

Directed endozoochory: a hitchhiker's guide to successful sexual reproduction in clonal ericaceous plants

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FACULTY OF BIOSCIENCES AND AQUACULTURE

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guide to successful sexual reproduction in
clonal ericaceous plants

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Preface

This thesis was submitted in fulfilment of the requirements for the degree of Philosophiae Doctor (PhD) at the faculty of Biosciences and Aquaculture (FBA), Nord University, Steinkjer, Norway. The presented original research was performed as part of the Stipendiat program. The candidate and project were funded by Nord University and Paper I was partially funded by a National Geographic Society's (NGS) explorer grant.

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Mie Prik Arnberg

Steinkjer, March 2023

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When I arrived in Steinkjer almost four years ago, I remember thinking ‘What have I done? There are no people under 40 here’ (sorry all that felt hit by that). But then our Steinkjer community slowly grew to incorporate many important people. To my fellow PhDs Gabriel, Maya and Annabel, thank you guys for all of the dinners, board game nights, long talks over a beer, or ten and being a constant support when life seemed hard. Quentin, you have been the best roommate and friend I could ever have wanted even when you ‘by accident’ eat all the good cheese. You have consistently made me laugh when life has ‘vacuumed the smile from me’ as you say. Celeste, thank you for brightening my day every time we met and for the countless

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Abstract

Berry-producing ericaceous species are widely distributed in the northern hemisphere and they are a keystone resource across their temperate, boreal and alpine ranges. Species of the genera *Vaccinium* and *Empetrum* have long presented a 'reproductive paradox'. Every year they produce staggering amounts of berries containing viable seeds which are dispersed by a wide array of animals through endozoochory. Nevertheless such ericaceous species are reported to expand by clonal propagation almost exclusively. Their seeds are underrepresented in the soil seed bank and seedling establishment is thought to be rare. The apparent lack of sexual reproduction has been ascribed to a combination of microsite and dispersal limitation. That is, seedling establishment is constrained to small-scale disturbances, and even if such recruitment windows of opportunity (RWO) occurs, seeds fail to arrive at them. However, previous research on seedling recruitment in *Vaccinium* and *Empetrum* has been based on field experiments without considering endozoochorous seed dispersal. This thesis aimed to disentangle the reproductive paradox of clonal berry-producing ericaceous species by elucidating pathways of sexual reproduction. Specifically, we connect vertebrate disperser species which have the potential for directed endozoochory to viable recruitment windows for seedling establishment.

Carrion has previously been identified as an endpoint of directed endozoochory by vertebrate scavengers at a mass-mortality site of 323 reindeer in the alpine tundra of south-eastern Norway. Within the same site, we showed that carrion decomposition created extensive disturbances in vegetation layers, also known as 'cadaver decomposition islands' (CDIs), which were characterized by high soil cover and absence of conspecific adults. Further, the CDIs provided suitable RWOs for ericaceous species as the probability of seedling establishment was positively related to carcass density. Similarly, we showed that carrion from single-mortality events can facilitate sexual recruitment in ericaceous species in a boreal forest. However, the recruitment pathway was contingent on the nature of the carcass itself. Large

ungulate carrion (moose and reindeer carcasses and hunting remains) created a spatiotemporal hotspot of vertebrate activity. Importantly, 93 % of the observed activity was of vertebrates that are known to consumer and/or disperse ericaceous seeds through endozoochory. Subsequently, large carcasses generally created CDIs which were viable RWOs for ericaceous species. Seedlings were significantly more abundant in CDIs compared with sites that were mechanically disturbed (suitable microsite but limited seed rain) and control plots (unsuited microsite with limited seed rain). In comparison, smaller carcasses did not aggregate disperser species nor did they generate CDIs, and seedling establishment was not observed at those sites.

Within forest habitats, large woody debris is another form of decomposing biomass which can offer a suitable microsite for seedling establishment of various plant species. We demonstrated that passerine birds (order Passeriformes) directed ericaceous seed dispersal towards cut stumps from forest management through their perching behaviour. Tree stumps were considerably more likely to have bird droppings compared to the forest floor and droppings consistently contained viable *Vaccinium* seeds. Finally, the decomposing stumps also served as viable RWOs with higher probability of seedling establishment compared with the forest floor. However, as with the carcass pathway, functionality of this pathway is rather contextual. The probability of scat deposition increased with higher complexity of the vertical forest structure and lower canopy cover, whereas seedling establishment required bryophyte cover and larger stumps, or alternatively smaller stumps with competition-free spaces.

Overall, this thesis illustrates that seedling recruitment in clonal ericaceous species occurs relatively frequently when coupled with directed endozoochorous dispersal. Their wide disperser guild ensures at least two complementary pathways to sexual reproduction, elevating the probability of seedling establishment within landscapes.

Sammendrag på norsk

Bærproduserende arter i lyngfamilien (Ericaceae) er vidt utbredte på den nordlige halvkule, og de er en nøkkelressurs på tvers av tempererte, boreale og alpine habitater. Arter av slektene *Vaccinium* og *Empetrum* har lenge dannet et 'reproduksjons paradoks'. Hvert år produserer de svimlende mengder med bær som inneholder mange spiredyktige frø, og disse spres av et bredt spekter av dyr via endozookori. Likevel er det rapportert at slike lyngarter nesten utelukkende brer seg via klonal vekst. Frøene deres er underrepresentert i jordfrøbanken, og det antas at frøspirende planter sjeldent forekommer. Den tilsynelatende mangelen på seksuell reproduksjon har blitt tilskrevet en kombinasjon av egnet mikrosteds- og spredningsbegrensning. Frøspiring er begrenset til småskala forstyrrelser, og selv om slike rekrutteringsvinduer oppstår, kommer frø ikke frem til dem. Tidligere forskning på rekruttering av frøspirende planter har imidlertid vært basert på felteksperimenter som ikke tok hensyn til endozookorisk frøspredning. Målet for denne avhandlingen var å belyse det reproduktive paradokset til klonale bær produserende lyngarter. Spesifikt kobler vi arter av virveldyr som har potensiale for å rette endozookorisk frøspredning mot rekrutteringsvinduer som egner seg for frøspiring og etablering.

Åtsler har tidligere blitt identifisert som et endepunkt for endozookorisk spredning fra åtseletere på et massedøds punkt for 323 rein i den alpine tundraen i Sørøst-Norge. På den samme plassen har vi vist at nedbrytingen av åtsler skapte omfattende forstyrrelser i vegetasjonslag, også kjent som 'kadaver nedbryting-øyer' (CDIs), som var karakterisert av høy forekomst av bar jord og fravær av voksne planter. Videre var CDI-ene egnede rekrutteringsvinduer for lyngarter siden sannsynligheten for etablering av frøspirende individer var positivt korrelert med kadavertetthet. Tilsvarende viste vi at åtsler fra enkeltdøds hendelser kan fasilitere rekruttering av frøspirende lyngplanter i boreal skog. Imidlertid var effekten av denne rekrutteringsveien avhengig av kadaveret. Store kadaver (elg- og reinkadavre og kadaverrester fra jakt) skapte en aggregering av virveldyr i rom og tid. Totalt var 93 %

av virveldyrs-observasjonene ved kadavrene av arter som er kjent for innta og spre lyngfrø via endozookori Samtidig genererte store kadaver generelt CDI-er som var gode rekrutteringsvinduer for lyngarter. Frøplanter var betydelig mer tallrike i CDI-er sammenlignet med mekaniske forstyrrelser (egnet mikrosted, men begrenset frøregn) og kontrollplott (uegnet mikrosted med begrenset frøregn). Til sammenligning aggregerte ikke mindre kadavre frøspredende virveldyr, genererte ikke CDI-er, og frøplantetablering ble ikke observert på disse stedene.

Innenfor skogshabitater er dødt trevirke en annen form for nedbrytende biomasse som kan fungere som et egnet mikrosted for frøplantetablering av ulike plantearter. Vi påviste at spurvefugler (orden Passeriformes) rettet spredning av lyngfrø mot trestubber fra skogsdrift gjennom sin sitteatferd. Det var betydelig større sannsynlighet for å finne fugleeskremer på trestubber sammenlignet med skogbunnen, og slike ekskremer inneholdt oftest spiredyktige *Vaccinium* frø. Videre fungerte stubbene også som rekrutteringsvinduer med høyere sannsynlighet for etablering av frøspirende lyngplanter sammenlignet med skogbunnen. Imidlertid, som med kadaver-rekrutteringsveien, var funksjonaliteten av denne rekrutteringsveien kontekstuell. Sannsynligheten for avsetning av ekskremer økte med høyere kompleksitet av den vertikale skogsstrukturen og lavere kronedekke, mens frøplantetablering krevde mosedekke og større stubber, eller alternativt mindre stubber med konkurransefrie områder.

Samlet illustrerer denne avhandlingen at seksuell reproduksjon i klonale lyngarter forekommer relativt ofte når det tas høyde for endozoorisk frøspredning rettet mot rekrutteringsvinduer. De mange dyrearter som utgjør frøspredningslauget til lyngarter sikrer minst to komplementære veier til seksuell reproduksjon, noe som øker sannsynligheten for etablering av frøplanter i landskapet.

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List of abbreviations

CDI – Cadaver decomposition island

IRS – Initial seedling recruitment

RSR – Repeated seedling recruitment

RWO – Recruitment window of opportunity

List of papers

Paper I: Arnberg, M. P., Frank, S. C., Blaaid, R., Davey M. L., Eycott, A. E. & Steyaert, S. M. J. G. (2022). Directed endozoochorous dispersal by scavengers facilitate sexual reproduction in otherwise clonal plants at cadaver sites. *Ecology and Evolution*, 12(1), e8503.

Paper II: Arnberg, M. P., Eycott, A. E. & Steyaert, S. M. J. G. (2023). From death comes life: characterizing the role of carcasses in seedling establishment for clonal ericaceous shrubs. (Manuscript).

Paper III: Arnberg, M. P., Patten, M. A., Klanderud, K., Haddad, C. Larsen, O. & G. Steyaert, S. M. J. (2023). Perfect poopers; Passerine birds facilitate sexual reproduction in clonal keystone plants of the boreal forest through directed endozoochory towards dead wood. *Forest Ecology and Management*, 532, 120842.

1. Introduction

1.1 Plant reproduction

Reproduction is the singular process responsible for continuity of life and is directly linked to an organism's fitness, survival and ecological success (Wiens and Worsley, 2016). In plants, recruitment of new individuals into a population is a spatially structured process that determines the distribution, dynamics and genetic structure of populations and communities (Schupp, 1995; Nathan and Muller-Landau, 2000)

Many plant species can reproduce through both asexual and sexual reproduction. In contrast to most animal species both reproductive modes usually occur simultaneously (Vallejo-Marín et al., 2010). The most common form of asexual reproduction in flowering plants (angiosperms) is vegetative reproduction, also referred to as clonal growth or clonal propagation (Harper, 1977). In fact, approximately 80 % of flowering plants are capable of clonal growth (Klimeš, 1997) where new ramets are produced by for example budding from stolons, rhizomes, roots or stems (Silvertown, 2008). This results in genetically identical individuals capable of independent growth and reproduction.

In clonal species, the balance between the two reproductive modes is a trade-off in resource allocation from a finite pool of resources (Zhang and Zhang, 2007). Regulation of the trade-off is linked to factors like plant age, soil moisture, disturbance, nutrient availability, air temperature, and population density (Zhang and Zhang, 2007; Silvertown, 2008; Fu et al., 2010). However, with increased resource allocation to asexual reproduction, allocation to sexual reproduction is correspondingly reduced, and *vice versa* (Thompson and Eckert, 2004; Van Drunen and Dorken, 2012). In general, clonality is often favored in habitats where sexual recruitment is restricted by unfavorable conditions for seed production (including

pollination and crossing incompatibility), germination or seedling establishment (Eckert, 2001; Vallejo-Marín et al., 2010; Barrett, 2015).

Clonal growth has several important advantages which contribute to population maintenance, survival, and expansion at local scales. For example, lateral clonal growth can facilitate rapid, short-distance spread (Lenssen et al., 2004). Physiological integration allows ramets (shoots) of one clone to share resources such as water and nutrients in heterogenous environments (i.e. clonal foraging; Alpert and Mooney, 1986; Hutchings and Wijesinghe, 1997; Liu et al., 2016). In turn, this also provides higher tolerance of genets to stress such as herbivory and drought (Zhang et al., 2012; Liu et al., 2020). Furthermore, clonal growth requires less energy and time (Wang et al., 2018) and can be a low-risk alternative to establishment from seed which is susceptible to seed predation, fungal decay and establishment failure (Aarssen, 2008). Despite the advantages of clonal growth, most clonal plants also reproduce sexually. Sexual reproduction promotes genetically diverse offspring through recombination, mutation and geneflow within and between populations. In addition, sexually produced propagules (seeds) are capable of dispersal over long distances and establishment in areas outside the range of clonal growth which usually aggregates around the mother ramet (Crawley, 1997). This further increases genetic variation within and between populations through potential long-distance dispersal. Theory predicts that genetic diversity increases adaptive potential to environmental variation, disease, insect outbreaks and disturbances (Silvertown, 2008; Yang and Kim, 2016). The most severe consequence of persistently relying on clonal reproduction is the total loss of sexual reproduction which could lead to extinction (Eckert, 2001).

Studying sexual reproduction in clonal species can be challenging. Genets are usually very long-lived and when ramets are not physically integrated, determining the extent of a genet is challenging without applying genetic methods. Seedling establishment in clonal plants is often considered to be infrequent or irregular (Eriksson, 1992; Eriksson, 1993), with considerable variation in sexual reproduction

among clonal plants (Zhang and Zhang, 2007). Two end points on a recruitment strategy spectrum have been described for plants in which the main population expansion relies on clonal growth (Eriksson, 1993): Initial seedling recruitment (ISR) where populations consist of the original members from an initial colonization event; and repeated seedling recruitment (RSR) where genets are continuously recruited in local populations.

Between these endpoints are plants that show spatial variation in recruitment among populations by switching between ISR and RSR in response to environmental pressure and species where seedling establishment occurs at 'recruitment windows of opportunity' (RWOs; Jelinski and Cheliak, 1992; Eriksson, 2011). Under a RWO strategy continuous seedling recruitment occurs within local conspecific populations but only under specific conditions that are spatially unpredictable (Eriksson and Fröborg, 1996; Eriksson, 2011). Irrespective of recruitment strategies, even occasional seedling recruitment can be sufficient for maintaining genetic diversity in long-lived clonal plant populations (De Witte et al., 2012; Watkinson & Powell, 1993). Thus, identifying constraints and pathways to sexual reproduction is important for understanding demography, life-history evolution, long-term persistence and population dynamics (Eriksson, 1993; Beckman and Rogers, 2013; Bonte and Doherty, 2017)

1.1.1 Constraints to sexual reproduction in plants

Sexual reproduction is a multi-stage process involving several sequential life-history stages (i.e. reproductive adults, seeds, seedlings, juveniles). The stage between seed production and seedling establishment is a particular bottleneck in many plant populations, as it is characterized by high mortality (Clark et al., 2007; Terborgh et al., 2014). Many seeds lose their viability over time, decay in the soil or are eaten before germination (Kumari et al., 2018). If they do germinate, seedlings no longer have the ability to withstand harsh conditions tolerated by seeds, and are often much less robust than later life stages (Kitajima and Fenner, 2000).

Recruitment limitation, defined as the failure of a species to recruit new individuals (genets) in all available favorable sites, is a combination of factors limiting seed production, dispersal, germination, seedling emergence and establishment (Crawley, 1990; Nathan and Muller-Landau, 2000). These limiting factors can be partitioned into three major components: Source limitation, seed limitation and microsite limitation (Fig 1; Turnbull et al., 2000; Beckman and Rogers, 2013). Source and dispersal limitation are often grouped under the more general term seed limitation which is the failure of seeds to arrive at all microsites suitable for seedling establishment (Nathan and Muller-Landau, 2000; Beckman and Rogers, 2013). In source limitation, seed production is too low to reach suitable microsites even if seeds have the dispersal ability to reach all sites. In dispersal limitation, seeds do not reach suitable microsites even though seed production is plentiful (Eriksson and Ehrlén, 1992; Clark et al., 1998b). On the other hand, microsite limitation (also called site or establishment limitation; Beckman and Rogers, 2013) occurs when recruitment is constrained by the number or quality of available sites for germination, establishment and survival of seedlings (Clark et al., 1998b). The suitability of a microsite is species-specific and determined by abiotic and biotic conditions. Such local barriers to recruitment include seed predation (Calviño-Cancela, 2007; Garzon-Lopez et al., 2022), competition from both conspecific and heterospecific plants (Garzon-Lopez et al., 2022), or pathogens (Wenny and Levey, 1998).

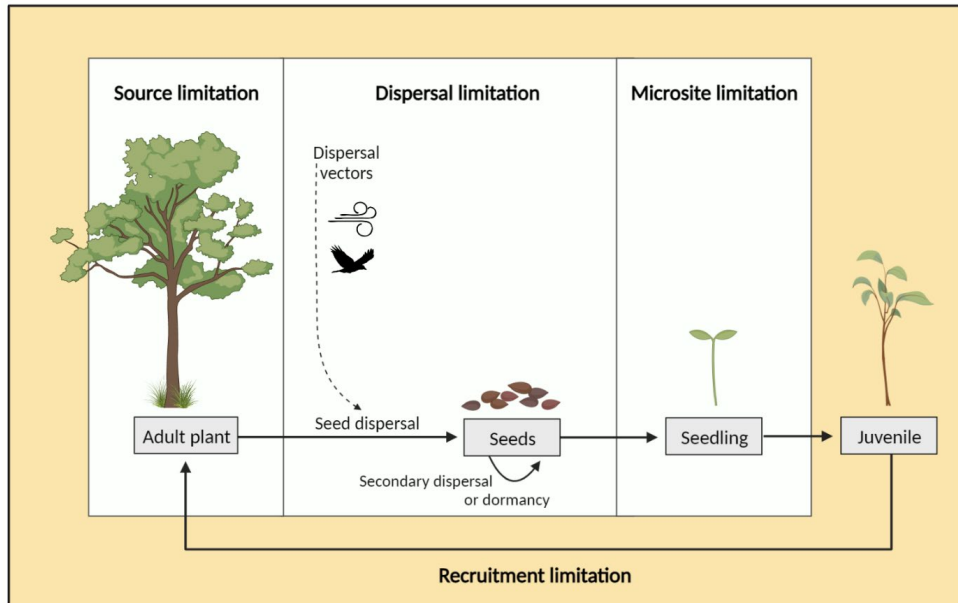


Figure 1. Hindrances to sexual recruitment partitioned over the main limitations imposed at sequential life-history stages (i.e. adult, seed, seedling, juvenile). Recruitment limitation can result from low seed production in plants (source limitation), seeds failing to arrive at suitable microsites (dispersal limitation) or unsuitable conditions for germination and seedling establishment at the seed deposition site (microsite limitation). Figure adapted from Beckman and Rogers (2013) and Beckman et al. (2020).

Sexual reproduction is for the most part determined by both seed and microsite availability although at varying degrees in heterogenous landscape (Myers and Harms, 2009; Long et al., 2014). That is, sexual recruitment cannot occur without seed arrival yet seed arrival is no guarantee of recruitment. To establish a new individual via sexual reproduction, a seed must be deposited in a suitable microsite and germinate. Further, the developing seedling must survive dynamic environmental conditions during later life history stages until it reaches sexual maturity (Schupp et al., 2010).

1.2 Seed dispersal: a critical link in sexual reproduction

Seed dispersal is the movement of seeds from the parent plant to another location where they might establish and reproduce (Schupp et al., 2010). The spatial pattern of seed deposition (i.e. seed shadow) creates the initial template for subsequent abiotic and biotic interactions that determine seed fate and influence seedling survival (Nathan and Muller-Landau, 2000; Levine and Murrell, 2003). As such, seed dispersal has profound effects on gene flow (Bacles et al., 2006), population dynamics and persistence (Kendrick et al., 2012; González-Castro et al., 2022), community composition, and allows plants to shift or expand their geographic ranges (Clark et al., 1998a; LaRue et al., 2019).

Since plants are sessile organisms, they rely on vectors (e.g. wind, water, animal) to disperse their seeds across the landscape. As a result, plants have adapted a myriad of different diaspore morphologies to enhance dispersal via specific vectors, such as wings and plumes, fleshy fruits, ballistic mechanisms or flotation devices (van der Pijl, 1982). For the large energy investment in flower, fruit, and seed production, plants can attain several advantages that increase the likelihood of seedling establishment: 1) escape higher density- and distance-dependent mortality near parents, such as pathogens, seed predators, and/or herbivores (Janzen–Connell mechanism, escape hypothesis); 2) seeds are randomly dispersed, allowing some to colonize newly available habitat patches (colonization hypothesis); or 3) non-random dispersal towards microsites with environmental conditions suitable for seedling establishment (directed dispersal hypothesis; Howe and Smallwood, 1982; Wenny, 2001). These are not mutually exclusive; there are several examples of plant species which benefit from multiple advantages concurrently (Wenny, 2001).

1.2.1 Endozoochory

Worldwide, approximately 50-60 % of flowering plants have adapted to seed dispersal via animals or zoochory (Aslan et al., 2013; Rogers et al., 2021). Many of these produce fleshy fruits that attract and are consumed by animals. In this

mutualistic interaction, animals consume fruits for nutrient acquisition and simultaneously provide dispersal services for plants by transporting seeds across landscapes (i.e. 'endozoochory'; Herrera, 2002). The mutualistic coupling between fleshy-fruited plants and their animal partners is in most cases characterized as 'diffuse co-evolution' (Janzen, 1980). That is, frugivores consume fruit from several plant species and each fruit-bearing plant often has more than one disperser species, creating complex networks of interactions (Herrera, 1982; Bascompte et al., 2003; Bascompte and Jordano, 2007).

From a plant's perspective, not all animals are equally good partners and the effectiveness of a dispersal event will depend on the disperser's relative contribution to plant fitness, namely the number of new reproductive adults to the population (Schupp et al., 2010; Schupp et al., 2017). As different animals show both inter- and intraspecific variability in morphology, physiology, and behaviour (Muller-Landau et al., 2008; Zwolak, 2018), seed dispersal effectiveness is context-dependent and influenced by how seed traits interact with disperser traits (Schupp et al., 2010). For instance, frugivores can exhibit differences in dietary preferences (Quintero et al., 2020) and the amount of seeds ingested and dispersed per visit is positively correlated with body size (Jordano et al., 2007). Long gut retention time and large home ranges can facilitate dispersal over considerable distances (Dennis and Westcott, 2007), while treatment of seeds passing through the gut can affect germination (Traveset et al., 2007). Further, animal behaviour and habitat-use largely determines seed deposition patterns (Cortes and Uriarte, 2013; Escribano-Avila et al., 2014; García-Cervígon et al., 2017) and thus the biotic and abiotic factors affecting seed fate in post-dispersal processes. Ultimately, seed dispersal effectiveness is the product of the quantity (visitation rate and seeds consumed) and the quality (probability of recruitment of a dispersed seed involving seed treatment, seed shadow, post-dispersal factors) of the dispersal event (Schupp et al., 2010).

In many complex endozoochorous systems, different animals or functional groups within disperser communities play complementary rather than redundant roles in plant recruitment (Jordano et al., 2007; McConkey and Brockelman, 2011; Escribano-Avila et al., 2014; Morán-López et al., 2020; García-Rodríguez et al., 2022). Specifically, dispersers with different movement behaviours, habitat use and faecal deposition patterns contribute to distinct parts of the seed shadow in space and time (Rother et al., 2016; Tochigi et al., 2022). For example, animals may move seeds over short and long distances contributing to both local and metapopulation dynamics of a plant (Jordano et al., 2007; Spiegel and Nathan, 2007). Seed dispersing animals may also consume seeds at different times during the fruiting season, ensuring dispersal through the whole season (García-Cervígon et al., 2017).

Maybe the most important aspect of the dispersal service in complementary networks is the dispersal to many different microsites, as seed fate and recruitment depends on it (Nathan and Muller-Landau, 2000). As such, the most effective and functionally most important seed dispersers would disperse many seeds to microsites suitable for seedling establishment (Schleuning et al., 2015). In fact, it has been recently shown that the number of seeds ingested and dispersed (interaction frequency) is not correlated with seedling establishment. Rather, dispersal quality is determined by the microsite of seed deposition (Donoso et al., 2016; González-Castro et al., 2022).

1.2.2 Directed endozoochory

In directed dispersal, seeds are disproportionately deposited in particularly favourable microsites that results in increased seedling establishment and growth (Wenny, 2001). Animal-mediated dispersal is often non-random because animals use space in a non-random way (Nathan et al., 2008). For instance, animal behaviour or use of habitat structures (e.g. perches or latrines) contribute to aggregation points in the seed shadow that overlap with suitable microsites for seedling establishment (Wenny and Levey, 1998; Bravo and Cueto, 2020). However, this process is rarely

recognized as directed endozoochory (Brodie et al., 2009; Escribano-Avila et al., 2014; García-Cervigón et al., 2017), which has commonly been considered a rare process (Wenny, 2001). This could be due to factors such as secondary dispersal obscuring seed fate, temporally-dependent detection (the timing of observation), or that even directed dispersal performed by ‘high-quality’ dispersers can be subtle as most seeds die (Wenny, 2001; Mason et al., 2022). Also contributing to directed dispersal’s perceived rarity is the restrictive definition that plant adaptations should actively direct dispersal vectors to favourable microsites after propagule removal (active directed dispersal; Mason et al., 2022). Yet directed dispersal may occur in a ‘passive’ form where plant adaptations allow plants to take advantage of reliable vector behaviour to arrive in disproportionate numbers at suitable microsites (Mason et al., 2022).

In diffuse plant-animal mutualisms, passive directed dispersal is likely widespread with important implications for population dynamics as different dispersers within a community shape the overall seed shadow (Morán-López et al., 2020; Mason et al., 2022). For example, small birds generally transport seeds over short distances and direct seed dispersal to perching points in closed canopy areas (Jordano et al., 2007; Escribano-Avila et al., 2014; González-Varo et al., 2017). In comparison, larger mammals can transport seeds over long distances and between habitat patches depositing seeds in favourable microsites both in open and forested habitat (Jordano et al., 2007; Tochigi et al., 2022). Recruitment will depend on a plants ability to utilize multiple vectors with varying behaviours and movement ability to arrive at favourable microsites in heterogenous landscapes (Mason et al., 2022). This demonstrates the importance of considering the contribution of multiple frugivores to plant recruitment and linking animal behaviour to suitable microsites for recruitment. Understanding the mechanisms and effects of directed endozoochorous dispersal on plant recruitment is critical for understanding plant population dynamics of endozoochorously dispersed species. Such dispersal pathways might be crucial for

species with limited seed availability to locate otherwise elusive microsites for regeneration in heterogenous landscapes.

1.3 Ericaceous dwarf shrubs

Ericaceae (the heath family) is a globally distributed and morphologically diverse family of mostly woody plants (trees, shrubs, lianas) that can be found in a variety of habitats (Stevens et al., 2004; Kron and Luteyn, 2005). Among the ericaceous species, dwarf shrubs (< 50 cm) dominate field layer vegetation in many habitats throughout temperate, boreal, alpine, and arctic regions of the northern hemisphere (Nilsson and Wardle, 2005; Nestby et al., 2019). Despite their small stature, they have large effects on ecosystem function both above and below ground. For example, in forested areas they exert strong filtering effects on tree seedling survival and subsequently forest succession and composition (Mallik, 2003; Nilsson and Wardle, 2005). Furthermore, ericaceous shrubs and their root-associated ericoid mycorrhizal fungi are key components to maintenance of microbial activity (Fanin et al., 2019), exerting direct control on processes regulating nutrient cycling, and carbon sequestration (Fanin et al., 2022). Perhaps most conspicuous is the keystone plant resource (Peres, 2000) from genera producing fleshy fruits (berries).

Ericaceous berries have great trophic importance as they provide a reliable food source sustaining a wide diversity of frugivore species from large mammals, mesopredators and birds, down to insects (e.g. Guitian et al., 1994; Atlegrim and Sjoberg, 1996; Schaumann and Heinken, 2002; Wegge and Kastdalen, 2008; Hertel et al., 2018). For example, during peak fruiting season, berries can constitute up to 30 % of the diet in red fox (*Vulpes vulpes*; Needham et al., 2014). For brown bears (*Ursus arctos*), berries can account for as much as 82 % of food consumption (Dahle et al., 1998) and constitute 68 % of their daily energy intake during fruiting season (Stenset et al., 2016).

The most frequent and abundant berry-producers of the boreal and alpine biomes include three species of the genus *Vaccinium* (subfamily Vaccinioideae): bilberry (*V. myrtillus*), lingonberry (*V. vitis-idaea*) and bog bilberry (*V. uliginosum*), and one species of genus *Empetrum* (subfamily Ericoideae): crowberry (*E. nigrum*) (Fig. 2). These species have circumpolar distributions and wide natural ranges that stretch through temperate and boreal forests to alpine and arctic regions more or less continuously in northern and central Europe, northern Asia and North America. The populations grow predominantly on acidic, nutrient poor substrates such as mountainous mineral heath, organic forest soils, and peat bogs (Bell and Tallis, 1973; Nestby et al., 2019). They have extensive horizontal creeping subterranean rhizome systems which produce ramets. Clones form discrete patches with multiple ‘individual’ shrubs (i.e. ramets) which can be relatively large, in some cases extending over 30 meters (Persson and Gustavsson, 2001; Albert et al., 2003; Bienau et al., 2016). They are slow growing and long-lived. Although actual life-span is unknown, genet age has been estimated to between 100 and 750 years (Flower-Ellis, 1971; Bienau et al., 2016). Bilberry, lingonberry, bog bilberry and crowberry usually coexist within habitat patches (Hultén and Fries, 1986; Jacquemart, 1996) although the relative abundance of each species is determined by various abiotic and biotic factors (Nilsson and Wardle, 2005).



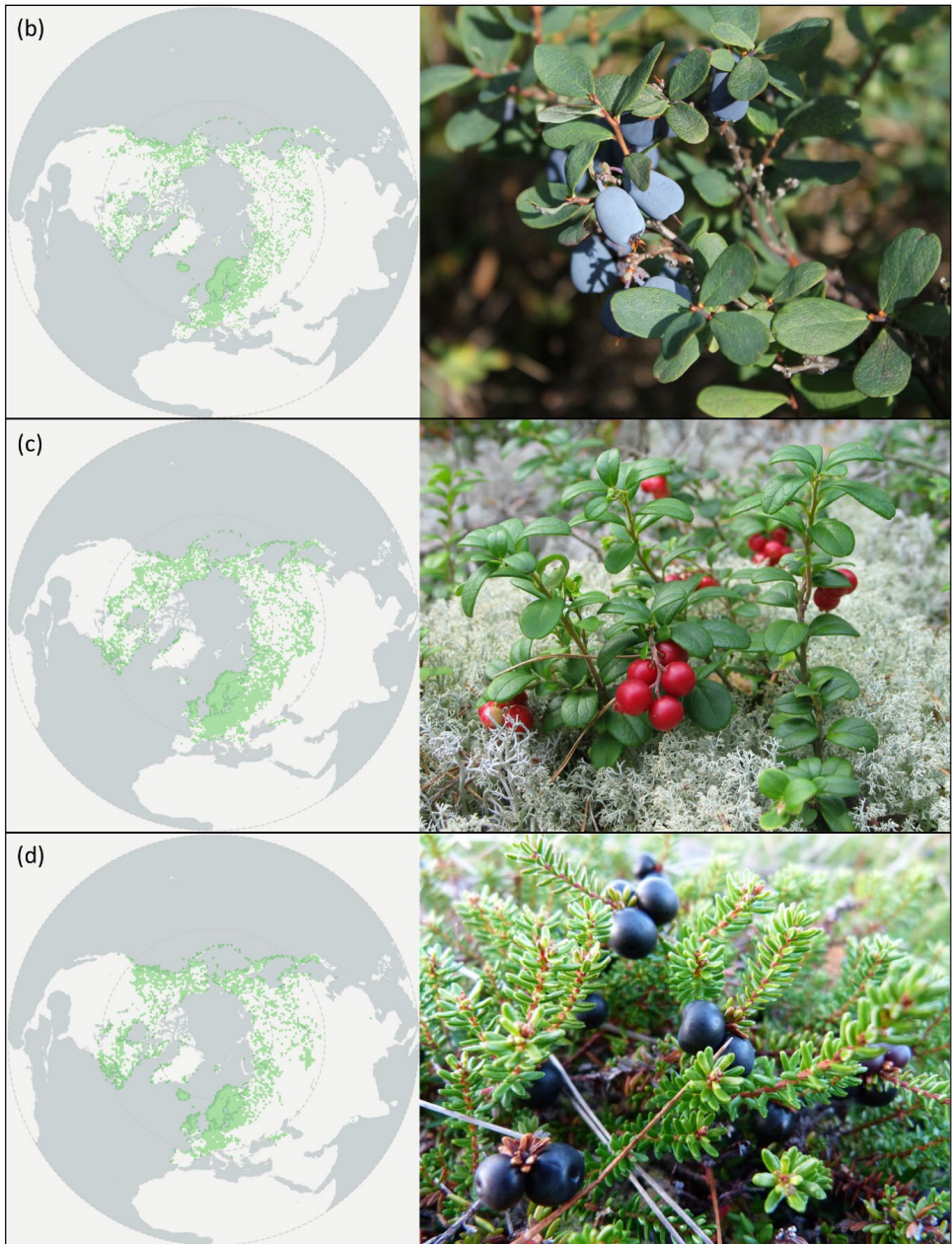


Figure 2. Species distribution maps of (a) bilberry (*Vaccinium myrtillus*), (b) Bog bilberry (*Vaccinium uliginosum*), (c) lingonberry (*Vaccinium vitis-idaea*) and (d) black crowberry (*Empetrum nigrum*) in the northern hemisphere. The maps were created using occurrence data from the Global Biodiversity Information Facility (GBIF) database. The true distributions of these species are likely larger than displayed in the maps. Note that observations in the southern hemisphere are not shown here.

1.3.1 From seed to seedling - the ericaceous reproductive paradox

Clonal ericaceous berry-producing species present an intriguing ‘reproductive paradox’ (Vander Kloet and Hill, 1994). Most clonal plants that rely mainly on clonal propagation exhibit lower energy allocation for sexual reproduction (Eckert, 2001). However, berry-producing ericaceous species invest heavily in sexual reproduction by producing numerous berries during summer that contain viable seeds (Ranwala and Naylor, 2004; Miina et al., 2009). The seeds are endozoochorously dispersed in large numbers by a wide animal community every fruiting season (García-Rodríguez et al., 2022). Further, a large proportion of seeds remain viable after passage through the gastro-intestinal system of disperser species (Honkavaara et al., 2007; Steyaert et al., 2018). In fact, germination rates can be significantly higher when seeds are defecated by frugivores compared with seeds embedded within berries (i.e. undispersed; Schaumann and Heinken, 2002; García-Rodríguez et al., 2021). Despite this, these species are reported to expand by clonal propagation almost exclusively (Hautala et al., 2001; Welch et al., 2000). Their seeds are underrepresented in the soil seed bank even when they dominate the field layer (Hester et al., 1991; Vander Kloet and Hill, 1994; Welch et al., 2000) and seedling recruitment is rarely observed under conspecific stands (Hester et al., 1991; Eriksson and Fröborg, 1996).

The discrepancy between seed production, soil seed bank formation and realized seedling establishment becomes even more bewildering when considering the magnitude of their annual seed production. On average, berries of the *Vaccinium* species contain 12-66 viable seeds (Jacquemart, 1996; Nuortila et al., 2002; Ranwala and Naylor, 2004; Nuortila et al., 2006; Manninen and Tolvanen, 2017), while *E. nigrum* contain fewer (7-8) but larger viable seeds (Bell and Tallis, 1973; Manninen and Tolvanen, 2017). Although seed yield is affected by variation in pollination dynamics (Fröborg, 1996; Nuortila et al., 2002) and climatic conditions (Krebs et al., 2009), ericaceous berry-producing plants can generate between 1200 to 12 000 seeds per m² (Vander Kloet and Hill, 1994; Hill et al., 2012). In productive stands, *V. myrtillus* can produce nearly 20 000 viable seeds per m² (Ranwala and Naylor, 2004).

There are two major contributors to the apparent lack of sexual regeneration in such species. Firstly, ericaceous species are microsite limited (Graae et al., 2011; Manninen and Tolvanen, 2017). Niche requirements for seedlings and established adults differ, which has implications for sexual regeneration (Eriksson, 2002; Auffret et al., 2010). The seedlings are weak competitors with very slow growth (Ritchie, 1955; Ritchie, 1956). Even after four years growth under natural conditions seedlings may not be taller than 4 cm (Eriksson and Fröborg, 1996) and thus typically do not survive competition from established adults. Eriksson and Fröborg (1996) showed that clonal ericaceous shrubs follow a recruitment strategy where seedling establishment occurs in spatially unpredictable RWOs within stands of mature conspecifics. Such recruitment windows consist of disturbances that remove barriers to recruitment such as field- and ground-layer vegetation and have moist soil with high organic content (Eriksson and Fröborg, 1996; Graae et al., 2011). Secondly, despite large seed production, seeds are not available or do not reach viable recruitment windows (i.e. dispersal limitation; Manninen and Tolvanen, 2017). Burial experiments have shown that seeds can retain high levels of viability over many years in the soil (Granstrøm, 1987; Vander Kloet and Hill, 1994; Hill and Vander Kloet, 2005). Yet, most seeds die between deposition and incorporation into the soil column due to factors such as germination in unsuited microsites or ineffective defense against fungal attack (Welch et al., 2000). Hence, if a disturbance occurs, ericaceous seeds are not available unless deposited directly into it. That is, in disturbances, ericaceous species grow and recover mainly clonally without additional seed rain (Hautala et al., 2001).

To date, research has focussed on mechanical disturbances with seed addition experiments (e.g. Eriksson and Fröborg, 1996; Hautala et al., 2001; Eriksson, 2002; Manninen and Tolvanen, 2017) to assess recruitment dynamics in clonal ericaceous species. However, such sites are unlikely to attract disperser species. This becomes problematic when recruitment is dependent upon dispersing seeds reaching suitable sites for germination, seedling establishment and survival.

A recruitment window was proposed by Steyaert et al. (2018), who observed directed seed dispersal by vertebrate scavengers towards carcasses of large ungulates. Carcass decomposition can generate discrete vegetation-denuded disturbances also called 'cadaver decomposition islands' (CDI; Towne, 2000; Carter et al., 2007). In addition, CDIs have previously been linked to seedling establishment in long-lived clonal trees (Bump et al., 2009). Further, Eriksson and Fröborg (1996) observed seedling establishment on decomposing woody debris and hypothesized that such substrates could be possible regeneration microsites for ericaceous species. Neither Steyaert et al.'s (2018) observations of directed seed dispersal, nor Eriksson and Fröborg's (1996) observations of seedlings on decomposing wood provide a complete and definitive picture of viable recruitment pathways. In combination they provided the motive for this thesis: that vertebrate dispersal vectors direct endozoochorous dispersal towards suitable microsites which facilitates seedling establishment in for berry-producing ericaceous species (Figure 3).

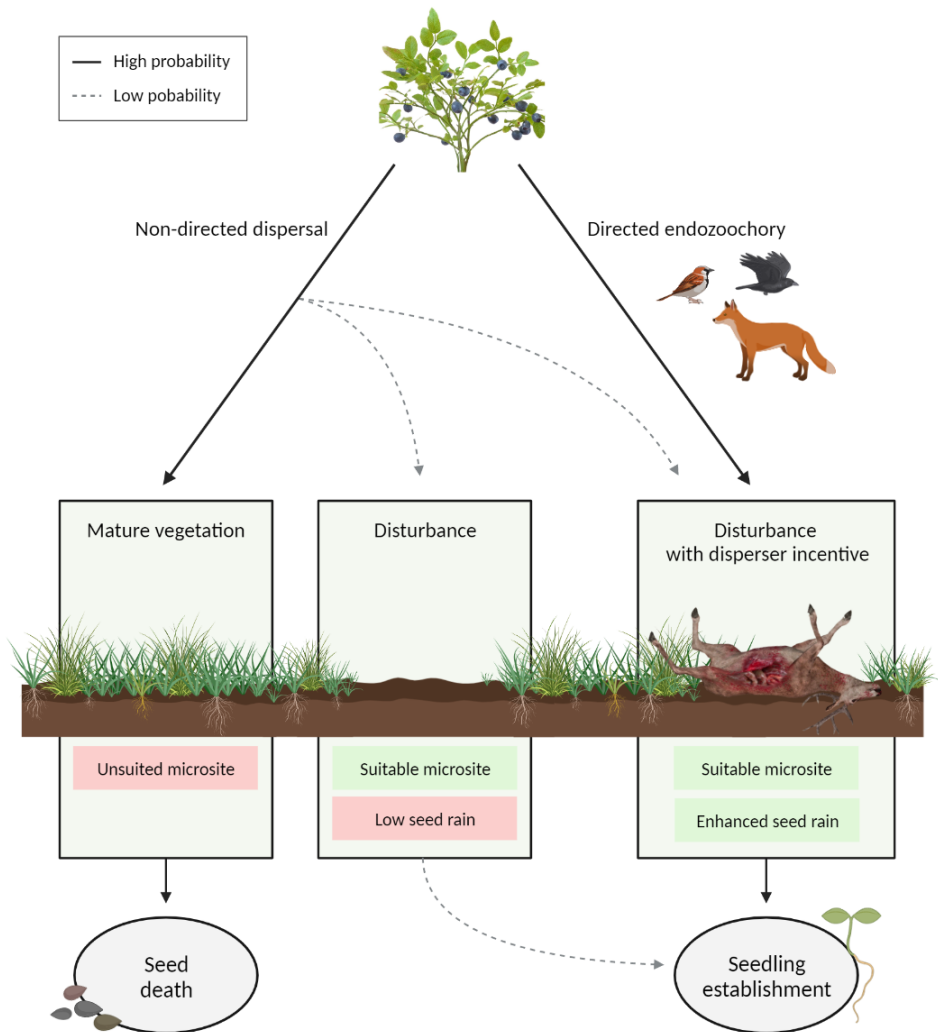


Figure 3. Schematic diagram showing directed seed dispersal by endozoochorous dispersal vectors towards favorable microsites as a pathway to successful sexual reproduction in clonal berry-producing ericaceous shrub species. Non-directed dispersed seeds have a limited encounter rate with temporally and spatially unpredictable recruitment windows of opportunity. By linking the endozoochorous dispersal capacity of frugivorous vertebrates and disperser-attractive microsites, dispersal limitation is overcome at ideal microsites due to (1) vectors facilitating their (2) directed dispersal (i.e. enhanced seed rain) into (3) favorable microsites for seedling establishment. Figure adapted from Arnberg et al. (2022).

2. Objectives

The overall objective of this thesis was to disentangle the ericaceous reproductive paradox by elucidating pathways of sexual reproduction (i.e. recruitment from seed) in clonal berry-producing ericaceous species. Specifically, we aimed to connect vertebrate disperser species which have the potential for directed endozoochory to viable recruitment windows for seedling establishment (Figure 3). This thesis focuses on two possible regeneration pathways: 1) Vertebrate scavengers provide directed dispersal towards cadaver decomposition islands by opportunistically consuming both ericaceous berries and carrion, and 2) Frugivorous passerine birds, also known as perching birds (order Passeriformes) direct seed dispersal towards perching points in the landscape, which can be suitable microsites for seedling establishment of ericaceous plants. Both recruitment pathways entail that seed deposition sites also accommodate seedling establishment.

The goal of **Paper I** was to extend the findings of Steyaert et al. (2018). In an alpine ecosystem, the authors found that scavenging birds and mammalian mesopredators provided directed seed dispersal towards a mass die-off site where 323 tundra reindeer had been killed by a lightning strike. Furthermore, animal feces consistently contained viable seeds from the ericaceous shrub *Empetrum nigrum*. Within the same mass die-off site, we used a permanent grid of survey plots spanning a gradient from high carcass-induced disturbance to intact vegetation, surveying environmental variables and seedling establishment concurrently. Specifically, this paper investigated I) if seedling establishment was associated with decomposing carcasses and II) the influence of other microsite conditions important for seedling establishment such as reduced competition.

Although mass mortality events are not necessarily rare (Fey et al., 2015), the majority of mammal carcasses are distributed individually across landscapes as most die from predation, hunting, starvation, or disease (Barton et al., 2019; Moleón et al., 2019). **Paper II** aimed to characterize the role of single mortality events in sexual

reproduction of ericaceous species in a boreal forest ecosystem. Specifically the aim was to elucidate links between carcass-induced disturbances in the vegetation, the scavenger community (i.e. documented dispersal vectors), and seedling establishment of keystone ericaceous species. By using an experimental control-intervention study design with control, mechanically disturbed and carcass plots, this paper assessed how carcass size and time of death influenced the I) vertebrate disperser community, II) development of CDIs (i.e. recruitment windows); then testing III) if seedling establishment was more abundant in CDIs compared to mechanical disturbances and control plots which have little disperser incentive.

Decomposing wood is an important habitat and regeneration site for many forest-associated plant species (Harmon et al., 1986; Santiago, 2000; Bače et al., 2012; Chmura et al., 2016). Within intensively-managed boreal forest, cut stumps constitute the majority of large woody debris (Rouvinen et al., 2002). Although passerines have not been directly associated with such man-made woody debris, they often use low coarse woody debris in natural forests, for example to perch on while foraging for insects (Hagelin et al., 2015). The aims of **Paper III** were to I) document directed endozoochorous dispersal of viable seeds towards cut stumps by passerines; II) assess if seedling establishment is more likely in cut stumps than random points on the forest floor; and III) uncover environmental factors modulating the two important components of this proposed recruitment pathway, i.e. scat deposition and seedling establishment.

3. Main results

Paper I: Directed endozoochorous dispersal by scavengers facilitate sexual reproduction in otherwise clonal plants at cadaver sites

The large and spatially-concentrated input of carrion biomass from 323 reindeer carcasses of animals that died from lightning in 2016 in the alpine tundra in southcentral Norway had drastic effects on the vegetation layer in the immediate vicinity of the mass die-off. Over the course of three years, the decomposing carcasses had created one mega CDI (25×25 m) in the most carcass-dense area and several smaller CDIs from scattered carcasses. Furthermore, the disturbance from carcass decomposition and scavenger activity had created patches of bare soil that extended far beyond carcass positions.

Our results showed that CDIs provided microsites that were suitable for ericaceous seedling establishment. In total, we registered 43 ericaceous seedlings within 67 survey plots. *Empetrum nigrum* was most abundant (n = 22), followed by *Vaccinium vitis-idaea* (n = 11), *V. uliginosum* (n = 7) and *V. myrtillus* (n = 1). Two seedlings could not be identified beyond genus level (*Vaccinium* spp.). The probability of ericaceous seedling establishment within survey plots was positively affected by carcass density. All other microhabitat conditions such as soil or vegetation cover were poor predictors of seedling establishments. Even plots with high amounts of soil cover and thus low competition did not have seedling establishment unless they were also near a carcass.

Together with Steyaert et al. (2018) our findings in Paper I established understanding of a novel, viable recruitment pathway. Seedlings of berry-producing ericaceous shrubs are more likely to establish within CDIs due to dispersal vectors facilitating directed dispersal of viable seeds into favorable microsites.

Paper II: Characterizing the role of carcasses in seedling establishment for clonal ericaceous shrubs

Across 30 experimental sites, each consisting of one experimentally deployed carcass, one control and one mechanically disturbed plot, we quantified vertebrate activity, microsite changes and ericaceous seedling establishment. After carcass deposition, plots with carrion material effectively created a spatiotemporal hotspot of animal activity. Of the 16 886 vertebrate observations from wildlife cameras, carcass plots accounted for 97 % of all observations with only the remaining 3 % of observations occurring at controls (i.e. baseline vertebrate community; we did not place cameras on mechanically-disturbed plots). The aggregation of vertebrates was contingent on carcass size: larger carcasses (e.g. moose, reindeer) attracted similar communities to one another whereas observations at small carcasses (e.g. red fox) resembled those at control plots. Crucial to plant recruitment, animals with the potential for ericaceous seed dispersal constituted an overwhelming 93 % of all observations at carcass plots. Further, the greatest occurrence of such species overlapped with berry ripening and the peak time of ericaceous seed dispersal.

Carcass size also played an important role in the formation of CDIs (i.e. recruitment microsites). Larger carcasses effectively created disturbances in the forest floor vegetation, while small carcasses had no or little effect on vegetation cover. Disturbances from large carcasses were characterized by a decrease in field- and ground-layer vegetation, and increase of bare soil in discrete patches. Thus, they closely fit the requirements for RWOs for ericaceous species. Season of carcass deposition did not affect animal aggregation or CDI formation. In fact, larger carcasses persisted for a surprisingly long time, often through multiple seasons.

Lastly, our results indicated that CDIs from single mortality events can be viable RWOs for ericaceous species. Seedlings were significantly more abundant in CDIs compared to mechanical disturbances and control plots. Our study demonstrates how individual carcasses in a forest landscape facilitates sexual reproduction in

ericaceous keystone species. However, the recruitment pathway is a multistep process where each step is modulated by the nature of the carcass itself. Smaller carcasses did not aggregate disperser species nor did they generate CDIs, and seedling establishment was never observed at those sites.

Paper III: Perfect poopers; Passerine birds facilitate sexual reproduction in clonal keystone plants of the boreal forest through directed endozoochory towards dead wood

Within a boreal forest landscape in Trøndelag, Norway, we quantified passerine scat deposition and seedling establishment at 142 cut stumps from forest management and paired forest floor plots. We used this data to evaluate how and to what extent passerine birds can direct ericaceous seed dispersal towards cut stumps, which have been suggested to be suitable microsites for ericaceous seedlings. Our result showed that passerine birds directed seed dispersal towards cut stumps in a managed forest landscape. Scat deposition was 24 times more likely on stumps compared to forest floor plots suggesting that passerine birds actively perch and regularly defecate on stumps. Importantly, bird droppings consistently contained viable seeds. In a germination trial of bird droppings collected at stumps, *Vaccinium* seeds germinated from 81 %. Stumps were also suitable recruitment windows for *Vaccinium* species, with a higher probability of seedling establishment at stumps compared with the forest floor. In total, we recorded 126 *Vaccinium* seedlings, 121 of which were on stumps (range: 0–24; mean: 0.85) and only 5 of which were in forest-floor plots (range: 0–2; mean: 0.03).

Our study shows how directed endozoochorous seed dispersal by passerine birds towards tree stumps provides another pathway to successful sexual reproduction in berry-producing *Vaccinium* spp. shrubs. Notably, our results indicate that the functionality of this recruitment pathway is rather contextual. That is, not all stumps were used for perches and not all stumps supported seedling establishment. The probability of seed deposition and seedling establishment varied strongly with

environmental context. If stumps were located in areas with higher complexity of the vertical forest structure and relatively low canopy cover, probability of scat deposition at stumps increased from 0.11 to 0.73. Seedling establishment was regulated by environmental variables at the stump level. Without bryophyte cover, seedlings never established on stumps while a combination of increasing bryophyte cover and stump diameter elevated the probability of seedling establishment from 0 to 0.74.

4. General discussion

This thesis demonstrates how berry-producing ericaceous species utilize different pathways to attain seedling establishment. Although seedling establishment has been categorised as rare in the *Vaccinium* and *Empetrum* genera (Eriksson and Ehrlen, 1992; Vander Kloet and Hill, 1994; Ranwala and Naylor, 2004), we show that it is a relatively frequent phenomenon when coupled with directed endozoochorous dispersal. Specifically, we demonstrate two functional pathways of sexual reproduction: 1) Scavenging vertebrate species direct endozoochorous seed dispersal towards CDIs (Steyaert et al., 2018) which are viable RWOs for seedling establishment (Papers I and II), and 2) Passerines direct endozoochorous seed dispersal towards decomposing tree stumps, i.e. viable RWOs, through their perching behaviour (Paper III). As such, this thesis adds to the growing body of evidence showing that (passive) directed endozoochory can be an important driver for population dynamics in plants (Mason et al., 2022)

4.1 Ecological consequences of the discovered pathways

4.1.1 Seedling establishment when connected to dispersal strategy

Our results support recent studies indicating that seedling recruitment in clonal ericaceous plants occurs much more frequently in nature than previously expected (García-Rodríguez and Selva, 2021; García-Rodríguez et al., 2022). However, it is all a matter of looking in the right place: the success of sexual reproduction is tightly linked to endozoochorous disperser activity at habitat disturbances (Fig. 4; Papers I, II and III). On average, microsites from carrion decomposition at single mortality events had 17 seedlings/m² (Paper II) while decaying stumps had 18.12 seedlings/m² (paper III). In comparison, seedling establishment under mature conspecific plants ranged between 0.72 - 0.97 seedlings/m² (Papers III and II, respectively). Mechanical disturbances, which are not necessarily attractive to disperser species but offer suitable conditions for seedling establishment, averaged 4.2 seedlings/m² (Paper II).

The seedling abundance we found in mechanical disturbances and among adult plants are similar to those reported in other studies (Hautala et al., 2001; Manninen and Tolvanen, 2017). These seedlings are likely the product of ‘background’ seed rain generated by berries falling directly to the ground (i.e. undispersed) or undirected dispersal by frugivorous animals (Fig. 4c; Graae et al., 2011). Considering the vast expanse of habitat covered by mature ericaceous vegetation in boreal and alpine biomes, nearly one seedling per square meter could potentially account for considerable annual recruitment. However, such seedlings are usually short-lived as they are easily outcompeted by the adult plants (Eriksson and Fröberg, 1996); a common end to life in many plant species that do not have seed or seedling traits which favor survival when faced with abiotic and biotic stress (e.g. large seeds or fast growth; Kitajima and Fenner, 2000; Moles and Westoby, 2004). Hence, the probability of ericaceous seedlings assimilating into the adult population as new reproductive individuals in mature vegetation is likely very low.

High levels of seedling establishment appeared to be achieved only when 1) landscape structures or resources were attractive to dispersal vectors and animal activity was concentrated at such points, and 2) those points were also viable RWOs for ericaceous seedling establishment. Although not comparable in size, CDIs from single mortality events could have up to 126 seedlings and decomposing stumps up to 24 seedlings at the time of observation (Papers II and III, respectively). The maximum abundance within survey plots (0.25 m²) at mass-mortality induced CDIs was 10 seedlings (Paper I).

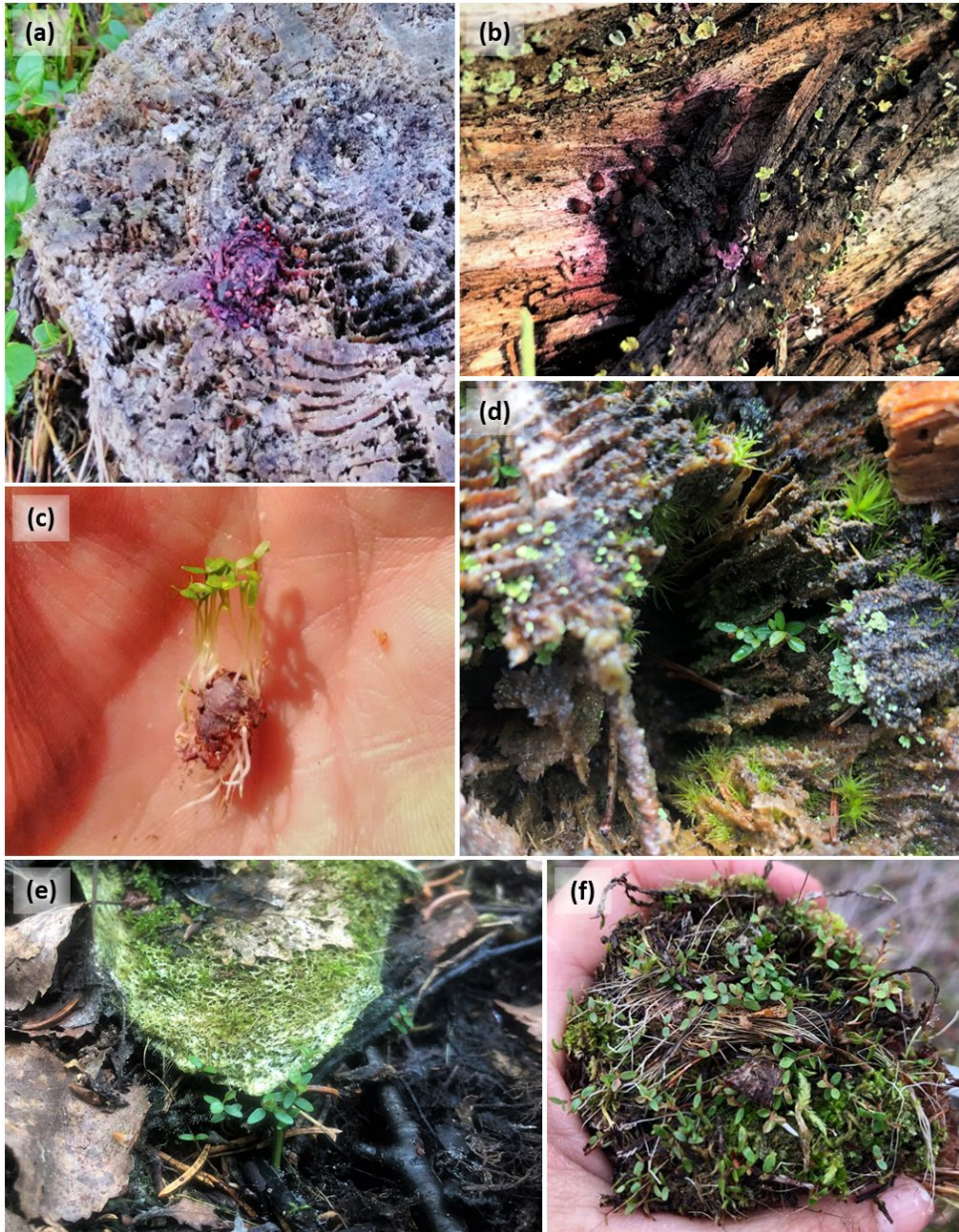


Figure 4. Pictures of: (a-b) bird droppings on decaying wood, colored blue by berries and with visible seeds of *Vaccinium* spp.; (c) *Vaccinium* spp. seedlings germinating directly out of an undispersed berry; (d) *V. myrtillus* seedlings on a tree stump; (e) *V. myrtillus* and *V. vitis-idaea* seedlings in a cadaver decomposition island; (f) ericaceous seedlings emerging from a red fox scat deposited at a moose carcass. Picture credit a and c: Sam Steyaert

The genetic diversity found in *Vaccinium* spp. and *Empetrum nigrum* populations, which is comparable to that of nonclonal species, supports frequent recruitment from seed (Persson and Gustavsson, 2001; Albert et al., 2003; Bienau et al., 2016). In *Vaccinium* populations, the majority of the genetic variation (86-89%) resides within populations (Persson and Gustavsson, 2001; Albert et al., 2004; Albert et al., 2005) and multiple genets can be found in relatively small patches (Persson and Gustavsson, 2001). For instance, Albert et al. (2004) found up to 21 genets of *Vaccinium myrtillus* in 3×3 meter plots in a temperate forest ecosystem. Together, this points to continuous seedling recruitment within conspecific plants and that such establishment is, at least to some extent, a result of long-distance dispersal events between populations (Hamrick and Godt, 1996).

Previous attempts to understand recruitment patterns in clonal plants, including berry-producing ericaceous shrubs, have not accounted for seed dispersal strategies (Eriksson, 1993; Vander Kloet and Hill, 1994; Welch et al., 2000). As such, ericaceous species have produced a perceived paradoxical set of life-history traits: profuse clonal growth, costly berry production that favours dispersal, relatively small seeds with poor defence mechanisms, slow growing seedlings with low stress and competitive abilities, and rare seedling establishment at suitable microsites. Yet, seed dispersal is crucial for explaining life-history traits and evolution (Bonte and Doherty, 2017; Beckman et al., 2018). In the case of ericaceous species, frugivorous dispersal vectors form the red thread which ties it all together. We show the importance of dispersal services provided by avian and mammalian dispersal vectors to successful sexual reproduction in clonal ericaceous species (Papers I, II and III). Seed dispersal directed towards suitable RWOs results in seedling establishment at much higher frequency than earlier thought.

By neglecting endozoochorous seed dispersal by vertebrates and their distinct contribution to the seed shadow, the importance of seedling recruitment has undoubtedly been underestimated. Sexual recruitment likely contributes to

population dynamics at both local and regional scales as evidenced by the genetic structure of the populations (Persson and Gustavsson, 2001; Albert et al., 2004; Albert et al., 2005). Notably, an array of plants primarily thought to propagate clonally have also shown high genetic diversity (Ellstrand and Roose, 1987; Nybom, 2004; Jankowska-Wróblewska et al., 2016; West et al., 2023). This may indicate that many plant species are dependent on previously overlooked complex and multistage processes related to successful seedling recruitment

4.1.2 When multiple species eat and poop

Within the documented recruitment pathways of this thesis, the disperser community of ericaceous seeds consists of many species that can direct seed dispersal towards suitable microsites (Paper III; Steyaert et al., 2018). At carcass sites, the most commonly observed species were the mammalian scavengers red fox and European pine marten (*Martes martes*), and corvids such as Eurasian jay (*Garrulus glandarius*), hooded crow (*Corvus cornix*) and Eurasian magpie (*Pica pica*) (Paper II). While we did not document the species of passerines that perched and defecated on stumps, more than 40 passerine species inhabit the area during summer and autumn. Hence, it is highly likely that more than one species contributed to droppings observed at stumps (Paper III).

When considering the two recruitment pathways in parallel, the disperser communities provided complementary seed dispersal services in two ways. Firstly, they directed dispersal towards two distinct microsites (carrion and stumps) in the landscape (Paper III; Steyaert et al., 2018;). Secondly, the dispersal communities included species with varying movement ranges which may contribute differently to particular regions of the seed shadow (i.e. seed deposition at differential distances from the source plant; Jordano et al., 2007; Papers II and III). The combination of both recruitment pathways allows ericaceous species to reach more RWOs and increase the frequency of sexual recruitment (Papers I, II and III) – a pattern found in several other plant-frugivore mutualisms (Escribano-Avila et al., 2014; González-Castro et al.,

2015; Morán-López et al., 2020). The medium sized scavengers, such as the red fox and corvids observed at carcass sites (Paper III), are considered long-distance seed dispersers with dispersal distances that can reach nearly 3 kilometres in a Mediterranean study system (González-Varo et al., 2013; Green et al., 2019). Importantly, such long distance dispersal is crucial to metapopulation dynamics as it allows for genetic connectivity between populations (Spiegel and Nathan, 2007; Jordano, 2017). For example, Jordano et al. (2007) found that 74 % of seeds from the mahaleb cherry (*Prunus mahaleb*) were deposited outside the genetic neighborhood of the source population when dispersed by medium sized mammals (foxes, badgers, and stone martens). In comparison, passerines which direct seed dispersal towards stumps (Paper III) and likely also CDIs (Badía et al., 2019; Paper I) mainly move seeds over short distances and deposit them within the source population (Jordano et al., 2007). Such short distance dispersal is also important to population dynamics as it promotes gene flow and population persistence at local scales (Jordano, 2017). Still, passerines such as robins or thrushes can also disperse seeds over very long distances, particularly during autumn migration (Costa et al., 2014).

The division of seed dispersers according to their potential dispersal distances also suggest that some functional redundancy exists within each dispersal pathway. That is, multiple species provide similar dispersal services and if one species becomes extinct other species could replace its function without a reduction in plant recruitment (Schleuning et al., 2015). Seed dispersal patterns by vertebrate scavengers are comparable in their contribution to the seed shadow: seeds are transported over long distances and deposited into the same microsite type (CDIs; González-Varo et al., 2013; Steyaert et al., 2018). Similarly, the passerine community disperses seeds over short distances to decomposing stumps or alternatively CDIs (Jordano et al., 2007; Paper III). Functional redundancy plays an important role in ecosystem resilience during environmental perturbations (Peterson et al., 1998) and can buffer the effects of disperser loss (García et al., 2011; Rumeu et al., 2017). Due to the similar dispersal services provided by subsections of the dispersal community,

dispersal patterns would persist if some frugivore species experienced population declines or even extinction.

4.2 The magnitude of overlooked recruitment opportunities

RWOs for seedling establishment and survival in clonal ericaceous species likely occur at relatively high frequencies across landscapes. Although the occurrence of RWOs in natural ecosystems at any given time point is unknown, many papers report relatively high frequencies of carrion input and coarse woody debris – material which we know can become suitable RWOs for ericaceous species (Papers I, II and III).

The annual input of carrion biomass to terrestrial systems from ungulates (wild and domestic) that died from natural causes such as predation, disease or starvation ranges from 10 to almost 700 kg/km² (Moleón et al., 2019 and references therein). Human activities can further increase the influx of carrion material (e.g. vehicle collisions, supplementary feeding; Moreno-Opo and Margalida, 2019). For example, remains from moose hunting (e.g. viscera, head, vertebral column, lower legs and hide) can annually subsidize carrion available biomass with almost 83 kg/km² (Lafferty et al., 2016). However, in many European countries, sanitary regulations has led to systematic removal of carrion from domestic livestock following the outbreak of bovine spongiform encephalopathy (mad cow disease; Margalida et al., 2010). Nevertheless, considering that experimentally-placed carcasses weighing from 70 kilos and upwards created CDIs within our study site (Paper II), ‘natural’ carcasses could potentially generate several RWOs per km² each year. In addition, estimates of carrion biomass are likely conservative due to carrion’s ephemeral nature: carrion has rapid turnover and is also a highly sought after resource by organisms of the necrobiome (e.g. scavengers, insects; Barton et al., 2019).

In Paper III, we showed that stumps from timber production can be viable RWOs for ericaceous species but decomposing wood comes in variety of forms. These include standing dead trees (snags), dead branches, fallen trees, coarse roots or

fragmentated pieces from larger snags and logs. The amount of decomposing wood (m^3/ha) can vary with climate, forest age, site fertility and stand density (Bujoczek et al., 2021). Forest management for timber production, however, is the most important driver of dead wood availability in most Scandinavian forests (Linder and Östlund, 1998). Managed forest stands consistently contain less woody debris compared to old growth forest across biomes and the woody debris that remains largely consists of stumps (e.g. Kirby et al., 1998; Siitonen et al., 2000; Lombardi et al., 2008; Bujoczek et al., 2021). Similarly, within managed stands, the volume of dead wood decreases with intensity of logging practices (Green and Peterken, 1997; Paletto et al., 2014). For seedling establishment, downed woody debris such as logs has been identified as an important microsite for many species (Chmura et al., 2016), and incidentally these are also seed deposition sites (Rehling et al., 2022). Directed endozoochorous dispersal towards stumps in an intensively managed forest (Paper III) might represent a subset of a much larger plant-frugivore dispersal network. The potential contribution of this reproductive pathway to recruitment is likely much bigger in more intact forests which host more potential regeneration sites and a more diverse avian disperser community.

Besides the recruitment pathways we have shown in this thesis, recent studies have shown that brown bears disperse bilberry seeds towards their daybeds which are small disturbed areas in which seeds can germinate and establish (Steyaert et al., 2019; García-Rodríguez and Selva, 2021). Undiscovered pathways likely exist and piecing together ecological clues and animal behaviour can thus reveal potential pathways. For example, windthrows are part of the natural disturbance regime and drivers of forest dynamics (Mitchell, 2013). When trees are uprooted by wind, they leave a pit at the former root position and an adjacent mound forms from falling soil released as the upturned root plate decomposes, creating discrete patches of bare soil in the forest floor (Schaeztl et al., 1989). Passerines use upturned root plates for perching and nesting (Thompson, 1980; Karpińska et al., 2022), and thereby deposit seeds into the pit and mound (Thompson, 1980). On a larger scale, extensive

windthrow gaps with multiple downed trees could provide a ‘mega’ opportunity for ericaceous species being dispersed by passerines. First, they immediately create exposed soil at upturned root plates and second, downed logs eventually decompose and become suitable for seedling establishment. In conclusion, there is likely a permanent supply of viable RWOs from natural disturbances in heterogeneous habitats for ericaceous shrubs or even other species relying on directed endozoochorous dispersal. The main barrier to recruitment for RWO strategy species is to locate such microsites. For RWO pathways to be better recognised by the scientific community, the main barrier seems to be linking seed dispersal to suitable microsites, for example through animal behaviour.

4.3 Seed dispersal in a changing world

For endozoochorous plants, particularly those which require specific microsites for seedling establishment, recruitment depends on the reliability of dispersal vectors – an increasing challenge in the Anthropocene. Many vertebrates world-wide are facing population declines, extinctions at local and global scales, altered spatial distributions and reduced movement ranges. Such ‘defaunation’ is caused by human-driven overharvesting, habitat fragmentation, degradation and loss, and invasion of alien species (Dirzo et al., 2014; Ceballos et al., 2015; Ceballos et al., 2017; Tucker et al., 2021). Here, I consider defaunation a larger threat to interactions between ericaceous species and their animal partners due to the generalist nature of both ericaceous berry-producing species and their disperser community. Changes in dispersal vector populations or behavior can have cascading effects (Rogers et al., 2021). They can severely impact plant-animal interactions such as seed dispersal (Neuschulz et al., 2016; Teixido et al., 2022) which may lead to reduced or even failed plant recruitment and increased risk of local extinction (Rodríguez-Cabal et al., 2007; Moran et al., 2009; Rogers et al., 2021).

We have shown that sexual recruitment through directed endozoochory occurs in both undisturbed (Paper I) and human-impacted habitats (Paper III). Although the

suggested redundancy of dispersal services discussed above offers some buffer to human disturbance, defaunation processes likely affect sexual reproduction in ericaceous plants. The impact on plant recruitment is tied to which members of the disperser assembly are susceptible to defaunation hazards: Animals with large body mass usually have the highest chance of population decline and local extinction (Dirzo et al., 2014; Rogers et al., 2021). Within Norwegian boreal forests (Papers II and III), the largest seed disperser in terms of body size and berry consumption, is the brown bear, which occupies a fraction of their original habitat due to overexploitation, habitat loss, and management policies favoring free ranging livestock husbandry (Swenson et al., 1995; Bischof et al., 2020). This implies not only loss of unique recruitment pathways (i.e. bear beds) but also loss of long distance dispersal opportunities (Lalleroni et al., 2017), with potential consequences for population connectivity and genetic diversity (Pérez-Mendez et al., 2016; Jordano, 2017). Similarly, species abundance and richness within scavenger assemblages are highly affected by human activity (Sebastián-González et al., 2019). A major driver is hunting and persecution, often due to misconceptions and livestock conflicts, while the important ecosystem services that scavengers provide are overlooked (Ogada et al., 2012; Moleón et al., 2014). In fact, many municipalities in Norway still have bounty payments in place for scavengers such as red fox, European pine marten, common raven (*Corvus corax*) and hooded crow to actively reduce their populations. This is a process which also results in a reduction of the seed dispersal services provided by such omnivorous scavengers. In addition, population declines are also evident in smaller mammals and birds (Donald et al., 2006; Davidson et al., 2009). There is, however, little knowledge on how loss of small disperser species, such as passerines (Paper III), affects seed dispersal (Rogers et al., 2021).

How anthropogenic interference in key ecosystem functions has altered and most importantly continues to impact sexual recruitment in keystone ericaceous plants is largely unknown. However, the abundance and diversity of seed dispersers is positively correlated with the number of seeds arriving at suitable microsites for

seedling establishment across landscapes (García et al., 2018; García-Rodríguez et al., 2022). Maintaining diverse disperser communities can thus be important for safeguarding complete dispersal networks and its associated biodiversity.

5. Conclusion and further perspectives

This thesis shows that ericaceous berry producing species do not necessarily present a reproductive paradox. Instead, they possess life-history traits (fleshy fruit) to overcome dispersal limitation and reach suitable microsites. Seedling establishment occurs at relatively high frequencies when endozoochorous dispersal vectors direct their seed dispersal towards RWOs. This approach also explains the observed high genetic diversity within relatively small patches of mature ericaceous stands. Although our findings elucidate a solution to the reproductive paradox, important questions remain unanswered.

The relative fitness contribution of a dispersal event to plant populations is only realised when seedlings persist and grow into new reproductive adults (Schupp et al., 2010). There are several factors besides reduced competition which might facilitate seedling persistence at RWOs within our study sites. For example, elevated levels of growth-restrictive nutrients from carrion decomposition can enhance seedling growth (Bump et al., 2009), and partnerships with ericoid mycorrhizal fungi can increase nutrient assimilation from decomposing wood (Perotto et al., 2018). However, long-term studies are needed to evaluate the survival of ericaceous seedlings, including both those which emerge under conspecific adults and those emerging in RWOs. Although such studies are challenging in long-lived clonal plants, they would also help in assessing the comparative importance of our dispersal pathways. For example, which pathway offers the most return in form of new adults to the ericaceous population and which disperser species are the functionally most important to sexual recruitment. In parallel, studies on population genetics would be necessary to evaluate how seed dispersal contributes and structures gene pools within and across populations of ericaceous plants. Preferentially, such investigations would connect seedling establishment (propagule) from known disperser species to the maternal plant or population (source). Then the actual frequency of long-distance

dispersal events which transport seeds between population can be quantified and inference made regarding which species provides such dispersal events.

6. References

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Paper I

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Directed endozoochorous dispersal by scavengers facilitate sexual reproduction in otherwise clonal plants at cadaver sites

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Abstract

1. The regeneration niche of many plant species involves spatially and temporally unpredictable disturbances, called recruitment windows of opportunity. However, even species with clear dispersal adaptations such as fleshy berries may not successfully reach such elusive regeneration microsites. Ericaceous, berry-producing species in the northern hemisphere demonstrate this dispersal limitation. They are said to display a reproductive paradox owing to their lack of regeneration in apparently suitable microsites despite considerable investment in producing large quantities of berries.
2. Cadavers generate vegetation-denuded and nutrient-rich disturbances termed cadaver decomposition islands (CDIs). Cadavers attract facultative scavengers with considerable capacity for endozoochorous seed dispersal. We hypothesize that CDIs facilitate recruitment in berry-producing ericaceous species due to endozoochorous dispersal directed toward favorable microsites with low competition.
3. We examined seedling establishment within a permanent, semi-regular 10 × 10 m grid across an ungulate mass die-off on the Hardangervidda plateau in southeastern Norway. Competing models regarding the relative importance of factors governing recruitment were evaluated, specifically cadaver location (elevated seed rain) and microsite conditions (competition).
4. We found that CDIs did facilitate seedling establishment, as cadaver density was the best predictor of seedling distribution. Other important factors governing seedling establishment such as percentage cover of soil and vascular plants alone were inadequate to explain seedling establishment.
5. *Synthesis*: This study provides a novel understanding of sexual reproduction in species with cryptic generative reproduction. The directed nature of endozoochorous dispersal combined with long-distance dispersal abilities of medium to large vertebrate scavengers toward cadavers allows plants to exploit the advantageous but ephemeral resource provided by CDIs.

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KEYWORDS

cadaver decomposition island, directed dispersal, Ericaceae, recruitment window of opportunity, reproductive paradox

JEL CLASSIFICATION

Life history ecology; Movement ecology; Seed ecology

1 | INTRODUCTION

Berry-producing ericaceous shrubs are keystone species throughout many of the temperate, boreal and alpine habitats in the Northern hemisphere, with important effects on ecosystem function (Mallik, 2003). Ericaceous vegetation dominates the boreal understory, regulating seedling survival and subsequently species composition (Nilsson & Wardle, 2005). Removal of this functional group has detrimental effects on soil microbial activity and soil quality (Fanin et al., 2019). Furthermore, their vegetative structures and berries are an important food source for many mammal, bird, and insect species (Atlegrim, 1989; Dahlgren et al., 2007; Wegge & Kastdalen, 2008).

While their importance for ecosystem function is well known, berry-producing genera such as *Vaccinium* and *Empetrum* present a reproductive paradox (Kloet & Hill, 1994). These species invest in the annual production of large crops of conspicuous fleshy fruits (berries) that contain viable seeds. The berries are consumed by a wide range of mammals and birds (e.g., brown bear, *Ursus arctos*; red fox, *Vulpes vulpes*; tetraonids and corvids) and are an adaptation for endozoochory, that is, seed dispersal via ingestion by animals (Howe & Smallwood, 1982; Willson, 1993). Despite their substantial investment in sexual reproduction, *Vaccinium* and *Empetrum* spp. are reported to propagate almost exclusively clonally (Hautala et al., 2001; Welch et al., 2000). Furthermore, their seeds are consistently under-represented in the soil seed bank and seedlings are rarely observed in the wild (Hester et al., 1991; Kloet & Hill, 1994; Ranwala & Naylor, 2004; Welch et al., 2000). This apparent reproductive paradox and its implications for the population biology of many ericaceous berry-producing shrubs are poorly understood and infrequently addressed (Kloet & Hill, 1994; Welch et al., 2000).

Recruitment in plants via endozoochory is closely tied to mutualistic interactions with frugivorous and omnivorous animal partners (Schupp et al., 2017). Animals remove fruits for resource acquisition and simultaneously provide dispersal services for plants by transporting and depositing seeds. This allows plant offspring to escape higher density- and distance-dependent mortality near conspecifics (Janzen–Connell mechanism; Comita et al., 2014), to locate ephemeral microsites suited for establishment and even to colonize newly available habitat patches (Escribano-Avila et al., 2014; Howe & Smallwood, 1982). The seed dispersal effectiveness, that is, contribution of a dispersal agent to the recruitment likelihood of a given plant species, is the outcome of a complex and multistage process (Schupp et al., 2010). Firstly, fruits must be detected and ingested. The number of seeds dispersed is dependent on the number of seeds removed per visit and the number of visits, which is related to the abundance of dispersers and their feeding behavior. Secondly, the

recruitment probability of dispersed seeds will be affected by the rate of successful scarification versus the rate of viability loss incurred during passage through the gastro-intestinal system and the quality of the seed deposition site (Schupp et al., 2010 and Schupp et al., 2017).

The microsite of seed deposition is critical for seed dispersal effectiveness (Schupp et al., 2010), as it must accommodate species-specific requirements for germination and subsequent seedling establishment and survival (Eriksson & Ehrlén, 1992; Grubb, 1977). Both abiotic and biotic microsite conditions (e.g., competition, nutrients, and seed predation) will be spatially and temporarily variable throughout a landscape (Riedel et al., 2005; Spasojevic et al., 2013). Situations where favorable microsite conditions are relatively short-lived are referred to as recruitment “windows of opportunity” (RWOs; Jelinski & Cheliak, 1992). Seed addition experiments have demonstrated that ericaceous species readily germinate and establish in suitable RWO-type microsites (Eriksson & Fröberg, 1996; Manninen & Tolvanen, 2017). These RWOs consist of disturbances within mature stands of ericaceous vegetation that remove potential barriers to recruitment such as field- and ground-layer vegetation (i.e., competition) and are typically characterized by high moisture and organic soil content (Eriksson & Fröberg, 1996; Graae et al., 2011). Such RWOs, however, are often spatio-temporally unpredictable, highlighting the need for dispersing seeds to reach suitable areas for germination, seedling survival, and growth (Eriksson & Fröberg, 1996; Hautala et al., 2001; Manninen & Tolvanen, 2017).

Cadavers of large animals generate small-scale disturbances in the landscape and may represent an ecologically important RWO for berry-producing ericaceous species (Steyaert et al., 2018). Nearby and underneath a cadaver, vegetation is either killed by abrupt shifts in soil nutrients and acidity or smothered, creating vegetation-denuded and nutrient-rich patches, termed “cadaver decomposition islands” (CDIs; Carter et al., 2007; Towne, 2000). In addition, cadavers are a food source for several scavenging species during decomposition (DeVault et al., 2003) leading to an aggregation of fecal deposition (Steyaert et al., 2018) that further contributes to organic input at the CDI (Carter et al., 2007). Thus, the disturbance from a CDI increases nutrient availability and removes competition in spatially discrete areas (Barton et al., 2016; Bump et al., 2009) which closely resemble the microsites described as ideal for ericaceous seedling establishment.

The majority of scavenging vertebrates that utilize cadavers as a food source are facultative scavengers (DeVault et al., 2003), that is, they are not solely dependent on carrion material and can include plant material as part of their diet. For example, during peak fruiting season, berries can constitute up to 30% of the diet

in red fox (Needham et al., 2014) and as much as 82% in brown bears (Dahle et al., 1998). Such facultative scavengers often have large home ranges and thus considerable capacity as vectors for long-distance endozoochorous seed dispersal (González-Varo et al., 2013; Schaumann & Heinken, 2002). In addition, the attractiveness of cadavers for berry-dispersing vertebrate scavengers suggests that such long-distance seed dispersal may be directed toward the CDIs (Steyaert et al., 2018).

The directed dispersal hypothesis, namely the disproportionate arrival of seeds at targeted microsites with particularly favorable conditions for recruitment, has been proposed to explain some plants' costly investment in nutritious fruit production (Howe & Smallwood, 1982; Wenny, 2001). Directed endozoochorous seed dispersal toward CDIs by facultative scavengers has been postulated as an important mechanism for sexual reproduction in ericaceous shrub species. Steyaert et al. (2018) demonstrated that ungulate cadavers are endpoints for directed endozoochory at a wild tundra reindeer (*Rangifer tarandus*) mass mortality event in south-central Norway. They found that defecation by scavengers was concentrated around cadavers and scavenger feces contained large numbers of viable seeds of the berry-producing ericaceous shrub crowberry (*Empetrum nigrum*). However, seed dispersal is only effective if it results in seedling establishment (Schupp et al., 2010, 2017).

We aim to further disentangle the reproductive paradox described for berry-producing ericaceous shrubs by extending the finding of Steyaert et al. (2018) that cadavers aided in directed seed dispersal to incorporate the seedling establishment stage. We hypothesize that seedlings of berry-producing ericaceous species are more likely to establish within CDIs due to (1) vectors facilitating their (2) directed dispersal into (3) favorable microsites (Figure 1). By examining seedling establishment in and around the same large CDI as Steyaert et al. (2018), we assess (I) whether cadaver presence facilitates successful seedling establishment and (II) the influence of other microsite conditions potentially important for seedling establishment such as reduced competition within the CDI. We predict that seedling occurrence will be more likely in close proximity to cadavers due to the combined effect of enhanced seed rain and favorable microsite conditions.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted at the site of an ungulate mass die-off event near the Vesle Saure Lake (N: 60.021, Lon: 8.034) on the mountainous plateau of Hardangervidda in Southeastern Norway, previously described by Steyaert et al. (2018). The site is located 1220 m asl and is part of a large alpine tundra ecosystem. On August 26, 2016, a lightning strike killed almost an entire herd ($n = 323$) of wild tundra reindeer (*Rangifer tarandus*). National authorities removed the heads from all dead reindeer for disease monitoring, but the remaining biomass was left on site. The cadavers are distributed

over a relatively small area (240×100 m), with the highest density confined to a 50×50 m area (Appendix 1).

The plant community is relatively species poor. In 2016, the field layer was dominated by dwarf birch (*Betula nana*) and ericaceous shrub species interspersed with graminoids and herbs and the ground layer had a consistent cover of bryophytes and lichens. However, over the course of 3 years the plant community within the most cadaver-intense area had drastically changed. In 2019, the decomposing cadavers had created one large (25×25 m) and several small CDIs. Extensive areas were dominated by bare soil and re-establishing bryophytes and graminoids (Figures 2 and 3).

Several vertebrate species, including scavengers, have been observed during previous fieldwork and camera trapping campaigns at the study site. Among those were corvids (common raven *Corvus corax* and hooded crow *C. cornix*), golden eagle (*Aquila chrysaetos*), foxes (red fox *Vulpes* and arctic fox *V. lagopus*), wolverine (*Gulo gulo*), and several rodent species (e.g., in the Arvicolinae; Steyaert et al., 2018). Scavenging species continued to use the mass die-off site after the initial mortality event in 2016. Scats showed that mesopredator and corvid occurrence was highly concentrated around the most cadaver-dense part of the site in both 2017 and 2018 (Frank et al., 2020; Steyaert et al., 2018), although corvid scat density was considerably reduced in 2018 (Frank et al., 2020). Observations of scavengers and scats made during fieldwork coincided with the ericaceous berry-ripening and dispersal season (August).

2.2 | Data collection

Shortly after the mass die-off event (October 2016), a permanent, semi-regular 10×10 m grid of $75.0.5 \times 0.5$ m survey plots was established, covering a 179×66 m area incorporating the mass die-off and immediate surroundings (Appendix 1). The grid was established to monitor different aspects such as changes in vegetation, microbiota and animal interactions (e.g., by Steyaert et al., 2018 and Frank et al., 2020, though they used 1×1 m survey plots). Since it was difficult to predict the spatial scale of changes caused by the mass die-off, the main grid was supplemented by a 10×10 m grid of 25 survey plots superimposed over the area of highest cadaver density (Appendix 1). In this paper, we use the data from the 2019 sampling campaign which incorporates 59 plots from the main grid and eight from the supplementary grid making 67 plots with a total area of 16.75 m^2 (Figure 4b and Appendix 1; some plots from the original grids were not sampled in 2019 due to missing plot markers and logistical constraints). The grid overlays a gradient from undisturbed, intact vegetation cover through highly disturbed vegetation-denuded patches around the cadavers, to persistent cadaver remains.

During the summer of 2019, we quantified seedling abundance of four ericaceous focal species: bilberry (*Vaccinium myrtillus*), bog bilberry (*V. uliginosum*), lingonberry (*V. vitis-idaea*), and crowberry (*Empetrum nigrum*) within the 67 surveyed plots. To ensure constant sampling effort, each 0.5×0.5 m survey plot was divided into 16 subplots (12.5×12.5 cm), which were each systematically

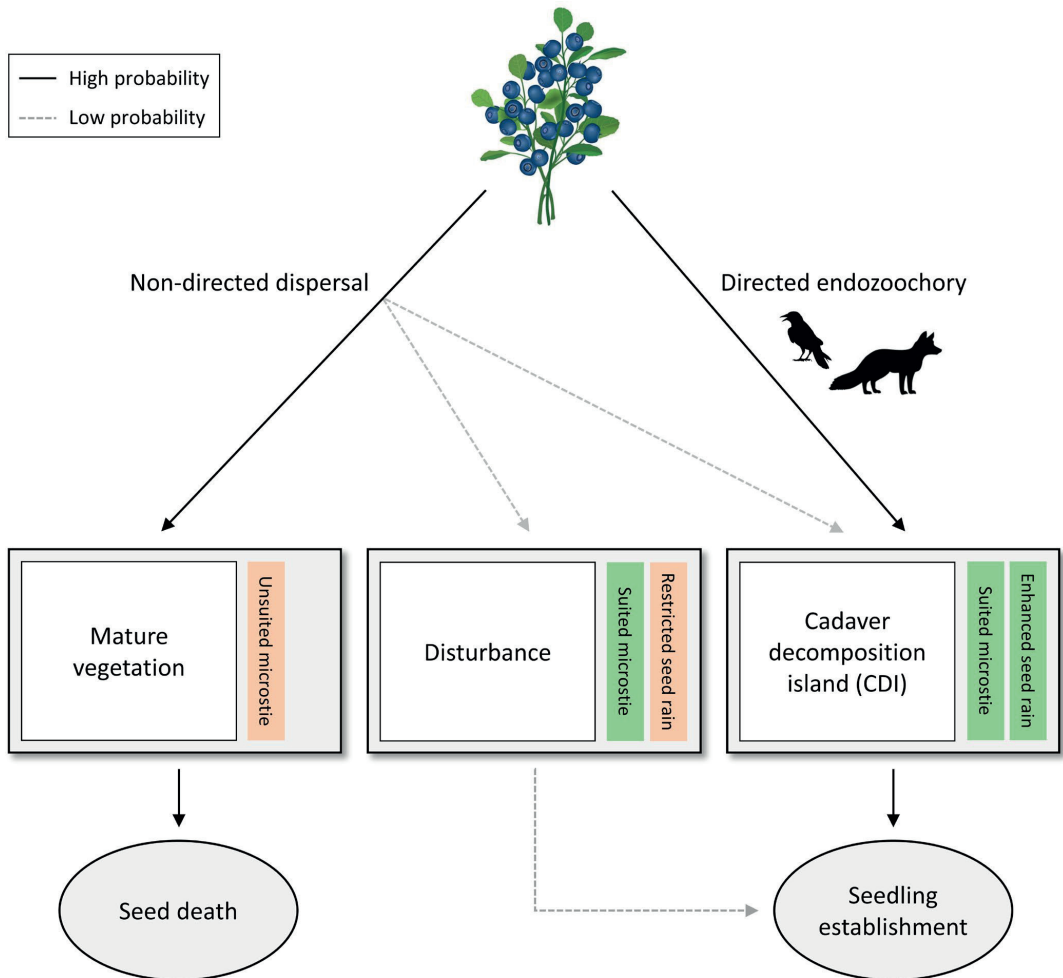


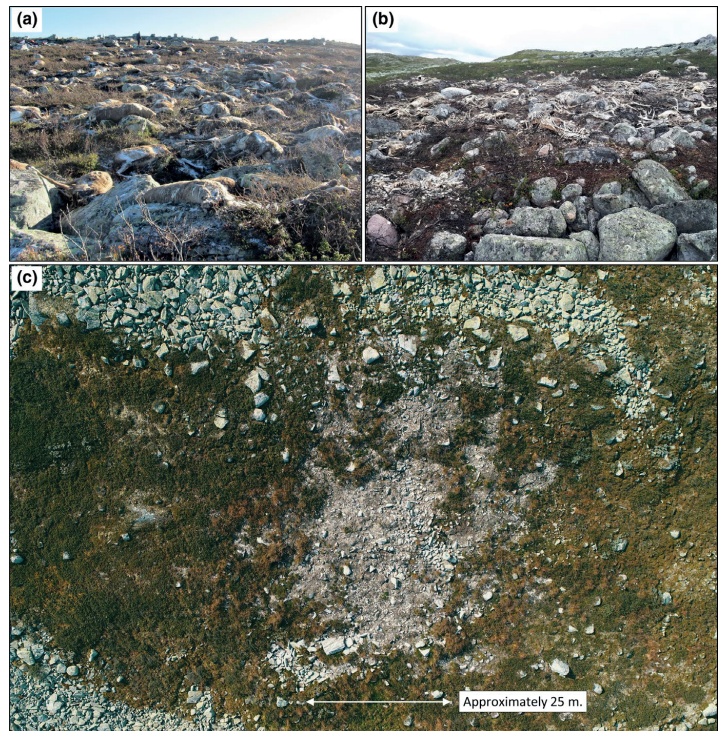
FIGURE 1 Schematic diagram showing directed seed dispersal by facultative scavengers toward cadaver decomposition islands as a pathway of successful sexual reproduction in berry-producing ericaceous shrub species. Non-directed dispersed seeds have a limited encounter rate with temporally and spatially unpredictable recruitment windows of opportunity. By linking the endozoochorous dispersal capacity of scavenging vertebrates and cadaver decomposition islands, seed limitation is overcome at ideal microsites due to (1) vectors facilitating their (2) directed dispersal (i.e., enhanced seed rain) into (3) favorable microsites for seedling establishment

searched for 15 s by one of two trained researchers, totaling 4 min search time per survey plot. Seedlings were distinguished from small ramets originating from clonal propagation by the presence of seed-leaves, while species identification was done using distinguishing features of the hypocotyl, seed-leaves, epicotyl and first leaves (Muller, 1978). In each 0.5×0.5 m survey plot, the total cover of vascular plants, soil, persistent cadaver remains, stones, bryophytes and lichens were estimated to the nearest 5%.

Seedling age was not recorded, although different cohorts were observed among the seedlings counted in 2019. Many individuals

had clearly germinated in 2019 appearing only with seed leaves and one or two first leaves—which also allowed for identification only to the genus level in some cases. However, some appeared to have germinated in the previous year and were elongated; amongst these, a few also had branching. Seedlings were not systematically inventoried in 2016–2018 but were expected to be remarked upon during vegetation surveys, given the importance of seedling establishment in the wider project at Vesle Saure. The presence of ericaceous seedlings at the site was indeed noted in the 2018 vegetation survey but not in 2016 or 2017.

FIGURE 2 The 323 reindeer cadavers have transformed the vegetation community drastically at the mass die-off site from 2016 (year of death) to 2019. (a) October 2016: The cadavers are relatively intact and the surrounding vegetation is alive. August 2019: (b) All soft tissue have either been removed by scavengers or decomposed while vegetation in the immediate vicinity has died off; (c) The mass die-off site seen from 60-m elevation. In the most cadaver-intense area one large cadaver decomposition island (CDI) has formed, surrounded by several smaller CDIs



2.3 | Statistical analysis

We followed an information-theoretic approach (Burnham & Anderson, 2002) to create and test candidate models as competing models for seedling establishment. We chose presence/absence of ericaceous seedlings at the survey plot (0.5 × 0.5 m) level as our response variable. Seedlings of ericaceous species were aggregated at the family level as there were too few observations for analysis of all but one species, *Empetrum nigrum*. Ericaceous seedling abundance was converted to a binary response variable (0 = seedlings not present, 1 = seedlings present) to avoid zero-inflation and violation of model assumptions.

We included two sets of explanatory variables. The first set contained percentage cover of persistent cadaver remains within survey plots, distance to nearest cadaver from survey plot center and interpolated cadaver density reflecting the elevated seed rain observed closer to cadavers (Steyaert et al., 2018). Cadaver density was estimated using the kernel density function from ArcGIS 10.4 and across several search radii (bandwidths: 1–10 m in 1-m increments). As a result, a smoothly curved surface was created over the study area based on cadaver density and the smoothness was determined by the number of cadavers within a neighborhood and the size of the neighborhood (bandwidth used). To determine the optimal spatial scale for seedling establishment, we fitted each bandwidth in one-predictor generalized linear models (GLMs) with a Bernoulli

distribution and seedling presence/absence as the response variable. We used Akaike Information Criterion corrected for small sample sizes (AICc) for model selection (Burnham & Anderson, 2002) and the “best” model with the lowest AICc value (search radius 2 m; Appendix 2) supplied the model term for further analysis. The second set of explanatory variables consisted of percentage cover of vascular plants, lichens, bryophytes and bare soil as measures of changed microsite conditions (e.g., competition) within the survey plots which have undergone disturbance. The rationale for including individual explanatory variables in each set is further elaborated in Table 1.

We assessed collinearity between explanatory variables prior to building candidate models using variance inflation factors (VIF) and Pearson's r correlation coefficient (Zuur et al., 2010). Collinear variables (VIF < 2 and Pearson's r < .6) were not included within the same candidate models.

Using the variables described above, a set of 14 biologically meaningful *a priori* candidate models were developed including a null model (intercept only) to explain seedling establishment. The candidate model set encompassed three subsets: (I) models based on cadaver location only (II) models based on microsite conditions only, (III) cadaver location and microsite condition combination models (Table 1). We allowed for interaction terms where such an interaction could plausibly have an effect on seedling establishment. Due to the relatively small sample size, we restricted our models

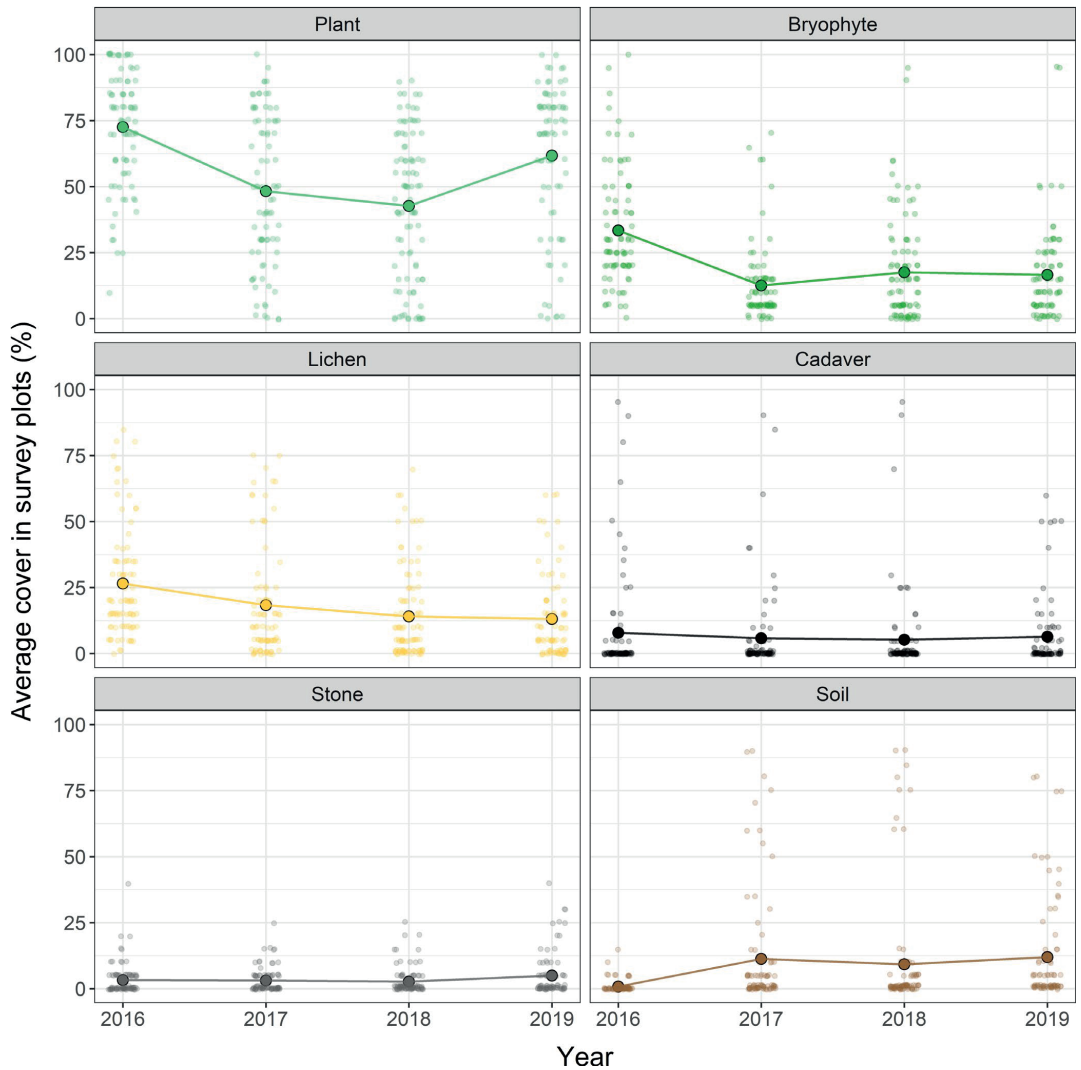


FIGURE 3 Average percentage cover of the functional groups (vascular plants, bryophytes, and lichen) and other microsite characteristics including persistent cadaver remains, stone, and soil within survey plots at the mass die-off site from 2016 to 2019

to combinations of ≤ 3 explanatory variables and fitted them using GLMs with a Bernoulli distribution.

We ranked the competing models according to AICc value and considered models within two AICc units of the top ranked model ($\Delta\text{AICc} \leq 2.0$) to have substantial support from the data and be part of the top model set (Burnham & Anderson, 2002). Nested models, that is, more complex versions of higher ranked models may produce “pretender variables” which have no relationship with the response variable and do not improve model fit (Burnham & Anderson, 2002). To avoid the inclusion of such uninformative variables (Cl

overlapping zero) within the top model set, nested models were not considered as competing models for seedling establishment (Arnold, 2010; Leroux, 2019).

We examined model residuals to ensure that assumptions were met and that effects were adequately accounted for by the model. Following Dormann et al. (2007) we assessed spatial autocorrelation of seedling presence/absence with a Moran's I test on model residuals using the R package “spdep” (Bivand & Wong, 2018) and detected no spatial dependency (p -value = .62). All statistical analyses were performed in R 4.0.2 (R Core Team, 2020).

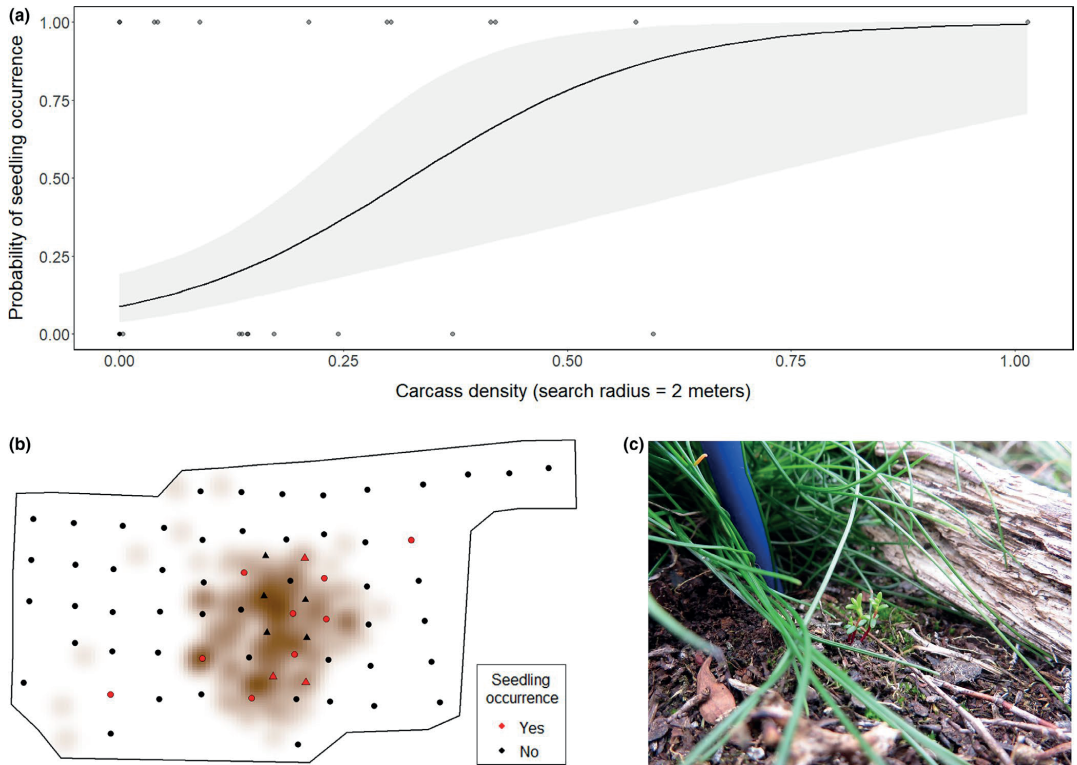


FIGURE 4 (a) The probability of seedling occurrence of berry-producing ericaceous species was positively correlated with cadaver density (search radius 2 m). The solid line is the Bernoulli generalized linear model predicted probability of seedling occurrence (0 = no seedling occurrence, 1 = seedling occurrence) relative to cadaver density. The 95% confidence interval for the model is shaded grey, and grey dots indicate the raw binary data of seedling occurrence ($n = 67$). (b) Graphical representation of the study site with dots as 0.5×0.5 m survey plots within the main sampling grid and triangles as 0.5×0.5 m survey plots within the superimposed grid. Positive seedling occurrences are indicated in red, and negative occurrences are indicated in black. The color-scaled background is a kernel density at two meters of cadavers where darker colors represent higher cadaver density. (c) Young seedlings of the ericaceous shrub *Empetrum nigrum* establishing on disturbed substrate within our study site. Picture by Marie Davey

3 | RESULTS

In total, we registered 43 ericaceous seedlings distributed over 12 of the 67 surveyed plots (range: 1–10 seedlings per survey plot). *E. nigrum* was most abundant ($n = 22$), followed by *V. vitis-idaea* ($n = 11$), *V. uliginosum* ($n = 7$) and *V. myrtillus* ($n = 1$). Because of their early juvenile state, two seedlings could not be identified beyond genus level (*Vaccinium* spp.).

The best model for predicting seedling presence contained the single explanatory variable cadaver density (Table 2). The probability of detecting ericaceous seedlings was positively associated with cadaver density ($\beta = 7.224$, $SE = 2.296$, p -value $< .01$; Figure 4a). Cadaver density was included in all four models within the top model set ($\Delta AICc \leq 2.0$) and of the next three models, two contained soil cover and one contained distance to nearest cadaver (Table 2). However, in none of these models either of the parameters or their interaction had a significant effect on seedling establishment.

4 | DISCUSSION

Cadaver decomposition islands created by ungulate cadavers provide microsites that are particularly suitable for ericaceous seedling establishment, as demonstrated by the findings within our study. This extends the findings of Steyaert et al. (2018), in which cadavers were identified as endpoints for directed endozoochorous dispersal by scavenging omnivores. Further, by encompassing a gradient from undisturbed, intact vegetation cover through highly disturbed denuded patches around the cadavers, to persistent cadaver remains, we show that favorable microsites characteristics alone are inadequate for seedling establishment. The amount of bare soil and vegetation cover—which represent important microhabitat conditions—were poor predictors of seedling establishments. Similarly, disturbed survey plots with low vegetation cover (i.e., low competition) which were adjacent to mature stands of ericaceous shrubs in which we observed ripe berries (and so seed

TABLE 1 The set of 14 *a priori* candidate models to explain seedling establishment (presence/absence) of berry-producing ericaceous shrub species

Model	Terms	Rationale	Category
1	Cadaver	Presence of persistent cadaver material facilitates continued elevated seed rain (i.e., scat deposition)	Cadaver location
2	CadDen	High cadaver density facilitates CDI's (i.e., RWOs) with elevated seed rain	
3	CadDist	Distance to nearest cadaver affects likelihood of CDI formation and scat deposition rate	
4	CadDen + CadDist	Cadaver density and proximity facilitates CDI's with elevated seed rain	
5	Cadaver + CadDist	Cadaver proximity facilitates CDI formation while persistent cadaver material within in plots provides continued seed rain	
6	Plant	Seedling establishment is reduced by competition from other vascular plants	Microsite conditions
7	Bryophyte	Bryophytes may either function as competition or nursery plants to establishing seedlings	
8	Soil	Areas with less competition will positively influence seedling establishment	
9	Plant + Lichen + Bryophyte	Competition negatively affects seedling establishment	
10	CadDen + Soil	Cadaver density facilitates CDI and elevated seed rain while high soil cover (i.e., low competition) positively affects seedling establishment	Combination
11	CadDist + Plant	Long distance to cadavers and competition from vascular plants negatively affects seedling establishment	
12	CadDen * Soil	Cadaver density facilitates CDI and enhanced seed rain but highly disturbed plots (i.e., high soil cover) are not ready for revegetation	
13	CadDen + CadDist + Soil	Cadaver density and proximity facilitates CDI and high seed rain while high soil cover positively affects seedling establishment	
14	Null	Intercept only	

Note: The candidate model set encompassed three subsets: (I) models based on cadaver location, reflecting the elevated seed rain (Steyaert et al., 2018) observed closer to cadavers, (II) models based on plant and soil cover, reflecting the reduced competition in the plots which have undergone disturbance, and (III) cadaver location and microsite condition combination models. Cover of cadaver, plant (i.e., vascular), lichen and bryophytes is expressed as percentage cover within survey plots. CadDen is cadaver kernel density (search radius = 2 m) and CadDist is distance to nearest cadaver from survey plot. Candidate models were fitted using generalized linear models (GLMs) with a Bernoulli distribution.

rain is expected to be relatively high due to berries falling; Graae et al., 2011) did not show seedling establishment unless they were also near a cadaver. Alternatively, this absence could be due to the short distance to conspecific adults where seeds and seedlings can suffer higher mortality from the activity of specialized natural enemies such as seed predators (Comita et al., 2014). However, ericaceous species such as *V. myrtillus* exhibit masting (Selås, 2000) and thus can be expected to experience weak density-distance regulation of seed and seedling mortality (Bagchi et al., 2011), possibly due to seed predator satiation (Janzen, 1970). The lack of observed seedling establishment under natural or experimental disturbance (e.g., Eriksson & Fröberg, 1996; Hautala et al., 2001; Hester et al., 1991; Manninen & Tolvanen, 2017) may be a case of looking for a needle in the wrong haystack: our results imply that seedling distribution may be related as much to the activity of endozoochorous dispersers (i.e., getting to the right place) as it is to habitat disturbance (García-Cervigón et al., 2018; Schupp et al., 2010).

The somewhat, but not entirely clustered seedling distribution in close proximity to cadavers precludes several alternative explanations for the occurrence of these seedlings. For example, Bråthen

et al. (2007) found approximately five viable seeds of ericaceous berry-producing species per liter of reindeer feces in northern Norway. If the source of the seedlings were the gut contents of the cadavers themselves, the seedlings would occur only directly upon the cadavers rather than around them. If frugivorous or granivorous species such as lemmings (*Lemmus lemmus*) or ptarmigan (*Lagopus muta*) were depositing seeds without acting as cadaver scavengers (i.e., random seed dispersal not directed at cadavers), seedling occurrence would not be clustered around the cadavers—quite possibly the opposite. Frank et al. (2020) found that the cadavers created a landscape of fear where rodents avoided the CDI due to the presence of facultative scavenger species which might predate the rodents. Finally, the seedbanks of ericaceous seed species are mostly transient and contain few seeds (Thompson et al., 1997; Welch et al., 2000). Although several studies report more persistent seedbanks (Thompson et al., 1997), if seedlings had originated from the seedbank we would expect a more even distribution within the CDI. Similarly, stronger seed limitation than microsite limitation has been described for recruitment of berry-producing ericaceous species in forest and alpine ecosystems (Manninen & Tolvanen, 2017): seedling recruitment into favorable microsites such as disturbances is

TABLE 2 The set of 14 *a priori* candidate models ranked according to decreasing AICc

Model	Model terms	df	AICc	Δ AICc	w_i
2	<i>CadDen</i>	2	51.708	0	0.308
12	<i>Soil</i> × <i>CadDen</i>	4	52.363	0.655	0.222
10	<i>Soil</i> + <i>CadDen</i>	3	52.923	1.215	0.168
2	<i>CadDen</i> + <i>CadDist</i>	3	52.927	1.219	0.168
13	<i>Soil</i> + <i>CadDen</i> + <i>CadDist</i>	4	54.566	2.858	0.074
3	<i>CadDist</i>	2	57.454	5.746	0.017
11	<i>Plant</i> + <i>CadDist</i>	3	57.826	6.118	0.014
5	<i>CadDist</i> + <i>Cadaver</i>	3	58.122	6.414	0.012
1	<i>Cadaver</i>	2	59.810	8.101	0.005
6	<i>Plant</i>	2	60.468	8.760	0.004
8	<i>Soil</i>	2	60.789	9.081	0.003
9	<i>Bryophyte</i> + <i>Plant</i> + <i>Lichen</i>	4	61.677	9.969	0.002
7	<i>Bryophyte</i>	2	63.232	11.524	0.001
14	<i>Null</i>	1	65.046	13.338	0.000

Note: Note that model 12, 10 and 2 (Δ AICc < 2) are not considered to be competing models as they are simply more complex versions of the top-ranked model.

Abbreviations: AICc, Akaike Information Criterion corrected for small sample size; df, degrees of freedom; w_i , model weight; Δ AICc, AICc difference values compared to the model with the lowest AICc value.

significantly enhanced by seed addition (e.g. Eriksson & Fröberg, 1996; Hautala et al., 2001; Manninen & Tolvanen, 2017; Welch et al., 2000). For example, in Hautala et al.'s (2001) unsown plots they recorded zero to four seeds m^{-2} depending on disturbance regimes, whereas sown plots had seedling densities ranging from 1.2 to 56.4 seedlings m^{-2} . Our survey plot with the most seedlings had ten seedlings m^{-2} .

For those berry-producing ericaceous species which present a reproductive paradox, the apparent conundrum lies in the absence of a seedbank. Such species are dependent on elevated seed rain at suitable microsites for germination and subsequent establishment (Eriksson & Fröberg, 1996; Manninen & Tolvanen, 2017). We show that vertebrate facultative scavengers may be a critical component of the regeneration niche of ericaceous species: plants may rely upon directed endozoochorous seed rain arriving at suitable microsites, in this case a relatively short-lived RWO provided by a CDI (Figure 1).

More recent studies on several *Vaccinium* and *E. nigrum* populations have documented higher genetic diversity than expected for clonal populations (Albert et al., 2004, 2005; Bienau et al., 2016; Persson & Gustavsson, 2001). This indicates that they establish from seed to a greater extent than previously thought including from outside their immediate genetic neighborhood (Jordano, 2017). For long-lived clonal plant populations even occasional seedling recruitment can be sufficient for maintaining genetic diversity in (De Witte et al., 2012; Watkinson & Powell, 1993).

The large home ranges of medium- to large-sized scavenger species, such as those observed within our study site, combined with their long gut retention times (Cunze et al., 2013), suggests the potential for long-distance dispersal *sensu stricto*, that is dispersal outside the range and genetic neighborhood of the parental population (Jordano, 2017). Despite their apparent rarity, such

“true” long distance dispersal events are known to play a major role in large-scale dynamics of plant populations as they promote gene flow between populations, colonization of unoccupied habitat and range expansion (Cain et al., 2000; Nathan et al., 2008). Even medium-sized scavengers considerably outperform co-occurring smaller seed dispersal vectors such as small and medium-sized passerine birds in providing a long-distance seed dispersal service for fruit-producing species (Jordano, 2017; Jordano et al., 2007). The combination of scavengers' potential effectiveness as long-distance dispersal vectors and the directed nature of the seed dispersal shadow (Steyaert et al., 2018) indicate their possible efficacy and importance as dispersers for plant species exploiting ephemeral RWOs.

We took advantage of a large mass die-off event in a relatively undisturbed mountain area to demonstrate that directed dispersal toward CDIs facilitates seedling establishment. Cadavers at the study site persisted over several years and continued to attract scavenging omnivores during the ericaceous berry season (Frank et al., 2020)—a crucial point for this mechanism to work. Although mass die-off events have been consistently reported over the past decades (Fey et al., 2015), large numbers of terrestrial herbivores also die from natural causes (e.g., predation, starvation, or disease) leaving single cadavers in the landscape (Barton et al., 2019; Moleón et al., 2019). Such single cadavers may be regularly provided throughout the year by for example large predators that only partly consume prey (Wilmers et al., 2003). However, at northern latitudes, maximum cadaver availability is in late winter when ungulate mortality is high due to starvation and thermal stress, creating temporally aggregated pulses of available carrion (Pereira et al., 2014). Factors such as the spatial and temporal distribution of cadavers, cadaver size, and environmental variables affect both the development and

size of CDIs (Towne, 2000). Moreover, the assembly of scavenger guilds (i.e., disperser species) utilizing cadavers (Selva et al., 2005; Turner et al., 2017) and the interactions between a cadaver, scavengers and surrounding habitat may have a considerable impact on whether CDIs, directed dispersal, or seedlings occur. For example, a cadaver deposited in winter might be either completely consumed or scattered over the landscape by scavengers within a relatively short time (Towne, 2000; Turner et al., 2017) and thus not persist until berry season or form a CDI. In alpine and arctic regions, however, cadavers may persist longer within the landscape, as we observed at Vesle Saure where cadaver material was still in place in 2019. Hence, it remains unclear how this mechanism works with single carcass events, across different ecosystems, and with different scavenger guilds.

Anthropogenic pressures on ecosystems continue to rise (Dirzo et al., 2014) and humans are likely disrupting key ecosystem functions, for example those provided by vertebrate scavengers (Mateo-Tomás et al., 2017; Sebastián-González et al., 2019, 2020). This could be particularly detrimental to long-term plant population resilience when, as we show, some plant species may benefit from the endozoochorous dispersal service provided by facultative scavengers to facilitate recruitment and so completion of their life cycle (Traveset et al., 2012). Our study area had a relatively intact scavenger guild, but anthropogenic pressures are significantly affecting scavenger richness and abundance on a global scale (Sebastián-González et al., 2019, 2020). Humans can affect scavenger species directly through persecution (Swenson et al., 1995) but also indirectly through cadaver removal (Margalida et al., 2010), habitat fragmentation and destruction (Sebastián-González et al., 2019). Furthermore, a reduction in cadaver availability would also decrease the frequency of CDIs, that is, reduce microsite availability. Seed dispersal shadows and long-distance dispersal events strongly depend on the relative contributions of different scavenging disperser species (González-Varo et al., 2013). The loss of a vector providing effective directed dispersal could decrease genetic diversity at the population level, potentially resulting in a marked reduction in population fitness (Wenny, 2001).

Our study provides a novel understanding of sexual reproduction in species with cryptic generative reproduction and to our knowledge, we are the first to observe this mechanism in action. This is proof-of-concept and demonstrates how directed dispersal toward CDIs mediates a higher probability of seedling establishment, giving support that directed seed dispersal by facultative scavengers toward CDIs provides a pathway to successful sexual reproduction in berry-producing ericaceous shrubs. However, the relative importance of this dispersal mechanism to population persistence in the long term and how humans influence it is not clear and may only be elucidated through studies on the genetic structure of populations of these plants.

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CONFLICT OF INTEREST

The authors have no competing interests.

AUTHOR CONTRIBUTIONS

Mie Prik Arnberg: Formal analysis (lead); investigation (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Shane C. Frank:** Conceptualization (equal); formal analysis (supporting); investigation (equal); methodology (equal); writing – review and editing (equal). **Rakel Blaalid:** Investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Marie Louise Davey:** Investigation (equal); methodology (equal); writing – review and editing (equal). **Amy Elizabeth Eycott:** Writing – original draft (supporting); writing – review and editing (equal). **Sam M. J. G. Steyaert:** Conceptualization (equal); investigation (equal); methodology (equal); visualization (supporting); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

The data used in this study is deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fn2z34ttz>.

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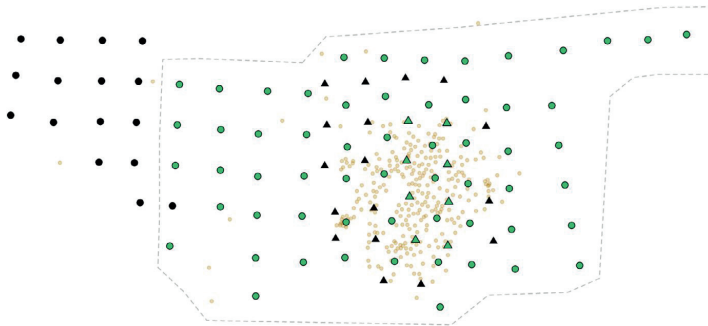
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APPENDIX 1



Graphical representation of the sampling grid setup at the study site. Dots represent the 75 survey plots (0.5×0.5 m) in the semiregular 10×10 m main grid. Triangles are the supplementary 25 survey plots superimposed in a 10×10 m grid over the area of highest cadaver density. Both grids were established shortly after the mortality event in October 2016. The grey dotted line indicates the 2019 study area, in which green colored survey plots were sampled, while black survey plots were not due to missing plot markers or logistical constraints. Brown dots are cadaver positions ($n = 323$).

APPENDIX 2

Model selection results from single predictor models (GLMs) relating seedling establishment (yes/no) to the different spatial scales for estimating cadaver kernel density (search radii 1–10 m in 1 m increments). The search radius for estimating the cadaver kernel density follows the “Cadaver density” model term in parentheses. AICc, Akaike Information Criterion corrected for small sample size; Δ AICc, AICc difference values compared to the model with the lowest AICc value; w_i , model weight.

Model term	df	AICc	Δ AICc	w_i
Cadaver density (2 m)	2	51.708	0	0.370
Cadaver density (3 m)	2	52.649	0.941	0.231
Cadaver density (4 m)	2	54.263	2.554	0.103
Cadaver density (5 m)	2	55.013	3.304	0.071
Cadaver density (6 m)	2	55.578	3.870	0.053
Cadaver density (7 m)	2	55.826	4.117	0.047
Cadaver density (8 m)	2	55.992	4.284	0.043
Cadaver density (9 m)	2	56.199	4.491	0.039
Cadaver density (10 m)	2	56.382	4.673	0.036
Cadaver density (1 m)	2	60.290	8.581	0.005

Paper III

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Perfect poopers; passerine birds facilitate sexual reproduction in clonal keystone plants of the boreal forest through directed endozoochory towards dead wood

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ABSTRACT

Berry-producing *Vaccinium* shrubs are keystone species in boreal forest ecosystems and their berries provide an essential food source for many vertebrates. In Fennoscandia, both the abundance and cover of *Vaccinium* have decreased in forests, with intensive forestry practice as a main driver. *Vaccinium* seedling recruitment is constricted to recruitment windows of opportunity and appears to be infrequent, mainly due to seed dispersal limitation. Passerine birds are key players in seed dispersal, which can be directed towards perching points such as coarse woody debris.

In this study, we investigated the potential for directed endozoochory by passerine birds towards cut stumps and if such stumps were viable recruitment windows for *Vaccinium* species, in an intensively managed boreal forest landscape of central Norway. We surveyed stump and paired forest floor microsites for passerine scat (i.e. potential seed rain) and *Vaccinium* seedlings. We collected passerine scat and conducted germination experiments to assess if they contained viable seed. We tested the microsite effect (i.e. forest floor/stump) on scat deposition and seedling establishment and then used modified ensemble classifiers to identify important environmental factors affecting scat deposition and seedling establishment patterns.

We found that passerine scat was disproportionately deposited on stumps, and that the vast majority of scat contained viable *Vaccinium* seed. Stumps were also suitable recruitment windows for *Vaccinium* species, as a higher probability of seedling establishment occurred at stumps compared with the forest floor. However, scat deposition and seedling establishment at stumps were rather contextual and determined by environmental variables. The probability of scat deposition increased with higher complexity of the vertical forest structure and lower canopy cover, whereas seedling establishment required bryophyte cover and larger stumps, or alternatively smaller stumps with competition-free spaces.

Our results highlight a pathway to successful sexual reproduction for *Vaccinium* species in managed forests: passerine birds direct endozoochorous seed dispersal towards tree stumps, which can offer suitable conditions for seedling establishment. However, the spatiotemporal variability both in forest stand structure and in stump conditions have a strong influence on the success of sexual recruitment via this pathway.

1. Introduction

Sexual recruitment is a key process in plant population dynamics that supports species diversity and richness (Myers and Harms, 2009). The recruitment stage between seed production and seedling establishment is a particular bottleneck for many plant populations, as it is characterized by high mortality (Clark et al., 2007). Recruitment may be

constrained by seed production, dispersal limitation or microsite availability (Clark et al., 2007; Uriarte et al., 2010). This implies that the spatial distribution of recruitment is a result of complex filtering of seed dispersal and post-dispersal factors that affect seed fate at the microsite (Schupp et al., 2010). The main constraints to seedling establishment at microsites are (i) the number of available microsites with suitable biotic and abiotic conditions for germination and seedling establishment

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(microsite limitation), and (ii) few seeds enter or persist in the soil seedbank or reach potential recruitment microsite (dispersal limitation/seed limitation; Eriksson and Ehrlen, 1992; Muller-Landau et al., 2002).

In heterogeneous landscapes, suitable microsites may be spatially unpredictable, and favourable conditions for seedling establishment can be ephemeral (Jelinski and Cheliak, 1992; Riedel et al., 2005). Yet, successful recruitment in long-lived plants is often restricted to such elusive recruitment “windows of opportunity”, such as canopy gaps, uprooted tree mounts, or ungulate carcasses (Eriksson and Fröberg, 1996; Dupuy and Chazdon, 2008; Arnberg et al., 2022). Plants do not actively choose the habitat into which their seeds disperse, although adaptations to dispersal mechanisms may direct them towards specific habitats or microsites (Howe and Smallwood, 1982). Evidence for such environmental coupling exists for frugivorous animals that disperse the seeds of fleshy fruits towards favorable recruitment windows (Wenny, 2001; Cavallero et al., 2012). For example, Wenny and Levey (1998) showed that male three-wattled bellbirds (*Procnias tricarunculata*) disproportionately dropped seeds of the forest tree *Ocotea endresiana* under song perches in canopy gaps far from parent trees. Those canopy gaps favored seedling survival (e.g. less fungal pathogens) and enhanced seedling growth, compared to random sites in the forest. Linking dispersal vectors to microsites can thus increase our understanding of spatial reproduction patterns in plant populations (Nathan and Muller-Landau, 2000; Hampe et al., 2008).

Berry-producing *Vaccinium* species dominate the field layer of the Eurasian boreal forest (Nilsson and Wardle, 2005). Like most long-lived clonal shrubs, seedling recruitment is infrequent (Eriksson and Ehrlen, 1992), despite considerable investment in annual berry production (Kloet and Hill, 1994). Dispersal limitation is part of the reason for their apparent recruitment rarity. Although a high number of seeds are dispersed by a wide guild (Steyaert et al., 2019; García-Rodríguez et al., 2021), few seeds reach the soil seed bank, and if they do, seeds are relatively short-lived and are close to absent in the soil seed bank (Kloet and Hill, 1994; Thompson et al., 1997; Ranwala and Naylor, 2004). At the same time, *Vaccinium* species are also microsite limited, and depend on recruitment windows of opportunity within stands of conspecific adults for successful sexual recruitment (Eriksson and Fröberg, 1996). For *Vaccinium* species, these recruitment windows consist of disturbances that remove barriers to recruitment such as field- and ground-layer vegetation within mature stands of ericaceous shrubs with high moisture and organic soil content (Eriksson and Fröberg, 1996; Graae et al., 2011). Such disturbances could once have been generated by the forest fires which were a frequent occurrence in much of the boreal forest biome but are now suppressed (Rolstad et al., 2017; Granath et al., 2018).

Vaccinium species, most notably bilberry (*Vaccinium myrtillus*), are keystone species and their parts (i.e. berries, leaves, and shoots) are essential food for many invertebrates and vertebrates of the boreal forest (Atlegrim, 1989; Dahlgren et al., 2007; Hertel et al., 2016). Further, they regulate tree seedling survival and subsequently forest succession and composition (Nilsson and Wardle, 2005), and are key components to maintain microbial activity and soil quality within boreal forests (Fanin et al., 2019). In fact, since ericaceous shrubs and their associated ericoid mycorrhizal fungi promotes belowground accumulation of organic matter, they contribute to boreal forest soils role as carbon and nitrogen sinks (Fanin et al., 2022).

Seedling establishment in long-lived clonal shrubs might not be as rare as previously expected as recent studies have revealed establishment via directed endozoochory (i.e. the process in which dispersal vectors deposit seeds disproportionately into favourable microsites). For example, scavengers in alpine ecosystems direct seed dispersal to cadaver decomposition islands, which facilitate seedling establishment of several *Vaccinium* species and *Empetrum nigrum* (Steyaert et al., 2018; Arnberg et al., 2022). In forested areas brown bears (*Ursus arctos*) disperse bilberry seeds towards their daybeds, in which seeds can germinate and establish (Steyaert et al., 2019; García-Rodríguez and

Selva, 2021).

Downed coarse woody debris can be important sites for regeneration for various tree species (e.g. Santiago, 2000; Mori et al., 2004; Bace et al., 2012) and forest herbs (Kirchner et al., 2011; Chmura et al., 2016). The temporal window for seedling establishment on coarse woody debris usually occurs in advanced stages of decomposition. At this time, decaying wood can offer a relatively competitor-free space compared to the forest floor (Kennedy and Quinn, 2001; Mori et al., 2004; Kirchner et al., 2011). It is typically characterized by a high moisture nutrient content although poor in nitrogen (Harmon et al., 1986; Zimmerman et al., 1995). In addition, bryophytes often colonize decaying wood early, and can act as seed traps and nursery substrate for establishing seedlings (Fukasawa and Ando, 2018). Within forest ecosystems, decomposing woody debris has been described as a possible regeneration microsite for *Vaccinium* species (Eriksson and Fröberg, 1996; García-Rodríguez et al., 2021).

Passerine birds or perching birds (order Passeriformes) often use coarse woody debris, especially snags (i.e. standing dead trees) and downed logs for perching, nesting, foraging and singing posts (Short and Horne, 1982; Rost et al., 2010; Robertson, 2012), and can direct seed dispersal towards such sites (McClanahan and Wolfe, 1993). During autumn, *Vaccinium* berries are an important food source for passerines at northern latitudes (Honkavaara et al., 2007; García-Rodríguez et al., 2021), as many switch from a mainly insectivorous diet to high levels of frugivory before the autumn migration (Bairlein, 2002). This implies that passerines, which are effective dispersers of *Vaccinium* seeds (García-Rodríguez et al., 2021), frequently may disperse seeds to decomposing wood and by doing so facilitate seedling establishment.

This environmental coupling between passerines and *Vaccinium* species might not be as straightforward in landscapes which are under increasing anthropogenic pressures. In Fennoscandia, up to 90 % of the boreal forest is managed, mostly for wood production (Burton et al., 2010). Intensive forestry has transformed the Scandinavian forest landscape during the last century, and replaced a rather contiguous, heterogeneous forest structure with younger, even-aged, more dense, and often very small and fragmented forest cohorts of commercially-interesting tree species such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Östlund et al., 1997; Kuuluvainen et al., 2012). Cut stumps are nowadays by far the most common form of coarse woody debris (Dahlberg et al., 2011) and may locally constitute up to 90 % of all woody debris (Rouvinen et al., 2002). Initially, cut stumps are often somewhat taller than the herbaceous layer, and it is well known that passerines often associate with low coarse woody debris in natural forests for example to perch on while foraging for insects (Skutck, 1971; Laven and MacNally, 1998; Hagelin et al., 2015), whereas this remains, to our knowledge, not documented for cut stumps in intensive forestry systems.

We hypothesize that tree stumps function as end-points of directed endozoochory of ericaceous species by passerine birds. Specifically, we ask the following questions; 1) Are bird scat and hence potential seed deposition and seedling establishment more frequent at stumps compared to the forest floor? and 2) Does bird scat contain viable *Vaccinium* seeds? In addition, we analyze and identify which environmental factors (e.g. forest stand characteristics derived from LiDAR data, vegetation cover on stumps, etc.) affect two important components of directed endozoochory, i.e. scat deposition and seedling establishment.

2. Methods

2.1. Study area

Our study took place in a boreal forest ecosystem in Trøndelag county, central Norway (N: 64.042, Lon: 11.899). The landscape is characterized by rolling hills from 50 to 800 m a.s.l., although we did not survey areas above tree line (ca. 500 m a.s.l.). The region has a mild oceanic climate with mean temperatures of 14.9 °C in the warmest

month (July) and -4.0 °C in the coldest month (January), and a mean annual precipitation of about 960 mm distributed relatively even across the year (Norwegian Meteorological Institute).

The majority of this forest is managed for timber production and logged at intervals of 70–120 years, pending soil fertility (Bergseng et al., 2018). Trees are harvested primarily by clear-cut logging, although some retention cutting is applied. The forest is dominated by the conifers Norway spruce and Scots pine, either in monoculture stands or mixed patches interspersed with broadleaf trees such as downy birch (*Betula pubescens*) and grey alder (*Alnus incana*). Logging activity divides the forest into a mosaic of successional stages ranging from newly logged clear-cuts or retention cuts to mature stands with a smaller proportion of old stands, the last mainly within nature reserves. The forest floor is largely dominated by the dwarf shrubs *Vaccinium myrtillus* and *V. vitis-idaea*. Other ericaceous shrubs such as *V. uliginosum* and *Empetrum nigrum* occur in the study area, but not as common as the above-mentioned *Vaccinium* species.

Approximately 80 bird species inhabit the forested area during summer. This avian assemblage includes a large proportion of small to medium-sized passerine species from families such as Fringillidae (true finches), Muscicapidae (Old World flycatchers), Turdidae (thrushes), and Paridae (tits). Larger species such as the black grouse (*Lyrurus tetrix*), Western capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*) occur in the area year-round (Norwegian Species Map Service, 2022). Although diet may vary throughout a season, many species consume berries when ripe or ripening (Bairlein, 2002), and several species found in our study area, including the Eurasian jay (*Garrulus glandarius*), song thrush (*Turdus philomelos*) and field fare (*T. pilaris*) are known to be effective dispersers of ericaceous seeds (García-Rodríguez et al., 2021).

2.2. Scat and seedling surveys

Scat and seedling surveys were carried out on tree stumps and paired random sites in August and September 2021. These months coincide with berry ripening and peak of the ericaceous berry season and therefore the period in which most seeds are dispersed. We restricted our sampling of decomposing woody microsites to decaying stumps from logged trees (hereafter 'stumps') as they: I) are by far the most frequent decomposing woody material in the managed forests, II) present relatively uniform microsites (i.e. surface structure, height) compared to naturally generated stumps created by windfall, for example, and are III) therefore also easier than logs to quantify and survey systematically. We only considered stumps that reached above the surrounding vegetation and that had no mature ericaceous vegetation established on their surface. This ensured that observed seedlings on stumps could only be a product of directed endozoochory and that no seedling establishment could originate from falling berries from mature overhanging *Vaccinium* plants or *Vaccinium* plants already established on the focal stump. In addition, we did not sample stumps where the vegetation succession had advanced to the point that the stump vegetation was visually indistinguishable from the surrounding forest floor vegetation and no longer resembled viable recruitment windows.

We randomly placed 50 belt transects perpendicular to roads within the study area using QGIS version 3.28. Each transect was 2000 m long and 8 m wide (16,000 m²) and the start point was at least 1 km from the starting point of another transect. We only selected transects (43) for sampling if they did not cross major roads, rivers or lakes, consisted of less than 60 % forest, or intersected rural or agricultural areas. Due to time constraints, we sampled 18 transects chosen at random from list of selected transects. We walked the transects along the center line, and a GPS reading was obtained for each stump that we encountered and met the criteria for surveying. We paired each surveyed stump with a forest floor plot. The forest floor plot was located 4 m from the stump, in a line perpendicular to and crossing the transect midline. We estimated the stump surface area by laying a rope at the stump surface contours, and

used the approximate dimensions of the stump surface for the forest floor plot. When the forest plot could not be located on a vegetated forest floor (e.g. rocks, standing trees), we selected a forest floor plot 4 m away from the stump in the opposite direction of the transect midline. When multiple stumps that met the survey criteria were observed at a location, only the first detected stump was surveyed and other stumps within 10 m of the focal stump were not considered for surveying to avoid over-sampling certain stump types, for example in newly logged areas. At both forest-floor and stump microsite plots, we recorded the number of bird droppings and ericaceous seedlings. We collected scats at microsites in individual vials whenever possible (e.g. not when smeared or washed out). We distinguished seedlings from small ramets that originated from clonal propagation by checking if seed leaves were present. Seedlings were determined to species level using characteristic features of the hypocotyl, cotyledons, epicotyl and first leaves (Muller, 1978) when possible, and otherwise determined to genus level.

2.3. Explanatory variables

We recorded and calculated explanatory variables for each stump (stump level variables) and its surroundings (habitat variables). Variables from each group were included either in a subset for assessing factors that potentially affect scat deposition (hereafter 'scat predictors'), a subset to assess factors that might modulate seedling establishment (hereafter 'seedling predictors'), or both (Table 1).

2.3.1. Stump-level variables

We recorded three variables that described stump-characteristics: the diameter of stump surface ('diameter'), the height of a stump from the forest floor ('height'), and decomposition stage ('decomposition'). Decomposition stage was classified according to a four class system after Motta et al. (2006): (1) bark intact, wood hard; (2) bark almost completely intact, wood hard in the outermost part and decay in the innermost part of the stump, texture with large pieces; (3) traces of bark only, decay spread in most of the stump, texture with blocky pieces; (4) bark absent, wood soft and powdery. If the decay stage varied in different parts of the stump, an average was taken (Table 1).

We also recorded five variables for explaining seedling establishment or bird usage at the stump level (Table 1): percentage cover of mosses and liverworts ('bryophytes') which can serve as seed traps and nurseries (Fukasawa, 2018) or act as barriers for seedling emergence (Zamfir, 2000); percent cover of vascular plants ('vascular') and plant litter ('litter') which both could potentially inhibit or facilitate seedling establishment (Xiong and Nilsson, 1999; Fukasawa and Ando, 2018); percent cover of bare decomposing wood for establishing seedlings or birds foraging for insects ('free niches'); and tree crown density ('shade') estimated as the mean of spherical densiometer measurements in four cardinal directions taken from a plot center (Lemmon, 1956).

2.3.2. Habitat variables

We used discrete return light detection and ranging (LiDAR) data to calculate forest stand characteristic and habitat heterogeneity commonly used in bird habitat studies (e.g. Clawges et al., 2008; Bakx et al., 2019; Herniman et al., 2020) around the surveyed stumps. Detailed explanation of the LiDAR metadata, preprocessing, and variable calculation is given in the supplementary materials (Appendix A). We calculated the maximum ('Hmax'), mean ('Hmean') and standard deviation (i.e. horizontal heterogeneity; 'Hsd') of vegetation height within a 50 m radius of each stump in R 4.2.0 (R Core Team, 2022). Within the same radius, we also calculated the foliage height diversity ('FHD') which describes the vertical heterogeneity and structural layering of vegetation (Table 1).

We derived the Euclidian distance from each stump location to the nearest habitat edge (i.e. where forest habitat was discontinued by other nature types like mires or lakes, 'distH') and to the nearest gravel or paved road ('distR') in ArcGIS Pro version 2.8. Distances were obtained

Table 1

Potential explanatory variables measured at 142 stumps in managed forest in Ogdalen, central Norway, with summary statistics. Variables were measured at the stump level or derived from LIDAR or land-use map data within a 50 m radius of the stumps. Values are denoted as mean \pm SD followed by the range in brackets. Predictor inclusion is if the variable was used to model scat deposition, seedling establishment or both. Abbreviations: distH = distance from each stump location to the nearest habitat edge and distR = distance to the nearest gravel or paved road; Hmax = maximum, Hmean = mean and Hsd = standard deviation (i.e., horizontal heterogeneity) of vegetation height and FHD = foliage height diversity (i.e., vertical heterogeneity) calculated from LiDAR data within a 50 m radius of each stump; DomTree = dominant tree type within a 50 m radius of each stump.

Variable	Data type	Value	Predictor inclusion
Diameter	Continuous (cm)	22.99 \pm 9.78	Scat/Seedling
Height	Continuous (cm)	(10, 51)	Scat/Seedling
		37.34 \pm 12.17	
Decomposition Bryophytes	Ordinal (1–4)	(9, 65)	Scat/Seedling
	Continuous (%)	I-IV 33.25 \pm 34.68	
Shade	Continuous (0–96; open-closed)	(0, 100)	Scat/Seedling
		35.57 \pm 34.18	
Vascular	Continuous (%)	(0, 96)	Seedling
		0.57 \pm 1.69	
Litter	Continuous (%)	(0, 10)	Seedling
		11.72 \pm 17.00	
Free niches	Continuous (%)	(0, 95)	Scat/Seedling
		41.95 \pm 37.47	
DistR	Continuous (m)	(0, 100)	Scat
		335.15 \pm 339.90 (5.23, 1836.97)	
DistH	Continuous (m)	(0, 100)	Scat
		131.55 \pm 146.96 (0.00, 545.71)	
Hmax	Continuous (m)	(0, 100)	Scat
		18.41 \pm 4.01 (8.05, 27.47)	
Hmean	Continuous (m)	(0, 100)	Scat
		4.94 \pm 2.92 (0.21, 12.20)	
Hsd	Continuous	(0, 100)	Scat
		3.87 \pm 1.21 (0.78, 6.40)	
FHD	Continuous	(0, 100)	Scat
		1.28 \pm 0.23 (0.49, 1.67)	
DomTree	Nominal	Spruce, pine, conifer mix, broad-leaf	Scat

using the land cover map N50 developed by the Norwegian Mapping Authority. We also assigned dominant tree type ('domTree') of the surrounding forest to each stump from the land cover map SR16 (16 \times 16 m resolution) developed by the Norwegian Institute of Bioeconomy Research (Table 1).

2.4. Germination trial

Scat samples were deposited into individual pots (8 \times 8 cm), on top of peat based commercial potting soil that was sterilized with a microwave treatment (Trevors, 1996). Most scat was deposited into a pot the same day they were collected. If that was not possible, the sample was stored in dark and cool conditions and potted the following day. We inspected collected scat for the presence of *Vaccinium* or *Empetrum* seeds (yes/no) rather than attempting to count seeds, which can be damaged during extraction and the counting process.

Potted seeds were incubated in a growth cabinet under a constant air temperature of 21 °C (\pm 0.5 °C) with alternating 12 h fluorescent light (38 W/m²) and 12 h darkness. The samples were watered regularly (every 2–3 days) so that the soil remained moist. If pots showed signs of

extensive fungi growth, they were watered with a sodium bicarbonate solution to reduce fungal growth. We recorded initial germination in pots and removed seedlings as soon as species identification was possible. When germination ceased, a cold stratification was applied (2 °C for 4 weeks) to break seed dormancy of ungerminated but viable seeds (Baskin et al., 2000). Pots were then placed back in the growth chamber under the previously described conditions and monitored for germination and seedling identification.

We conducted two independent germination trials. The first trial consisted of scat that were collected during surveys at focal stumps. This trial failed due to excessive fungi growth. We therefore initialized a second germination trial in which scat was collected from stumps in our study area, but independent of the original surveys. Both trials followed the same procedure outlined above.

2.5. Data analysis

To assess whether microsite (stump vs. forest floor) affected scat occurrence and seedling establishment, we created a Bayesian analogue to a G-test for 2 \times 2 contingency tables. We coded the abundance of scat and seedlings to binomial response variables (0 = scat/seedlings not present, 1 = present) and assigned flat priors (beta distribution with shape parameters = 1) to both scat and seedling occurrence. The models were built in JAGS (Plummer, 2017) and called through the rjags package (Plummer, 2021) in R version 4.2.0 (R Core Team, 2022). We estimated the posterior probability distributions via three chains in Markov chain Monte Carlo (MCMC) with 10,000 iterations and a burn-in of 2000 iterations. We examined the convergence of the MCMC chains with standard trace plots. If the 95 % highest density credible intervals (HDI) of the mean difference between microsites did not overlap zero, we considered there to be an effect on the parameter of interest. We also report the proportion of times the mean difference was larger than zero through all the iterations as a measure of how strong the signal was.

We used decision trees to explore which stumps would be susceptible for scat deposition (a proxy for seed rain) and which stumps would represent a viable recruitment window for seedling establishment. The possible complexity of our predictor variables' relationship to scat and seedling occurrence made decision trees a good choice for several reasons: 1) a large number of predictors can be included in the model regardless of sample size and collinearity; 2) the technique is non-parametric and can fit non-linear relationships between response and predictors; 3) high-order interactions can be fit; and 4) analysis results can be visualized as a hierarchical tree structure, making it easy to interpret (De'ath and Fabricius, 2000). Despite the apparent advantages, single decision trees can have estimation problems because they can be sensitive to the data which they are applied on. In other words, a slight change in the data might significantly change the structure of a tree (Breiman, 1996). Bootstrap aggregation, also called 'bagging', solves this problem by performing separate decision tree analysis on a high number of bootstrapped datasets and then averaging predictions (Breiman, 1996). Even though the accuracy of bagged trees is often higher than for a single tree (Prasad et al., 2006), visualisation and interpretation of variable interactions are lost. Further, unbalanced data can have profound effects on tree model performance (Zhou et al., 2019; Shin et al., 2021). Both response variables - i.e. scat occurrence and seedling establishment - were imbalanced with prevalence of the negative responses (0.68 and 0.84, respectively). To retain the visual exploration of important predictor variables and mitigate class imbalance, we adopted a modified version of the ensemble classifier technique SMOTEBagging (Wang and Yao, 2009).

We constructed 1000 data subsets each from the scat predictors and seedling predictors in which the minority classes were upsampled to match the majority classes for both response variables. This was done with a Synthetic Minority Over-Sampling Technique (SMOTE) for the scat predictors and a SMOTE-NC (-Nominal Continuous) for the seedling predictors which contained both continuous and nominal explanatory

variables. Both algorithms generate synthetic replicates at random locations along the vector between a minority class instance and its k-nearest neighbors (Chawla et al., 2002). We applied a classification and regression tree (CART; Breiman et al., 1984) model to each of the data subsets relating scat and seedling occurrence to their respective predictor variables (described in Table 1) using the recursive partitioning and regression trees package for R (RPART; Therneau and Atkinson, 2022). Each tree was built with a 10-fold cross-validation and a stopping criterion that each terminal node had to contain minimum 5 % of the data. To reduce overfitting, we pruned the trees back to an optimal size using the complexity parameter corresponding to the lowest cross-validation error. Lastly, we used the SMOTEBagging support (conceptually equivalent to bootstrap support, hereafter 'support') defined as the percentage of times a variable was used for splitting or when a terminal node occurred in hierarchical order over the 1000 trees to construct a visual tree typology. The splitting variable or terminal node with the most support was chosen until all terminal nodes were defined. We imposed splitting values and incident probabilities from an average of 20 representative trees.

We applied a Bayesian model selection procedure using Bayes Factors to evaluate support for potential explanatory variable assemblies identified as important by the ensemble trees when modeling scat occurrence and seedling establishment. We computed Bayes Factors relative to a null model (intercept only) for all restrictions on a full model and allowed for interactions indicated by the CART models using the 'BayesFactor' package (Morey and Rouder, 2021). We considered Bayes Factor values > 3 to indicate support in favor of the alternative model where values between 3 and 10 indicate substantial support; values between 10 and 100 indicate strong support; and values > 100 indicate very strong ('decisive') support (Kass and Raftery, 1995).

3. Results

We searched 288.000 m² of the forest habitat in our study area. Across the transects, we surveyed 142 stumps which met our selection criteria and their paired forest floor microsites (range: 2–19 pairs per

transect).

3.1. Scat and seedling occurrence at stumps and the forest floor

We detected bird scat on 33.8 % of the stumps compared to 1.41 % on the forest floor plots. In total, we registered 76 droppings, where 74 of those were on stumps (range: 0–4 droppings per stump; mean: 0.52 / stump) compared to only 2 in the forest floor plots (range: 0–1; mean: 0.01). Microsite had a clear effect on the probability of scat deposition: scat was more prevalent on stumps compared to the forest floor. Bird scat was 24 times more likely to occur on stumps with a posterior estimate of 0.340 (HDI [0.261, 0.416]) compared to 0.021 on the forest floor ([0.002, 0.044]; Fig. 1). Further, the microsite effect on scat deposition was consistent over the 10,000 MCMC iterations. Through all iterations, the mean difference in probability for scat occurrence between the stumps and forest floor were always higher than zero (proportion = 1).

Seedling establishment occurred on 16.2 % of the surveyed stumps compared to 2.82 % in the paired forest floor plots. In total, we recorded 126 *Vaccinium* seedlings, 121 of which were on stumps (range: 0–24; mean: 0.85) and only 5 of which were in forest-floor plots (range: 0–2; mean: 0.03). *Vaccinium myrtillus* was the most abundant species (n = 47), followed by *V. vitis-idaea* (n = 36) and *V. uliginosum* (n = 2; Fig. 2). Ericaceous seedlings are very slow growing; as a result, 41 seedlings could not be identified beyond genus level (*Vaccinium* spp; Fig. 2).

Although the microsite effect was smaller than for scat deposition, stumps supported increased probability of seedling establishment compared to the forest floor (mean difference: 0.020; HDI [0.006; 0.197]; Fig. 1). The effect of microsite on seedling establishment was consistent over the 10,000 MCMC iterations and mean difference in probability between the stumps and forest floor was always higher than zero (proportion = 1).

3.2. *Vaccinium* seed occurrence and germination in bird scat

We collected 138 bird droppings deposited on stumps from collection

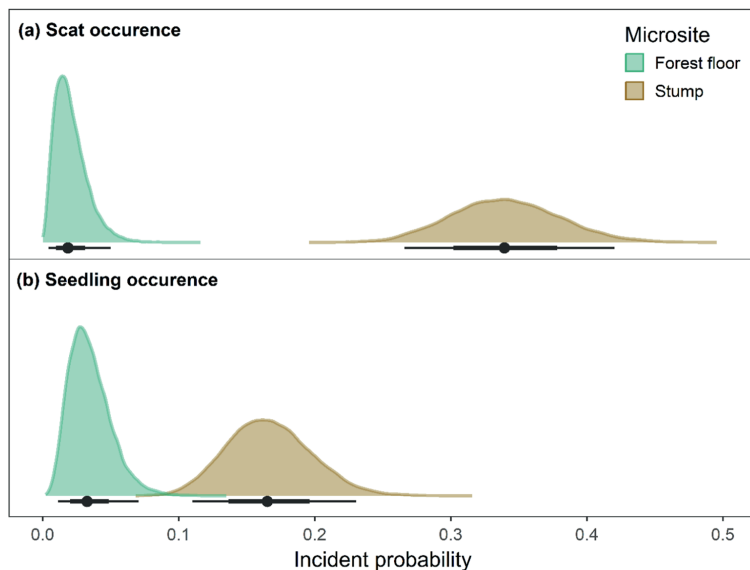


Fig. 1. Probability of (a) bird scat occurrence and (b) ericaceous seedling establishment in the microsites forest floor and decomposing stumps in a forest landscape. Points represent medians of posterior probability distributions, thick lines represent 66 % credible intervals, and thin lines represent 95 % credible intervals. Green (forest floor) and brown (stump) lines and shading represents posterior distributions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

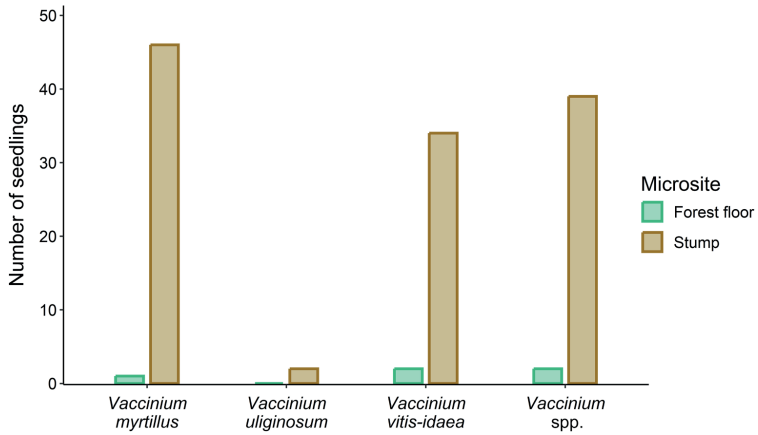


Fig. 2. Number of *Vaccinium* seedlings found at the microsites forest floor and decomposing stump. Due to their juvenile stage, 48 seedlings could not be identified beyond the genus level (*Vaccinium* spp.).

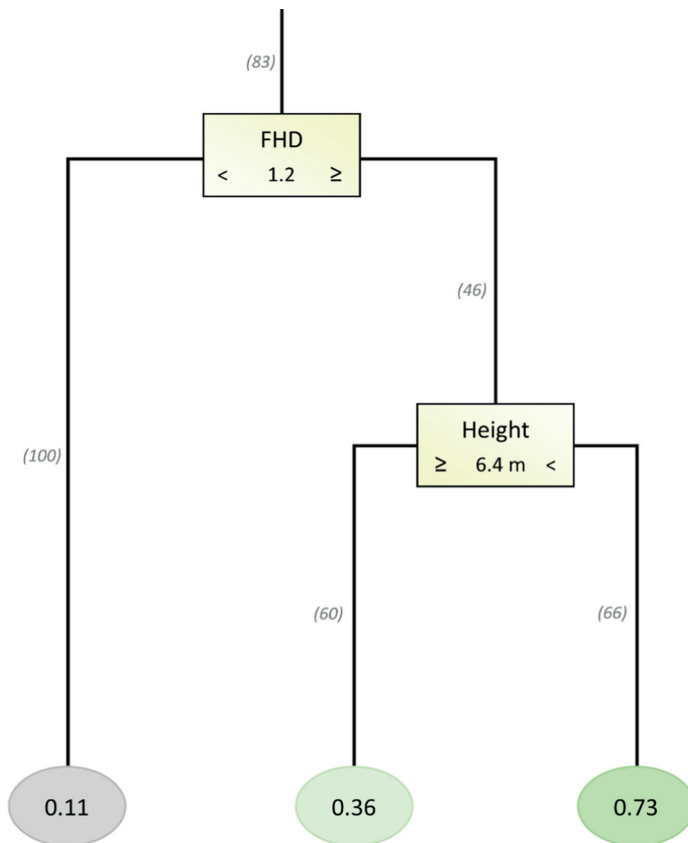


Fig. 3. The most supported tree topology for modeling scat occurrence over 1000 CART trees. Each split is characterized by a splitting criterion in square boxes with comparison operators to indicate which reading direction to proceed. Numbers in terminal nodes depict the probability of scat occurrence under the given predictor variables. Support values (SMOTEBagging support, conceptually equivalent to bootstrap support) for the branching pattern are indicated as grey numbers in parentheses. Abbreviations: FHD = foliage height diversity and Hmean = mean tree height. Both were calculated within a 50 m radius of a stump using LiDAR data.

rounds one and two (71 and 47, respectively). In the first germination trial, 54 (76 %) of the collected droppings contained ericaceous seeds, and of those, germination occurred in 20 (37 %) before the fungal infection, but only one seedling could be identified as *V. myrtillus*. Of the 47 droppings collected for the second germination trial, 43 (91 %) contained ericaceous seeds, of which 35 had germination of *Vaccinium* seeds (81 %). For those 35 droppings, on average 3.1 seed germinated per scat (range: 1 – 17 seeds per scat).

Over the course of the germination trial, 22 seedlings died before species identification was possible, however for 85 seedlings species identification was possible. Most seedlings identified were *V. vitis-idaea* (n = 58), followed by *V. myrtillus* (n = 22), and *V. uliginosum* (n = 5). In nine droppings the germinated seeds were from a single *Vaccinium* species and eight droppings had a combination of two species while no scat had seedlings from all three *Vaccinium* species.

3.3. Variables affecting scat deposition and seedling occurrence at stumps

The tree topology recovered most commonly recovered for modeling scat occurrence on stumps retained the variables Foliage height diversity (FHD) and mean tree height (Hmean) with two splits and three terminal nodes (Fig. 3). Foliage height diversity was assigned as the most important splitting variable (support: 85), where diversity in the vertical forest structure less than 1.2 led to lower probability of scat occurrence (probability = 0.10) as a terminal node (support: 100). FHD values higher than 1.2 was followed by branch split created of mean of canopy height at 6.4 m (support: 46). Higher canopy resulted in lower probability of scat deposition (probability: 0.36; support: 60). Stands that had a combination of higher FHD and canopy height lower than 6.4 m increased the probability of scat deposition to 0.73 (support: 66; Fig. 3). The importance of foliage height diversity on scat deposition was supported by Bayes Factors and included in all three models that had substantial support over the null hypothesis. If the term was dropped, the Bayes Factor fell to support for the null hypothesis. Mean tree height was only important when models also contained foliage height diversity (Table 2).

When modelling the probability of seedling establishment on stumps, we obtained a slightly more complex tree topology. The most supported topology retained the variables bryophyte cover, Diameter and Free niches with three splits and four terminal nodes (Fig. 4). Although several factors contributed to establishment, bryophyte cover was consistently the most important predictor being the first split over all the bagged trees (support: 100). If a stump had less than 3 % bryophyte cover, no seedlings would establish (probability = 0.00). With increasing bryophyte cover, seedlings were most likely to establish on stumps > 21 cm in diameter (probability = 0.74). Smaller stumps (less than 21 cm) could support seedlings if those stumps also offered free niches for establishment (probability = 0.70). The support for the stump diameter and free niches as splitting variables were lower than for bryophytes (43 and 45, respectively). However, this could be a result of collinear variables and Bayes Factors supported the importance of the variables identified by the ensemble CART trees. In total, six models had

substantial support or more over the model representing the null hypothesis (Table 3), and all six included the variables Bryophyte, Free niches and their interaction while stump diameter was included in five models. When these variables were excluded from the models, the Bayes Factor fell to support for the null hypothesis.

4. Discussion

In our study we show how directed endozoochorous seed dispersal by passerine birds towards tree stumps in a managed forest landscape provides a pathway to successful sexual reproduction in berry-producing *Vaccinium* shrubs. Not only was bird scat aggregated on tree stumps, they also consistently contained viable *Vaccinium* seeds. This allowed *Vaccinium* plants to track the window of suitable conditions for seedling establishment. However, the spatio-temporal variability between forest stands and stump conditions were important determinants for this reproduction pathway.

Mutualistic fruit–frugivore seed dispersal interactions are one of the most important ecosystem services provided by birds (Whelan et al., 2008). Within second growth forest and regenerating landscapes, perching birds are known to be key players in seed dispersal directed towards perching points (Wunderle, 1997; Holl, 1998; Wenny and Levey, 1998). Surprisingly, despite stumps being recognized as the largest coarse woody debris component in intensively managed forests (Rouvinen et al., 2002) very little is known about their potential as perches or as recipients of endozoochorous seed dispersal. To our knowledge, we are the first to link seed dispersing perching behavior to decomposing stumps from intensive forest management. We found that stumps were 24 times more likely to receive bird scat compared to the forest floor, suggesting that passerine birds actively perch on such stumps, regularly defecate on stumps, and by doing so also facilitate directed endozoochory towards such sites. Forest floor microsites had slightly less bird droppings than seedlings, whereas the opposite pattern held on stumps. This apparent difference could have resulted from recruitment when berries drop from mature plants and seeds deposited at random by defecating birds or because scat on the forest floor has lower detectability.

Generally, a perch becomes attractive to avian seed dispersers when it is taller than surrounding herbaceous vegetation (McDonnell, 1986). However, not all stumps had the same probability of being used by the passerine disperser guild and seed deposition was regulated by several forest structure variables. We found that the most important variable for predicting scat/seed deposition on stumps was complexity of the vertical forest structure, such as foliage height diversity. Stumps in more complex forest stands were noticeably more likely to have scat compared to stumps in low complexity stands, such as newly harvested or plantation stands. Stumps in complex stands with lower average canopy heights further increased the probability of seed deposition. Frugivore assembly and habitat use, and associated seed deposition can be strongly influenced by changes in local habitat structure (Schupp et al., 2010; Albrecht et al., 2012). Habitats with higher bird densities generally have higher seed deposition (Garcia et al., 2010). Foliage height diversity is an important driver of bird abundance and richness (Baril et al., 2011; Sam et al., 2019), because structurally complex forests provide a greater variety of microhabitats that offer diverse roosting, foraging and nesting opportunities (MacArthur and MacArthur, 1961; Garcia et al., 2010). Also, fruit removal is often resource-driven (Albrecht et al., 2012). Stands of Norway spruce in our study area have low complexity and low berry production, and are therefore probably not the most attractive habitats for frugivorous birds. Intensively managed forests in Scandinavia have a characteristic vegetation structure, consisting of an even-aged tree layer and an understory of woody ericaceous shrubs (Östlund et al., 1997; Nilsson and Wardle, 2005). They have little or no midstory vegetation once they have passed the initial regeneration phase and there is little foliage or possible perching branches beneath immediate tree crowns. In areas where the average tree height was

Table 2

Variable inclusion and Bayes Factor values of models relating scat occurrence on decomposing stumps to those predictor variables identified as important by the modified ensemble trees. Models with BF values > 3 have substantial support compared to the null model (intercept only). Abbreviations: FHD = foliage height diversity and Hmean = mean tree height. Both were calculated from LiDAR data within a 50 m radius of each stump.

Model ID	FHD	Hmean	Hmean:FHD	BF
1	x			5.692
2	x	x		4.419
3	x	x	x	3.947
4		x		0.256

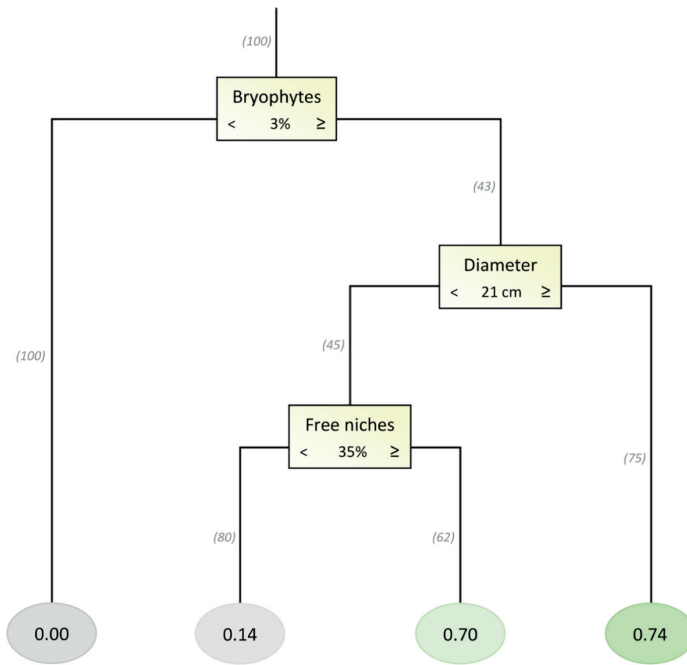


Fig. 4. The most supported tree topology for modeling seedling occurrence over 1000 CART trees. Each split is characterized by a splitting criterion in square boxes with comparison operators to indicate which in which reading direction to proceed. Numbers in terminal nodes depict the probability of seedling occurrence under the given predictor variables. Support values (SMOTEBagging support, conceptually equivalent to bootstrap support) for the branching pattern are indicated as grey numbers in parentheses.

Table 3

Variable inclusion and Bayes Factor values of the top-ranked models relating seedling establishment on decomposing stumps to those predictor variables identified as important by the modified ensemble trees. Models with BF values > 3 have substantial support compared to the null model (intercept only). Abbreviations: dia = stump diameter, bryo = percentage cover of bryophytes, free niches = percentage cover of bare decomposing wood.

Model ID	Dia	Bryo	Free niches	Bryo: niches	Bryo: dia	Free niches: dia	Bryo: niches: dia	BF
1	x	x	x	x				78.700
2		x	x	x				70.142
3	x	x	x	x	x			64.381
4	x	x	x	x		x		38.165
5	x	x	x	x	x	x		23.587
6	x	x	x	x	x	x		8.904
7	x	x					x	0.882
8	x							0.808
9		x						0.732
10	x	x			x			0.674
11	x		x					0.315
12	x	x	x					0.305
13	x	x	x		x			0.283
14			x					0.255
15		x	x					0.227
16	x	x				x		0.156
17	x		x			x		0.144
18	x	x	x		x	x		0.117

under 6 m, passerines might choose stumps as song perches as there is little foliage density to obstruct song transmission and few alternative song post before the tree crowns. In summary, it is likely that the heterogeneity increases bird abundance while the canopy height affects bird perching behavior, increasing their use of stumps.

Decomposing wood is initially a seed-free substrate and species using such microsites to attain sexual reproduction are dependent on dispersal

mechanisms to get there. The potential for seedling establishment has generally been focused on species with anemochores dispersal syndrome (Motta et al., 2006; Bace et al., 2011; Fukasawa, 2018) although zoochorous plants often are associated with a decaying wood substrate (Checko et al., 2015; Chmura et al., 2016). Stumps within our study not only received disproportionate seed rain per unit area through directed endozoochory compared to the forest floor, they also appeared to be

suitable recruitment windows for *Vaccinium* species. The number of stumps in our study site that supported seedling establishment might have been higher as we excluded those with overhanging or established ericaceous vegetation. Birds might perch on excluded stumps as much as our surveyed stumps and so provide seed dispersal towards those.

Although it has recently been argued that recruitment within conspecific adults might be a common feature in *Vaccinium* (García-Rodríguez and Selva, 2021), our results indicate that seedling establishment was rather contextual. Seedling establishment on the forest floor was near absent and not all stumps supported seedlings. Seedling establishment required bryophyte cover and larger stumps, or alternatively smaller stumps with competition-free spaces. In contrast to expectations, decomposition stage was not an important environmental variable for ericaceous seedling establishment although being described as important to many other species germinating on decomposing wood (e.g., Mori et al., 2004; Kirchner et al., 2011; Fukasawa, 2012). In our study, seedlings occurred indiscriminately in early to late decomposition stages (stage 2–5). Several non-exclusive processes possibly contribute to this. In general, a stump microsite is available for seedling establishment earlier than logs (Bace et al., 2011) as stumps decompose more rapidly than logs because they are rooted in the soil, allowing nutrients to be transported from the soil via fungal mycelia (Zimmerman et al. 1995). For slow growing species, such as *Vaccinium*, seedlings may establish in early decomposition stages and follow the gradual progressive decomposition of wood (Zielonka, 2006). Bryophytes colonize decaying wood early (Zielonka and Piatek, 2004) and may therefore be a better predictor of seedling establishment. Lastly, seedlings often emerged from small depressions in the stump surface. Such depression could be further in decomposition stage than the overall stump and therefore not reflected in the results. Nevertheless, it seems that passerine birds allow dispersing *Vaccinium* seeds to locate spatiotemporal availability and suitability of decomposing stumps.

An important and unanswered question is whether young seedlings persist to adult individuals and contribute to the population, particularly given the low area of stumps compared with the surrounding forest floor. We did find seedlings both in forest floor and stump microsites but speculate that seedlings on tree stumps are more likely to survive to adulthood. Seedling growth is very slow for the three *Vaccinium* species in our study (Jacquemart, 1996; Ritchie, 1955, 1956); *Vaccinium myrtillus* does not develop rhizomes until at least the third year of life (Flower-Ellis, 1971) and branching is observed around 4 years (Eriksson and Fröberg 1996). Thus, young seedlings cannot extend laterally or vertically to escape competition. Therefore a seedling's expected life span in mature vegetation is usually short: each of the six seedlings which Eriksson and Fröberg (1996) observed germinating in mature vegetation died shortly after emergence. In contrast, seedlings they observed on decaying woody substrates grew much faster and were significantly bigger than seedlings of the same age on non-woody disturbances (Eriksson and Fröberg 1996). This may be due to mycorrhizal fungi, which are often associated with decomposing wood (Fukasawa, 2021 and references therein). Ericaceous species benefits strongly from their mycorrhizal partnerships (Mallik, 2003) which have been demonstrated to be particularly efficient in extracting nutrients from recalcitrant compounds of plant cell walls (Perotto et al., 2018). The reduced competition on stumps combined with the efficiency of ericoid mycorrhizal assimilation of nutrients from deadwood likely increase long-term persistence and survival into adulthood for ericaceous shrub seedlings. However, the true extent of seedling survival, growth and assimilation to adult population may only truly be elucidated through long-term or genetic studies.

Several recent studies have found that seedling establishment of berry producing ericaceous plants is closely linked with non-exclusive pathways of directed endozoochory in intact ecosystems (García-Rodríguez and Selva, 2021; Arnberg et al., 2022). *Vaccinium* populations have shown higher genetic diversity than expected for clonal populations (Persson and Gustavsson, 2001; Albert et al., 2004; Albert et al.,

2005) indicating they might establish from seed to a greater extent than previously thought (Jordano, 2017). Here we have shown that at least one such a pathway is functional in a managed forest landscape. Passerines can be more effective seed dispersers compared to mesopredators and brown bears (García-Rodríguez et al., 2021). That is, their contribution to the recruitment likelihood of a given plant species is higher (Schupp et al., 2010; Schupp et al., 2017). However, spatiotemporal contribution of diverse frugivory guilds to seed dispersal and subsequently seed dispersal shadows enhances plant recruitment (García and Martínez, 2012; Schupp et al., 2017). For example, an intact disperser guild provides complementarity dispersal services that ensures seed deposition at different microsites throughout the fruiting season for *Vaccinium myrtillus* (García-Rodríguez et al., 2021).

Intensive forest management has severe consequences for disperser species and microsite frequencies within forest stands (Paillet et al., 2010; Chaudhary et al., 2016), and can reduce seedling establishment and early survival of fleshy-fruited plants (Rehling et al., 2022). Consequently, it is highly likely that forestry practices have affected sexual reproduction of *Vaccinium* species. Small birds usually perform complementary seed dispersal and are drivers of population dynamics and genetic flow at a local scale (Spiegel and Nathan, 2007; Jordano, 2017). In managed forests the diversity of avian dispersers is lower compared to intact forests (Schieck and Song, 2006; Söderström, 2009) and functional complementary seed dispersal is reduced as the remaining species deposits seeds in fewer and overlapping microsites (Rehling et al., 2022). The loss of a vector providing effective directed dispersal or an impoverished set of dispersal vectors could decrease genetic diversity at the population level, potentially resulting in a marked reduction in population fitness (Wenny, 2001; Voigt et al., 2009). The microsite of seed deposition is equally important to successful sexual reproduction (Jordano, 2017). Logging activities reduce the diversity and abundance of seed deposition sites (Rehling et al., 2022) and although stumps are a direct consequence of intensive forest management, logging severely reduces the amount of dead wood compared to natural forests (Siitonen, 2001). Our suggested recruitment pathway might be a remnant of a once much larger complimentary plant-frugivore network with diverse species interactions. However, the impact of intensive forest management on the genetic structure of Scandinavian *Vaccinium* species and the population level implications for these important keystone species in boreal ecosystems is for now unknown. Recently, removal of cut stumps has been suggested to control invasive pathogens in forest management (Roberts et al., 2020), a practice that seems particularly detrimental to this recruitment pathway.

5. Conclusion

Intensive forestry practices has reduced both abundance and cover of berry-producing shrubs in Fennoscandian forests (Hedwall et al., 2013; Hedwall et al., 2019) and likely disrupted plant-frugivore networks. Our study demonstrates that directed endozoochorous seed dispersal by passerine birds towards tree stumps in a managed forest landscape provides an important pathway to successful sexual reproduction in berry-producing of *Vaccinium* shrubs. The effectiveness of the pathway is contingent on seed deposition patterns modulated by forest structure and the presence of stumps, which we have shown present an important window of opportunity for *Vaccinium* recruitment. Given important role of ericaceous shrubs to ecosystem functioning, elucidating and preserving recruitment pathways likely plays an important role in long-term persistence and population health of ericaceous keystone species.

CRedit authorship contribution statement

Mie P. Arnberg: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Michael A. Patten:** Formal analysis, Visualization, Writing –

review & editing. **Kari Klanderud**: Writing – review & editing. **Camela Haddad**: Conceptualization, Methodology, Writing – review & editing. **Oddbjørn Larsen**: Investigation, Writing – review & editing. **Sam M.J. G. Steyaert**: Conceptualization, Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

The data used are available at: <https://doi.org/10.18710/D99INQ>.

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Author contributions

Mie Prik Arnberg: Conceptualization (equal); methodology (equal); investigation (lead); Formal analysis (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). Michel A. Patten: Formal analysis (supporting); visualization (supporting); writing – review and editing (equal). Kari Klanderud: Writing – review and editing (equal). Camela Haddad: Conceptualization (equal); methodology (equal); writing – review and editing (equal). Oddbjørn Larsen: Investigation (supporting); writing – review and editing (equal). Sam M. J. G. Steyaert: Conceptualization (equal); methodology (equal); investigation (supporting); writing – review and editing (equal).

Data availability

The data used are available at: <https://doi.org/10.18710/D99INQ>

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120842>.

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Berries are not just a treat for humans – they are also a vital resource for many animals. From small insects to large bears, creatures in temperate, boreal, and alpine habitats across the northern hemisphere rely on the nutritious bounty provided by berry-producing plants in the heather family. In return, animals help plants spread by moving and depositing seeds through their digestive systems. However, scientists have long been puzzled by the ‘reproductive paradox’ of the heather species bilberry, lingonberry, bog bilberry and crowberry. These species produce countless berries containing viable seeds, yet rarely seem to reproduce through seeds themselves. In this thesis, we show that seedling establishment of berry-producing species is actually relatively common when the behavior of animals is considered and that at least two pathways to sexual reproduction exist. By opportunistically consuming berries and carrion, scavenging animals provide seed dispersal directed towards carcasses, which during decomposition creates viable sites for seedling recruitment. Meanwhile, passerine birds direct seed dispersal towards perching points on tree stumps, another form of decomposing microsite that is a viable location for seedling establishment for berry-producing heather plants. Our findings add to the growing body of evidence that highlights the vital interdependence between animals and plants.