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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ARTICLE INFO

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 disproportionally 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 Fröborg, 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 Fröborg, 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 Fröborg, 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 supressed (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 disproportionally 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 course 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 Fröborg, 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 abovementioned *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) therefor 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 m^2) 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 withing 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 Ogndalen, 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 ± 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 Hds = 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 ± 9.78 (10, 51)	Scat/Seedling
Height	Continuous (cm)	37.34 ± 12.17 (9, 65)	Scat/Seedling
Decomposition	Ordinal (1–4)	I-IV	Scat/Seedling
Bryophytes	Continuous (%)	33.25 ± 34.68 (0, 100)	Seedling
Shade	Continuous (0–96; open-closed)	35.57 ± 34.18 (0, 96)	Scat/Seedling
Vascular	Continuous (%)	0.57 ± 1.69 (0, 10)	Seedling
Litter	Continuous (%)	11.72 ± 17.00 (0, 95)	Seedling
Free niches	Continuous (%)	41.95 ± 37.47 (0, 100)	Scat/Seedling
DistR	Continuous (m)	335.15 ± 339.90 (5.23, 1836.97)	Scat
DistH	Continuous (m)	131.55 ± 146.96 (0.00, 545.71)	Scat
Hmax	Continuous (m)	18.41 ± 4.01 (8.05, 27.47)	Scat
Hmean	Continuous (m)	4.94 ± 2.92 (0.21, 12.20)	Scat
Hsd	Continuous	3.87 ± 1.21 (0.78, 6.40)	Scat
FHD	Continuous	1.28 ± 0.23 (0.49, 1.67)	Scat
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 × 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 × 8 cm), on top of peat based commercial potting soil that was sterilized with a micro-wave 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 (±0.5 °C) with alternating 12 h fluorescent light (38 W/m^2) 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 × 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 m^2 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 gemination in bird scat

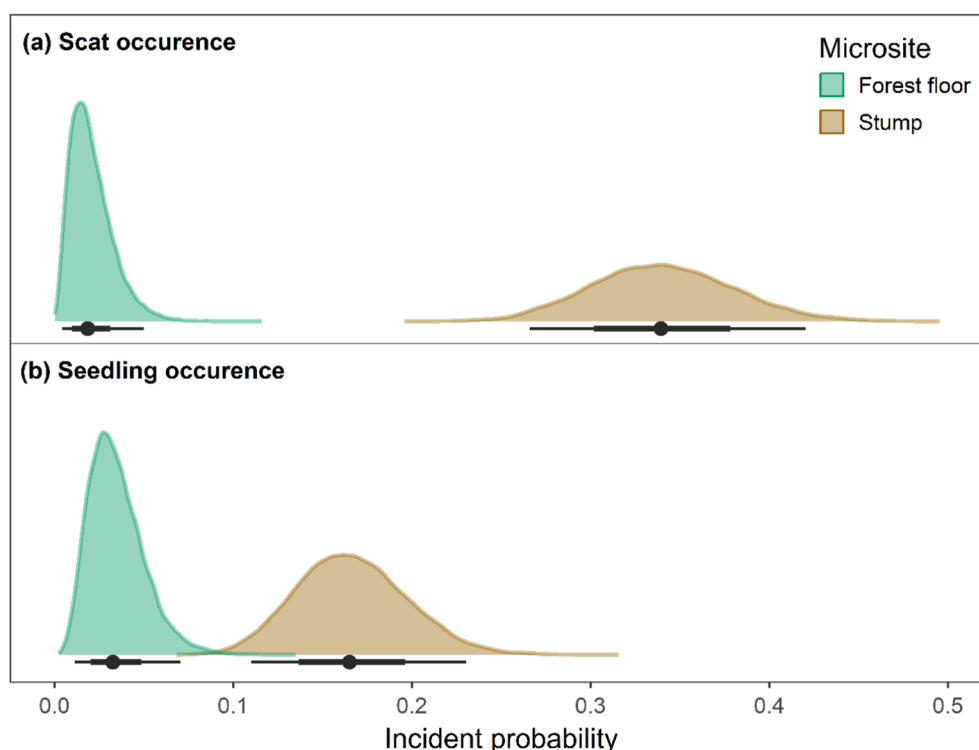We collected 138 bird droppings deposited on stumps from collection

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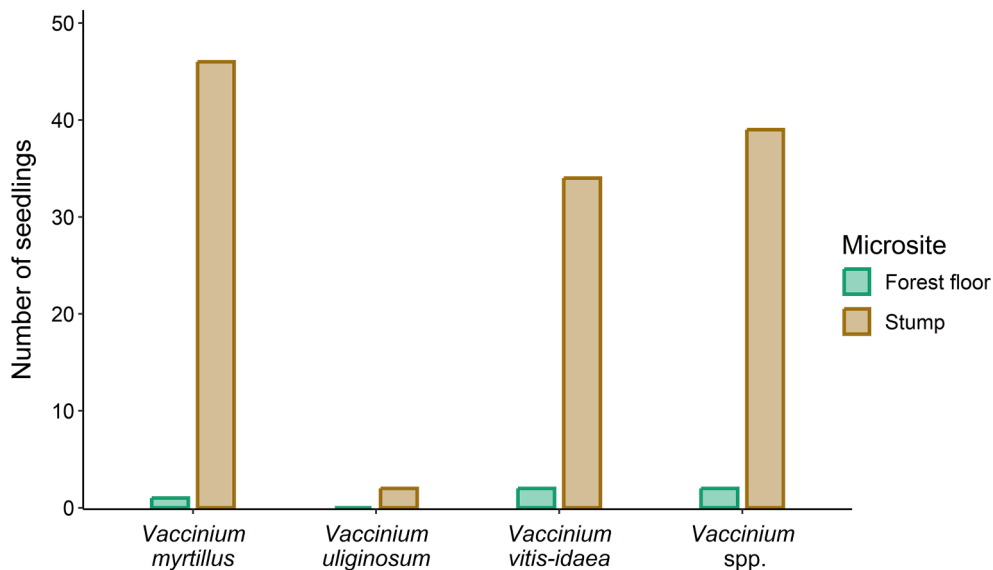
Fig. 2. Number of *Vaccinium* seedlings found at the microsites forest floor and decomposing stump. Due to their juvenile stage, 48 seedlings could not be identified beyond the genus level (*Vaccinium* spp.).
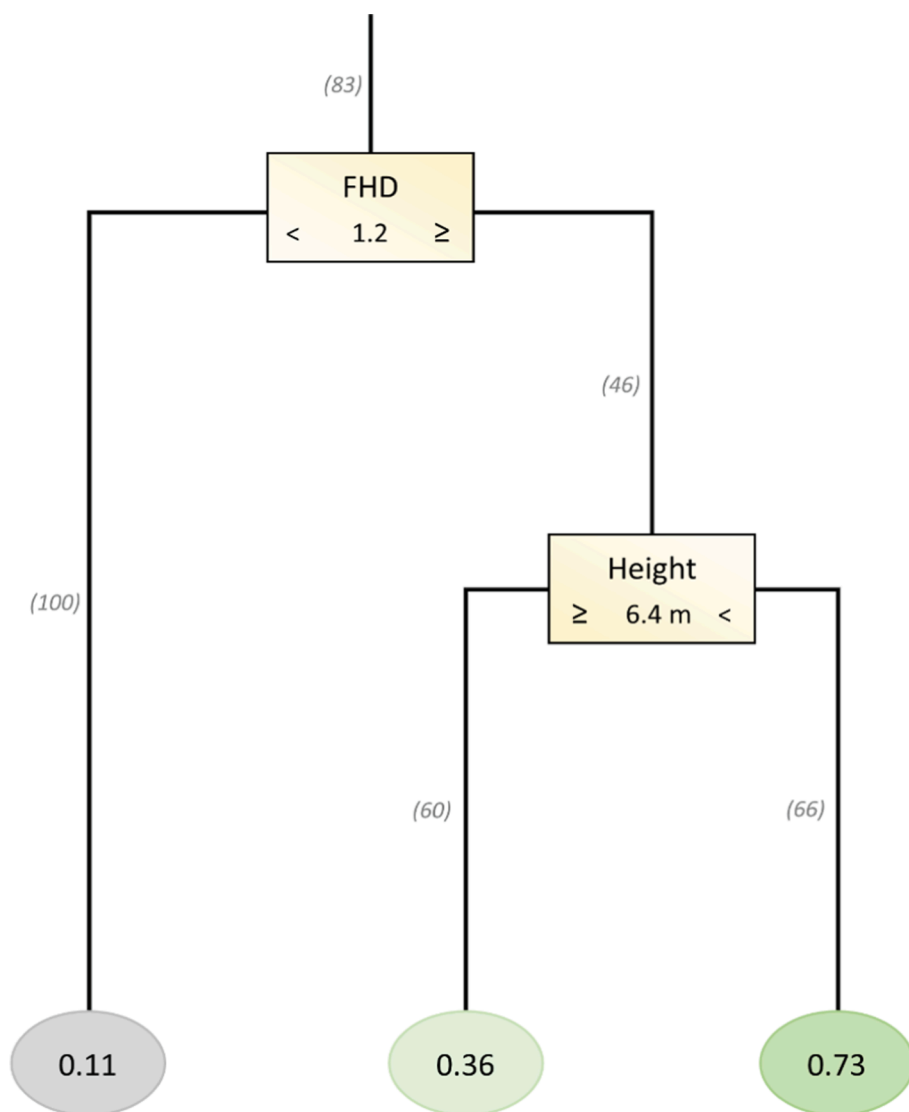

Fig. 3. The most supported tree topology for modelling scat occurrence over 1000 CART trees. Each split is characterized by a splitting criterion in square boxes with comparison operators to indicate which reading direction to proceed. Numbers in terminal nodes depict the probability of scat occurrence 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 calculates 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 modelling 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

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

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 (Ostlund 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
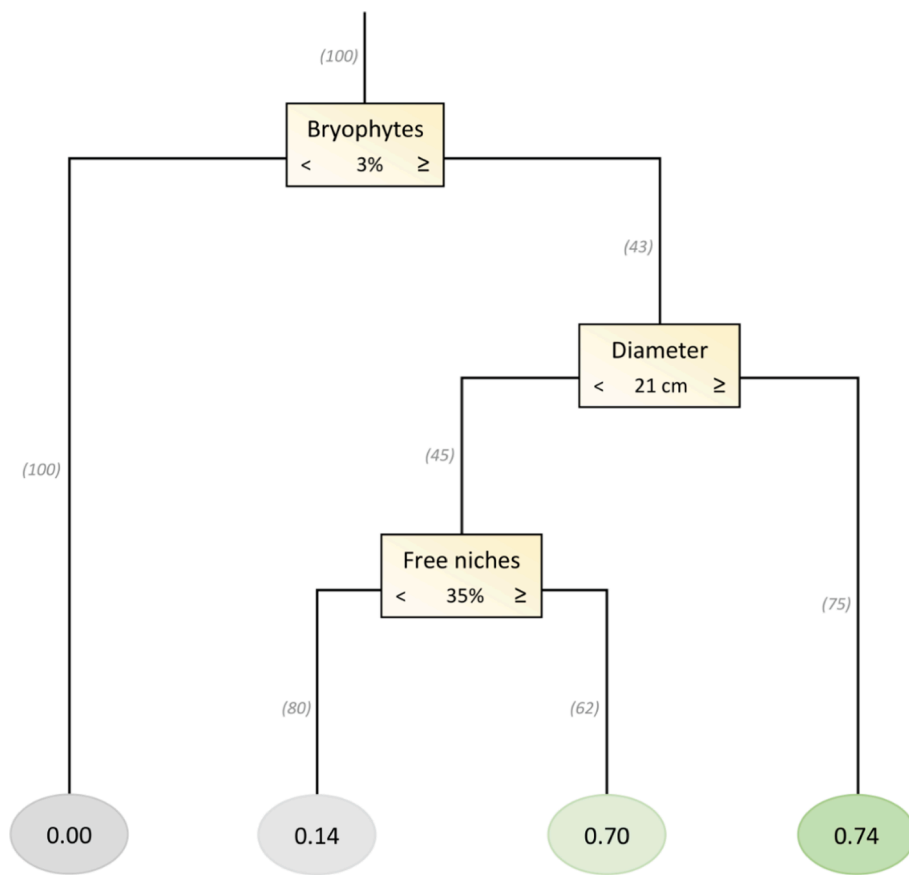
Fig. 4. The most supported tree topology for modelling seedling occurrence over 1000 CART trees. Each split is characterized by a splitting criterion in square boxes with comparison operators to indicate which in which reading direction to proceed. Numbers in terminal nodes depict the probability of 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 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	x	8.904
7	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 Fröborg 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 Fröborg (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 Fröborg 1996). This may be due to mycorrhizal fungi, which are often associated with decomposing wood (Fukasawa, 2021 and references there in). 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 –

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.

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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