystem functioning was measured in Papers 2, 3 and 4. In Paper 2, I measured predation rates with artificial caterpillars. The artificial caterpillars were made from plasticine, which was formed into cylinders by hand (20 - 30 mm long and 5 mm thick), and a metal wire was used to attach the caterpillars to a natural site of attachment. Six artificial caterpillars were placed 2-4 m from the trunk of the focal tree. Half were placed 1.5 - 2 m above the ground and the other half were placed at ground level. Three colors (green, brown and black) were chosen to mimic the variety of lepidoptera larvae commonly found in Scandinavian forests (Fig 3). The caterpillars were subjected to a 30-day exposure, and were collected and replaced once a month from May to August 2018. Attack marks on the artificial

caterpillars were documented in the field and verified in the lab. They were identified as being made by arthropods, birds, small mammals or an unknown source. In total, I deployed 720 artificial caterpillars, but 375 were found to be either missing or unidentifiable, presumably due to bird attacks. However, the remaining caterpillars (354) were well balanced within the experimental setup.

In Paper 3, I measured decomposition rates with small diameter oak branches using the methods previously described. Upon completing the process of extracting beetles from the bundles, the bundles were weighed, then oven dried at 103° C until the weight stabilized (approximately 7 days) before measuring dry mass and density. Density was calculated as the dry mass divided by the volume.

In Paper 4, I measured decomposition rates for the entire box and for each of the layers of material (leaves, sawdust and wood mould) as percent weight loss (PWL), which was calculated as start weight minus end weight, divided by the start weight. Moisture content for each of the layers was measured and the final weight was adjusted for this. I was not able to measure moisture content for the entire box, so the moisture content in the wood mould (presumably the most reliable measure of overall moisture in the box) was included as a covariate in the model. Additionally, 10 g of the wood mould was taken to measure the amount of nitrogen and phosphorus. Nitrogen and phosphorus concentrations were measured by *Landcare Research* (54 Gerald Street, Lincoln 7608 New Zealand). The samples were block digested using the Kjeldahl wet oxidation process (Rowland and Grimshaw 1985), and a QuikChem 8500 flow injection analyser was used to colorimetrically determine the nitrogen and phosphorus in the digested samples.

Data preparation and statistical analysis

Beetle trait information was used in Papers 1, 2 and 3 (Table 2). In Paper 1, I considered three functional groups of beetles: decomposers, predators and flower visitors. In Paper 2, I focused on beetle predators, while in Paper 3 I focused on wood-decomposing beetles. In all cases I chose traits that were relevant for the respective ecosystem function. Body size was used in all studies and for all functional groups, because it is closely linked to many life history traits such as life span and dispersal ability, and has been found to influence the amount and composition of resources used by the organism (Fountain-Jones et al. 2015, Gillespie et al. 2017, Moretti et al. 2017). For decomposers, I also used wood diameter and decay stage preference because a diversity of preferred habitats will likely aid the overall decomposition process of dead wood (Gossner et al. 2013). In Paper 1, I also included whether the species was a known polypore visitor because research suggests that beetles visiting polypores play a role in dispersing fungal spores (Birkemoe et al. 2018). However, this trait was not used in Paper 3 because I lacked information on too many species. For predators (Papers 1 and 2) and flower-visitors (Paper 1) I used peak activity date because having species active throughout the season will increase phenological overlap with potential prey species and flowering

plants (Gillespie et al. 2017, Moretti et al. 2017). In addition, I included the morphological traits of relative eye size for predators and body shape for flower-visitors. Eye size is linked to prey recognition as well as hunting strategy (Fountain-Jones et al. 2015, Moretti et al. 2017), and body shape may influence how the species interacts with floral architecture (Patt et al. 1997, Fountain-Jones et al. 2015). Trait information for beetle species was primarily collected from literature, but some trait information was calculated from available material.

Table 2: Overview of the traits used in the papers and the link to ecosystem functions.

Functional group	Trait	Paper	Link to ecosystem functions
Decomposer	Body size	1 & 3	Linked to many life history traits, and influences the amount and composition of resources that are used
	Decay stage	1 & 3	A diversity of preferred habitats aids the decomposition process
	Wood diameter	1 & 3	A diversity of preferred habitats aids the decomposition process
	Polypore visitor	1	Beetles visiting polypores play a role in dispersing fungal spores
Predator	Body size	1 & 2	Linked to many life history traits, and influences the amount and composition of resources that are used
	Activity time	1 & 2	Activity throughout the season increases phenological overlap with prey species
	Relative eye size	1 & 2	Linked to prey recognition and hunting strategy
Flower visitor	Body size	1	Linked to many life history traits, and influences the amount and composition of resources that are used
	Activity time	1	Activity throughout the season increases phenological overlap with flowering plants
	Body shape	1	Influence how the species interacts with floral architecture

I chose to use functional dispersion (FDis) as the measure of functional diversity in Papers 1, 2 and 3 because it accounts for species abundances, can be calculated for multiple traits and is only minimally sensitive to species richness (Laliberte and Legendre 2010). FDis is a measure of dispersion in trait space and is calculated as the mean distance of all species (weighted by abundances) to the centroid of the community in multidimensional trait space (Laliberte and Legendre 2010). In Paper 3, I also included the community weighted mean of each trait to gain insight into how mean trait values differed between veteran and young oaks. Community Weighted Mean (CWM) is defined as the mean values of a given trait present in the community, weighted by the relative abundance of the taxa bearing each trait value (Lavorel et al. 2007).

In order to incorporate substrate density at different spatial scales (Paper 1) and to verify that tree cover was similar between the veteran and the young trees (Papers 2 and 3), I used Copernicus tree cover density maps with 20 m resolution. I calculated the tree cover density at the 20 m scale, the 100 m scale and the standard deviation at the 100 m scale for all trees (CLMS 2012 & 15), which enabled

me to have one scale that was finer and one that was coarser than the habitat class variable obtained in the field (50 m). Since sampling ended in 2011, in Paper 1 I used the 2012 maps when possible, but when there was missing data, I included data from 2015, while in Papers 2 and 3 I only used maps from 2015. In Paper 1, I also included a measure of the connectivity of the study trees to other veteran oaks at different spatial scales. Connectivity was estimated with a published distribution model for veteran oaks (Skarpaas et al. 2017) by summing the predicted probabilities of occurrence of veteran oaks for all pixels in radii of 0.5-25 km of the focal tree (Table 3).

Table 3: Variables that describe the veteran oaks and the surrounding landscape.

Variable	Type	Measurement	Reference
Tree circumference	Continuous	Tree circumference at breast height in cm. Natural logarithm taken	Sverdrup-Thygeson et al. (2010)
Light availability	Continuous	Slope*cos(Aspect-45)	Stage (1976), Stage and Salas (2007)
Vitality	Categorical (2 levels)	Healthy: 20% or more living canopy Senescent: < 20% living canopy	Sverdrup-Thygeson et al. (2017)
Regrowth	Categorical (3 levels)	Open: no regrowth around oak Shrubs: low vegetation, shrubs or small trees Trees: trees with height similar to the focal tree	Sverdrup-Thygeson et al. (2017)
Connectivity (8 variables)	Continuous	Predicted number of hollow oaks within 0.5km, 1km, 2km, 3km,4km,5km,10km, and 25km of focal tree	Skarpaas et al. (2017)
Habitat class	Categorical (2 levels)	Forest or open landscape: based on 50 m radius surrounding the tree. Open landscapes were either parks or agricultural landscapes	Sverdrup-Thygeson et al. (2010)
Tree cover density (3 variables)	Continuous	20 m: the percent of the 20 m pixel with the focal tree that is covered by forest. 100 m: the percent of 20 m pixels covered by forests within 100 m radius of the focal tree. Standard deviation: the standard deviation of the percent of 20m pixels covered by forests within 100m radius of focal tree	Copernicus Tree Cover Density (2012 & 15)

In all papers, analyses were carried out in R version 3.4.0 (R Development Core Team 2017), and I also used similar statistical methods (Table 4). Prior to statistical analysis, I followed the steps for data exploration outlined by Zuur et al. (2010). The best model in each case was chosen with backward model selection based on Akaike Information Criterion (AIC). I modeled all response variables that were approximately normally distributed with linear mixed models (LMM), and all response variables that were count data with generalized linear mixed models (GLMM) with Poisson distribution. I subsequently visually checked the assumptions of the LMMs for normal distribution of the residuals and homoscedasticity (Zuur et al. 2009, Zuur et al. 2010) and checked the assumption of the GLMMs that the variance was equal to mean with the function *dispersion_glm* from the ‘blmeco’ package (Korner-Nievergelt et al. 2015). In the case of the invertebrate attack marks on the artificial caterpillars

(Paper 2) and macrofauna detritivores and diptera abundance (Paper 4), I detected overdispersion ($\sigma^2 > \mu$), and subsequently modeled them with negative binomial distribution (Zuur et al. 2009). Additionally, I checked for influential observations, and spatial and temporal structure that was not accounted for by the model (Zuur et al. 2009).

Table 4: A summary of statistical methods (LMM is linear mixed models and GLMM is generalized linear mixed models).

Statistical method	Response variable			
	Paper 1	Paper 2	Paper 3	Paper 4
LMM	FDis	FDis	FDis and wood density	Weight loss and nematode indices
GLMM (Poisson)	Species richness	Species richness	Species richness	Species richness and abundances
GLMM (negative binomial)		Attack marks		Macrofauna detritivores and diptera abundance
Random effect	Year and tree	Sampling block	Sampling block	Tree

Main results

In Paper 1, I found that the features and surroundings of the veteran oaks influenced species richness and functional diversity of beetles, whether classified as decomposers, predators or flower-visitors (Figure 5). For all groups, I found that when the veteran trees were situated in forest rather than open landscapes both species richness and functional diversity were higher. Apart from this, the additional predictors differed between groups, and between species richness and functional diversity. I found that decomposer species richness responded to the vitality of the tree, being higher in senescent trees, while their functional diversity increased with connectivity in open landscapes. Predator species richness increased with shrub regrowth, while their functional diversity increased with tree circumference. There were no additional predictors of flower-visitor species richness or functional diversity.

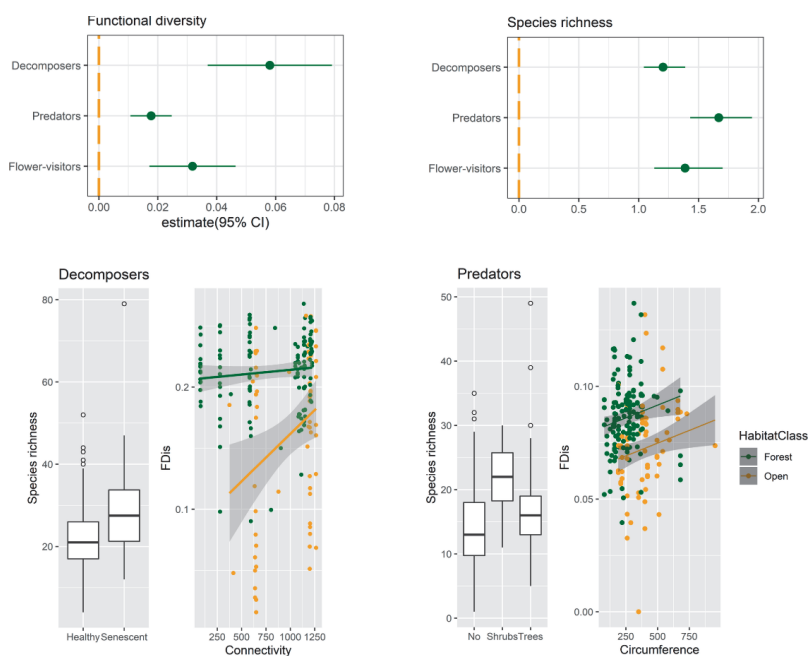


Figure 5: Main results from Paper 1. *Top plots:* across all groups, functional diversity (left plot) and species richness (right plot) was significantly higher in traps mounted on veteran oaks surrounded by forest (green) than those in open landscapes (yellow). *Bottom left plots:* decomposer species richness was significantly higher in traps mounted on senescent trees than healthy ones, and functional diversity (FDIs) increased significantly with connectivity (X-axis, measured as the number of predicted veteran oaks within a 5km radius of the focal tree) in open landscapes, while there was no effect in forests. *Bottom right plots:* predator species richness was significantly higher when there was regrowth of shrubs around the trees, and functional diversity (FDIs) increased significantly with tree circumference. All boxplots show the median, first and third quartiles, with whisker that extend 1.5 times the interquartile range. In all plots, the veteran oaks in open landscapes are colored yellow and the ones in forests are colored green.

In Paper 2, I found that there was higher predatory beetle diversity (both taxonomic and functional) and invertebrate attack rates around veteran oaks than around young oaks (Figure 6). I also found that the diversity of predatory beetles and invertebrate attack rates decreased in parallel through the season, indicating that they were interrelated. Additionally, I found that arthropod predators attacked the green artificial caterpillars less, and the caterpillars placed on the ground were attacked more.

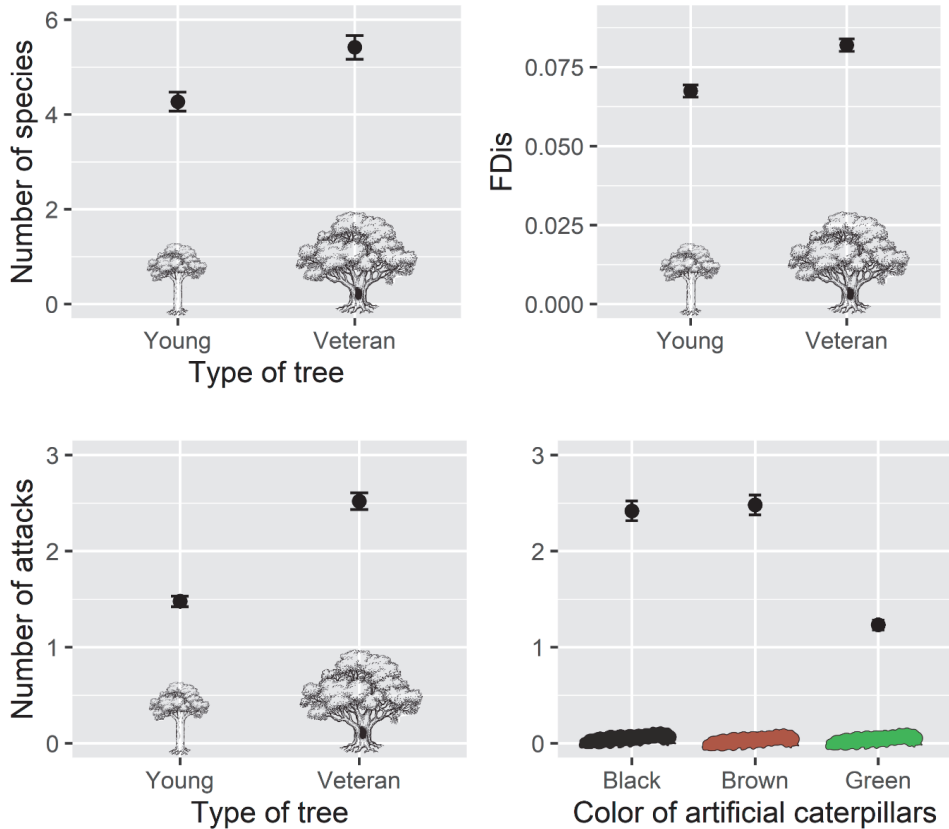


Figure 6: Main results from Paper 2. The top plots are estimates from the models that predicted species richness (left plot) and functional diversity (right plot) of predatory beetles (\pm SEM; $n=238$ from 40 trees). The bottom plots are of the estimated invertebrate attack rates on the artificial caterpillars (\pm SEM; $n=345$).

In Paper 3, I found that the number of beetle species involved in decomposition of wood was higher around veteran than young oaks (Figure 7). This pattern was mirrored by a significant, although less pronounced, increase in functional diversity around veteran oaks. I also found that the main difference in the wood decomposing beetles' traits was that beetles around the veteran trees preferred larger diameter wood than the communities around the young tree. The greater diversity of beetles did not result in higher colonization rates of the wood bundles, and the density of the bundles was significantly higher around the veteran trees, indicating lower decomposition rates.

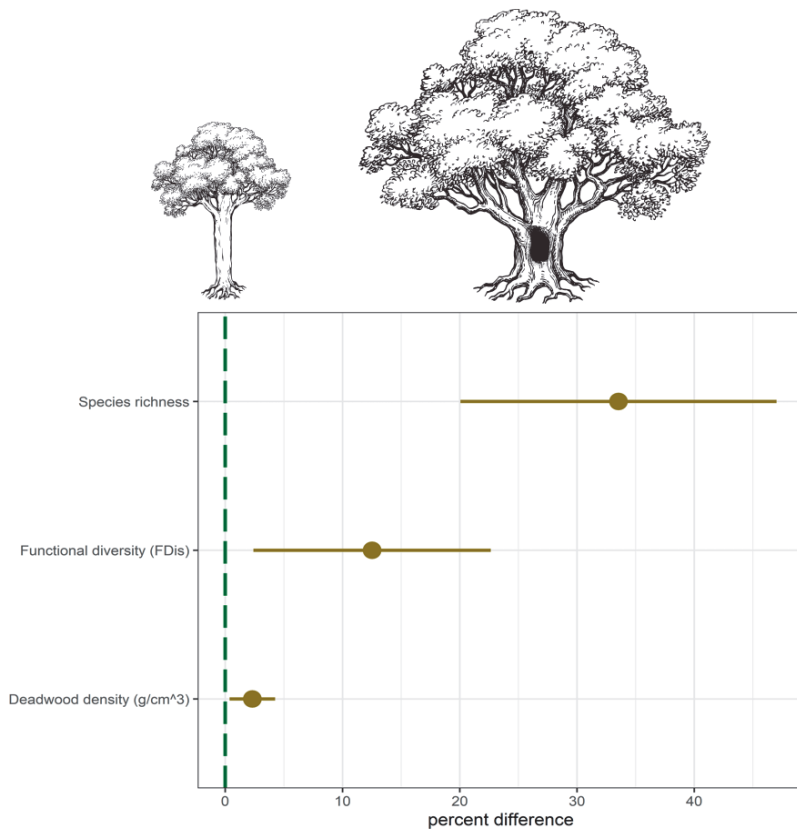


Figure 7: Main results from Paper 3. The percent difference between paired young (green line) and veteran (brown points) oak trees for wood-decomposing beetle species richness, beetle community functional diversity, and the post-experiment density of the wood bundles. Error bars show 95% confidence intervals, based on regression models.

In Paper 4, I found that the decomposition rate of all the organic material combined was highest in the complex community treatment (Table 5). I also found that the complex community treatment had the most wood mould, and contained the highest concentration of nitrogen and phosphorus. Additionally, there was mixing of the organic layers (leaves, sawdust and wood mould) in the complex community treatment. This contrasted with the other treatments, where layers remained distinct and the nutrients were significantly lower in the mould. The results thus indicate that within the complex community treatments wood mould was being created from the sawdust and leaves, whereas it was primarily being diminished in the other treatments. Also, the complex community treatment remained the most complex in terms of community structure at the end of the experiment; it had a greater diversity of organisms and trophic structuring in both the macrofauna and the mesofauna.

Table 5: Model results from Paper 4. Decomposition was measured as percent weight loss (PWL), and was calculated as start weight minus end weight divided by the start weight. Nitrogen and phosphorus were only measured in the wood mould. All response variables related to decomposition and nematodes were modeled with a linear mixed effect model, while response variables related to macrofauna were count data and subsequently modeled with generalized linear mixed models with Poisson distribution. In all models, treatment was included as a fixed effect and tree as a random effect. Treatments that were significantly different are reported in the column ‘Significant treatment’, and the corresponding direction of this effect is reported in the column ‘Direction of the effect’. When all treatments were significantly different, I reported All, and when there were not different, I reported Not significant.

	Response	Significant treatment	Direction of the effect	P value
Decomposition				
	Box (PWL)	Complex community	-	0.006
	Sawdust (PWL)	Complex community	-	0.023
	Leaves (PWL)	Defaunated	+	0.036
	Wood mould (PWL)	Complex community	+	0.002
	Nitrogen	Simple community	-	0.005
	Phosphorus	Complex community	+	0.03
Macrofauna				
	Predators	Complex community	+	0.004
	Detritivores	Not significant		0.733
	Beetle SR	Complex community	+	>0.001
	Diptera abundance	Defaunated	+	0.028
Nematodes				
	Structure index	Complex community	+	>0.001
	Maturity index	All	Increasing with complexity	>0.001
	Channel index	All	Simple, Complex, Defaunated (high to low)	>0.001
	Omnivores %	Complex community	+	>0.001
	Fungivores %	Simple community	+	>0.001
	Bacterivores %	Defaunated	+	>0.001

Discussion

The aim of this project has been to explore the multifaceted drivers of diversity within veteran oak invertebrate communities, and to measure the communities' contribution to ecosystem functioning. In the following section, I discuss some of the central findings of this research and address the questions identified in the introduction. I begin by discussing biodiversity in veteran trees, and then move to discussing this in context of the habitat heterogeneity hypothesis. Next, I discuss the relationship between veteran trees biodiversity and ecosystem functioning, and then focus more directly on decomposition and predation in this context. I end with some reflections on the implications for management and possibilities for future research.

Veteran trees and biodiversity

The strongest trend, that held across all my research, was that veteran oaks in Norway have a very high number of beetle species associated with them. These findings are supported by other work in Norway (Sverdrup-Thygeson 2009, Gough et al. 2014, Pilskog et al. 2016) and are consistent with findings related to veteran trees throughout Europe (Müller et al. 2013, Siitonen and Ranius 2015, Parmain and Bouget 2018, Sánchez-Galván et al. 2018). Prior studies, however, have focused exclusively on veteran oaks, and Papers 2 and 3 are the first studies to contrast differences in diversity of beetles around veteran and young oaks in Norway. In Papers 2 and 3, I found 20-30% more species of predatory and wood-decomposing beetles around veteran oaks than young oaks in the same landscape and with similar immediate surroundings. These high levels of beetle diversity included both taxonomic and functional diversity. In addition to being important for conservation, the greater levels of functional diversity are likely to promote multiple ecosystem processes and make these processes more resistant and resilient to change (Grime et al. 1997, Diaz and Cabido 2001, Folke et al. 2004, Reiss et al. 2009, Tilman et al. 2014).

I also captured many species of beetles around the young oaks in Papers 2 and 3, and it is possible that these numbers were higher due to the presence of veteran trees in the area. Results from Paper 1 indicates the number of veteran trees in an area (at scales up to 10 km) is a positive predictor of beetle diversity, and this is supported by similar findings from other research (Sverdrup-Thygeson et al. 2010, Pilskog 2016, Sverdrup-Thygeson et al. 2017). Thus, the differences in diversity between the veteran and the young oaks that I observed may be even greater if there were no veteran trees in the landscapes surrounding the young trees. Additionally, the results from Paper 4 indicate that the presence of macrofauna (especially beetles) in tree hollows can have far reaching effects that influence multiple trophic levels and increase habitat quality and ecosystem functioning.

Habitat heterogeneity

As described in the introduction, the habitat heterogeneity hypothesis suggests that as the number of habitats increases within an area so will the number of species (Simpson 1949, Tews et al. 2004). Support for this hypothesis has been found in regards to beetle diversity in dead wood and in veteran trees (Müller et al. 2013, Seibold et al. 2016b). In Paper 1, I found that different aspects of the trees and their landscapes influence different groups of beetles. This highlights the importance of habitat heterogeneity provided by veteran trees, and indicates that it affects multiple spatial scales. Landscape-scale habitat heterogeneity may positively contribute to diversity, even within communities that have poor dispersal ability, because it provides different niches and refuges (Vanbergen et al. 2007). Additionally, the different functional groups diverged in their response to tree qualities and the landscape, which indicates that habitat heterogeneity is not only important for taxonomic diversity, but can also increase functional diversity (Müller et al. 2013).

Predatory beetle diversity seemed to be strongly influenced by habitat heterogeneity at the local scale. In Paper 1, I found that their diversity increased with tree size and regrowth of shrubs around the trees, both of which were measured at the local scale and have a strong link to habitat heterogeneity (Ranius and Jansson 2000, Parmain and Bouget 2018). In Paper 2, there was a significant difference between the veteran and the young trees, and predation rates were higher at the ground level. This latter finding indicates that carabids (ground beetles) may be important predators associated with veteran trees. A greater diversity of habitats increase invertebrate prey diversity and promote diverse hunting strategies (Snyder 2019), which can result in a greater diversity of invertebrate predators. These findings are supported by research on ground beetles, which have been found to be positively influenced by habitat heterogeneity (including vegetation cover) at the local scales, but less so at large scales (Brose 2003a, Brose 2003b, Tews et al. 2004, Lilleeng et al. 2018).

On the other hand, there was more of an overlap between the importance of habitat amount and heterogeneity in relation to beetles involved with decomposition, and the effects were at both the local and the landscape scale. In Paper 1, decomposer beetles responded to the number of veteran trees in the landscape and tree senescence. In both cases, there was a strong correlation between habitat amount and heterogeneity. Experimental studies with dead wood highlight the importance of habitat heterogeneity at the local scale for saproxylic beetle diversity (Seibold et al. 2016b), whereas studies related to habitat amount have been inconclusive (Seibold et al. 2017). In Paper 3, I did not find an effect of number of veteran trees in the landscape and tree senescence, but there was likely not enough variation in these to measure an effect. I did, however, find that there were more wood decomposing beetles that preferred large diameter dead wood around veteran trees, which also indicates that heterogeneity in wood diameter may be an important driver of beetle diversity around veteran trees.

Although habitat heterogeneity seems to be important, it is not the only factor leading to high levels of biodiversity in veteran trees. In Paper 4, I found that starting a simulated tree hollow with a complex community resulted in greater habitat quality and diversity in both the macrofauna and the mesofauna. These communities were also more structured and mature, even in the groups that were not directly manipulated. The results thus indicate a positive feedback, where a greater diversity within a community creates a higher quality habitat. Results from Paper 4 also highlight the role of stochastic processes, specifically priority effects (the order in which the species arrived), in creating and maintaining diversity at larger scales, and this has been found in other research as well (Fukami et al. 2010). However, this may have been a temporary effect, and it remains unknown if given enough time, the communities would have become similar, or if the differences that I observed would have persisted.

Biodiversity and ecosystem functioning

Linking biodiversity to ecosystem functioning has been a central theme of my research, but it has also posed considerable challenges. In Paper 1, I did not measure ecosystem functioning directly, but instead inferred that ecosystem functions would be greater with a diversity of relevant traits within functional groups. Traits information is difficult and time consuming to collect, and it is typically more detailed and readily available for common and pest species. Additionally, it is difficult to choose the most relevant traits. While I have based my choices on other research (Fountain-Jones et al. 2015, Moretti et al. 2017), this research remains limited and speculative. Another issue related to traits is that I have only considered interspecific variation, which is the most common method (Wong et al. 2019). However, some research on the topic indicates that intraspecific trait variation may also influence ecosystem functions (Johnson et al., 2012), but the importance of intraspecific trait variation remains an open question in regards to terrestrial arthropods and ecosystem functioning (Wong et al. 2019).

In Papers 2 and 3, I attempted to directly measure the effect of biodiversity on ecosystem functioning with field experiments that contrasted ecosystem functions around veteran trees with young trees in the same landscapes. I found that the assumption of Paper 1 held for invertebrate predation (Paper 2), or in other words, greater diversity of beetle predators coincided with higher levels of invertebrate predation. However, I found the opposite effect in Paper 3, where decomposition of small diameter wood in early decay was negatively related to the presence of the veteran tree, even though veteran trees had greater diversity of wood decomposing beetles around them. In Paper 4, I manipulated an entire tree hollow system, and found evidence that community complexity does indeed increase decomposition rates. Thus, the results from my research indicate that the biodiversity associated with veteran trees influences ecosystem functions, but that the effects are not always positive.

On one hand, high levels of diversity, especially functional diversity, are usually associated with increased ecosystem functioning (Lefcheck and Duffy 2015). Facilitative interactions and resource and time partitioning are likely to increase ecosystem functioning (Gessner et al. 2010), and this may

explain the positive effects that were observed in Paper 2 and 4. On the other hand, antagonistic relationships, such as competition, predation and parasitism, may slow ecosystem functioning (Gessner et al. 2010, A'Bear et al. 2014). Research indicates that high levels of fungal diversity can slow decomposition rates because competing fungi release inhibitory compounds (Cox et al. 2001, Yang et al. 2016, Skelton et al. 2019). I speculate that this may explain the results in Paper 3 (slower decomposition rates around veteran trees) as there is strong evidence to support the assumption that there was greater fungal diversity around the veteran trees (Heilmann-Clausen and Christensen 2004, Bütler et al. 2013, Parmain and Bouget 2018). Nevertheless, I did not measure fungal diversity or attempt to control for it in my experimental design, so this remains highly speculative and requires more research.

Decomposition

Decomposition is a complex process, and broad trends that relate biodiversity to decomposition are lacking (Hättenschwiler et al. 2005). Specifically, the role macrofauna plays in the process of decomposition remains poorly understood and highly debated (Gessner et al. 2010, A'Bear et al. 2014, David 2014, Ratcliffe et al. 2017, Joly et al. 2020). One of the main issues is that the effects are often context dependent (Gessner et al. 2010, A'Bear et al. 2014, Joly et al. 2018). The results in Paper 4 support this assertion, as the effect of community complexity was mediated by the quality of the decomposing material. Importantly, only considering one aspect of decomposition may lead to different results than if the process was considered more holistically. For instance, in Paper 4 when the layers of material were considered independently, greater diversity did not always lead to higher levels of decomposition, but when considered together, overall decomposition was greater in the complex community treatment.

In Paper 3, decomposition was narrowly defined (early decay and small diameter wood), and this may have influenced the results. However, evidence suggests the net cumulative effect of all invertebrates on wood decomposition is accelerative, especially during the early stages of decomposition (Ulyshen 2016). In Paper 3, I collected much fewer beetles from the bundles of experimentally added wood than previous research that used similar methodology (Ferro et al. 2009, Brin et al. 2011, Seibold et al. 2018). The most likely reason for this difference is that I left the bundles of wood out for two seasons (to increase the amount of time for decomposition to progress), but most beetles specialized on fresh deadwood only take a year to complete their life cycles (Seibold et al. 2018). Therefore, the beetles colonizing the bundles likely dispersed before they were collected. While this did not introduce systematic differences between the veteran and the young tree, it would have been informative to determine if there were differences in colonizing beetles and how this related to decomposition rates. The results related to the differences in traits between the beetle communities around veteran and young trees indicate that there were not large differences in the beetles that inhabit the small diameter wood. Therefore, it seems most likely that the results were not driven by beetles but

rather difference in fungal diversity, as previously discussed. It should also be pointed out that this was a short-term study and the long-term effects remain unknown. In fact, there is a general need for long-term studies on the role of invertebrates in wood decomposition (Ulyshen 2016).

Predation

The results from Paper 2 are the first to find that the diversity of natural enemies and invertebrate predation rates are higher around veteran trees than young trees, given an otherwise similar habitat. These findings are not so surprising, however, considering that research related to predation by natural enemies highlights the importance of landscape structure (Snyder 2019) and that veteran trees are considered keystone structures (Müller et al. 2013, Parmain and Bouget 2018). Results from Paper 1 indicate that the benefits of veteran trees for predation may increase with size and age (since they are correlated) of the tree. These findings also indicate it may be possible for managers to enhance the benefits of invertebrate predators associated with veteran trees by allowing some regrowth around the trees.

The effects of large-scale landscape features on predation around veteran trees remains largely unexplored. Paper 2 focused on the dichotomy between veteran and young trees at rather small spatial scales (200 m or less), but large scale anthropogenic factors such as urbanization gradients have also been found to influence predation rates by natural enemies (Ferrante et al. 2014, Perez-Alvarez et al. 2019). In contrast, Paper 1 only found effects at relatively small spatial scales. This is more in line with research within agroecosystems that found that strips of non-agriculture area with resources for natural enemies reduce pests and crop plant damage independent of landscape complexity (Tschumi et al. 2015). Thus, while it is clear that veteran trees should not be considered independent units (Sverdrup-Thygeson et al. 2010), the interaction between local and regional landscape effects and predation around veteran trees needs more research.

Conservation and management implications

As previously discussed, my findings support the large body of other work indicating that veteran trees support high levels of biodiversity. Most of the work on veteran trees has focused on species richness and red listed species (Sverdrup-Thygeson 2009, Müller et al. 2013, Gough et al. 2014, Gough et al. 2015, Sverdrup-Thygeson et al. 2017, Parmain and Bouget 2018, Pilskog et al. 2020), and both aspects of insect diversity are important. However, recent reports regarding global insect declines indicate that insects are not just declining in terms of species but also in abundances (Wagner 2020). In my research, all measures of functional diversity were abundance weighted, but I did not consider overall beetle abundances independently. Nevertheless, results from Papers 2 and 3 also indicate that veteran oaks have greater abundances of beetles than young oaks. Other research has also found that abundances

within certain groups of beetles increase with the size of the tree (Pilskog et al. 2020). This further highlights the benefits of veteran oaks for biodiversity, and indicates that their conservation may be a step in the critical process of halting the global insect decline.

Results from Paper 1 indicate that veteran trees in forests are especially valuable for diversity of beetles. The results from Papers 2 and 3 also indicate that veteran trees are influencing ecosystem functioning. The modern forestry practice of clear cutting has been identified as a main threat to forest biodiversity (Kuuluvainen 2009), but the retention of a few trees and large diameter deadwood has been found to offset some of these adverse effects (Rosenvald and Löhmus 2008, Rudolphi et al. 2014). However, findings from a recent review indicate that the prevailing retention practices in northern Europe lack ecological credibility in safeguarding biodiversity and are in urgent need of development to meet ecological sustainability goals (Kuuluvainen et al. 2019). Norwegian forest guidelines suggest that veteran oaks should be left during cutting (MiS 2017). However, in many cases trees are not allowed to grow old, and this is a major barrier for veteran tree recruitment (Lindenmayer and Laurance 2016). If managers commit to long-term protection of certain younger trees that can grow old (e.g.: oak), my findings indicate that this could be beneficial for both conservation and ecosystem functioning. The time scale that is required for these practices to have an effect is daunting, and this highlights the need for rapid action to support recruitment and strict protection of the veteran trees that currently exists.

Large wooden boxes, like the ones used in Paper 4, have been suggested as a conservation tool that could be used to reduce the impact of habitat loss on beetles that are dependent on tree hollows (Jansson et al. 2009, Carlsson et al. 2016). Although I used these boxes primarily to test ecological theory, our results might also add information about their use for conservation purposes. I found that specialized invertebrates in tree hollows were able to survive and reproduce when they were introduced into the boxes, and others were able to colonize the boxes as well. These findings are in line with previous research (Jansson et al. 2009, Carlsson et al. 2016, Mestre et al. 2018). However, the boxes in my study dried out, and many of the introduced beetles died during the study. To some extent, this could have been mitigated with a better design for the boxes that prevented moisture loss (the metal trays placed in the bottom of the boxes to prevent moisture loss degraded during the study), but our results indicate that even under the best circumstances large wooden boxes provide short term and low-quality habitat.

Large wooden boxes have much lower habitat heterogeneity than actual tree hollows. For instance, the walls of a tree hollow are comprised of a gradient of dead and dying wood, have complex structure created by insect galleries and can have fungal fruiting bodies growing out of them (Stokland et al. 2012, Bütler et al. 2013, Quinto et al. 2014). I found that after 3 years in the field, the walls of the boxes remained homogenous, with smooth structure and limited decay. The results also indicated that organic material needs to be added to the boxes, as it decomposed relatively quickly, and even the best made boxes would likely last no more than one or two decades (Carlsson et al. 2016). This contrasts

greatly with tree hollows, which improve as a habitat with time and can persist for hundreds of years. Although there is limited amount of research on the topic, veteranisation of younger trees likely has greater conservation value and broader application. It is possible to create multiple habitats associated with veteran trees in younger trees (Bengtsson et al. 2012, Rueegger 2017), and these habitats may improve with time (Menkis et al. 2020). However, large wooden boxes could be used in some specific conservation settings, such as steppingstones to connect isolate habitats or as a tool to introduce species into an area. The results from Paper 4 indicate that boxes will provide higher quality habitat for a longer period of time if they are started with a full community of invertebrates. Large wooden boxes designed to simulate tree hollows are an innovative tool with some conservation applications but are in no way a substitute for adequate protection of veteran trees.

Future outlook

There are many questions related to biodiversity and ecosystem functioning raised by my work that could be addressed in future research. The most obvious is to further explore the relationship between wood decomposition and veteran trees. It would be very interesting to determine the mechanisms behind the finding in Paper 3, that decomposition was slower around veteran trees. A better understanding of the conditions that lead to biodiversity being negatively related to ecosystem functioning would greatly add to the field and provide insights valuable for managers. With the data that I currently have, it would be possible to look more broadly at differences in beetle abundances and species richness between the veteran and the young oaks, and relate this to their red list status and rareness. This would provide additional information about the conservation value of veteran trees and might highlight species that are especially dependent on these trees. A possibility for a more applied avenue of research would be to attempt to boost the diversity in an agricultural system (perhaps an orchard) with large wooden boxes, and measure how this influences ecosystem functions such as predation by natural enemies or pollination. This research may provide an example of how veteran trees and their communities can be integrated into sustainable agriculture, and help develop practical methods and tools to carry this out.

Conclusion

The findings from my research support the conclusion that veteran trees are important for biodiversity, and indicate that veteran trees and their communities influence ecosystem functions, such as invertebrate predation and decomposition. They also highlight the importance of community complexity and habitat heterogeneity for promoting biodiversity and ecosystem functioning. This is extremely important due to the current global decline in veteran trees (Lindenmayer et al. 2012) and insects (Sánchez-Bayo and Wyckhuys 2019, Wagner 2020) which is likely to compromise important ecosystem functioning. Since habitat destruction is a primary driver of insect declines (Sánchez-Bayo and Wyckhuys 2019), the conservation of veteran oaks is an important measure to prevent a continuation of this process and to preserve these valuable entities. Veteran oaks offer a unique habitat for a wide range of insects, and these trees and their communities influence ecosystem processes. My findings also indicate that there is a potential for synergies between the conservation of veteran trees and sustainable agriculture and forestry. Protecting and valuing veteran trees and their communities, and reintegrating them into land use practices, is an essential step towards a more sustainable system of management, and has the possibility of enhancing the wellbeing of people while promoting biodiversity.

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Paper I

Hollow oaks and beetle functional diversity: Significance of surroundings extends beyond taxonomy

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Abstract

Veteran hollow oaks (*Quercus* spp.) are keystone structures hosting high insect diversity but are declining in numbers due to intensification of land use and the abandonment of traditional management. The loss of this vital habitat is resulting in a reduction of biodiversity, and this likely has consequences for ecosystem functioning, especially if functional diversity is reduced. A considerable amount of research has been done on predictors of beetle taxonomic diversity in veteran oaks, but predictors of functional diversity have remained largely unexplored. The aim of this study was to establish whether the features and surroundings of veteran oaks are related to functional diversity within three functional groups of beetles (decomposers, predators, and flower visitors) and determine whether species richness and functional diversity within the groups are dependent on the same predictors. Sampling was carried out intermittently between 2004 and 2011 on 61 veteran oaks in Southern Norway. Of the 876 beetle species that were collected, 359 were determined to be decomposers, 284 were predators, and 85 were flower visitors. Species richness and functional diversity in all groups were consistently higher in traps mounted on veteran oaks in forests than in open landscapes. However, additional predictors differed between groups, and for species richness and functional diversity. Decomposer species richness responded to tree vitality, while functional diversity responded to habitat connectivity, predator species richness responded to regrowth of shrubs while functional diversity responded to tree circumference, and flower visitor richness and functional diversity did not respond to any additional predictors. Previous studies have found that the features and surroundings of veteran oaks are important for conservation of taxonomic diversity, and the results from this study indicate that they are also important for functional diversity within multiple functional groups.

KEYWORDS

biodiversity and ecosystem functioning, coleoptera, functional diversity, invertebrate conservation, *Quercus* spp., saproxylic beetles, veteran trees

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1 | INTRODUCTION

Human activities are converting and degrading ecosystems at unprecedented levels (Newbold et al., 2015), and this has resulted in dramatic biodiversity loss in the last 50 years (Reid et al., 2005). This decline is predicted to continue or even accelerate in the coming years (Newbold et al., 2015). Biodiversity regulates ecosystem processes such as energy and matter fluxes over space and time, and maintenance of life on earth depends on these processes (Laureto, Cianciaruso, & Samia, 2015). Therefore, this is a greater problem than a reduction in the number of species, as there is robust evidence that biodiversity has a positive effect on ecosystem functioning (Brose & Hillebrand, 2016; Cardinale et al., 2012; Laureto et al., 2015).

Although there is a link between biodiversity and ecosystem functioning, the relationship is not straightforward (Lefcheck & Duffy, 2015). Ecosystem functioning is more closely related to species trait diversity than to species richness (Heemsbergen et al., 2004; Lefcheck & Duffy, 2015). A diversity of effect traits, that is, an aspect of an organism's morphology, physiology, phenology, or behavior with an effect of ecosystem processes (Reiss, Bridle, Montoya, & Woodward, 2009), promotes multiple ecosystem processes and makes these processes more resistant and resilient to change (Diaz & Cabido, 2001; Folke et al., 2004; Grime et al., 1997; Reiss et al., 2009; Tilman, Isbell, & Cowles, 2014). Studies on functional diversity have the potential to reveal patterns that studies on taxonomic diversity are unable to detect and allow for the possibility to draw inferences about effects on ecosystem functioning (Cadotte, Carscadden, & Mirotnick, 2011; Hooper et al., 2005; Laureto et al., 2015; Mouillot et al., 2013). Therefore, identifying drivers of functional diversity is a crucial step in the process of predicting and possibly mitigating reduction of ecosystem functioning.

Veteran trees are keystone structures in forest, agricultural landscapes, and urban areas (Lindenmayer, Laurance, & Franklin, 2012; Müller, Jarzabek-Müller, Bussler, & Gossner, 2013; Parmain & Bouget, 2018). The size and age of veteran trees, as well as their coarse bark, structurally complex canopies, and sheltered nutrient-rich cavities provide features that support high biodiversity (Lindenmayer et al., 2012; Parmain & Bouget, 2018). However, veteran trees are in decline globally as a result of intensification of land use and the abandonment of traditional management (Siitonen & Ranius, 2015). Veteran oaks (*Quercus* spp.) are especially important for biodiversity in Northern European forest (Siitonen & Ranius, 2015). The community of invertebrates associated with veteran oaks is of high management interest and is important for decomposition and nutrient recycling, and also has high diversity of predators and flower visitors (Ranius, Niklasson, & Berg, 2009b; Sverdrup-Thygeson, Skarpaas, & Ødegaard, 2010).

A considerable body of work has gone into identifying the main predictors of taxonomic diversity of veteran oak beetle communities, and it is well established that the features and surroundings of the tree influence the community (Micó, 2018). The main factors that have been shown to affect species richness are tree size, regrowth around the tree, sun exposure and temperature, amount and

diversity of dead wood, height of the hollow, hollow and wood mold volume, habitat isolation, and stand maturity (Gossner et al., 2016; Gough, Birkemoe, & Sverdrup-Thygeson, 2014; Micó, García-López, Sánchez, Juárez, & Galante, 2015; Miklín et al., 2018; Parmain & Bouget, 2018; Pilskog, Birkemoe, Framstad, & Sverdrup-Thygeson, 2016; Ranius & Jansson, 2000; Ranius, Niklasson, & Berg, 2009a; Sverdrup-Thygeson et al., 2010). Furthermore, there has been a noted distinction between beetle communities in veteran trees in forests and similar trees in open landscapes (Parmain & Bouget, 2018; Sverdrup-Thygeson, Skarpaas, Blumentrath, Birkemoe, & Evju, 2017; Sverdrup-Thygeson et al., 2010). Research has also found that oak-dependent saproxylic species respond to substrate density across different spatial scales (Bergman, Jansson, Claesson, Palmer, & Milberg, 2012; Sverdrup-Thygeson et al., 2017).

Although recent studies have begun to focus on traits in addition to taxonomic diversity, this work has been primarily focused on trophic levels (Pilskog et al., 2016), patterns associated with specialists and generalists (Sverdrup-Thygeson et al., 2017), and the response of traits to management strategies (Gossner et al., 2013; Janssen, Fuhr, Cateau, Nusillard, & Bouget, 2017). To our knowledge, no work has been done on veteran oak beetle community effect traits, and it is unknown how the features and surroundings of veteran oaks will affect this community's functional diversity.

The aim of this study was to establish how the features and surroundings of veteran oaks are related to functional diversity within three functional groups (decomposers, predators, and flower visitors) and determine whether species richness and functional diversity within the groups are dependent on the same set of predictors. We chose traits that were relevant for their respective ecosystem function and therefore considered different effect traits within each group. The advantage of this approach is that it is possible to observe patterns that are relevant for both conservation and ecosystem functioning (Brose & Hillebrand, 2016; Fountain-Jones, Baker, & Jordan, 2015; Laureto et al., 2015; Mayfield et al., 2010; Tilman et al., 2014).

Since the functional groups depend on different resources and we considered different traits within the groups, we expected different predictors to be important for the groups. We expected diversity in decomposers to respond to predictors associated with the amount and diversity of dead wood (e.g., forest cover, tree vitality, and presence of other hollow trees), predator diversity to respond to predictors associated with the amount and diversity of prey (e.g., tree size, which increase the number and diversity of microhabitats), and flower visitor diversity to the abundance and richness of flowering plants (e.g., light and openness, and regrowth around the trees).

2 | MATERIAL AND METHODS

Sampling was carried out on 61 veteran hollow oaks (*Quercus robur* and *Q. petraea*) at 27 sites in the main distribution of oaks in Southern Norway (Figure 4). Sites were originally selected based on forest inventories of hollow oaks from the forestry sector and the municipalities. Some of the sites had cluster of up to five trees, while

others had just one tree. The data set used in this study was collected intermittently between 2004 and 2011 and is part of a long-term study of veteran oaks and the National Program for Surveying and Monitoring Biodiversity in Norway (ARKO, 2011). A veteran hollow oak was defined with national management regulations, as a tree of at least 95cm circumference with a visible cavity in the trunk (Lovdata, 2011).

Sampling was conducted with flight intercept traps: 20 × 40 cm windows with a funnel below leading to a vial containing ethylene glycol, water (4:1 mixture), and a drop of detergent used as a surfactant. It is important to note that flight intercept traps are the least selective method of sampling tree hollows and are biased toward flying beetle species (Micó, 2018). They are activity traps that capture dispersing insects and have been extensively used to measure veteran tree insect communities (Micó, 2018; Parmain & Bouget, 2018; Sverdrup-Thygeson et al., 2017, 2010). Although flight interception traps detect activity, the beetle communities caught in this type of trap hanging from a dead or hollow tree have been shown to reflect species associated with the dead wood resource (Isaksen, 2015; Sverdrup-Thygeson & Birkemoe, 2009). It has also been found that the same proportion of dead wood associated insects has been collected in flight intercept traps as in other sampling techniques, such as emergence traps (Birkemoe & Sverdrup-Thygeson, 2015), and the same responses have been identified along gradients (Müller et al., 2015). Furthermore, the presence of exit holes on the dead wood source has been correlated with species caught in flight intercept traps. Thus, they represent a widely used and efficient way of estimating beetles in dead wood. In this study, we were interested in the entire veteran oak beetle community, not just the communities within the hollows. Each tree was therefore sampled with two traps: one directly in front of the hollow and one hanging in the canopy. Traps were activated in May and emptied once a month until the middle of August. Due to the methodology of the Program for Surveying and Monitoring Biodiversity in Norway (ARKO, 2011), some trees were sampled over multiple years: 20 trees were sampled for 1 year, 27 trees were sampled for 4 years, and 14 trees were sampled for 5 years.

All beetles were identified to the species level following the taxonomy of The Norwegian Biodiversity Information Centre (NBIC 2018). The species were subsequently divided into the three functional groups: decomposers, predators, and flower visitors based on published literature (Figures 1–3, Appendix II). Species were assigned to the groups based on both adult and larval diet and were therefore not mutually exclusive. Species that we could not find trait information for or did not fit into at least one of the three functional groups were removed from the data set. This came to 30% of the total number of sampled species (262 species). Important effect traits related to decomposition, predation, and pollination were identified based on previous studies (Gossner et al., 2013; Pilskog et al., 2016; Seibold et al., 2015; Sverdrup-Thygeson et al., 2017) and protocols for selecting insect functional traits (Fountain-Jones et al., 2015; Moretti et al., 2017).



FIGURE 1 Example a beetle that is a decomposer: *Pogonocherus hispidulus*



FIGURE 2 Example of a predatory beetle: *Phosphuga atrata*



FIGURE 3 Example of a flower-visiting beetle: *Ctenicera pectinicornis*

We used body size (measured as length in mm) for all functional groups, because it is closely linked to many life-history traits such as life span and dispersal ability, and it influences the amount and composition of resources used by the organism (Fountain-Jones et al., 2015; Gillespie, Birkemoe, & Sverdrup-Thygeson, 2017; Moretti et al., 2017). For decomposers, we also used wood diameter and decay stage preference, because a diversity of preferred habitats will aid the decomposition process (Gossner et al., 2013); and if the species was a known polypore visitor, because recent research suggests that beetles visiting polypores play a role in dispersing fungal spores (Birkemoe, Jacobsen, Sverdrup-Thygeson, & Biedermann, 2018). For predators and flower visitors, we used peak activity date, because having species active throughout the season will increase phenological overlap with prey species and flowering plants (Gillespie et al., 2017; Moretti et al., 2017). In addition, we included the morphological traits of relative eye size for predators and body shape for flower visitors. Eye size is linked to prey recognition as well as hunting strategy (Fountain-Jones et al., 2015; Moretti et al., 2017), and body shape may influence how the species interacts with floral architecture (Patt, Hamilton, & Lashomb 1997, Fountain-Jones et al., 2015). Trait information for beetle species was primarily collected from literature, but some trait information was calculated from available material (Table 1).

Functional diversity was calculated based on all traits within each of the functional groups. Since functional diversity indices are sensitive to missing trait information, we verified that at least 80% of all species in the functional groups had trait information (Majekova et al. 2016). All species that were excluded as a result of lack of data

were rare in the data set (less than five individuals). We chose to use functional dispersion (FDIs) to measure functional diversity because it accounts for species abundances, species richness has limited effect on it (Figure 4 in Appendix I), and it can be calculated for multiple traits and can include both continuous and categorical measurements (Laliberte & Legendre, 2010). FDis is a measure of dispersion in trait space, is calculated as the mean distance of species to the centroid of the community and is weighted by abundances (Laliberte & Legendre, 2010).

Since all traits within the functional groups had Pearson correlation coefficient less than 0.7, we considered them to add independent contributions and chose not to weigh any of the traits when calculating the FDis (Appendix I). FDis was also calculated for all traits individually and then tested for correlations with the tree and landscape variables in order to verify that there were no counter-acting effects (Appendix I). We calculated species richness and FDis with the *dbFD* function in the "FD" package (Laliberte & Legendre, 2010; R Development Core Team, 2017). FDis was calculated using a Gower dissimilarity matrix and the "cailliez" correction method (Cailliez, 1983; Lalibert & Legendre, 2010).

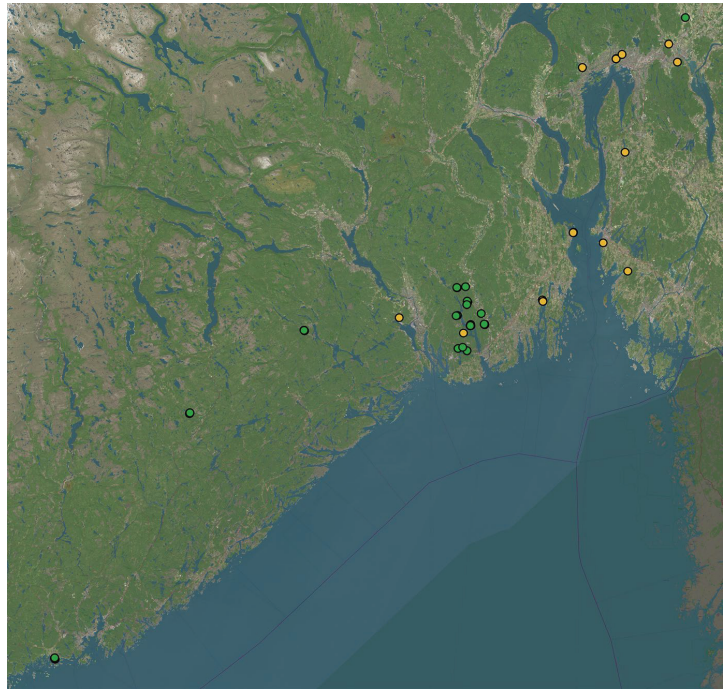
Following a protocol set by Sverdrup-Thygeson et al. (2017), we classified veteran oaks into two habitat classes based on the dominating habitat within a 50 m radius of the tree. Oaks were located either in forests or in open landscapes (Table 2). Forests trees were primarily in multiple-use managed forests, which contained a diversity of other tree species and decaying wood. Trees in open landscapes were either in parks or in agricultural landscapes and were surrounded by fields or gardens with low amounts of dead

TABLE 1 A summary of species richness and functional diversity for each of the functional groups, along with the traits used to calculate functional diversity

Functional group	Species richness	Functional diversity	Traits	Type/unit of measurement	Collection source
Decomposer	Total: 359	Mean:0.20	Body length	Continuous: mm	Literature
	Mean: 23	Max:0.27	Polypore visitor	Binomial	Literature
	Max: 52	Min:0.02	Wood diameter preference	Continuous: developed by Gossner et al. (2013)	Literature
	Min: 4		Decay preference	Continuous: developed by Gossner et al. (2013)	Literature
Predator	Total: 284	Mean:0.08	Body length	Continuous: mm	Literature
	Mean: 15.8	Max:0.14	Eye size	Continuous: eye size divide by length	Photogrammetric analysis
	Max: 39	Min:0.03	Peak activity date	Continuous: year days	Literature and predictions from GBIF data
Flower visitor	Total: 85	Mean: 0.13	Body length	Continuous: mm	Literature
	Mean: 6.1	Max: 0.25	Body shape	Continuous: width at widest place divide by length	Photogrammetric analysis
	Max: 25	Min: 0.02	Peak activity date	Continuous: year days	Literature and predictions from GBIF data
	Min: 1				

Functional dispersion was used as a measure of functional diversity and was calculated from different traits within each of the functional groups. Important effect traits related to the respective ecosystem function were identified based on previous studies and protocols for selecting insect functional traits. Species richness and functional diversity were calculated for each veteran oak for every year of sampling ($N = 202$, 61 trees sampled intermittently from 2004 to 2011).

FIGURE 4 Sampling was carried out on 61 hollow oaks (*Quercus* sp.) in forest (green circles) and open landscapes (yellow circles) at 27 sites located in the main distribution of oaks in Southern Norway. Data were collected intermittently between 2004 and 2011 as part of the National Program for Surveying and Monitoring Biodiversity in Norway (ARKO 2009)



wood (forest trees = 38 and open landscape trees = 23). Variables that described the tree and its surrounding were collected at the time of sampling (Table 2) and were chosen because they have been shown to have an effect in other oak-beetle studies (Parmain

& Bouget, 2018; Pilskog et al., 2016; Ranius & Jansson, 2002; Sverdrup-Thygeson et al., 2017, 2010). We also included a measure of the connectivity of the study tree to other veteran oaks at different spatial scales (Table 2). Connectivity was estimated

TABLE 2 Variables that described the veteran oak and its surrounding landscape and were used to predict species richness and functional diversity of beetles captured around the tree

Variable	Type	Measurement	Reference
Tree circumference	Continuous	Tree circumference at breast height in cm. Natural logarithm taken	Sverdrup-Thygeson et al. (2010)
Light availability	Continuous	$\text{Slope} \cdot \cos(\text{Aspect} - 45)$	Stage (1976), Stage and Salas (2006)
Vitality	Categorical (2 levels)	Healthy: 20% or more living canopy Senescent: <20% living canopy	Sverdrup-Thygeson et al. (2017)
Regrowth	Categorical (3 levels)	Open: no regrowth around oak Shrubs: low vegetation, shrubs or small trees Trees: trees with height similar to the focal tree	Sverdrup-Thygeson et al. (2017)
Connectivity (8 variables)	Continuous	Predicted number of hollow oaks within 0.5 km, 1 km, 2 km, 3 km, 4 km, 5 km, 10 km, and 25 km of focal tree	Skarpaas et al. (2017)
Habitat class	Categorical (2 levels)	Forest: tree situated in a forest Open landscape: tree in either a park or agricultural landscape	Sverdrup-Thygeson et al. (2010)
Tree cover density (3 variables)	Continuous	20 m: the percent of the 20 m pixel where focal tree is located that is covered by forest. 100 m: the percent of 20 m pixels covered by forests within 100 m radius of focal tree. Standard deviation: the standard deviation of the percent of 20 m pixels covered by forests within 100 m radius of focal tree	CLMS (2012 & 15)

Trees were either located in forest ($n = 38$) or open landscapes ($n = 23$).

with a published distribution model for veteran oaks (Skarpaas, Blumentrath, Evju, & Sverdrup-Thygeson, 2017) by summing the predicted probabilities of occurrence of veteran oaks for all pixels in radii of 0.5–25 km of the focal tree. The model was based on a stratified random sample of veteran oak presences and absences across the oak distribution in Southern Norway and geographic and land cover predictors that represent a mixture of ecological and anthropogenic factors.

In order to incorporate substrate density at different spatial scales, we used Copernicus tree cover density maps with 20 m resolution to calculate the tree cover density (TCD) at the 20 m scale, the 100 m scale, and the standard deviation at the 100 m scale for all trees (CLMS, 2012, & 15). We chose these two scales so that we would have one that was finer and one that was coarser than the habitat class variable (50 m), which was obtained in the field. This approach gave us the possibility to consider continuous landscape variables measured at different scales. Since sampling ended in 2011, we used the 2012 maps when possible, but when there was missing data, we included data from 2015 maps (Table 2). However, preliminary analysis indicated that there was very little overlap in TCD between the habitat classes. Furthermore, when the response variables were separated into habitat classes, TCD was not a significant predictor (Appendix I). We concluded that habitat class was a better variable at describing the landscape and at predicting how functional groups respond to it. We therefore dropped TCD from further analysis.

Since trees were sampled repeatedly over a varying number of years, we included year and tree as crossed random effects in the models to adjust for repeated sampling of the trees and year-to-year variation. We also considered using site in the random effect structure but found that it did not improve the models, so it was dropped from the analysis. We used linear mixed models with Gaussian error distribution to model the influence of the tree and landscape variables on FDis since it was approximately normally distributed in our data set. We also used generalized linear mixed models with the same random effect structure and Poisson error distribution to model the effects on species richness. Prior to statistical analysis, we followed the steps for data exploration outlined by Zuur, Ieno and Elphick (2010). All continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation of the data matrix using the *scale* base function in R (version 3.4.0). In order to avoid collinearity, no model contained variables with Pearson correlation coefficient of 0.5 or higher, and no model had a variation inflation factor (VIF) greater than three (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The best model was chosen with backward model selection based on Akaike information criterion (AIC) (Zuur et al., 2009). We carried out model selection separately for correlated variables and subsequently compared the final models using AIC to determine the optimal model (Arnold, Sabom, Nisbet, & Hatch, 2006). The residuals of the final linear models were checked for normality and homogeneity, and the generalized linear models were checked for overdispersion. Models were also checked for influential observations, as well as patterns between the residuals and all potential

predictor variables, sampling date, and geographic location (Zuur et al., 2009).

Statistical analysis was carried out in R version 3.4.0 (R Development Core Team, 2017). Linear mixed models were created using the *lmer* function, and generalized linear mixed models were created with the *glmer* function in the "lme4" package (Bates, Machler, & B. B. and S. Walker., 2015). The R-squared and P values were calculated for the models with packages "MuMIn" and "lmerTest" (Barton, 2018; Kuznetsova, Brockhoff, & Christensen, 2017). The following packages were also used for data manipulation, statistical analysis, and graphical visualization: "Lattice" (Sarkar, 2008), "e1071" (Meyer, Dimitriadou, Hornik, Leisch, & W. A., 2018), "nlme" (Pinheiro, Bates, & D. S., and S. D., 2018), "predictmeans" (Luo, Ganesh, & K. J., 2018), "ggplot2" (Wickham, 2016), "Hmisc" (Harrel & Dupont, 2018), and "dplyr" (Wickham, F. R., H. L., & K. Müller., 2018).

3 | RESULTS

In total, 31,617 individuals from 876 species were collected between 2004 and 2011. Of these 27,314 individuals from 614 species could be included in at least one of the functional groups and had available trait information. A total of 359 species were determined to be decomposers, 284 were determined to be predators, and 85 were flower visitors. The groups were not mutually exclusive, so 45 species were determined to be both decomposers and predators, 44 were decomposers and flower visitors, 25 were predators and flower visitors, and three species were included in all groups. The mean decomposer species richness per tree and year was 23 (min-max: 4–52); mean predator species richness was 16 (1–39); and mean flower visitor species richness was 6 (1–25).

Species richness and functional diversity in all groups (decomposers, predators, and flower visitors) was consistently higher in traps mounted on veteran oaks surrounded by forest than those in open landscapes (Table 3 and Figure 5). The magnitude of this effect, however, varied between functional groups, and for species richness and functional diversity. For functional diversity, forest surroundings had the strongest effect on decomposers and a weaker effect on predators and flower visitors, and for species richness, this trend was reversed (Figure 5).

3.1 | Decomposers

In addition to the difference between forest and open landscape, we found that decomposer species richness responded to the vitality of the tree, being higher in senescent trees ($\beta = 0.265$, $p = .002$, Table 3 and Figure 6). Functional diversity, meanwhile, was affected by connectivity in open landscapes ($\beta = 0.026$, $p = .041$, Table 3 and Figure 6). Connectivity was significant at 2–10 km scale in open landscapes, and the strongest effect and least amount of error around the estimate was at the 5 km scale

TABLE 3 Results from the best generalized linear mixed model (species richness) and linear mixed models (functional diversity) with year and tree as random effects.

Species richness	Decomposers β	Predators β	Flower visitors β
intercept	3.136***	2.894***	1.866***
Habitat class (forest)	0.186***	0.512***	0.328**
Tree vitality (Senescent)	0.265**		
Regrowth (shrubs)		0.207*	
Regrowth (trees)		-0.037	
AIC	1,391	1,213	1,060
R ² fixed	0.14	0.32	0.07
R ² full	0.52	0.62	0.33
Functional diversity			
intercept	0.211***	0.087***	0.132***
Habitat class (forest)	0.058***	0.018***	0.032**
Connectivity: Habitat class (forest)	0.003		
Connectivity: Habitat class (open)	0.026*		
Tree circumference		0.004*	
AIC	-660	-1032	-672
R ² fixed	0.22	0.15	0.10
R ² full	0.60	0.31	0.21

The models were used to test the effects of the tree and landscape variables on the functional group's species richness and functional diversity. Species richness and functional diversity were calculated for each veteran oak for every year of sampling ($N = 202$, 61 trees sampled intermittently from 2004 to 2011). The best models were identified with backward model selection based on AIC. All continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation of the data matrix (Significance codes: *** <0.001 , ** <0.01 , * <0.05).

($\beta = 0.026$, $p = .407$), but there was no significant effect of connectivity in forests ($\beta = 0.003$, $p = .693$, Table 3 and Figure 6). The model predicting species richness explained less of the fraction of the variation than the model predicting functional diversity (R² fixed = 0.14 and 0.22, Table 3).

3.2 | Predators

Independent of whether the tree was in a forest or open landscape, predator species richness increased with shrub regrowth ($\beta = 0.207$, $p = .003$, Table 3 and Figure 7). Functional diversity, on the other hand, increased with tree circumference ($\beta = 0.004$, $p = .014$, Table 3 and Figure 7). The model that predicted species richness explained twice as much of the variation as the model predicting functional diversity (R² = 0.31 and 0.15, Table 3).

3.3 | Flower visitors

The only significant predictor of flower visitor species richness and functional diversity was whether the tree was in a forest or in an open landscape, with greater values being measured in traps mounted on trees in forests (Table 3). In addition, the fixed part of the models only explained a small fraction of the variation in

species richness and functional diversity (R² = 0.07 and R² = 0.10, Table 3).

4 | DISCUSSION

In this study, we found that the features and surroundings of the veteran oaks influenced species richness and functional diversity of beetles, whether classified as decomposers, predators, or flower visitors. There was one trend that held for all groups: When the trees were situated in forest rather than open landscapes, both species richness and functional diversity were higher. Apart from this, the additional predictors differed between groups, and for species richness and functional diversity. This indicates that focusing on only species richness or functional diversity may result in missing predictors that are relevant for conservation and ecosystem functioning.

4.1 | Forest versus open landscapes, across functional groups

The result that species richness was higher in traps mounted on trees in forest than in open landscapes for all groups matches the general trends that have been identified for veteran oak beetle

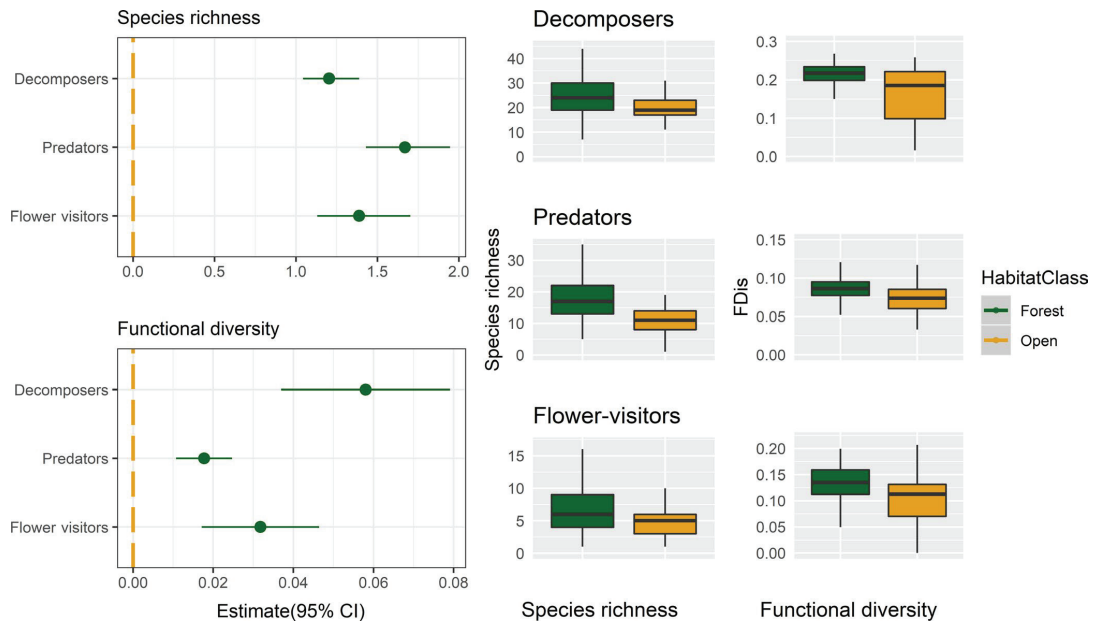


FIGURE 5 Species richness and functional diversity in all groups were significantly higher in traps mounted on veteran oaks surrounded by forest (green) than those in open landscapes (yellow). The magnitude of this effect varied between functional groups, and for species richness and functional diversity. The plots on the left are partial regression coefficients (with 95% CI) for the effect of forest surroundings on species richness (top) and functional diversity (bottom). The boxplot on the right is observations of species richness (middle plots), and functional diversity (right plots) in forests and open landscapes for each of the functional groups. The boxplots show the median, first, and third quartiles, with whisker that extend 1.5 times the interquartile range. In all plots, the veteran oaks in open landscapes are colored yellow and in forests are green

communities in Northern Europe (Bergman et al., 2012; Pilskog et al., 2016; Sverdrup-Thygeson et al., 2017, 2010), but the result that functional diversity was higher in all groups is a new finding. Both results, however, contrast to research done in France, where Parmain and Bouget (2018) found more rare species in veteran trees in open landscapes than veteran trees in forests and no difference between total species richness. It is possible that the higher number of rare species would result in higher functional diversity (Jain et al., 2014; Mouillot et al., 2013; Soliveres et al., 2016; Violle et al., 2017). If that was the case, it would be an intriguing contrast to our results, but this currently remains unverified.

Another interesting result is that there was some indication that decomposers were responding differently than the other groups to forests surroundings. Decomposer species richness was the least affected by forest surroundings, while functional diversity was the most. This indicates that more often than the other functional groups, the additional decomposer species in forests had trait combinations that were not present in open landscapes. Understanding how species are filtered from communities according to their traits remains a fundamental question in community ecology (McGill et al., 2007; Sutherland et al., 2013). One explanation for our results is that the decomposer communities captured

in traps mounted on trees in forests were more influenced by surrounding because their traits were tightly linked to amount and diversity of dead wood, which was clearly higher and more diverse in forests. On the other hand, the resources that drove predator and flower visitor functional diversity may not have been so tightly linked to the differences between forest and open landscapes. However, it is also possible that these results were an artifact of our trait choices (we considered a different set of traits for each group) and therefore should not be overstated.

4.2 | Decomposers

In addition to the results above, we found that reduced connectivity had a negative effect on decomposer functional diversity, but forests surroundings modulated this effect. We found that habitat connectivity in open landscaped increased functional diversity, but it did not have an effect in forests. Communities within isolated trees may have a strong selective pressure for traits that can be sustained by the veteran tree. This likely results in environmental filtering and reduced dispersion of the community's traits (Córdova-Tapia, Hernández-Marroquín, & Zambrano, 2018; Mason, Bello, Mouillot, Pavoine, & Dray, 2013; Mason et al., 2012).

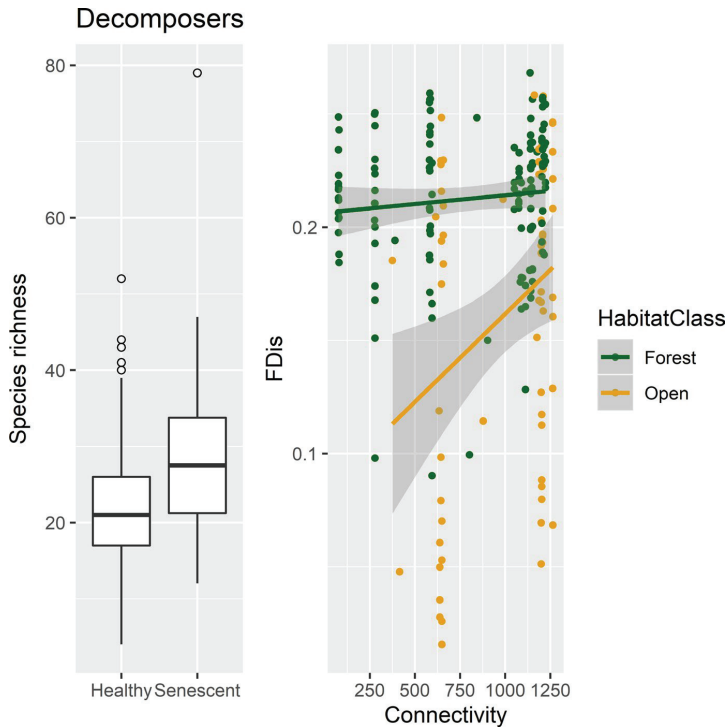


FIGURE 6 *Left plot:* Boxplot of species richness and health of the tree. Decomposer species richness was significantly higher in traps mounted on senescent trees than healthy ones. The plot shows the median, first, and third quartiles, with whisker that extend 1.5 times the interquartile range, and observations beyond the end of the whiskers as points. *Right plot:* Decomposer functional diversity (FDIs, y-axis) was significantly higher in traps mounted on trees in forests (green) than in open landscapes (yellow), and connectivity (x-axis, measured as the number of predicted veteran oaks within a 5 km radius of the focal tree) had a significant positive effect in open landscapes but no effect in forests. Regression lines are the results from a linear mixed model that predicted FDIs with year and tree as random effects, and the gray area around the lines is the 95% confidence interval. Values in the figure have been back transformed, but for the analysis all continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation of the data matrix

Effects of habitat connectivity have also been observed on species richness and abundances of veteran oak-dependent beetles (Pilskog et al., 2016; Sverdrup-Thygeson et al., 2017). Our results add to these findings by indicating that isolation may cause functional homogenization of decomposers. This is potentially problematic, as a recent study has experimentally linked isolation with reduced functional diversity and shown that it has a negative impact on decomposition rates (Mestre, Jansson, & Ranius, 2018).

Decomposer species richness did not respond to connectivity, but instead increased with decreasing tree vitality. This finding matched our predictions as tree vitality relates to the amount of dead wood available in the veteran tree. However, other studies found mixed results when considering the effects of veteran oak vitality on taxonomic diversity of saproxylic beetles. Vitality of veteran oaks did not have an effect on rare and threatened beetles or on generalist saproxylic species richness (Sverdrup-Thygeson et al., 2017, 2010), but did affect species richness of oak specialist and abundances within diverse feeding guilds (Pilskog et al., 2016; Sverdrup-Thygeson et al., 2017).

In this study, the effect of tree vitality on species richness was not paralleled by an effect on functional diversity. The mechanism for this discrepancy remains unknown, but these results indicate that a large patch of dead wood might ensure high species richness, which may not necessarily correspond to higher rates of decomposition. However, functional redundancy of communities can make the ecosystem function they support more resilient to species loss and environmental changes (Fonseca & Ganade, 2001; Hooper et al., 2005).

4.3 | Predators

Predator functional diversity increased with tree size. As tree size increases, so does structural heterogeneity, which increases the number of microhabitats available for potential prey species (Parmain & Bouget, 2018; Ranius & Jansson, 2000). Many of the habitats, such as coarse bark, moss covering the tree trunk, sap flows, dendrotelms (water-filled hollows), and vertebrate nests,

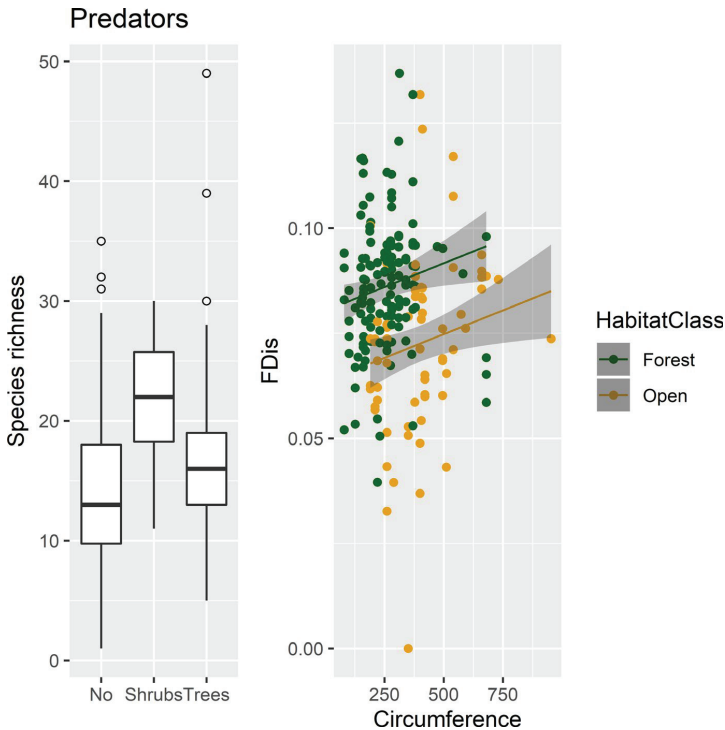


FIGURE 7 *Left plot:* Boxplot of species richness and regrowth around the tree. Predator species richness was significantly higher when there was regrowth of shrubs around the trees. The plot shows the median, first, and third quartiles, with whisker that extend 1.5 times the interquartile range, and observations beyond the end of the whiskers as points. *Right plot:* Predator functional diversity (FDIs, y-axis) was significantly higher in traps mounted on trees in forests (green) than in open landscapes (yellow), and tree circumference had a significant positive effect. Regression lines are the results from a linear mixed model that predicted FDIs with year and tree as random effects, and the gray area around the lines is the 95% confidence interval. Values in the figure have been back transformed, but for the analysis all continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation of the data matrix and tree circumference was log-transformed to reduce the effect of extreme observations

are beneficial to species other than decomposing or flower-visiting beetles and may be related to higher numbers and greater diversity of prey species. Thus, we predicted that predator diversity would increase with tree size, and our prediction was supported for functional diversity but not species richness. Earlier research has found that total saproxylic beetle species richness increased with tree size (Gough et al., 2014; Parmain & Bouget, 2018; Ranius & Jansson, 2000; Sverdrup-Thygeson et al., 2010), but the only study focusing on predators as a group found no such correlation for species richness (Pilskog et al., 2016).

We found that predator species richness instead increased with regrowth of shrubs. There is some precedent for this result, as Pilskog et al. (2016) found that regrowth influenced predatory beetles around veteran oaks. Furthermore, the family of Carabidae, which are primarily predators and an important family in our data set, has been shown to have a link to plant taxonomy and traits (Brose, 2003; Niemelä, Koivula, & Kotze, 2006; Niemelä, Spence, & Spence, 1992; Pakeman & Stockan, 2014), but it should be pointed out that our trapping methods were not ideal for sampling this group as they are biased toward flight dispersing beetles (Micó, 2018). Nevertheless, regrowth of shrubs around the veteran trees likely increases habitat heterogeneity and this has been shown to have a positive effect on species diversity (Tews et al., 2004). Functional diversity, however, was not affected by regrowth, which may indicate that there is not a benefit of regrowth for biological control, as it has been found that an increase in functionally

similar predators does not necessarily increase predation rates of invertebrate pests (Snyder, 2019; Straub & Snyder, 2006).

4.4 | Flower visitors

In contrast to the other functional groups, no additional predictors of functional diversity or species richness were identified for flower visitors. Also, the best models that predicted flower visitor species richness and functional diversity explained only a small fraction of the variation. Clearly, major predictors of this group remain unknown. It is important to note that flower-visiting activity is only applicable to adult beetles and that the pollen or nectar acquired is typically a supplementary diet. Of the 85 species of flower visitors, only 18 were not included among the decomposer and/or predators. It is likely that species within this group were responding differently to the predictors. Nevertheless, given the abundance and diversity of flower-visiting beetles that this study found, it is likely that these communities contribute to pollination in the surrounding landscapes.

4.5 | Conclusion and management implications

The importance of forests surrounding veteran trees has been demonstrated for the conservation of rare and threatened beetles (Sverdrup-Thygeson et al., 2010), and our results indicate that surrounding forest

cover is also important for supporting multiple ecosystem processes. We also suggest that managers should promote high densities of veteran oaks over large areas. Our results support the concept that these trees are not independent units and that veteran trees collectively add value across large spatial scales (Sverdrup-Thygeson et al., 2017, 2010). Furthermore, large veteran trees provide a source of predators and are likely beneficial to pest control when the trees are near agricultural fields or in managed forests. Another possible benefit of veteran oaks for agriculture is pollination from the diverse flower-visiting beetle communities. Our results indicate that management strategies can be implemented to support decomposition, predation, and flower visitation, and good practices have the potential to add value for conservation and ecosystem functioning.

In conclusion, a large body of work has shown that features and surroundings of veteran oaks are important for conservation of species diversity, and the results from this study indicate that they are also important for functional diversity within multiple functional groups. We also conclude that functional and taxonomic diversity respond to different drivers between and within the functional groups, so both measures should be considered as complimentary and potentially relevant for future research focused on conservation and ecosystem functioning.

CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

RTW contributed to the study design, analyzed the data, and wrote the first draft of the manuscript. TB contributed to the study design and critical review of the draft. OS contributed to the study design, supervised data analysis, and contributed critical review of the draft. AS was responsible for the data set, contributed to the study design, and critical review of the draft. All authors assisted in the writing of the manuscript and approve the final version.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study complied with the appropriate institutional, national, and international guidelines.

DATA ACCESSIBILITY

All data used in this study is deposited in DataverseNO (<https://doi.org/10.18710/VF2FTT>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Appendix

Appendix I

Functional groups and traits

Trait information for beetle species was primarily collected from literature, but some trait information was calculated from available material. Peak activity time was established by Gillespie et al. (2017) and was estimated using flight activity period data. For species that we did not have a measurement of peak activity time, we calculated one based on a linear model using GBIF data. We calculated the mean event date in the GBIF data and then used a linear model to predict peak flight date. We then used the model to make predictions for peak activity time for species that were missing in Gillespie et al. (2017) data (Figure 1). In the GBIF data, we only took observations from Norway that happened between March and September. We also removed species from the dataset that had fewer than 20 observations.

We also chose to include the morphological traits of relative eye size for predators and body shape for flower-visitors. We gathered photographs of the beetles from online databases. In order to obtain a relative measure of eye size, we measured each eye and length of the beetle using the program *imageJ*. We then divided the mean of the eye measurements by the length of the beetle. We followed a similar protocol to obtain a relative measure of shape. We measured the beetle at the widest place and its length. We then divided width at the widest place by length.

Functional dispersion

Before calculating the functional dispersion (FDis) of all the traits, we first calculated the Pearson correlation coefficient between the traits. Since all traits within the functional groups had a correlation coefficient less than 0.7, we considered them to add independent contributions, and chose not to weigh any of the traits when calculating the FDis (Figure 2). FDis was also calculated for all traits individually and then tested for correlations with the landscape and site variables, in order to verify that there were no counteracting effects (Table 2).

Tree cover density

Habitat class (whether the trees was in a forest or open landscape) and tree cover density at the 100m scale (TCD) had the strongest effect on both species richness and functional diversity in all the functional groups. However, preliminary analysis indicated that there was very little overlap in TCD between the habitat classes (Figure 3), and the effect of these variables was very similar: species richness and functional diversity increased with tree cover and from open landscapes to forests. However, when the response variables were separated into habitat classes, TCD was not a significant predictor (Table 3). We therefore, conclude that the primary effect is a result of differences in habitat class, and TCD also captured this difference. TCD was subsequently dropped from the analysis.

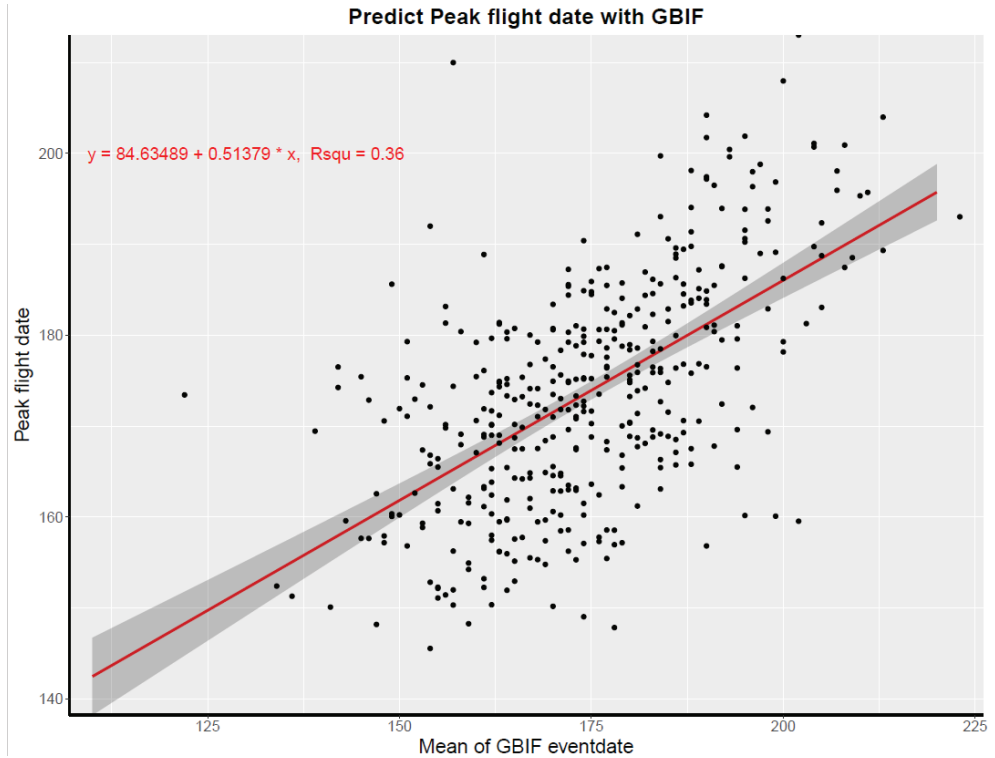


Figure 1: Results from a linear model that predicted Gillespie et al. (2017) measure of peak flight date with the mean event date from GBIF data. We only took observations from Norway that occurred between March and September, and removed species from the data that had fewer than 20 observations. We then used this model to predict the peak flight date for species that were not present in Gillespie et al. (2017) data.

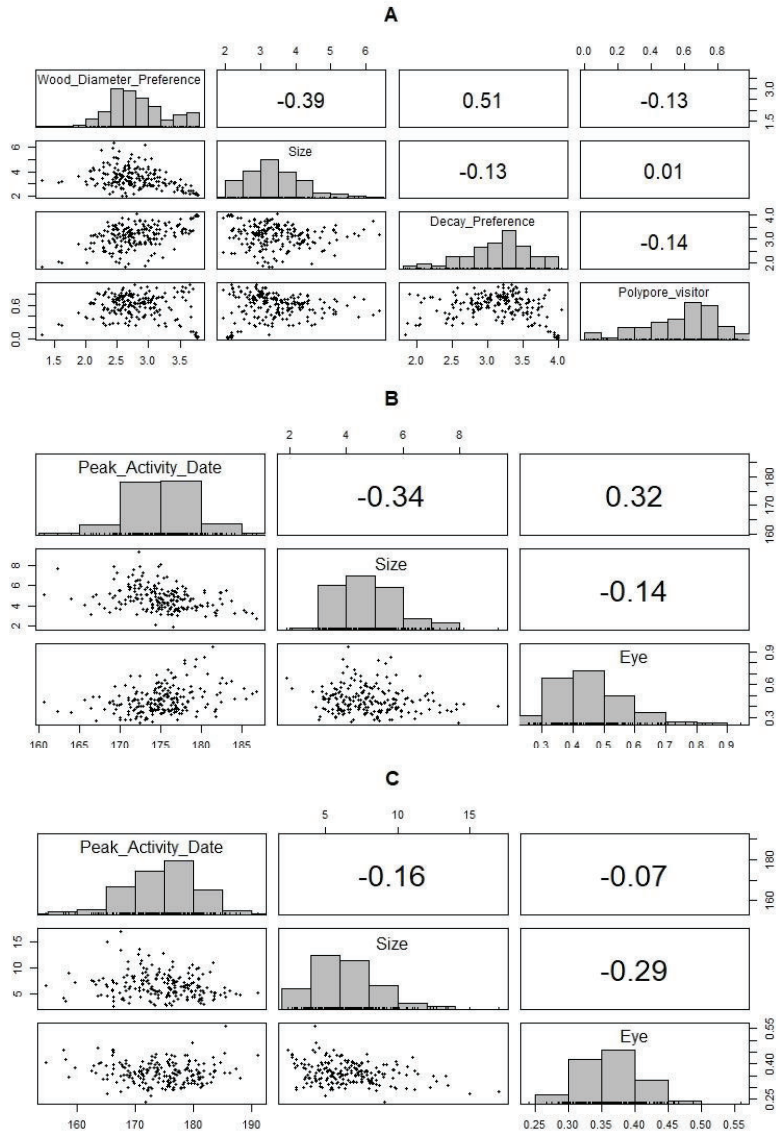


Figure 2: Plots of the CWM of the traits for decomposer (plot A), predators (plot B) and flower-visitors (plot C). Plots below the diagonal are bivariate scatter plots, on the diagonal are histograms on the diagonal, and above the diagonal is the Pearson correlation coefficient.

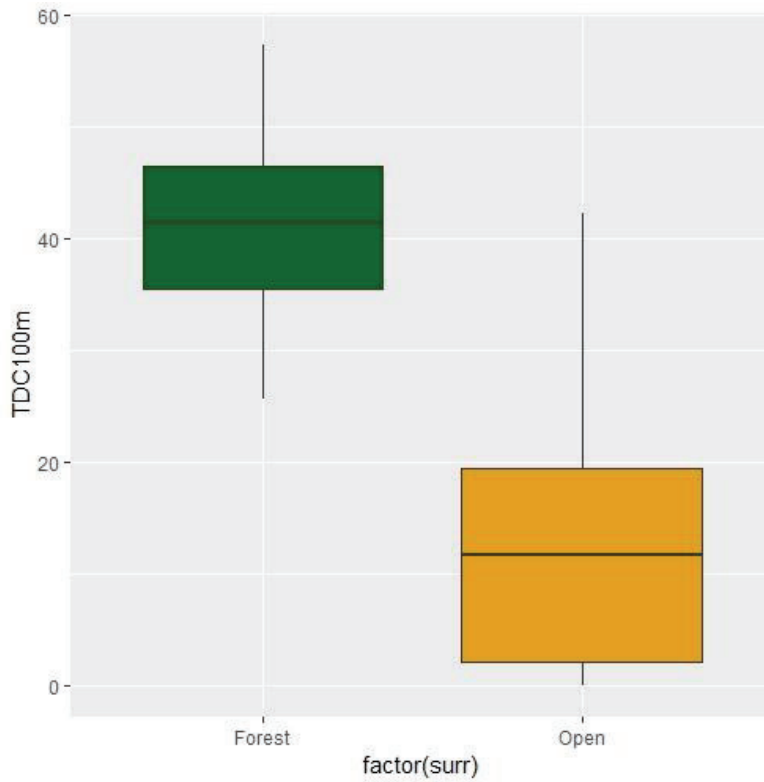


Figure 3: Boxplot of TCD at the 100m scale and Habitat class around the veteran tree. There was very little overlap in TCD between the habitat classes. The plot shows the median, first and third quartiles, with whisker that extend 1.5 times the inter-quartile range. Veteran oaks in open landscapes are colored yellow and in forests are green.

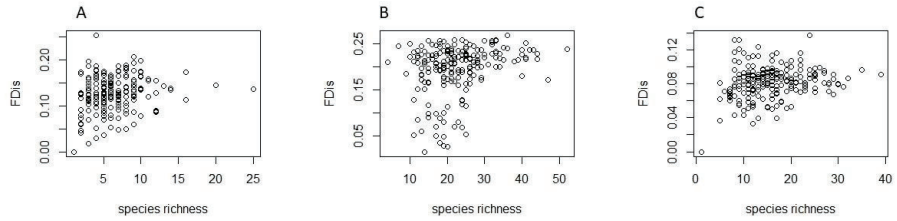


Figure 4: Scatter plot of FDis (y axis) and species richness (x axis) for predators (plot A), decomposers (plot B) and flower-visitors (plot C). The person correlation coefficient for predators was 0.17, for decomposer was 0.28, and for flower-visitor was 0.18.

Table 1: Pearson correlation coefficient between FDis for each trait and the landscape and site variables. FDis was calculated for each trait and for all the traits and tested for counteracting effects.

Decomposers								
traits	Tree Circ.	Habitat class	Connectivity	Vitality	Tree form	Regrowth	Slope	Aspect
Size	-0.13	-0.53	>0.01	0.31	0.09	0.44	0.09	0.14
Polypore visitor	-0.19	-0.41	>0.01	0.22	0.07	0.33	0.24	0.09
Decay preference	-0.28	-0.36	>0.01	0.19	0.25	0.22	0.34	>0.01
Wood Diameter preference	-0.29	-0.25	0.11	0.10	0.24	>0.01	0.29	0.18
All	-0.23	-0.45	0.01	0.24	0.14	0.34	0.29	>0.01
Predators								
traits								
Size	-0.15	-0.35	>0.01	0.17	>0.01	0.16	0.27	0.08
Activity time	0.15	-0.12	>0.01	-0.06	-0.13	>0.01	>0.01	>0.01
Eye size	>0.01	>0.01	-0.12	>0.01	>0.01	-0.17	>0.01	>0.01
All	>0.01	-0.33	>0.01	-0.09	>0.01	0.16	0.16	>0.01
Flower-visitor								
traits								
Size	>0.01	-0.16	>0.01	>0.01	>0.01	0.17	0.11	0.10
Activity time	-0.14	-0.33	>0.01	>0.01	>0.01	0.14	0.19	0.34
Body shape	>0.01	-0.18	>0.01	>0.01	>0.01	0.11	0.10	0.15
All	>0.01	-0.32	>0.01	>0.01	>0.01	0.22	0.18	0.26

Table 2: Pearson correlation coefficient between community weighted mean (CWM) for each continuous trait and the landscape and site variables. CWM was calculated using the dbFD function in the 'FD' package (Laliberté and Legendre 2010, R Development Core Team 2017).

Decomposers								
traits	Tree Circ.	Habitat class	Connectivity	Vitality	Tree form	Regrowth	Slope	Aspect
Size	-0.11	-0.48	0.11	0.26	0.1	0.45	0.23	0.11
Decay preference	0.22	>0.01	>0.01	>0.01	-0.22	>0.01	>0.01	>0.01
Wood Diameter preference	0.34	0.45	>0.01	>0.01	>0.01	-0.3	-0.2	-0.11
Predators								
traits								
Size	>0.01	-0.16	>0.01	>0.01	-0.15	>0.01	>0.01	>0.01
Activity time	>0.01	-0.21	0.1	>0.01	>0.01	0.13	0.1	>0.01
Eye size	0.13	0.3	>0.01	-0.11	>0.01	-0.22	-0.22	>0.01
Flower-visitor								
traits								
Size	>0.01	-0.1	>0.01	>0.01	>0.01	0.18	>0.01	0.1
Activity time	>0.01	-0.11	>0.01	0.1	0.12	-0.14	0.16	-0.1
Body shape	>0.01	>0.01	0.12	>0.01	0.17	>0.01	>0.01	>0.01

Table 3: Results from generalized linear mixed model (species richness) and linear mixed models (functional diversity) with year and tree as random effects. Species richness and functional diversity were calculated for each veteran oak for every year of sampling (N=203, 61 trees sampled intermittently from 2004 to 2011) and were predicted with an interaction between TCD and habitat class (Significance codes: 0 '***', 0.001 '**', 0.01 '*').

Species richness			
	Decomposers	Predators	Flower-visitors
	β	β	β
intercept	2.945***	2.904***	1.764***
TCD: Habitat class (open)	-0.002	-0.002	0.006
TCD: Habitat class (forest)	0.006	-0.041	0.002
Functional diversity			
intercept	0.228***	0.082***	0.142
TCD: Habitat class (open)	-0.001	-0.000	0.000
TCD: Habitat class (forest)	-0.047	0.006	0.000

Appendix II

Table of species with abundances and functional group (for reference list see published material).

Species	Total abundance	Forest abundance	Open landscape abundance	Decomposer	Predator	Flower visitor
<i>Abraeus parvulus</i>	1	1	0	0	1	0
<i>Acalles ptinoides</i>	3	3	0	1	0	0
<i>Acidota crenata</i>	9	6	3	0	1	0
<i>Acrotona orbata</i>	11	9	2	0	1	0
<i>Acrotrichis cognata</i>	3	2	1	1	0	0
<i>Acrotrichis intermedia</i>	72	63	9	1	0	0
<i>Acrotrichis rugulosa</i>	3	3	0	1	0	0
<i>Acrotrichis sericans</i>	1	0	1	1	0	0
<i>Acrulia inflata</i>	4	4	0	1	1	0
<i>Adalia bipunctata</i>	8	2	6	0	1	0
<i>Adalia decempunctata</i>	29	18	11	0	1	0
<i>Agaricochara latissima</i>	10	10	0	1	0	0
<i>Agathidium badium</i>	1	1	0	1	0	0
<i>Agathidium confusum</i>	18	15	3	1	0	0
<i>Agathidium nigripenne</i>	1	1	0	1	0	0
<i>Agathidium pisanum</i>	4	3	1	1	0	0
<i>Agathidium rotundatum</i>	1	1	0	1	0	0
<i>Agathidium seminulum</i>	65	65	0	1	0	0
<i>Agathidium varians</i>	28	26	2	1	0	0
<i>Agrilus angustulus</i>	4	4	0	1	0	0
<i>Agrilus laticomis</i>	2	2	0	1	0	0
<i>Agrilus sulcicollis</i>	11	10	1	1	0	0
<i>Aloconota gregaria</i>	45	6	39	0	1	0
<i>Alosterna tabacicolor</i>	28	27	1	1	0	1
<i>Amara familiaris</i>	1	0	1	0	1	0
<i>Amara lunicollis</i>	1	1	0	NA	1	0
<i>Amara plebeja</i>	1	0	1	0	1	0
<i>Amischa analis</i>	28	11	17	0	1	0
<i>Amischa decipiens</i>	1	0	1	0	1	0
<i>Amischa nigrofusca</i>	2	0	2	0	1	0
<i>Ampedus balteatus</i>	366	343	23	1	1	0
<i>Ampedus cinnabarinus</i>	2	2	0	1	0	0
<i>Ampedus hjorti</i>	114	72	42	1	0	0
<i>Ampedus nigrinus</i>	106	106	0	1	1	0
<i>Ampedus nigroflavus</i>	6	5	1	1	0	0
<i>Ampedus pomorum</i>	6	6	0	1	0	0
<i>Ampedus praeustus</i>	4	4	0	1	0	0
<i>Ampedus sanguineus</i>	1	1	0	1	0	1
<i>Ampedus tristis</i>	3	3	0	1	1	0

<i>Anaspis frontalis</i>	42	19	23	1	0	1
<i>Anaspis marginicollis</i>	167	140	27	1	1	0
<i>Anaspis rufilabris</i>	290	245	45	1	1	1
<i>Anaspis thoracica</i>	60	20	40	1	0	1
<i>Anastrangalia sanguinolenta</i>	5	5	0	1	0	1
<i>Anatis ocellata</i>	1	1	0	0	1	0
<i>Anchomenus dorsalis</i>	1	0	1	0	1	0
<i>Anisandrus dispar</i>	84	69	15	1	0	0
<i>Anisotoma axillaris</i>	1	1	0	1	0	0
<i>Anisotoma castanea</i>	17	16	1	1	0	0
<i>Anisotoma glabra</i>	4	4	0	1	0	0
<i>Anisotoma humeralis</i>	81	79	2	1	0	0
<i>Anisotoma orbicularis</i>	7	7	0	1	0	0
<i>Anitys rubens</i>	10	4	6	1	0	0
<i>Anomognathus cuspidatus</i>	3	1	2	0	1	0
<i>Anoplodera sexguttata</i>	6	6	0	1	0	1
<i>Anotylus rugosus</i>	5	1	4	0	1	0
<i>Anthaxia morio</i>	1	1	0	1	0	1
<i>Antherophagus pallens</i>	16	12	4	0	1	1
<i>Anthrenus muscorum</i>	56	20	36	1	1	0
<i>Anthribus nebulosus</i>	3	2	1	0	1	0
<i>Aphidecta oblitterata</i>	8	8	0	0	1	0
<i>Aphodius ater</i>	2	1	1	1	0	0
<i>Aphodius fimetarius</i>	1	1	0	1	0	0
<i>Aplocnemus nigricornis</i>	7	5	2	0	1	1
<i>Arpedium quadrum</i>	1	1	0	0	1	0
<i>Aspidiphorus orbiculatus</i>	15	14	1	1	0	0
<i>Atheta aeneipennis</i>	1	0	1	1	1	0
<i>Atheta basicornis</i>	2	1	1	0	1	0
<i>Atheta britanniae</i>	2	2	0	1	0	0
<i>Atheta castanoptera</i>	5	3	2	1	1	0
<i>Atheta celata</i>	1	1	0	0	1	0
<i>Atheta corvina</i>	2	2	0	0	1	0
<i>Atheta crassicornis</i>	7	6	1	1	1	0
<i>Atheta euryptera</i>	1	0	1	0	1	0
<i>Atheta harwoodi</i>	8	2	6	1	NA	0
<i>Atheta hypnorum</i>	1	0	1	0	1	0
<i>Atheta incognita</i>	6	6	0	1	1	0
<i>Atheta laticollis</i>	1	0	1	0	1	0
<i>Atheta macrocera</i>	1	1	0	0	1	0
<i>Atheta myrmecobia</i>	7	5	2	1	1	0
<i>Atheta pilicornis</i>	13	6	7	0	1	0
<i>Atheta sodalis</i>	15	14	1	1	0	0
<i>Atheta vaga</i>	58	32	26	1	0	0

<i>Athous haemorrhoidalis</i>	125	58	67	0	1	1
<i>Athous subfuscus</i>	272	271	1	0	1	0
<i>Atomaria affinis</i>	1	1	0	1	0	0
<i>Atomaria apicalis</i>	4	0	4	1	0	0
<i>Atomaria atricapilla</i>	5	1	4	1	0	0
<i>Atomaria fuscata</i>	15	3	12	1	0	0
<i>Atomaria lewisi</i>	10	0	10	1	0	0
<i>Atomaria morio</i>	3	2	1	1	0	0
<i>Atomaria nigrirostris</i>	8	6	2	1	0	0
<i>Atomaria nitidula</i>	2	0	2	1	0	0
<i>Atomaria omata</i>	1	1	0	1	0	0
<i>Atomaria subangulata</i>	2	2	0	1	0	0
<i>Atomaria testacea</i>	4	2	2	1	0	0
<i>Atomaria turgida</i>	15	11	4	1	0	0
<i>Atrecus affinis</i>	9	9	0	1	1	0
<i>Atrecus longiceps</i>	1	1	0	0	1	0
<i>Atrecus pilicomis</i>	1	1	0	0	1	0
<i>Attagenus pello</i>	10	4	6	1	0	1
<i>Baeocrara variolosa</i>	1	1	0	1	0	0
<i>Batrisodes delaporti</i>	4	1	3	0	1	0
<i>Batrisodes venustus</i>	12	8	4	0	1	0
<i>Bembidion lampros</i>	2	0	2	0	1	0
<i>Bembidion quadrimaculatum</i>	18	16	2	0	1	0
<i>Bibloporus bicolor</i>	209	208	1	0	1	0
<i>Bibloporus minutus</i>	25	21	4	0	1	0
<i>Bisnius fimetarius</i>	1	1	0	0	1	0
<i>Bisnius nigriventris</i>	1	1	0	0	1	0
<i>Bisnius puella</i>	1	1	0	0	1	0
<i>Bolitochara mulsanti</i>	2	2	0	0	1	0
<i>Bolitophagus reticulatus</i>	2	2	0	1	0	0
<i>Bryaxis bulbifer</i>	1	1	0	0	1	0
<i>Bryaxis puncticollis</i>	6	6	0	0	1	0
<i>Bryophacis maklini</i>	1	1	0	0	1	0
<i>Byturus ochraceus</i>	2	1	1	0	0	1
<i>Byturus tomentosus</i>	8	7	1	0	0	1
<i>Cacotemnus rufipes</i>	5	0	5	1	0	0
<i>Calambus bipustulatus</i>	14	9	5	1	0	0
<i>Cantharis decipiens</i>	5	5	0	0	1	1
<i>Cantharis obscura</i>	6	5	1	0	1	0
<i>Cantharis pellucida</i>	1	1	0	0	0	1
<i>Cantharis rustica</i>	6	0	6	0	1	0
<i>Carabus violaceus</i>	7	7	0	0	1	0
<i>Cardiophorus ruficollis</i>	20	20	0	1	0	0
<i>Carpelimus corticinus</i>	14	4	10	0	1	0

<i>Cartodere constricta</i>	1	0	1	1	1	0
<i>Cartodere nodifer</i>	17	13	4	1	0	0
<i>Cercyon lateralis</i>	1	0	1	0	1	0
<i>Cerylon deplanatum</i>	2	2	0	0	1	0
<i>Cerylon fagi</i>	3	3	0	0	1	0
<i>Cerylon ferrugineum</i>	168	128	40	1	1	0
<i>Cerylon histeroideus</i>	53	49	4	1	1	0
<i>Cetonia aurata</i>	5	5	0	1	0	1
<i>Cis bidentatus</i>	12	12	0	1	0	0
<i>Cis boleti</i>	18	14	4	1	0	0
<i>Cis castaneus</i>	2	2	0	1	0	0
<i>Cis comptus</i>	1	0	1	1	0	0
<i>Cis dentatus</i>	7	7	0	1	0	0
<i>Cis fagi</i>	64	19	45	1	0	0
<i>Cis festivus</i>	10	9	1	1	0	0
<i>Cis glabratus</i>	1	1	0	1	0	0
<i>Cis micans</i>	1	1	0	1	0	0
<i>Cis punctulatus</i>	2	2	0	1	0	0
<i>Cis submicans</i>	13	7	6	1	0	0
<i>Cis vestitus</i>	56	51	5	1	0	0
<i>Cis villosulus</i>	10	6	4	1	0	0
<i>Clytus arietis</i>	5	5	0	1	0	1
<i>Coccinella septempunctata</i>	4	2	2	0	1	0
<i>Coccinula quatuordecimpustulata</i>	4	4	0	0	1	0
<i>Colydium elongatum</i>	2	2	0	0	1	0
<i>Conopalpus testaceus</i>	45	44	1	1	0	0
<i>Cordylepherus viridis</i>	1	1	0	NA	NA	1
<i>Corticaria interstitialis</i>	1	1	0	1	0	0
<i>Corticaria longicollis</i>	92	86	6	1	0	0
<i>Corticaria longicornis</i>	6	5	1	1	0	0
<i>Corticaria rubripes</i>	1	0	1	1	0	0
<i>Corticaria serrata</i>	1	1	0	1	0	0
<i>Corticarina minuta</i>	18	8	10	1	0	0
<i>Corticarina similata</i>	312	227	85	1	0	0
<i>Corticeus fasciatus</i>	3	3	0	0	1	0
<i>Corticaria gibbosa</i>	102	51	51	1	0	0
<i>Crepidophorus mutilatus</i>	7	6	1	0	1	0
<i>Cryphalus asperatus</i>	7	6	1	1	0	0
<i>Cryptarcha strigata</i>	115	83	32	1	1	0
<i>Cryptarcha undata</i>	50	25	25	1	1	0
<i>Cryptolestes corticinus</i>	7	6	1	0	1	0
<i>Cryptophagus badius</i>	10	9	1	1	0	0
<i>Cryptophagus confusus</i>	1	0	1	1	0	0
<i>Cryptophagus dentatus</i>	165	107	58	1	0	0

<i>Cryptophagus dorsalis</i>	12	12	0	1	0	0
<i>Cryptophagus intermedius</i>	1	1	0	1	0	0
<i>Cryptophagus labilis</i>	4	1	3	1	0	0
<i>Cryptophagus lapponicus</i>	3	3	0	1	0	0
<i>Cryptophagus micaceus</i>	386	327	59	1	0	0
<i>Cryptophagus parallelus</i>	1	1	0	1	0	0
<i>Cryptophagus populi</i>	86	49	37	1	0	0
<i>Cryptophagus scanicus</i>	350	223	127	1	0	0
<i>Cryptophagus setulosus</i>	1	1	0	1	0	0
<i>Cryptophagus subdepressus</i>	1	1	0	1	0	0
<i>Cryptopleurum minutum</i>	1	0	1	1	0	0
<i>Crypturgus cinereus</i>	10	7	3	1	0	0
<i>Crypturgus hispidulus</i>	4	4	0	1	0	0
<i>Crypturgus pusillus</i>	3	3	0	1	0	0
<i>Ctenicera pectinicornis</i>	1	1	0	1	NA	1
<i>Ctesias serra</i>	126	28	98	1	0	0
<i>Curtimorda maculosa</i>	1	1	0	1	0	0
<i>Cychramus luteus</i>	47	34	13	1	0	1
<i>Cychramus variegatus</i>	10	4	6	1	0	1
<i>Cychnus caraboides</i>	4	4	0	0	1	0
<i>Cyphon coarctatus</i>	36	27	9	0	1	0
<i>Cyphon ochraceus</i>	18	15	3	0	1	0
<i>Cyphon variabilis</i>	5	2	3	0	1	1
<i>Dacne bipustulata</i>	42	2	40	1	0	0
<i>Dadobia immersa</i>	6	6	0	1	1	0
<i>Dalopius marginatus</i>	312	265	47	0	1	0
<i>Dascillus cervinus</i>	2	2	0	0	0	1
<i>Dasytes aeratus</i>	3	1	2	0	1	1
<i>Dasytes caeruleus</i>	62	44	18	0	1	1
<i>Dasytes niger</i>	222	220	2	0	1	1
<i>Dasytes obscurus</i>	3	3	0	0	1	1
<i>Dasytes plumbeus</i>	381	191	190	0	1	1
<i>Dendrophilus punctatus</i>	3	2	1	0	1	0
<i>Dendrophilus pygmaeus</i>	4	4	0	0	1	0
<i>Denticollis linearis</i>	11	11	0	1	1	1
<i>Dermestes lardarius</i>	1	0	1	1	0	0
<i>Diaperis boleti</i>	2	1	1	1	0	0
<i>Dienerella filum</i>	1	1	0	1	0	0
<i>Dienerella vincenti</i>	12	4	8	1	NA	0
<i>Dorcatoma chrysomelina</i>	1827	442	1385	1	0	0
<i>Dorcatoma dresdensis</i>	5	4	1	1	0	0
<i>Dorcatoma flavicomis</i>	79	76	3	1	0	0
<i>Dromius agilis</i>	42	30	12	0	1	0
<i>Dromius angustus</i>	3	3	0	0	1	0

<i>Dromius fenestratus</i>	3	3	0	0	1	0
<i>Dromius quadrimaculatus</i>	40	19	21	0	1	0
<i>Drusilla canaliculata</i>	1	1	0	0	1	0
<i>Dryocoetes alni</i>	7	7	0	1	0	0
<i>Dryocoetes autographus</i>	4	2	2	1	0	0
<i>Dryocoetes hectographus</i>	1	1	0	1	0	0
<i>Dryocoetes villosus</i>	35	29	6	1	0	0
<i>Dryophilus pusillus</i>	5	3	2	1	0	1
<i>Dyschirius globosus</i>	3	3	0	0	1	0
<i>Elater ferrugineus</i>	9	9	0	1	0	0
<i>Elateroides dermestoides</i>	16	16	0	1	0	1
<i>Eledona agricola</i>	21	17	4	1	0	0
<i>Encephalus complicans</i>	1	1	0	0	1	0
<i>Endomychus coccineus</i>	1	1	0	1	0	0
<i>Enicmus fungicola</i>	5	5	0	1	0	0
<i>Enicmus histrio</i>	1	0	1	1	0	0
<i>Enicmus planipennis</i>	4	1	3	1	0	0
<i>Enicmus rugosus</i>	697	659	38	1	0	0
<i>Enicmus testaceus</i>	199	174	25	1	0	0
<i>Enicmus transversus</i>	7	1	6	1	0	0
<i>Ennearthron cornutum</i>	64	39	25	1	0	0
<i>Eपुरaea aestiva</i>	21	21	0	1	0	1
<i>Eपुरaea biguttata</i>	3	1	2	1	1	0
<i>Eपुरaea binotata</i>	1	1	0	0	1	1
<i>Eपुरaea guttata</i>	6	4	2	0	1	0
<i>Eपुरaea marseuli</i>	3	3	0	0	1	0
<i>Eपुरaea melanocephala</i>	29	23	6	0	0	1
<i>Eपुरaea neglecta</i>	2	2	0	0	1	1
<i>Eपुरaea pallescens</i>	3	2	1	0	1	1
<i>Eपुरaea pygmaea</i>	2	1	1	1	0	0
<i>Eपुरaea terminalis</i>	5	5	0	0	1	0
<i>Eपुरaea unicolor</i>	127	9	118	0	1	1
<i>Ernobius abietinus</i>	1	1	0	1	0	0
<i>Ernobius abietis</i>	1	1	0	1	0	0
<i>Ernoporicus caucasicus</i>	6	6	0	1	0	0
<i>Ernoporus tiliae</i>	20	17	3	1	0	0
<i>Eucnemis capucina</i>	20	19	1	1	0	0
<i>Euconnus claviger</i>	14	13	1	0	1	0
<i>Euconnus maklinii</i>	3	3	0	0	1	0
<i>Euglenes oculatus</i>	6814	234	6580	1	0	0
<i>Euglenes pygmaeus</i>	2	0	2	1	0	0
<i>Euplectus brunneus</i>	2	1	1	0	1	0
<i>Euplectus decipiens</i>	6	6	0	0	1	0
<i>Euplectus karstenii</i>	197	184	13	0	1	0

<i>Euplectus mutator</i>	18	17	1	0	1	0
<i>Euplectus nanus</i>	24	20	4	0	1	0
<i>Euplectus piceus</i>	35	34	1	0	1	0
<i>Euplectus punctatus</i>	87	81	6	0	1	0
<i>Euplectus signatus</i>	9	9	0	0	1	0
<i>Euryusa sinuata</i>	3	1	2	0	1	0
<i>Eusphalerum luteum</i>	107	105	2	0	0	1
<i>Euthiconus conicicollis</i>	9	9	0	0	1	0
<i>Exochomus quadripustulatus</i>	1	1	0	0	1	0
<i>Gabrius appendiculatus</i>	1	1	0	0	1	0
<i>Gabrius expectatus</i>	1	1	0	0	1	0
<i>Gabrius splendidulus</i>	30	29	1	0	1	0
<i>Gastrallus immarginatus</i>	62	57	5	1	0	0
<i>Glischrochilus hortensis</i>	42	35	7	1	0	0
<i>Glischrochilus quadriguttatus</i>	3	3	0	1	1	0
<i>Gnathoncus buyssoni</i>	68	53	15	1	1	0
<i>Gnorimus nobilis</i>	31	31	0	1	0	1
<i>Grammoptera ruficornis</i>	3	2	1	1	0	1
<i>Grynobius planus</i>	41	41	0	1	0	0
<i>Grynocharis oblonga</i>	22	16	6	1	0	0
<i>Gyrophaena affinis</i>	2	2	0	1	0	0
<i>Gyrophaena manca</i>	2	2	0	1	0	0
<i>Gyrophaena strictula</i>	2	1	1	1	0	0
<i>Hadrobregmus pertinax</i>	15	4	11	1	0	0
<i>Hallomenus axillaris</i>	2	2	0	1	0	0
<i>Hallomenus binotatus</i>	8	4	4	1	0	0
<i>Halyzia sedecimguttata</i>	14	3	11	0	1	0
<i>Hapalaraea pygmaea</i>	31	27	4	0	1	1
<i>Haploglossa gentilis</i>	85	85	0	0	1	0
<i>Haploglossa marginalis</i>	17	8	9	1	0	0
<i>Haploglossa villosula</i>	3069	2115	954	1	0	0
<i>Harpalus latus</i>	1	1	0	0	1	0
<i>Harpalus rufipes</i>	1	0	1	0	1	0
<i>Helophorus brevipalpis</i>	5	0	5	0	1	0
<i>Hemicoelus canaliculatus</i>	22	8	14	1	0	0
<i>Hemicrepidius hirtus</i>	2	2	0	0	1	0
<i>Holobus apicatus</i>	2	2	0	0	1	0
<i>Holobus flavicornis</i>	128	119	9	0	1	0
<i>Hylastes brunneus</i>	3	2	1	1	0	0
<i>Hylastes cunicularius</i>	34	29	5	1	0	0
<i>Hylesinus crenatus</i>	6	2	4	1	0	0
<i>Hylesinus fraxini</i>	17	15	2	1	0	0
<i>Hylesinus toranio</i>	1	1	0	1	0	0
<i>Hylis foveicollis</i>	1	1	0	1	0	0

<i>Hylobius abietis</i>	5	4	1	1	0	0
<i>Hypebaeus flavipes</i>	2	2	0	0	1	1
<i>Hypulus quercinus</i>	1	1	0	1	0	0
<i>Ilyobates nigricollis</i>	1	1	0	1	1	0
<i>Ipidia binotata</i>	2	1	1	0	1	0
<i>Ips acuminatus</i>	3	3	0	1	0	0
<i>Ips typographus</i>	21	20	1	1	0	0
<i>Ischnoglossa elegantula</i>	3	3	0	1	0	0
<i>Ischnoglossa prolixa</i>	7	7	0	1	1	0
<i>Ischnomera caerulea</i>	2	2	0	1	0	1
<i>Ischnomera cinerascens</i>	1	1	0	1	0	1
<i>Ischnosoma splendidum</i>	6	6	0	1	0	0
<i>Isomira murina</i>	63	62	1	0	1	0
<i>Isorhipis marmottani</i>	1	1	0	1	0	0
<i>Korynetes caeruleus</i>	7	0	7	0	1	1
<i>Kyklioacalles roboris</i>	5	5	0	1	0	0
<i>Lagria hirta</i>	1	1	0	0	0	1
<i>Lathrobium fulvipenne</i>	1	1	0	0	1	0
<i>Latridius gemellatus</i>	3	0	3	1	0	0
<i>Latridius hirtus</i>	31	19	12	1	0	0
<i>Latridius minutus</i>	7	4	3	1	0	0
<i>Latridius porcatus</i>	2	1	1	1	0	0
<i>Leiestes seminiger</i>	4	4	0	1	0	0
<i>Leioderes kollari</i>	1	1	0	1	0	0
<i>Leiodes obesa</i>	1	1	0	1	0	0
<i>Leiopus linnei</i>	1	1	0	1	NA	0
<i>Leiopus nebulosus</i>	20	16	4	1	0	0
<i>Leptophloeus alternans</i>	1	1	0	0	1	0
<i>Leptura quadrifasciata</i>	2	1	1	1	0	1
<i>Leptusa fumida</i>	17	17	0	1	1	0
<i>Leptusa pulchella</i>	3	3	0	1	1	0
<i>Leptusa ruficollis</i>	165	162	3	1	1	0
<i>Lissodema cursor</i>	8	0	8	0	1	0
<i>Litargus connexus</i>	3	0	3	1	0	0
<i>Lordithon exoletus</i>	1	1	0	0	1	0
<i>Lordithon lunulatus</i>	11	11	0	0	1	0
<i>Lordithon pulchellus</i>	1	1	0	0	1	0
<i>Lordithon trinotatus</i>	1	1	0	1	1	0
<i>Lymexylon navale</i>	10	10	0	1	0	0
<i>Magdalis carbonaria</i>	1	0	1	1	0	0
<i>Magdalis cerasi</i>	2	2	0	1	0	0
<i>Magdalis duplicata</i>	2	2	0	1	0	0
<i>Malachius bipustulatus</i>	9	2	7	0	1	1
<i>Malthinus flaveolus</i>	16	14	2	0	1	0

<i>Malthinus frontalis</i>	75	13	62	0	1	0
<i>Malthinus seriepunctatus</i>	5	5	0	0	1	0
<i>Malthodes brevicollis</i>	15	15	0	0	1	1
<i>Malthodes crassicornis</i>	14	14	0	0	1	0
<i>Malthodes flavoguttatus</i>	1	1	0	0	1	0
<i>Malthodes fuscus</i>	14	14	0	0	1	0
<i>Malthodes guttifer</i>	83	82	1	0	1	0
<i>Malthodes marginatus</i>	49	27	22	0	1	0
<i>Malthodes minimus</i>	1	1	0	0	1	0
<i>Malthodes mysticus</i>	3	3	0	0	1	0
<i>Malthodes pumilus</i>	19	19	0	0	1	1
<i>Malthodes spathifer</i>	40	35	5	0	1	0
<i>Margarinotus merdarius</i>	1	1	0	0	1	0
<i>Margarinotus striola</i>	1	0	1	0	1	0
<i>Megarthus depressus</i>	9	7	2	0	1	0
<i>Megarthus nitidulus</i>	1	1	0	0	1	0
<i>Megatoma undata</i>	15	8	7	1	0	1
<i>Melanotus castanipes</i>	117	102	15	1	0	1
<i>Melanotus villosus</i>	38	9	29	1	1	1
<i>Melasis buprestoides</i>	7	7	0	1	0	0
<i>Meligethes aeneus</i>	45	16	29	0	1	1
<i>Meligethes carinulatus</i>	1	1	0	NA	NA	1
<i>Meligethes corvinus</i>	1	0	1	NA	NA	1
<i>Meligethes denticulatus</i>	21	20	1	0	0	1
<i>Meligethes flavimanus</i>	3	2	1	NA	NA	1
<i>Meligethes ovatus</i>	3	0	3	0	0	1
<i>Meligethes pedicularius</i>	6	5	1	NA	NA	1
<i>Micrambe abietis</i>	44	40	4	1	0	0
<i>Micropeplus porcatus</i>	1	0	1	1	0	0
<i>Microrhagus lepidus</i>	3	3	0	1	0	0
<i>Microrhagus pygmaeus</i>	3	3	0	1	0	0
<i>Microscydmus minimus</i>	5	5	0	0	1	0
<i>Microscydmus nanus</i>	14	14	0	0	1	0
<i>Molorchus minor</i>	2	2	0	1	0	1
<i>Mordella aculeata</i>	2	2	0	1	0	1
<i>Mordella holomelaena</i>	1	1	0	1	0	1
<i>Mordellistena variegata</i>	2	0	2	1	0	1
<i>Mordellochroa abdominalis</i>	8	6	2	1	0	1
<i>Mycetochara axillaris</i>	3	2	1	1	0	0
<i>Mycetochara flavipes</i>	2	2	0	1	0	0
<i>Mycetochara humeralis</i>	18	0	18	1	0	0
<i>Mycetochara maura</i>	198	98	100	1	0	0
<i>Mycetophagus fulvicollis</i>	5	5	0	1	0	0
<i>Mycetophagus piceus</i>	60	59	1	1	0	0

<i>Mycetophagus populi</i>	10	9	1	1	0	0
<i>Mycetoporus baudieri</i>	1	1	0	1	0	0
<i>Mycetoporus erichsonianus</i>	3	3	0	1	0	0
<i>Mycetoporus lepidus</i>	18	8	10	0	1	0
<i>Mycetoporus longulus</i>	5	1	4	0	1	0
<i>Mycetoporus punctus</i>	2	2	0	1	0	0
<i>Myrmetes paykulli</i>	1	1	0	0	1	0
<i>Myzia oblongoguttata</i>	6	6	0	0	1	0
<i>Necydalis major</i>	1	1	0	1	0	1
<i>Nemadus colonoides</i>	20	19	1	1	0	0
<i>Nemozoma elongatum</i>	8	7	1	0	1	0
<i>Nevraphes elongatulus</i>	12	7	5	1	1	0
<i>Nicrophorus vespilloides</i>	40	40	0	1	1	0
<i>Notiophilus biguttatus</i>	1	1	0	0	1	0
<i>Notothecta flavipes</i>	23	22	1	0	1	0
<i>Nudobius lentus</i>	1	1	0	0	1	0
<i>Oiceoptoma thoracicum</i>	5	5	0	1	1	0
<i>Omalium rivulare</i>	1	1	0	0	1	0
<i>Omalium rugatum</i>	1	1	0	1	0	0
<i>Orchesia fasciata</i>	3	3	0	1	0	0
<i>Orchesia luteipalpis</i>	2	2	0	1	0	0
<i>Orchesia micans</i>	1	1	0	1	0	0
<i>Orchesia undulata</i>	15	12	3	1	0	0
<i>Orsodacne cerasi</i>	70	70	0	0	0	1
<i>Orthocis alni</i>	38	31	7	1	0	0
<i>Orthoperus atomus</i>	1	0	1	0	1	0
<i>Orthoperus corticalis</i>	10	10	0	1	0	0
<i>Orthoperus punctatus</i>	2	2	0	0	1	0
<i>Osphya bipunctata</i>	25	25	0	1	0	1
<i>Othius subuliformis</i>	6	6	0	0	1	0
<i>Oxymirus cursor</i>	1	1	0	1	0	1
<i>Oxypoda arborea</i>	290	288	2	0	1	0
<i>Oxypoda bicolor</i>	1	1	0	0	1	0
<i>Oxypoda brevicornis</i>	2	1	1	0	1	0
<i>Oxytelus laqueatus</i>	1	1	0	0	1	0
<i>Palorus depressus</i>	2	2	0	1	0	0
<i>Paraphotistus impressus</i>	18	18	0	0	1	0
<i>Paromalus flavicornis</i>	2	0	2	0	1	0
<i>Paromalus parallelepipedus</i>	1	1	0	0	1	0
<i>Pediacus depressus</i>	1	0	1	0	1	0
<i>Philonthus addendus</i>	2	2	0	0	1	0
<i>Philonthus carbonarius</i>	16	0	16	0	1	0
<i>Philonthus decorus</i>	1	0	1	0	1	0
<i>Philonthus marginatus</i>	1	0	1	0	1	0

<i>Philonthus varians</i>	1	0	1	0	1	0
<i>Phloeocharis subtilissima</i>	1	1	0	0	1	0
<i>Phloeonomus punctipennis</i>	3	3	0	0	1	0
<i>Phloeopora corticalis</i>	49	23	26	0	1	0
<i>Phloeopora testacea</i>	25	12	13	0	1	0
<i>Phloeostiba plana</i>	5	4	1	0	1	0
<i>Phloeotribus spinulosus</i>	1	0	1	1	0	0
<i>Phloiotrya rufipes</i>	16	15	1	1	0	0
<i>Phosphuga atrata</i>	5	2	3	0	1	0
<i>Phyllodrepa ioptera</i>	35	25	10	0	1	0
<i>Phyllodrepa linearis</i>	10	8	2	0	1	0
<i>Phyllodrepa melanocephala</i>	27	19	8	0	1	0
<i>Phymatodes testaceus</i>	18	8	10	1	0	0
<i>Pityogenes bidentatus</i>	4	3	1	1	0	0
<i>Pityogenes chalcographus</i>	70	61	9	1	0	0
<i>Pityogenes quadridens</i>	3	3	0	1	0	0
<i>Pityogenes trepanatus</i>	46	26	20	1	0	0
<i>Pityophagus ferrugineus</i>	3	0	3	0	1	0
<i>Pityophthorus lichtensteini</i>	3	1	2	1	0	0
<i>Pityophthorus micrographus</i>	30	26	4	1	0	0
<i>Pityophthorus pubescens</i>	2	2	0	1	0	0
<i>Placusa tachyporoides</i>	19	12	7	1	1	0
<i>Plagionotus arcuatus</i>	2	2	0	1	0	0
<i>Platycerus caraboides</i>	4	4	0	1	0	0
<i>Platydracus stercorarius</i>	3	3	0	0	1	0
<i>Platynus assimilis</i>	4	0	4	0	1	0
<i>Platystomos albinus</i>	1	1	0	1	0	0
<i>Plectophloeus nitidus</i>	1	0	1	0	1	0
<i>Plegaderus caesus</i>	26	23	3	0	1	0
<i>Plegaderus vulneratus</i>	1	1	0	0	1	0
<i>Podabrus alpinus</i>	4	4	0	0	1	0
<i>Podistra schoenherri</i>	3	3	0	0	1	0
<i>Pogonocherus fasciculatus</i>	1	1	0	1	0	0
<i>Polygraphus poligraphus</i>	10	9	1	1	0	0
<i>Polygraphus punctifrons</i>	4	4	0	1	0	0
<i>Prionocyphon serricornis</i>	15	11	4	1	0	0
<i>Prionychus ater</i>	33	12	21	1	0	0
<i>Prionychus melanarius</i>	1	0	1	1	0	0
<i>Procrærus tibialis</i>	16	0	16	1	0	0
<i>Propylea quatuordecimpunctata</i>	7	2	5	0	1	0
<i>Prostemon tessellatum</i>	79	78	1	0	1	0
<i>Protaetia marmorata</i>	5	2	3	1	0	1
<i>Pseudocistela ceramboides</i>	196	116	80	1	0	1
<i>Psyllobora vigintiduopunctata</i>	33	33	0	0	1	0

<i>Ptenidium formicetorum</i>	3	3	0	0	1	0
<i>Ptenidium turgidum</i>	44	43	1	1	0	0
<i>Pterostichus melanarius</i>	3	1	2	0	1	0
<i>Pterostichus niger</i>	9	8	1	0	1	0
<i>Pterostichus oblongopunctatus</i>	4	4	0	0	1	0
<i>Pteryx suturalis</i>	2	2	0	1	0	0
<i>Ptilinus fuscus</i>	3	3	0	1	0	0
<i>Ptilinus pectinicornis</i>	19	19	0	1	0	0
<i>Ptinomorphus imperialis</i>	17	8	9	1	0	1
<i>Ptinus fur</i>	25	13	12	1	0	0
<i>Ptinus rufipes</i>	53	3	50	1	0	0
<i>Ptinus subpillosus</i>	571	381	190	1	0	0
<i>Quedius brevicornis</i>	10	10	0	0	1	0
<i>Quedius brevis</i>	4	3	1	0	1	0
<i>Quedius cruentus</i>	10	5	5	0	1	0
<i>Quedius lucidulus</i>	1	1	0	0	1	0
<i>Quedius maurus</i>	13	12	1	0	1	0
<i>Quedius mesomelinus</i>	11	8	3	0	1	0
<i>Quedius microps</i>	4	4	0	0	1	0
<i>Quedius plagiatus</i>	4	4	0	0	1	0
<i>Quedius scitus</i>	6	0	6	0	1	0
<i>Quedius tenellus</i>	1	1	0	0	1	0
<i>Quedius xanthopus</i>	97	89	8	0	1	0
<i>Rabocerus gabrieli</i>	1	1	0	0	1	0
<i>Rhagium mordax</i>	25	24	1	1	0	1
<i>Rhagonycha lignosa</i>	57	50	7	0	1	1
<i>Rhagonycha lutea</i>	10	7	3	0	1	0
<i>Rhagonycha nigriventris</i>	11	8	3	0	1	0
<i>Rhizophagus bipustulatus</i>	52	25	27	1	1	0
<i>Rhizophagus cribratus</i>	22	19	3	0	1	0
<i>Rhizophagus dispar</i>	2	1	1	0	1	0
<i>Rhizophagus fenestralis</i>	2	2	0	0	1	0
<i>Rhizophagus ferrugineus</i>	1	1	0	0	1	0
<i>Rhizophagus nitidulus</i>	1	1	0	0	1	0
<i>Rhizophagus parallelocollis</i>	1	0	1	1	1	0
<i>Rhyncolus ater</i>	111	101	10	1	0	0
<i>Rhyncolus elongatus</i>	4	4	0	1	0	0
<i>Rhyncolus sculpturatus</i>	15	15	0	1	0	0
<i>Ropalodontus perforatus</i>	1	1	0	1	0	0
<i>Rugilus rufipes</i>	2	1	1	1	0	0
<i>Rutpela maculata</i>	5	5	0	1	0	1
<i>Salpingus planirostris</i>	106	82	24	0	1	0
<i>Salpingus ruficollis</i>	52	42	10	0	1	0
<i>Saperda scalaris</i>	7	7	0	1	0	1

<i>Scaphidium quadrimaculatum</i>	1	1	0	1	0	0
<i>Scaphisoma agaricinum</i>	50	46	4	1	0	0
<i>Scaphisoma assimile</i>	1	1	0	1	0	0
<i>Scaphisoma balcanicum</i>	1	1	0	1	0	0
<i>Scaphisoma boleti</i>	1	1	0	1	0	0
<i>Scaphisoma boreale</i>	3	3	0	1	0	0
<i>Schizotus pectinicornis</i>	3	3	0	1	1	0
<i>Sciodrepoides fumatus</i>	3	3	0	1	0	0
<i>Scolytus intricatus</i>	419	64	355	1	0	0
<i>Scolytus laevis</i>	130	1	129	1	0	0
<i>Scolytus ratzeburgi</i>	1	1	0	1	0	0
<i>Scolytus rugulosus</i>	13	9	4	1	0	0
<i>Scraptia fuscula</i>	93	1	92	0	1	0
<i>Scraptia testacea</i>	43	3	40	1	0	0
<i>Scydmaenus hellwigii</i>	9	9	0	0	1	0
<i>Scydmorephes minutus</i>	8	8	0	0	1	0
<i>Scymnus suturalis</i>	4	4	0	0	1	0
<i>Selatosomus aeneus</i>	75	61	14	0	1	0
<i>Sepedophilus constans</i>	1	1	0	1	0	0
<i>Sepedophilus littoreus</i>	5	4	1	1	0	0
<i>Sepedophilus testaceus</i>	11	11	0	1	0	0
<i>Sericoderus lateralis</i>	1	0	1	1	0	0
<i>Silvanoprus fagi</i>	4	3	1	0	1	0
<i>Sinodendron cylindricum</i>	19	16	3	1	0	0
<i>Soronia grisea</i>	12	4	8	1	0	0
<i>Soronia punctatissima</i>	9	5	4	1	0	0
<i>Sphaeriestes castaneus</i>	4	4	0	0	1	0
<i>Sphaerosoma pilosum</i>	1	0	1	1	0	0
<i>Sphindus dubius</i>	4	4	0	1	0	0
<i>Stenichnus bicolor</i>	21	19	2	0	1	0
<i>Stenichnus collaris</i>	20	20	0	1	1	0
<i>Stenichnus godarti</i>	11	7	4	0	1	0
<i>Stenichnus scutellaris</i>	29	26	3	0	1	0
<i>Stenostola dubia</i>	4	4	0	1	0	1
<i>Stenurella melanura</i>	53	53	0	1	0	1
<i>Stenus clavicornis</i>	6	6	0	0	1	0
<i>Stephostethus rugicollis</i>	6	2	4	1	0	0
<i>Stictoleptura maculicornis</i>	29	29	0	0	0	1
<i>Sulcacis fronticornis</i>	1	1	0	1	0	0
<i>Synchita humeralis</i>	6	2	4	1	0	0
<i>Synuchus vivalis</i>	1	0	1	0	1	0
<i>Tachinus elongatus</i>	1	1	0	1	1	0
<i>Tachinus rufipes</i>	4	1	3	1	1	0
<i>Tachyporus chrysoelinus</i>	2	0	2	1	1	0

<i>Tachyporus dispar</i>	9	1	8	0	1	0
<i>Tachyporus nitidulus</i>	2	1	1	0	1	0
<i>Tetratoma ancora</i>	3	3	0	1	0	0
<i>Tetropium castaneum</i>	1	1	0	1	0	0
<i>Tetrops praeustus</i>	1	0	1	1	0	1
<i>Thalycra fervida</i>	2	2	0	1	0	0
<i>Thamiaraea cinnamomea</i>	41	27	14	0	1	0
<i>Thamiaraea hospita</i>	6	4	2	1	1	0
<i>Thanasimus femoralis</i>	1	1	0	0	1	0
<i>Thanasimus formicarius</i>	3	3	0	0	1	0
<i>Thiasophila inquilina</i>	1	0	1	1	0	0
<i>Thiasophila wockii</i>	1	1	0	0	1	0
<i>Thymalus limbatus</i>	28	28	0	1	0	0
<i>Tillus elongatus</i>	25	25	0	0	1	1
<i>Tinotus morion</i>	2	0	2	0	1	0
<i>Tomoxia bucephala</i>	4	4	0	1	0	1
<i>Trachodes hispidus</i>	8	8	0	1	0	0
<i>Trichius fasciatus</i>	19	19	0	1	0	1
<i>Trichocele memnonia</i>	7	3	4	0	1	0
<i>Trichonyx sulcicollis</i>	1	0	1	1	1	0
<i>Trimium brevicorne</i>	10	10	0	0	1	0
<i>Triphyllus bicolor</i>	14	14	0	1	0	0
<i>Triplax aenea</i>	3	3	0	1	0	0
<i>Triplax rufipes</i>	3	2	1	1	0	0
<i>Triplax russica</i>	21	20	1	1	0	0
<i>Tritoma bipustulata</i>	2	2	0	1	0	0
<i>Trixagus carinifrons</i>	12	5	7	1	0	0
<i>Trixagus dermestoides</i>	155	141	14	1	0	0
<i>Trixagus meyhohmi</i>	12	9	3	1	0	0
<i>Trox scaber</i>	3	2	1	1	0	0
<i>Trypodendron domesticum</i>	2	2	0	1	0	0
<i>Trypodendron lineatum</i>	6	4	2	1	0	0
<i>Trypophloeus binodulus</i>	3	3	0	1	0	0
<i>Trypophloeus granulatus</i>	4	4	0	1	0	0
<i>Tyrus mucronatus</i>	8	8	0	0	1	0
<i>Xantholinus linearis</i>	2	2	0	0	1	0
<i>Xantholinus tricolor</i>	8	8	0	1	1	0
<i>Xestobium rufovillosum</i>	201	172	29	1	0	1
<i>Xyleborinus saxesenii</i>	279	141	138	1	0	0
<i>Xyleborus cryptographus</i>	1	1	0	1	0	0
<i>Xyleborus monographus</i>	6	0	6	1	0	0
<i>Xylechinus pilosus</i>	9	7	2	1	0	0
<i>Xyletinus longitarsis</i>	1	1	0	1	0	0
<i>Xylita laevigata</i>	1	1	0	1	1	0

<i>Xylophilus corticalis</i>	31	25	6	1	0	0
<i>Xylostiba monilicornis</i>	1	0	1	0	1	0
<i>Zyras lugens</i>	5	4	1	0	1	0

Paper II



OPEN Veteran trees are a source of natural enemies

Ross Wetherbee[✉], Tone Birkemoe & Anne Sverdrup-Thygeson

Predation of invertebrate pest by natural enemies is a critical contribution of nature to people, because invertebrate pests cause a vast amount of economic damage and pesticides use has many long-term costs. Veteran trees are keystone structures and hotspots for biodiversity, and are a potential source of natural enemies. To explore this, we used a balanced experimental design where we measured predatory beetle diversity and attack marks on three colors of artificial caterpillars placed around 20 veteran oaks and 20 nearby young oaks, in Southern Norway. We predicted that around the veteran oaks there would be a greater diversity of predatory beetles and more invertebrate attacks on artificial caterpillars. Sampling for predatory beetles was conducted in summer 2017 and 2018, and invertebrate attacks were measured in 2018. We found support for the predictions: diversity of predatory beetles was higher around veteran trees and there were more arthropod attack marks on artificial caterpillars placed around veteran trees. Our results indicated that veteran trees are a source of natural enemies. Valuing and protecting veteran trees and their communities is an essential step towards a more sustainable system of management that has the possibility of promoting both the wellbeing of people and biodiversity.

Biodiversity loss and the associated environmental and social problems are considered some of the central challenges of our time¹, in part, because all societies are dependent on the functioning of ecosystems for the support of human existence and wellbeing². Nature's contribution to people [NCP] has been suggested as a framework to help societies better understand and relate to the ecosystems on which they depend³. NCP can be defined as all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to people's quality of life⁴.

Invertebrate pests are an example of an NCP with considerable negative impacts on society. Agricultural intensification has exacerbated this problem by simplifying the landscape and reducing biodiversity⁵, and the pervasive method of using pesticides to control invertebrate pests has many interrelated costs for local people, future generations and biological communities^{6–8}. One viable alternative to the use of pesticides is to preserve or enhance predation by the natural enemies in a target area⁹. While pest control with natural enemies is an ancient method, with records of it being implemented as early as 900 AD⁹, it has recently gained new interest as an beneficial NCP^{10,11}. Additionally, research has shown that landscape complexity is critical for this NCP, because higher levels of habitat heterogeneity have positive effects on the ability of multiple enemies to coexist due to the presence of additional non-pest prey and greater range of microhabitats^{11,12}.

Veteran trees have played a prominent role in many cultures around the world and throughout the ages¹³. They are 'keystone structures' for biological communities^{14,15}, and are an integral aspect in many traditional landscapes and sacred sites^{13,16,17}. Veteran oaks are a hotspot for biodiversity in Northern Europe^{18,19} and enhance the structural complexity of the landscape²⁰. Large trees in agroforestry systems have been found to enhance functional biodiversity and promote beneficial NCP including invertebrate pest control²¹. Veteran oaks provide food resources and shelter for a diverse set of species¹⁹, including arthropod predators^{22,23} and may be a source of a natural enemies of invertebrate pests.

However, high levels of biodiversity do not necessarily result in enhanced ecosystem functioning; ecosystem functioning is instead more closely related to a diversity in traits [functional diversity] rather than taxonomic diversity^{24,25}. Therefore, functional diversity can be considered the link between biodiversity and ecosystem functioning. When specifically considering predation by natural enemies, mounting evidence suggests that predation increases when the natural enemies have complementary traits^{10,11}. Natural enemies are complementary when they attack different pest species, have differences in their phenologies and diurnal/nocturnal activities, and have different hunting behaviors¹¹. Although it has been established that veteran trees increase the structural complexity of the landscape¹⁵ and are a source of diverse predator²², the link between biodiversity and ecosystem

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functioning has received less attention and it is unknown to what extent the presences of these trees influences the beneficial NCP of predation by natural enemies.

Assessing differences in the predation by natural enemies is not straight forward²⁶. Attacks by predators on invertebrate prey are usually cryptic and rarely leave any evidence of the event, and visual observations are seldom possible and complicated by presence of the observer²⁷. Other methods such as examination of predator gut contents, or radioactive labelling of the prey have difficulties distinguishing between “real” predation and scavenging or secondary predation²⁸. An alternative method of measuring predation intensity is with the use of artificial caterpillars. The technique involves fashioning prey from malleable, non-hardening material, deploying them in the field and then measuring depressions left on the models by predators^{29,30}. The marks left on the artificial caterpillars from attempted predation event can be used to identify the predator³⁰. Additionally, different colors of artificial caterpillars can be deployed to mimic different prey species^{27,31}. The level of identification of predator attack marks has varied between studies, but identification at a coarse taxonomic level (bird, mammal, or invertebrates) has been shown to be the most prudent approach²⁹. Invertebrate attacks on artificial caterpillars have been attributed to ants, ground beetles, predatory bugs, predatory wasps, parasitoid wasps, spiders²⁷ and in some cases non-predatory insects^{26,27,31}. Although the method of deploying artificial caterpillars to measure predation rates has limitations, it has been found to be suitable for measuring predation rates in comparative studies²⁷.

In order to measure the contribution of veteran oaks to the beneficial NCP of predation by natural enemies, we employed a balanced experimental design. We matched twenty veteran oaks with twenty nearby young oaks, which were taken to represent the background levels, and measured the diversity of predatory beetles and the number of invertebrate attack marks on artificial caterpillars placed around the trees. We included trees from open landscapes and forests to span the variation that is observed in veteran oak distribution in Northern Europe, but we were primarily focused on the dichotomy between the veteran and the young tree. The study had two main predictions related to this dichotomy: first, there would be a greater diversity of beetle predators around veteran trees, and second, there would be more attacks on artificial caterpillars deployed around veteran trees. The first prediction was based on the fact that veteran oaks have high diversity of arthropods associated with them¹⁹. We defined diversity as including both taxonomic and functional diversity, and for our measure of functional diversity we chose to focus on traits that were identified as being complementary for natural enemies^{10,22,32}. The next prediction was rooted in the first: a community of predators with diverse complementary traits (i.e. predators with different hunting strategies, prey species and phenologies) will have high predation levels. If these predictions are supported, veteran trees should be considered as enhancing predation by providing a source of natural enemies.

Results

Over the course of the two summers we captured a total of 465 beetle species of which 173 were predators. Both species richness and functional diversity of complementary traits were higher around veteran than young trees (Table 1, $P = 0.01$ and 0.037 , respectively). Independent of the type of tree, there was a yearly and seasonal effect on both measures of diversity, which decreased through the season and was significantly lower at the end of the summer in 2018 (Table 1, Fig. 1).

In total we placed out 720 artificial caterpillars, however we found that many (52%) of them were either missing or damaged to the point of obscuring other attack marks. Despite this, the remaining caterpillars were well balanced within the experimental setup. We found that arthropods attacked 47% of the remaining artificial caterpillars ($n = 345$). The optimal model that predicted the number of arthropod attack marks on the artificial caterpillars included the type of tree, the color of the caterpillars, the position of caterpillars and a seasonal effect (Table 1, Fig. 2). Attack rates were higher around veteran trees than young trees ($P = 0.007$). Green caterpillars were attacked less than caterpillars with other colors ($P = 0.005$), and all caterpillars were attacked more when they were placed at ground level ($P = 0.016$). There was also a decrease in attacks towards the end of the summer ($P = 0.041$).

Discussion

In the present study, we found that our predictions that there would be higher predatory beetle diversity (both taxonomic and functional) and invertebrate attack rates around veteran oaks were supported. We also found that the diversity of predatory beetles and invertebrate attack rates decreased in parallel through the season, indicating that they were interrelated. Veteran trees have been identified as a hotspot for invertebrate diversity in Northern Europe¹⁹ and have a greater diversity of beetles associated with them than younger trees¹⁵. Building on these findings, our results are the first to show that both the diversity of natural enemies and invertebrate predation rates were higher around veteran trees than young trees, given an otherwise similar habitat. Our results considered in conjunction with each other, provide strong evidence to support the conclusion that veteran trees are a source of natural enemies.

Habitat heterogeneity is important for predation by natural enemies, as it increases the possibility of multiple invertebrate enemies to coexist^{11,12} and has been linked to a greater diversity of invertebrate predators^{22,33}. The coexistence of natural enemies with complementary traits has been found to be the most important predictor of pest control by natural enemies¹⁰. Müller et al.¹⁷ attributes the finding that veteran trees had greater diversity of beetles associated with them than young trees to the structural heterogeneity proved by the veteran trees. As the size and age of a tree increases so does its structural heterogeneity, and this increases the number of micro-habitats available for shelter and potential prey species^{34,35}. In our study it is likely that the structural heterogeneity proved by the veteran trees allowed for the coexistence of natural enemies and promoted complementary trait diversity, which lead to the higher predation rates that we observed around veteran trees. It should be noted however, that we did not determine the identity of the invertebrate predators attacking the artificial caterpillars, and it is therefore unknown to what extent our findings were a result of attacks from specialized predators that are

Response variable and predictors		Estimate	Standard error	P value	Pseudo R2
Species richness					0.7
Intercept		1.781	0.087	<0.001	
Type of tree	(Veteran)	0.235	0.095	0.010	
Sampling period	(Middle)	- 0.046	0.087	0.600	
	(last)	- 0.881	0.114	<0.001	
Year	(2018)	0.116	0.084	0.168	
Sampling period: year	(Middle: 2018)	- 0.483	0.129	<0.001	
	(last: 2018)	- 0.917	0.190	<0.001	
FDis					0.28
Intercept		0.075	0.007	<0.001	
Type of tree	(Veteran)	0.015	0.007	0.038	
Sampling period	(Middle)	0.007	0.009	0.417	
	(Last)	- 0.02	0.009	0.025	
Year	(2018)	0.0129	0.009	0.152	
Sampling period: year	(Middle: 2018)	- 0.023	0.013	0.069	
	(Last: 2018)	- 0.036	0.013	0.005	
Invertebrate attack marks					0.32
Intercept		0.326	0.224	0.145	
Type of tree	(Veteran)	0.537	0.198	0.007	
Color	(Brown)	- 0.012	0.239	0.961	
	(Green)	- 0.716	0.251	0.004	
Position	(Low)	0.493	0.204	0.015	
Sampling period	(Middle)	0.269	0.232	0.247	
	(Last)	- 0.481	0.267	0.041	

Table 1. Summary of the optimal Linear (LMM) and Generalized linear (GLM) mixed effect models predicting species richness (GLM, Poisson error distribution) and functional diversity (LMM, Gaussian error distribution) of predatory beetles, and invertebrate attack rates (GLM, Negative binomial error distribution) on artificial caterpillars related to veteran and young oaks in Southern Norway. Species richness and functional diversity were based on 40 paired trees (young and veteran) during three sampling periods in summer 2017 and 2018 (n = 238 from 40 trees). The number of invertebrate attack marks left on the artificial caterpillars placed around the trees were identified for the same periods in summer 2018 (n = 345). Bold text indicates significant relationships (P < 0.05).

dependent on veteran trees and more generalist predators that were attracted to veteran trees for shelter and as a source of prey. It is likely that it was the later, as it has been shown that ground beetles are important predators in Northern European forests^{26,36,37}. In either case however, veteran trees provide resources that are beneficial for invertebrate predators and are lacking or of lower quality in younger trees¹⁷.

Although this study focused on the dichotomy between veteran and young trees at rather small spatial scales (200 m or less), other research has established that the immediate surroundings and the wider landscape around the veteran trees can influence invertebrate diversity^{22,38–41} and that large scale anthropogenic factors such as urbanization gradients influence predation rates by natural enemies^{12,26}. In contrast, research within agroecosystems has found that strips of non-agriculture area with resources for natural enemies reduce pests and crop plant damage independent of landscape complexity⁴². It is clear that veteran trees should not be considered independent units because invertebrate diversity has been shown to be influenced by habitat connectivity at spatial scales up to 25 km^{22,38,39}, but the interaction between local and regional landscape effects with predation around veteran trees needs more research.

The findings that green artificial caterpillars were attacked less by arthropod predators and that artificial caterpillars were attacked more when they were placed at ground level are interesting results that have implications for pest control with natural enemies and future research with artificial caterpillars. It is likely that green caterpillars were less detectable due to lower contrast with the background³⁶ and that ground dwelling predators were responsible for the increase in attack marks on artificial caterpillars placed at ground level. It has been found that visual signals have a strong influence on hunting arthropods^{43–45}, and artificial prey coloration had an effect on invertebrate attacks in Northern Europe³⁶ but less so in the tropics³¹. This difference may be due to the dominance of ants in tropics, which are more chemically oriented and therefore less influenced by the prey coloration³¹. Certain ant species such as *Lasius brunneus* and *L. ferrugineus*, are associated with tree hollows in Europe⁴⁶, but ants were only observed in high numbers at three of the study trees (one veteran and two young). On the other hand, predation by beetles has been observed to be influenced by prey coloration, although this has been found to vary between even related species⁴⁷, and ground beetles are likely the dominant invertebrate predator attacking artificial caterpillars in Northern European forests^{26,36,37}. The conclusion that beetles were the dominant predator attacking the artificial caterpillars in our study is further supported by the fact that we found ground beetles in our traps, and as discussed previously, invertebrate attack rates paralleled the trapping data of predatory beetles. It would, however, be beneficial to know the identity of the invertebrate predators so that these findings could be more clearly integrated into an understanding of predation by natural enemies.

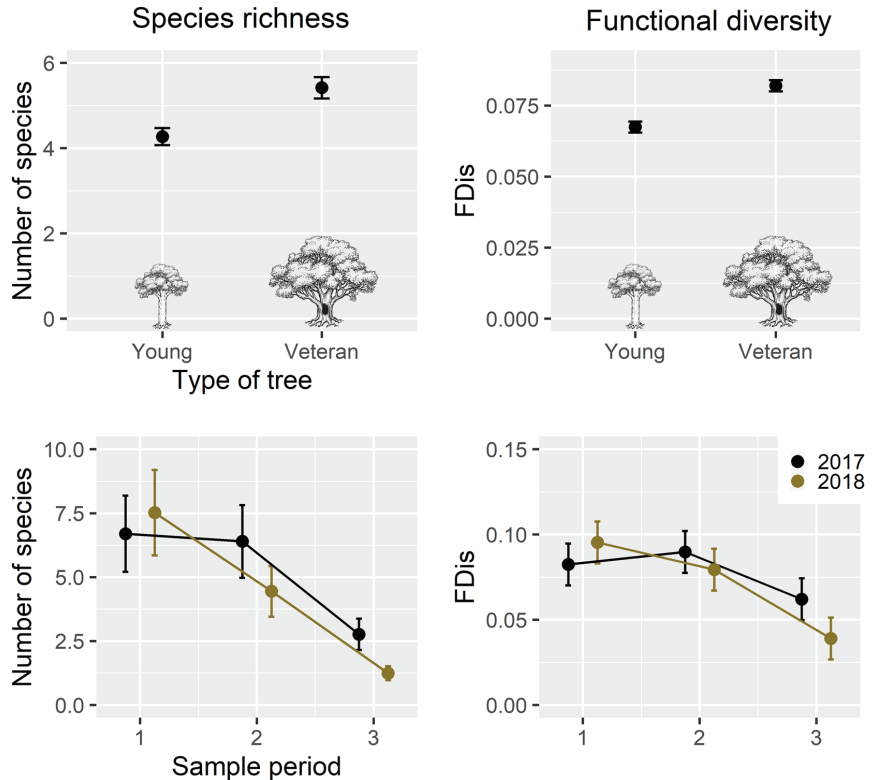


Figure 1. Estimates from the models that predicted species richness (left plot) and functional diversity (right plot) of predatory beetles (\pm SEM; $n = 238$ from 40 trees). Species richness was modeled with a generalized liner mixed effect model with Poisson error distribution, and functional diversity was calculated as functional dispersion (FDIs) and modeled with a Liner mixed effect model with Gaussian error distribution. Both measures of diversity were higher around veteran trees ($P = 0.01, 0.037$, top), and independent of the type of tree there was a yearly and seasonal effect where diversity decreased through the season and was significantly lower at the end of 2018 ($P = 0.001, 0.017$, bottom). Window trap samples were collected once a month from May to August 2018, at the same time as the artificial caterpillars were collected. A summary of the models is presented the Table 1 (Ill. by Matthew Cooper).

Finally, it should be noted that a large portion of the artificial caterpillars placed out during this study were found to be missing or damaged to the point of obscuring other attack marks. It does not appear that this influenced the results related to invertebrate attacks because the remaining caterpillars were well balanced within the experimental setup. We presume that the missing and damaged caterpillars were a result of bird attacks²⁹. Our study was not designed to measure avian predation and the relatively short distance between the two types of trees likely allowed birds to easily move between them. The influence of veteran trees on avian predation is clear avenue of future research, but a different study design would be needed to further explore this relationship.

Conclusions

Our results that species richness and complementary trait diversity of invertebrate predators responded in parallel through the season with predation rates and were higher around the veteran trees clearly indicate that veteran trees are a source of natural enemies. Veteran trees are valuable because of their cultural significance⁶ and their importance for biodiversity¹⁹. They increase the structural complexity of landscapes³⁵ and based on our results, their communities may contribute to invertebrate pest control. These results give clear incentive to protect veteran trees and their associated communities. Veteran trees also provide additional contributions of benefits to people that are both economic and cultural^{48–50}. Hartel et al.⁵¹ goes on to state that wood-pastures with veteran scattered trees provide a model ecosystem for the sustainable integration of food production and biodiversity conservation. Protecting and valuing veteran trees and their communities and reintegrating them into agricultural systems is an essential step towards a more sustainable system of management and has the possibility of enhancing the wellbeing of people while promoting biodiversity.

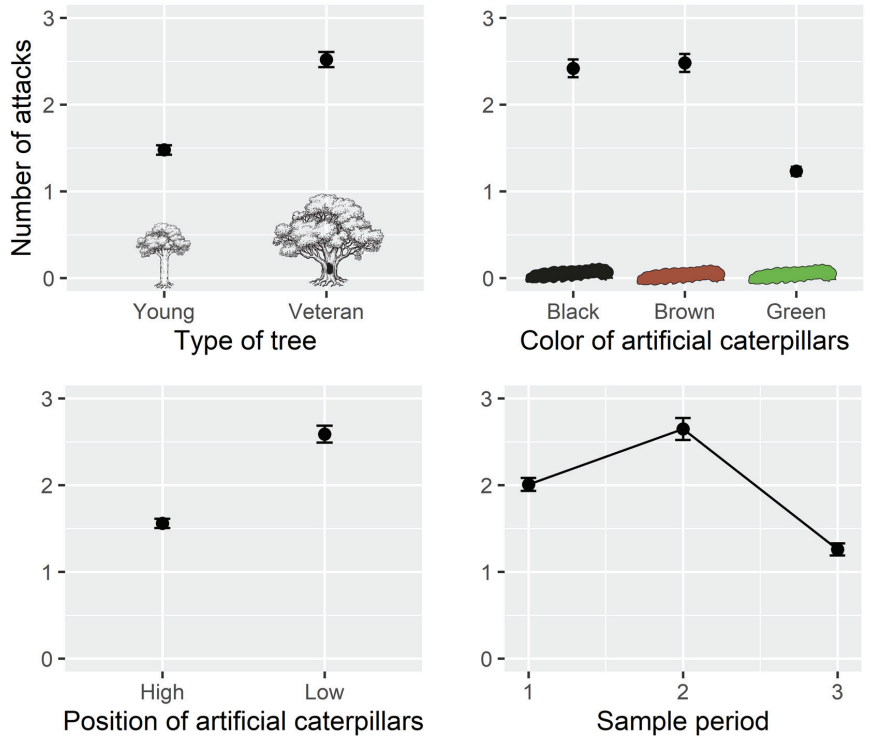


Figure 2. Estimated invertebrate attack rates on the artificial caterpillars from the Generalized liner mixed effect model with Negative binomial error distribution (\pm SEM; $n = 345$). Artificial caterpillars were subjected to a 30-day exposur, being collected and replaced once a month from May to August 2018, at the same time as the window trap samples were collected. A summary of the model is presented the Table 1 (Ill. by Matthew Cooper).

Material and methods

In order to test our predictions, we established a balanced experimental design where we chose 20 veteran oaks in the central distribution of oaks in Southern Norway from the Norwegian database of veteran oaks⁵¹ and matched them with 20 young oaks from the nearby surroundings. We used stratified random sampling to include veteran trees in forest and open landscapes ($n = 12$ and 8, respectively), had trunks with circumferences of 2 m or greater (measured at the height of 130 cm) and had young oaks in the immediate surroundings. Young oaks were within 200 m of the focal veteran oak, had similar immediate surroundings (e.g. openness, sun exposure and surrounding tree species) and were at least 50 m from any other veteran oak. The mean circumference of the veteran oaks was 283 cm (200–405 cm) and mean circumference of the young oaks was 74.5 cm (25–148 cm). The trees were originally identified within 500 × 500 m blocks, which we will refer to as the sampling blocks⁵¹. Twelve pairs of trees were nested in clusters of three within a sampling block, but all tree pairs were more than 100 m apart. All trees were within a 30 km radius of the city of Larvik.

To measure the functional and taxonomic diversity of predatory beetles, we sampled the beetle communities around the focal tree with flight intercept traps over the course of summer 2017 and 2018. The traps were made of two intersecting 20 × 40 cm windows with a funnel below leading to a vial containing propylene glycol, water (4:1 mixture) and a drop of detergent used as a surfactant. The traps were hung from a branch in the canopy of the focal tree and were placed out in May and emptied once a month until August (Fig. 3).

Predation rates were measured with artificial caterpillars made from plasticine (JOVIE) formed into 20–30 mm long and 5 mm thick cylinders by hand. A metal wire (\varnothing 1.1 mm) extending from the core of each caterpillar were used for attachment. Six artificial caterpillars were placed 2–4 m from the trunk of the focal tree and split equally by two positions: 1.5–2 m and at ground level (0–10 cm). The caterpillars were attached to a natural site of attachment (branch or stem). Although it has been shown that the plant species had little effect on invertebrate predation of artificial caterpillars³¹, the caterpillars was either attached to a branch of the focal tree or to a branch of a nearby deciduous tree. Three colors (green, brown and black) were chosen to mimic the variety of lepidoptera larvae commonly found in Scandinavian forests (Fig. 3). Artificial caterpillars were subjected to a 30-day exposur, being collected and replaced once a month from May to August 2018, at the same

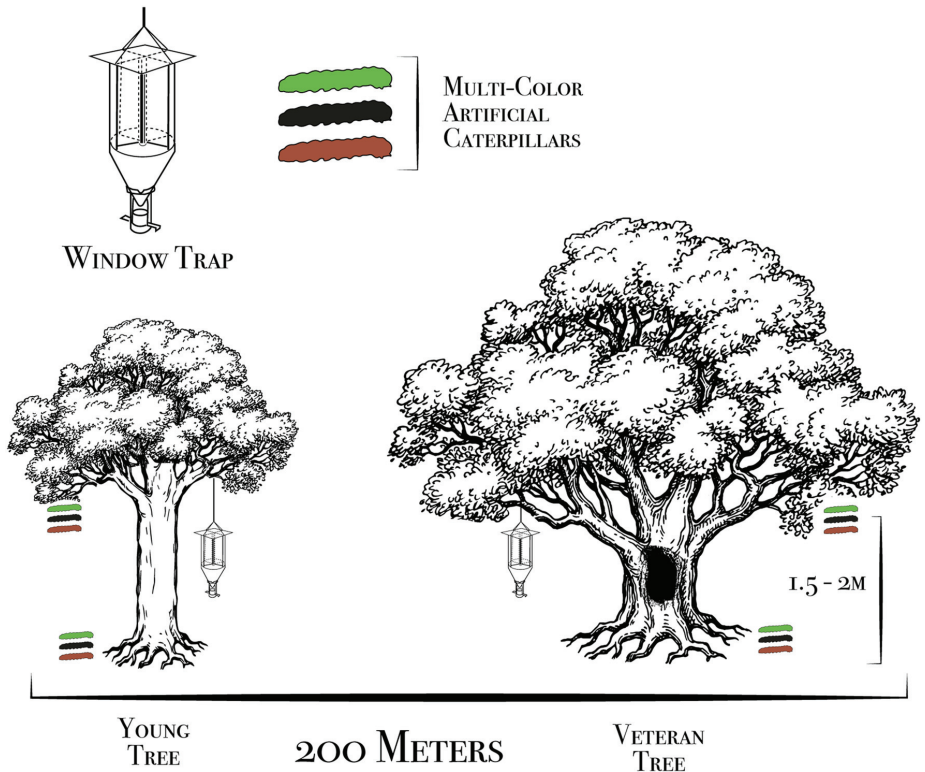


Figure 3. A figure of the study design that we used to measure the contribution of veteran oak invertebrate communities to predation by natural enemies. We measured predatory beetle diversity with window traps and predation rates with attack marks left on artificial caterpillars around 20 pairs of young and veteran oaks in Southern Norway. The window traps were active through the summer in 2017 and 2018 and artificial caterpillars were placed out in the summer 2018. The artificial caterpillars were secured to a natural attachment sites 2–4 m from the trunk of the focal tree (Ill. by Matthew Cooper).

time as the window trap samples were collected. The location of the caterpillars remained the same through the experiment, but to avoid bias the colors were randomized within the location so that the order was not same between sampling periods.

Attack marks on the artificial caterpillars were documented in the field and verified in the lab. They were identified as being made by either arthropods, birds, small mammals or an unknown source based on a key provided by Low et al.²⁹, and counted for each taxonomic group. In total we placed out 720 artificial caterpillars, but 375 were found to be either missing or unidentifiable, presumably due to bird attacks²⁹. Despite this, the remaining caterpillars were well balanced within the experimental setup. There were 162 caterpillars remaining around the veteran trees and 183 around the young trees, 187 remaining at the high and 158 at the low location, and regarding the different colors there were 110 black, 116 brown and 119 green caterpillars. However, the number of caterpillars remaining through the sampling period did decrease as the summer progressed: we collected 177 caterpillars in the first period, 96 in the second period and 72 in the last period.

All beetles collected in the flight intercept traps were identified to the species level following the taxonomy of The Norwegian Biodiversity Information Centre⁵² by an expert. Following the protocol set by Wetherbee et al.²⁴ species were classified as predators based on both adult and larvae diets, and adult trait information (body length, relative eye size and peak activity date) was collected from literature or calculated from available material (Table 2). Functional diversity was subsequently calculated based on all traits. Since functional diversity indices are sensitive to missing trait information, we verified that at least 80% of all species in the functional groups had trait information⁵³. All species that were excluded as a result of lack of data were rare in the data set (abundance less than 5). We chose to use functional dispersion (FDIs) to measure functional diversity because it accounts for species abundances, it can be calculated for multiple traits, and species richness has limited effect on it⁵⁴. FDis is a measure of dispersion in trait space and is calculated as the mean distance of species to the centroid of the community and is weighted by abundances⁵⁴.

Trait	Link to predation	Type/unit of measurement	Collection source
Body length	Closely linked to many life history traits such as life span and dispersal ability, and it influences the amount and composition of resources used	Millimeters	Literature
Relative eye size	Linked to prey recognition as well as hunting strategy	Mean eye circumference divided by length (measured in pixels)	Photogrammetric analysis
Peak activity date	More species being active throughout the season will increase phenological overlap with prey species and decrease intraguild predation	Year days	Literature and predictions from GBIF data

Table 2. Traits included in our measure of functional diversity (trait information is from adult beetles).

Prior to statistical analysis, we followed the steps for data exploration outlined by Zuur et al.⁵⁵. Statistical analysis was carried out in R version 3.4.0⁵⁶. Species richness and FDis were calculated with the *dbFD* function in the 'FD' package^{54,56}. FDis was calculated using a Gower dissimilarity matrix and the "cailliez" correction method^{154,57}. All models were created with the function *glmmTMB* from the package 'glmmTMB'⁵⁸. The following predictor variables were initially included in all models: whether the tree was veteran or young, the sampling period (early, mid or late), whether the tree was in an open landscape or a forest, a land use gradient, the tree cover density in a 50 and 100 m radius of the focal tree, and the circumference of the focal tree. Additionally, the sampling year was included in the beetle diversity models and the color and location of the artificial caterpillars were included in the invertebrate attack model. The best model was chosen with backward model selection based on Akaike information criterion (AIC) and non-significant predictors were removed ($P > 0.05$)⁵⁵. We also determined the best error distribution and random effect structure by comparing the AIC of candidate models using the *AICtab* function in the package 'bmlme'⁵⁹. We compared three different random effect structures to deal with spatial correlation between the tree pairs (the veteran/young tree pair, the sampling blocks and a crossed random effect of tree pair and sampling block) and a model with no random effect, and found that a random intercept model with sampling block as the random effect was the best random effect structure for all models. The coefficient of determination (pseudo R^2) was calculated for the models using the *r.squaredGLMM* function in the MuMIn package⁶⁰.

We modeled species richness of predatory beetles with a Generalized linear mixed effect model with Poisson error distribution. We found that arthropod attack marks were overdispersed, and used a Generalized linear mixed effect model with Negative binomial error distribution with the "NB2" parameterization (variance = $\mu(1 + \mu/k)$) to deal with the additional dispersion^{58,61}. Although FDis is bound between 0 and 1, in our dataset it was approximately normally distributed, so we used a Linear mixed model with Gaussian error distribution to model it. The data also appeared to have slight zero inflation, but the Linear mixed effect model had a lower AIC and was chosen as our final model⁶². The final models were checked for patterns in the residuals, influential observations, and spatial and temporal structure that was not accounted for by the model⁵⁵. The following packages were also used for data manipulation, statistical analysis and graphical visualization: 'lattice'⁶³, 'ggplot2'⁶⁴, 'dplyr'⁶⁵.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Author contributions

R.W., T.B. and A.S. conceived the ideas and designed methodology. R.W. collected and analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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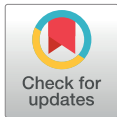
Paper III

RESEARCH ARTICLE

Veteran trees have divergent effects on beetle diversity and wood decomposition

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Abstract

Veteran hollow trees are keystone structures in ecosystems and provide important habitat for a diverse set of organisms, many of which are involved in the process of decomposition. Since veteran trees are 'islands' of high biodiversity, they provide a unique system in which to study the relationship between biodiversity and decomposition of wood. We tested this relationship with a balanced experimental design, where we quantified the taxonomic and functional diversity of beetles directly involved in the process of decomposing wood, and measured the decomposition of experimentally added bundles of small diameter wood around 20 veteran trees and 20 nearby young trees in southern Norway. We found that the diversity (both taxonomic and functional) of wood-decomposing beetles was significantly higher around the veteran trees, and beetle communities around veteran trees consisted of species with a greater preference for larger diameter wood. We extracted few beetles from the experimentally added wood bundles, regardless of the tree type that they were placed near, but decomposition rates were significantly lower around veteran trees. We speculate that slower decomposition rates around veteran trees could have been a result of a greater diversity of competing fungi, which has been found to decrease decay rates. Veteran trees provide an ecological legacy within anthropogenic landscapes, enhance biodiversity and influence wood decomposition. Actions to protect veteran trees are urgently needed in order to save these valuable organisms and their associated biodiversity.

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Data Availability Statement: All species observations related to this study are registered in Global Biodiversity Information Facility (GBIF) and are publicly available (<https://doi.org/10.15468/5bxyph>), and all data that was used in this study

Introduction

Veteran hollow trees are valuable entities in forests, farmlands, traditional landscapes and urban areas because they are keystone structures that increase habitat heterogeneity and biodiversity [1–3]. However, they are declining globally [4]. The decline of veteran trees is adding to the existential threat of global biodiversity loss, which is especially problematic because biodiversity contributes to critical ecosystem functions on which humans rely [5]. Research clearly indicates that loss of biodiversity results in reductions in these contributions [6, 7], but the exact relationship between biodiversity and ecosystem functioning continues to be debated [8–11].

A community's contribution to ecosystem functioning is more closely related to its diversity of relevant functional traits than to the number of species within the community [12–14]. A

has been archived in NMBU Open Research Data (<https://dataverse.no/dataverse/nmbu>).

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diversity of functional traits in a community is thought to promote multiple ecosystem processes and make these processes more resilient to change [15–19]. Veteran trees are, in a sense, ‘islands’ of high biodiversity, as they are surrounded by other trees that support less species-rich communities [1]. This provides the opportunity for paired study designs that examine ecosystem functioning at different levels of diversity within the same landscape context [20]. Thus, research related to the influence of veteran trees, and their associated biodiversity, on ecosystem functioning has a two-fold advantage, in that it can elucidate the relationship between biodiversity and ecosystem function and simultaneously provide incentives to protect these valuable organisms.

Dead wood is a particularly important form of plant biomass, as there are more than 73 billion tons of carbon stored in naturally occurring dead wood globally [21]. Small diameter wood in particular may be of great importance regarding carbon cycling and storage in forest ecosystems [22]. However, biodiversity mediates the rate at which wood decomposes and this in turn effects the rate at which carbon dioxide is released to the atmosphere [23]. Veteran trees have larger circumference, a greater diversity of dead wood and more fungal fruiting bodies than typical forests trees [2], and this increases the diversity of wood-decomposing organisms associated with them [24–26]. However, the relationship between biodiversity and decomposition is complex, with many interactions among diverse organisms [11, 27].

Insects are extraordinarily diverse, interact with many organisms involved in decomposition [28, 29], and likely play an important role in the process of decomposing wood [30]. In northern ecosystems, where termites are absent, beetles are one of the primary insect decomposers [26, 31] and both beetle species richness and abundance are often high in small diameter wood [32–35]. Beetles contribute to decomposition both directly, by consuming dead wood and the fungi living within it [36–39], and indirectly, most likely by acting as dispersers of fungal spores to dead wood [40, 41]. These indirect effects are especially relevant, because fungi are a primary driver of wood decomposition [42, 43], and decomposition rates have been shown to decrease in response to insect exclusion [41]. It is therefore likely that the diversity of organisms associated with veteran trees has some effect on decomposition of wood, yet this remains relatively unexplored.

Combining an analysis of functional diversity with a study exploring the relationships between biodiversity and decomposition of wood may help to expand the current understanding of that relationship. For example, the body size of an insect is tightly connected to its resource use [14] and, in the case of wood-boring beetles, also influences how tunnels and galleries within the wood are created [38, 39]. Additionally, features of the dead wood, such as the diameter, decay stage, vertical position within the canopy and tree species, have been found to influence insect communities and decomposition rates [25, 32, 33, 44, 45]. Therefore, a diversity of niche preferences within an insect community may decrease competition and increase resource partitioning [46–48], thus potentially increasing decomposition rates [8].

In order to test the influence of veteran trees on wood-decomposing beetle diversity and wood decomposition rates, we employed a paired experimental design. We matched veteran oaks with nearby young oaks in southern Norway, experimentally added bundles of recently cut small diameter oak branches, and sampled beetle communities with window traps over a two-year period. We measured the diversity of wood-decomposing beetle communities and quantified wood decay rates. The study had four aims: 1) measure the number of beetles species associated with wood decomposition around veteran and young trees, 2) compare the two communities’ functional diversity, 3) investigate whether this diversity increased the number of beetles colonizing the experimentally added wood, and 4) measure the decay rates of the wood bundles. We predicted that there would be a greater diversity of wood-decomposing beetles around veteran trees, in terms of both number of species and functional diversity, and

that this would result in more beetles colonizing the wood bundles, which in turn would increase decomposition rates.

Methods

This study complied with the appropriate institutional, national, and international guidelines and was approved by the Norwegian University of Life Sciences, Faculty of Environmental Sciences and Natural Resource Management (Project number: 7101212). The study sites were on public and private land, and we confirm that Vestfold Fylkeskommune and the private land-owners provided permission to conduct the study at these sites.

We established a paired experimental design, in which we randomly chose twenty veteran oaks in the central distribution of oaks in Norway from the Norwegian database of veteran oaks [49]. Each of these trees had a circumference of 2 m or greater (measured at the height of 130 cm). We subsequently matched each veteran tree with a young oak that was within 200 m and had similar immediate surroundings (e.g. similar openness, sun exposure and surrounding tree species). The tree-pairs were in either forests or open landscapes ($n = 12$ and 8 , respectively) and were within a 30 km radius of the city of Larvik. The higher number of tree-pairs in the forest was due to the difficulty of finding suitable young oaks near the veteran oaks in open landscapes. A young tree was defined as an oak that had a circumference less than 150 cm and no visible hollow. The tree-pairs were always more than 100 meters apart, but 12 of these pairs were clustered within four 500 m x 500 m sampling blocks that were established by the survey which originally identified the veteran oaks [49]. These same tree-pairs were also used by Wetherbee et al., (2020b). The mean circumference of the veteran oaks was 283 cm (200–405 cm) and mean circumference of the young oaks was 74.5 cm (25–148 cm).

We measured beetle diversity, and decomposition rates of experimentally added wood, from spring 2017 to fall 2018. To measure beetle diversity, we hung one flight intercept trap in the canopy of each tree. The flight intercept traps were made of two intersecting 20 x 40 cm windows with a funnel below leading to a vial containing propylene glycol, water (4:1 mixture) and a drop of detergent used as a surfactant. They were hung from a branch in the canopy, on the opposite side of the tree as the experimentally added wood. The traps were active from May to August in both years and emptied once a month during that time.

In order to measure colonization and decomposition of small diameter wood, we transported a total of 149.5 kg of fresh oak branches into the forest. The branches were divided evenly into bundles that were held together with zip ties, and two bundles were placed near each tree (one on the ground at the base of the tree and one hanging in the mid-canopy, 3–4 m high). The wood bundles consisted of six 50 cm long freshly cut branches that were 1–3 cm in diameter, and the average wet weight of the bundles was 1.9 kg (min = 1.4, max = 2.6). All branches originated from three living oaks and were collected on the 9th of May 2017. Subsequently, the branches were transported back to the lab, where they were randomly mixed, sorted into bundles and weighed. The bundles were then transported to the field sites between the 16th and the 25th of May 2017. Bundles were retrieved between the 13th and the 18th of August 2018.

After the bundles were collected from the field, they were placed directly into rearing chambers. The rearing chambers consisted of non-transparent cardboard barrels (50 cm diameter and 150 cm length) with a plastic lid and a transparent collection vial mounted on it. The bundles were then reared for one year in an open-air building at the ambient temperature (September 2018 to October 2019). The collection vials were emptied regularly and at the end of rearing all invertebrates found inside the barrels were collected. Subsequently, the bundles were weighed, then oven dried at 103^o C until the weight stabilized (approximately 7 days)

before measuring dry mass. In order to measure bundle densities, we cut off 5 cm from both ends of the sticks (from here on referred to as ‘tips’) before and after the field experiment. All tips were oven dried at 103°C until the weight had stabilized (approximately 4 days). The tips were then weighed, and the volume was measured by water displacement. The density of the tips was then calculated as the dry mass divided by the volume [41].

All beetles collected in both the flight intercept traps and in the bundle extractions were identified to the species level by an expert, following the taxonomy of The Norwegian Biodiversity Information Centre [50]. Additionally, all species observations were registered in Global Biodiversity Information Facility (GBIF) and are publicly available [51]. Following the protocol set by Wetherbee et al. (2020a), a literature survey was carried out and beetles were classified as wood-decomposers if they were described as xylophagous, mycetophagous (fungivore) or saprophagous and polyphagous (including a life stage that feeds on wood either directly or indirectly) at any point in their life stages (S1 Table). Available trait information that was relevant for wood decomposition rates was collected from the literature (Table 1).

Functional diversity was subsequently calculated based on all traits, and a community weighted mean (CWM) was calculated for each trait individually. We verified that at least 80% of all species used in the statistical analysis had trait information, since functional diversity indices are sensitive to missing trait information [52]. All species that were excluded due to a lack of trait data were rare in our data set (total abundance < 3). We chose to use functional dispersion (FDis) as our measure of functional diversity because it accounts for species abundances, can be calculated for multiple traits, and is only minimally sensitive to species richness [53]. FDis is a measure of dispersion in trait space and is calculated as the mean distance of all species (weighted by abundances) to the centroid of the community in multidimensional trait space [53]. We also choose to use CWMs of each trait to gain insight into how mean trait values differed between veteran and young oaks. CWM is defined as the mean values of a given trait present in the community, weighted by the relative abundance of the taxa bearing each trait value [54].

All analyses were carried out in R version 3.4.0 [55]. Species richness and FDis of saproxylic beetles, as well as CWM for each trait, were calculated with the *dbFD* function in the ‘FD’ package. FDis was calculated using a Gower dissimilarity matrix and the “cailliez” correction method [53, 56]. Additionally, the percent weight loss (PWL) of the dead wood bundles was calculated as the start weight minus the end weight, divided by the start weight.

In order to test the effect of the tree type on beetle diversity and decomposition rates, we fit a set of models to predict beetle species richness, FDis, CWM for each trait, and the density and PWL of the bundles. Although we were primarily focused on the dichotomy between the veteran and the young trees, we also included relevant tree and landscape predictor variables and, in the case of the wood bundles, location (hanging or on the ground) as fixed effects in the models (Table 2, S1 Fig). We determined that the response variables of density of the bundles, FDis and CWM for each trait were all approximately normally distributed and modeled

Table 1. Traits included in our measure of wood-decomposing beetle functional diversity (for species list and trait values see S1 Table).

Trait	Link to decomposition	Type	Collection source
Body length	Closely linked to many life history traits such as life span and dispersal ability, and influences the amount and composition of resources used	Continuous	See Wetherbee et al. 2020a, Appendix II
Wood diameter preference	Diversity of preferred habitats may aid the decomposition process	Continuous	Gossner et al. 2013, Seibold et al. 2014, Janssen et al. 2017
Decay stage preference	Diversity of preferred habitats may aid the decomposition process	Continuous	Gossner et al. 2013, Seibold et al. 2014, Janssen et al. 2017

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Table 2. Variables that describe the oak trees and their surrounding landscape in southern Norway.

Experimental variables	Type	Measurement	Reference
Type of tree	Categorical (2 levels)	Veteran or young tree: a veteran tree was defined as a tree of at least 200 cm circumference with a visible cavity in the trunk, and a young tree was defined as having a circumference less than 200 cm, and not having a visible hollow if it was larger than 95 cm	Lovdata (2011)
Location of the wood bundle	Categorical (2 levels)	Ground or canopy: bundles were either placed on the ground or hung from a branch in the middle of the canopy	Seibold et al. (2018)
Additional variables			
Habitat class	Categorical (2 levels)	Forest or open landscape: based on 50 m radius surrounding the tree. Open landscapes were either parks or agricultural landscapes	Sverdrup-Thygeson et al. (2010)
Tree cover density (2 variables)	Continuous	Measured at two scales (20 and 100 m): the 20 m scale was measured as the percent of the 20 m pixel where focal tree is located that is covered by forest. The 100 m scale was measured as the percent of 20 m pixels covered by forests within 100 m radius of focal tree.	Copernicus Tree Cover Density (2012 & 15)
Tree circumference	Continuous	Tree circumference at breast height.	Sverdrup-Thygeson et al. (2010)

These variables were used to predict species richness and functional diversity of beetles, as well as the decomposition rates of the experimentally added bundles of wood.

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them with a linear mixed model with Gaussian distribution (LMM). Additionally, we modeled species richness (count data) with a Generalized linear mixed effect model with a Poisson distribution (GLMM) (see [S2 Fig](#) for variable distributions). We also included a random effect in each model with sampling block as a random intercept to deal with the spatial correlation introduced by the study design. Since decomposition is heavily influenced by abiotic conditions, we also tested if tree cover ([Table 2](#)) or moisture in the bundles differed between the two tree types. To calculate the tree cover, we used we used Copernicus tree cover density maps with 20 m resolution and measured the tree cover density within a 20 m and a 100 m radius of the focal tree [[57](#)].

Prior to statistical analysis, we followed the steps for data exploration outlined by Zuur et al. (2010) for all statistical models. The best model in each case was chosen with backward model selection based on Akaike information criterion (AIC). We subsequently visually checked the assumptions of the final LMMs of normal distribution of the residuals and homoscedasticity [[58](#)]. We also checked the final GLMM for over/under dispersion with the function *dispersion_glm* from the 'blmeco' package [[59](#)]. Additionally, we checked for influential observations, and spatial and temporal structure that was not accounted for by the model, by plotting the model residuals against the spatial coordinates and looking for patterns [[58](#)]. The following packages were also used for data manipulation, statistical analysis and graphical visualization: 'lattice' [[60](#)], 'ggplot2' [[61](#)], and 'dplyr' [[62](#)].

Results

Over the course of the two summers we captured a total of 465 beetle species (4,539 individuals) in the flight intercept traps, of which 160 (1,405 individuals) were wood decomposers ([S1 Table](#)). The total number of wood-decomposing beetle species captured around veteran trees was 132 (787 individuals), compared to 114 (618 individuals) around young trees. Both species richness and functional diversity of wood-decomposing beetles were higher around veteran trees than young trees ([Fig 1](#) and [Table 3](#), $P < 0.001$ and $P = 0.021$, respectively). This effect was especially pronounced for species richness, where there were on average 22 (min = 10, max = 24) species around veteran trees and 16 (10, 29) around young trees. The community weighted mean (CWM) of wood diameter preference for beetles captured around the veteran trees was significantly higher than for those captured around the young trees ($P = 0.011$),

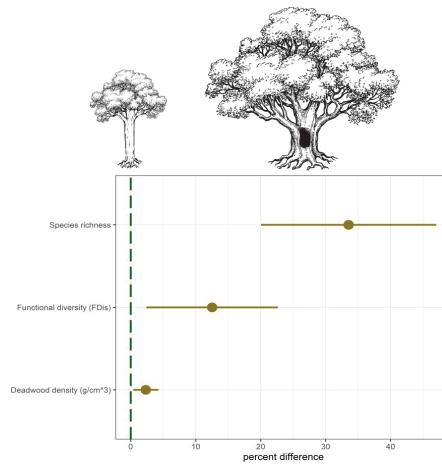


Fig 1. The percent difference between paired young (green line) and veteran (brown points) oak trees for wood-decomposing beetle species richness, beetle community functional diversity, and the post-experiment density of the experimentally added dead wood. Error bars show 95% confidence intervals, based on regression models (see [Table 3](#) for model outputs). All sites were located in southern Norway.

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Table 3. Estimated regression parameters, standard errors and P-values from the best models.

Response variable and predictors	Estimate	Standard error	P value	R ² (or pseudo R ²)
Species Richness				
intercept	2.746	0.086	<0.001	0.18
Type of tree (veteran)	0.289	0.074	<0.001	
FDIs				
intercept	1.293	0.047	<0.001	0.13
Type of tree (veteran)	0.162	0.067	0.021	
CWM wood diameter				
intercept	2.202	0.047	<0.001	0.15
Type of tree (veteran)	0.180	0.067	0.012	
Wood density				
intercept	0.640	0.005	<0.001	0.16
Type of tree (veteran)	0.015	0.006	0.023	
Surroundings (forest)	0.019	0.007	0.007	
Percent weight loss				
intercept	0.482	0.003	<0.001	0.16
Type of tree (veteran)	-0.009	0.003	0.011	
Surroundings (forest)	-0.010	0.004	0.03	

The intercept represents young oaks or, in models with a ‘surroundings’ covariate, young trees in open landscapes. Species richness of wood decomposing beetles was modeled with a GLMM with Poisson distribution (N = 40). Beetle functional diversity (FDIs) and community weighted mean (CWM) of their wood diameter preference were modeled with LMM with Gaussian distribution (N = 40), as was the density of the experimentally added bundles of wood (N = 80). The best models were identified with backward model selection based on the AIC. Note: the model estimates for species richness have not been back transformed. Results from additional models that did not have significant effects are presented in text.

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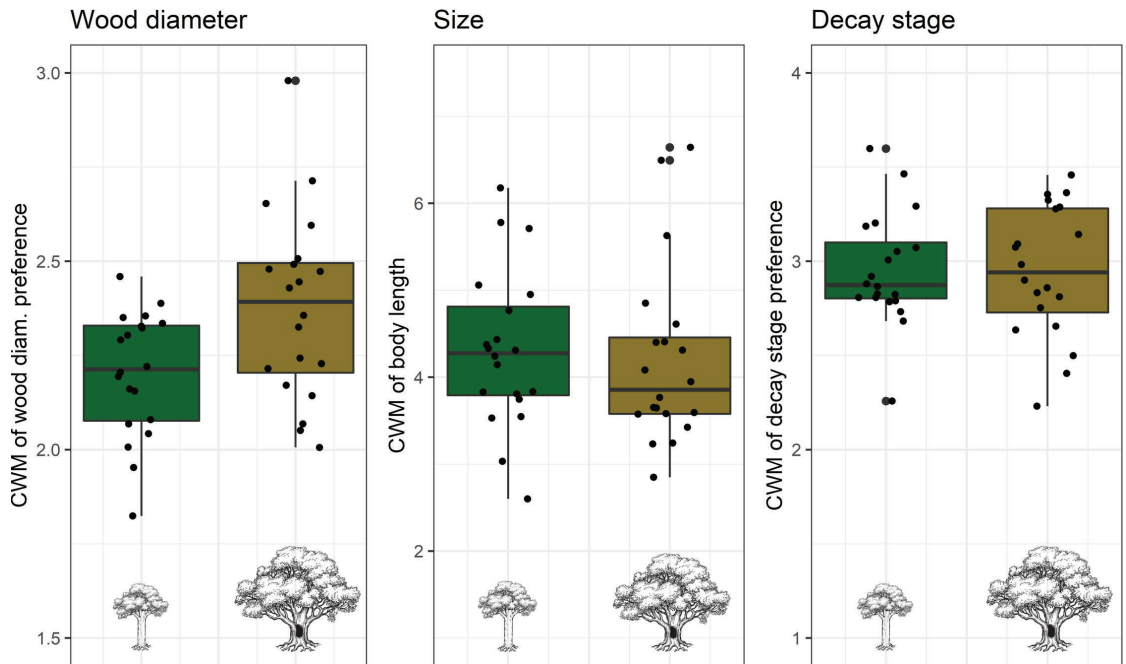


Fig 2. Community weighted mean (CWM) of the three traits that we included in the measure of functional diversity for wood decomposing beetles captured around young (green) and veteran (brown) oak trees in southern Norway. The plots show the median, first and third quartiles, with whiskers that extend 1.5 times the interquartile range. All observations as shown as points on the plots. Beetle communities around veteran trees preferred significantly larger diameter wood (middle plot) than those around young trees ($P = 0.01$), whereas the CWM of decay stage preference (left plot) and beetle body length (right plot) did not differ among tree types.

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whereas the CWM of body length and wood decay stage preference did not differ between the two tree types (Fig 2).

The diversity and abundance of beetles reared from the experimental wood bundles was low (19 individuals from five species), but most of the species and individuals came from bundles that had been placed around veteran trees (Table 4). However, the type of tree (veteran or young) did influence the final density of the wood and the percent weight loss of the bundles

Table 4. Species and abundances of beetles extracted from the experimentally added bundles of small diameter wood.

Species	Veteran tree abundance	Young tree abundance
<i>Orchestes fagi</i>	1	0
<i>Phymatodes testaceus</i>	1	0
<i>Poecilium alni</i>	0	2
<i>Salpingus planirostris</i>	2	0
<i>Scolytus intricatus</i>	13	0

The bundles of wood were placed around either a veteran or a young tree and left in the field for two seasons and then extracted for one year. The study was carried out in southern Norway.

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(PWL). After two seasons in the field, the density of the experimentally added wood was, on average, 2.3% higher in the bundles placed around the veteran trees than those around young trees, and this effect was mirrored in the PWL, which was significantly lower around the veterans (Fig 1 and Table 4, $P = 0.023$ and $P = 0.011$, respectively). Independent of the type of tree, wood density was 2.9% higher in forests than in open landscapes and again this result was mirrored in the PWL, which was significantly lower in forests (Table 3, $P = 0.007$ and $P = 0.03$, respectively). We also found that there were no significant differences between the veteran and young trees regarding tree cover density, or the amount of moisture in the bundles at the end of the study (S2 Table, $P = 0.484$ and 0.166 , respectively).

Discussion

Overall, the number of beetle species involved in decomposition of wood was higher around the veteran oaks than the young oaks. This finding is consistent with previous research in Germany, which found higher species richness of saproxylic beetles around veteran trees [1], and provides reasons to protect veteran trees as valuable habitat for beetle diversity. Our results indicate that veteran trees contribute greatly to a landscape's biodiversity. We observed that beetle species richness was more than thirty percent higher around veteran oaks than around nearby (only 50 to 200 meters) young oaks in the same landscape context. This pattern was mirrored by a less pronounced, yet still significant, increase in functional diversity around veteran oaks.

The number of beetle species that we collected in this study, although high, is in line with other observations around veteran oaks in Norway [48, 63–65], and a significant subset of these species appear to specialize on oaks [66]. Prior studies, however, have focused exclusively on veteran oaks and this is, to our knowledge, the first study to measure the diversity of beetles around young oaks in Norway. Although we captured many species around the young oaks, these numbers were likely higher due to the presence of veteran trees in the area. Research indicates that the number of veteran trees in an area (at scales up to 10 km) is a positive predictor of beetle diversity [48, 67, 68].

As our measure of functional diversity indicated, the species captured around veteran trees had greater differences in traits than those captured around the young trees. The main difference we detected in beetle functional diversity was that the beetles around veteran trees included species that preferred larger diameter dead wood, while fewer such species occurred around the young trees. Examples of these beetles were *Ptinus subpillosus*, *Cryptophagus micaceus*, *Dorcatoma chrysomelina*, and *Euglenes oculus*. Of these, *E. oculus* is on the Norwegian red list as near threatened. Also, *C. micaceus* and *D. chrysomelina* are primarily fungivores, and this highlights the importance of fungal fruiting bodies that are associated with large diameter wood as a habitat provided by veteran trees.

Additionally, several species of bark beetle (family: *Curculionidae*) were observed in higher numbers around the veteran trees than the young trees, and this finding has implications for colonization of small diameter wood that we added around the trees. Specifically, *Scolytus intricatus* was observed in higher numbers around the veteran trees. The species is known to have a strong oak association [69], and is specialized in small diameter wood in early decay [70]. This seems to be supported by our data, as most of the beetles extracted from the bundles were *S. intricatus*. However, we only extracted 13 individuals from five different bundles. In fact, there were surprisingly few beetles extracted from the bundles, especially considering how many beetles we captured in the flight intercept traps. This may be explained by the fact that *S. intricatus*, like most bark beetles, colonize wood in June and overwinter as larvae, then emerges the following summer [69]. In this study we left the bundles in the field for two seasons to

measure decomposition over a longer period, which may have reduced the number of beetle that we captured in the extractions.

In general, previous research has found high abundance and diversity of beetles in small diameter wood [32, 33, 35]. Our results contrast greatly with these findings, but is more in line with Ferro and Gimmel (2014), who found much lower colonization rates. To some extent the differences between the findings may result from differences in the amount and diversity of dead wood that was placed out in the various studies, as this is important for saproxylic species richness and abundance [26, 71–73]. Additionally, beetles colonizing small diameter wood are known to be sensitive to freshness of the wood and seasonality [74], and many emerge as adults after one year [32, 33]. As mentioned above, it is quite likely that since the bundles were in the field for two seasons, we missed the early emerging beetles. Also, freshness of the sticks may have played a role in the results, as the sticks were not placed out immediately after cutting. It is less likely that seasonality was important, because the bundles were placed out in spring before the peak flight activity of most beetles in Norway [75].

In addition to few beetles being extracted from the bundles, we found that the bundles placed around the young trees had lower density and greater weight loss than those placed around the veteran trees. This indicates that, contrary to what we had expected, the higher levels of beetle diversity that we observed around the veteran oaks did not increase decomposition rates. While functional dispersion has been shown to be an important measure of trait diversity for decomposition [12], this of course depends on what traits are used to estimate this measure of functional diversity [76]. As discussed above, we found that the main difference in beetle functional diversity between the tree types was that the beetles around veteran trees preferred larger diameter dead wood. Since we only measured decomposition of small diameter wood, it is perhaps not surprising that functional diversity of beetles was not positively correlated with decomposition rates in our study.

However, this does not explain why we observed lower decomposition rates of bundles placed around veteran trees. Lower decomposition rates are unlikely to be attributed to differences in abiotic conditions since we found no differences in tree cover density at the 20 m and 100 m scale, or in the amount of moisture in the wood bundles, between the veteran and young trees. One possible explanation for this finding is related to differences in fungal diversity between the two tree types. High levels of fungal diversity have been shown to slow decomposition rates [23, 27, 77]. Fungal diversity also increases with the diameter of the tree [25], and veteran trees have more fungal fruiting bodies than typical forest trees [2, 78]. It has also been found that beetles may act as targeted dispersers of fungal spores even when not directly colonizing the dead wood themselves [40]. It is therefore possible that more fungal spores arrived, directly or indirectly via beetle dispersal, in the bundles of wood placed around the veteran trees, and that this slowed decomposition. Unfortunately, we did not measure fungal diversity; an experimental design with a series of beetle and fungi exclusions could be used to verify these findings and gain a better understanding of the underlying mechanisms.

Conclusion

Our results highlight that veteran trees have a high conservation value and have species-rich beetle communities with high functional diversity. This has often been assumed but rarely measured, and these results provide hard evidence of the benefits that arise from protecting veteran trees. Our results also indicate that the presence of veteran trees is linked to slower decomposition rates of small diameter wood during early decay. The mechanism behind this finding remains unknown, but could potentially be caused by higher fungal diversity, which has been linked to slower wood decomposition rates. Veteran trees provide an ecological

legacy within anthropogenic landscapes that influence ecosystem functions and services. Actions to protect veteran trees are urgently needed in order to save these valuable organisms and their associated biodiversity.

Supporting information

S1 Fig. Correlation matrix with continuous variables used in the analysis of beetle diversity and wood decomposition rates around oaks in Southern Norway. Values on top right are the Pearson's correlation coefficient.

(DOCX)

S2 Fig. Distribution of values from beetle sampling and experimentally added wood bundles around oaks in southern Norway. Histograms show beetle species richness, density of wood bundles, functional diversity (FDIs), community weighted mean (CWM) of species' wood decay stage preference, species' wood diameter preference, and beetle body length.

(DOCX)

S1 Table. Beetle species captured in flight intercept traps in veteran (VT) and young (YT) trees and characterized as wood-decomposers. Beetles were classified as being wood decomposers based on being involved in primary or secondary wood decomposition at any point in their life stages. This included the following feeding types (FT): xylophagous (x), mycetophagous (m), saprophagous (s) and polyphagous (p). Additionally, the trait data regarding the beetle's body length (mm), wood diameter preference (WD pref) and wood decay stage preference (D pref), and references for their feeding type is provided.

(DOCX)

S2 Table. Estimated regression parameters, standard errors and P-values from models that predicted the starting wet weight and density of the bundles, bundle wetness after the experiment, and Tree Cover Density (TCD) at 20 m and 100 m scales. All models compare values between veteran and young oak trees. All response variables were modeled with LMMs with Gaussian distribution.

(DOCX)

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Appendix

Appendix I

Additional information about statistical analysis

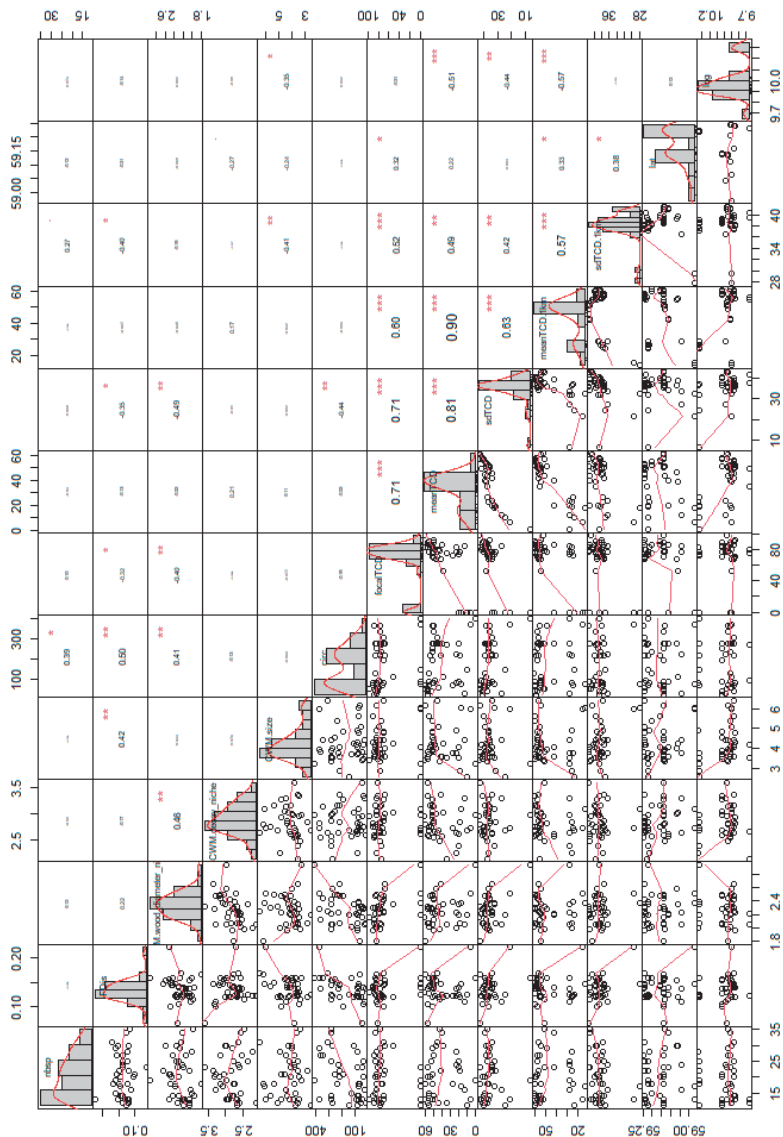


Fig S1: Correlation matrix with continuous variables used in the analysis of beetle diversity and wood decomposition rates around oaks in Southern Norway. Values on top right are the Pearson's correlation coefficient.

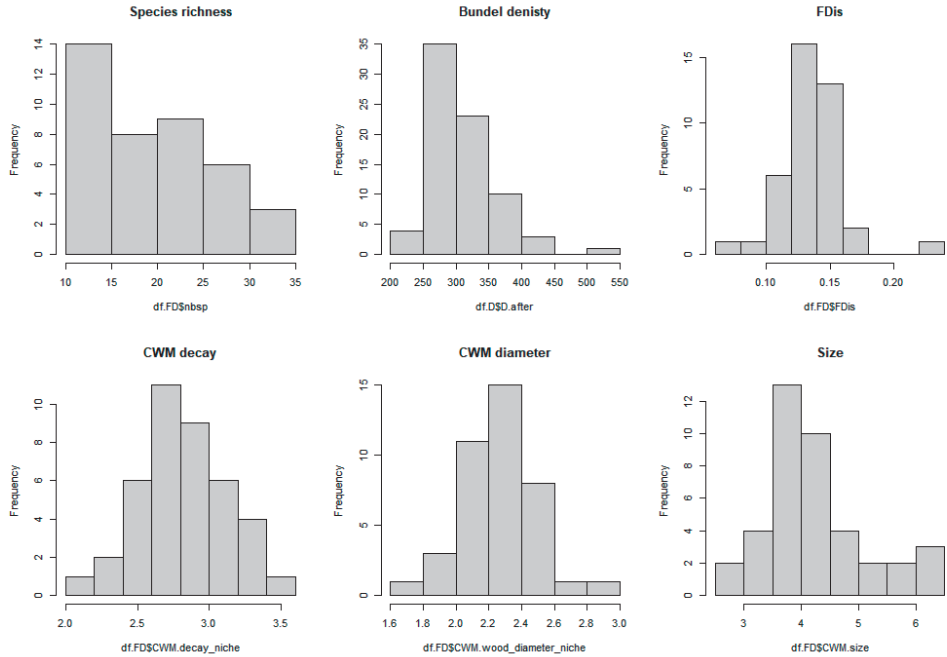


Fig S2: Distribution of values from beetle sampling and experimentally added wood bundles around oaks in southern Norway. Histograms show beetle species richness, density of wood bundles, functional diversity (FDIs), community weighted mean (CWM) of species' wood decay stage preference, species' wood diameter preference, and beetle body length.

Table S1: Beetle species captured in flight intercept traps in veteran (VT) and young (YT) trees and characterized as wood-decomposers. Beetles were classified as being wood decomposers based on being involved in primary or secondary wood decomposition at any point in their life stages. This included the following feeding types (FT): xylophagous (x), mycetophagous (m), saprophagous (s) and polyphagous (p). Additionally, there is trait data regarding the beetle's body length (mm), wood diameter preference (WD pref) and wood decay stage preference (D pref), and references for their feeding type.

Species	Family	VT	YT	FT	Length	WD pref	D pref	Reference
<i>Agathidium nigripenne</i>	Leiodidae	1	0	x	2.75		2	3 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Agathidium varians</i>	Leiodidae	2	2	m	2.75		2	3 Janssen et al 2017
<i>Agrilus angustulus</i>	Buprestidae	0	4	x	5.25		1	2 Seibold et al 2015;Gossner et al 2013
<i>Alosterna tabacicolor</i>	Cerambycidae	9	16	x	7		2.5	3.6 Seibold et al 2015;Gossner et al 2013
<i>Ampedus balteatus</i>	Elateridae	13	6	x	8.75		2.5	3.4 Seibold et al 2015;Gossner et al 2013
<i>Ampedus hjorti</i>	Elateridae	5	0	x	10		3.75	3.7 Ehnstrom and Axelsson 2002
<i>Ampedus nigrinus</i>	Elateridae	17	12	m	7.5		2.5	3.7 Seibold et al 2015;Gossner et al 2013
<i>Ampedus nigroflavus</i>	Elateridae	1	0	x	11		3	3.4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Ampedus pomonae</i>	Elateridae	2	1	x	9.25		2	3.5 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Anaspis frontalis</i>	Scraptiidae	6	26	s	3.4		2.3	4 Seibold et al 2015;Gossner et al 2013
<i>Anaspis marginicollis</i>	Scraptiidae	11	13	m	3.5		2.29	4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Anaspis rufilabris</i>	Scraptiidae	69	106	x	3		2.3	4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Anaspis thoracica</i>	Scraptiidae	1	8	p	2.75		2.3	4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Anisotoma humeralis</i>	Leiodidae	1	0	s	3.35		2.5	4 Seibold et al 2015;Janssen et al 2017
<i>Anoplodera sexguttata</i>	Cerambycidae	4	1	p	9		2.5	3.4 Seibold et al 2015;Gossner et al 2013
<i>Anthaxia morio</i>	Buprestidae	1	0	m	7.5		1.25	2 Seibold et al 2015;Gossner et al 2013
<i>Atomaria bella</i>	Cryptophagidae	0	1	m	1.7		2	3 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Atomaria diluta</i>	Cryptophagidae	1	0	m	1.8		2	3.3 Seibold et al 2015;Gossner et al 2013
<i>Atomaria morio</i>	Cryptophagidae	1	0	x	2		4	4.5 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Atomaria ornata</i>	Cryptophagidae	1	0	x	2		1	2 Seibold et al 2015;Gossner et al 2013
<i>Atomaria turgida</i>	Cryptophagidae	3	11	m	1.85		1	2 Seibold et al 2015;Gossner et al 2013
<i>Calambus bipustulatus</i>	Elateridae	2	0	x	7.4		2.7	3.5 Seibold et al 2015
<i>Calopus serraticornis</i>	Oedemeridae	1	0	x	19		2.3	3.4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Cartodere nodifer</i>	Latridiidae	2	2	m	1.75		2	2 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Cerylon ferrugineum</i>	Cerylonidae	19	9	m	1.9		2.5	2.4 Seibold et al 2015;Janssen et al 2017
<i>Cerylon histeroides</i>	Cerylonidae	7	2	x	2.05		2.5	3.7 Seibold et al 2015
<i>Cetonia aurata</i>	Scarabaeidae	2	0	x	17		3	4 Seibold et al 2015;Janssen et al 2017
<i>Cis bidentatus</i>	Giidae	1	1	m	2.4		3	3.4 Seibold et al 2015
<i>Cis boleti</i>	Giidae	2	1	x	3		2.5	3.4 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Cis festivus</i>	Giidae	3	4	p	2.2		1.9	3 Seibold et al 2015;Gossner et al 2013
<i>Cis jacquemartii</i>	Giidae	0	1	x	2		2.5	3.25 Seibold et al 2015;Gossner et al 2013
<i>Cis micans</i>	Giidae	3	3	x	2.55		2.5	3.25 Seibold et al 2015
<i>Cis vestitus</i>	Giidae	6	2	p	1.85		1.9	3 Janssen et al 2017
<i>Cis villosulus</i>	Giidae	3	0	x	2		2.5	3.25 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013
<i>Clytus arietis</i>	Cerambycidae	1	0	m	10.5		2	2.5 Seibold et al 2015;Janssen et al 2017;Gossner et al 2013

Table S2: Estimated regression parameters, standard errors and P-values from models that predicted the starting wet weight and density of the bundles, bundle wetness after the experiment, and tree cover density (TCD) at 20m and 100m scales. All models compare values are veteran and young oak trees. All response variables were modeled with LMM with Gaussian distribution.

Response variable and predictors		Estimate	Standard error	P value
Bundle start weight				
intercept		1866.08	47.45	<0.001
Type of tree	(veteran)	25.86	47.15	0.585
placement	(hanging)	-57.39	47.15	0.228
Bundle start density				
intercept		0.5644666	0.0169000	<0.001
Type of tree	(veteran)	-0.0001062	0.0184897	0.995
placement	(hanging)	-0.0024019	0.0185061	0.897
Bundle wetness				
intercept		179.616	6.050	<0.001
Type of tree	(veteran)	8.280	5.911	0.166
placement	(hanging)	-6.714	5.910	0.260
TCD 20m				
intercept		13.258	3.794	<0.001
Type of tree	(veteran)	-3.794	5.366	0.484
Surroundings	(forest)	29.801	2.915	<0.001
TCD 100m				
intercept		31.404	2.0058	<0.001
Type of tree	(veteran)	0.1734	2.5179	0.945
Surroundings	(forest)	25.1818	2.915	<0.001

Appendix II

Table of species with abundances around veteran trees (VT) and young trees (YT) and their trait information. Length is in mm, wood diameter preference and decay stage preference were originally developed by Seibold et al (2015) (for reference list see published material).

Species	Family	VT	YT	FT	Length	WD pref	D pref
<i>Agathidium nigripenne</i>	Leiodidae	1	0	x	2.75	2.00	3.00
<i>Agathidium varians</i>	Leiodidae	2	2	m	2.75	2.00	3.00
<i>Agrilus angustulus</i>	Buprestidae	0	4	x	5.25	1.00	2.00
<i>Alosterna tabacicolor</i>	Cerambycidae	9	16	x	7.00	2.50	3.60
<i>Ampedus balteatus</i>	Elateridae	13	6	x	8.75	2.50	3.40
<i>Ampedus hjorti</i>	Elateridae	5	0	x	10.00	3.75	3.67
<i>Ampedus nigrinus</i>	Elateridae	17	12	m	7.50	2.50	3.67
<i>Ampedus nigroflavus</i>	Elateridae	1	0	x	11.00	3.00	3.40
<i>Ampedus pomonae</i>	Elateridae	2	1	x	9.25	2.00	3.50
<i>Anaspis frontalis</i>	Scaptiidae	6	26	s	3.40	2.29	4.00
<i>Anaspis marginicollis</i>	Scaptiidae	11	13	m	3.50	2.29	4.00
<i>Anaspis rufilabris</i>	Scaptiidae	69	106	x	3.00	2.29	4.00
<i>Anaspis thoracica</i>	Scaptiidae	1	8	p	2.75	2.29	4.00
<i>Anisotoma humeralis</i>	Leiodidae	1	0	s	3.35	2.50	4.00
<i>Anoplodera sexguttata</i>	Cerambycidae	4	1	p	9.00	2.50	3.40
<i>Anthaxia morio</i>	Buprestidae	1	0	m	7.50	1.25	2.00
<i>Atomaria bella</i>	Cryptophagidae	0	1	m	1.70	2.00	3.00
<i>Atomaria diluta</i>	Cryptophagidae	1	0	m	1.80	2.00	3.29
<i>Atomaria morio</i>	Cryptophagidae	1	0	x	2.00	4.00	4.50
<i>Atomaria ornata</i>	Cryptophagidae	1	0	x	2.00	1.00	2.00
<i>Atomaria turgida</i>	Cryptophagidae	3	11	m	1.85	1.00	2.00
<i>Calambus bipustulatus</i>	Elateridae	2	0	x	7.40	2.71	3.50
<i>Calopus serraticornis</i>	Oedemeridae	1	0	x	19.00	2.29	3.40
<i>Cartodere nodifer</i>	Latridiidae	2	2	m	1.75	2.00	2.00
<i>Cerylon ferrugineum</i>	Cerylonidae	19	9	m	1.90	2.50	2.40
<i>Cerylon histeroides</i>	Cerylonidae	7	2	x	2.05	2.50	3.67
<i>Cetonia aurata</i>	Scarabaeidae	2	0	x	17.00	3.00	4.00
<i>Cis bidentatus</i>	Ciidae	1	1	m	2.40	3.00	3.40
<i>Cis boleti</i>	Ciidae	2	1	x	3.00	2.50	3.40
<i>Cis festivus</i>	Ciidae	3	4	p	2.20	1.86	3.00
<i>Cis jacquemartii</i>	Ciidae	0	1	x	2.00	2.50	3.25
<i>Cis micans</i>	Ciidae	3	3	x	2.55	2.50	3.25
<i>Cis vestitus</i>	Ciidae	6	2	p	1.85	1.86	3.00
<i>Cis villosulus</i>	Ciidae	3	0	x	2.00	2.50	3.25
<i>Clytus arietis</i>	Cerambycidae	1	0	m	10.50	2.00	2.50
<i>Conopalpus testaceus</i>	Melandyriidae	4	1	x	6.00	1.20	3.40
<i>Corticaria rubripes</i>	Latridiidae	1	0	x	1.90	1.00	2.25
<i>Cryphalus asperatus</i>	Curculionidae	1	1	m	1.45	1.00	2.00
<i>Cryptarcha strigata</i>	Nitidulidae	6	1	x	3.00	2.50	1.14
<i>Cryptarcha undata</i>	Nitidulidae	7	2	x	2.60	2.50	1.14
<i>Cryptophagus dorsalis</i>	Cryptophagidae	0	1	m	2.20	3.20	4.00

<i>Cryptophagus fuscicornis</i>	Cryptophagidae	1	0	m	2.00	3.75	4.00
<i>Cryptophagus micaceus</i>	Cryptophagidae	12	1	m	2.00	3.80	4.60
<i>Cryptophagus parallelus</i>	Cryptophagidae	1	1	m	1.00	1.00	2.00
<i>Cryptophagus subdepressus</i>	Cryptophagidae	0	1	m	2.25	1.50	2.50
<i>Crypturgus cinereus</i>	Curculionidae	3	2	x	1.30	2.20	2.00
<i>Crypturgus hispidulus</i>	Curculionidae	0	4	x	1.25	2.20	2.00
<i>Crypturgus pusillus</i>	Curculionidae	1	0	m	1.10	1.20	2.00
<i>Ctesias serra</i>	Dermestidae	4	1	x	4.00	3.40	4.17
<i>Cychramus luteus</i>	Nitidulidae	7	45	x	4.30	2.50	3.40
<i>Cychramus variegatus</i>	Nitidulidae	2	7	x	6.00	3.00	3.40
<i>Dacne bipustulata</i>	Erotylidae	16	16	x	2.90	2.50	3.17
<i>Dadobia immersa</i>	Staphylinidae	3	2	x	1.75	1.25	2.50
<i>Denticollis linearis</i>	Elateridae	3	7	x	10.75	2.50	3.40
<i>Dorcatoma chrysomelina</i>	Ptinidae	37	0	x	2.00	3.80	3.40
<i>Dryocoetes alni</i>	Curculionidae	6	1	x	2.15	1.00	2.00
<i>Dryocoetes autographus</i>	Curculionidae	8	11	m	3.85	2.40	2.00
<i>Dryocoetes villosus</i>	Curculionidae	9	0	m	3.00	3.00	2.00
<i>Dryophilus pusillus</i>	Ptinidae	0	3	x	2.10	1.00	2.50
<i>Elateroides dermestoides</i>	Lymexylidae	2	3	x	12.00	3.00	2.00
<i>Enicmus rugosus</i>	Latridiidae	22	14	x	1.00	2.60	4.00
<i>Enicmus testaceus</i>	Latridiidae	33	4	x	1.00	1.67	3.00
<i>Enicmus transversus</i>	Latridiidae	0	1	m	2.00	2.00	3.00
<i>Ennearthron cornutum</i>	Ciidae	9	1	m	1.70	2.29	3.40
<i>Ernobius abietis</i>	Ptinidae	0	1	m	3.05	1.00	1.86
<i>Ernobius mollis</i>	Ptinidae	1	3	x	4.50	1.20	2.50
<i>Ernoporus tiliae</i>	Curculionidae	3	0	x	1.30	1.00	2.00
<i>Eucnemis capucina</i>	Eucnemidae	1	0	m	5.00	3.80	3.50
<i>Euglenes oculatus</i>	Aderidae	13	1	x	2.00	3.80	4.00
<i>Gastrallus immarginatus</i>	Ptinidae	4	0	m	2.00	3.00	2.00
<i>Gaurotes virginea</i>	Cerambycidae	0	1	m	10.50	2.29	3.40
<i>Glischrochilus hortensis</i>	Nitidulidae	18	8	m	5.50	2.00	2.00
<i>Glischrochilus quadriguttatus</i>	Nitidulidae	1	0	x	4.35	2.20	1.50
<i>Gnorimus nobilis</i>	Scarabaeidae	3	0	x	16.50	3.80	4.20
<i>Grammoptera ruficornis</i>	Cerambycidae	0	1	x	5.75	1.00	2.75
<i>Grammoptera ustulata</i>	Cerambycidae	1	0	p	7.00	1.00	3.00
<i>Hadrobregmus pertinax</i>	Ptinidae	0	1	x	5.25	3.00	3.00
<i>Hallomenus binotatus</i>	Tetratomidae	1	0	x	4.75	2.50	3.40
<i>Hemicoelus canaliculatus</i>	Ptinidae	2	2	x	3.75	3.00	3.00
<i>Hylastes cunicularius</i>	Curculionidae	13	20	x	3.85	2.50	2.00
<i>Hylesinus crenatus</i>	Curculionidae	1	0	x	5.00	3.00	2.00
<i>Hylesinus varius</i>	NA	1	3	x	3.00	2.71	2.00
<i>Hylis cariniceps</i>	Eucnemidae	0	2	x	5.00	2.29	3.50
<i>Hylobius abietis</i>	Curculionidae	0	2	x	10.25	2.50	2.00
<i>Ips typographus</i>	Curculionidae	4	6	x	4.85	2.50	1.75
<i>Ischnoglossa prolixa</i>	Staphylinidae	8	4	x	2.90	2.33	3.25
<i>Ischnomera cinerascens</i>	Oedemeridae	1	1	x	8.00	3.00	3.40
<i>Judolia sexmaculata</i>	Cerambycidae	1	0	x	11.00	2.29	3.40
<i>Latridius hirtus</i>	Latridiidae	1	1	m	1.90	2.20	4.00

<i>Leiopus nebulosus</i>	Cerambycidae	0	6	m	8.00	1.20	2.00
<i>Leptura quadrifasciata</i>	Cerambycidae	2	1	p	15.00	2.50	3.25
<i>Leptusa fumida</i>	Staphylinidae	4	3	x	2.70	2.60	3.80
<i>Leptusa pulchella</i>	Staphylinidae	3	1	p	2.95	2.60	3.80
<i>Lymexylon navale</i>	Lymexylidae	1	0	x	11.00	3.00	2.00
<i>Megatoma undata</i>	Dermestidae	1	0	m	5.00	3.00	3.50
<i>Melasis buprestoides</i>	Eucnemidae	1	1	x	7.00	2.29	3.00
<i>Micrambe abietis</i>	Cryptophagidae	0	6	m	2.30	1.00	2.00
<i>Microrhagus lepidus</i>	Eucnemidae	1	4	m	2.50	3.20	2.00
<i>Microrhagus pygmaeus</i>	Eucnemidae	2	2	m	4.25	2.29	3.50
<i>Molorchus minor</i>	Cerambycidae	5	10	x	11.00	1.20	2.00
<i>Mordella aculeata</i>	Mordellidae	1	1	m	6.50	2.29	3.00
<i>Mordella holomelaena</i>	Mordellidae	0	1	m	7.25	2.29	3.00
<i>Mordellochroa abdominalis</i>	Mordellidae	3	6	x	5.25	2.29	3.50
<i>Mycetochara humeralis</i>	Tenebrionidae	1	0	s	4.50	3.80	4.17
<i>Mycetochara maura</i>	Tenebrionidae	15	1	m	5.00	3.00	4.29
<i>Mycetophagus piceus</i>	Mycetophagidae	2	0	m	4.00	3.00	3.50
<i>Orchesia micans</i>	Melandryidae	0	1	m	4.50	2.50	3.25
<i>Orchesia minor</i>	Melandryidae	1	2	p	3.50	1.00	3.40
<i>Orchesia undulata</i>	Melandryidae	13	21	x	4.50	2.50	3.50
<i>Orthocis alni</i>	Ciidae	5	6	x	2.35	1.00	2.75
<i>Phloeotribus spinulosus</i>	Curculionidae	0	1	s	2.05	1.50	1.30
<i>Phloiotrya rufipes</i>	Melandryidae	4	3	p	7.00	1.20	3.40
<i>Phymatodes testaceus</i>	Cerambycidae	4	0	x	11.50	2.29	2.00
<i>Pityogenes bidentatus</i>	Curculionidae	2	1	x	2.50	1.00	2.00
<i>Pityogenes chalcographus</i>	Curculionidae	44	22	x	2.15	1.67	1.75
<i>Pityophthorus lichtensteinii</i>	Curculionidae	4	2	x	1.00	1.00	2.00
<i>Pityophthorus micrographus</i>	Curculionidae	1	1	m	1.00	1.00	2.00
<i>Placusa tachyporoides</i>	Staphylinidae	1	0	x	2.00	2.60	1.60
<i>Plagionotus arcuatus</i>	Cerambycidae	1	1	x	13.00	3.00	2.00
<i>Platycerus caraboides</i>	Lucanidae	1	0	x	11.00	2.00	3.40
<i>Polygraphus poligraphus</i>	Curculionidae	25	3	x	2.60	1.80	2.00
<i>Prionocyphon serricornis</i>	Scirtidae	2	0	m	4.15	3.00	3.00
<i>Prionychus ater</i>	Tenebrionidae	3	1	x	13.00	4.00	4.60
<i>Ptilinus fuscus</i>	Ptinidae	0	2	x	4.00	3.00	3.00
<i>Ptilinus pectinicornis</i>	Ptinidae	4	4	m	4.50	2.50	3.00
<i>Ptinomorphus imperialis</i>	Ptinidae	4	2	x	4.15	1.86	3.00
<i>Ptinus subpillosus</i>	Ptinidae	11	2	x	2.40	3.80	0.25
<i>Rhagium inquisitor</i>	Cerambycidae	0	2	x	15.50	2.50	2.40
<i>Rhagium mordax</i>	Cerambycidae	7	7	x	17.50	2.50	2.25
<i>Rhizophagus bipustulatus</i>	Monotomidae	12	10	x	2.90	2.50	2.50
<i>Rhyncolus elongatus</i>	Curculionidae	1	0	x	4.50	3.00	3.00
<i>Rusticoclytus rusticus</i>	Cerambycidae	1	0	p	14.00	2.25	2.00
<i>Rutpela maculata</i>	Cerambycidae	3	1	s	17.00	2.50	3.25
<i>Scaphisoma agaricinum</i>	Staphylinidae	5	4	x	2.20	2.33	4.00
<i>Schizotus pectinicornis</i>	Pyrochroidae	3	1	x	8.50	1.20	2.50
<i>Scolytus intricatus</i>	Curculionidae	40	7	x	3.00	1.20	1.75
<i>Scolytus laevis</i>	Curculionidae	1	0	x	4.00	1.20	1.75

<i>Sinodendron cylindricum</i>	Lucanidae	0	2	x	14.00	3.00	3.25
<i>Soronia grisea</i>	Nitidulidae	33	22	m	4.50	2.50	1.50
<i>Spondylis buprestoides</i>	Cerambycidae	1	0	x	18.00	2.50	2.75
<i>Stenostola dubia</i>	Cerambycidae	0	1	p	11.00	1.00	3.00
<i>Stenurella melanura</i>	Cerambycidae	8	0	m	7.50	1.00	3.40
<i>Stephostethus alternans</i>	Latridiidae	1	0	x	2.50	1.50	3.00
<i>Stephostethus pandellei</i>	Latridiidae	0	1	m	2.10	2.00	2.40
<i>Stephostethus rugicollis</i>	Latridiidae	0	2	x	1.80	1.00	2.50
<i>Sulcaxis nitidus</i>	Ciidae	2	0	x	1.50	2.50	3.40
<i>Tetratoma ancora</i>	Tetratomidae	1	2	m	3.25	1.86	3.00
<i>Tetropium castaneum</i>	Cerambycidae	1	1	m	13.50	2.20	2.00
<i>Tetropium fuscum</i>	Cerambycidae	1	2	m	12.50	2.20	2.00
<i>Thymalus limbatus</i>	Trogossitidae	1	0	x	6.00	2.50	3.25
<i>Tomoxia bucephala</i>	Mordellidae	0	5	x	7.00	2.29	3.00
<i>Trichius fasciatus</i>	Scarabaeidae	1	0	x	10.50	2.50	3.50
<i>Triplax aenea</i>	Erotylidae	3	4	p	3.80	3.00	3.40
<i>Triplax russica</i>	Erotylidae	1	1	m	5.75	3.00	3.40
<i>Tritoma bipustulata</i>	Erotylidae	0	1	m	3.75	2.50	3.40
<i>Trypodendron lineatum</i>	Curculionidae	3	0	x	3.20	2.29	2.00
<i>Xestobium rufovillosum</i>	Ptinidae	1	1	p	7.00	3.00	3.25
<i>Xyleborinus saxesenii</i>	Curculionidae	3	2	m	1.80	2.29	2.00
<i>Xylechinus pilosus</i>	Curculionidae	0	1	x	2.35	2.17	2.00
<i>Xylophilus corticalis</i>	Eucnemidae	4	0	x	5.00	2.71	3.50

Paper IV

It takes a community to maintain a tree hollow: macrofauna increase decomposition, enhance wood mould production and structure lower tropic levels

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Abstract

Background: Veteran trees are keystone structures, but declining in numbers globally because of land-use changes and modern forestry practices. One of the most unique and important microhabitats associated with veteran trees is the hollow, and a key element of the hollow is its wood mould. However, little is known about wood mould creation and how invertebrate diversity (insects, isopods, myriapods and nematodes) living in tree hollows affects decomposition. The aim of this project was to test how community complexity affects decomposition rates and wood mould creation in tree hollows

Study design: We randomly selected 20 veteran oaks in southern Norway. We then used large wooden boxes to simulate tree hollows and test how differences in community complexity influence decomposition. The boxes were filled with material to imitate a tree hollow (wood mould, oak leaf litter and oak sawdust) and started with one of three treatments: i) a complex community with macrofauna and mesofauna, ii) a simple community without macrofauna and iii) only the defaunated material. Boxes were subsequently transported into the field, and a box with each of the treatments was hung from every veteran oak (N = 60). The boxes remained in the field from May 2017 to October 2019. They were then transported back to the lab where the macrofauna and mesofauna were extracted and identified, and the material was weighed and the nutrients in the wood mould was determined.

Results: After three seasons in the field, we found that the complex community treatment had the highest rates of decomposition overall, but also had the greatest amount of wood mould with the highest concentrations of nitrogen and phosphorus. Additionally, we found that the nematodes within the complex community treatment had greater trophic structuring and a higher maturity index. Lastly, as indicated by the nematode communities, the simple community treatment had a fungal based decomposition pathway and the defaunated community had a bacterial based pathway, while the complex community remade intermediate.

Conclusions: Our results support the hypothesis that community complexity increases decomposition rates and wood mold production in tree hollows. Additionally, our results indicate that macrofauna provide a considerable contribution to tree hollow communities, as they influence the decomposition pathway and the nematode community structure and maturity.

Key words: veteran tree, decomposition, biodiversity and ecosystem functioning, tree hollow, wood mould, beetle, nematode

Introduction

Veteran hollow trees are keystone structures in forest, agricultural landscapes and urban areas (Manning et al. 2006, Lindenmayer and Laurance 2016). The size and the age of the trees affect the quantity and quality of microhabitat, and as a result, they harbor many species (Sverdrup-Thygeson 2009, Siitonen and Ranius 2015, Parmain and Bouget 2018). However, veteran trees are declining in numbers globally as a result of development, changes in land use and modern forestry practices (Lindenmayer et al. 2012). One of the most unique and important microhabitats associated with veteran trees is the hollow (Stokland et al. 2012). The tree's hollow provides a stable, nutrient rich habitat that hosts many rare and threatened invertebrates (Bütler et al. 2013, Siitonen and Ranius 2015).

Tree hollow development typically begins when the tree is damaged, and the sapwood and heartwood is exposed. Subsequently, fungi and invertebrates begin a decaying process within the tree (Stokland et al. 2012), and this process can develop for over hundreds of years when hollows form in slow growing and long-lived trees, such as *Quercus* sp. (Ranius et al. 2009). The partially degraded organic material that gathers inside of tree hollows is known as wood mould. Wood mould is a humus like material that consist of partially decomposed wood, fungal material, leaf litter and animal excrements (Stokland et al. 2012, Landvik et al. 2016). It is a nitrogen-rich habitat and is a central element of tree hollows. The amount of wood mould that a veteran tree contains is a positive predictor of beetle species richness (Ranius et al. 2009, Landvik et al. 2016). Although tree hollows are considered a vital habitat, little is known about wood mould creation and how the diversity within the hollows affects decomposition.

Tree hollows are in many ways analogous to soil systems, in that they consist of a resource base of decomposing organic matter, and similar groups of organisms that contribute to the process of decay and nutrients turnover rates. Soil food webs associated with decomposition are extraordinarily complex, and this diversity significantly influences carbon and nutrient turnover rates (Hättenschwiler et al. 2005, Gessner et al. 2010). Since these systems are so complex, a key tool in this research is mesocosms. Mesocosms can be defined as “bounded and partially enclosed outdoor experiments to bridge the gap between the laboratory and the real world” (Odum 1984). With these experiments research has begun to peer into the black box of soil food webs (A'Bear et al. 2014).

Soil food webs consist of three major groups of organisms: the microbes (bacteria and fungi), various groups of mesofauna and macrofauna (Wardle et al. 1998). The microbes are considered to be the primary decomposer group (Gessner et al. 2010). Their relative abundance is driven by nutrient availability, where more nutrients commonly leads to a more bacteria-dominated energy channel and thus faster turnover rates than fungi-dominated communities (Bell et al. 2009). However, microbial growth and activity has been demonstrated in some cases to be regulated by the mesofauna (0.1 - 2 mm) (Wardle et al. 1998), which consists primarily of nematodes, mites and collembola (Neher 2001).

Nematodes are generally considered to be the most important group within the mesofauna, while mites and collembola have weak roles in carbon and nitrogen cycling (Filser 2002, Ferris 2010). Nematodes are extraordinarily abundant and diverse, and nearly ubiquitous in the soil environments (Ferris et al. 2001). They influence carbon and nutrient turnover rates, both directly by feeding on the resource base, and indirectly by feeding on and spreading the microbes (Ferris 2010). They also act as regulators of other nematodes and mesofauna populations through predation, and macrofauna populations through parasitism (Ettema 1998, Ferris 2010). Nematode community structure can be regulated by productivity in a bottom-up control and by predators in a top-down control (Moore et al. 2003). Additionally, nematodes are easily classified into functional groups, and this combined with their importance and ubiquity makes them excellent indicators of microbial communities, food web structure and energy channels (Ferris 2010). Although Mites and collembola generally have weak roles in carbon and nitrogen cycling, they are an important part of soil food webs (Filser 2002, Read et al. 2006). They have been considered important fungal feeders (Wardle et al. 1998), but more recent work indicates that regulation of fungi through grazing by collembola is less important in natural systems with diverse fungal communities (A'Bear et al. 2014). In some case predacious mites and omnivorous collembola have been shown to exert top-down control of nematode populations (Filser 2002, Read et al. 2006). Mites and collembola may also be an important food source for predatory macrofauna (Halaj et al. 2000).

Macrofauna (>5 mm) are involved in many soil processes related to decomposition and nutrient release (David 2014, Menta and Remelli 2020). However, this relation remains poorly understood (Hättenschwiler et al. 2005, Gessner et al. 2010), and all trends that have been identified come with caveats. Macrofauna that feed directly on dead organic material have been found to enhance decomposing, with a particularly strong impact on nitrogen dynamics through litter fragmentation and compaction (Joly et al. 2018). It is clear that this process of bioturbation enhances decomposing, but it remains debated if this is achieved by enhancing microbial activity or if it has a direct effect (David 2014). Additionally, it has also been shown that the effect of detritivores on decomposition is largely dependent on litter quality, with stronger effects on more recalcitrant and slow decomposing material, and neutral or even negative effects on high-quality material that has labile carbon and other nutrients (Gessner et al. 2010, Joly et al. 2020). Macrofauna are also important fungal feeders and have been shown to reduce fungal growth and increase decomposition, but the effect of fungal grazing activity is dependent on interaction-specific feeding preferences (A'Bear et al. 2014).

In tree hollows, certain macrofauna species have been linked to wood mould creation (Sanchez-Galvan et al. 2014, Sánchez et al. 2017), and greater levels of biodiversity have been shown to increase decomposition in tree hollows (Mestre et al. 2018). However, almost nothing is known about interactions between the major groups of organisms (the microorganisms, mesofauna and macrofauna). In fact, there has been little work even documenting any of the groups in three hollows, other than the

macrofauna (Stokland et al. 2012). Tree hollows have been described as mesocosms (Micó 2018), and previous research has found that they can be simulated with large wooden boxes (Jansson et al. 2009, Hilszczański et al. 2014, Carlsson et al. 2016, Mestre et al. 2018). These boxes have primarily been used in conservation, but could also be implemented in mesocosms experiments where communities are manipulated and decomposition is monitored.

The aim of this project was to test how community complexity affects decomposition rates, wood mould creation and community structure in tree hollows using a mesocosms experiment. Boxes made of oak and designed to simulate tree hollows were hung from 20 veteran trees in southern Norway. The boxes were filled with material to imitate a tree hollow (wood mould, oak leaf litter and oak sawdust) and started with one of three treatments: i) a complex community with macrofauna and mesofauna, ii) a simple community without the macrofauna, and iii) only the defaunated material. A box with each treatment was hung every tree (N = 60). We used this study design to test the following hypothesis: 1) decomposition will decrease with decreasing community complexity, 2) wood mold creation is dependent on a complex community with macrofauna, and 3) community complexity will influence the structure of the nematode communities, due to both top down and bottom up effects. This experiment will provide information about decomposition and wood mould creation in tree hollows that might contribute to future conservation efforts, as well as provide new insight into interactions between macrofauna and nematodes.

Methods

We hung three large boxes (50 x 30 x 30 cm) with different starting communities on 20 hollow oaks in southern Norway (n= 60). Boxes were transported into the field in May 2017 and hung from the hollow oaks (Lovdata 2011) 1.5-2m above the ground. These trees were randomly chosen from the Norwegian database of veteran oaks (ARKO 2011). The trees were in either forests or open landscapes (n=12 and 8, respectively) and were within a 30 km radius of the city of Larvik. The boxes were constructed using 28mm thick oak (*Quercus* spp.) boards. The bottom of the boxes was fitted with an aluminum tray to prevent moisture loss. An 8 cm (diameter) entrance hole was drilled into the front of the box and covered by wire mesh (to exclude vertebrates), and two 8mm holes were drilled into the top to allow water to enter the boxes. All boxes were filled with wood mould (1115 g), oak sawdust (480 g) and leaf litter (85 g) to mimic natural hollows (Figure 1). The wood mould was collected from a dead hollow oak in the same geographic region as the study sites. The leaf litter was also collected in the same area and was primarily oak. The sawdust was provided by the sawmill where the boards were purchased.



Figure 1: Pictures of two sets of boxes at the end of the experiment. The box sets are rows and treatments are columns.

All macrofauna were removed from the wood mould by hand and identified to order. The wood mould was then split into thirds. One third was treated with liquid nitrogen to remove the mesofauna (Steyn and Delwiche 1970, Setälä 1995), and was subsequently split evenly between 20 boxes as the defaunated treatment. The remaining wood mould was split evenly between 40 boxes. Macrofauna were then reintroduced to the wood mould in 20 of the boxes, as the complex community treatment. The remaining 20 boxes with the sorted wood mould and no macrofauna were the simple community treatment. Each box within the complex community treatment received 30 Coleoptera larvae, 60 Diplopoda adults, and 6 Diptera larvae, all originating from the collected wood mould. The number and identity of the invertebrates added to the boxes was based on the densities in which they originally occurred. During the material sort the Coleoptera larvae were separated into morphological groups, and one specimen from each group was preserved on 98% ethanol for later identification. All leaf litter and sawdust were defaunated with the same liquid nitrogen treatment and an additional freeze (-20° C) and thaw treatment. We also added two litterbags, each with two dried and weighed oak leaves, to every box at the top of the organic matter.

The boxes were left in the field for three seasons, and were collected in October 2019. Boxes were immediately placed into large, mesh game bags to prevent invertebrates from escaping or entering the boxes. The boxes were subsequently placed in a cooler room (5° C) for three months, to break possible diapauses. They were then moved to a warm room (15° C) with controlled light set on a 12-hour light/dark cycle, and a funnel leading to a collection vial with 98% ethanol was placed over the entrance hole of each box to collect dispersing invertebrates. After three months of this extraction process, the boxes were opened and the remaining invertebrates were captured by hand and each layer of organic material (leaves, sawdust and wood mould) was weighed (Figure 1). Moisture content was estimated by weighing approximately 10g of material before and after one week of drying at 50° C. Additionally, 100 g samples from the wood mould were taken for nematode extractions, and 10 g were taken to measure the amount of nitrogen and phosphorus in the samples. Nitrogen and phosphorus concentrations were measured by *Landcare Research* (54 Gerald Street, Lincoln 7608 New Zealand). The samples were block digested using the Kjeldahl wet oxidation process (Rowland and Grimshaw 1985). Subsequently, a QuikChem 8500 flow injection analyser was used to colorimetrically determine the nitrogen and phosphorus in the digested samples.

All adult beetles collected in the extraction traps and during the material sort were identified to species level following the taxonomy of The Norwegian Biodiversity Information Centre (NBIC 2018) by an expert. Additionally, the beetle larvae were sorted into morpho groups within each box. One larva was selected from each morpho group from every box and from the original wood mould and sent for DNA barcoding in collaboration with NorBOLD. All other macro-invertebrates were identified to order only. Nematodes were extracted by combination of sieving, decanting and funnel method (Renčo et al. 2012). After extractions, nematodes in water suspension were heat-killed, fixed in FAA and counted

under a stereomicroscope (LEICA S8APO, Germany, magnification up to 80×). When abundance was over 200, at least 100 randomly selected nematodes were identified, and abundance of all genera were expressed to total nematode abundance at the end of identification. All individuals from the sample were identified if total abundance was under 200. The nematode indicator joint analysis (NINJA) website was used to calculate the percent of nematodes within each feeding guild, and the structure, maturity, and channel index for the nematode communities (Sieriebriennikov et al. 2014). The structure index represents an aggregate of longevity, body size and disruption-sensitivity of functional guilds (Bongers 1990). The maturity index is defined as the weighted mean frequency of the colonizer-persister (cp) classes (Bongers 1990), and the channel index indicates the predominant decomposition pathway (Ferris et al. 2001).

All analyses were carried out in R version 3.4.0 (R Development Core Team 2017). We followed the steps for data exploration outlined by Zuur et al. (2010) for all statistical models. We determined that all response variables related to decomposition and nematodes were approximately normally distributed and modeled them with a linear mixed model with Gaussian distribution (LMM). Decomposition was measured as proportion of weight loss and was calculated as: $(\text{start weight} - \text{end weight}) / \text{start weight}$. The weight of the material was adjusted for moisture percent, but in the case of the boxes this was not possible, because we did not have a measure of the moisture in the boards. In this case, the amount of moisture in the wood mould was included in the final model as a fixed effect. Additionally, we modeled all macroinvertebrate abundance (predators, detritivores, coleoptera and diptera) with a Generalized linear mixed effect model with Poisson distribution (GLMM) because it was count data. Some of this data was determined to be overdispersed and in this case we used negative binomial distribution. We also included the tree as a random intercept to deal with the spatial correlation introduced by the study design. We subsequently checked the assumptions of the final LMMs of normal distribution of the residuals and homoscedasticity visually (Zuur et al. 2009, Zuur et al. 2010). We also checked the dispersion parameter of the final GLMM for over/under dispersion with the function *dispersion_glm* from the 'blmeco' package (Korner-Nievergelt et al. 2015). Additionally, we checked for influential observations, and spatial and temporal structure that was not accounted for by the model (Zuur et al. 2009).

Results

Decomposition

The boxes with the complex community treatment lost significantly more weight than the other treatments (Table 1, est. weight loss = 5.3%, $P = 0.006$), while the simple community and defaunated treatment did not differ (est. = 4.6% and 4.5% respectively). However, the effect of the treatments also varied between the layer of material in the boxes. The leaves in the litter bags lost the same amount of weight in the complex and the simple community treatments (est. weight loss = 17% and 16.9% respectively), but both lost significantly more weight than the defaunated treatment (est. = 12.7%, $P = 0.036$). We also found that the height of the remaining leaves was significantly lower in the boxes with the complex and simple community treatments than the defaunated treatment (Figure 2, $P = 0.001$). The sawdust, on the other hand, showed a pattern similar to the total box measurements: a significantly greater weight loss in the complex community than the other treatments (est. weight loss = 23.2%, $P = 0.023$), and no difference between the simple community and the defaunated treatments (est. = 17.3.9% and 17.4% respectively). We found that the simple community treatment lost the most weight in the wood mould (est. weight loss = 24.2%), followed by the defaunated treatment (est. = 19.1%), and the complex community treatment lost the least amount of weight (est. = 14.9%, $P = 0.002$). When considering the nutrients in the wood mould we found that complex community treatment had the greatest percent of both nitrogen and phosphorus, while the simple community had the least ($P = 0.005$ and 0.03 respectively) at the end of the experiment. The defaunated treatment on the other hand, had a similar amount of nitrogen as the complex community, and similar amount phosphorus as the simple community (see Table 1 for all results related to decomposition).

Table 1: Model results related to decomposition. Decomposition was measured as percent weight loss (PWL) and was calculated as start weight minus end weight divided by the start weight. Nitrogen and phosphorus were measured in the wood mould and are also in percentages. All response variables were modeled with a linear mixed effect model with treatment as the fixed effect and the tree as a random effect (* denotes a significant difference at the 0.05 threshold and the P value if for the entire term).

Response	Treatment	Estimate	SE	P value
Box (PWL)	Moisture	-11.041	0.619	>0.001
	Complex community*	5.352	0.293	0.006
	Simple community	4.604	0.315	
	Defaunated	4.362	0.303	
Sawdust (PWL)	Complex community*	23.227	1.662	0.023
	Simple community	17.32	2.296	
	Defaunated	17.39	2.37	
Leaves (PWL)	Complex community	16.99	1.465	0.036
	Simple community	16.896	1.944	
	Defaunated*	12.721	1.891	
Wood mould (PWL)	Complex community*	14.913	1.786	0.002
	Simple community	24.218	2.526	
	Defaunated	19.108	2.604	
Nitrogen	Complex community	1.34	0.027	0.005
	Simple community*	1.229	0.035	
	Defaunated	1.332	0.035	
Phosphorus	Complex community*	0.035	0.001	0.03
	Simple community	0.029	0.002	
	Defaunated	-0.031	0.002	

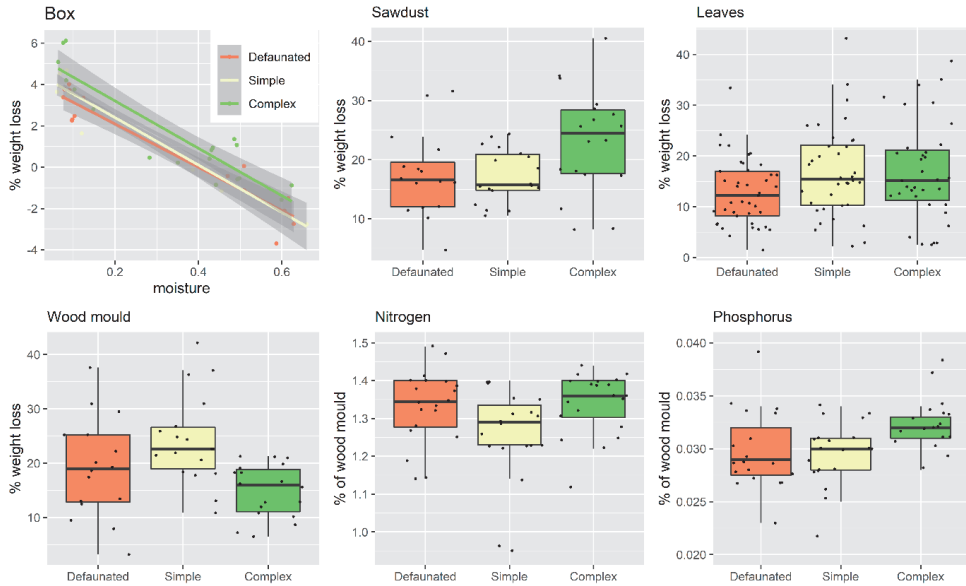


Figure 2: Measurements related to decomposition in the artificial tree hollows (boxes) with experimentally manipulated invertebrate communities. The boxes were mounted on veteran oaks in southern Norway for three seasons. Weight loss was measured as start weigh minus end weight divided by start weigh. The final weights of the sawdust, leaves and wood mould were adjusted for their moisture content. This was not possible for the weight of the boxes overall, so it was modeled with the moisture in the wood mould (top left plot, y-axis) and treatment as fixed effects in the model. Nitrogen and phosphorus concentration were only measured in the wood mould. The box plots show the median, first and third quartiles, with whiskers that extend 1.5 times the interquartile range (see Table 1 for model results related to decomposition).

Final communities

The effects of the treatments on the final nematode communities were clearly seen at the end of the experiment (Table 2, Figure 3 and Appendix: Table A1). The complex community treatment had nematodes communities with the highest maturity and structure index ($P < 0.001$ in both cases). Although less than the complex community treatment, the simple community had a significantly higher maturity index than the defaunated treatment, but there was not a significant difference regarding the structure index. There was also a clear effect of the treatment on nematode feeding guilds. The complex community treatment had the greatest percentage of omnivores ($P < 0.001$), the simple community had the greatest percentage of fungivores ($P < 0.001$), and the defaunated treatment had the greatest percentage of bacterivores ($P < 0.001$). The channel index was significantly higher in the simple community ($P < 0.001$), indicating that the decomposition pathway was dominated by fungi. Additionally, insect parasites were only observed in the complex and simple community treatment and were much higher in the complex community treatment.

Table 2: Model results related to nematode community composition at the end of the study. All response variables were modeled with a linear mixed effect model with treatment as the fixed effect and the tree as a random effect. The structure index (SI) represents an aggregate of longevity, body size and disruption-sensitivity of functional guilds. The maturity index (MI) is defined as the weighted mean frequency of the cp classes, and the channel index (CI) indicates the predominant decomposition pathway. Omnivores, fungivores and bacterivores are measured as the percent of all nematodes within the respective feeding guilds (* denotes a significant difference at the 0.05 threshold and the P value if for the entire term).

Response	Treatment	Estimate	SE	P value
SI	Complex community*	69.339	2.922	>0.001
	Simple community	50.822	4.061	
	Defaunated	51.314	4.006	
MI	Complex community*	2.46	0.042	>0.001
	Simple community*	2.265	0.059	
	Defaunated*	2.127	0.059	
CI	Complex community*	41.434	4.976	>0.001
	Simple community*	56.029	5.985	
	Defaunated*	27.773	6.080	
Omnivores %	Complex community*	13.675	1.271	>0.001
	Simple community	6.26	1.775	
	Defaunated	4.932	1.775	
Fungivores %	Complex community	29.975	3.314	>0.001
	Simple community*	44.47	3.939	
	Defaunated	23.244	4.002	
Bacterivores %	Complex community	50.145	3.325	>0.001
	Simple community	43.465	4.293	
	Defaunated*	62.696	4.357	

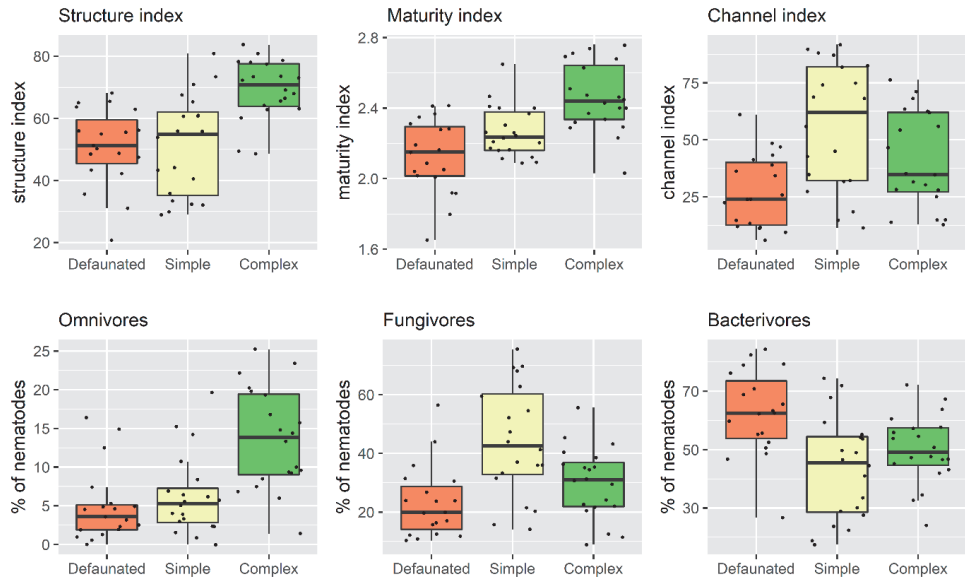


Figure 3: Measurements of nematodes in the artificial tree hollows (boxes) with experimentally manipulated invertebrate communities. The boxes were mounted on veteran oaks in southern Norway for three seasons. The structure index (top left plot) represents an aggregate of longevity, body size and disruption-sensitivity of functional guilds, while the maturity index (middle top) is a measure of the nematode communities age and functional group. The channel index (top right) indicates the primary decomposition pathways with higher values representing bacteria driven decomposition pathways and lower values representing fungal driven pathways. Omnivores, fungivores and bacterivores are measured as the percent of all nematodes within the respective feeding guilds. The box plots show the median, first and third quartiles, with whiskers that extend 1.5 times the interquartile range (see Table 2 for model results related to the nematodes).

The differences in the macrofauna at the end of the experiment were less pronounced than the differences in the nematodes (Table 3 and Figure 4). Nevertheless, the complex community treatment did have significantly more predatory macrofauna ($P = 0.004$), but there was not a difference in macrofauna detritivore abundances between the treatments at the end of the experiment. The overall number of beetles was greater in the complex and simple community treatment, while diptera were the primary detritivores in the defaunated treatment. Although they were not part of the starting communities, wood lice were common throughout the boxes independent of treatment. Additionally, the defaunated treatment was characterized by high variance in their macroinvertebrate communities.

Table 3: Model results related to macrofauna community composition at the end of the study. All response variables were count data and subsequently modeled with generalized linear mixed models, with treatment as a fixed effect and the tree as a random effect (* denotes a significant difference at the 0.05 threshold and the P value if for the entire term).

Response	Treatment	Estimate	SE	P value
Predators	Complex community*	40.7	2.908	0.004
	Simple community	32.211	4.166	
	Defaunated	26.45	4.112	
Detritivores	Complex community	80.30	17.92	0.733
	Simple community	61.05	25.03	
	Defaunated	74.8	25.03	
Beetle SR	Complex community*	1.209	0.1925	>0.001
	Simple community	0.742	0.2280	
	Defaunated	0.3	0.2467	
Diptera abundance	Complex community	1.77	0.246	0.028
	Simple community	1.583	0.107	
	Defaunated*	2.76	0.084	

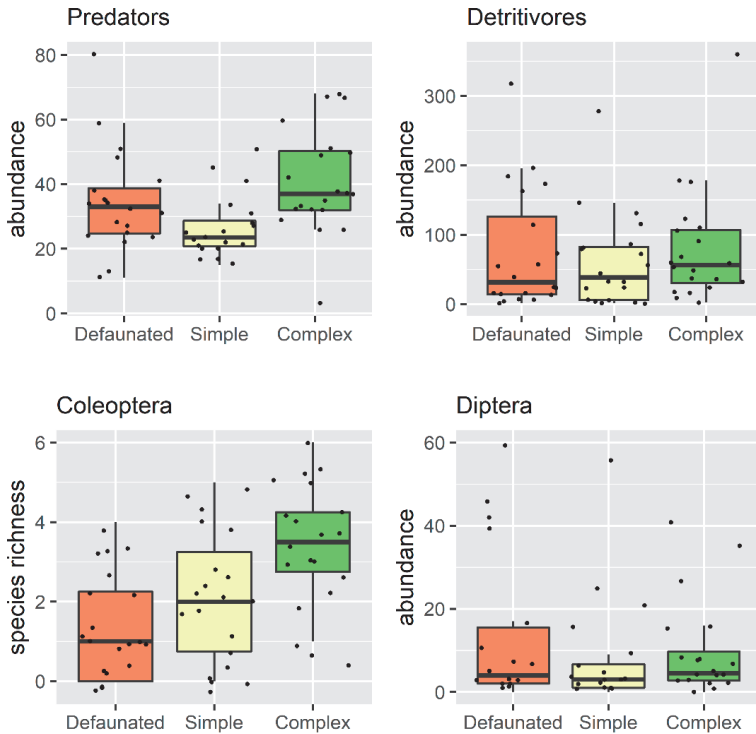


Figure 4: Measurements of the different groups of macrofauna in the artificial tree hollows (boxes) with experimentally manipulated invertebrate communities. The boxes were mounted on veteran oaks in southern Norway for three seasons. The box plots show the median, first and third quartiles, with whiskers that extend 1.5 times the interquartile range (see Table 3 for model results related to the macrofauna).

We collected a total of 337 beetles from a total of 39 species (Appendix: Table A2). The average number of individuals per box was 5.6 (min = 0, max = 49) and the average number of species was 2.3 (0, 6). The complex community treatment started with a beetle community, and at the end of the experiment, also had the highest number of beetle species ($P < 0.001$, Table 3 and Figure 4). There was a similar pattern for beetle abundance, but there was one outlier from the boxes with the defaunated treatment, with 49 individuals of one species. The complex community treatment had most individuals from the families Elateridae and Tenebrionidae, while simple community boxes had more Dermestidae. The defaunated treatment had the most individuals from Staphylinidae, but these were primarily the single previously mentioned box.

Discussion

To our knowledge, this is the first study to test the effects of community complexity on decomposition in tree hollows. We expected that i) complex communities would decompose the organic material faster than less complex communities, and ii) wood mould creation was dependent on macrofauna. We also expected that iii) community complexity would influence the structure of the nematode communities, due to both top down and bottom up effects. The first hypothesis was supported for the total amount of organic matter, although the effect of the treatment on decomposition of the individual layers (sawdust, leaves and wood mould) seemed to be mediated by the litter quality. We also found support for our second hypothesis that macrofauna were creating wood mould from the other layers in the boxes (sawdust and leaf litter). The complex community treatment (which included a starting community of macrofauna) had the greatest weight loss of sawdust and the lowest weight loss of wood mould. Also, the wood mold in this treatment had the highest concentrations of nitrogen and phosphorus, indicating that the nutrients derived from the decomposed leaves and sawdust. Lastly, there was support for our third hypothesis as well. The complex community treatment remained the most complex in terms of community structure even after three seasons in the field, which was not entirely surprising given that this was what we manipulated. Nevertheless, the complex community treatment had a greater diversity of organisms, and more pronounced trophic levels in both the macrofauna and the mesofauna than either of the other treatments.

The role macrofauna play in the process of decomposition remains poorly understood and debated (Gessner et al. 2010, A'Bear et al. 2014, David 2014, Ratcliffe et al. 2017, Joly et al. 2020). One of the main issues seems to be that in many cases the effects are context dependent (Gessner et al. 2010, A'Bear et al. 2014, Joly et al. 2018). Although decomposition in our study was higher overall in the complex community treatment, the relationship between community complexity and decomposition was also mediated by the litter quality. The rate of decomposition in the layer of sawdust was greater in the complex community treatment than in the other treatments. Sawdust is slow decomposing with recalcitrant organic carbon. Conversion of recalcitrant litter to faeces by macrofauna has been shown to significantly increase the organic matter lability and surface area, which then increases both leaching and the ability of smaller organisms to continue to break down the material (Joly et al. 2020). This effect seems to have been less important in the leaf litter. Leaf litter is of intermediate quality, and we found no difference in decomposition rate between the complex and simple community treatments in this substrate.

The processes of decomposition and wood mould creation are interconnected, and our results indicate that the macrofauna were contributing to both processes. Our experiment was not specifically designed to test which organisms play a primary role in wood mould creation. However, other research a laboratory setting has found that *Cetonia aurataeformis* larvae, which are specialized in tree hollows,

can decompose the polysaccharides in *Quercus* sp. wood, and produce frass with altered organic structure and higher concentration of nitrogen and phosphorus (Sánchez et al. 2017). Also, the presence of certain Cetoniidae and Cerambyx species has been linked to higher quality of physical and chemical features in tree hollows (Micó et al. 2015). In this study, *Prionychus ater* and *Pseudocistela ceramboides* were two species that were included at the start of the experiment in the complex community treatment, and at the end of the experiment their presence was correlated with higher percentages of nitrogen and phosphorus in the wood mould. This may indicate that these species are involved in wood mould creation, but more research needs to be done to verify this finding.

After three seasons in the field, the complex community treatment remained the most complex in terms of community structure. This treatment had a greater diversity of organisms, and more pronounced feeding guilds in both the macrofauna and the nematodes, as can be seen by the number of macrofauna predators, the presence of insect parasites and the nematode structure index. This finding is not surprising given that manipulating community complexity was part of the study design, but also indicates that dispersal from the veteran tree into the boxes was influenced by priority effects, and that macrofauna were influencing nematode communities. In fact, the effects of the treatment had far reaching consequences for community structure, even when the communities were not directly manipulated.

Based on our analysis of the nematodes, which act as bioindicators of energy flows and community structure (Ferris 2010), the communities within the complex community treatment had greater structure and maturity. This result is interesting, because we did not directly manipulate the nematodes in either the complex or the simple community treatments. Additionally, the channel index, which indicates decomposition pathways, changed to fungal driven pathways in the simple community treatment. Nematodes are affected directly by predators (primarily predatory mites), and indirectly by detritivores mixing and changing the conditions in the wood mould (Moore et al. 2003, Read et al. 2006), and our results suggest that macrofauna may have been altering these relationships. These results are in accordance with the findings of A'Bear et al. (2014) and indicate that macrofauna may have been altering decomposing pathways through fungal feeding activity. The channel index also indicated that the dominant decomposition pathway in the defaunated treatment was bacteria driven. The most likely explanations for this finding is that either liquid nitrogen treatments also reduced the fungal communities (Setälä 1995), or the increase in nitrogen led to a bacteria dominated community. This is a point we will discuss in more detail below.

Although the macrofauna remained most diverse in the complex community treatment, macrofauna detritivores also colonized the other treatments. We found that there were no differences in terms of overall abundances of macrofauna detritivores at the end of the experiment, even though they were initially removed from the simple and the defaunated treatments. This is in line with earlier

findings that large wooden boxes designed to simulate tree hollows have been colonized by macrofauna (Carlsson et al. 2016, Mestre et al. 2018). Nevertheless, the defaunated treatment was also characterized by high variance in the final macrofauna communities. For example, one box within this treatment had the most macrofauna predators (49 individuals from one species of beetle), and a different box had the most detritivores (estimated 2700 fly larvae). Thus, some macrofauna (especially diptera) were able to thrive in the absence of others (primarily coleoptera), and this indicates that competitive exclusion may play a role in structuring communities within tree hollows.

There were some limitations to this study. First of all, we extracted fewer beetles from the large wooden boxes than what has been reported from authors using similar methods in earlier studies (Jansson et al. 2009, Hilszczański et al. 2014, Carlsson et al. 2016, Mestre et al. 2018). The most likely explanation was the lack of moisture in our boxes, which might be critical for beetle larvae development (Landvik et al. 2016). To maintain moisture in the boxes, we placed a metal tray in the bottom of each box, but it degraded during the study and this reduced the water retention capacity of the boxes. We also extracted the boxes in the laboratory and this may have resulted in additional drying of the boxes. Although this dryness likely reduced survival in the boxes, the methodology was the same for all treatments, and there is no reason to believe that the effect differed between treatments.

Additionally, as previously mentioned our results indicated that the liquid nitrogen defaunation technique affected more than the fauna. We found that the defaunated treatment had similar concentration of nitrogen as the complex community, and a similar concentration of phosphorus as the simple community treatment. The most reasonable explanation for this result is that nitrogen levels in the defaunated treatment were elevated by the treatment and this is a known effect of this methodology (Setale 1995). The defaunated treatment may have also diminished the microbial communities. The effects of this versus the reduction of community complexity on our results are difficult to disentangle. Therefore, another defaunation technique would have been preferable.

Conclusion

In this research we have provided experimental evidence of the importance of macrofauna for maintaining tree hollows. Tree hollows are a critical habitat that is important for the large number of red listed and specialized insects. Thus, in a conservation context, artificial hollows should preferably be established with a macrofaunal community present. Although our experiment was not designed to test which organisms play a primary role in wood mould creation, our results do support other findings that large specialized insect species may have a critical function in tree hollows, and this further emphasizes the need to protect them. Additionally, the presence of macrofauna promotes a functionally diverse mesofauna, and a more complex community with a greater ability to decompose recalcitrant organic matter.

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Appendix

Appendix

Table A1: Summaries of the nematodes collected in the wood mould of boxes designed to simulate tree hollows. The boxes were started with one of three treatments: a complex community with macrofauna and mesofauna, a simple community without macrofauna, and only the defaunated material. There were 20 boxes within each treatment for a total of 60 boxes. Additionally, 3 samples were taken from the original wood mould so that we had a base line of the nematode communities. Nematodes are separated into colonizer-persister (cp) based on their life history strategy. The values range from 1 to 5 (extreme r- to extreme K-strategists).

Genus	Trophic group	cp	Original wood mould	Defaunated	Simple community	Complex community
<i>Acrobelles</i>	Bacterivore	2	71	81	93	275
<i>Acrobeloides</i>	Bacterivore	2	77	955	474	1146
<i>Alaimus</i>	Bacterivore	4	0	146	96	538
<i>Bunonema</i>	Bacterivore	1	19	176	109	131
<i>Cephalobus</i>	Bacterivore	2	60	150	128	169
<i>Cervidellus</i>	Bacterivore	2	0	204	43	259
<i>Diploscapter</i>	Bacterivore	1	0	55	45	54
<i>Eumonhystera</i>	Bacterivore	2	0	466	236	51
<i>Euteratocephalus</i>	Bacterivore	3	0	169	20	291
<i>Heterocephalobus</i>	Bacterivore	2	12	55	26	20
<i>Chiloplacus</i>	Bacterivore	2	17	156	0	54
<i>Mesorhabditis</i>	Bacterivore	1	0	180	141	340
<i>Panagrolaimus</i>	Bacterivore	1	123	408	91	331
<i>Plectus</i>	Bacterivore	2	102	1179	589	1448
<i>Prismatolaimus</i>	Bacterivore	3	56	1634	697	2267
<i>Rhabditis</i>	Bacterivore	1	41	2375	384	965
<i>Wilsonema</i>	Bacterivore	2	0	603	204	414
<i>Aphelenchoides</i>	Fungivore	2	351	1637	1494	1867
<i>Aphelenchus</i>	Fungivore	2	135	281	1360	1164
<i>Ditylenchus</i>	Fungivore	2	0	282	251	380
<i>Ecphyadophora</i>	Fungivore	2	0	110	76	311
<i>Tylencholaimus</i>	Fungivore	4	0	37	144	150
<i>Tylencholaimellus</i>	Fungivore	4	0	148	82	143
<i>Steinernema</i>	Insect parasite	NA	0	0	14	101
<i>Aporcelaimellus</i>	Omnivore	5	72	83	109	290
<i>Eudorylaimus</i>	Omnivore	4	58	335	305	1808
<i>Mesodorylaimus</i>	Omnivore	4	13	18	40	174
<i>Clarkus</i>	Predator	4	0	105	94	160
<i>Trypila</i>	Predator	3	0	33	21	59
<i>Prionchulus</i>	Predator	4	0	6	9	10
<i>Filenchus</i>	Root-fungal feeder	2	47	465	230	243
<i>Malenchus</i>	Root-fungal feeder	2	42	254	63	295
Tylenchida (unidentified)	Root-fungal feeder	2	5	40	30	114

Table A2: Table of the beetles collected in the wood mould of boxes designed to simulate tree hollows. The boxes were started with one of three treatments: a complex community with macrofauna and mesofauna, a simple community without macrofauna, and only the defaunated material. Additionally, beetle larvae collected taken from the original wood mould so that we had a base line of the communities.

Species	Original wood mould	Defaunated	Simple community	Complex community
<i>Ampedus balteatus</i>	2	16	18	55
<i>Ampedus</i> sp1*	2	0	1	3
<i>Ampedus hjorti</i>	0	0	1	2
<i>Ampedus pomorum</i>	0	0	1	0
<i>Ampedus</i> sp2	1	0	11	4
<i>Anaspis marginicollis</i>	0	1	0	0
<i>Anaspis rufilabris</i>	0	1	0	0
<i>Anaspis septentrionalis</i>	0	1	1	0
<i>Anthrenus museorum</i>	0	0	3	0
<i>Batrisodes venustus</i>	0	1	4	3
<i>Corticaria longicollis</i>	0	13	13	12
<i>Corticaria serrata</i>	0	2	0	1
<i>Cryptocephalus frontalis</i>	0	0	0	1
<i>Cryptocephalus querceti</i>	0	0	1	0
<i>Cryptophagus dentatus</i>	0	0	1	0
<i>Ctesias serra</i>	0	3	14	2
<i>Dasytes plumbeus</i>	0	1	0	0
<i>Dienerella vincenti</i>	0	1	1	4
<i>Epuraea unicolor</i>	0	1	0	0
<i>Euplectus karstenii</i>	0	2	1	12
<i>Euplectus nanus</i>	0	0	0	2
<i>Exomius pellucidus</i>	0	1	0	0
<i>Gabrius splendidulus</i>	0	55	6	0
<i>Latridius minutus</i>	0	0	1	0
<i>Malthodes brevicollis</i>	0	0	0	1
<i>Malthodes marginatus</i>	0	0	1	0
<i>Megatoma undata</i>	0	0	1	0
<i>Mycetochara humeralis</i>	0	0	0	1
<i>Orchestes quercus</i>	0	0	1	1
<i>Otiorhynchus scaber</i>	0	0	1	0
<i>Phosphuga atrata</i>	0	0	1	0
<i>Polydrusus pilosus</i>	0	0	0	1
<i>Prasocuris marginella</i>	0	0	1	0
<i>Prionychus ater</i>	1	0	1	20
<i>Pseudocistela ceramboides</i>	3	0	3	15
<i>Ptinus subpilosus</i>	0	2	0	4
<i>Quedius xanthopus</i>	0	1	1	0
<i>Tyrus mucronatus</i>	0	0	2	0

* the DNA barcoding returned the identification of *A. brunnicornis*, but this species has not been observed in Norway and we believe there was a mistake in the database.

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