

SUMMARY

Seed dispersal is an essential ecosystem service that, in temperate and boreal regions, is mainly provided by birds and mammals. Frugivores usually differ in their effectiveness as seed dispersers as a result of their different quantitative and qualitative contributions to seed dispersal. Long-distance seed dispersal events, mostly carried out by large frugivores, are key to guarantee gene flow among plant populations and the colonization of habitats, especially for clonal plants that rarely show seedling recruitment. The brown bear *Ursus arctos* is one of the most widely distributed terrestrial mammals and one of the few large-sized frugivorous species in non-tropical regions. In this PhD I evaluated the role of brown bears as seed dispersers, in particular of the bilberry *Vaccinium myrtillus*, a slow-growing clonal shrub common in Eurasian temperate and boreal regions and an important food resource for brown bears and many other animal species.

In Paper I I investigated the effectiveness of brown bears as seed dispersers worldwide. I analyzed their quantitative importance by extracting information about the species of fleshy fruits consumed and their importance in brown bears' diet from published data of 96 study areas. Brown bears consumed worldwide more than a hundred fleshy-fruited plant species whose fruits represented a quarter of the annual bears' diet. The bilberry was the second most commonly fruit eaten, only surpassed by the crowberry *Empetrum nigrum*, and it was consumed in most study areas located in Eurasian temperate and boreal regions. Ex-situ germination experiments with 11 species of fleshy fruits commonly eaten by brown bears (including the bilberry) were performed to check the quality of the seed dispersal service provided by the species. Ingestion by brown bears rarely damaged the seeds (99% of bilberry seeds were viable after bear ingestion), which usually germinated better than when embedded within the pulp. This study shows that, being one of the few megafaunal species inhabiting non-tropical areas, brown bears are pivotal seed dispersers across the entire range of the species.

In Paper II I analyzed the importance of fleshy fruits, and specifically of the bilberry, in the feeding ecology of brown bears inhabiting Tatra National Park (southern Poland). I assessed diet composition with DNA metabarcoding techniques in 246 bear scats collected between 2017 and 2019. Fleshy-fruited plant species were present in 56% of scats and across the whole bear activity period. The bilberry was the most common food (present in 42% of samples), followed by other fleshy-fruited plant species, the raspberry *Rubus idaeus* (20%). The bilberry was especially important during hyperphagia (from July to October), being detected in up to 73% of the scats in August. The prevalence of fleshy fruits in the diet of Tatra brown bears suggest that, even in areas highly humanized as Tatra National Park, bears may still provide essential ecosystem services such as seed dispersal.

In Paper III I analyzed the effectiveness of brown bears as bilberry dispersers in Tatra National Park in relation to the other frugivores inhabiting the area. To do that, in 2017 and 2018 I collected mammal scats and bird droppings containing bilberry seeds during transect inspections in coniferous forests and alpine meadows. Mammals were identified visually from their scats, and birds by DNA barcoding techniques. I counted the numbers of seeds in each faecal sample and conducted ex-situ germination experiments to address the quantity and quality of the bilberry dispersal services provided by each species. Among the three mammal and 13 bird species dispersing bilberry seeds in the study area, brown bears dispersed the vast majority of the seeds (more than 100,000 seeds per hectare and month). When quantitative and qualitative contributions were combined, brown bears were also among the most effective bilberry dispersers in the area, only surpassed by two species of thrushes. Additionally, brown bears complemented the dispersal activities provided by avian dispersers by defecating large amounts of bilberry seeds in alpine meadows and at the end of the fruiting season- areas and periods where seed dispersal by birds was less prevalent.

In Paper IV I investigated how important brown bears and other guilds of seed dispersers are for bilberry seedling recruitment in natural conditions. In 2018 and 2019 I marked 33 brown bear, 17 mesocarnivore (foxes *Vulpes vulpes* and martens *Martes sp.*) and 12 passerine faeces containing bilberry seeds in Tatra National Park. I revisited the locations of the faeces in 2019 and 2020 and counted the number of bilberry seedlings emerging. Bilberry germination was associated to all bear, 88% of mesocarnivore and 50% of bird faeces. The largest number of bilberry seedlings germinated from bear scats (154 seedlings/m²); this was significantly higher than in scats of the other two guilds of dispersers and in control plots. Up to 16% of the seedlings germinated from bear scats survived at least one year after germination. Additionally, seedling density was significantly higher when associated to bear scats located in bear daybeds than in animal paths. Thus, brown bear resting behavior in daybeds, which usually involves the creation of small disturbances in the soil, enhanced bilberry germination. This study shows that bilberry seedling germination and survival is common when associated to faeces of frugivores, including brown bears, which implies that, contrary to previous suggestions, repeated bilberry seedling recruitment may occur in nature. Endozoochory, and especially specific behaviors of frugivores that create suitable conditions for bilberry germination, must not be neglected when analyzing reproductive strategies of plants, especially in the case of clonal species.

The results of this PhD demonstrate the importance of brown bears as bilberry seed dispersers and suggest that this may apply for all areas where both species coexist. Some features of brown bears such as the long distances they can travel and the disturbances they create in their resting sites, together with the large amounts of seeds they defecate in a single scat and the matching between their hyperphagia period and the bilberry fruiting season, are key to understand the singularity of the seed dispersal services provided by the species, especially considering that

other large-sized frugivores are often missing in areas where brown bears are present. Proper management and conservation strategies are key to guarantee the essential ecosystem services brown bears still provide.