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Constant gardeners: Endozoochory promotes repeated seedling recruitment in clonal plants

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Abstract. Paradoxically, seedlings of clonal plants are rarely observed in nature, despite many of these species producing large amounts of seeds every fruiting season. Studies about clonal plants' recruitment strategies are usually based on experiments carried out under controlled conditions (e.g., laboratory) and rarely consider frugivores' effects. We tested the role of endozoochory in the seedling recruitment in natural conditions of the bilberry *Vaccinium myrtillus*, a widely distributed clonal species and a key resource in temperate and boreal regions of Eurasia, which has been suggested to recruit at occasional windows of opportunity (unpredictable conditions in which seedling recruitment may occur within conspecific adult stands). We marked brown bear *Ursus arctos*, mesocarnivore (red foxes *Vulpes vulpes* and martens *Martes* spp.) and passerine feces containing bilberry seeds in the Tatra Mountains (Carpathian Mountains, Southern Poland) and followed the fate of the embedded seeds during two years. We detected bilberry germination associated with 100%, 87.5%, and 50% of brown bear, mesocarnivore, and passerine feces, and also in 43.6%, 41.2%, and 23.1% of the control plots located 5, 10, and 30 m away from the bear scats, respectively. In bear scats, investigated in more detail, 15.7% of the seedlings survived at least one year. The largest numbers of seedlings were associated with bear scats (154.4 ± 237.3 seedlings/m^2), especially to those defecated upon the soil disturbances these animals create next to their resting sites. Our results demonstrate that endozoochory facilitates repeated bilberry seedling recruitment in nature, suggesting that studies on the reproductive strategies of clonal plants must consider the role of frugivores. Some frugivores' behaviors, such as the defecation by bears in the vicinity of their resting sites, may in fact be crucial for the reproduction of clonal plants and for the adaptation of these species to the current changing climatic conditions.

Key words: frugivory; germination; recruitment at windows of opportunity; seed dispersal; *Ursus arctos; Vaccinium myrtillus*.

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Introduction

Seedling recruitment is considered infrequent in most clonal plant species (Eriksson 1992). Different recruitment strategies in this plant group have been described, ranging from species in which seedlings are established only during one initial period ("initial seedling recruitment") to species presenting continuous recruitment within conspecific adults ("repeated seedling recruitment," Eriksson 1992, Eriksson and Fröborg 1996). A third and intermediate strategy, the "recruitment at windows of opportunity" (RWO), is proposed for species in which recruitment within conspecific adults is limited spatially or temporally to unpredictable conditions that may happen more than once but at very low frequencies (Jelinski and Cheliak 1992, Eriksson and Fröborg 1996). Recruitment events are challenging to investigate in long-lived clonal plants, especially in species following a RWO strategy, because recruitment can happen at intervals much longer than the average length of field studies. Still, recruitment events may be crucial for plant demography and gene flow (Eriksson and Fröborg 1996).

A classic example of a species following a RWO strategy is the bilberry *Vaccinium myrtillus* (Eriksson and Fröborg 1996), a clonal shrub widely distributed in Eurasian temperate and boreal regions (Ritchie 1956) and a key food for frugivores of different body sizes, ranging from brown bears *Ursus arctos* to passerines (Honkavaara et al. 2007, García-Rodríguez et al. 2021c). Despite their seeds being dispersed in high numbers, usually undamaged, by birds and mammals (Schaumann and Heinken 2002, Honkavaara et al. 2007, García-Rodríguez et al. 2021b), paradoxically bilberry populations mostly expand by clonal propagation, with seedling recruitment considered rare within conspecific stands and usually restricted to open gaps with high moisture and organic soil content. Due to this, RWO has been proposed and widely accepted as the bilberry' recruitment strategy (Eriksson and Fröborg 1996). However, the high genetic diversity found in many clonal plants, including the bilberry, suggests that recruitment in these species might often be underestimated (Ellstrand and Rose 1987, Eriksson 1989, Albert et al. 2004). The hypothesis of RWO as the bilberry' recruitment strategy relies on inferences from both sowing experiments and studies about the species' genetic diversity (Eriksson and Fröborg 1996, Albert et al. 2004), but no study has accounted for the real frequency of these windows of opportunity in natural ecosystems. Specific behaviors of frugivore species, such as defecation in the vicinity of resting sites in the case of brown bears ("daybeds" hereafter) or at marking points or in the vicinity of animal carcasses in the case of mesocarnivores (e.g., foxes *Vulpes vulpes*, martens *Martes* spp.), have been proposed as potentially important for seedling recruitment in the bilberry and other clonal plants because they may direct seed dispersal to microhabitats suitable for germination (Schaumann and Heinken 2002, Steyaert et al. 2018, 2019, García-Rodríguez et al. 2021b). However, information about the importance of frugivores in the actual recruitment of clonal plants in natural conditions is still very limited (García-Rodríguez et al. 2021a).

Here, we analyze the effects of endozoochory in the sexual reproduction of the bilberry. We assessed germination and survival of bilberry seedlings in a natural ecosystem with a diverse community of seed dispersers and evaluated how endozoochory by the main disperser guilds in the area—brown bears, mesocarnivores, and passerines—affects the frequency of bilberry germination and survival under natural conditions. We discussed our results in the context of the RWO strategy and how they may be extrapolated to other clonal plants as well as the importance of considering the community of frugivores when analyzing the reproductive strategies of clonal plant species.

Materials and Methods

Study area

The study was conducted in Tatra National Park, a 211-km^2 protected area located in the Tatra Mountains—Northwestern Carpathians (southern Poland). The area ranges from 774 to 2499 meters above sea level (m asl). Mean annual temperatures in the area are 5.4 and 2.4°C at the lowest elevations and timberline areas (1550 m asl), respectively, whereas annual precipitation averages 1100 mm at the lowest elevations and increases up to 1700 mm at the timberline. Snow cover lasts for about 100 d in lower parts and up to 290 in the mountain tops. Montane (below 1550 m asl) and subalpine (1550–1800 m asl) areas are dominated by Norway spruce *Picea abies* and dwarf pine *Pinus mugo* formations, respectively. Montane, subalpine, and alpine (up to 2300 m asl) floors are dominated by bilberry (Appendix S1: Fig. S1), which forms highly productive patches during the fruiting season, from July to October (up to 1050 berries per m^2 in specific locations, Mirek and Piekos-Mirkowa 1992; authors', *unpublished data*). At least 16 frugivore species consume bilberry fruits in the area, with small- to medium-sized passerines (mostly Turdidae), mesocarnivores (red foxes and martens), and especially brown bears dispersing the majority of seeds (García-Rodríguez et al. 2021a).

Field sampling

During the fruiting seasons of 2018 and 2019, we marked 62 feces containing bilberry seeds belonging to the three main bilberry disperser guilds in the area (33 brown bear and 17 mesocarnivore scats, 12 passerine droppings). We inspected each feces visually in the field and confirmed that the bilberry was the most predominant food item in all the feces marked (i.e., all the marked feces were purple and embedded bilberry seeds were visible). All mesocarnivore and passerine feces and 21 bear scats were found during periodical inspections of animal paths, whereas 12 bear scats were marked at daybeds ($n = 5$) used by GPS-tracked collared brown bears. Following Steyaert et al. (2019), we defined bear daybeds as small dug-out areas with signs of bear presence (scats, hairs) and located in areas where bear's GPS relocations clustered for at least 4 h within a range of 50 m. We put each mammal scat in a plastic bag and weighted it with the help of a spring scale. After that, we put each sample back at its exact original location. We assigned 0.1 g to the weight of each passerine dropping based on previous research (García-Rodríguez et al. 2021a). We delimited each fecal sample with ropes and metal nails stuck to the ground, recorded its GPS location, and assigned an individual ID (Appendix S1: Fig. S2).

We revisited the samples a year later, in September 2019 and 2020, using a metal detector to find the marking nails when the relocation of the marked feces was difficult. Most feces were no longer visible after one year in the field and only the nails and ropes used to delimit each sample remained. Due to this, for each fecal sample whose marking nails were recovered ($n = 59$ out of 62), we delimited a 1-m^2 square plot ("sample plot" hereafter) centered at the sample location with the help of wooden measurement sticks. In order to assess differences in bilberry seedling germination between bear scats and surrounding areas, in 2019 we established six additional 1-m^2 square "control plots" for 27 bear fecal samples recovered out of the 29 bear scats marked in 2018. Although seeds are expected to concentrate in the vicinity of the defecation places, they can also potentially move from the feces' original locations due to several reasons (e.g., rain, snow and subsequent melting, wind, secondary seed dispersal). To account for this potential area of influence of feces, we established control plots at three different distances (5, 10, and 30 m from the marked bear scats) in two opposite directions from each sample plot. These two opposite directions were not necessarily established based on geographical coordinates, but rather on the topography of the feces location, the accessibility by foot and the possibility to set the 1-m^2 plots at those distances from the location of the bear scat. To avoid overlapping, we established control plots only in one direction from each sample plot when two or more bear scats were clustered, that is, located less than 30 m away from each other. Thus, for a given location we established one sample plot and a maximum and minimum of six and three control plots, respectively. We recorded the number of new bilberry seedlings (younger than one year), the bilberry cover (visual estimate of the percentage of ground covered by adult bilberry ramets), the canopy cover (visual estimate of the percentage of sky covered by tree canopy), and the predominant substrate (vegetation/bryophytes or denuded soil) in each sample and control plot. In 2020, and only for the bear scats marked in 2018, we distinguished new and one-year-old seedlings based on morphological differences (new seedlings present entire leaf margins, whereas one-year-old seedlings already show the toothed shape common in adult shrubs; Appendix S1: Fig. S3). In total, we assessed bilberry seedling germination in 59 sample and 117 control plots, and seedling survival in 26 sample plots (one out of the 27 plots could not be recovered in 2020, Appendix S1: Table S1).

Statistical analysis

We used Kruskal-Wallis tests to check the effect of the disperser guild (bears, mesocarnivores, and passerines) on the number of bilberry seedlings germinating per m^2 and per gram of fresh feces separately. We performed Dunn tests for pairwise comparisons between guilds. We also used Kruskal-Wallis tests to explore differences in seedling numbers per m^2 and per gram of fresh scat between bear scats located in daybeds and in animal paths. We performed a Generalized Linear Mixed Model (GLMM) fitted to a binary distribution to analyze the effect of the distance to the bear scats on the probability of seedling germination (absence/presence of bilberry seedlings in 1-m^2 plots) and a zero-inflated GLMM fitted to Poisson distribution to analyze the effect of distance on the number of seedlings germinated per m^2. We included data from both sample (only bears, distance = 0 m) and control plots and used their location as a random factor in both models. In the case of bear scats, we performed two Generalized Linear Models (GLMs), fitted to a Poisson and a gamma distribution, to check the combined effects of bilberry cover, canopy cover, and type of substrate on the number of seedlings per m^2 and per gram of fresh scat, respectively. We used GLMs fitted to a binomial distribution to assess the proportion of seedlings surviving the first winter after germination in bear scats in relation to the number of seedlings germinated the previous year per m^2 and per gram of fresh scat, separately. We performed all the analyses in R environment, version 3.4.0 (R Development Core Team 2017), using the *dunn.test* and *glmmTMB* packages for the implementation of the Dunn tests and the zero-inflated mixed models, respectively (Dinno 2017, Magnusson et al. 2017).

Results

We found bilberry germination in 100%, 87.5%, and 50% of the sample plots associated with bear, mesocarnivore, and passerine feces, respectively. New germination occurred in 77.8% of two-year-old bear scats. We detected bilberry germination in 35.9% of controls (43.6%, 41.2%, and 23.1% in plots 5, 10, and 30 m away from bear scats, respectively; Appendix S1: Table S1). The disperser guild influenced the number of bilberry seedlings germinated per m^2 (Kruskal-Wallis $\chi^2 = 23.374$, $P < 0.001$; Fig. 1a). The largest numbers of seedlings were associated with bear scats (154.4 ± 237.3 seedlings/m^2), followed by mesocarnivores and passerines (18.3 ± 24.4 and 1.8 ± 3.1 seedlings/m^2 respectively; Fig. 1a; Appendix S1: Table S2). The number of seedlings germinated per gram in passerine droppings (17.5 ± 31.1 seedlings/g) was larger than in mesocarnivore and bear scats (1.6 ± 1.8 and 0.2 ± 0.2 seedlings/g, respectively; Kruskal-Wallis $\chi^2 = 6.898$, $P = 0.032$; Fig. 1b; Appendix S1: Table S2). More seedlings germinated from bear scats in daybeds than in animal paths, both per m^2 (360.83 ± 277.22 vs. 24.05 ± 23.21 seedlings/m^2, respectively; Kruskal-Wallis $\chi^2 = 12.002$, $P < 0.001$) and per gram of scat (0.32 ± 0.26 vs. 0.13 ± 0.13 seedlings/g, respectively; Kruskal-Wallis $\chi^2 = 5.486$, $P = 0.019$; Fig. 1).

Distance to bear scats significantly and negatively affected the probability of germination of at least one bilberry seedling within control plots, but not the number of seedlings germinating per m^2 (Fig. 2, Appendix S1: Table S3). Larger bilberry cover, lower canopy cover, and denuded soil were associated with larger numbers of seedlings per m^2, whereas only the substrate had an effect on seedling germination per gram of fresh scat (Appendix S1: Table S4). We detected seedling survival in 84.6% of the bear scats monitored for two years, specifically in 91.7% and 78.6% of scats located in daybeds and in animal paths, respectively. In total, 15.7% of all seedlings germinated in 2019 from bear scats were still alive in 2020 (Appendix S1: Table S1). Neither the number of seedlings per m^2 nor per gram of fresh scat influenced survival rates of one-year-old seedlings dispersed by bears (Appendix S1: Table S5).

Discussion

We have shown that bilberry seedling recruitment is a widespread phenomenon in natural ecosystems when associated with endozoochory. Thousands of seedlings germinated and survived from just an insignificant subset of all feces defecated by frugivores in the study area during the fruiting season, implying that the actual numbers of bilberry seedlings recruited every year are several orders of magnitude higher than the numbers we detected. In line with this, previous research conducted in the area found that more than 50,000 bilberry seeds are dispersed by frugivores per hectare and month upon substrates suitable for bilberry germination (decaying wood and bare soil; García-Rodríguez et al. 2021a). According to these numbers, and given that the probability of a bilberry seed becoming an established adult when deposited upon a suitable substrate is around 0.3% (Eriksson and Fröborg 1996), a minimum of about 150 of the bilberry seeds dispersed by frugivores per hectare and month would become part of adult populations across the entire area. Our findings suggest that bilberry seedling germination and survival in the Tatra Mountains is not restricted spatially nor temporally to very rare windows of opportunity, but that these windows occur at frequencies much larger than previously assumed. Moreover, the germination and survival of bilberry seedlings in areas occupied by adult stands, a feature also found in coniferous forests of Sweden (Eriksson 2002), also suggests that repeated seedling recruitment in the bilberry (and other related species) might be a common feature in temperate and boreal ecosystems of Eurasia, especially if they are inhabited by a diverse community of frugivores. Our results, thus, put in question the traditional hypothesis stating that bilberry seedling recruitment always occurs at very low frequencies in nature. In this context, long-term studies would still be extremely helpful to disentangle to which extent bilberry seedlings recruited from endozoochorous seed dispersal activities may survive and become part of adult populations.

Seed arrival to suitable germination sites may be enhanced by the segregation of seed dispersal services, both spatially (e.g., different disperser guilds depositing seeds in different (micro)habitats) and/or temporally (either by developing seed banks or by differences in the quantitative and qualitative contributions of different frugivore species along the fruiting season, Eriksson 1989, González-Varo et al. 2019). The spatiotemporal complementarity of seed dispersal services provided by birds and mammals in the Tatra Mountains guarantees the arrival of large quantities of bilberry seeds to different microsites across the entire fruiting season (García-Rodríguez et al. 2021a). This, together with a high bilberry germination and survival rates from feces, supports a repeated bilberry seedling recruitment in the study area. This might also apply to other areas inhabited by a diverse and rich community of bilberry dispersers and to other clonal plants heavily consumed by frugivores, for instance Ericaceae and Rosaceae species such as *Empetrum* spp., *Vaccinium* spp., or *Rubus* spp., whose seeds remain viable in important proportions after being ingested by birds and mammals (Traveset and Willson 1997, Traveset 1998, Steyaert et al. 2018). In this line, Ericaceae species other than the bilberry, such as *Arctostaphilos uva-ursi* and *V. angustifolium*, are known to present repeated seedling recruitment (Eriksson 1992 and references therein). In addition to frugivore effects, natural disturbances such as wind storms or bark beetle outbreaks, relevant and common components of boreal and temperate forest dynamics, may also facilitate recruitment of bilberry and other clonal plants by increasing the availability of suitable substrates for establishment (decaying wood or dug-out soil, Eriksson and Fröborg 1996). Consequently, natural disturbances at different spatial scales, ranging from landscape disturbances such as bark beetle outbreaks to local ones such as bear resting sites, might be relevant for the sexual reproduction of the bilberry and other related species.

Sexual reproduction is essential for the establishment of new populations of clonal plants (Eriksson 1989) and may also be crucial for the adaptation of these plant species to the ongoing changes in climatic conditions. In this context, medium- and large-sized carnivores, such as martens, foxes, and bears, are likely to play an essential role in plant adaptation to climate change as they can track the phenology of fruiting plants across elevation gradients, facilitating seed dispersal toward upper elevations and helping plants to escape global warming (Naoe et al. 2016, González-Varo et al. 2017). Additionally, local disturbances in the soil surface created by these carnivore species may enhance seedling germination in clonal plants (Eriksson 1989 and references therein, Steyaert et al. 2019). Our results show that specific behaviors of large frugivores, particularly bear defecation next to their resting sites, can direct seed dispersal to locations suitable for seedling recruitment of clonal plants. Brown bears usually dig out the vegetation in the vicinity of their resting sites, mobilize nutrients, and expose the soil surface to later deposit on it the seeds embedded in the scat (Appendix S1: Fig. S4). This "sowing" behavior may facilitate recruitment in the bilberry and other related clonal plants. This would explain why larger numbers of bilberry seedlings germinated in association with bear scats located in day beds than upon animal paths. Moreover, we found bilberry seeds germinating after two years embedded within bear scats, whereas manually extracted bilberry seeds cannot germinate after 45 weeks under controlled moisture conditions (Ranwala and Naylor 2004). This suggests that

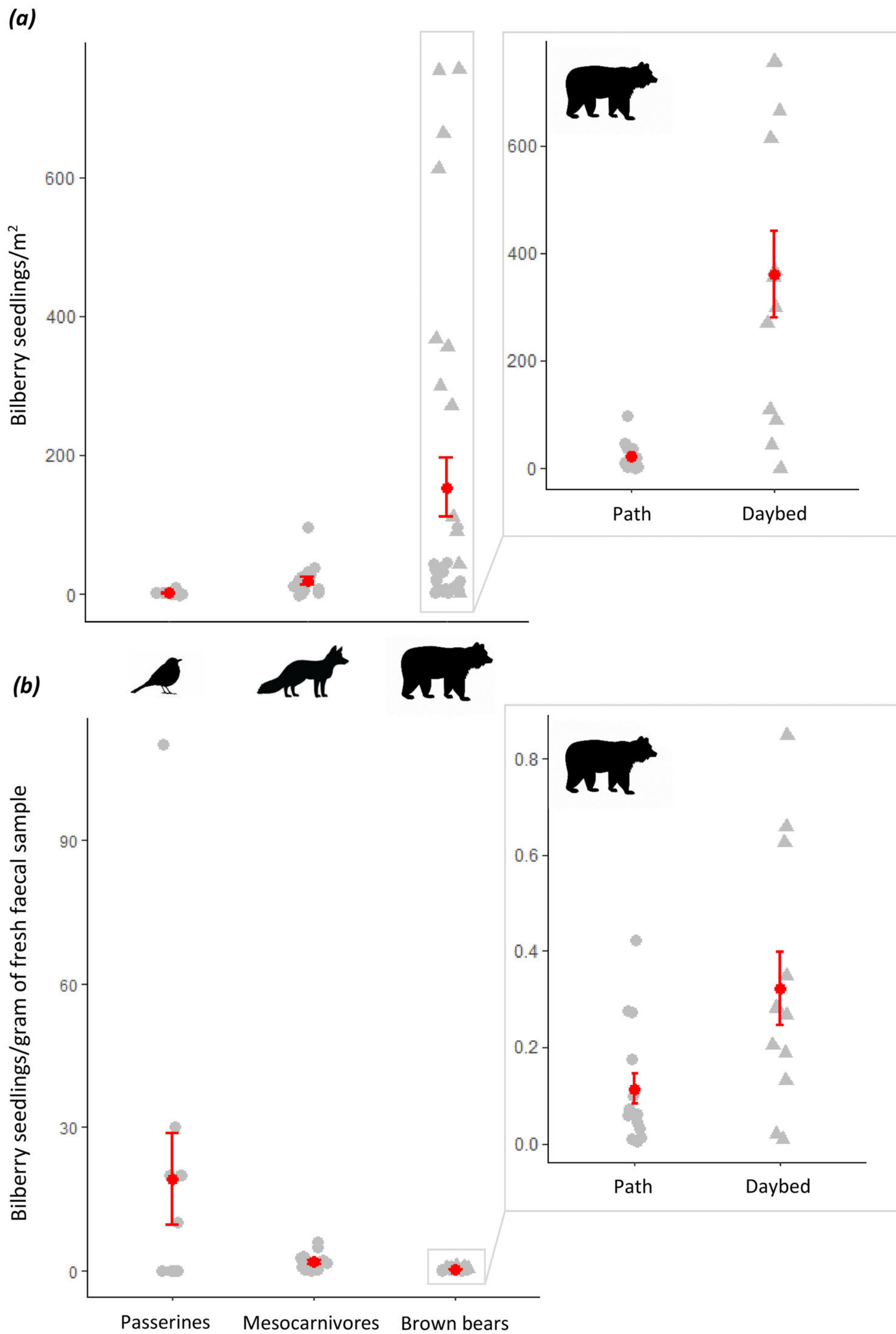

Fig. 1. Bilberry recruitment mediated by passerines ($n = 12$ feces), mesocarnivores ($n = 16$), and brown bears ($n = 31$) indicated as number of seedlings germinated (a) per m^2 and (b) per gram of fresh feces. Red dots and arrows represent mean values and standard errors, and gray dots the actual observed values. Embedded figures represent the numbers associated with bear scats located in daybeds ($n = 12$; triangles) and in animal paths ($n = 19$; circles). Please note that the Y-axes are represented in different scales.

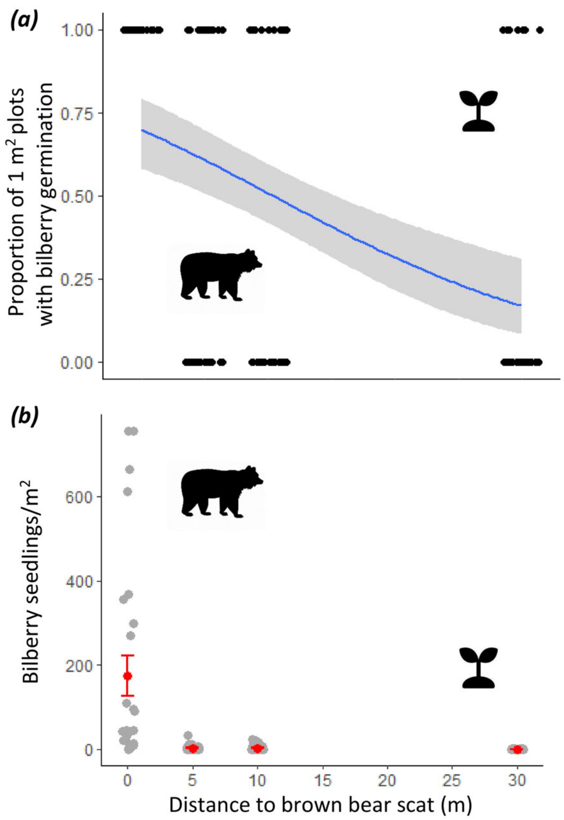

Fig. 2. Effects of the distance to brown bear feces on (a) the probability of bilberry germination and (b) the number of bilberry seedlings germinated per m^2. In (a), the blue line and gray-shaded area represent mean and standard error model predictions, and black dots the actual observed values. In (b), red dots and arrows represent mean values and standard errors, and gray dots the actual observed values (distance = 0 represents the location of the brown bear scats).

the fecal envelope, especially in large feces as bears', may have additional positive effects for seedling establishment in clonal plants as it may protect the seeds, allowing longer viability. We detected a strong negative relationship between the distance to bear feces and the proportion of control plots with bilberry recruitment, as well as much larger numbers of bilberry seedlings germinating from bear scat locations than from control plots. These two results combined suggest that bilberry germination in the area is strongly associated with endozoochory and concentrated primarily next to the deposition sites, with only a small proportion of seeds moving further than a few meters away from the feces locations. The analysis of the factors affecting the relocation of seeds away from the feces deposition site is a research topic that could help to better understand recruitment processes.

Besides the important contributions of medium- and large-sized frugivores to long-distance seed dispersal events, small birds are also important dispersers, which mobilize seeds usually over short distances (Jordano et al. 2007, but see González-Varo et al. 2021, and references therein for long-distance seed dispersal events provided by migratory birds). We found bilberry seedlings associated with half of the passerine droppings and in a third of the control plots. As germination rates of bilberry seeds are significantly lower when seeds are embedded within whole fruits than when defecated by frugivores (Honkavaara et al. 2007, García-Rodríguez et al. 2021b), we believe that bilberry seedlings detected in control plots are most likely derived from dispersal activities of frugivorous animals. In this context, bilberry seedlings detected in control plots, especially in those located the most far away from the bear scats, might also be a consequence of scattered avian defecations throughout the area. Selective pressures, such as sibling and adult competition, herbivory, and pathogen attacks, are different according to the region of the seed shadow (i.e., the spatial pattern of seed distribution relative to parent trees), being usually stronger next to parent plants (Janzen 1970, Connell 1971). Due to this, dispersal strategies, apparently opposite, might be equally optimal in different portions of the seed shadow. For instance, seedling recruitment far away from parent plants, where sibling competition is expected to be low, might be enhanced by mammal scats containing large seed loads, whereas recruitment next to their parents might benefit from the scattered deposition of many passerine droppings containing small numbers of seeds each. Moreover, avian short-distance seed dispersal events may complement clonal propagation by increasing genet numbers, which reduces extinction risk and promotes the persistence of specific genotypes within a population (Eriksson 1992). The vast majority of the genetic diversity of the bilberry is known to be explained by within-population variation (up to 86% of the total bilberry genetic variation, Albert et al. 2004), with several clones being present even in small patches; for instance, an average of 8 clones and up to 21 were found in 3×3 m plots in Belgium (Albert et al. 2003). Thus, we believe that endozoochory by both birds and mammals might explain, at least partially, the high genetic diversity found not only in the bilberry but in a wide variety of clonal plants (Ellstrand and Rose 1987). Interestingly, the high within-population genetic diversity, the relevance of short-distance dispersal events and the small seed size are bilberry traits that have traditionally been associated with clonal species showing repeated seedling recruitment (Eriksson 1992).

Here, we have demonstrated that endozoochory must be definitively considered when defining the reproductive strategies of clonal plants. Despite our results referring only to germination and to one-year survival, they already suggest that bilberry recruitment is more frequent in natural conditions than previously assumed and that frugivores may be a key, and yet overlooked, component to understand the apparent reproductive paradox of plant species reproducing mainly by clones but still producing huge amounts of seeds (Kloet and Hill 1994). Neglecting the effects of both mammalian and avian frugivores on seedling recruitment may lead to inaccurate information about population dynamics and life history evolution of clonal plants. For instance, our results support the assumption made by Eriksson (1989), who linked the high genetic diversity of clonal plants, comparable to that of nonclonal species, to a possible underestimation of seedling recruitment in clonal species. Preserving an intact community of frugivores seems crucial to guarantee repeated seedling recruitment in clonal plants. Endozoochory-mediated seed dispersal by diverse and intact frugivore guilds is an essential component in the assessment of the recruitment strategies of clonal plants.

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Data Availability

R scripts are also available from Figshare: https://figshare.com/articles/dataset/R_code_RSR_paper/15044433

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3861/full