Integrating animal seed dispersal into plant regeneration

Dissertation von Finn Rehling

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Integrating animal seed dispersal into plant regeneration

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Illustration front page: *Turdus merula* feasting on fruits of *Sorbus aucuparia*.
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Erstgutachterin:	Dr. Dana G. Schabo
Zweitgutachterin:	Prof. Dr. Nina Farwig

Tag der mündlichen Prüfung:

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Declaration of the author contributions

The thesis ‘Integrating animal seed dispersal into plant regeneration’ is based on the work I carried out from March 2017 to November 2021 at the Philipps University of Marburg, under the supervision of Dr. Dana G. Schabo and Prof. Dr. Nina Farwig. **Chapters 2 - 4** of this thesis include three independent scientific manuscripts, each with co-authorship, and have been published or will be published. My contributions to other manuscripts and projects not being part of the dissertation are also described. The contributions of the authors for each manuscript or project is stated as following:

Chapter 2 – Within-species trait variation can lead to size limitations in seed dispersal of small-fruited plants

Finn Rehling, Bogdan Jaroszewicz, Leonie Victoria Braasch, Jörg Albrecht, Pedro Jordano, Jan Schlautmann, Nina Farwig, Dana G. Schabo

Published in *Frontiers in Ecology and Evolution*, 9: 698885 (2021).

Author contributions: FR, NF and DS conceived and designed the experiments. FR and LB collected and measured fruits and seeds, and performed a pilot germination study. BJ administrated field work. JA and JS provided data on species interactions in Białowieża Forest. PJ provided data on within-species variation in gape widths of the main seed dispersers. FR analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Chapter 3 – Forest degradation limits the quality and complementarity of animal seed dispersal

Finn Rehling[1], Jan Schlautmann[1], Bogdan Jaroszewicz, Dana G. Schabo[2], Nina Farwig[2]

[1]shared co-first authorship; [2]shared co-senior authorship.

Not published.

Author contributions: FR, JS, NF and DGS conceived and designed the experiments. FR and JS collected the deposited seeds, JS carried out the laboratory analyses, FR and JS performed the recruitment experiments, BJ organized permissions and administrated field work. JS and FR analysed the data. FR and JS wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Chapter 4 – How many seeds do animals have to disperse for a tree to grow?

Finn Rehling, Eelke Jongejans, Jan Schlautmann, Jörg Albrecht, Hubert Fassbender, Bogdan Jaroszewicz, Diethart Matthies, Lina Waldschmidt, Nina Farwig, Dana G. Schabo

Not published.

Author contributions: FR, JA, JS, NF and DGS conceived and designed the experiments. JA observed the fruit removal, FR and JS collected the deposited seeds, JS carried out the laboratory analyses, FR, JS, HF and LW performed the recruitment experiments and recorded the tree vital rates, BJ organised permissions and administrated field work. FR and EJ analysed the data, conducted the modelling and discussed details with DM, NF and DGS. FR wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Other (co-)author contributions

Responses of a legume to inbreeding and the intensity of novel and familiar stresses

Finn Rehling, Diethart Matthies, Tobias M. Sandner

Published in *Ecology and Evolution*, 9 (3): 1255-1267 (2019).

Author contributions: FR, TMS, and DM conceived and designed the experiments. TMS conducted a pilot study and collected the original seeds. FR performed the experiments. FR, TMS, and DM analyzed the data and wrote the manuscript.

Biomass partitioning in response to intraspecific competition depends on nutrients and species characteristics: A study of 43 plant species

Finn Rehling, Tobias M. Sandner, Diethart Matthies.

Published in *Journal of Ecology*, 109 (5): 2219-2233 (2021).

Author contributions: F.R., T.M.S. and D.M. conceived and designed the experiments. F.R. conducted a pilot study and performed the experiments. All authors analyzed the data. F.R. wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Observing frugivores or collecting scats: a method comparison to construct quantitative seed dispersal networks

Jan Schlautmann, **Finn Rehling**, Jörg Albrecht, Bogdan Jaroszewicz, Dana G. Schabo and Nina Farwig

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Author contributions: Jan Schlautmann: Formal analysis (equal); Investigation (equal); Visualization (equal); Writing – original draft (equal). Finn Rehling: Investigation (equal); Writing – review and editing (equal). Jörg Albrecht: Investigation (equal); Methodology (equal); Writing – review and editing (equal). Bogdan Jaroszewicz: Writing – review and editing (equal). Dana G. Schabo: Conceptualization (equal); Writing – review and editing (equal). Nina Farwig: Conceptualization (equal); Writing – review and editing (equal).

Frugivory community composition and interaction frequency are vertically stratified in a liana species fruiting across forest strata

Sarina Thiel, Franziska Willems, Nina Farwig, **Finn Rehling**, Dana G. Schabo, Matthias Schleuning, Ney Shahuano Tello, Till Töpfer, Marco Tschapka, Eckhard W. Heymann, Katrin Heer

Not published.

Author contributions: KH, EWH, MT, FMW and ST concepted and designed the study. ST, FMW and NST collected the field data, and TT contributed the bird traits data. ST compiled and analyzed all data with input from FR, MS, KH, DS, NF. ST wrote the manuscript with all co-authors contributing to revisions.

Summary

Ecological interactions build the backbone of biodiversity and ecosystems. Understanding how species interactions are structured across ecological scales, how they work, and how they are disrupted by anthropogenic pressure is important to predict and reverse the ongoing decline in biodiversity worldwide.

Silvicultural practices change the structure and spatial composition of forest ecosystems and can strongly affect species interactions such as seed dispersal by frugivorous animals. Quantifying these effects, however, is complex as it requires in-depth knowledge of the delayed effects of seed dispersal on the regeneration of plant communities, and the effect of humans on the underlying processes.

In this thesis, the seed dispersal mutualism between 41 frugivores (31 birds and 10 mammals) and 15 fleshy-fruited plant species was investigated in ash-alder forests in the degraded and intact part of the Białowieża Forest (BF) in Eastern Poland.

The results presented here together with previous findings in the studied temperate forest indicate that seed dispersal of fleshy-fruited plants is robust against the loss of single animal species for four reasons: (i) the small fruits of plants can be consumed by most animals and species extinctions will not lead to size mismatches between species during seed dispersal, (ii) most species are not effective seed dispersers, (iii) seed dispersal is qualitatively redundant, and (iv) the dispersal by gravity can also result in successful plant regeneration.

However, before species are lost due to forest degradation, the physical environment and ecological interactions change. These 'background' effects of species loss on seed dispersal and plant populations are complex, and plant species will respond differently, but the regeneration of the fleshy-fruited plant community is likely to decrease overall.

This thesis highlights the value of intact forest ecosystems for the conservation of plant-frugivore communities and their interactions. It further indicates that restoring environmental heterogeneity and the frequency of ecological interactions will improve the functioning of degraded ecosystems and maintain biodiversity.

Chapter 1: General introduction

Ecological interactions structure the (co-)evolution of species, and contribute to the functioning, stability and persistence of ecosystems (Hutchinson, 1959; Loreau, 2020). Humans benefit from a series of ecological functions and services provided by high-quality ecosystems (Whelan et al., 2008; Haines-Young and Potschin, 2010). Simultaneously, humans have strongly altered the abiotic environment and ecological interactions in a way that the rate of species extinctions will soon be about five times higher than a few hundred years ago (Johnson et al., 2017). In face of this dramatic loss of biodiversity, the increasing awareness of the human dependency on ecological interactions has led to a recent paradigm shift in the fields of ecology and conservation. From managing and conserving small-scale habitats and rare species, the focus has shifted towards maintaining interaction networks and ecosystem functions, with the superordinate aim of conserving high-quality ecosystems and biodiversity (MEA, 2005; Harvey et al., 2017; Heleno et al., 2020).

Seed dispersal of plants by animals is an important function of ecosystems: plants provide nutritious fruits to animals for energy uptake and animals move plants to new locations through the dispersal of their seeds (Howe and Smallwood, 1982; Rogers et al., 2021). On a global scale, roughly 50% of plants are dispersed by animals (Aslan et al., 2013; Jordano, 2014; Rogers et al., 2021). Thus, seed dispersal by animals is indispensable for the regeneration of various terrestrial plant communities and the stability and persistence of ecosystems. Humans benefit directly from animal seed dispersal through the production of wood, fruits and other non-timber products, and indirectly through succession, ecosystem structure, nutrient cycling, carbon storage, and climate regulation (Rogers et al., 2021).

Seed dispersal is a provision-service type of interaction, and is expected to be beneficial for both contributing partners (Bronstein, 2009; Guimarães, 2020). The benefits of seed dispersal to animals are direct (Jordano, 2014; Albrecht et al., 2018; Quintero et al., 2020; González-Varo et al., 2021). Plants benefit from seed dispersal directly by improving conditions for seed germination (Rogers et al. *preprint*), and temporally delayed by the dispersal of seeds to habitats which may or may not promote plant recruitment and growth, and the colonization of new habitats. At large scales, seed dispersal can contribute to long-distance dispersal, and gene flow within and between populations (Nathan, 2006; Browne et al., 2018). It has long been noted that animals might differ in their behaviour during seed dispersal and thus also in their effect on plant populations and communities (McKey, 1975). The context-dependency of seed dispersal, however, has made it difficult to quantify the long-term, demographic effects of animals on plant populations and communities (Wang and Smith, 2002; Godínez-Alvarez and Jordano, 2007; Rogers et al., 2019).

The demographic effect of animal seed dispersal on plants cascades through a set of stages: Starting with the removal of fruits by animals, tracking the fate of animal-dispersed seeds requires knowledge on where seeds are deposited, and how these seeds germinate and grow to adult plants in the respective environment. In isolation, each of these processes, and therefore also the benefits of seed dispersal to plants is well understood in theory (Howe and Smallwood, 1982; Godínez-Alvarez and Jordano, 2007; Rogers et al., 2021). However, because most studies were unable to track the fate of animal-dispersed seeds through the life cycle of plants, it is poorly understood how strongly plants benefit from animal seed dispersal, and which role single animal species play for the effectiveness of seed dispersal. The few studies that have integrated animal dispersal into plant population dynamics found large differences in the effectiveness of seed dispersal by different animals (Godínez-Alvarez et al., 2002; Brodie et al., 2009a, 2009b; Loayza and Knight, 2010; Yang et al., 2011; Horvitz et al., 2015; Elwood et al., 2018).

The effectiveness framework of ecological interactions offers a possibility to characterize the net interaction strength of a species population on another (*sensu* Schupp, 1993; Schupp et al., 2010, 2017). Accordingly, the effectiveness of seed dispersal by an animal on plants can be described by the product of quantity and quality of the provided services. The quantity of seed dispersal describes the relative number of removed fruits by each animal species. Often fruit removal varies strongly among species, with a few species removing most of the fruits (Bascompte et al., 2003). The quality of seed dispersal represents a fitness measure, for example the dispersed seed developing into a reproductive plant. The effects of qualitative components can outweigh that of quantitative components and *vice versa* (Schupp et al., 2017). For instance, animals removing most of the available seeds do not necessarily contribute most to population growth if they deposit seeds close to parental plants, where growth conditions might be poor due to competition by conspecific individuals or other detrimental factors (Comita et al., 2014; Jansen et al., 2014; McConkey et al., 2018). In contrast, animals that disperse only a few seeds, but at particularly favourable sites, may be crucial for plant populations (Wenny, 2001; Carlo et al., 2013).

Differences in the quality of seed dispersal among animal species further describe to which extent single species are redundant or complementary in their function. If only one animal species provides high-quality seed dispersal, the loss of this one species could potentially result in the functional decline of seed dispersal (Terborgh et al., 2008; Pérez-Méndez et al., 2016) and, in the long-term, to co-extinctions of plant populations (Traveset and Riera, 2005; Traveset et al., 2012) or entire species (Brodie et al., 2014; Emer et al., 2019). In turn, the loss of a functionally redundant species may not affect plant communities much, as the lost interaction could be compensated by other animal species in the community (Lawton and Brown, 1994; Zamora, 2000). Understanding the role of species richness for the effectiveness of animal dispersal may help to answer the question to what extent the conservation of ecosystem functions and services will also lead to the conservation of biodiversity (Silvertown, 2015; Winfree, 2020). The few studies that integrated animal dispersal into plant regeneration and used the effectiveness framework found that seed dispersal quality differed strongly across animal species. Total seed dispersal effectiveness thus depended on only one of the two (Loayza and Knight, 2010), three (Brodie et al., 2009b) and five animal species studied (Godínez-Alvarez et al., 2002), respectively.

Each of the above-mentioned processes are altered by anthropogenic pressure (Tylianakis et al., 2008; McConkey et al., 2012). Over 75% of forests worldwide (Potapov et al., 2017) and over 99% of European temperate forests have been degraded by humans (Hannah et al., 1995; Sabatini et al., 2018). Forest degradation changes the spatial structure, the species and functional composition of animal-plant communities, species richness and abundance (Bobiec, 2002; Watson et al., 2018). These changes in forest structure increase the vulnerability of forests to further degradation through ongoing human interventions and interactions with natural disturbances such as windthrows, fires or insect outbreaks (Lindenmayer et al., 2017; Mikusiński et al., 2018; Watson et al., 2018). Large-bodied animals and forest specialists are vulnerable to the changes in forest structure following degradation (Albrecht et al., 2013; Cooke et al., 2019; Boissier et al., 2020). As these animals may provide complementary seed dispersal, their loss can have severe effects on the regeneration of associated animal-dispersed plants. Strong evidence of this is the correlation between the decline of large animals and the regeneration of large-fruited plant species (Peres and Palacios, 2007; Terborgh et al., 2008; Markl et al., 2012; McConkey et al., 2012; Galetti et al., 2013; Emer et al., 2019; Boissier et al., 2020; Carvalho et al., 2021a). Small animals cannot consume the large fruits of plants or only small portions of them, and thus are unlikely to fully compensate the seed dispersal of large animals after loss (but see Donatti et al., 2009; González-Varo and Traveset, 2016; Mittelman et al., 2020). Large-fruited plants will then respond to disperser loss by going extinct or by producing smaller fruits (Galetti et al. 2013, Onstein et al. 2018). However, even the seed dispersal of plants with small fruits might be size-limited (Gonzàlez-Varo and Traveset, 2016), and the production of small fruits might correlate to a reduction in seed size and plant regeneration (e.g. Galetti et al. 2013). Overall, a decline of large-fruited plants may lead to a decline in the carbon storage capacity of forests because the size of fruits and seeds is correlated to the wood density and height of plants (Bello et al., 2015; Doughty et al., 2016).

However, not all effects of forest degradation on seed dispersal need to be linked to the loss of animal species. Changes in the environment, the availability of food resources or species composition in degraded forests may influence the behaviour of animals during seed dispersal and plant regeneration (Jansen and Zuidema, 2001; Farwig and Berens, 2012; McConkey and O'Farrill, 2016). For example, the dispersal of seeds by animals into suitable microhabitats will depend on the availability of these microhabitats (Jansen and Zuidema, 2001). It has been shown that animals move farther and faster in intact than degraded forests which might increase their potential for long-distance dispersal (Uriarte et al., 2011). Simultaneously, forest degradation does not only affect seed dispersal, but also seed predation, herbivory and carnivory (Struhsaker et al., 1996; Kollmann and Buschor, 2003; Tylianakis et al., 2008; Bubnicki et al., 2019; van Ginkel et al., 2019). The impact of forest degradation on seed dispersal is thus multi-layered and context-dependent, which makes it difficult to generalize about the direction and magnitude of changes in the pattern of seed dispersal, especially with respect to the redundancy and complementarity of animal species (Farwig and Berens, 2012; McConkey and O'Farrill, 2016). So far, the findings of previous studies indicate that later stages of seed dispersal may be more strongly affected by forest degradation than fruit removal (except for the large-fruited plant species) (Brodie et al., 2009a; Uriarte et al., 2011; Albrecht et al., 2014; McConkey and O'Farrill, 2016; Farwig et al., 2017; Carvalho et al., 2021a). This might suggest that the quantitative compensations of the lost dispersers by generalist frugivores in degraded forests can mask declines in the effectiveness of seed dispersal, but these processes are poorly understood (McConkey and O'Farrill, 2016).

1.1. Aims of the thesis

In this thesis, I investigated the seed dispersal interactions of a plant-frugivore community in a temperate forest. My research focussed on three aspects of the seed dispersal mutualism between fleshy-fruited plants and frugivorous animals: (i) the size-dependency of seed dispersal of small-fruited plants (Chapter 2), (ii) the effect of forest degradation on seed dispersal quality and complementarity (Chapter 3, a shared study with Jan Schlautmann), and (iii) the long-term effects of animal seed dispersal on plant populations (Chapter 4).

The studies took place in the Białowieża Forest that covers an area of c. 1500 km² across the border of Poland and Belarus. At present, the 630 km² of forest in Poland are divided into the Białowieża National Park (c. 105 km²) and forests managed by state forestry. In an area of about c. 48 km² of the

Białowieża National Park, human interference has been minimal for over half a millennium and has been strictly protected since 1921, making it the best-preserved lowland forest in Europe. In contrast, commercial logging has shaped more than 80% of the Polish state forest since the First World War (Mikusiński et al., 2018; Jaroszewicz et al., 2019). The comparison of the old-growth core of the Białowieża National Park with the surrounding, managed forest provides the unique opportunity to study the effect of forest degradation on species communities and ecosystem functions in a 'natural experiment'. In the Białowieża Forest, up to 20% of the forest is dominated by alder (Jaroszewicz et al., 2019) which is home to a diverse community of at least fifteen woody, fleshy-fruited plant species (Albrecht et al., 2015). The seeds of these plants are dispersed by at least 41 animal species, including common small-bodied passerines (e.g. *Sylvia atricapilla, Erithacus rubecula*), rare woodpecker species (e.g. *Dendrocopos leucotos*) and forest specialists (e.g. *Tetrastes bonasia*), a suite of smaller and larger mammals (e.g. *Martes martes*, *Vulpes vulpes*, *Cervus elaphus*) and the largest European forest herbivore, the European Bison (*Bison bonasus*) (Albrecht et al., 2013; Jaroszewicz et al., 2013; Schlautmann et al., 2021).

This dissertation builds upon comprehensive datasets from previous studies on the plant-frugivore interactions in the Białowieża Forest (Albrecht et al., 2013, 2014, 2015; Farwig et al., 2017). In these studies, plant-frugivore networks have revealed that forest degradation causes a structural loss of 27% in the number of partners in plant-frugivore associations and a 50% decline in interaction frequencies as compared to intact forest (Albrecht et al., 2014). This loss of partners and interactions was partly attributable to a loss of forest specialists and large-bodied frugivores (Albrecht et al., 2013; Farwig et al., 2017) and a lower density of fruiting plants (Albrecht et al., 2014) in degraded forest. However, small-bodied generalists were able to establish equally high removal rates and quantitatively compensated the loss of disperser species (Albrecht et al., 2014; Farwig et al., 2017).

To link the behaviour of animals during fruit removal to the deposition of their seeds, over 3000 scats of animals were collected in the Białowieża Forest from 2016-2018, and the animal species of the defecated or regurgitated seeds were identified in a laboratory using DNA barcoding. In Schlautmann et al. (2021, see 'Other contributions'), it was found that both methods, the observation of frugivores during fruit removal and the collection of animal scats, identified the same disperser species. Only by collecting scats, however, mammals were identified as frequent seed dispersers. Schlautmann et al. (2021) identified the disperser species responsible for different dispersal events in the forest, which provides the link between frugivory and seed deposition, necessary for and used in the studies presented in chapters two to four.

In Chapter 2, I expected that the observed size limitation in seed dispersal of large-fruited plant species may similarly occur in small-fruited plant species. Specifically, I characterized the community-wide and (for the quantitatively most important species) the within-species trait variation in fruit diameter of plants and the gape widths of dispersers. For the species subset, I further investigated fruit-seed trait relationships to determine if the restricted access of small-gaped animals to large fruits results in the dispersal of fewer or smaller seeds per fruit.

In Chapter 3, we expected that forest degradation might affect the structure of the environment or the behaviour of animals in the forest. Changes in the environment and the behaviour of animals could potentially influence the deposition patterns of animals and lead to a reduction in the quality and complementarity of seed dispersal across animal species. Specifically, we used a niche-based approach to investigate the effect of forest degradation on changes in the forest structure and seed deposition patterns of the animal community along three environmental gradients. This allowed us to determine to what extent seed deposition in the intact and degraded forest is functionally redundant across animal species in complex environments. To show that the observed differences in deposition patterns across animal species and environmental gradients may be important for later life stages of plants, we complemented the analyses of seed deposition patterns with a four-year recruitment study of the plant community along two of the three studied environmental gradients.

In Chapter 4, I expected that the population growth of plants increases with the proportion of fruits removed, and that differences in the seed deposition pattern between animal species along environmental gradients affect plant regeneration. The resulting differences in the effectiveness of seed dispersal may determine the susceptibility of animal-dispersed plants to the extinction of single disperser species. Specifically, I used integral projection models to link the fruit removal, seed handling and seed deposition patterns of animal species along the natural gradient of canopy cover in the Białowieża Forest to their later effects on plant regeneration. I calculated the contribution of each animal species to population growth of *F. alnus*. This further allowed me to simulate changes in the total effectiveness of seed dispersal of *F. alnus* with the loss of interactions with single species or the loss of single species but not interactions.

This is a cumulative dissertation. The chapters two to four can be read independently as the scientific background, material and methods and the results are presented and discussed independently in each chapter. Please note that I use the term "we" frequently throughout the thesis to indicate that I was part of a large team conducting the research (see also author contribution).

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Chapter 2[a]: Within-species trait variation can lead to size limitations in seed dispersal of small-fruited plants

2.1. Abstract

The inability of small-gaped animals to consume very large fruits may limit seed dispersal of the respective plants. This has often been shown for large-fruited plant species that remain poorly dispersed when large-gaped animal species are lost due to anthropogenic pressure. Little is known about whether gape-size limitations similarly influence seed dispersal of small-fruited plant species that can show a large variation in fruit size within species. In this study, fruit sizes of 15 plant species were compared with the gape sizes of their 41 animal dispersers in the temperate, old-growth Białowieża Forest, Poland. The effect of gape-size limitations on fruit consumption was assessed at the plant species level, and for a subset of nine plant species, also at the individual level, and subindividual level (i.e., fruits of the same plant individual). In addition, for the species subset, fruit-seed trait relationships were investigated to determine whether a restricted access of small-gaped animals to large fruits results in the dispersal of fewer or smaller seeds per fruit. Fruit sizes widely varied among plant species (74.2%), considerably at the subindividual level (17.1%), and to the smallest extent among plant individuals (8.7%). Key disperser species should be able to consume fruits of all plant species and all individuals (except those of the largest-fruited plant species), even if they are able to consume only 28-55% of available fruits. Fruit and seed traits were positively correlated in eight out of nine plant species, indicating that gape size limitations will result in 49% fewer (in one plant species) or 16-21% smaller seeds (in three plant species) dispersed per fruit by small-gaped than by large-gaped main dispersers, respectively. Our results show that a large subindividual variation in fruit size is characteristic for small-fruited plant species, and increases their connectedness with frugivores at the level of plants species and individuals. Simultaneously, however, the large variation in fruit size leads to gape-size limitations that may induce selective pressures on fruit size if large-gaped dispersers become extinct. This study emphasizes the mechanisms by which gape-size limitation at the species, individual and subindividual level shape plant-frugivore interactions and the co-evolution of small-fruited plants.

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2.2. Introduction

The fleshy fruits of plants are an important food source for many animals (Snow & Snow 1988, Jordano 2014, Albrecht et al. 2018b, Quintero et al. 2020, González-Varo et al. 2021). In exchange for the provided pulp, animals disperse the seeds of the fruits, which is critical to the recruitment of plant populations (Howe & Smallwood 1982). Seed dispersal is typically carried out by multiple species of animals; conversely, those animals feed on the fruits of multiple species of plants (Zamora 2000, Blüthgen et al. 2007). Nevertheless, the morphological, physiological, and behavioral traits of plants and animals have co-evolved such that certain plant-animal interactions are favored over others (Gautier-Hion et al. 1985, Jordano 1987, Albrecht et al. 2015, 2018b).

Co-evolved traits include the sizes of the fruits and the gapes of their animal dispersers (Moermond & Denslow 1985, Wheelwright 1985, Jordano 1995a, Eklöf et al. 2013, Albrecht et al. 2018a/b, Schleuning et al. 2020). Because animals can poorly feed on fruits that are larger than their gape (Levey 1987, Rey et al. 1997), the diversity of dispersing animals decreases with increasing fruit size, such that large-fruited plant species are dispersed only by a few large-gaped animals (Janzen & Martin 1982, Guimarães et al. 2008). The reliance of a plant species on large-gaped animals for seed dispersal may result in strong population declines, once their main dispersers become functionally lost. This has been observed especially in the tropics (e.g., Galetti et al. 2013, Kurten 2013, Correa et al. 2015, Lim et al. 2020) and on islands (e.g., Perez-Mendez et al. 2016, Brodie 2017, Case & Tarwater 2020), where, following anthropogenic pressure, the inability of simplified, down-sized animal communities to consume large fruits limits the regeneration of the respective plants (Terborgh et al. 2008, Brodie et al. 2009). Despite these strong examples, the diameters of the vast majority of fruits and gapes are < 1.2 cm (Wheelwright 1985, Wenny et al. 2016), and the extent to which gape-size limitations determine the interactions between small-fruited plants and small-gaped seed dispersers is unclear.

Within-species levels of trait variation may lead to gape-size limitations that do not take place at the species level (as observed in the large-fruited plant species), but subtler at the individual or subindividual level. Fruits of plants can vary in their size among different plant individuals (interindividual variation) due to genetic differences, differences in plant size or the environment (Foster 1990, Wheelwright 1993, González-Varo & Traveset 2016). Simultaneously, fruit size also varies within individuals (subindividual variation), because flowers receive a different amount of pollen during pollination, or fruits differ in their vertical position, or light conditions (Jackson & Sharples 1971, Lloyd 1984, Dogterom et al. 2000, Herrera 2009, 2017). Thus, for example, in the common myrtle *Myrtus communis*, while all of its main dispersers are able to feed on its fruits, the actual disperser assemblage differs between plant individuals bearing fruits of different sizes, such that some individuals have potentially only two and others up to five main dispersers (González-Varo & Traveset 2016). In the olive tree *Olea europaea*, the large fruits of cultivated plants can be consumed by only one disperser whereas the small fruits of wild individuals are consumed by all four main dispersers (Rey et al. 1997). On top of the variation in plants, substantial interindividual variation occurs in the gape width of seed-dispersing animals, due either to ontogenetic differences or due to sexual dimorphism (González-Varo & Traveset 2016, Zwolak 2018).

The resulting community-wide trait variation in fruit and gape sizes not only determine the interactions among plants and animals at different ecological levels (species, individual, subindividual level), they may also play a role in the success and effectiveness of seed dispersal (Schupp et al. 2010). Within plant species, fruit size was shown to positively correlate with the number or mass of dispersed seeds per fruit (e.g., Sallabanks 1993, Alcántara & Rey 2003, Hernàndez 2009). Seed size, in turn, mediates other dispersal-related processes, such as the dispersal ability of seeds, the seed's susceptibility to natural enemies, and the performance of the seedlings after germination (Leishman et al. 2000, Muller-Landau 2010, Fricke et al. 2019). If the animal's gape size constrains its fruit choice, then large-gaped animals will be able to disperse more or larger seeds per fruit than small-gaped animals, because they are able to consume larger fruits (Alcantera & Rey 2003, Hernández 2009, Herrera 2009, Galetti et al. 2013, González-Varo et al. 2014, Carvalho et al. 2021). Thus, the within-species trait variation in fruit size could potentially have direct and indirect consequences for both the quantity and the quality of seed dispersal, even in plant species with small fruits.

In this study, we describe the extent to which gape-size limitations structure species interactions between small-fruited plants and their associated frugivores, and how gape-size limitations influence the mass or number of dispersed seeds by small-gaped frugivores. We combined data on fruit removal (Albrecht et al. 2013), seed deposition (Schlautmann et al. 2021), fruit and seed traits, and gape widths (Herrera 1984, Jordano 1984a) of a diverse plant-frugivore community of the lowland temperate forests in Białowieża Forest (Eastern Poland). First, we characterized the community-wide trait variation in both the fruit diameter of plants and the gape widths of seed dispersers at the species level. In addition, we characterized the within-species trait variation for a subset of nine plant species and their six main dispersers. Second, we tested and quantified to which extent the different levels of trait variation of fruit diameter and gape width affect the interactions between plants and their seed dispersers at the species level (all species) and within species at the individual and subindividual level (subset only).

For the species subset, we further tested, third, if fruit size is positively related to the key determinants of post-dispersal seedling establishment, i.e. the number and mean mass of seeds per fruit. Finally, we described the consequences of gape-size limitations for seed dispersal by testing whether fruit diameter and gape width affected the number and mass of dispersed seeds.

2.3. Materials and Methods

2.3.1. Study area and species

The study was conducted in the Białowieża Forest, which covers an area of 1,506 km² and spans the borders of Poland and Belarus. The Polish part of the forest (~ 625 km²) is divided into the Białowieża National Park (~105 km²) and state forests. The 48-km² Białowieża National Park has been continuously protected for almost 500 years, first as a royal hunting ground and since 1921 strictly as a national park. It is therefore the best-preserved lowland forest in Europe (Samojilik et al. 2019, Jaroszewicz et al. 2019). By contrast, commercial logging has been allowed in > 80% of Polish state forests since the First World War (Mikusinski et al. 2018, Jaroszewicz et al. 2019).

Up to 20% of the Białowieża Forest is dominated by alder (Jaroszewicz et al. 2019), which is home to a diverse community of at least 15 woody, fleshy-fruited plant species (Table S1, see also Albrecht et al. 2015). For the study of within-species trait variation and fruit-seed trait relationships of small-fruited plant species, we focused on the nine most abundant plant species in the middle layer and understory of the forest: *Euonymus europaeus* (European spindle)*, Frangula alnus* (alder buckthorn)*, Prunus padus* (bird cherry)*, Rhamnus cathartica* (European buckthorn)*, Ribes nigrum* (black currant)*, Ribes spicatum* (downy currant)*, Sambucus nigra* (elder)*, Sorbus aucuparia* (rowan), and *Viburnum opulus* (guelder rose). These species belong to five plant families and are either trees (n = 6 species) or shrubs (n = 3). They produce red (n = 4) or black (n = 5) fruits and their fruiting season starts in June (*P. padus* and *R. spicatum*) and ends in October (*E. europaeus*). The seeds of these plants are dispersed by many different animal species (Table S2), including at least 10 mammalian and 31 avian frugivores (Albrecht et al. 2013, Jaroszewicz et al. 2013, Schlautmann et al. 2021). However, the contribution of these species to the total seed dispersal of the plant community in the Białowieża Forest is highly heterogeneous, as only five bird species, i.e., *Erithacus rubecula* (European robin), *Sylvia atricapilla* (Eurasian blackcap), *S. borin* (garden warbler), *Turdus merula* (common blackbird), *T. philomelos* (song thrush) and one mammal, the European pine marten *Martes martes*, account for 97.0% of the fruit removal interactions and 98.6% of the seed rain (Schlautmann et al. 2021). In the following, these six species are referred to as the main seed dispersers in the studied community.

2.3.2. Fruit and seed traits of plants at the species, individual and subindividual levels

To describe the community-wide trait variation in fruit diameter of small-fruited plants, we collected data for 15 woody, fleshy-fruited plant species at the species level, and for a subset of nine plant species also at the individual and subindividual levels. The data on the fruit diameters at species level were based on the fruit measurements performed in this study (see next section) and on the measurements reported in Albrecht et al. (2018b) for the remaining six plant species (Table S1). For *Rubus ideaus* (raspberry), a fruit-size diameter of 0.34 cm (Robbins & Moore 1991) was assumed because animals feed on single drupelets of the polydrupe.

For the subset of nine plant species, fruit samples from (7–)12–15 individual adult plants per species (mean ± SD: 12.8 ± 2.5) were collected in the Białowieża Forest, for a total of 115 adult plant individuals (Table S1). Ripe fruits were sampled between June and September 2018, aligned with the fruiting phenologies of the species. The collected fruits were stored in a freezer at −4°C. Between 4 and 22 fruits per plant individual (8.8 ± 2.8) were depulped for use in the analysis, resulting in 99–151 fruits per plant species (112.4 ± 22.0, Table S1). The diameters of the frozen fruits were recorded to the nearest 0.01 cm (mean length and width of the fruit; referred to hereafter as fruit diameter). Intact seeds were extracted and then dried at room temperature for two days. The number of seeds per fruit and the mean dry mass of the seeds per fruit, defined as the total mass of seeds divided by the number of seeds per fruit, were determined. Fruits of *R. cathartica* often contained aborted seeds (mass < 7 mg) that seldom germinated (data not shown). Those seeds were excluded from estimates of the number and mass of seeds per fruit. In addition, because some fruits of *S. aucuparia* were infested by larvae of *Argyresthia conjugella* and seed-dispersing species tend to avoid eating infested fruits (Manzur & Courtney 1984), only the non-infested fruits of *S. aucuparia* were considered.

2.3.3. Gape width of animals at the species and individual levels

Data from three sources (Herrera 1984, Jordano 1984a, specimen collection, unpublished) were used to determine the gape width for 30 of the 41 studied disperser species from the Białowieża Forest at the species level. Herrera (1984) and Jordano (1984a) measured the gape width of mist-netted birds from Southern Spain (1978–1982) and Northern Spain (1980–1983), respectively. In the Appendix of the report by Herrera (1984), only the mean values were listed whereas in the dataset provided by Jordano (1984a) the gape widths of up to 20 individuals per bird species were recorded. Because gape widths can differ between animals of different populations and depending on the observer (see

Supplement of González-Varo et al. 2016), in this study the mean values of Herrera (1984) and Jordano (1984a) were averaged when data from both sources were available. In the absence of information on the gape width of living individuals, the values were based on measurements of up to four mounted specimens within the animal collection of Philipps-Universität Marburg (Table S2). However, the gape of mounted animals is stiff, such that the mean gape width was consistently smaller ($F = 14.08$, $p < 0.001$) than reported by Herrera (1984) and Jordano (1984a). In all three data sources, the gape width of birds was measured at the internal commissures of the mouth using a caliper and recorded to the closest 0.01 cm. For *Carpodacus erythrinus* (common rosefinch), no data were available and the gape width was therefore predicted based on bird species with a similar body mass and diet as reported by Herrera (1984) (Supplementary material 1.2, Fig. S1). For mammalian dispersers, information on gape width was rare and all mammalian species ($n = 10$) were therefore expected to have a gape width of ≥ 2 cm.

Because the gape width of bird species was averaged from measurements reported in different studies, interindividual differences in the gape width of the main dispersers were simulated by sampling 50 individuals with the species-specific mean gape width and the variation of gape width reported by Jordano (1984a, SD in *E. rubecula* = 0.036 cm, *S. atricapilla* = 0.033 cm, *S. borin* = 0.037 cm, *T. philomelos* = 0.037 cm, *T. merula* = 0.101 cm). Small-gaped, intermediate-gaped, and large-gaped individuals within species were defined accordingly, based on the 10% quantile, the mean, and the 90% quantile of the gape width of simulated individuals (Table S3).

2.3.4. Statistical analyses

Trait variation in fruit diameter and gape width at the species, individual and subindividual level

We summarized the community-wide trait variation in the fruit diameter of plants and the gape width of frugivores at the species level (Fig. 1). Frugivores were defined as all animal species recorded eating fruits of any of the studied plant species at least once, either during fruit removal observations in 2011/2012 (Albrecht et al. 2013) or based on the seeds found in the scat of animals collected in 2016–2018 (Schlautmann et al. 2021). Because we did not have direct measures of the gape widths of mammals, a cut-off was set at 2 cm. The black woodpecker *Dryocopus martius* (the only bird with a gape size > 2 cm) was grouped with mammals, thus yielding a group of large-gaped animals whose choice of fruits was not limited by gape width (Fig. 1, Table S1, S2).

We tested if the gape width of seed disperser species was related to the maximum and mean diameters of the consumed fruits at the species level. The maximum diameter of the consumed fruits was defined

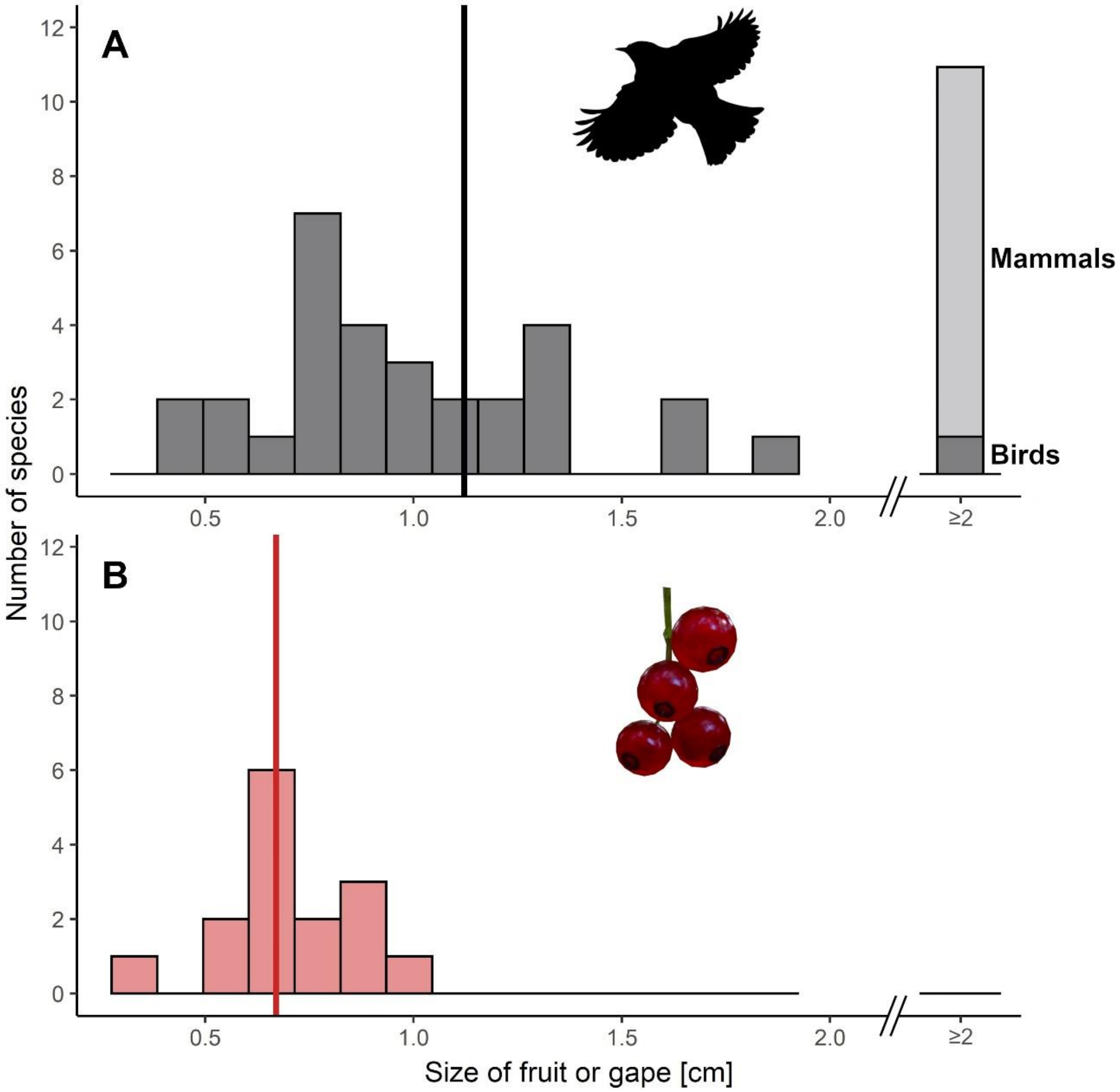

Fig. 1: Distribution of (A) the gape widths of animal dispersers and (B) the fruit diameter of associated plants at species level in temperate forests in Białowieża Forest, Poland. This is a summary of the local plant-frugivore community, whose contributing species were identified either based on fruit removal observations (Albrecht et al. 2013) or based on seeds in scats of animals (Schlautmann et al. 2021). Vertical lines illustrate the median value of a distribution.

as the mean fruit diameter of the largest-fruited plant species fed upon by a given seed disperser species, based either on observations of fruit removal (Albrecht et al. 2013) or on seed deposition (Schlautmann et al. 2021). The mean diameter of fruits removed by a given seed disperser species was calculated by weighting the fruit diameter of each plant species by the disperser-specific fruit consumption rate. The mean fruit diameter was determined solely on the basis of fruit-removal observations (Albrecht et al. 2013), not on seed depositions, because the mean fruit consumption rate cannot be adequately calculated from the number of seeds in scats. This is because birds usually deposit only a few seeds at most (not all seeds of one or more fruits) at the same place, and this behavior might depend on the plant species. Similarly, the number of seeds in scats might have been confounded by within-species differences in fruit choice among animal species. The effect of gape width on an animal's choice of fruits at the species level was evaluated using linear models in which the maximum and mean diameters of the fruits removed by each seed disperser species served as the response variable and the gape width of the respective seed disperser species as the continuous explanatory variable. In the analyses of maximum and mean fruit diameters, mammals were not included due to the missing values for gape width (n = 4). The nine avian seed disperser species that were observed less than six times were also excluded because the sample size was too low to consider their fruit choices as representative. Thus, the maximum and mean diameters of consumed fruits were analyzed for 17 seed disperser species. To test if the number of disperser species of a plant species decreases with the increasing diameter of fruits at the species level, generalized linear effect models were used with the number of disperser species as the response variable and fruit diameter as the fixed explanatory variable. The models included a logit link and a Poisson error distribution (analysis of deviance, Quinn & Keough 2002).

For a subset of the nine most abundant plant species and their six main dispersers (see 2.1 Study species), we quantified the extent to which gape-size limitations could potentially affect fruit removal and fruit consumption within species. To do so, we calculated the proportion of fruits from each plant species that could be swallowed (i.e., falling within the size interval of the gape widths) by the six main seed disperser species (proportion of accessible fruits for consumption, i.e., animal perspective; or proportion of fruits that can be dispersed by different animals respectively, i.e., plant perspective; see Table S3). In addition, we quantitatively compared the different levels of trait variation in fruit diameter of the nine plant species. The coefficient of variation (CV), defined as the sample variability (standard deviation) divided by the mean of the sample, and variance partitioning were used to compare the levels of trait variation in fruit diameter and the mean seed mass in plants among species, among individuals, and within individuals (subindividual). The CV was chosen because it provides a measure of trait variability from the individual perspective and is thus well-suited for comparisons of individuals within species. As a second measure, we used variance partitioning as it is able to provide a measure of trait variability from the community perspective and was thus well-suited for comparing the variability within and among species. In this study, it was used to separate the total community variability in fruit diameter and mean seed mass per fruit into the underlying contributions of species, individual, and subindividual variation. As both the CV and variance partitioning have different mathematical drawbacks and describe different aspects of trait variation, they were used in combination (Herrera 2009). The variance component (VC) models were fitted using an ANOVA-type (type I sums of squares) estimation for unbalanced mixed models, with the fruits nested in plant individuals nested in plant species as random factors (Searle et al. 1992). Significant differences between factors were based on 95% confidence intervals (95%CIs) using Satterthwaite's correction. Differences in the subindividual variation in fruit diameter between plant species were tested using the subindividual CV of individuals as replicates and by constructing linear models with plant species as the fixed factor. A potential relationship between the individual and subindividual CVs among plant species was investigated by averaging the subindividual CV per species and using a Spearman correlation.

Fruit-seed trait relationships

For the subset of the nine most abundant plant species, the relationship between fruit diameter and the seed traits of the plant species was assessed using (generalized) linear mixed models. In these models, the number or the mean mass of seeds per fruit served as the response variable, the fruit diameter, plant species and their interaction as the continuous explanatory variables, and the individual plant (from which the fruits had been collected) as a random factor. However, these models performed poorly which may have been due to the following reasons: first, the number of seeds per fruit was morphologically constrained in five of the nine plant species (*E. europaeus, F. alnus, P. padus, S. nigra*, and *V. opulus*) and hardly varied among fruits. Second, a linear mixed model with a normal error distribution performed best in the analyses of the number of seeds of *R. cathartica* and *S. aucuparia*, but a Poisson error distribution performed better in the models of *R. nigrum* and *R. spicatum*. Third, the number of seeds, the mean seed mass, and fruit size strongly differed between plant species, and the absence of overlap in the ranges of the values of the different plant species cast doubt on the accuracy of the model outcome. Thus, each of the nine plant species was tested separately and the probability values for multiple comparisons were adjusted using a Bonferroni correction to avoid a type I error.

The consequences of gape-size limitations for dispersed seeds

For the subset of the nine most abundant plant species and the six main dispersers, a possible effect of the gape width of the seed disperser species on the number or mean mass of seeds per fruit was analyzed. The number or mean mass of seeds per fruit was bootstrapped by randomly sampling 50 fruits of the studied plant species with 1000 replacements. For each of the bootstrap replicates, the maximum fruit diameter that could be sampled was limited according to the gape width of the animal species or individual. Pairwise mean value comparisons of the bootstrapped data were performed to test whether differences in the gape width of seed disperser species was the sole explanation for the differences in the number or mass of dispersed seeds, i.e., the probability that the mean value of the dispersed seeds of small-gaped seed dispersers was larger than that of large-gaped seed dispersers (based on one-tailed p-values). This was achieved by grouping the large-gaped main seed disperser species (*M. martes, T. merula*, *T. philomelos*), because they were not limited in their fruit choices, and adjusting the probability values for multiple comparisons between the main seed disperser species using a Bonferroni correction, to avoid a type I error. Because the results were slightly variable among iterations (i.e. seeds), we present the mean effect sizes and mean probability values of 50 iterations of the pairwise mean value comparisons of the bootstrapped data.

All statistical analyses were conducted using the R program version 4.0.3 (R Core Team 2020). Variance component analyses were performed using the R-package VCA version 1.4.3 (Schuetzenmeister & Dufey 2020). Generalized linear mixed models were constructed using the package lme4 version 1.1-23 (Bates et al. 2015). Significance values for the effect of fixed factors were obtained using Wald-χ^2 tests (type II sums of squares) in the package car version 3.0-9 (Fox & Weisberg 2019).

2.4. Results

2.4.1. Trait variation in fruit diameter and gape width at the species, individual and subindividual level

In Białowieża Forest, 15 fleshy-fruited plant species are dispersed by 41 animal species (10 mammal and 31 bird species, Fig. 1) (Albrecht et al. 2013, Schlautmann et al. 2021). At the species level, the mean fruit diameter ranged from 0.51 cm in *S. nigra* to 0.96 cm in *V. opulus* and was therefore smaller (median = 0.67 cm) than the gape width of the associated seed disperser assemblage (median = 1.12 cm). From the community perspective, trait variation in fruit diameter was largely explained by differences among plant species ($VC_{species}$ = 1.87, 95% CI: 0.84–6.99). However, more of the total variation in the fruit diameter within a plant species was explained by the subindividual than by the interindividual variation ($VC_{subindividual}$ = 0.43, 95%CI: 0.39–0.47 and $VC_{individual}$ = 0.22, 95%CI: 0.16–0.31, respectively; Table 1). The subindividual variation in fruit diameter differed significantly between plant species ($F_{8, 106}$ = 11.8, $p < 0.001$) and was smallest in *V. opulus* and largest in *R. spicatum* (Fig. 2, Fig. S2). The interindividual and subindividual variation in fruit diameter were not significantly rank-correlated across species (n = 9, Spearman's ρ = 0.45, p = 0.230).

Table 1. Analyses of variance components of fruit diameter and mean seed mass per fruit across nine fleshy-fruited plant species in Białowieża Forest, Poland.

	Fruit diameter			
	VC	**%Var**	**CV [%]**	
Community	2.51	100	22.16	
Species	1.87	74.17	19.08	a
Inter-individual	0.22	8.71	6.54	c
Intra-individual	0.43	17.11	9.16	b
	Mean seed mass			
	VC	**%Var**	**CV [%]**	
Community	833.53	100	103.76	
Species	765.5	91.84	99.44	a
Inter-individual	31.3	3.76	20.11	b
Intra-individual	36.74	4.41	21.78	b

VC; ANOVA-type estimation of variance components (Searle et al. 1992).
%Var; Proportion of total community-level variance in plant traits explained by different ecological scales: variation among species (species), variation among individuals of the same species (inter-individual), variation within individuals of the same species (intra-individual).
CV [%]; Coefficient of variation of different ecological scales.
Lower cases indicate significant differences between VC, %Var and CV [%] of the different ecological scales based on 95% confidence levels using 'Satterthwaite' approach (Schuetzenmeister & Dufey 2020).

The gape width of seed dispersers also varied considerably among species (Fig. 1) and among individuals of the same species (Fig. 2). When the community-wide trait variation in gape width and fruit diameter was considered, all plant species produced fruits small enough to be swallowed by all of the main seed dispersers in the studied plant-frugivore community (*E. rubecula, M. martes, S. atricapilla, S. borin, T. merula, T. philomelos*). In five of the nine studied plant species, the main seed disperser could potentially feed on > 90% of the total available fruits (based on the mean gape width of seed disperser species, Figs. 2 and 3, Table S3). In three plant species (*F. alnus*, *R. nigrum, S. aucuparia*), the main small-gaped seed dispersers (*E. rubecula*, *S. atricapilla*, *S. borin*) could feed only on 28–55% of the available fruits, but could interact with most individuals in the population (66–100%, based on the mean gape width of the studied species, Fig. 3). The fruits of *V. opulus* seemed to be barely accessible to small-gaped main dispersers (*E. rubecula*, *S. atricapilla*, *S. borin*) whereas the three main large-gaped seed dispersers (*M. martes*, *T. philomelos*, and *T. merula*) were potentially not size-limited in their fruit choices, neither among nor within plant species (Figs. 1, 2, and 3, Table S3).

Fruit size did not affect the number of seed disperser species feeding on the fruits ($\chi^2 = 0.07$, p= 0.794, Fig. 4a). However, the maximum ($F_{1,15} = 4.69$, p = 0.047) and mean ($F_{1,15} = 5.50$, p = 0.033) diameters of the consumed fruits increased with the increasing gape width of the seed disperser species (Fig. 4b). Only in 16.4% of the interactions did seed dispersers consume the fruits of plant species that were on average larger than their mean gape width (Fig. 4b).

2.4.2. Fruit-seed trait relationships

The number of seeds per fruit was biologically constrained in five of the nine studied plant species (1–3 seeds per fruit). For example, *P. padus* and *V. opulus* have drupaceous fruits, always with one seed per fruit. Fruit diameter correlated positively with the number of seeds per fruit only in three plant species (Fig. 5): *R. cathartica* (Wald-$\chi^2 = 10.61$, $p = 0.004$), *R. nigrum* (Wald-$\chi^2 = 199.97$, $p < 0.001$) and *R. spicatum* (Wald-$\chi^2 = 75.15$, $p < 0.001$). The variation in the mean seed mass per fruit was mostly explained by the differences between species, with only small contributions by individual and

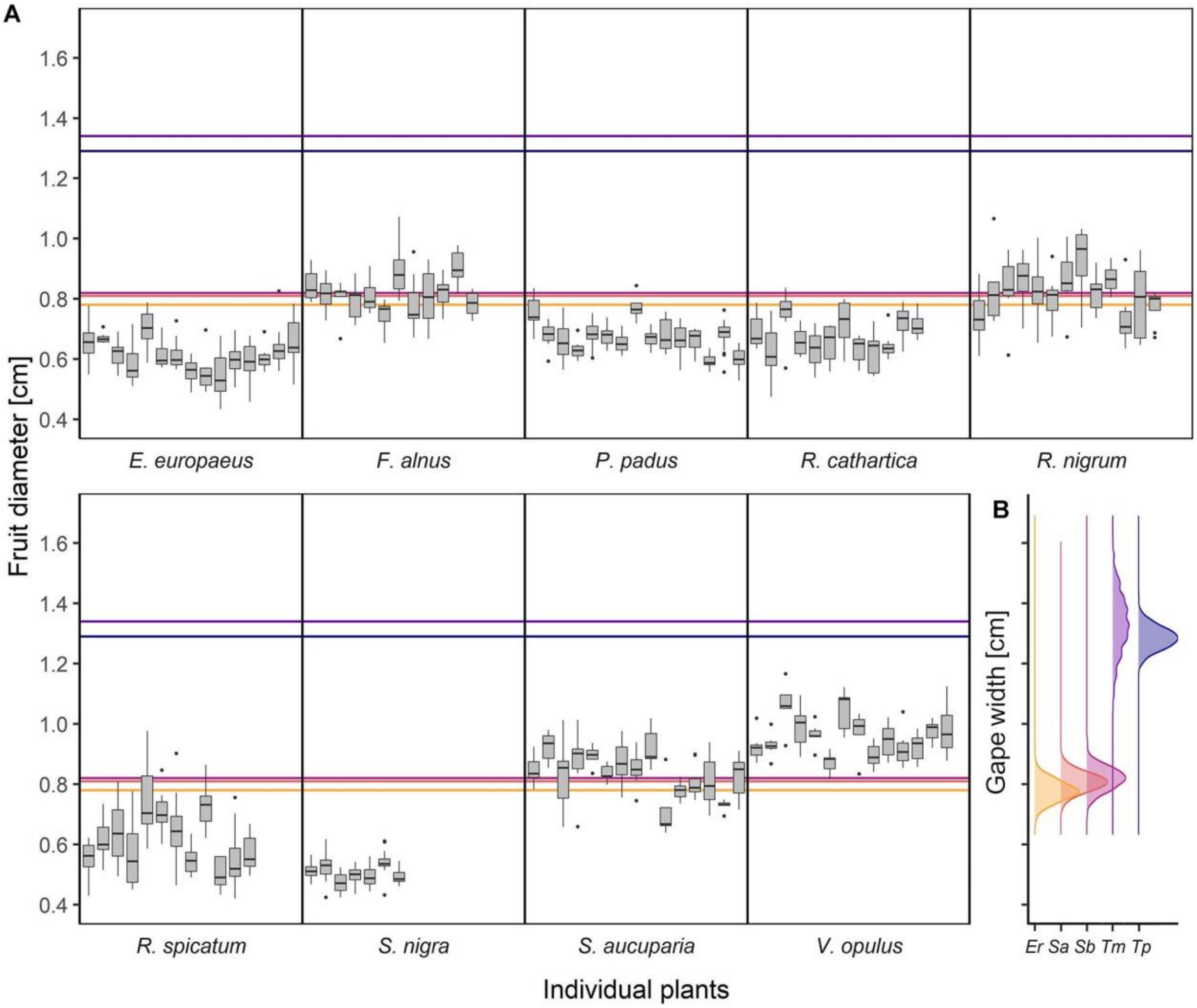

Fig. 2: (A) Boxplots showing sub- and interindividual variation in fruit diameter across nine fleshy-fruited plant species in Białowieża Forest, Poland. (B) Density plot of gape width of the five most important frugivore species (Er = *Erithacus rubecula*, Sa = *Sylvia atricapilla*, Sb = *Sylvia borin*, Tm = *Turdus merula*, Tp = *Turdus philomelos*). Together with *M. martes* (gape width > 2 cm), these disperser species account for 97.0% of fruit removal interactions and 98.6% of the seed rain in the Białowieża Forest, Poland. The color of horizontal lines in (A) depict the mean gape width of disperser species in (B), respectively.

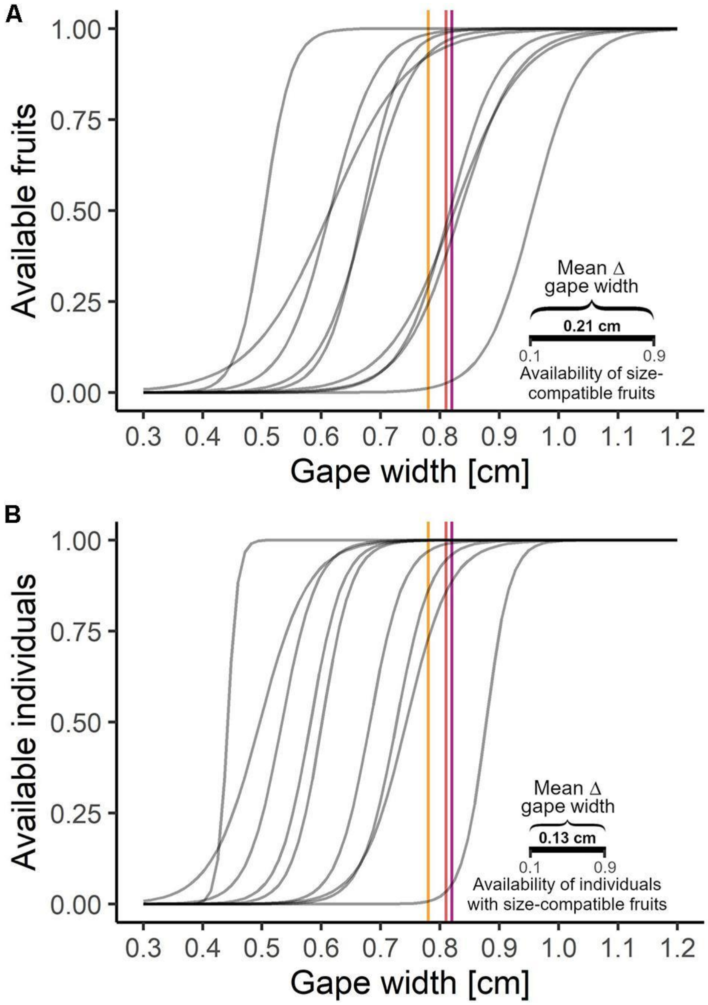

Fig. 3: Availability of (A) fruits or (B) individuals with size-compatible fruits as a function of the gape width of frugivorous animals. Each grey solid line displays one plant species. The black horizontal line illustrates the mean difference in the gape width of animals that allows animals to feed on either 10% or 90% of (A) fruits, or (B) plant individuals, respectively. The colored vertical lines depict the mean gape width of the small-gaped disperser *E. rubecula* (0.78 cm), *S. atricapilla* (0.82 cm) and *S. borin* (0.83 cm), respectively.

subindividual differences (Table 1). The mean seed mass per fruit correlated positively with fruit diameter in five of the nine studied plant species (Fig. 6): *F. alnus* (Wald-$\chi^2 = 57.53$, $p < 0.001$), *P. padus* (Wald-$\chi^2 = 14.83$, $p = 0.001$), *S. nigra* (Wald-$\chi^2 = 7.06$, $p = 0.071$), *S. aucuparia* (Wald-$\chi^2 = 17.55$, $p = 0.010$) and *V. opulus* (Wald-$\chi^2 = 26.63$, $p < 0.001$).

2.4.3. Consequences of size limitations for dispersed seeds

Tests for pair-wise differences between the main seed disperser species with respect to the number or mass of dispersed seeds per fruit showed significant differences for four of the nine plant species (Figs. 5 and 6). For *R. nigrum*, the small-gaped *E. rubecula* tended to disperse, on average, seeds from fruits with fewer seeds per fruit than did *S. borin* ($p = 0.033$) or the three main large-gaped seed dispersers *M. martes*, *T. merula, T. philomelos* ($p < 0.001$). *S. atricapilla* and *S. borin*, in turn, dispersed seeds from fruits with fewer seeds than did the three main large-gaped seed dispersers (both $p \leq 0.002$, Fig. 5d). The mean mass of the dispersed seeds did barely differ between the main small-gaped seed dispersers (*E. rubecula, S. atricapilla, S. borin*). However, in all but one comparison, *E. rubecula, S. atricapilla* and *S. borin* dispersed smaller seeds than the main large-gaped seed dispersers for three plant species, namely, *F. alnus*, *S. aucuparia* and *V. opulus* ($p < 0.001$ for two, $p < 0.05$ for one, and $p < 0.1$ for three species comparisons, respectively). Only in *F. alnus*, *S. borin* did not disperse seeds smaller than those dispersed by the large-gaped dispersers ($p = 0.148$), but differences between the main seed dispersers (even between the small-gaped seed dispersers) became significant ($p < 0.001$), when we strongly increased the number of samples for bootstrapping (e.g., 500 instead of 50 fruits).

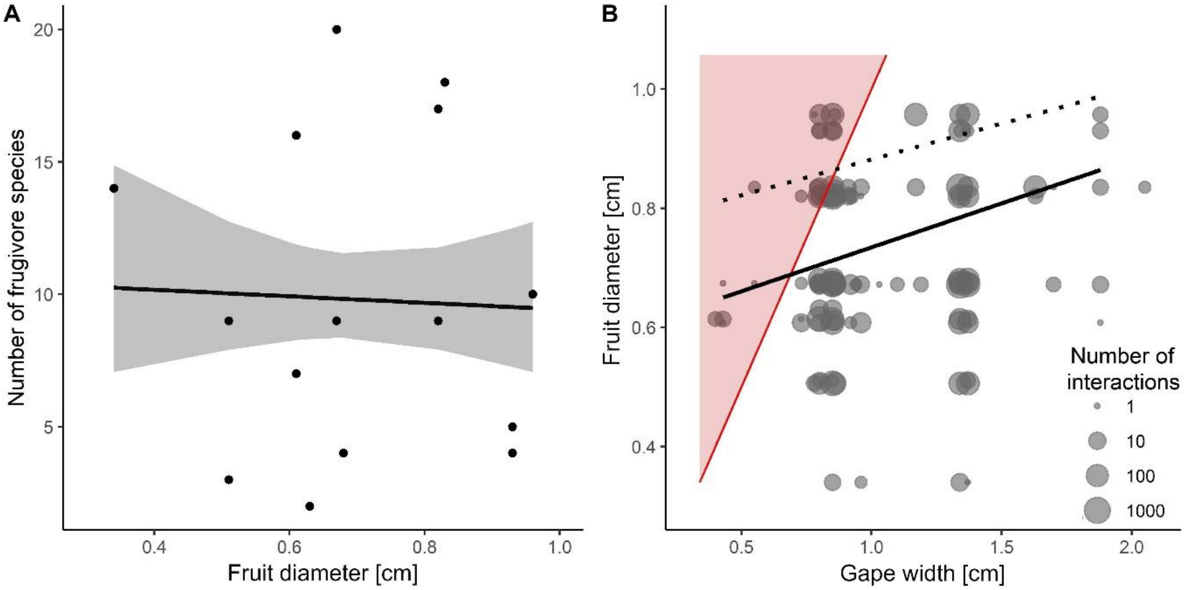

Fig. 4: (A) The effect of fruit diameter on the number of disperser species per plant species. The grey-shaded area indicates 95% confidence intervals. (B) The maximum and mean diameter of fruits of plant species dispersed by animals with different gape widths during fruit removal observations (Albrecht et al. 2013, Schlautmann et al. 2021) in Białowieża Forest, Poland. The red-shaded area displays morphological 'forbidden links' between plants and animals based on mean trait-values.

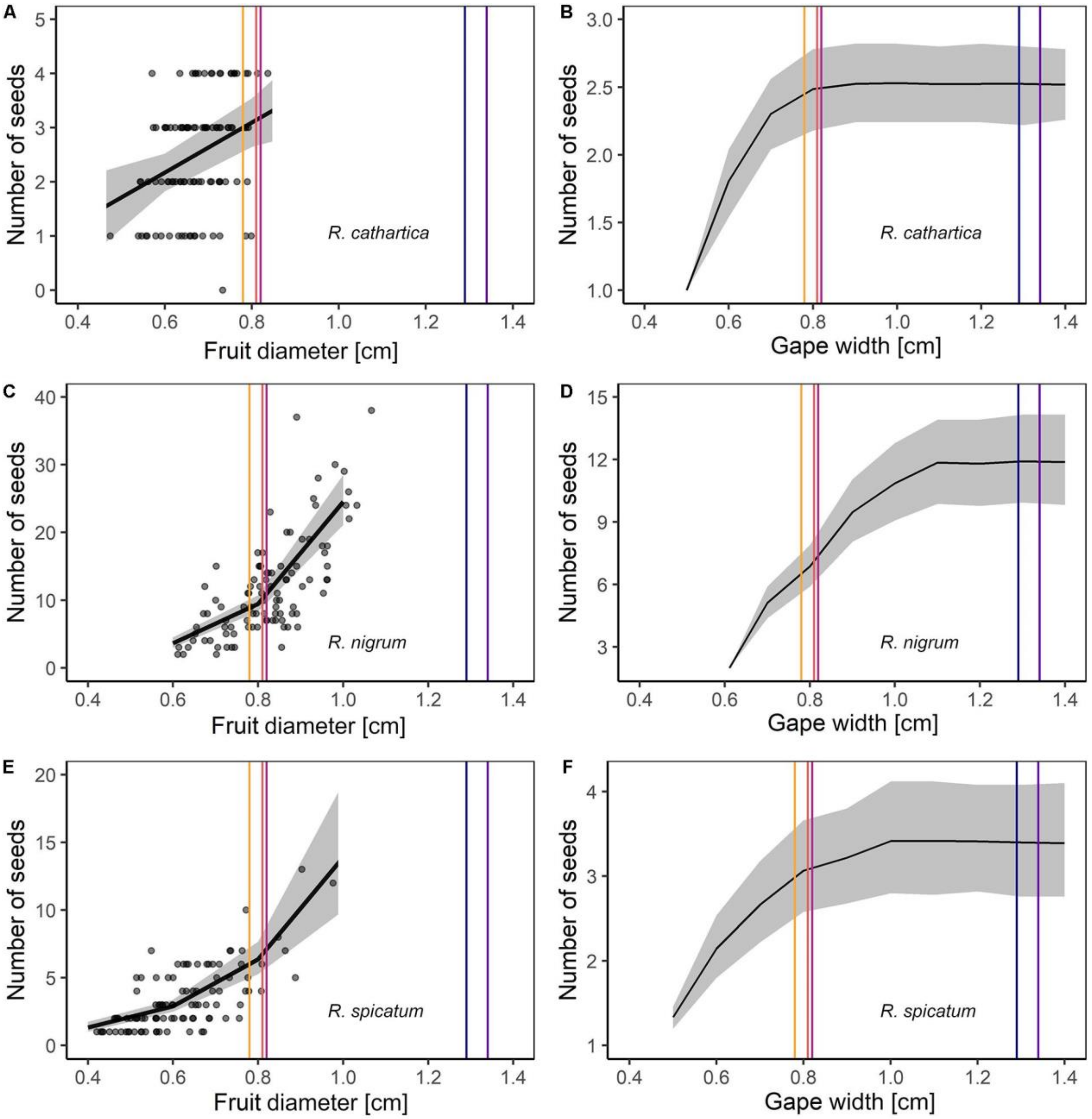

Fig. 5: (A, C, E) The number of seeds per fruit in relation to fruit diameter and (B, D, F) the predicted number of seeds per fruit taken up by animals depending on their gape width in *Rhamnus cathartica* (A, B), *Ribes nigrum* (C, D) and *Ribes spicatum* (E, F). The number of seeds per fruit was not related to the diameter of fruits in the other study species in Białowieża Forest, Poland. Shaded areas indicate the 95% confidence intervals. The colored vertical lines display the mean gape width of the most important animal dispersers of the plant species (but *M. martes* with a gape width > 2 cm). Please see Fig. 2 for more information.

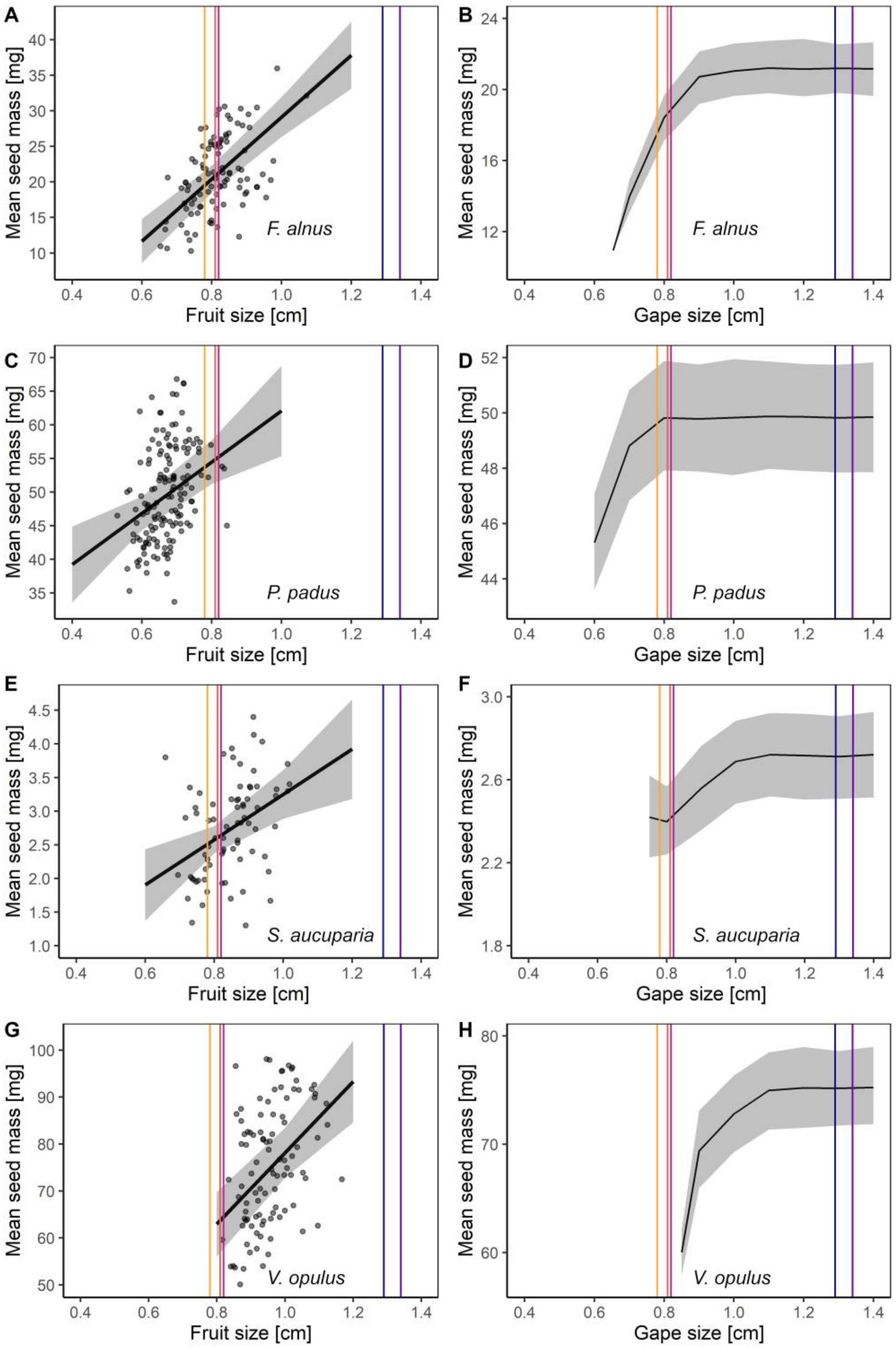

Fig. 6: The mean mass of seeds per fruit in relation to fruit diameter (A, C, E, G) and the mean mass of seeds per fruit taken up by animal dispersers depending on their gape width (B, D, F, H) in *F. alnus* (A, B), *P. padus* (C, D), *S. aucuparia* (E, F) and *V. opulus* (G, H). In *S. nigra*, mean mass of seeds per fruit was related to fruit diameter, but the largest fruit was 0.617 cm and, thus, too small to induce gape-size limitations in the main disperser. Shaded areas indicate the 95% confidence intervals. The colored vertical lines display the mean gape width of the most important animal dispersers of the plant species (but *M. martes* with a gape width > 2 cm). Please see Fig. 2 for more information.

2.4. Discussion

The importance of within-species trait variation in structuring species interactions such as seed dispersal has long been noted (Wheelwright 1985, Jordano 1995b), but only recently ecologists have started to investigate the eco-evolutionary consequences (Herrera 2009, Bolnick et al. 2011, González-Varo & Traveset 2016, Des Roches et al. 2018, Schupp et al. 2019, Snell et al. 2019). Our study showed that the community-wide trait variation in fruit diameter of plants and the gape width of frugivores is large among species, but also considerable within species. Every plant species produced fruits of a size that could be swallowed by the six seed disperser species previously shown to be quantitatively important for seed dispersal in this community (Albrecht et al. 2013). Only the fruits of *V. opulus* were too large to be consumed and dispersed by all main seed disperser species. However, these fruits are usually eaten several months after their appearance, when they have become smaller due to desiccation (Hernández 2009). The dried, smaller fruits provide a food source in winter that is accessible even to small-gaped dispersers (Hernández 2009). Consequently, mismatches in size between plants and their disperser are rare in temperate forests at the species level (González-Varo & Traveset 2016), which might render the associated seed dispersal processes relatively robust against anthropogenic pressures (Albrecht et al. 2013, 2014, Farwig et al. 2017, Emer et al. 2019).

By contrast, at the subindividual plant level, the fruit choices of small-gaped seed dispersers were limited for the plants *F. alnus*, *R. nigrum*, and *S. aucuparia*, with the main small-gaped seed dispersers being able to feed only on 31–55% of the accessible fruits. Such size mismatches between dispersers and fruits may in part explain why 47–78% of the fruits in previously described populations of *F. alnus* remained undispersed (Hampe 2008, Szewczyk et al. 2019). However, because the fruit size of each plant species varied more strongly within than between individuals, the main seed dispersers were still able to feed on the fruits of individual plants (except those of large-fruited *V. opulus*). On average, plants were able to interact with animals, whose gape width was 0.082 cm smaller, only due to subindividual trait variation in fruit size. These tiny differences in size could correspond to a potential increase of 0-7 disperser species (mean = 2.1) at the level of plant individuals. Herrera (2009) found that, in terms of the total variation in fruit size, subindividual variation was larger than variation among individuals in 20 of 25 fleshy-fruited plant species. Together, these findings indicate that the large subindividual trait variation is characteristic for fleshy-fruited plant species, and allows for a broader range of interaction partners than would be expected based on the mean fruit sizes of plant species in plant-frugivore communities.

The number of disperser species did not decline with increasing fruit diameter, although species with larger gape widths preferentially fed on larger fruits. Large-gaped frugivores were usually heavier (Supplementary information 1.2) and their feeding on energy-rich resources would maximize their energy intake (Albrecht et al. 2018a, b, Quintero et al. 2020). An increase in preferred fruit size with increasing gape width has been observed in other plant-frugivore communities as well, especially in tropical ecosystems, where at the species level there is a much larger trait variation in both fruit diameter and gape width (Wheelwright 1985, Jordano 1987, Lambert 1989, Noma & Yumoto 1997, Moran & Caterall 2010, Burns 2013, Chen & Moles 2015, Dehling et al. 2016, Bender et al. 2018). Even within the same plant species, dispersers not limited by gape width were shown to preferentially feed on larger fruits (Sallabanks 1993, Sobral et al. 2010).

In previous studies, birds were observed to peck rather than to swallow fruits that were larger than their gape (Levey 1987, Rey et al. 1997, Hernández 2008, Rey 2011), but the birds were either kept under captive conditions and forced to feed on the fruits (Levey 1987, Rey et al. 1997) or large fruits were the only food resource in the close vicinity (Hernández 2008, Rey 2011). In our study, there was no evidence of pecking with increasing fruit diameter, as the pecking of fruits was very rarely observed during fruit removal (< 2% of all interactions). In addition, pecking may reflect responses other than gape-size limitations, such as difficulty in approaching less accessible fruits or exploratory probing (Supplementary figure S3). These observations suggest that fruit pecking is not frequently used to overcome gape-size limitations, at least in most seed dispersers and as long as multiple food sources are available. A recent study likewise showed that the diet and body conditions of the small-gaped Sardinian warbler *Curruca melanocephala* could be primarily predicted by the local density of accessible fruits, not by the total fruit density (González-Varo et al. 2021).

The finding that no plant species only produced fruits larger than the gapes of *E. rubecula*, *S. atricpilla*, and *S. borin* suggests more effective seed dispersal by the six main seed dispersers than by the three large-gaped seed dispersers (*T. merula*, *T. philomelos*, and *M. martes*) alone. For fruit plants, interactions with many seed disperser species may increase the overall quantity of dispersed seeds, the probability of plant recruitment, and therefore parental fitness (Herrera 1984, Schupp et al. 2010). In addition, the reliance on a large diversity of seed disperser species provides a bet-hedging strategy of plant individuals to guarantee constant seed dispersal even during years when the population sizes of single disperser species are low (Herrera 1998, Blüthgen et al. 2016). This suggests that subindividual variation in plant traits can influence the fecundity of plant species and may thus be under selection (Herrera 2009, 2017), especially in animal-dispersed plants (Jordano 1995b, Sobral et al. 2013, 2019). However, rather than increases or decreases in subindividual trait variation *per se*, natural selection might affect the variation in fruit diameter among plant individuals to promote interactions with key seed dispersers.

Our study showed that fruit diameter correlated positively with the number or the mean mass of seeds in eight of the nine studied plant species. This suggests that a positive relationship between fruit diameter and seed traits is common in fleshy-fruited plants, in line with the findings of many single-species studies (e.g., Herrera 1988, Sallabanks 1993, Herrera et al. 1994, Jordano 1995b, Alcantera & Rey 2003, Hernandez 2009, Rodriguez-Perez & Traveset 2010, González-Castro et al. 2019, Traveset et al. 2019, Carvalho et al 2021). Potential mismatches between gapes and fruits can, therefore, decrease the mass and the number of dispersed seeds in small-gaped dispersers, as this was shown for four of the nine studied plant species. Even small differences in the gape width among species, such as those between *E. rubecula* (gape width = 0.78 cm) and *S. atricapilla* (0.82 cm) or *S. borin* (0.83 cm), might be large enough to induce selective pressures on fruit traits on the long-term.

A similar pattern was found in an *in-situ* study conducted in the Mediterranean areas, where for *Olea europea* the fruit choice by dispersers was limited by their gape size (Rey et al. 1997). The positive correlation between fruit size and seed size (Alcantara & Rey 2003) also explains the smaller seeds dispersed by *S. atricapilla* than by large-gaped *T. philomelos* (González-Varo et al. 2014). For the spurge olive *Cneuorum tricoccon*, larger seeds were found in the scat of *M. martes* than in that of small-gaped lizards (Traveset et al. 2019). Even in aggregated fruits such as *Rubus* spp., avian frugivores may select for seeds of different sizes by selecting fruits of different sizes (e.g., Jordano 1984b). Seed size can, in turn, affect the post-dispersal regeneration of plants. Larger seeds are usually less susceptible to soil pathogens and produce larger seedlings, especially in adverse environments, but they may also be poorly dispersed (Murray et al. 1993, Leishman et al. 2000, Fricke et al. 2019, González-Castro et al. 2019). This suggests that gape-size limitations play a pivotal role in seed dispersal and influence the effectiveness of seed disperser species by constraining the efficiency of fruit handling (Schupp et al. 2010), even in small-fruited plants. This mechanism provides an explanation how the co-evolution of large seeds and animal seed dispersal started from small seeds 80 million years ago (Eriksson 2016). However, as the effect of seed size on plant performance during and after seed dispersal may differ between plant species and disperser species, the effects of gape-size limitations on the efficiency of seed dispersal may not always be straightforward (Fricke et al. 2019, Schupp et al. 2019). The consequences of the patterns identified in this work may be a promising avenue for future research (e.g., Fricke et al. 2019, Carvalho et al. 2021).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, or are available online from Dryad Digital Repository https://doi.org/10.5061/dryad.0vt4b8gzk (Rehling et al., 2021).

Ethic statement

Ethical review and approval was not required for the animal study because this study relied on previously published data and indirect methods for assessing the behaviour of animals.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary Material

The Supplementary Material for this article can be found online at:
https://www.frontiersin.org/articles/10.3389/fevo.2021.698885/full#supplementary-material

2.5. References

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2.6. Supplementary Material

Table S1. Fruit and sample size of woody plants in Białowieża Forest.

No.	Plants	Fruit diameter (cm)		Sample size	
		Albrecht et al. 2018	This study	No. of individuals	No. of fruit
1	*Cornus sanguinea*	0.68	-	-	-
2	*Crataegis monogyna*	0.93	-	-	-
3	*Euonymus europaeus*	0.51	0.61	15	151
4	*Euonymus verrucosus*	0.51	-	-	-
5	*Frangula alnus*	0.69	0.82	12	101
6	*Lonicera xylosteum*	0.93	-	-	-
7	*Prunus padus*	0.79	0.67	15	151
8	*Rhamnus cathartica*	0.74	0.67	12	102
9	*Ribes alpinum*	0.63	-	-	-
10	*Ribes nigrum*	0.73	0.82	13	101
11	*Ribes spicatum*	0.62	0.61	12	99
12	*Rubus idaeus*	1.23	-	-	-
13	*Sambucus nigra*	0.40	0.51	7	100
14	*Sorbus aucuparia*	0.93	0.83	15	107
15	*Viburnum opulus*	0.74	0.96	14	100

Table S2. List of frugivores of fleshy-fruited plants in Białowieża Forest.

ID	Frugivore species	Occurence	Class	Gape width (cm)			
				study	**Jordano**	**Herrera**	**Collection**
1	*Apodemus flavicollis*	B	Mammalia	≥ 2.0			
2	*Bos bonasus*	D	Mammalia	≥ 2.0			
3	*Carpodacus erythrinus*	D	Aves	0.99**			
4	*Cervus elaphus*	D	Mammalia	≥ 2.0			
5	*Coccothraustes coccothraustes*	B	Aves	1.63		1.63	1.41
6	*Columba palumbus*	B	Aves	1.16			1.16
7	*Dendrocopos leucotos*	R	Aves	1.7			1.7
8	*Dendrocopos major*	B	Aves	0.96			0.96
9	*Dendrocopos medius*	R	Aves	0.91			0.91
10	*Dryocopus martius*	R	Aves	2.05			2.05
11	*Dryomys nitedula*	D	Mammalia	≥ 2.0			
12	*Erithacus rubecula*	B	Aves	0.78	0.77	0.8	0.61
13	*Ficedula hypoleuca*	R	Aves	0.78	0.77	0.79	0.75
14	*Ficedula parva*	R	Aves	0.4			0.4
15	*Fringilla coelebs*	R	Aves	0.80		0.8	0.74
16	*Garrulus glandarius*	B	Aves	1.88		1.88	1.53
17	*Hippolais icterina*	R	Aves	0.78			0.78
18	*Luscinia luscinia*	B	Aves	0.92			0.92
19	*Martes martes*	B	Mammalia	≥ 2.0			
20	*Muscardinus avellanarius*	B	Mammalia	≥ 2.0			
21	*Muscicapa striata*	R	Aves	0.84	0.88	0.8	0.8
22	*Myodes glareolus*	D	Mammalia	≥ 2.0			
23	*Oriolus oriolus*	R	Aves	1.33			1.33
24	*Parus major*	B	Aves	0.73		0.73	0.58
25	*Periparus ater*	R	Aves	0.53		0.53	0.36
26	*Phylloscopus trochilus*	R	Aves	0.52	0.49	0.55	0.53
27	*Poecile palustris*	R	Aves	0.43			0.43
28	*Prunella modularis*	D	Aves	0.68		0.68	
29	*Pyrrhula pyrrhula*	D	Aves	1.02		1.02	0.93
30	*Sciurus vulgaris*	B	Mammalia	≥ 2.0			
31	*Sitta europaea*	R	Aves	0.83		0.83	0.7
32	*Sus scrofa*	D*	Mammalia	≥ 2.0			
33	*Sylvia atricapilla*	B	Aves	0.81	0.76	0.85	0.85
34	*Sylvia borin*	B	Aves	0.82	0.78	0.86	0.72
35	*Tetrastes bonasia*	R	Aves	1.17			1.17
36	*Turdus iliacus*	R	Aves	1.12	1.12		0.94
37	*Turdus merula*	B	Aves	1.34	1.35	1.34	1.33
38	*Turdus philomelos*	B	Aves	1.29	1.21	1.37	1.2
39	*Turdus pilaris*	R	Aves	1.10			1.1
40	*Turdus viscivorus*	B	Aves	1.27	1.27		1.03
41	*Vulpes vulpes*	D*	Mammalia	≥ 2.0			

Observation; information on whether frugivore species were observed based fruit removal observations (R, Albrecht et al. 2013), based on seed deposition pattern (D, Schlautmann et al. 2021), or based on both approaches (B).

Gape width; The width of gapes used in this study was based on three sources, measurements on mist-netting birds (Herrera 1984, Jordano 1984) and mounted individuals of an animal collection in the Philipps-University Marburg (‘Collection’).

*unpublished results.

**Estimated based on body mass and type of diet of the animal species (see supplementary figure S1)

Table S3: Proportion of fruits accessible to the main animal dispersers.

Plant species	**Main animal dispersers**					
	E. rubecula			***S. atricapilla***		
	Small	Intermediate	Large	Small	Intermediate	Large
	(0.734 cm)	(0.780 cm)	(0.826 cm)	(0.768 cm)	(0.810 cm)	(0.849 cm)
E. europaeus	0.93	0.98	0.99	0.97	0.99	1.00
F. alnus	0.14	0.31	0.59	0.26	0.47	0.72
P. padus	0.88	0.97	0.98	0.96	0.98	1.00
R. cathartica	0.78	0.90	0.99	0.90	0.98	1.00
R. spicatum	0.83	0.93	0.95	0.89	0.95	0.96
R. nigrum	0.21	0.30	0.52	0.26	0.43	0.61
S. nigra	1.00	1.00	1.00	1.00	1.00	1.00
S. aucuaparia	0.15	0.28	0.42	0.24	0.37	0.53
V. opulus	0.00	0.00	0.01	0.00	0.00	0.04
	S. borin			***M. martes, T. merula, T. philomelos***		
	Small	Intermediate	Large	Small	Intermediate	Large
	(0.772 cm)	(0.820 cm)	(0.867 cm)			
E. europaeus	0.97	0.99	1.00	1.00	1.00	1.00
F. alnus	0.26	0.54	0.76	1.00	1.00	1.00
P. padus	0.97	0.98	1.00	1.00	1.00	1.00
R. cathartica	0.90	0.99	1.00	1.00	1.00	1.00
R. spicatum	0.91	0.95	0.97	1.00	1.00	1.00
R. nigrum	0.26	0.48	0.69	1.00	1.00	1.00
S. nigra	1.00	1.00	1.00	1.00	1.00	1.00
S. aucuaparia	0.24	0.38	0.58	1.00	1.00	1.00
V. opulus	0.00	0.01	0.08	1.00	1.00	1.00

The proportion of accessible fruit depends on the gape width of the animal dispersers (in brackets).

Supplementary information and figure on estimating gape widths based on the body size of birds

We predicted the gape size of *Carpodacus erythrinus* by using body mass as a predictor. To do so, we used a linear model to test for the relationship between body mass and gape size of birds in Herrera (1984, Appendix). This relationship, however, is affected by the type of diet of the frugivores (body mass * diet interaction, $F_{2,34} = 23.55$, $p < 0.001$, Fig. S1). The information on the main diet of birds in Herrera (1984) was based on the Elton database (Wilman et al., 2014).

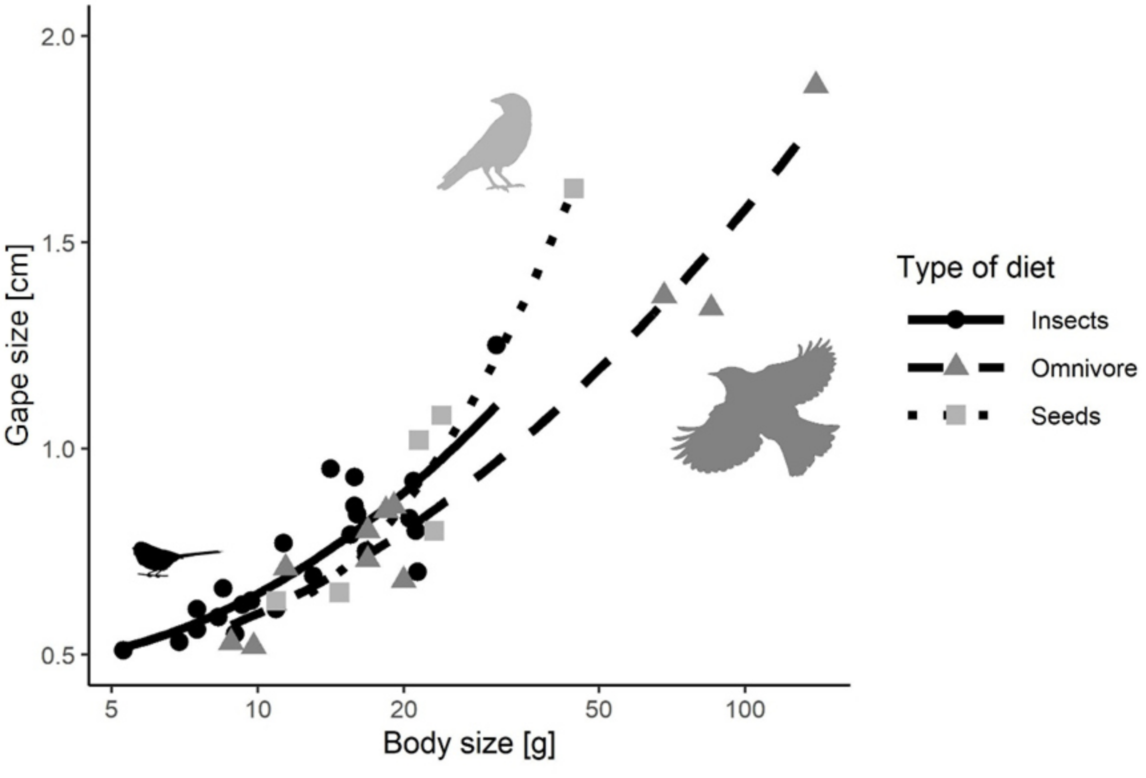
The gape size *y* of birds can be predicted by

$$y = 0.60826 - 0.55917x + 0.59909x^2 \text{ (Eqn 1)}$$

$$y = 0.51495 - 0.36283x + 0.44771x^2 \text{ (Eqn 2)}$$

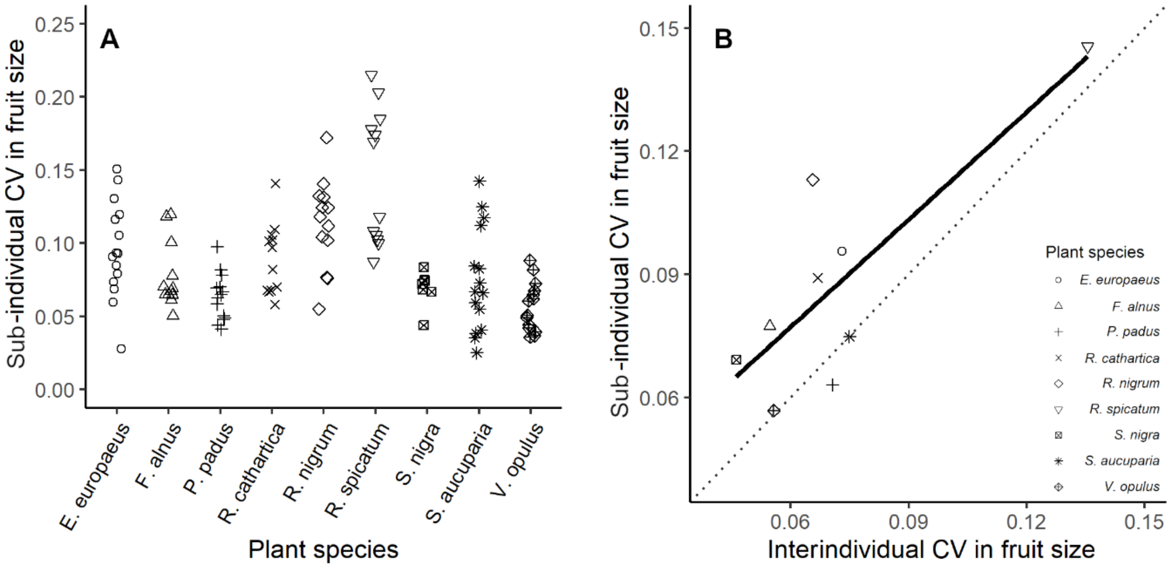
$$y = 2.35794 - 3.80050x + 2.03923x^2 \text{ (Eqn 3)}$$

where x is the log-transformed body size of bird species with an insectivorous diet (Eqn 1), an omnivorous diet (Eqn 2) or a diet mainly based on seeds (Eqn 3), respectively (Fig. S1).



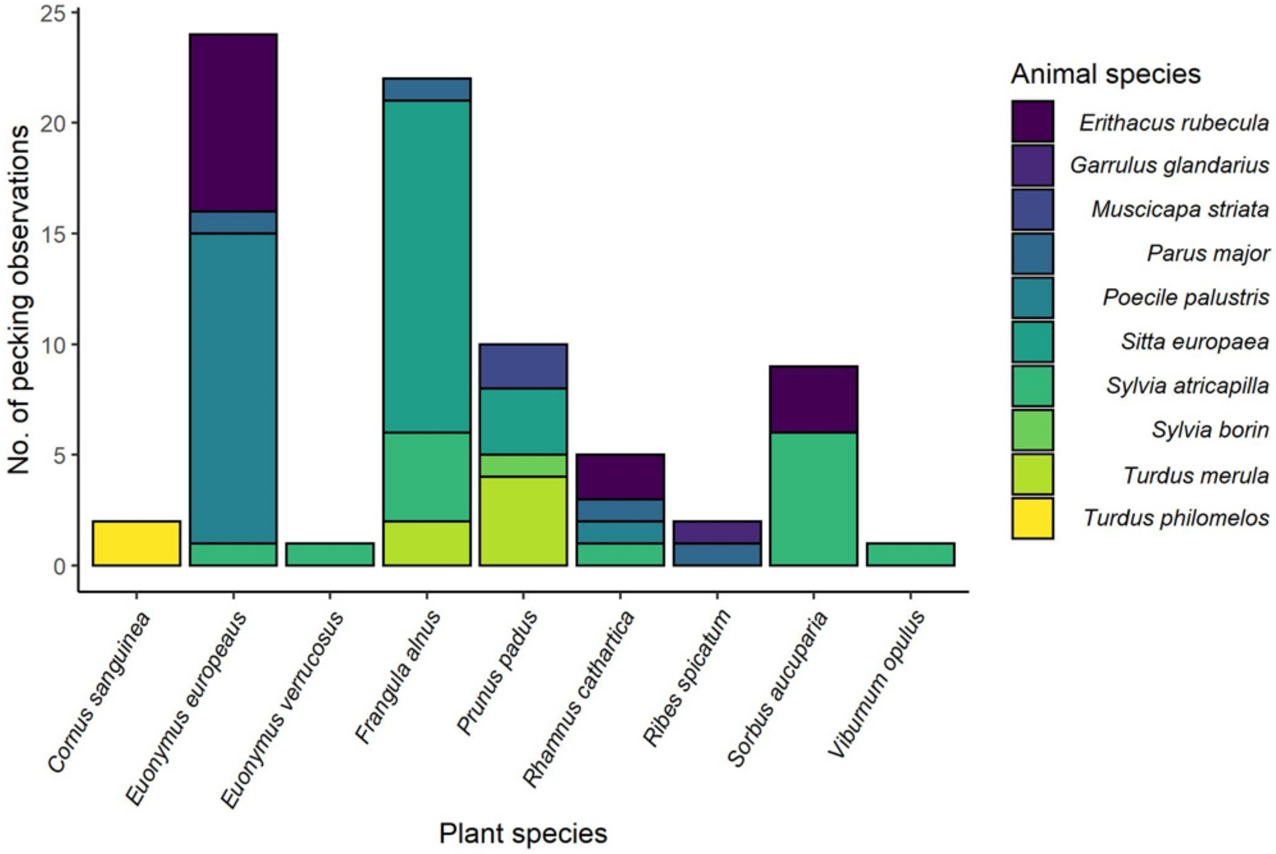
Supplementary figure S1. The relationship between body size and gape size of animals with different types of diet. The gape size of bird species and body size is based on Herrera (1984). Information about the diet of birds is based on the Elton database (Wilman et al. 2014). Note the log-scale for body size.

Correlation of sub-individual CV and interindividual CV among plants



Supplementary figure S2. (A) Coefficient of variation (CV) in fruit size of individuals of different fleshy-fruited plant species. (B) Correlation between mean sub-individual CV and interindividual CV in fruit size (n = 9, Spearman's ρ = 0.45, p = 0.230).

Pecking of fruits



Supplementary Figure S3. Total number of pecking attempts of different disperser species on fruits of different plant species during fruit removal observations in Albrecht et al. (2013).

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Chapter 3[b]: Forest degradation limits the quality and complementarity of animal seed dispersal

3.1. Abstract

When intact forests are degraded to secondary habitats, their structural heterogeneity and species communities are altered, with potential consequences for ecosystem functions including seed dispersal by frugivorous animals. While the quantity of seed dispersal by frugivorous animals is relatively robust towards forest degradation, the qualitative changes are poorly understood. In this study, extensive field sampling in Europe's last lowland primeval forest (Białowieża, Poland), DNA barcoding of animal-dispersed seeds, and a niche-based hypervolume approach were combined to evaluate the effect of forest degradation on the seed deposition patterns of frugivores along three forest microhabitats (canopy cover, ground vegetation, deadwood). Forest degradation was shown to (1) reduce the niche space of microhabitats important for plant recruitment by half, (2) homogenize seed deposition patterns of frugivores, and (3) increase the redundancy of low-quality seed deposition. Our study shows that the environmental heterogeneity of intact forests safeguards not only the diversity of animal and plant species but also the diversity of their interactions providing the basis for high-quality ecosystem functions.

3.2. Introduction

Humans have degraded >75% of forest ecosystems worldwide (Venter et al., 2016; Potapov et al., 2017), with much of the remaining intact forests at risk of degradation to secondary habitats (Mikusiński et al., 2018; Paiva et al., 2020; Namkhan et al., 2021). Forest degradation alters the forest's structure, reduces its overall biodiversity, and changes species interactions, which may ultimately lead to a functional "meltdown" of ecosystems and the services they provide to humans (Pecl et al., 2017; Watson et al., 2018). A key biotic function of ecosystems is seed dispersal by frugivorous animals, as it determines the spatial distribution and genetic composition of plants at small and large scales (Howe and Smallwood, 1982; Nathan, 2006; Rogers et al., 2021). Forest degradation results in a loss of frugivores and changes plant-frugivore interactions (Albrecht et al., 2013, 2014; Galetti et al., 2013; Rogers et al., 2021).

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However, because seed dispersal is characterized by a low specialization between plants and frugivores (Blüthgen et al., 2007; Albrecht et al., 2018b, 2018a; Rehling et al., 2021; Vizentin-Bugoni et al., 2021), it is largely insensitive to the loss of vulnerable frugivores in degraded areas, as it is instead maintained by other, less sensitive species (Moran et al., 2004; Kirika et al., 2008; Albrecht et al., 2013, 2014; Farwig et al., 2017; Vizentin-Bugoni et al., 2021). Consequently, seed dispersal is relatively robust to forest degradation (Zamora, 2000).

Most research on the effects of forest degradation on seed dispersal has been limited to quantitative investigations of seed dispersal, i.e., assessments of the number of removed fruits. However, the effectiveness of seed dispersal is also determined by qualitative factors, which determine the probability of a seed reaching maturity in a given environment (Schupp et al., 2010). In degraded habitats, quantitative compensation by generalist frugivores for the loss of fruit removal by specialists can mask severe declines in the effectiveness of seed dispersal, when changes in its quality are not detected (González-Varo et al., 2012; Rey and Alcántara, 2014). Forest degradation can alter the quality of seed dispersal via different pathways: by altering the availability and characteristics of microhabitats, especially those important for plant growth, including light conditions, plant competition, and herbivory rates (González-Varo et al., 2012; Rey and Alcántara, 2014; Bubnicki et al., 2019), and by changing the behavior of frugivores and their (non-)random use of microhabitats, thus altering patterns of seed deposition. For example, the direct deposition by frugivores of seeds in forest gaps will depend on the availability of those gaps and may differ in intact vs. degraded forests (Brodie et al., 2009; González-Varo et al., 2017). Little is known about qualitative changes in seed dispersal in degraded forests, mostly due to the difficulty in tracking the effect of frugivores on the later stages of seed dispersal in complex environments such as forest ecosystems (Wang and Smith, 2002; Rogers et al., 2019). However, with the aid of DNA barcoding, deposited seeds can be traced back to the frugivores responsible for their dispersal, and the effects of forest degradation on seed dispersal quality accordingly monitored (González-Varo et al., 2014, 2017; Schlautmann et al., 2021).

In this study, a comprehensive niche-based approach was used to investigate the effect of forest degradation on the seed deposition patterns of a diverse plant-frugivore community in the temperate lowland forest of Białowieża, Poland (Albrecht et al., 2013; Rehling et al., 2021; Schlautmann et al., 2021). The Białowieża Forest harbors a 45-km² old-growth forest that has largely remained intact, without substantial direct human interference. The remaining 625 km² of forest has been subjected to logging during the last century (Mikusiński et al., 2018; Jaroszewicz et al., 2019). For the purposes of our study, 12 sites (4 in the intact forest, 8 in the degraded forest, Table S1) were established, each with five transects. In those transects, three different microhabitat characteristics important for plant recruitment to the adult stage were recorded: canopy cover (as an inverse proxy for light availability), ground vegetation (as a proxy for seed predation and early competition), and the volume of deadwood (as an inverse proxy for the intensity of herbivory, as tree logs are often avoided by herbivores when top predators are present, thus reducing the intensity of herbivory close to the logs (van Ginkel et al., 2019)). In addition, ~4,000 seed-containing scats of frugivores were collected from the forest transects during three consecutive years and the dispersing frugivore species for each scat was identified using DNA barcoding (Schlautmann et al., 2021). With this approach, seed deposition by frugivores could be linked to forest microhabitats.

A hypervolume approach (Blonder et al., 2014) was subsequently applied to construct three-dimensional microhabitat spaces representing the intact and degraded forest (hereafter referred to as "forest microhabitat space") and therefore the niche space potentially available for seed deposition within those microhabitats. The number of deposited seeds in the transects was then used to construct the deposition microhabitat spaces of frugivores in each forest type (hereafter referred to as "deposition microhabitat spaces"). The activities of the three generalist frugivore species most important for fruit removal in Białowieża Forest (Albrecht et al., 2013), i.e., *Sylvia atricapilla* (blackcap), *Turdus merula* (blackbird), and *Turdus philomelos* (song thrush), were distinguished from those of the remaining 20 frugivores for which scats were collected and subsequently combined (hereafter referred to as "mixed dispersers"; Table S2). The resulting niche spaces were used to describe two independent properties influencing the quality of microhabitats for plant growth and therefore the quality of seed dispersal by frugivores (Schupp et al., 2010): (i) the volume of the microhabitat space (i.e., the niche space of available microhabitats), which was expected to correlate with the number of microhabitats supporting the persistence of plant species over time, and (ii) the centroid of the niche space, which was expected to directly influence the probability of a seed reaching maturity, because the microhabitat dimensions have been shown to correlate with plant fitness (Kollmann and Buschor, 2003; Brodie et al., 2009; van Ginkel et al., 2019) (see also Supplement S3). Bootstrapped subsamples of each microhabitat space were created to allow pair-wise comparisons of the volume or centroid between the microhabitat spaces of (i) intact and degraded forest, (2) each forest type and its frugivores (i.e. intact/degraded forest vs. frugivore community/species), and (3) the frugivores in each forest type. Comparisons of the centroids of the forest microhabitat spaces with those of the deposition microhabitat spaces of the frugivores revealed whether the seed deposition patterns of either the frugivore community or single species were random and thus whether those patterns corresponded to the availability of forest microhabitats. In addition, the fraction of the total volume of the deposition microhabitat space of the frugivore community filled by different combinations of single frugivores in intact vs. degraded forest was determined.

In studying the effect of forest degradation on the quality of seed dispersal we sought answers to the following questions: How does forest degradation affect the niche space and characteristics of forest microhabitats (canopy cover, ground vegetation, deadwood)? What is the impact of forest degradation on seed deposition by the frugivore community and by single frugivores therein? Do frugivores disperse seeds non-randomly depending on the forest type (in contrast to what would be expected based on the availability of microhabitats)? By depositing seeds in similar microhabitats, are frugivores functionally redundant or complementary during seed deposition in intact and degraded forests?

3.3. Results

The degraded forests of Białowieża Forest were characterized by correlated changes, both in the niche space and the characteristics of the forest microhabitats and in seed depositions by the frugivore community therein. The volume of the three-dimensional forest microhabitat space was 2.4 times larger in intact than in degraded forest (118 SD3 vs. 50 SD3, Fig. 1). This result could be attributed to the rarity in degraded forest of forest gaps with a very low canopy cover and of microhabitats with a large volume of deadwood (Fig. 1). In general, intact forest had a larger volume of deadwood (centroid: 143.5 vs. 51.0 m^3/ha, $p < 0.01$), denser ground vegetation (centroid: 34.7 vs. 31.4%, $p < 0.01$), and less canopy cover (centroid: 82.5 vs. 84.1%, $p = 0.03$) than degraded forest (Table S4).

The volume of the deposition microhabitat space of the frugivore community was ~2.7 times larger in intact than in degraded forest (102 SD^3 vs. 38 SD^3). The centroids of the forest microhabitat space in both forest types were largely equal to those of the deposition microhabitat space of the frugivore community ($p > 0.05$, Fig. 2, Table S5). However, in degraded forest, the frugivore community preferentially deposited seeds within microhabitats with a lower volume of deadwood and a denser ground vegetation, in contrast to what was expected based on the availability of forest microhabitats ($p < 0.01$, Fig. 2, Table S5).

At the level of single frugivores, both metrics of the deposition microhabitat space, i.e., volume and centroid, followed complex patterns in the two forest types (Fig. 2, 3). The deposition

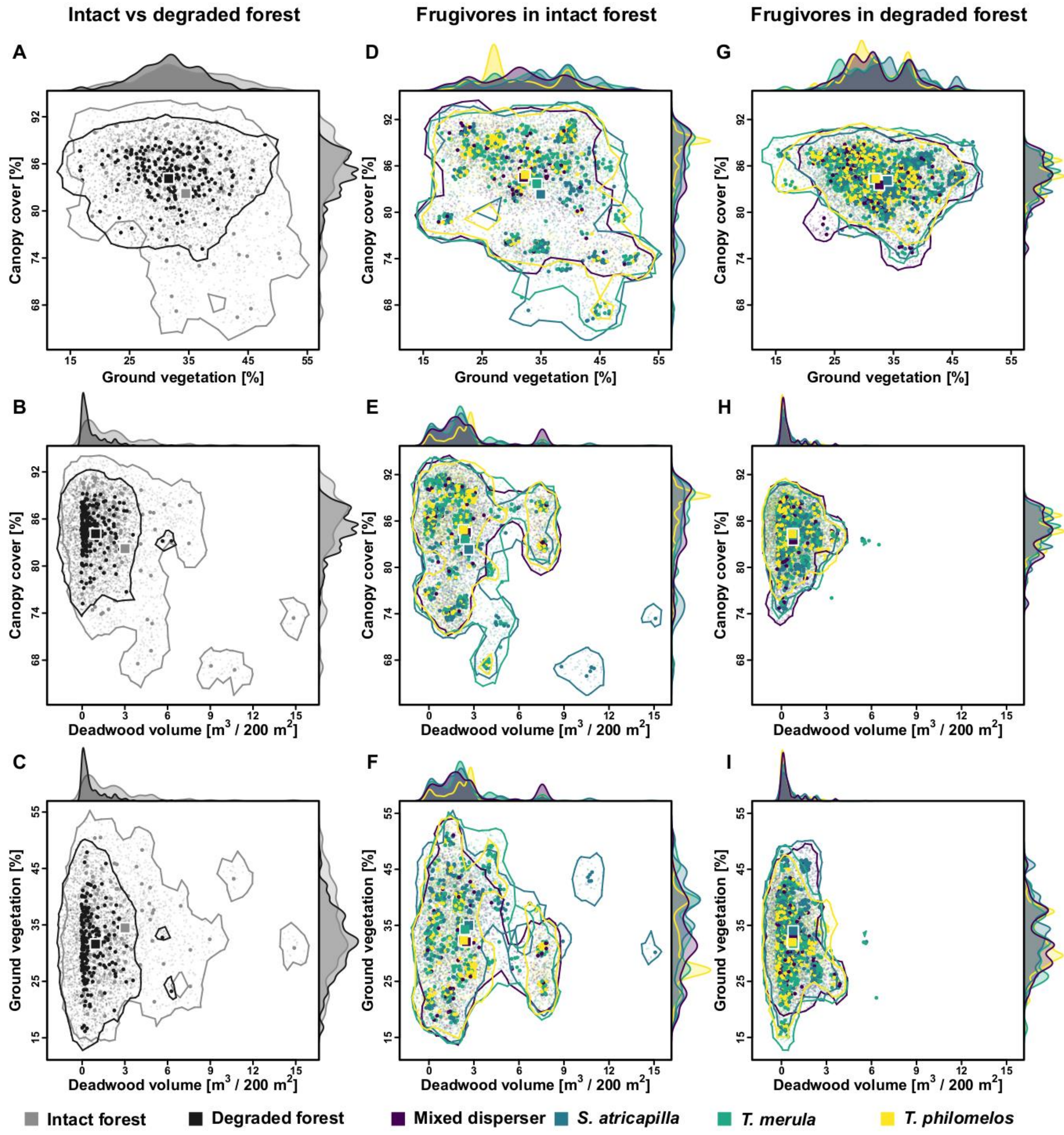

Fig. 1: The three-dimensional forest microhabitat space of intact and degraded forest in Białowieża Forest (left panels), and the deposition microhabitat space of frugivores (mixed dispersers, *S. atricapilla*, *T. merula*, *T. philomelos*) in intact (center panels) and degraded (right panels) forest, illustrated by two-dimensional representations of (top) canopy cover and ground vegetation, (center) canopy cover and the volume of deadwood, and (bottom) ground vegetation and the volume of deadwood. Circles represent the transect segments of the forest (left panels) or the deposited seeds of the frugivores therein (center and right panels). The centroids (squares) indicate the center of the forest (left panels) and the deposition microhabitat spaces (center and right panels) along each of the three environmental dimensions (canopy cover, ground vegetation, volume of deadwood).

microhabitat spaces of *S. atricapilla*, *T. merula*, and the mixed dispersers were generally larger than those of *T. philomelos*, independent of the forest type ($p \leq 0.04$, Fig. 3, Table S6). Furthermore, in intact forest, compared to the mixed dispersers and to *T. philomelos*, *S. atricapilla* deposited seeds more frequently in microhabitats characterized by a high light

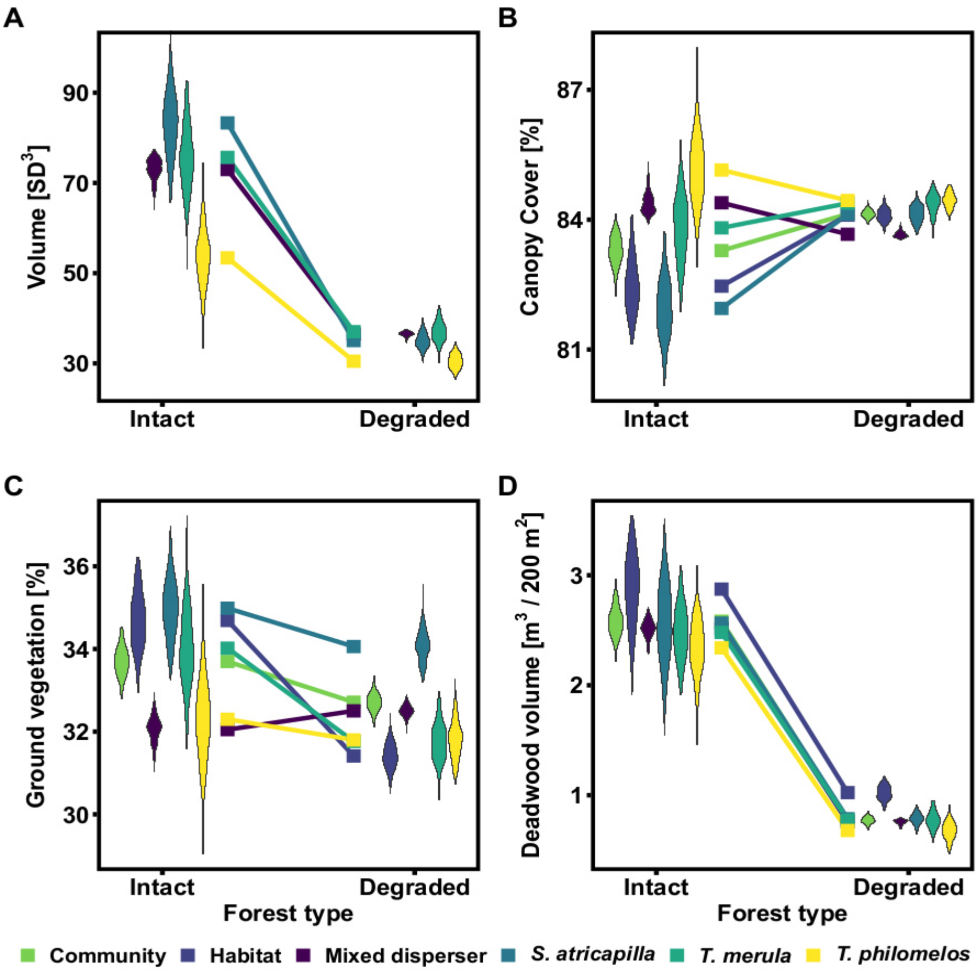

Fig. 2: (A) Volume of the deposition microhabitat space of single frugivore species (*S. atricapilla*, *T. merula*, *T. philomelos*, mixed dispersers) in Białowieża Forest, Poland. (B, C, D) Centroids of the forest microhabitat spaces and the deposition microhabitat spaces of the combined frugivore community and of single frugivores along the three environmental dimensions of forest microhabitats in intact and degraded forest: (A) canopy cover, (B), ground vegetation, (C) volume of deadwood.

availability and a dense ground vegetation (Figure 2, $p \leq 0.01$, Tables S7–S9). Differences in the volumes and centroids of the deposition microhabitat spaces between frugivores were more pronounced in intact than in degraded forest, especially with respect to canopy cover and ground vegetation (Fig. 2).

Comparisons between the seed deposition patterns of the frugivores and the microhabitat structure of the respective forest types showed that seed deposition by frugivores was non-random, but mostly at the level of single frugivores and only rarely at the level of the frugivore community. The frequent seed depositions of mixed dispersers and *T. philomelos* in microhabitats with a high canopy cover and less ground vegetation did not correspond to microhabitat availability, especially in intact forest but also often in degraded forest. *Sylvia atricapilla* deposited seeds significantly more often in microhabitats with extensive ground

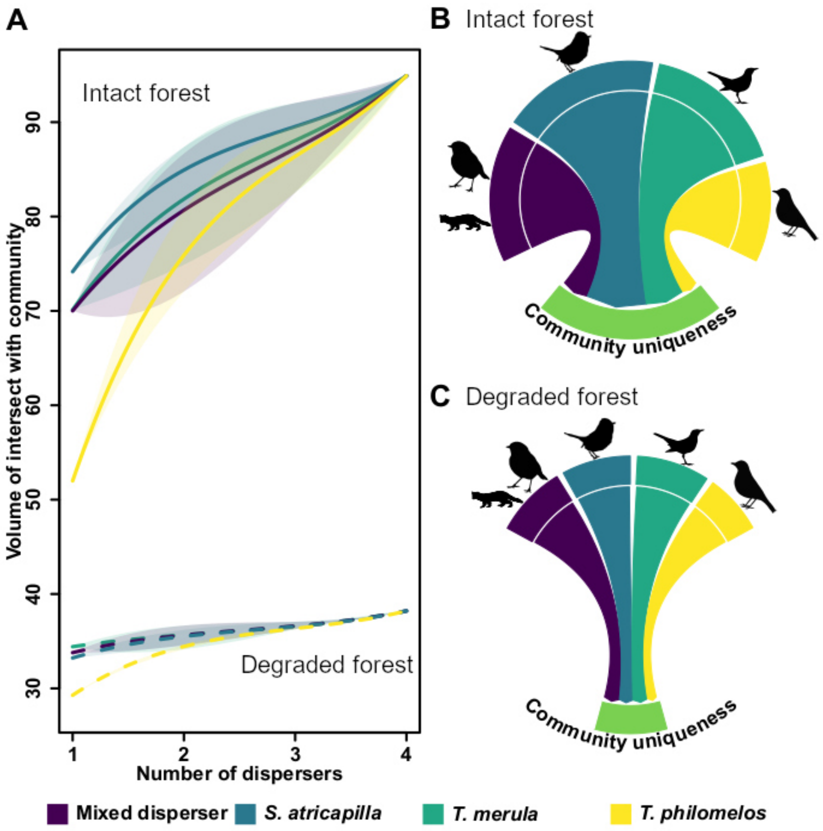

Fig. 3: (A) Volume of the deposition microhabitat space in intact (solid lines) and degraded (dotted lines) forest as a function of different combinations of single frugivores (*S. atricapilla*, *T. merula*, *T. philomelos*, mixed dispersers) in Białowieża Forest, Poland. The lines indicate the mean volume of the bootstrapped deposition microhabitat spaces for each combination of singles frugivores, and the shaded areas the best and worst combinations of the different single frugivores. (B, C) The volume and uniqueness of the deposition microhabitat space of the different frugivores, and the uniqueness of the community in the (B) intact and (C) degraded forest. The upper part of the chord-diagram shows the niche space of seed deposition (i.e. the volume of the microhabitat space) of the different frugivores; the lower chord-diagram shows the proportion of each frugivore's deposition to community uniqueness (i.e. part of the microhabitat space only filled by one frugivore), and the summed proportions of the uniqueness of depositions of single frugivores ('community uniqueness', light green).

vegetation. Similarly, in degraded forest, all frugivores deposited seeds in microhabitats with a smaller volume of deadwood with a higher frequency than would be expected by chance. Otherwise, the seed deposition patterns in both forest types mostly corresponded to the availability of microhabitats along the studied environmental dimensions (Table S10).

The amount of the deposition microhabitat space of the frugivore community filled by different combinations of single frugivores was examined in intact and degraded forest, as a measure of the complementarity of single frugivores to the seed deposition patterns of the community. In intact forest, 50–70% of the volume of the deposition microhabitat space of the community was filled by only one frugivore, with additional frugivores contributing an average of 15.0%, 7.3%, and 7.5% (Figure 3). The deposition microhabitat space of intact forest was consistently reduced when *T. philomelos* was part of the frugivore combination, because the deposition microhabitat space of this species was the smallest and it had the highest overlap with that of the other frugivores ($p \leq 0.03$, Fig. 2A, 3, Table S11). In degraded forest, the deposition microhabitat space of one frugivore accounted for 86% of the total volume of the community, and any combination of two frugivores resulted in a mean completeness of 92–96% of the total volume of the deposition microhabitat space.

3.4. Discussion

Our results showed that forest degradation simplified the forest structure—by altering the characteristics of forest microhabitats and reducing the available niche space—and thus homogenized the deposition patterns of frugivores across the reduced niche space. Single frugivores often provided non-random seed dispersal in certain microhabitats, especially within intact forest. However, the effects of those differences among those frugivores cancelled each other out, such that the overall deposition pattern of the frugivore community mostly corresponded to the structure of both forest types (intact and degraded). Ultimately, forest degradation increased the redundancy of low-quality seed deposition.

Pronounced changes in forest structure may partially explain the strong decline in forest specialists and large-bodied frugivores observed in previous studies of degraded forests (Albrecht et al., 2013, 2014; Farwig et al., 2017). Nevertheless, those studies also showed that, during fruit removal, small-bodied generalist bird species quantitatively compensate for the loss of frugivores in those forests. It was therefore concluded that forest degradation has only minor effects on the removal of fruits from small-fruited plants (Markl et al., 2012; Fontúrbel et al., 2015; Neuschulz et al., 2016; Rehling et al., 2021). However, our study revealed that, while the quantity of seed dispersal is robust, forest degradation strongly affects the quality of seed dispersal. Because the seed deposition patterns of the frugivores largely corresponded to the availability of microhabitats in each forest type, the narrowed niche space of the microhabitats in degraded forest led to an agglomeration of seeds in less heterogeneous microhabitats, i.e., those with a relatively small volume of deadwood and a high canopy cover. A decline in recruitment can thus be expected, as a diversity of forest microhabitats, including with respect to the availability of light and the volume of deadwood, foster plant regeneration (Brodie et al., 2009; Bubnicki et al., 2019). Accordingly, our study showed that the overall recruitment rate of seedlings was higher in intact than in degraded forest, and that greater light availability improved the early survival of first-year seedlings (Supplement S3). Thus, forest degradation may ultimately reduce plant population growth, especially the growth of light-dependent pioneer species, thereby altering plant composition compared to intact forest (Brodie et al., 2009; Rey and Alcántara, 2014; Bubnicki et al., 2019; Jaroszewicz et al., 2019).

Overall, our findings are a further demonstration of seed dispersal as a rather generalized plant-animal interaction (Blüthgen et al., 2007; Albrecht et al., 2018a, 2018b; Rehling et al., 2021; Vizentin-Bugoni et al., 2021). In tropical forests, bellbirds (Wenny and Levey, 1998), lemurs (Razafindratsima and Dunham, 2015), and muntjac deer (Brodie et al., 2009) show distinct seed deposition patterns in forest gaps. By contrast, the seed deposition patterns among the frugivores of Białowieża Forest were comparably small, and no single species played an outsized role in seed deposition within a certain microhabitat. These findings highlight that the key frugivores in temperate forests are small-bodied generalists that make use of microhabitats with similar characteristics. Functional similarities between frugivore species may explain why previous studies reported that frugivore abundance is usually more important than frugivore diversity for seed deposition in temperate forests (Garcia et al., 2010; García et al., 2018). However, even small differences between the deposition patterns of single frugivore species, as demonstrated herein for *S. atricapilla* (centroid = 81.95%) and *T. philomelos* (85.15%) along the canopy cover of intact forest, can lead to large increases in the survival of first-year seedlings (15% on average, up to 44% in *Viburnum opulus*, see Supplement S3). If these effects persist until plants reach reproduction (Wang and Smith, 2002), small-bodied frugivores will ultimately differ in the overall quality of their seed dispersal for the plant species and the plant community (Schupp et al., 2010).

Importantly, in our study differences in the deposition niche spaces of the different frugivore species occurred almost exclusively in intact forest. Thus, while the frugivores were functionally redundant in the degraded forest, they provided complementary functions in the intact forest. However, the need to pool all rare dispersers into a single group of mixed dispersers may have obscured more subtle differences in the complementarity of the contributing frugivore species. In isolation, the high redundancy of seed dispersal in degraded forests would seem to indicate its robustness towards forest degradation; yet, in truth, it should instead be interpreted as an increased homogenization of seed dispersal, with a reduction in the quality of seed dispersal compared to intact forests, resulting from a decrease in structural heterogeneity, species loss, and a loss of heterogeneous interactions (that is independent of species loss). A decrease in the functional complementarity of seed dispersal may pose a challenge to the population dynamics of plant species in degraded forests and may eventually modify the community composition of forest ecosystems.

Our study is one of the very few to show the shift in ecosystem function that accompanies forest degradation, evidenced by a shift from the high-quality, partially complementary functions of frugivores in complex environments to the low-quality, almost entirely redundant functions of those same frugivore species in simple environments (also described for plant-pollinator interactions (Burkle et al., 2013)). These observations evidence both the importance of heterogeneous environments in maintaining biodiversity and species interactions, and the need to ensure structural heterogeneity, not only at the landscape scale but also at the local scale, in order to preserve the ecosystem functions of forests (Garcia et al., 2010; García et al., 2018). The species losses that commonly follow anthropogenic disturbances imply a simultaneous loss of the complementary functions provided by other co-occurring species (McConkey and O'Farrill, 2016). The assumption that functional redundancy will protect species and ecosystem functions may thus be erroneous, if the original distributions and interactions of species are unknown (Rosenfeld, 2002). Our study demonstrates the need to incorporate qualitative aspects in assessments of the effects of forest degradation on biodiversity, ecosystem functionality, and the ecosystem services provided to humans.

3.5. Materials and Methods

3.5.1. Study area and sites

The study was conducted in Białowieża Forest, which spans the borders of Poland and Belarus and is the last intact forest in European lowlands. The Polish part of the forest (~675 km²) is divided into Białowieża National Park (~105 km²) and forests managed by the state forestry department. The forest is structurally rich and consists of a mosaic of unevenly aged, species-rich tree stands as well as a large amount of deadwood (Jaroszewicz et al., 2019). A 47.5-km² area within the current Białowieża National Park was protected as a royal hunting area before it was declared as a national park, such that it has remained largely pristine for roughly 500 years, with only minor disturbances by humans (Jaroszewicz et al., 2019). By contrast, in > 80% of the Polish part of the forest, commercial logging has been conducted since the First World War (Mikusiński et al., 2018; Jaroszewicz et al., 2019).

Our study was conducted at 12 of 17 sites previously used in studies of the interactions between frugivores and fleshy-fruited plants in the ash-alder floodplain forests of Białowieża Forest

(Albrecht et al., 2013, 2014, 2015; Farwig et al., 2017; Schlautmann et al., 2021). The 12 sites were scattered over ~ 400 km², covering two-thirds of the Polish part of Białowieża Forest. Pair-wise distances between study sites ranged from 1.5 to 23 km. Four study sites were situated in Białowieża National Park (stand age: ~70–150 years) and eight in the managed forests (stand age: ~60 years), referred to respectively herein as “intact” and “degraded” forest.

3.5.2. Study species

Fourteen commonly occurring woody plant species producing fleshy fruits were included in this study: *Cornus sanguinea, Euonymus europaeus, Frangula alnus, Prunus padus, Rhamnus cathartica, Ribes alpinum, R. nigrum, R. spicatum, Rubus fruticosus agg., R. ideaus, Sambucus racemosa, S. nigra, Sorbus aucaparia, and Viburnum opulus.* The fruiting season of this plant community starts in mid-June, with *P. padus* and *R. spicatum*, and ends in mid-October, with *E. europaeus*. Although previous studies documented as many as 41 animal species acting as seed dispersers within the study sites (Schlautmann et al., 2021), we chose to examine seed deposition by *Sylvia atricapilla* (blackcap), *Turdus merula* (blackbird), and *T. philomelos* (song thrush), as they are among the quantitatively most important seed dispersers not only in Białowieża Forest (Albrecht et al., 2013; Schlautmann et al., 2021) but also in most of Europe (González-Varo et al., 2021). For the 20 other frugivores, made up of small- and large-bodied bird and mammal species and represented by their scats, a single “mixed dispersers” group was established (see Table S2).

3.5.3. Seed deposition

The seed deposition patterns of the four groups in Białowieża Forest from 2016 to 2018 were assessed along five transects per study site. These transects had a length of 100 m and were separated from each other by at least 20 m. Scats containing seeds of the plant species of interest found within a range of 1 m to the left and right of each transect (total area of 1000 m² per site) were collected. During the fruiting period of the plant community, the transects were checked every 10 days for new scats. This resulted in 11 repetitions of the transect walks in 2016 and 2018, and, due to a shorter fruiting season, 9 repetitions in 2017. In case of heavy rainfall events, scats were collected at least 2 days after they had ended. The scats of most mammals were identified in the field; otherwise, they were stored in sterile tubes at −20°C and analyzed following extraction of their DNA. A modification of the barcoding protocol (González-Varo et al., 2014) was used to extract DNA of animal origin from the surfaces of the deposited seeds (success rate = 90.1%). Additional information on disperser identification using DNA barcoding is provided in the Supplement S12.

3.5.4. Assessing microhabitats

To identify the microhabitats where frugivores deposited plant seeds, each transect was split into five 20-m-long segments and each deposited scat was then assigned to the closest segment. At each of these segments, the following microhabitats characteristics were recorded: canopy cover, ground vegetation cover, and the volume of deadwood. Canopy cover was determined based on up to six (5.4 ± 0.49) hemispherical photos taken at the center of each segment using a fish-eye lens. All photos were taken during the fruiting period (from June to October) and the area covered by forest canopy was then analyzed using DHPT 1.0 (Loffredo et al., 2016). Canopy cover was calculated as the mean of the forest coverage as depicted in up to six photos. In addition, the relative coverage of vegetation at heights of 0 m, 0.5 m, and 1 m located within a radius of 10 m around the center of each transect segment was estimated. Ground vegetation was calculated as the mean vegetation cover across the different heights. The amount of deadwood was determined within a range of 5 m to the right and left of the transect, by measuring the diameter and length of all dead tree logs with a minimum diameter of 10 cm and the diameter and height of all tree stumps with a minimum height of 50 cm. The measurements were made in August 2017. The volume of deadwood was calculated as the sum of standing or lying deadwood per transect segment.

3.5.5. Statistical analyses

The microhabitat niche space of the seed deposition sites of the different frugivores was calculated based on the data obtained from 100 transect segments in the intact forest (5 segments × 5 transects × 4 sites) and 200 transect segments in the degraded forest (5 segments × 5 transects × 8 sites). One segment was excluded from the analyses because ~1,000 scats, mostly of *S. atricapilla*, containing seeds of *S. nigra* were found underneath a parental plant of the same species, which thus acted as a hub tree in the forest matrix and affected the overall seed deposition pattern of the local plant-frugivore community.

The analyses were conducted using a hypervolume approach with a Gaussian kernel density estimation, which allowed a relatively loose fit of the data by the hypervolume and the inclusion of data points away from the centroid (Blonder et al., 2014; Blonder, 2018). Standardized canopy cover, ground vegetation, and the volume of deadwood were used as environmental dimensions of the hypervolume to assess the niche space of microhabitats in intact and degraded forest (“forest microhabitat space”) and the seed deposition of frugivores therein (“deposition microhabitat space”). The deposition microhabitat spaces of *S. atricapilla, T. merula*, and *T. philomelos* were evaluated separately; however, those of the remaining 20 dispersers were combined, due to the low number of replicates (Table S2). In addition, the deposition microhabitat space of the frugivore community was assessed in intact and degraded forest, by combining the microhabitat spaces of the three frugivore species and the mixed dispersers in intact and degraded forest, respectively. The volume of the deposition microhabitat space increased with the number of replicates. To correct for differences in the volume of the deposition microhabitat space due to difference in the sample size of the transect segments and frugivores, 55 (lowest n of a single frugivore = 61) and 150 (lowest n = 157, respectively) replicates of the locations (forest type) and scats (frugivore species) in the intact and degraded forest, respectively, were subsampled. Uncertainties in the microhabitat spaces of the forest type and in the deposition of frugivores were determined by bootstrapping (n = 200) the subsamples without replacement and then creating the forest microhabitat spaces and the deposition microhabitat spaces of single frugivores and the frugivore community for each subsample as described above. A constant bandwidth over all bootstraps was maintained using the mean of the Silverman estimates of all combinations of forest type × frugivore × bootstrap subsample for the forest microhabitat space and the deposition microhabitat space of single frugivores, respectively.

Statistical analyses of microhabitat spaces remain a challenge (Blonder, 2018), and, to our knowledge, the use of an integrated approach is currently not possible. Thus, instead, the volumes and centroids of the bootstrapped subsamples of the forest and seed deposition microhabitats were compared pair-wise to determine the probability that the value of one group was larger than that of another group (based on two-tailed p-values). The comparisons were aimed at determining: (1) whether forest degradation affects the availability and characteristics of forest microhabitats, based on comparisons of the volumes and centroids of intact and degraded forest; (2) whether seed deposition by the frugivore community corresponds to the availability of forest microhabitats, based on comparisons of the centroids of the forest microhabitat space with the centroids of the deposition microhabitat space of the frugivore community in intact and degraded forest; (3) whether frugivores in either forest type differ in their seed deposition patterns, based on comparisons of the volumes and centroids of the deposition microhabitat spaces of different frugivores in intact and degraded forest; and (4) whether seed deposition by single frugivores in certain forest microhabitats in either forest type is non-random, based on comparisons of the centroids of the forest microhabitat space and the deposition microhabitat space of single frugivores in intact and degraded forest. All statistical analyses were performed using R version 4.1.1 (R Core Team, 2021), and the hypervolumes were created using the package ‘hypervolume’ version 2.0.12 (Blonder and Harris, 2019).

Data availability statement

The original contributions and R code presented in the study are included in the article, Supplementary Material, or will be made available online from Dryad Digital Repository https://doi.org/10.5061/dryad.wdbrv15q1.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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3.7. Supplementary Material

for "Forest degradation limits the quality and complementarity of animal seed dispersal"

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The supplementary materials include:

Supplementary information text S1 and S2
Figures S1
Tables S1 to S11
SI References

Table S1. Geographical coordinates, the number of scats and the forest types of the 12 study sites in Białowieża forest, Eastern Poland.

plot	N_scats	Latitude	Longitude	Forest type
013	371	52.832209	23.772104	Degraded
015	287	52.691722	23.840740	Degraded
030	268	52.688673	23.877749	Degraded
035	268	52.854070	23.729802	Degraded
036	210	52.872765	23.722445	Degraded
102	7	52.703070	23.653528	Degraded
112	330	52.733813	23.789229	Degraded
203	113	52.704294	23.622402	Degraded
301	429	52.742522	23.833125	Intact
303	277	52.789420	23.844638	Intact
314	70	23.844638	23.822146	Intact
315	132	52.798711	23.826023	Intact

Table S2. List of frugivores depositing seeds in Białowieża forest, Eastern Poland.

Disperser	# scats in degraded forest	# scats in intact forest	class
Turdus merula	363	622	Aves
Turdus philomelos	260	515	Aves
Sylvia atricapilla	224	560	Aves
Erithacus rubecula	21	32	Aves
Martes martes	16	14	Mammal
Sylvia borin	8	66	Aves
Dryomys nitedula	4	NA	Mammal
Dendrocopos major	3	2	Aves
Luscinia luscinia	3	NA	Aves
Bos bonasus	1	NA	Mammal
Carpodacus erythrinus	1	11	Aves
Cervus elaphus	1	5	Mammal
Myodes glareolus	1	2	Mammal
Sciurus vulgaris	1	NA	Mammal
Turdus viscivorus	1	NA	Aves
Coccothraustes coccothraustes	NA	8	Aves
Pyrrhula pyrrhula	NA	5	Aves
Muscardinus avellanarius	NA	4	Mammal
Garrulus glandarius	NA	3	Aves
Parus major	NA	2	Aves
Apodemus flavicollis	NA	1	Mammal
Columba palumbus	NA	1	Aves
Prunella modularis	NA	1	Aves

3.7.1. Supplementary information text 1: Regeneration pattern of the fleshy-fruited plant species

Results and discussion

The rate of seedling recruitment and the first-year survival of seedlings was studied along the canopy cover gradient and the ground vegetation gradient in intact and degraded forest (Figure S1, Table S3). In short, the recruitment rate of seedlings of the fleshy-fruited plant species was higher in intact than degraded forest (Fig. S1A). Independent of forest type, seedling recruitment of the plant species was higher in microhabitats with a less dense ground vegetation (Fig. S1B). Seedling recruitment was not related to canopy cover, but early survival of seedlings was higher in light environments for *E. europaeus*, *F. alnus*, *S. aucuparia* and *V. opulus*, but not that of *R. spicatum* (Fig. S1C). The forest type and ground vegetation did not affect early survival of seedlings (Table S2).

Although we did not directly study the effect of the volume of deadwood on plant regeneration of the fleshy-fruited plant community, other studies have shown that the seed germination and seedling growth of fleshy-fruited plant species was improved on deadwood (Eriksson & Fröborg, 1996, García-Rodríguez et al. *submitted*). In addition, the presence of large tree logs altered browsing patterns of large herbivores in the Białowieża Forest (Bubnicki et al., 2019;

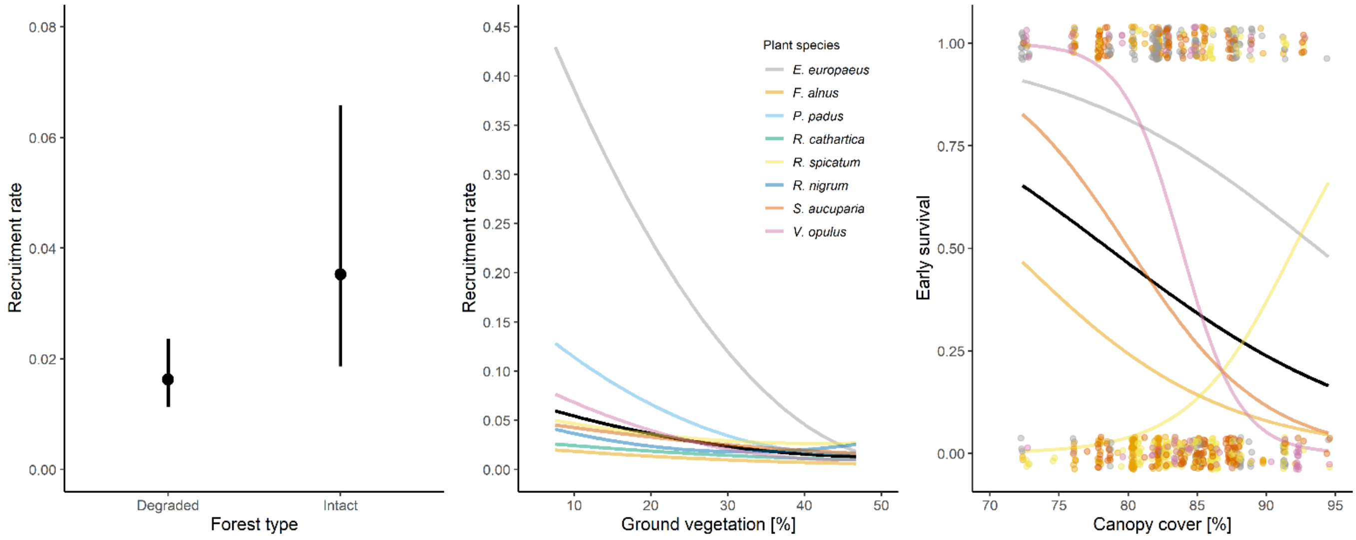

Fig. S1: Seedling recruitment in the peak year and early survival of the fleshy-fruited plant community in Białowieża Forest, Poland. (A) The effect of forest type (intact vs. degraded) on seedling recruitment. Mean ± 95%CI. (B) The relationship between ground vegetation and seedling recruitment. (C) The relationship between canopy cover and early survival of the seedlings. In (B) and (C), the black line represents the predicted mean of the plant community, and the coloured lines represent the mean of the plant species.

Table S3: Mixed model analyses of variance of the effects of standardized canopy cover, standardized ground vegetation and forest type on the recruitment rate and early survival of seedlings of 8 fleshy-fruited plant species in Białowieża, Poland.

	Recruitment rate				Early survival		
	df	χ^2	p		df	χ^2	p
Fixed effects				Fixed effects			
Forest type	1	7.21	**0.007**	Forest type	1	2.02	0.154
z-Ground vegetation	1	10.64	**0.001**	z-Ground vegetation	1	2.71	0.100
z-Canopy cover	1	2.20	0.138	z-Canopy cover	1	5.10	**0.024**
Forest * Vegetation	1	2.64	0.104	Plant species	4	45.34	**<0.001**
Forest * Canopy	1	0.07	0.784	Forest * Vegetation	1	2.74	0.098
Vegetation * Canopy	1	0.26	0.612	Forest * Canopy	1	0.46	0.499
Forest * Vegetation * Canopy	1	1.89	0.169	Vegetation * Canopy	1	0.63	0.429
Residuals	324			Forest * Species	4	5.22	0.266
				Vegetation * Species	4	7.54	0.110
				Canopy * Species	4	18.82	**0.001**
				Forest * Vegetation * Canopy	1	1.46	0.228
				Forest * Vegetation * Species	4	8.16	0.086
				Forest * Canopy * Species	4	2.92	0.571
				Vegetation * Canopy * Species	4	6.80	0.147
				Forest * Veg. * Can. * Spec.	4	5.93	0.205
				Residuals	538		
Random effects				Random effects			
Plots	41			Sites	7		
Plant species	7						
Species * Forest type	7						
OLRE	332						

Early survival of seedlings was analyzed only for a subset of plant species (n = 5). The effect of plant species was included as a fixed effect in this analysis.

van Ginkel et al., 2019). These studies together with our own findings support the expectation that the microhabitat characteristics used in the main manuscript (canopy cover, ground vegetation, volume of deadwood) affect plant regeneration of the studied fleshy-fruited plant community in the Białowieża Forest.

Material & Methods

Sowing experiments

We conducted *in situ*-sowing experiments from 2016-2018 at four study sites (2 in degraded forest, 2 in intact forest) that we also used for the study of seed deposition (main document).

Each year, we collected fruits of at least six conspecific adults of the nine plant species in each forest type, removed the pulp, dried the seeds for 48 h at room temperature and mixed them afterwards. Because the introduction of external genetic material into the intact forest was prohibited, we used seeds from the intact forest only for sowing experiments in the intact forest and seeds from the degraded forest only in the degraded forest. We established 10 plots at each of the four study sites. At these 40 plots, we established one subplot per plant species and sowed 25 seeds within an area of 50 cm x 50 cm in 2016. In 2017 and 2018, we repeated these sowing experiments and established new subplots next to the plots established in 2016, but in 2017 we sowed them only at ten of the twenty locations in each forest type. One study site was partially flooded in 2017, and another one in 2018 in the degraded forest. Thus, we established one additional study site in 2018, and in 2019 in degraded forest (n of study sites = 42 in total). *Sambucus nigra* did not occur in the intact forest and was only studied in the degraded forest. Due to late frosts in spring, *P. padus* did not produce any fruits in 2016 and 2017 and was only studied in 2018. Taken together, we performed sowing experiments with nine fleshy-fruited plant species at four study sites, and at each study site, we established 10 plots with independent species-specific subplots for three years of sowing experiments; 2016 (n = 40 subplots), 2017 (n = 20) and 2018 (n = 40). This results in 2,500 sown seeds for seven of the nine plant species, 1,250 for *S. nigra* (only degraded forest) and 1,000 for *P. padus* (only in 2018).

To check for external seed input in our sowing experiments, we counted seedlings of the plant species on 'control' plots next to each subplot once in the first year after sowing. Control plots had the same area (50 cm^2), but no sown seeds. We found only four seedlings on these 'control' subplots over the three years (one seedling of *F. alnus* and *R. cathartica* and two seedlings of *R. spicatum*), indicating no relevant external seed input into our sowing experiments.

In 2016, we sowed the seeds directly after their collection. However, no seedlings of the plant community emerged in the year of sowing indicating that seeds of the fleshy-fruited plant community need cold-stratification before germination (Baskin & Baskin, 2014). For logistic reasons, in 2017 and 2018 we stored the depulped seeds after their collection in a fridge at 4-8 °C and sowed seeds of all species at the same time in late September. From 2017 to 2019, we checked all subplots for the number of emerging seedlings once in June.

To investigate first-year survival of the seedlings of the plant community, we tracked the survival of the emerging seedlings from the sowing experiments. In addition, we searched for seedlings at eight study sites, that we used for studies on seed removal and seed deposition of the frugivore-plant community from 2017 to 2019 (Albrecht et al., 2013, 2014; Farwig et al., 2017; Schlautmann et al., 2021). We only considered seedlings with cotyledons. We were able track the survival of 477 seedlings as part of the sowing experiment, and 101 seedlings that 'naturally' occurred in the forest.

Assessing microhabitats

At the 40 plots used for the sowing experiment, and at the locations where we investigated the survival of first-year seedlings, we used the same method to estimate canopy cover and vegetation density as for the seed deposition pattern of the frugivores (see material and method section of main document). However, for logistic reasons, we performed the microhabitat assessment at these locations up to three times, and used the mean values for the analyses.

Statistical analyses

Sowing experiment

To analyse the effect of the interaction between the microhabitat dimensions and forest type on the recruitment pattern of the plant species, we used a mark-recapture design which assumes that all seeds in the soil remain viable throughout the study period, i.e. if seeds had not recruited in the first year, seeds were able to recruit in the next year. However, we found that the recruitment pattern and seed bank dynamics were very variable among plant species. For example, some plant species (*F. alnus*, *R. cathartica*, *R. nigrum*, *S. aucuparia*) only recruited in the first year and did not produce a persistent seed bank. *Ribes spicatum* recruited especially in the first year, but kept on recruiting from a seed bank afterwards. *Euonymus europaeus* and *Viburnum opulus* germinated either entirely (*V. opulus*) or in particular (*E. europaeus*) in the second year, and both species produced a persistent seed bank from which they kept recruiting afterwards. This resulted in differences in the number of replicates for study year for different plant species. In addition, for some year × forest type × plant species combinations, we did not find recruiting seedlings (zero-observations). Especially, *Sambucus nigra* recruited very poorly overall (n = 4 seedlings, ~0.3% germination rate). To allow a full-factorial approach of analyzing the data, we entirely excluded *S. nigra* from the analyses, pooled the data from the sowing experiment among years and analysed only the year of peak recruitment for each plant species (assuming that the high recruitment rate of *P. padus* in the first year resembles its peak recruitment year).

We used a generalised linear mixed model (binomial error distribution and a logit link) with the number of seedlings in the year of peak recruitment (successes) and the number of seeds that had remained in the soil until then (failures) as a response variable (binomial denominator). We used the standardized canopy cover, the standardized mean of ground vegetation, the forest type (intact vs. degraded) and their interactions as fixed factors in this model. We included a maximal random effects structure (Barr et al., 2013) by including random intercepts for the species and the plots, and random slopes for the species responses to forest type. In these models, we also included observation level random effects (Harrison 2014) to account for overdispersion.

First-year survival of seedlings

To analyse the effect of the interaction between microhabitat dimensions and forest type on early survival of seedlings, we used a generalized linear mixed model (binomial error distribution and a logit link) with survival as a binary response variable, the standardized canopy cover, the standardized mean of ground vegetation, the forest type (intact vs. degraded) and their interactions as fixed factors, and the study site as a random effect. To allow a non-zero fit of the data, we pooled seedlings from different study years. However, in 2016 and 2017, *P. padus* barely produced viable seeds. Thus, the number of seedlings of *P. padus* was very low in our study period (four individuals). In addition, the number of surviving seedlings of *R. nigrum* was very low (six individuals), and surviving seedlings of *R. cathartica* and *S. nigra* were spatially aggregated (only at two locations within the study sites). We thus excluded these four plant species from the analysis, and included plant species ($n = 5$, too low to estimate random intercepts and slopes) and their interactions with canopy cover, ground vegetation and forest type as fixed factors in the analysis (number of tracked seedlings for each species: *E. europaeus* = 179, *F. alnus* = 54, *R. spicatum* = 155, *S. aucuparia* = 127, *V. opulus* = 63).

All statistical analyses were conducted using the R program version 4.0.3 (R Core Team, 2020). Generalized linear mixed models were constructed using the package glmmTMB version 1.0.2.1 (Brooks et al., 2017). Significance values for the effect of fixed factors were obtained using Wald-χ^2 tests (type II sums of squares) in the package car version 3.0-9 (Fox & Weisberg, 2019).

Table S4. Pairwise comparisons of the centroids of the forest microhabitat space in the intact and degraded forest of Białowieża forest, Eastern Poland. Significant differences at the α = 0.05 level are highlighted in boldface. Mean volumes and 95 % confidence intervals are shown.

Habitat 1	Habitat 2	Centroid habitat 1	Centroid habitat 2	*P*
Canopy cover [%]				
Intact	**Degraded**	**82.5 [81.3 – 83.9]**	**84.1 [83.8 – 84.4]**	**0.03**
Ground cover [%]				
Intact	**Degraded**	**34.7 [33.3 – 36.0]**	**31.4 [30.8 – 32.0]**	**< 0.01**
Deadwood volume [m^3 / 200 m^2]				
Intact	**Degraded**	**2.87 [2.19 – 3.44]**	**1.02 [0.89 – 1.14]**	**< 0.01**

Table S5. Pairwise comparisons of the environmental centroids of the forest microhabitat space and the deposition microhabitat space of the frugivore community in the intact and degraded forest of Białowieża forest, Eastern Poland. Significant differences at the α = 0.05 level are highlighted in boldface. Mean (± 95% CI) is shown.

Intact forest

Habitat	Community	Centroid habitat	Centroid community	*P*
		Canopy cover [%]		
Habitat	Community	82.5 [81.3 – 83.9]	83.3 [82.5 – 83.9]	0.28
		Ground cover [%]		
Habitat	Community	34.7 [33.3 – 36.0]	33.7 [32.9 – 33.4]	0.2
		Deadwood volume [m^3 / 200 m^2]		
Habitat	Community	2.87 [2.19 – 3.44]	2.58 [2.34 – 2.83]	0.46

Degraded forest

Habitat	Community	Centroid habitat	Centroid community	*P*
		Canopy cover [%]		
Habitat	Community	84.1 [83.8 – 84.4]	84.1 [83.9 – 84.3]	0.92
		Ground cover [%]		
Habitat	**Community**	**31.4 [30.8 – 32.0]**	**32.7 [32.2 – 33.2]**	**< 0.01**
		Deadwood volume [m^3 / 200 m^2]		
Habitat	**Community**	**1.02 [0.89 – 1.14]**	**0.77 [0.71 – 0.83]**	**< 0.01**

Table S6. Pairwise comparison of the volume of the deposition microhabitat space [SD^3] between different combinations of frugivores in the intact and degraded forest. Significant differences at the $\alpha = 0.05$ level are highlighted in boldface. Mean (± 95% CI) is shown.

Disperser 1	Disperser 2	Volume disperser 1	Volume disperser 2	*P*
Intact forest				
Mixed disperser	*S. atricapilla*	73 [67.4 - 76.5]	83.3 [68.6 - 96.5]	0.17
Mixed disperser	*T. merula*	73 [67.4 - 76.5]	75.7 [62.3 - 90.2]	0.77
Mixed disperser	***T. philomelos***	**73 [67.4 - 76.5]**	**53.4 [40 - 66.1]**	**0.02**
S. atricapilla	*T. merula*	83.3 [68.6 - 96.5]	75.7 [62.3 - 90.2]	0.51
S. atricapilla	***T. philomelos***	**83.3 [68.6 - 96.5]**	**53.4 [40 - 66.1]**	**< 0.01**
T. merula	***T. philomelos***	**75.7 [62.3 - 90.2]**	**53.4 [40 - 66.1]**	**0.01**
Degraded forest				
Mixed disperser	*S. atricapilla*	36.5 [35 - 37.3]	35.1 [31.9 - 38.8]	0.46
Mixed disperser	*T. merula*	36.5 [35 - 37.3]	37 [33.2 - 41.6]	0.87
Mixed disperser	***T. philomelos***	**36.5 [35 - 37.3]**	**30.5 [27.2 - 33.7]**	**< 0.01**
S. atricapilla	*T. merula*	35.1 [31.9 - 38.8]	37 [33.2 - 41.6]	0.49
S. atricapilla	***T. philomelos***	**35.1 [31.9 - 38.8]**	**30.5 [27.2 - 33.7]**	**0.04**
T. merula	***T. philomelos***	**37 [33.2 - 41.6]**	**30.5 [27.2 - 33.7]**	**0.02**

Table S7. Pairwise comparisons of the volume reduction [SD³] due to forest degradation between different combinations of frugivores. Significant differences at the α = 0.05 level are highlighted in boldface. Mean (± 95% CI) is shown.

Disperser 1	Disperser 2	Slope disperser 1	Slope disperser 2	*P*
Mixed disperser	*S. atricapilla*	- 36.5 [- 31.1 - - 40.5]	- 48.2 [-34.5 - - 62.6]	0.11
Mixed disperser	*T. merula*	- 36.5 [- 31.1 - - 40.5]	- 38.6 [-54.2 - - 24.6]	0.84
Mixed disperser	***T. philomelos***	**- 36.5 [- 31.1 - - 40.5]**	**-22.9 [- 36.5 - - 10.3]**	**0.04**
S. atricapilla	*T. merula*	- 48.2 [-34.5 - - 62.6]	- 38.6 [-54.2 - - 24.6]	0.38
S. atricapilla	***T. philomelos***	**- 48.2 [-34.5 - - 62.6]**	**-22.9 [- 36.5 - - 10.3]**	**< 0.01**
T. merula	*T. philomelos*	- 38.6 [-24.6 - - 54.2]	-22.9 [- 36.5 - - 10.3]	0.16

Table S8. Pairwise comparisons of the environmental centroids of the deposition microhabitat space between different combinations of frugivore species in the intact forest. Significant differences at the α = 0.05 level are highlighted in boldface. Rescaled mean centroid positions and 95 % confidence intervals are shown.

Disperser 1	Disperser 2	Centroid position 1	Centroid position 2	*P*
		Canopy cover [%]		
Mixed disperser	***S. atricapilla***	**84.39 [84 - 84.97]**	**81.95 [80.63 - 83.34]**	**< 0.01**
Mixed disperser	*T. merula*	84.39 [84 - 84.97]	83.81 [82.06 - 85.13]	0.48
Mixed disperser	*T. philomelos*	84.39 [84 - 84.97]	85.15 [83.61 - 86.64]	0.43
S. atricapilla	*T. merula*	81.95 [80.63 - 83.34]	83.81 [82.06 - 85.13]	0.10
S. atricapilla	***T. philomelos***	**81.95 [80.63 - 83.34]**	**85.15 [83.61 - 86.64]**	**< 0.01**
T. merula	*T. philomelos*	83.81 [82.06 - 85.13]	85.15 [83.61 - 86.64]	0.20
		Ground cover [%]		
Mixed disperser	***S. atricapilla***	**32.05 [31.32 - 32.66]**	**34.99 [33.68 - 36.42]**	**< 0.01**
Mixed disperser	***T. merula***	**32.05 [31.32 - 32.66]**	**34.02 [32.09 - 35.85]**	**0.03**
Mixed disperser	*T. philomelos*	32.05 [31.32 - 32.66]	32.3 [30.56 - 34.32]	0.85
S. atricapilla	*T. merula*	34.99 [33.68 - 36.42]	34.02 [32.09 - 35.85]	0.42
S. atricapilla	***T. philomelos***	**34.99 [33.68 - 36.42]**	**32.3 [30.56 - 34.32]**	**0.03**
T. merula	*T. philomelos*	34.02 [32.09 - 35.85]	32.3 [30.56 - 34.32]	0.24
		Deadwood volume [m^3 / 200 m^2]		
Mixed disperser	*S. atricapilla*	2.52 [2.32 - 2.66]	2.57 [1.85 - 3.21]	0.93
Mixed disperser	*T. merula*	2.52 [2.32 - 2.66]	2.48 [2.01 - 2.97]	0.88
Mixed disperser	*T. philomelos*	2.52 [2.32 - 2.66]	2.34 [1.68 - 2.88]	0.57
S. atricapilla	*T. merula*	2.57 [1.85 - 3.21]	2.48 [2.01 - 2.97]	0.84
S. atricapilla	*T. philomelos*	2.57 [1.85 - 3.21]	2.34 [1.68 - 2.88]	0.61
T. merula	*T. philomelos*	2.48 [2.01 - 2.97]	2.34 [1.68 - 2.88]	0.69

Table S9. Pairwise comparisons of the environmental centroids of the deposition microhabitat space between different combinations of frugivore species in the degraded forest. Significant differences at the α = 0.05 level are highlighted in boldface. Rescaled mean centroid positions and 95 % confidence intervals are shown.

Disperser 1	Disperser 2	Centroid position 1	Centroid position 2	*P*
		Canopy cover [%]		
Mixed disperser	***S. atricapilla***	**83.66 [83.54 - 83.85]**	**84.13 [83.73 - 84.47]**	**< 0.01**
Mixed disperser	***T. merula***	**83.66 [83.54 - 83.85]**	**84.38 [83.92 - 84.78]**	**0.01**
Mixed disperser	***T. philomelos***	**83.66 [83.54 - 83.85]**	**84.44 [84.08 - 84.74]**	**< 0.01**
S. atricapilla	*T. merula*	84.13 [83.73 - 84.47]	84.38 [83.92 - 84.78]	0.42
S. atricapilla	*T. philomelos*	84.13 [83.73 - 84.47]	84.44 [84.08 - 84.74]	0.24
T. merula	*T. philomelos*	84.38 [83.92 - 84.78]	84.44 [84.08 - 84.74]	0.79
		Ground cover [%]		
Mixed disperser	***S. atricapilla***	**32.5 [32.21 - 32.79]**	**34.06 [33.36 - 34.76]**	**< 0.01**
Mixed disperser	*T. merula*	32.5 [32.21 - 32.79]	31.76 [30.81 - 32.79]	0.15
Mixed disperser	*T. philomelos*	32.5 [32.21 - 32.79]	31.8 [31 - 32.66]	0.18
S. atricapilla	***T. merula***	**34.06 [33.36 - 34.76]**	**31.76 [30.81 - 32.79]**	**< 0.01**
S. atricapilla	***T. philomelos***	**34.06 [33.36 - 34.76]**	**31.8 [31 - 32.66]**	**< 0.01**
T. merula	*T. philomelos*	31.76 [30.81 - 32.79]	31.8 [31 - 32.66]	0.86
		Deadwood volume [m^3 / 200 m^2]		
Mixed disperser	*S. atricapilla*	0.76 [0.7 - 0.78]	0.79 [0.69 - 0.87]	0.56
Mixed disperser	*T. merula*	0.76 [0.7 - 0.78]	0.77 [0.63 - 0.92]	0.89
Mixed disperser	*T. philomelos*	0.76 [0.7 - 0.78]	0.68 [0.49 - 0.86]	0.38
S. atricapilla	*T. merula*	0.79 [0.69 - 0.87]	0.77 [0.63 - 0.92]	0.93
S. atricapilla	*T. philomelos*	0.79 [0.69 - 0.87]	0.68 [0.49 - 0.86]	0.29
T. merula	*T. philomelos*	0.77 [0.63 - 0.92]	0.68 [0.49 - 0.86]	0.43

Table S10. Pairwise comparisons of the environmental centroids of the deposition microhabitat space and the forest microhabitat space for different combinations of frugivores and forest type. Significant differences at the α = 0.05 level are highlighted in boldface. Rescaled mean centroid positions and 95 % confidence intervals are shown.

Disperser	Habitat	Centroid position Disperser	Centroid position Habitat	*P*
Canopy cover				
Mixed disperser	**Intact**	**84.39 [84 - 84.97]**	**82.5 [81.3 – 83.9] %**	**0.01**
S. atricapilla	Intact	81.95 [80.63 - 83.34]	82.5 [81.3 – 83.9] %	0.6
T. merula	Intact	83.81 [82.06 - 85.13]	82.5 [81.3 – 83.9] %	0.23
T. philomelos	**Intact**	**85.15 [83.61 - 86.64]**	**82.5 [81.3 – 83.9] %**	**0.02**
Mixed disperser	**Degraded**	**83.66 [83.54 - 83.85]**	**84.1 [83.8 – 84.4] %**	**0.03**
S. atricapilla	Degraded	84.13 [83.73 - 84.47]	84.1 [83.8 – 84.4] %	0.91
T. merula	Degraded	84.38 [83.92 - 84.78]	84.1 [83.8 – 84.4] %	0.34
T. philomelos	Degraded	84.44 [84.08 - 84.74]	84.1 [83.8 – 84.4] %	0.16
Ground cover				
Mixed disperser	**Intact**	**32.05 [31.32 - 32.66]**	**34.7 [33.3 – 36.0]**	**< 0.01**
S. atricapilla	Intact	34.99 [33.68 - 36.42]	34.7 [33.3 – 36.0]	0.8
T. merula	Intact	34.02 [32.09 - 35.85]	34.7 [33.3 – 36.0]	0.56
T. philomelos	**Intact**	**32.3 [30.56 - 34.32]**	**34.7 [33.3 – 36.0]**	**0.04**
Mixed disperser	**Degraded**	**32.5 [32.21 - 32.79]**	**31.4 [30.8 – 32.0]**	**0.02**
S. atricapilla	**Degraded**	**34.06 [33.36 - 34.76]**	**31.4 [30.8 – 32.0]**	**< 0.01**
T. merula	Degraded	31.76 [30.81 - 32.79]	31.4 [30.8 – 32.0]	0.52
T. philomelos	Degraded	31.8 [31 - 32.66]	31.4 [30.8 – 32.0]	0.5
Deadwood volume				
Mixed disperser	Intact	2.52 [2.32 - 2.66]	2.87 [2.19 – 3.44]	0.32
S. atricapilla	Intact	2.57 [1.85 - 3.21]	2.87 [2.19 – 3.44]	0.57
T. merula	Intact	2.48 [2.01 - 2.97]	2.87 [2.19 – 3.44]	0.37
T. philomelos	Intact	2.34 [1.68 - 2.88]	2.87 [2.19 – 3.44]	0.21
Mixed disperser	**Degraded**	**0.76 [0.7 - 0.78]**	**1.02 [0.89 – 1.14]**	**< 0.01**
S. atricapilla	**Degraded**	**0.79 [0.69 - 0.87]**	**1.02 [0.89 – 1.14]**	**< 0.01**
T. merula	**Degraded**	**0.77 [0.63 - 0.92]**	**1.02 [0.89 – 1.14]**	**0.01**
T. philomelos	**Degraded**	**0.68 [0.49 - 0.86]**	**1.02 [0.89 – 1.14]**	**< 0.01**

Table S11. Pairwise comparison of the proportion of uniqueness between dispersers in intact and degraded forest. Significant differences at the α = 0.05 level are highlighted in boldface. Mean volumes and 95 % confidence intervals are shown.

Disperser 1	Disperser 2	Uniqueness 1 in %	Uniqueness 2 in %	*P*
		Intact forest		
Mixed disperser	***S. atricapilla***	**5.68 [3.57 – 8.95]**	**12.95 [7.01 - 19.1]**	**0.03**
Mixed disperser	*T. merula*	5.68 [3.57 – 8.95]	8.26 [4.10 – 13.5]	0.35
Mixed disperser	*T. philomelos*	5.68 [3.57 – 8.95]	3.3 [2.21 - 4.85]	0.07
S. atricapilla	*T. merula*	12.95 [7.01 - 19.1]	8.26 [4.10 – 13.5]	0.30
S. atricapilla	***T. philomelos***	**12.95 [7.01 - 19.1]**	**3.02 [2.17 – 4.37]**	**< 0.01**
T. merula	***T. philomelos***	**8.26 [4.10 – 13.5]**	**3.3 [2.21 - 4.85]**	**< 0.01**
		Degraded forest		
Mixed disperser	*S. atricapilla*	5.16 [3.34 - 7.36]	4.65 [2.89 – 7.21]	0.74
Mixed disperser	*T. merula*	5.16 [3.34 - 7.36]	5.07 [2.47 - 8.65]	0.94
Mixed disperser	***T. philomelos***	**5.16 [3.34 - 7.36]**	**3.89 [2.55 - 5.31]**	**0.03**
S. atricapilla	*T. merula*	4.65 [2.89 – 7.21]	5.07 [2.47 - 8.65]	0.91
S. atricapilla	*T. philomelos*	4.65 [2.89 – 7.21]	3.89 [2.55 - 5.31]	0.19
T. merula	*T. philomelos*	5.07 [2.47 - 8.65]	3.00 [2.09 - 4.12]	0.17

3.7.2. Supplementary information text 2: Frugivore identification via DNA barcoding

We performed DNA extractions in a laboratory dedicated to low DNA concentration procedures and included negative controls in each extraction to check for contamination. The following barcoding protocol was modified after González-Varo et al. (2014). Seed-containing scats, which were stored after field collection are referred to as samples. Scats, which contained 1 or 2 seeds were processed as a whole, scats with > 2 seeds were split.

For DNA extraction 500 µL of extraction buffer (0.1 M Tris HC ph 8, 0.1 M EDTA ph 8, 0.01 M NaCl, 0.5 % SDS), 6 µL of Proteinase K (20 mg / mL), 22 µL of PVP (10 %) and 8 mg of TCEP were added to the sample. The sample was then incubated at 50°C in a shaker (1500 rpm) for 1 h 40 min. After centrifugation (2 min at 10,000 rpm) the supernatant (400 – 450 µL) was transferred to a new 2.0 mL tube. 250 µL of binding buffer (5 M guanidine thiocyanate, 0.1 M Tris HCl ph 6.4, 0.02 M EDTA pH 8, 1.3 % Triton X-100) and 80 µL of silica suspension were added and the mix was incubated in a shaker (1,500 rpm) at room temperature for 1 h 40 min. After centrifugation (1 min at 3,500 rpm) the supernatant was discarded and the silica pellet – containing the DNA – was resuspended in 300 µL binding buffer and transferred to the columns (MoBiTec, Germany) lined with a glass microfiber filter (Whatman Grade DF/b 1.0 µm). After centrifugation (1 min at 13,000 rpm), the silica pellet was washed twice by adding 450 µL washing buffer (50 % ethanol, 0.01 M Tris HCl ph8, 0.001 M EDTA ph 8, 0.125 M NaCl) and subsequently centrifuged (1 min at 13,000 rpm). The columns were then placed in a new, clean tube and the DNA was eluted twice by centrifugation (1 min at 13,000 rpm), first with 50 µL of ultrapure water and then with 50 µL of diluted TE buffer (5 mM Tris HCl ph 8 and 0.1 mM EDTA ph 8).

The eluted DNA was subsequently amplified using PCR. The 30 µL volume of PCR cocktail contained 8 µL of sample DNA, 3 µL 1x-buffer, 1.2 µL $MgCl_2$ (2 mM), 1,05 µL BSA, 0.3 µL dNTPs (0.25 mM), 2 x 1.8 µL of forward and reverse primer (0.6 µM), 0.2 µL Taq (Bioline) and 12,65 µL ultrapure water. PCR amplification was done with primers COI-fsd-degF and COI-fsdR for degraded samples (González-Varo et al., 2017). Samples without successful amplification underwent a nested PCR where we used the COI-fsd-degF / COI-fsdR (González-Varo et al., 2017) primer set on the amplicon of AWCintF2 / AWCintR4 (avian DNA barcodes, Lijtmaer et al., 2012). The PCR was performed in a Biometra TOne cycler. Four minutes of initial denaturation at 94 °C were followed by 42 cycles of denaturation at 94°C, annealing at 54°C and extension for 72°C, each for 45s, respectively. The PCR was then finished with a final extension of 6 min at 72°C. After PCR amplification we used LGC Genomics (Berlin, Germany) or Macrogen Europe (Amsterdam, Netherlands) to purify and sequence the samples. The resulting sequences were edited with CodonCode Aligner (Version 9.0.1, CodonCode Corporation) and we used the Barcode of Life identification system (BOLD, Ratnasingham and Hebert 2007) to identify the disperser. For our analysis, we only used samples with a > 98% similarity to recorded sequences in BOLD. We successfully identified the disperser of 90.1% of our samples. In four instances, we found many scats containing seeds or regurgitations of seeds (n = 49, 60, 132, 826) directly underneath a single fruiting tree individual. In these cases, we only barcoded a subset of the samples (n = 14, 27, 28, 260, respectively) and extrapolated the relative contribution of the identified dispersers to the entire seed rain.

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Chapter 4[c]: How many seeds do animals have to disperse for a tree to grow?

4.1. Abstract

Mutualistic interactions are beneficial for each contributing partner. Apart from the immediate effects, however, how mutualistic interactions influence partners in real-world ecosystems in the long-term is insufficiently understood. Here, we used spatial integral projection models to link seed dispersal of 20 animal species to the demography of the fleshy-fruited tree *F. alnus*. Our analysis showed that animal dispersal increased the population growth of *F. alnus* through improved germination and through the deposition of seeds in favourable habitats. Seed dispersal by gravity, nevertheless, led to population growth close to equilibrium indicating that animal-dispersed plants might potentially be independent of the mutualism. The effectiveness of animals for seed dispersal was strongly related to the quantity of removed fruit. Modelling species extinctions therefore predicted the loss of seed dispersal with the loss of interactions rather than species. We conclude that conserving the abundance of participating individuals ensures the functionality of mutualisms in species-rich communities.

4.2. Introduction

Mutualisms are by definition beneficial for each contributing partner, structure the (co-)evolution of species, and contribute to the functioning of ecosystems (Hutchinson 1959, Bronstein 1994, Loreau 2020). Seed dispersal by frugivorous animals is a provision-service mutualism: in return for the provided pulp of fruits (Snow & Snow 1988, Jordano 2014, Albrecht et al. 2018), animals deposit seeds in favourable microhabitats, help plants to colonize new habitats and provide long-distance dispersal (e.g. Howe & Smallwood 1982, Wenny 2001, Nathan 200). However, evidence for the benefits of animal seed dispersal for plant populations has often been indirect. It was determined, for example, through changes in the spatial genetic structure of parental plants and their offspring (Ismail et al., 2017; Wandrag et al., 2017), through studies observing disrupted patterns of plant regeneration after animal dispersers had become extinct (Christian, 2001; Terborgh et al., 2008; Galetti et al., 2013; Correa et al., 2015; Wandrag et al., 2017), or through mechanistic or simulation modelling of dispersal (Doughty

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et al., 2016; Szewczyk et al., 2019; Fedriani et al., 2020). Direct investigations of the effects of animal seed dispersal on the full life cycle of plants are surprisingly rare (Godínez-Alvarez et al., 2002; Brodie et al., 2009; Loayza and Knight, 2010; Yang et al., 2011; Rey and Alcántara, 2014; Horvitz et al., 2015). This is perhaps due to the difficulty of linking the behaviour of animals to their later effects on plant populations in complex environments (Wang and Smith, 2002; Rogers et al., 2019). Studies that tracked the fate of animal-dispersed seeds to the early recruitment of plants suggest that animal species strongly differ in the amount of fruits removed and in the sites of seed deposition (Bascompte et al., 2003; Jordano et al., 2007; Donoso et al., 2016; González-Varo et al., 2017; Timóteo et al., 2018; Rumeu et al., 2020). Although multiple animals act as seed dispersers of plants, seed dispersal to favourable environments seems to rely on only a minority of disperser species, even in species-rich communities (Wenny and Levey, 1998, Chapter 3). Yet, little is known about whether the observed complementary effects of animals on fruit removal, seed deposition and plant recruitment translate into later life stages of plants (Fig. 1) (Wang and Smith, 2002; Rogers et al., 2019). Therefore, it also poorly understood how strongly plant populations depend on single animal species and whether the extinction of key species could functionally be compensated by other animal species, or even by seed dispersal through gravity (Hampe, 2008; Jongejans et al., 2015). Understanding the long-term consequences of seed dispersal will provide new insights into the coevolution of plants and animals (Howe and Smallwood, 1982; Albrecht et al., 2015, 2018; Eriksson, 2016; Rehling et al., 2021), and may provide guidance for identifying key disperser species particularly important for ecosystem functioning and services (Whelan et al., 2008; Farwig and Berens, 2012; Schleuning et al., 2020).

In this study, we explored the long-term effects of the seed dispersal mutualism between a frugivore community of 20 animal species and the population of the early-successional tree *Frangula alnus* in the old-growth Białowieża Forest, Poland (Supplementary figure 1-2, Supplementary table 1-3). *Frangula alnus* produces black fruits and relies on animals for seed dispersal to forest gaps (Godwin, 1943). We used integral projection models to study the effect of animal seed dispersal on the full life cycle of *F. alnus* along the natural gradient of canopy cover in the forest (Fig. 1, Supplementary figure 3). The models were built on comprehensive datasets from our previous studies: We combined 936 h of seed removal observations (Albrecht et al., 2013, 2014; Farwig et al., 2017) with DNA barcoding of 1,726 scat samples with seeds of *F. alnus* and other fleshy-fruited plants to assess frugivore-specific deposition patterns (Schlautmann et al., 2021, **Chapter 3**), recruitment experiments using 2,500 seeds (see Supplement 3.7.1 in Chapter 3), and demographic data for 938 individuals of *F. alnus* over three years. This allowed us to test to whether and how seed dispersal by animals positively affects population growth rates. Second, we quantified if the quantity (fruit removal) or the quality of seed dispersal (seed handling and deposition) structures the dispersal-dependent

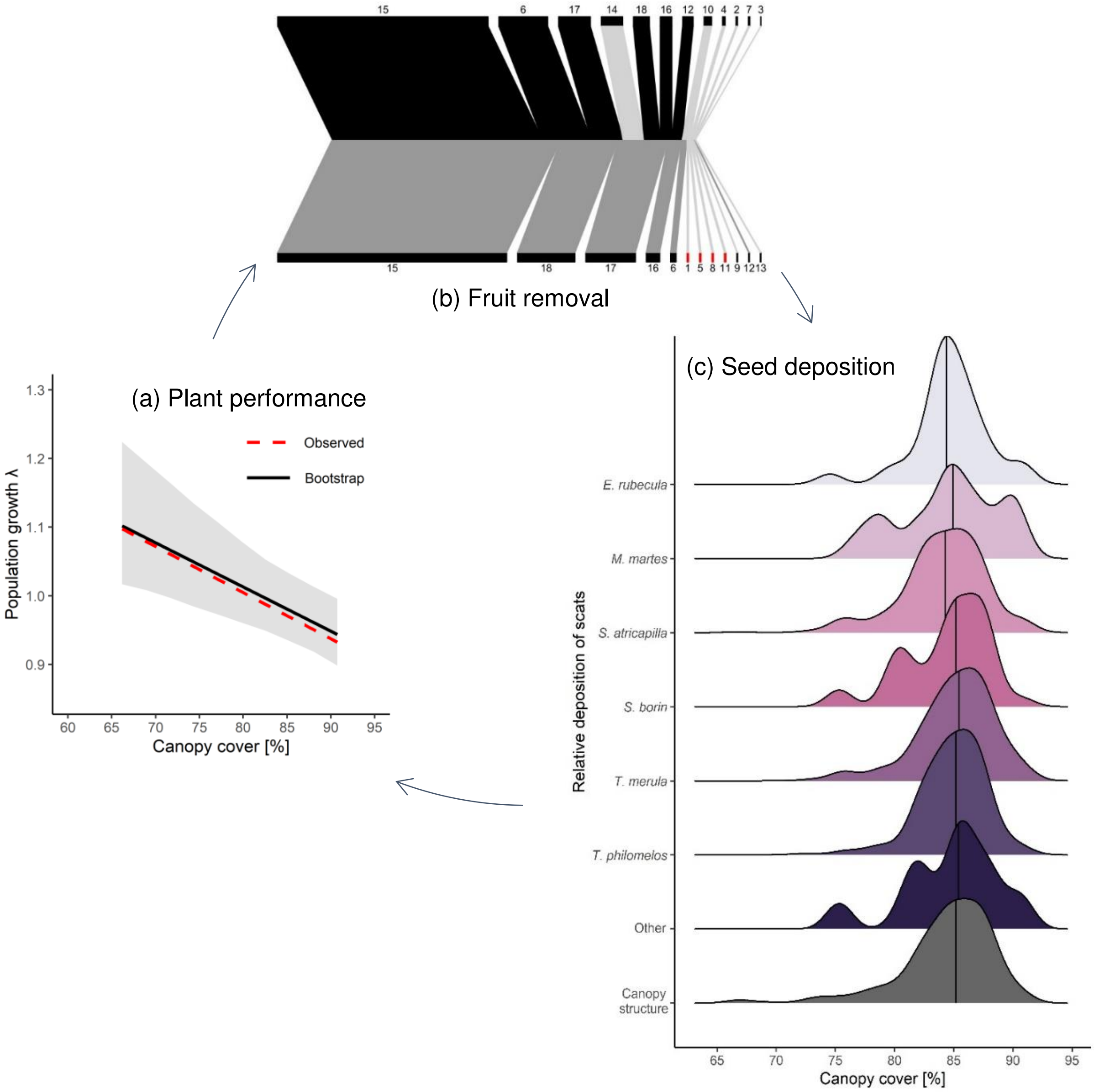

Fig. 1: The seed dispersal loop (*sensu* Wang and Smith, 2002) - animal seed dispersal as a demographic bridge between reproductive adults and new plant recruits. (a) Plant performance: Relationship between canopy cover and population growth of the temperate fleshy-fruited tree *Frangula alnus* in Białowieża Forest, Eastern Poland, when seeds are solely dispersed by gravity. Mean ± 95% prediction interval based on 500 bootstraps of plant data. The dashed red line displays the actually observed local population growth of *F. alnus* along the canopy cover gradient. (b) Fruit removal: The fruit removal (Albrecht et al., 2013) (top, black) and seed deposition network (Schlautmann et al., 2021) (bottom, dark grey). The linkage width of bars represents the number of visits of an animal species on *F. alnus* (removal network) or the number of scats with seeds of *F. alnus* (deposition network). Links of animal species that only occur in one type of network are shown in light grey. Bars of birds are shown in black and bars of mammals in red. The labels display different frugivorous animal species (for species names, see Supplement table S3). Two species were only observed using camera traps and not part of the interaction networks. (c) The effect of animal species on seed deposition pattern, as well as the microhabitat structure along the canopy gradient in the forest.

change in population growth (i.e. seed dispersal effectiveness (Schupp et al., 2010). Lastly, we characterized how strongly extinctions of single animal species reduce dispersal-dependent population growth, i.e. the relative functional loss of animal seed dispersal with species loss. For this, we simulated two scenarios: a scenario where the seed dispersal function of an animal is inevitably lost (i.e. interaction deficit), and another scenario where the remaining animal community quantitatively compensates the lost interactions (i.e. interaction compensation) (Brodie et al., 2014; Fricke et al., 2018).

4.3. Results and Discussion

4.3.1. Vital rates and population growth of *F. alnus* along the natural gradient of canopy cover in the forest

We found no effects of canopy cover on seedling recruitment, but strong negative effects on survival, growth and reproduction of *F. alnus* (see Supplementary table 4-5 and Supplementary figure 3-8, Supplementary information text 1). Assuming that the observed population of *F. alnus* was fully established along the canopy gradient and was only dispersed by gravity (i.e. all produced seeds would be deposited in the same environment as their parents), population growth gradually declined with increasing canopy cover (Fig. 1a), from being positive (λ = 1.16, 95%CI: 1.02-1.22) in light environments (canopy cover = 66.3%), over being in balance (λ = 1.00, 0.96-1.08) at intermediate sites (canopy cover = 79.9%), to shrinking (λ = 0.95, 0.89-1.00) in closed forest (canopy cover = 90.7%). These results emphasize the functional niche of *F. alnus* as a gap-dependent, mid-successional plant in temperate forests, in line with the observations of previous studies in this species (Cunard and Lee, 2009; Szewczyk et al., 2019). When we corrected for the relative availability of microhabitats along the canopy gradient, our IPM predicted that the gravity-dispersed meta-population of *F. alnus* (i.e. the population aggregated over the entire forest) was close to equilibrium (λ = 0.97, 0.94-1.04).

4.3.2. Fruit removal and seed deposition

In total, we observed 20 animal species (14 birds and 6 mammals) acting as seed dispersers of *F. alnus* in the Białowieża forest, of which we observed six species only by observing fruit removal, six species only by collecting scats, six species with both methods (Schlautmann et al. 2021), and two species only by camera trapping in a pilot study (*master thesis* by Kohlbrecher 2015). The relative interaction frequency of animals with *F. alnus* was highly heterogeneous: Four bird species accounted for 86.6% (95%CI: 82.4-89.8%) of interactions, namely *Sylvia atricapilla* (58.7%, 53.2-63.9%), *Turdus merula* (15.0%, 9.8-20.6%), *Erithacus rubecula* (8.3%, 6.2-10.4%) and *T. philomelos* (4.6%, 2.9-6.5%), and fourteen animal species contributed ~1% or less to total fruit removal (Fig. 1b, Supplementary table 3, Supplementary figure 9). Over three study years we collected fewer than 30 scats with seeds of *F. alnus* for all, but three animal species, which strongly limited the identification of animal species-specific deposition pattern for *F. alnus* along the canopy cover gradient in forest (Supplementary table 3). For the modelling of seed deposition, we used all scats with seeds of any fleshy-fruited plant that were found at the same time as the deposited seeds of *F. alnus*, as scats with seeds of the species were rare and only covered few disperser species. For *Martes martes*, we used all seeds assuming that it deposits scats at the same locations independent of season (see material and methods). Ultimately, we were able to distinguish the seed deposition pattern of six animal species with more than 30 scat replicates. All species with fewer scat replicates were pooled as 'other' (Fig. 1c, Supplementary figure 10-11). We found that the bird species *T. merula*, *T. philomelos*, and *E. rubecula* dispersed only 3-4% of seeds to the 50%-lightest environments along the natural canopy gradient, which is less than expected by a random pattern of seed dispersal along a gradient of available microhabitats (i.e. 7.3% of available microhabitats). In contrast, the deposition pattern of the other animal species corresponded to a random dispersal of seeds to available microhabitats (Fig. 1c, Supplementary Fig. S10-11). This shows strong evidence for the presence of non-random seed dispersal within plant populations in a temperate forest at the animal species level, and has been similarly observed for bellbirds (Wenny and Levey, 1998), muntjacs (Brodie et al., 2009) and lemurs (Razafindratsima and Dunham, 2015) along canopy cover gradients in tropical forests.

4.3.3. Effects of animal seed dispersal over the full life cycle of a plant

By combining data on plant vital rates, fruit removal and seed deposition with spatial- and animal species-explicit integral projection models along a canopy cover gradient in the forest, we found that within-population seed dispersal by animals was beneficial for plants and increased population growth (100% animal seed dispersal, $\Delta\lambda = 0.025 \pm 0.001$, Fig. 2a). This effect was strongly related to the improved germination of seeds after fruit consumption (c. +70%, Rogers et al. *preprint*). If we additionally assumed that *F. alnus* only occurred in closed forest and relied on animal seed dispersal to reach forest gaps, the effect of animal dispersal on the plant population was increased by 13.7% ($\Delta\lambda = 0.029 \pm 0.001$, Fig. 2a), although the relative availability of forest gaps was low (7.3%). This shows that animal dispersal in plants is generally beneficial, especially due to the improved seed germination after dispersal, during forest succession and the colonization of new habitats. These results provide direct evidence for a long history of natural observations and theoretical predictions (Howe and Smallwood, 1982; Wang and Smith, 2002; Yang et al., 2011; Makoto and Wilson, 2019; Rogers et al., 2021).

4.3.4. Seed dispersal effectiveness

The net effect of seed dispersal by an animal species on population growth of *F. alnus*, representing the species' seed dispersal effectiveness, can be divided into the contributions of the quantity and quality of seed dispersal (Schupp et al., 2010, 2017). To assess quantity, we used the relative interaction frequency of animal species with *F. alnus*. To assess quality, we calculated the probability of a seed to reach maturity after being dispersed by a certain animal species. The quality of animals for seed dispersal was a consequence of their fruit handling (removing vs. dropping fruits, seed predation), improved conditions for seed germination after

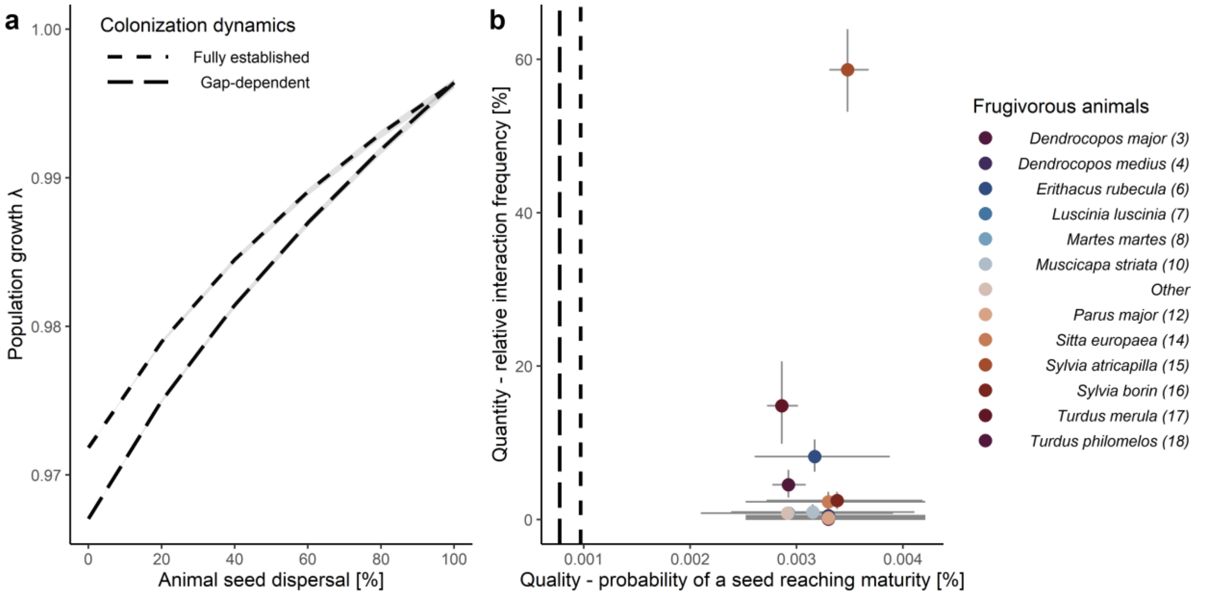

Fig. 2: (a) The effect of seed dispersal by 20 animal species on the population growth rate of *F. alnus* in Białowieża Forest, Eastern Poland; depending on whether the plant population (i) is fully established along the natural gradient of canopy cover in the forest (short-dashed), or (ii) is established only in the closed forest (the 50%-darkest microhabitats, i.e. 92.7% of all microhabitats) and animal seed dispersal is necessary for plant establishment in forest gaps ('gap-dependent', long-dashed line). The total effectiveness of animal dispersal on population growth was calculated as the inverse of gravity dispersal. (b) The 'landscape' of seed dispersal effectiveness of animal species and gravity dispersal for *F. alnus*. The y-axis represents the quantity of seed dispersal (i.e. the relative interaction frequency of the animal species with *F. alnus*) and the x-axis represents the quality of seed dispersal (i.e. the probability of a seed reaching maturity when dispersed by the respective animal species). The vertical lines depict the two modes of gravity dispersal in (a): gravity dispersal in closed forest only ('gap-dependent', long-dash) and along the entire canopy cover gradient ('fully established', short-dash). The group of 'other' frugivores refers to *Apodemus flavicollis*, *Cervus elaphus, Dryomys nitedula, Meleagris gallopavo, Myodes glareolus*, *Prunella modularis* and *Sus scrofa*, whose estimates are based on the same values for seed removal and deposition (see Supplementary Table S3). The 20th animal species, *Coccothraustes coccothraustes,* was not included, because it predated all seeds in most bootstraps (Quality = 0%). Mean ± 95% prediction intervals for seed dispersal quantity and quality based on 500 non-parametric bootstraps.

dispersal (Rogers et al., *preprint*), the deposition pattern of animals along the canopy gradient, and their later consequences for plant growth to adulthood (Supplementary figure 8-12). We found that, although the quality of seed dispersal differed significantly among animal species (Fig. 2b), the seed dispersal effectiveness across animals was very strongly related to the quantity (Spearman's $\rho = 0.98$, $p < 0.001$) and not to the quality of seed dispersal (Spearman's $\rho = 0.21$, $p = 0.662$).

The strong relationship between seed dispersal effectiveness and the relative interaction frequency of animals may have been due to the low environmental filtering in temperate forests. In this study, the forest environment, i.e. canopy cover, did not strongly affect the recruitment of seedlings. For example, first-year survival of seedlings of *F. alnus* decreased from c. 60% in light environments (canopy cover = 66.3%) to 20% in closed forest (canopy cover = 90.7%), which may be typical for fleshy-fruited plant species in temperate forests (Merges et al., 2020, Chapter 3). In contrast, in arid environments, most seedlings survive only in the shade of nursery plants where they are protected from heat stress (Fulbright et al. 1995, Nunez et al. 1999). In such cases, non-dispersed seeds or those deposited in open areas do not contribute to plant regeneration (Rey and Alcántara, 2000), and seed dispersal effectiveness will strongly depend on the few animal species that bring the seeds to favourable environments (Godínez-Alvarez et al., 2002; González-Varo et al., 2017). Alternatively, it has been emphasized that seed dispersal is especially important for escaping the increased mortality close to parental plants (Caughlin et al., 2014). However, a meta-analysis found only a reduction of 25% in recruit survival close to conspecific adults (Comita et al., 2014). We did not find a decreased seedling recruitment close to conspecific adults neither in *F. alnus* (see Supplementary text 2, supplementary figure 3 and supplementary information text 2), nor in any other fleshy-fruited plant species of the community (*bachelor thesis* by Waldschmidt 2019). In fact, gravity dispersal alone could have resulted in population growth of *F. alnus* close to equilibrium, similar to what has been observed in a fleshy-fruited Mediterranean plant population without animal disperser (Rodríguez-Pérez and Traveset, 2012). Similarly, other studies showed strong legacy effects of adult plants on the future distribution of individuals in animal-dispersed plant populations (Hampe, 2008; Arnell et al., 2021; Perea et al., 2021) which may be due to a combination of both, inefficient animal seed dispersal away from conspecific adults (Supplementary text 2) and gravity dispersal.

In addition, we found only small differences in the seed deposition pattern among animal species (see also Chapter 3). To test the sensitivity of seed dispersal quality to variation in deposition pattern, we simulated very strong, virtually unrealistic patterns of seed deposition (Supplementary figure 14). These extreme deposition pattern increased the differences in seed dispersal quality between animal species from 2 (Fig. 2b, except for the seed-predating *C. coccothraustes*) to 23-fold (Supplementary figure 14). This implies that population growth can be sensitive to differences in the deposition pattern, but the habitat use of animals may be too similar to lead to distinct deposition pattern. Independent of the contributing seed deposition pattern, differences in the quantity of seed dispersal will remain larger (972-fold) than those in seed dispersal quality.

A recent, extensive meta-analysis of over 2500 experiments showed that seed germination was strongly improved when the seeds were freed from the fruit pulp (c. +70% seed germination in temperate regions, 'deinhibition effect' *sensu* Rogers et al. *preprint*). The gut passage of animals did not further improve seed germination ('scarification effect' *sensu* Rogers et al., *preprint*). Ultimately, these findings suggest that the quality component with the largest effect on seed dispersal effectiveness does not strongly differ between animal species (Rogers et al. *preprint*, see also Fricke et al. 2018). Thus, the strong relationship between seed dispersal effectiveness and the relative interaction frequency of animals in this study was due to the combination of (i) a low environmental filtering in temperate forests (in comparison to harsh, microsite-limited environments), (ii) the low differences in seed deposition among animal species and (iii) the strong effect of fruit pulp on seed germination that does not differ among animal species (Fricke et al. 2018, Rogers et al. *preprint*).

These results showed that populations of typically 'animal-dispersed' plant species are potentially stable without the interactions with animals (see also Hampe 2004, Rodriguez & Traveset 2012), and might be independent of the seed dispersal mutualism. Nevertheless, being dispersed by animals leads to a suite of benefits increasing the growth of plant population, such as the improved seed germination (Rogers et al. *preprint*), and the dispersal to and colonization of favourable habitats. The underlying total effectiveness of animals during seed dispersal is strongly related to the number of removed fruit, and not to the quality of seed dispersal (Vázquez et al., 2005). Thus, observing the relative interaction frequencies together with the number of species partners (Bascompte et al., 2003) could provide ecologists with an easy tool to identify functionally important species across spatial and ecological scales (Eklöf et al., 2013; García-Callejas et al., 2018; Guimarães, 2020) and for multiple types of ecological interactions at the same time (Timoteo et al., *preprint*).

4.3.5. Robustness of animal seed dispersal to species extinctions

Assuming that interactions of animal species with *F. alnus* were quantitatively lost after extinction (i.e. interaction deficit of extinct species), we found an asymptotic pattern in the loss of seed dispersal with species loss: The seed dispersal effectiveness (i.e. the total net effect of seed dispersal on population growth) decreased the strongest when either of the dispersers *S. atricapilla* (-47.2%), *T. merula* (-10.1%), *E. rubecula* (-5.5%) or *T. philomelos* (-3.0%) were lost. These four bird species are quantitatively the most important seed dispersers not only of *F. alnus*, but for most fleshy-fruited plant species in Białowieża Forest (Albrecht et al., 2013; Rehling et al., 2021; Schlautmann et al., 2021), and Europe (González-Varo et al., 2021) beyond habitat boundaries (Breitbach et al., 2012; Rumeu et al., 2020). In contrast, the extinction of one of 14 animal species (70% of seed-dispersing animal species of *F. alnus*, 33% of the entire frugivore community in Białowieża Forest) led to a negligible loss (< 1%) in the effectiveness of animal seed dispersal. Many of these species were forest specialists and potentially rare (Albrecht et al., 2013; Farwig et al., 2017). Because the rarest species contribute the fewest to seed dispersal and are likely to be lost first, seed dispersal may be relatively robust to species loss (Farwig et al., 2017; Rehling et al., 2021). Such a pattern has been similarly observed for plant-pollination interactions (Kleijn et al., 2015; Winfree et al., 2015). Although these species are not yet functionally important for animal seed dispersal, they may become important under future conditions when they take over the role of declining disperser species.

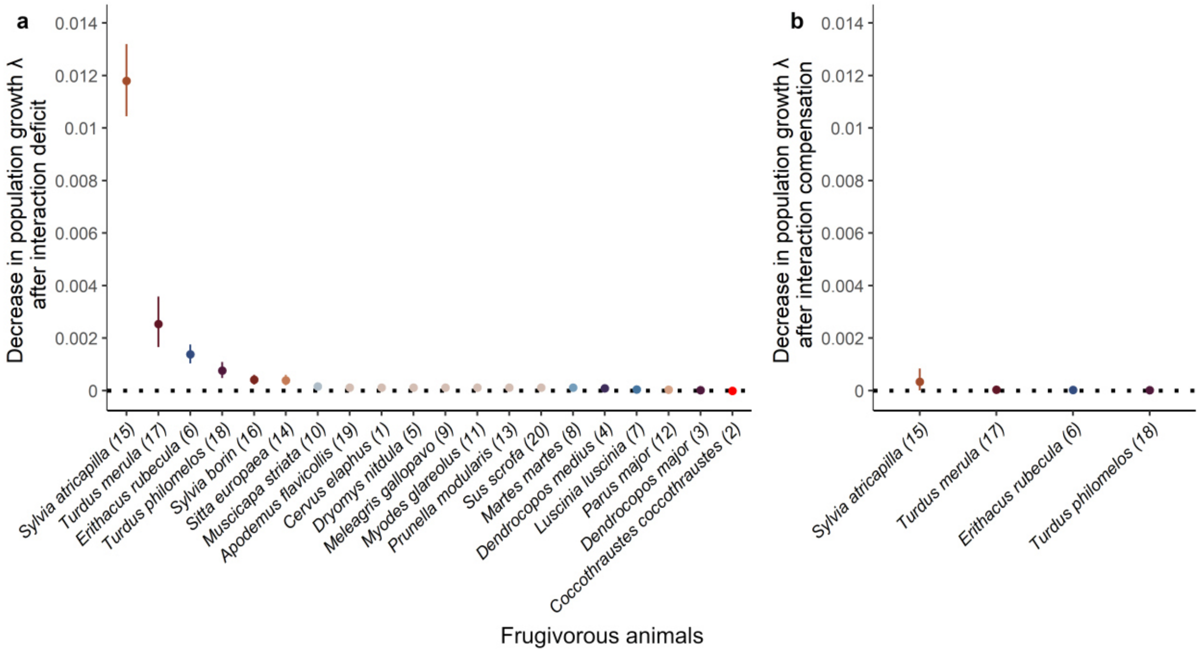

Fig. 3: Projected consequences of the extinction of each of 20 frugivorous animals on population growth of *F. alnus* under two scenarios: (a) interaction deficit (i.e. the interactions of an animal were entirely lost) and (b) interaction compensation (i.e. the species was lost, but the remaining animal community compensated interactions). Mean ± 95% prediction intervals based on 500 bootstraps of dispersal data.

In a second scenario, we therefore tested if the remaining animal community can keep up the effectiveness of seed dispersal when one of the four main disperser species goes extinct, and the remaining community compensates fruit removal of the lost species (i.e. interaction compensation of extinct species). In this second scenario, we found that the potential extinction of the main dispersers of *F. alnus* (*S. atricapilla*, T. *merula, E. rubecula*, and *T. philomelos*) was well buffered by the remaining animal community (< 2% functional loss), which is due to the small differences in the quality of seed dispersal among dispersers observed before. A high redundancy of seed dispersal might be a useful mechanism to buffer the large variation in the number of individuals of single animal species among different years (Herrera, 1998; Yachi and Loreau, 1999; Blüthgen et al., 2016). It further highlights that there is no key disperser of *F. alnus* whose contribution to population growth is unique (Lawton and Brown, 1994; Zamora, 2000).

However, before species are lost due to anthropogenic pressure, the environment has usually changed structurally and with it the effectiveness of the ecological interactions therein (McConkey and O'Farrill, 2015). In previous studies, we found that the loss of animal forest specialists in Białowieża Forest due to forest degradation (Albrecht et al., 2013, 2014; Farwig et al., 2017) was accompanied by a 50% loss of deposition microhabitats and an increase in the redundancy of low-quality seed dispersal (Chapter 3). Especially dispersal to forest gaps was lost, which are important for the recruitment of several fleshy-fruited plant species (Chapter 3) and here for population growth of *F. alnus*. Direct and indirect effects of changes in the environment and the ecological interactions independent of species loss are likely to disrupt seed dispersal processes (McConkey et al., 2012; McConkey and O'Farrill, 2016). Yet, little is known about the background effects of species loss on seed dispersal and other ecological interactions (McConkey and O'Farrill, 2015).

Within-population seed dispersal in temperate forests is relatively robust to the loss of single disperser species. However, if main dispersers go extinct, the effectiveness of seed dispersal can strongly decrease when the remaining community is not able to keep up the ecological interactions – a pattern which may reflect the seed dispersal disruption of animals observed on islands and for large-fruited plant species (Kurten, 2013; Doughty et al., 2016; Fricke et al., 2018; Onstein et al., 2018; Boissier et al., 2020; Lim et al., 2020), but see (Kistlera et al., 2015; Mittelman et al., 2020). This emphasizes the role of the abundance of individuals in addition to the role of species diversity for ecological interactions such as seed dispersal (Garcia et al., 2010; García et al., 2018). In recent decades, over 400 million birds have been lost in Europe and 2.5 billion in North America (Inger et al., 2015; Rosenberg et al., 2019). If the importance of the abundance of individuals for ecological functions hold true for other types of interactions as well (e.g. pollination, Vázquez et al., 2005; Winfree et al., 2015, Timoteo et al., *preprint*), then stopping and reversing the ongoing decrease in the abundance of animal individuals (e.g. Hallmann et al., 2014, 2017; Inger et al., 2015; Rosenberg et al., 2019; Kamp et al., 2021; Kim et al., 2021) should be a primary goal of nature conservation to reinforce multifunctionality and -services of ecosystems.

4.4. Materials and Methods

4.4.1. Study area and sites

Our study took place in the Białowieża Forest which covers an area of c. 1500 km² across the border of Poland and Belarus. At present, the 630 km² of forest in Poland are divided into the Białowieża National Park (c. 105 km²) and forests managed by state forestry. In an area of about c. 48 km² of the Białowieża National Park human interference have been minimal for over half a millennium and that part has been strictly protected since 1921, making it the best-preserved lowland forest in Europe. In contrast, commercial logging has shaped more than 80% of the Polish state forest since the First World War (Mikusiński et al., 2018; Jaroszewicz et al., 2019). In the Białowieża Forest, up to 20% of the forest is dominated by alder (Jaroszewicz et al., 2019) which is home to a diverse community of at least fifteen woody, fleshy-fruited plant species and 41 frugivorous animal species. The frugivore community consists of small-bodied passerines (e.g. *Sylvia atricapilla, Erithacus rubecula*, *Turdus merula*), forest specialists (e.g. *Tetrastes bonasia*), and mammals of different size (e.g. *Dryomys nitedula*, *Martes martes*, *Bison bonasus*) (Albrecht et al., 2013; Jaroszewicz et al., 2013; Rehling et al., 2021; Schlautmann et al., 2021).

All sampling took place at 17 studies sites in ash-alder floodplain forests (*Fraxino-alnetum* community, Albrecht et al., 2015) in both the managed (stand age: c. 50 years, n = 11) and the old-growth part (stand age: c. 100-150 years, n = 5) of the Białowieża Forest. Due to logistic constraints, we assessed each process important for the demography of *F. alnus* only at subsets of all study sites (Supplementary figure 1, supplementary table 1-2): Seed removal (at 15 sites), seed deposition (at 12), seedling recruitment (at 4 sites, of which each site consisted of 10 plots, each with three subplots) and plant demography (at 14). Our sites were scattered over an area of c. 400 km², i.e. two thirds of the Polish part of the Białowieża Forest.

4.4.2. Study species

Frangula alnus (Miller; family: Rhamnaceae) is distributed from Morocco throughout most of Europe to western Asia (Hampe et al., 2003). *F. alnus* grows as shrubs or as small trees in open environments or in the understorey of mid-successional forests (Godwin, 1943). In late-successional forests, shade-tolerant plants outcompete *F. alnus* (Cunard and Lee, 2009), but canopy gaps can improve growth and regeneration of *F. alnus* (Lee and Thompson, 2012). In Białowieża Forest, *F. alnus* is mainly associated with ash-alder floodplain forests and produces fruits from the end of July to October. Fruits are black with a diameter of 6.5-10.7 mm and contain on average two seeds with a mass of 21.2 mg (range: 10.3 – 36.0 mg, Rehling et al., 2021). Seeds are primarily dispersed by small birds and mammals, and secondarily by ants or water (Hampe, 2004). Seeds of *F. alnus* are physiologically dormant and both, light and cold-stratification improve germination (Godwin, 1943; Baskin and Baskin, 2014). *Frangula alnus* can produce clonal side-trunks and has the ability to resprout after breakage (Godwin, 1943), but relies entirely on the dispersal of seeds for the colonization of new habitats.

4.4.3. Seed removal

To quantify the interaction frequency of animal species with *F. alnus*, 17 people observed seed removal by frugivores, and their fruit handling, at 15 sites during the fruiting period of *F. alnus* in 2011 and 2012. Depending on the availability of fruiting individuals at the study sites, we selected one (at 2 sites), two (at 7 sites) or three (at 12 sites) reproducing individuals of *F. alnus* per year, overall 52 individuals in total (Supplementary table 1-2). Frugivores visiting these individuals were observed with binoculars from camouflaged tents on three separate days for a period of 6 h starting at sunrise, i.e. in total 936 h of observation. For each frugivore species, the number of visits, the number of fruits eaten during each of these visits and their fruit-handling was recorded. It was differentiated between three types of fruit-handling: (i) swallowing or removing, (ii) crushing and (iii) dropping of fruits. If groups of frugivores were visiting a tree at the same time, the observer recorded the number of visits and focussed only on one frugivore individual. 1006 frugivore visits were observed and whether frugivores handled fruits or not was successfully observed in 766 of 821 cases (93.3%). For further details on the methods for observing fruit removal see Albrecht et al. (2013).

4.4.4. Seed deposition

To quantify seed deposition patterns by the animal species along the canopy gradient in the forest, we collected scats of frugivores at 12 study sites during the fruiting period of *F. alnus* in 2016-2018. At each study site, we set up five 100 m transects which were at least 20 m apart.

Along each transect, we searched for animal scats within 1 m wide strips to the left and right of each transect, covering a total area of 1,000 m² per study site. The transects were checked every ten days during the entire fruiting season lasting from mid-June to mid-October. After heavy rains, scat collection was paused for two days. At each study site, we collected scats eleven times in 2016 and 2018 and nine times in 2017 due to a shorter fruiting season. We collected all bird scats with seeds to identify the frugivore in the laboratory. Mammal scats were assigned visually to species in the field and the seeds counted, or also collected for genetic identification. Scat samples were stored at -4 °C on the same day until they were used for frugivore identification in the laboratory.

To identify the frugivore species that had deposited the scat, we followed the DNA barcoding protocol of González-Varo and colleagues (2014; 2017). DNA extraction and the PCR amplification took place in the Conservation Ecology laboratory of the University Marburg. Our samples were sent to LGC Genomics (Berlin, Germany) or Macrogen Europe (Amsterdam, Netherlands) for DNA purification and sequencing. The final DNA sequences were edited with CodonCode Aligner (Version 9.0.1, CodonCode Corporation) and species were identified using the Barcode of Life identification system (BOLD, Ratnasingham & Hebert, 2007). For the analysis we only used samples whose sequences had a > 98 % similarity with recorded sequences in BOLD. We successfully identified the frugivore species of c. 90 % of our samples. For further details on the methods for collecting scats and identifying the frugivore species see Schlautmann et al. (2021).

4.4.5. Seedling recruitment

To assess the probability of a seed of *F. alnus* to develop into a seedling, we conducted recruitment experiments each year from 2016-2018. We collected fruits of at least six adults, removed the pulp, dried the seeds for 48 h at room temperature, and mixed them. At each of four study sites, we established 10 marked plots, and at each of these plots we established independent subplots for the different years of the recruitment experiments, 2016 (n = 40 plots), 2017 (n = 20, only half the plots) and 2018 (n = 40). We sowed 25 seeds per subplot, thus, 2,500 seeds in total. Each subplot had an area of 50 cm x 50 cm and was at least 5 m away from the next reproductive *F. alnus* individual. From 2017 to 2019, we checked the experimental subplots for the number and size of seedlings once per year in June and then tracked their fate as part of the demographic study. In addition, we checked once for emerging seedlings of *F. alnus* on a control subplot next to each subplot where we had not sown seeds. We found only one seedling of *F. alnus* in these control plots indicating only negligible external seed input in our recruitment experiments. No seedlings were emerging in the year sown indicating that seeds of *F. alnus* need cold-stratification before germination (Baskin and Baskin, 2014) and seeds of *F. alnus* did not produce a persistent seed bank. For further details on the methods for the seedling recruitment experiments see Supplementary Material 3.7.1 (Chapter 3).

4.4.6. Plant vital rates

To analyse the demography of *F. alnus*, we recorded survival, growth and reproduction of plant individuals during June-October from 2017-2019 at 14 study sites in the Białowieża Forest. We randomly tagged individuals of all sizes. To be able to locate plant individuals in the forest throughout the study period, we attached yellow plastic tags to each plant in the logged and green degradable plant tags in the old-growth forest. We measured the stem diameter of individuals at ground level with callipers or a tape measure and counted the number of fruits before the main period of fruiting of *F. alnus*. However, in c. 27% of cases, we assessed a plant later in the season. Because animals had eaten some or even all of the fruits by that time, we only checked for leftovers of fruits to see if an individual was reproductive or not. Throughout this manuscript, individuals are categorised as reproductive if they had produced at least one fruit which could be dispersed. Individuals that produced only flowers, but no seeds were not considered reproductive. In addition, a large proportion of plant tags was destroyed in each census year (c. 10-20%). This led to a high loss of marked individuals because we were able to retrieve only c. 10 % of the individuals. As a consequence, we recorded survival and death only for individuals which could be clearly identified throughout the study period. In total, we were able to record vital rates for 938 individuals, of which 341 were assessed once, 247 twice and 350 for three consecutive years (following outlier detection, see statistical analyses).

4.4.7. Canopy cover

To determine the effect of canopy on plant recruitment, growth and seed deposition, we took hemispherical photos with a fisheye lens at ground level. For studying effects on seed deposition, we split each of the 100 m transects into five segments with 20 m. Every scat that was found along these transects was assigned to the closest segment. As we tagged most plants close to the transects (within 10 m distance), we similarly assigned these individuals to the closest segment along the transects. If plant individuals were located further away from the transects, we took extra hemispherical photos within 10 m distance from the plant individuals. We also took photos at the centre of each of the 40 plots used to study plant recruitment. From 2016 to 2019, we took up to six hemispherical photos of the canopy along the transects used to study seed deposition, and up to three photos everywhere else. All photos were taken during the fruiting period of the fleshy-fruited plant community from June-October. The hemispherical photos were analysed with DHPT 1.0 (Loffredo et al., 2016) to receive the proportion of area that was covered by the canopy at each location. Comparing canopy cover of photos taken at the same location at different points in time, we found that canopy cover varied considerably resulting in a weak correlation between canopy cover measured in 2016 and 2017 at the same locations (Supplementary information text 3). As a consequence, we did not use these data to model natural, between-year dynamics of the canopy within the forest (as in Metcalf, Horvitz, Tuljapurkar, & Clark, 2009), but used average estimates instead.

4.4.8. Estimating seed deposition patterns

Investigating seed deposition patterns of all possible frugivores is time-consuming, and even after three years of collecting c. 4,000 scats, the number of scats with seeds of only *F. alnus* were too low for 15 of the 18 dispersers to predict animal-specific seed deposition patterns. To be able to include these animals in the analyses, we made the following assumptions: (1) We pooled data on seed deposition of all animals across study sites and years in the forest assuming no temporal or spatial differences in our population. (2) We did not differentiate between seeds deposited beneath conspecific adults and elsewhere as early recruitment of seedlings was not affected by conspecific adults (Supplementary information text 1). (3) We assumed that frugivores showed the same behaviour and dropped scats at the same locations along the canopy gradient independent of whether they had eaten fruits of *F. alnus* or one of the other 15 co-fruiting (i.e. temporally) plant species. Thus, scats with seeds of other species were equally representative for deposition patterns of the different frugivores across the canopy gradient, and could be used to inform seed deposition pattern of *F. alnus.* We only pooled scats with seeds that were found at the same time as scats with seeds of *F. alnus* in each year (but for *M. martes*, see next point). (4) *M. martes* is known to mark its home range using scats for the communication between individuals (Barja et al., 2011). In line with this, we found scats of *M. martes* at the same microhabitats (mostly the same tree logs) throughout the year. We pooled scats of *M. martes* with seeds of fleshy-fruited plants from the entire fruiting period to analyse the deposition of seeds. (5) In our spatial population models, we analysed the role of rare frugivores separately, but treated them as functionally equal. To do so, we pooled all data on fruit removal and seed deposition for frugivores with < 10 scats. However, by pooling scats with seeds of *F. alnus* and other plants, we also included scats of animals that did not interact with *F. alnus*. We kept them in the analyses by assuming that their patterns of deposition were equal to that of rare dispersers of *F. alnus* (Supplementary table 3). Over the course of three years we found > 1,000 scats with seeds of *Sambucus nigra* beneath only one parental tree of *S. nigra* acting as a hub tree in the forest ecosystem. As seeds deposited beneath this tree affected the overall pattern of seed deposition of frugivores when we pooled the deposition data, we used only scats with seeds of *F. alnus* from this transect segment in the analyses. Based on these assumptions, we differentiated the seed deposition pattern of seven frugivores, each with a minimum number of 30 replicates (Figure 1c, Supplementary table 3).

4.4.9. Composite integral projection models

To investigate plant population dynamics, we used integral projection models (IPMs) (Easterling et al., 2000; Ellner and Rees, 2006). For the tree *F. alnus*, we used standardised log10-diameter at ground level as a state variable for size z and the standardised, continuous canopy closure c as a continuous state variable for light availability. In the IPM, the individuals are thus characterised by two continuous state variables: their size and the degree of canopy cover of their location. The transition of the number of individuals n of size z in environment c at time t to the number of individuals n' with size z' in environment c' at time $t+1$ is given by

$$n'_{t+1}(z',c') = [\iint_L^U P(z',z,c) + \sum_{x=i} \iint_L^U F(z',c',z,c)]\ n_t(z,c)dzdc$$

(Eq 1).

Here $P(z',z,c)$ describes survival, breakage and growth of individuals as a function of their size and their environment, and $F(z',c',z,c)$ describes dispersal of seeds and their recruitment. When seeds are taken up by animal x, the dispersed seed acquires a new location along the canopy gradient c. In contrast, when seeds are dispersed only by gravity or when animal x drops the fruit beneath conspecific trees, the seeds will not be transferred to new locations and, thus, remain under the same canopy cover c in which they were produced.

We used the ‘cumulative kernel’ (or ‘bin-to-bin’) approach to numerically integrate the IPM as it has been shown to perform better for slow-growing, long-lived species than the commonly used ‘midpoint rule’ (Zuidema et al., 2010; Dawson, 2013; Ellner et al., 2016). The integration is set among U being 1.1 times the upper and L being 0.9 times the lower boundary of the observed size- and canopy-ranges within the forest. We added probabilities with smaller or larger values than the boundaries of the matrices to the outer classes to avoid eviction (Williams et al., 2012). We discretised the tree-IPM into 100x100 size classes with (standardised) sizes z ranging between -2.86 and 2.36, corresponding to a diameter of 0.06 cm and 89.68 cm, respectively. This resolution in size classes resulted in robust estimates of population growth rates (λ) as a doubling of the size dimension hardly affected estimates of λ (< 0.001). We split the canopy gradient into ten equally large segments and estimated the IPM separately for each of these canopy segments. The (standardised) canopy cover ranged from -4.279 to 2.178, corresponding to a canopy cover of 64.8% in light environments to 92.1% in dark environments.

The transition of the population of *F. alnus* is based on the following equations:

$$n'_{t+1}(z',c') =$$

$$\int_L^U S(z,c)\big(1-B(z)\big)G(z',z,c)\, n_t(z,c)dzdc$$

(Eq 2a)

$$+\int_L^U S(z,c)B(z)R(z',z)\, n_t(z,c)dzdc$$

(Eq 2b)

$$+\sum_{x=i}\iint_L^U \begin{array}{c} f_{repr}(z,c)f_{fruit}(z,c) \\ f_{rel.anim.disp}\, f_{rel.int.freq}(x)\, f_{nocrush}(x)\, f_{consumed}(x)\, f_{seed}\, f_{deposition}(c',x) \\ f_{recruit1}\, f_{dist}\,(z')\, n_t(z,c)dzdc \end{array}$$

(Eq 2c)

$$+\sum_{x=i}\iint_L^U \begin{array}{c} f_{repr}(z,c)f_{fruit}(z,c) \\ f_{rel.anim.disp}\, f_{rel.int.freq}(x)\, f_{nocrush}(x)\, f_{drop}(c',x)\, f_{seed} \\ f_{recruit1}\, f_{recfruit}\, f_{dist}(z')\, n_t(z,c)dzdc \end{array}$$

(Eq 2d)

$$+\sum_{x=1}\iint_L^U \begin{array}{c} f_{repr}(z,c)\, f_{fruit}(z,c) \\ \left(1-f_{rel.anim.disp}\right) f_{seed} \\ f_{recruit1}\, f_{dist}(z')\, n_t(z,c)dzdc \end{array}$$

(Eq 2e)

In Eq. 2a, $S(z,c)$ models survival and $G(z',z,c)$ models growth as a function of individual plant size z and canopy c. However, growth of *F. alnus* is complex and some of the large individuals of *F. alnus* randomly broke from one year to the next. Most of these individuals died, which is covered by the survival function, but a few, usually large individuals (n = 17 over three years) survived breakage as they either had a small side-trunk before breakage or were able to resprout thereafter. The diameter of these broken individuals was strongly reduced at time $t + 1$. Thus, we split growth of *F. alnus* into two processes: Eq. 2a describes growth of *F. alnus* for individuals that did not break with the probability $1 - B(z)$, while Eq. 2b models the probability to break $B(z)$ and the size distribution $R(z', z)$ of broken individuals after resprouting. However, this event was very rare and, because of the low sample size, $B(z)$ and $R(z', z)$ were only a function of size and were kept constant among years and different canopies.

We modelled the fecundity of *F. alnus* including seed dispersal by animals using a model for consumed fruit (Eq. 2c), a model for dropped fruit (Eq. 2d), and an frugivore-independent gravity model (Eq. 2e). Eq. 2c, Eq. 2d and Eq. 2e are conditioned on each other and can be distinguished into three independent parts which take place chronologically in nature: fruit production, seed dispersal and recruitment to the seedling stage thereafter. The first part describes the amount of fruit produced by *F. alnus* and is given by the probability to reproduce $f_{repr}(z, c)$ and the number of fruits $f_{fruit}(z, c)$ as a function of size and canopy. The second part describes the process of dispersal of seeds by frugivore x into canopy c. Here, $f_{rel.anim.disp}$ is the percentage of animal dispersal within the population. If we assume that all fruits are removed by frugivores, then $f_{rel.anim.disp} = 1$ applies and fecundity is only a function of Eq. 2c and Eq. 2d. However, when the overall relative contribution of dispersal to fecundity decreases up to a point where no seeds are dispersed ($f_{rel.anim.disp} = 0$), the gravity function (Eq. 2e) becomes more important as $(1 - f_{rel.anim.disp})$ increases, respectively. Thus, $f_{rel.anim.disp}$ can be interpreted as the level of relative total fruit removal of the animal community. The sum of Eq. 2c and Eq. 2d is the contribution of seed dispersal by a frugivore to population growth, conditional on dispersal by gravity (see also Eq. 3). $f_{rel.int.freq}(x)$ is the relative interaction frequency of frugivores with *F. alnus.* The interaction frequency was calculated as the product of the number of visits, the probability of handling a fruit during each of these visits and the mean number of fruits that are handled thereafter. It describes the quantity component of seed dispersal effectiveness. $f_{nocrush}(x)$ is the probability of a fruit not being crushed by frugivores x and therefore not destroyed, $f_{consumed}(x)$ is the probability of a fruit being consumed conditional on not being crushed, $f_{drop}(c', x)$ is the probability of a fruit being dropped beneath a conspecific adult in environment c, conditional on neither being crushed nor consumed, and is, thus, equivalent to $1 - f_{consumed}(x)$, respectively, f_{seed} displays the transition from fruit to seed and is the mean number of seeds per fruit, $f_{deposition}(c', x)$ is the probability of a seed being deposited along the canopy gradient c within the forest. Notably, the canopy c in f_{repr} and f_{fruit} refers to the environment of the reproductive tree, and as dropped fruits do not change their position along the canopy gradient, in Eq. 2d, the canopy c' in f_{drop} also refers to the canopy of the reproductive tree. In contrast, in Eq. 2c, the canopy c' in $f_{deposition}$ refers to the new environment in which the seed is deposited after being taken up by frugivore x, and thus represents the transport of seeds from one environment to another. The third part of Eq. 2c, Eq. 2d and Eq. 2e describes seedling recruitment; $f_{recruit1}$ is the probability of recruitment of seedlings, $f_{recfruit}$ is the factor by which $f_{recruit1}$ is inhibited if seedlings are recruiting from seeds in fruit (Rogers et al. *preprint*), i.e. when fruits fall or are dropped beneath parental trees, and $f_{dist}(z')$ is the size distribution of new seedlings at time $t+1$.

4.4.10. Calculating seed dispersal effectiveness

The IPM was first used to calculate local population growth rates (λ) along the canopy gradient assuming that only gravity dispersal takes place. We then included animal seed dispersal in the IPM and calculated a meta-population growth rate by weighing the local IPMs (with dispersal) by the relative abundance of canopy covers in the forest (Fig. 1c). To calculate the effect of animal seed dispersal on population growth rate, we gradually increased the relative importance of seed dispersal (by increasing $f_{rel.anim.disp}$ from 0 to 1). To investigate the effect of animal seed dispersal during the colonization of favourable habitats, we assumed that individuals were not present in forest gaps (i.e. the 50% lightest environments along the canopy cover gradient in the forest) and calculated long-term local and meta-population growth rate by proportionally increasing the abundance of the 50% darkest environments (such that the values added up to 1). We are aware that this is a simple approach to investigate the effect of seed dispersal during colonisations. At best, the effect of animal seed dispersal is modelled over time (see e.g. Yang et al., 2011). However, we were not able to track changes in the canopy structure of the forest over time (Supplementary information text 3), which prevented us from studying the effect of seed dispersal during forest succession (see e.g. Metcalf et al., 2009).

To quantify the net gain of dispersal by a single frugivore species in comparison to a situation, in which its function is absent (gravity), we calculated frugivore-specific gravity components,

$$\sum_{x=1} \iint_{L}^{U} \begin{matrix} f_{repr}(z,c) f_{fruit}(z,c) \\ f_{rel.anim.disp} f_{rel.int.freq}(x) f_{seed} \\ f_{recruit1} f_{recfruit} f_{dist}(z')\, n_t(z,c') dz dc dx \end{matrix}$$

(Eq 3)

which we later subtracted from the frugivore-specific dispersal effects (the sum of Eq. 2c and Eq. 2d). In these models, we kept the proportion of animal seed dispersal constant at ($f_{rel.anim.disp}$ = 1). Due to the non-linear relationship between population growth of *F. alnus* and the proportion of animal seed dispersal, the sums of the net effects of single dispersers to total population growth (i.e. the loss during the interaction deficit, Fig. 3a) do not add up to the total effect of animal dispersal (Fig. 2a). This is because the effectiveness of seed dispersal of animal species increases with the number of species lost, as population growth increased most with animal seed dispersal the fewer seeds were dispersed. Interaction compensation by the animal community was modelled by proportionally increasing the relative interaction frequency of the remaining animal community by the relative interaction frequency of the lost dispersers, such that the summed proportion of removed fruits added up to 1 again. Because this step was computationally extensive, we modelled interaction compensation only for the four main dispersers.

The seed dispersal effectiveness of frugivore x can be separated into the underlying contribution of quantity and quality (Schupp et al., 2010): For the quantity component, we took the relative interaction frequency of an animal with *F. alnus* as a variable. For the quality component, we took the survival probability of a seed until the age of first reproduction as a measure. This can be calculated using a Markov chain, in which reproduction is an absorbing state in addition to mortality (Ellner et al., 2016). The probability of a seed of *F. alnus* reaching maturity $f_{maturity}$ is then given by

$$f_{maturity}(z_0, c', x) =$$

$$\sum_{x=i} \iint_L^U f_{nocrush}(x)\, f_{consumed}(x)\, f_{deposition}(c', x)\, f_{recruit1}\, l_{(\bar{a}_{repr}-1)}(z_0, c')\, dz_0 dc$$

(Eq 4a)

$$+$$

$$\sum_{x=i} \iint_L^U f_{nocrush}(x)\, f_{drop}(c', x)\, f_{recruit1}\, f_{recfruit}\, l_{(\bar{a}_{repr}-1)}(z_0, c')\, dz_0 dc$$

(Eq 4b)

which is the sum of the probability of consumed fruits (Eq. 4a) and dropped fruits (Eq. 4b) reaching maturity conditional on seed dispersal of frugivore x, the initial size of seedlings z_0 and the canopy cover c'. Here, $l_{(\bar{a}_{repr}-1)}$ describes the probability of a seedling surviving until it has produced fruits at least once, and is a modification of formulas presented in (Ellner et al., 2016, chapter 3). A more detailed derivation of $l_{(\bar{a}_{repr}-1)}$ is given in Supplementary information text 4. Note that the unit for $f_{maturity}$ is one seed, and not the probability of the combined probability of two or more seeds in one fruit.

4.4.11. Statistical analyses

Fruit removal, handling and seed deposition

We analysed the effect of frugivorous animal species on different components of fruit removal (Supplementary figure 9) with generalised linear mixed models with site and observer as a random factor using the R-package glmmTMB version 1.1.2 (Brooks et al., 2017) and the R program version 4.1.1 (R Core Team, 2021). Significance values were obtained with a Wald-χ^2 test using the R-package car version 3.0-11 (Fox and Weisberg, 2019). To analyse the effect of animal species on the probability of handling a fruit during a visit to *F. alnus*, we used a logit link and a binomial error distribution. To analyse the effect of animal species on the number of fruits handled during each of these visits, we used a log link and a Poisson error distribution. In the analysis on the effect of animal species on the number of seeds per scat, we used site as a random factor, animal species as a fixed factor, and a log link and a Poisson error distribution. In this model, we excluded an outlier observation because it affected the model outcome, and included the scat ID as observation level random effect to account for overdispersion (OLRE, Harrison, 2014).

Seedling recruitment

To analyse the effect of canopy cover and year on seedling recruitment of *F. alnus*, we used generalised linear mixed models with the number of seedlings that had recruited in spring and the number of non-recruited seedlings in the same plot as a response variable. We included the plots within sites as a random factor. In these models, we used a logit link and a beta-binomial error distribution to account for overdispersion.

Plant vital rates

To analyse the effect of study year, size of individuals, forest canopy cover and their interaction on the vital rates of *F. alnus*, we used the study year, the standardized log10-transformed diameter and the standardized canopy cover as fixed factors and site as a random factor (see Supplementary table 4, 5). In addition, we added size^2 as a term in these models to test for non-linear relationships. We then identified potential outliers using 2.24*standard deviation of the studentised residuals of the global model of plant growth as a threshold (Aguinis et al., 2013). Of these outliers, we removed 55 transitions of plant individuals from the dataset (~3% of total transitions); either entirely, if they had erroneous values (n = 14) or by splitting up records of single individuals into that of two or more independent individuals, when two or more different individuals had been incorrectly classified to be the same individual in the field (n = 41). To analyse the effect of year, size and canopy cover on the survival, breakage and fruiting probability, we used a logit link and a binomial error distribution. In the analysis of the number of fruits, we used a log link, a Poisson error distribution and an observation level random effect (OLRE). To find the most parsimonious model for the analyses of survival, growth, fruiting probability and the number of fruits, the global model and 7 component models were ranked according to the small sample unbiased Akaike's information criterion (AICc, Supplementary Table 4, 5, Supplementary figure 4, 5), using the R-package MuMIn version 1.43.17 (Barton, 2020). As the sample size was very low in the analyses of breakage and resprouting, we analysed only the effects of size (linear) in the binomial models of breakage, and size and size^2 (linear and quadratic) in the growth analyses of resprouting individuals. In the analyses of resprouting, we further modelled the variance as a function of size and size^2 (Supplementary table 4, supplementary figure 6). The performance of all models was evaluated using the R-package DHARMa version 0.4.3 (Hartig, 2021).

Seed dispersal effectiveness

The change in population growth following the deficit of interactions with an animal disperser was used as a measure for seed dispersal effectiveness (*sensu* Schupp et al. 2017). To test if the mean seed dispersal effectiveness of animals among bootstraps was related to the mean quantity or mean quality of seed dispersal, we used Spearman rank and Pearson correlations. As the quality or quantity of seed dispersal for animal species was partially calculated using the same parameters (see e.g. Fig 1c, Supplementary table 3), we repeated the correlations with two subsets of animal species (n = 7, no pseudo-replication, see Fig. 1c; and n = 13, partial pseudo-replication, see Fig. 2b). The results of the correlations were qualitatively not affected in their direction or magnitude by the number of animal species included in the correlations, nor by the type of correlation analyses (Spearman vs. Pearson). We refer to the analyses of the Spearman rank correlation with no pseudo-replication throughout the study.

4.4.12. Quantifying uncertainty

We used bootstrapping to examine the uncertainty in the different demographic measures. We differentiated between uncertainty arising from different observations of plant individuals (hereafter 'growth uncertainty') and uncertainty arising from differences in the dispersal process (hereafter 'dispersal uncertainty'). To model uncertainty of growth, we resampled observations of plant individuals of *F. alnus* at each site in each year from the dataset, with replacement. By doing so, we created 500 datasets with three years of observation. We modelled the vital rates as described above and kept the remaining parameter constant. To model uncertainty of dispersal, we resampled 500 times the removal observations, seed deposition, seedling recruitment rates and, as a function of seed recruitment, the deinhibition of fruit pulp on seed germination (logit = -1.24, Rogers et al. *preprint*), with replacement. The bootstrapped data had the similar structure as the original field data with respect to the number of replicates for each combination of year and site. From these, we calculated the frugivore-specific dispersal rates as described above. The structure of the formulas of the IPM were held constant for the vital rates, i.e. we only allowed parameter estimation for the most parsimonious model across bootstraps (Supplementary figure 5).

Data availability statement

The original contributions and R code presented in the study will be made available online from Dryad Digital Repository https://doi.org/10.5061/dryad.h44j0zpmq.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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4.6. Supplementary Material

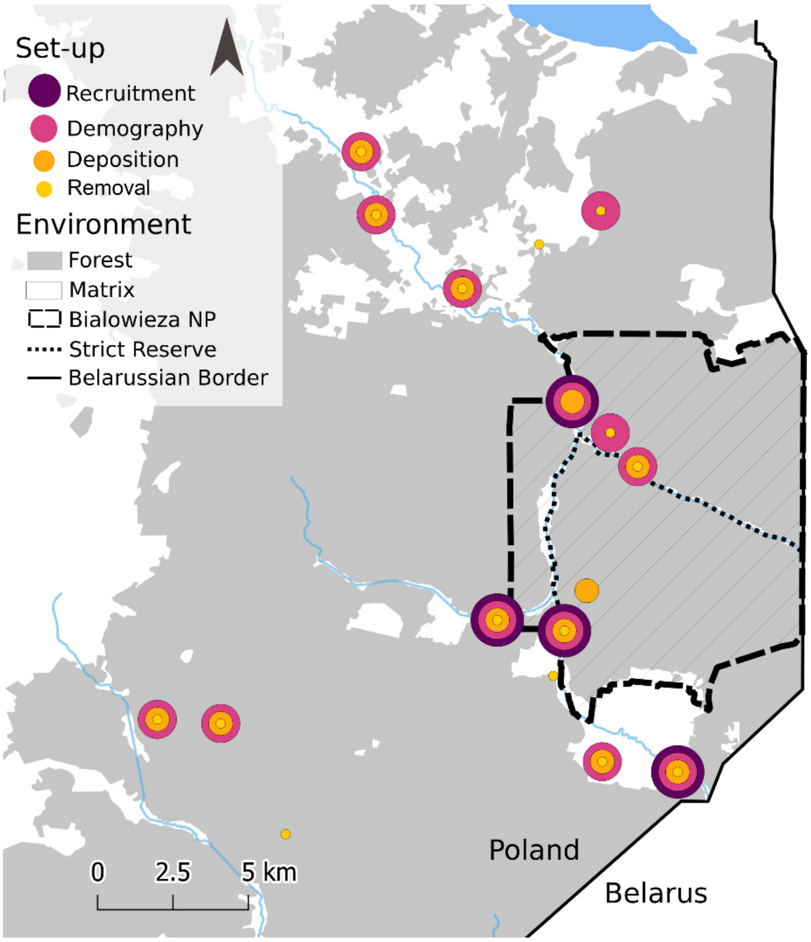
This supplement includes:

Supplementary text 1-4

Supplementary figures 1-15

Supplementary tables 1-5

Supplementary information references



Supplementary figure 1: Map showing the location of the 17 study sites in the Białowieża Forest, Eastern Poland, and the studies conducted at these locations

Supplementary table 1: Geographical coordinates and characteristics of the experimental setup in Białowieża Forest, Eastern Poland.

					Entire fleshy-fruited plant community				Only *Frangula*			
Plot	Site	Latitude	Longitude	Forest	Removal	Deposition	Demographie	Keimung	Removal	Deposition	Demographie	Keimung
301	1	52.7425223	23.8331253	Intact	1	1	1	0	0	1	1	0
312	2	52.7894196	23.8446378	Intact	1	0	1	0	1	0	1	0
303	3	52.7793992	23.8580859	Intact	1	1	1	0	1	1	1	0
314	4	52.7306426	23.8221458	Intact	1	1	1	1	1	1	1	1
315	5	52.7987112	23.8260231	Intact	1	1	1	1	0	1	1	1
102	6	52.7030703	23.6535284	Degraded	1	1	1	1	1	1	1	1
103	7	52.6701456	23.6853848	Degraded	1	0	0	0	1	0	0	0
203	8	52.7042936	23.6224021	Degraded	1	1	1	0	1	1	1	0
111	9	52.7172336	23.8167656	Degraded	1	0	0	0	1	0	0	0
112	10	52.7338132	23.7892289	Degraded	1	1	1	0	1	1	1	0
30	11	52.6886727	23.8777491	Degraded	1	1	1	1	1	1	1	1
11	12	52.8552399	23.8399927	Degraded	1	0	1	0	1	0	1	0
36	13	52.8540699	23.7298022	Degraded	1	1	1	0	1	1	1	0
33	14	52.8453121	23.8097584	Degraded	1	0	0	0	1	0	0	0
13	15	52.8322092	23.7721042	Degraded	1	1	1	0	1	1	1	0
15	16	52.6917217	23.8407402	Degraded	1	1	1	0	1	1	1	0
35	17	52.8727648	23.7224447	Degraded	1	1	1	0	1	1	1	0

Supplementary table 2: Summary of the sampling of seed removal, deposition and plant demography on *Frangula alnus* across 17 study sites in Białowieża Forest. The entries in each cell depict the year- and plot-specific sampling of (1) the number of individuals of *F. alnus* that have been selected for the three sessions of frugivore observations; (2) the number of scats with only *F. alnus* or all scats with seeds of the fleshy-fruited plant community found along the transects; (3) the number of individuals that were used for vital rate assessment of plant demography

		Seed removal		**Seed deposition**						**Plant demography**		
				Scats with seeds of *F. alnus*			**All scats with seeds**					
Plot	**Site**	**2011**	**2012**	**2016**	**2017**	**2018**	**2016**	**2017**	**2018**	**2017**	**2018**	**2019**
301	1			0	0	0	5	6	119	0	0	0
303	3	1		0	0	19	17	18	140	20	19	23
312	2	3								163	150	125
314	4	3	3	2	7	17	3	8	29	127	95	98
315	5	1		1	0	1	13	9	82	25	25	25
102	6	2	2	0	0	0	1	1	3	5	6	6
103	7	3										
203	8	3	3	0	0	37	22	6	63	11	10	10
111	9	2	2									
112	10	3	3	6	63	68	28	115	111	26	48	56
30	11		3	11	8	53	22	28	138	106	79	100
11	12		3							31	49	41
36	13		2	0	1	5	24	31	85	31	30	28
33	14		2									
13	15		3	44	57	29	44*	67*	120*	30	42	43
15	16		2	2	2	1	35	59	49	28	30	29
35	17		3	4	5	19	33	8	184	38	39	38
Total		21	31	70	143	249	247	356	1123	641	622	622

*We found almost 500 scats beneath one tree of *Sambucus nigra*, which acted as a hub tree in the local forest. We excluded scats from this transect other than *F. alnus* from the analyses, as these influenced the deposition pattern of frugivore species.

Supplementary table 3: List of codes, removal and deposition of animal seed disperser of *Frangula alnus* in Białowieża Forest**.**

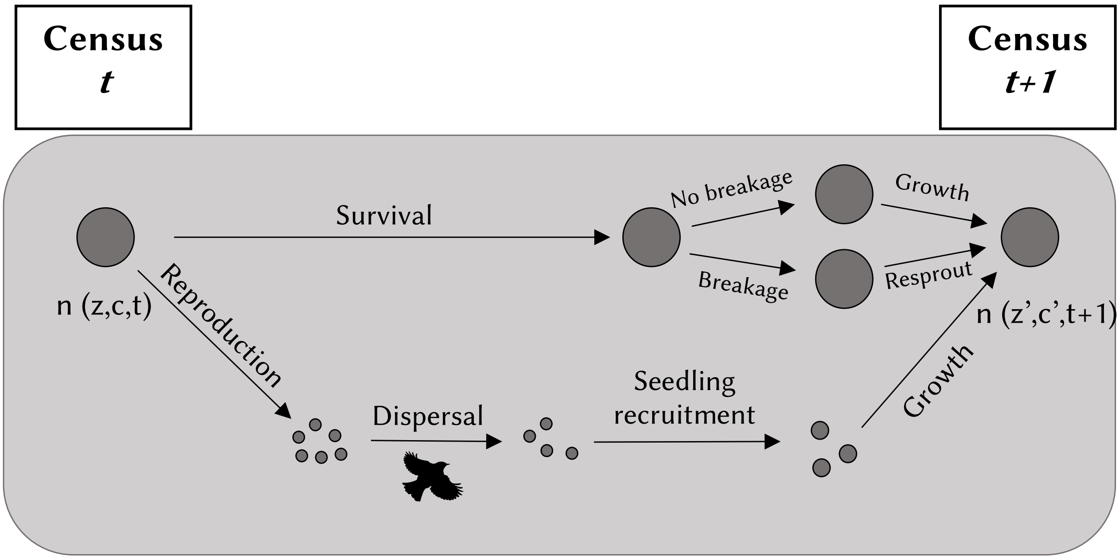
Order	**Family**	**Animal species**	**Code**	**Visits**	**Prob. of handling fruit**	**Mean no. of handled fruit**	**Interaction frequency**	**No. of observed handling**				**No. of scats with only *F. alnus***	**No. of scats with all seeds***
								swallow	**remove**	**crush**	**drop**		
Passeriformes	Fringillidae	*Coccothraustes coccothraustes*	2	4	0.75	1.67	5.00	0	1	4	0	0	0
Piciformes	Picidae	*Dendrocopos major*	3	1	1.00	1.00	1.00	11	0	0	0	0	1
Piciformes	Picidae	*Dendrocopos medius*	4	7	0.86	1.83	11.00	1	0	0	0	0	0
Passeriformes	Muscicapidae	*Erithacus rubecula*	6	135	0.73	1.89	185.97	155	5	0	1	7	30
Passeriformes	Muscicapidae	*Luscinia luscinia*	7	4	1.00	1.50	6.00	6	0	0	0	0	3
Passeriformes	Muscicapidae	*Muscicapa striata*	10	21	0.64	1.67	22.50	14	0	0	1	0	0
Passeriformes	Paridae	*Parus major*	12	29	0.17	1.00	4.83	2	0	0	0	1	2
Passeriformes	Sittidae	*Sitta europaea*	14	59	0.51	1.75	52.88	25	10	0	0	0	0
Passeriformes	Sylviidae	*Sylvia atricapilla*	15	582	0.90	2.49	1312.33	935	5	0	5	291	570
Passeriformes	Sylviidae	*Sylvia borin*	16	32	0.89	1.91	54.30	42	0	0	0	17	37
Passeriformes	Turdidae	*Turdus merula*	17	88	0.84	4.55	335.48	198	0	0	2	63	597
Passeriformes	Turdidae	*Turdus philomelos*	18	44	0.85	2.71	101.87	76	0	0	0	73	429
Artiodactyla	Cervidae	*Cervus elaphus*	1	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	2	4
Rodentia	Gliridae	*Dryomys nitedula*	5	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	2	4
Carnivora	Mustelidae	*Martes martes*	8	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	2	30‡
Galliformes	Phasianidae	*Meleagris gallopavo*	9	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	1	2
Rodentia	Cricetidae	*Myodes glareolus*	11	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	2	3
Passeriformes	Prunellidae	*Prunella modularis*	13	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	1	1
Rodentia	Muridae	*Apodemus flavicollis*	19	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	0	1
Artiodactyla	Suidae	*Sus scrofa*	20	17**	0.70**	1.49**	17.81**	0.79**	0.15**	0.05**	0.01**	0	0
Artiodactyla	Bovidae	*Bison bonasus*		0								0	1
Columbiformes	Columbidae	*Columba palumbus*		0								0	1
Passeriformes	Corvidae	*Garrulus glandarius*		0								0	3
Rodentia	Gliridae	*Muscardinus avellanarius*		0								0	4
Passeriformes	Fringillidae	*Pyrrhula pyrrhula*		0								0	5
Rodentia	Sciuridae	*Sciurus vulgaris*		0								0	1

*Scats with seeds of at least one fleshy-fruited plant species co-occuring with *F. alnus*. We included only those scats in the analyses, which were found at the same time as scats with seeds of *F. alnus* (see methods).

‡*Martes martes* uses scats to mark territories. We included all scat of *M. martes* in the analyses independent of the period of year when we found the scat (see methods).

** Fruit removal and fruit handling of these animals was not observed. We assigned them the mean values of fruit removal and handling probabilities of other rare animals in the seed deposition network (less than ten scats in total; see methods).

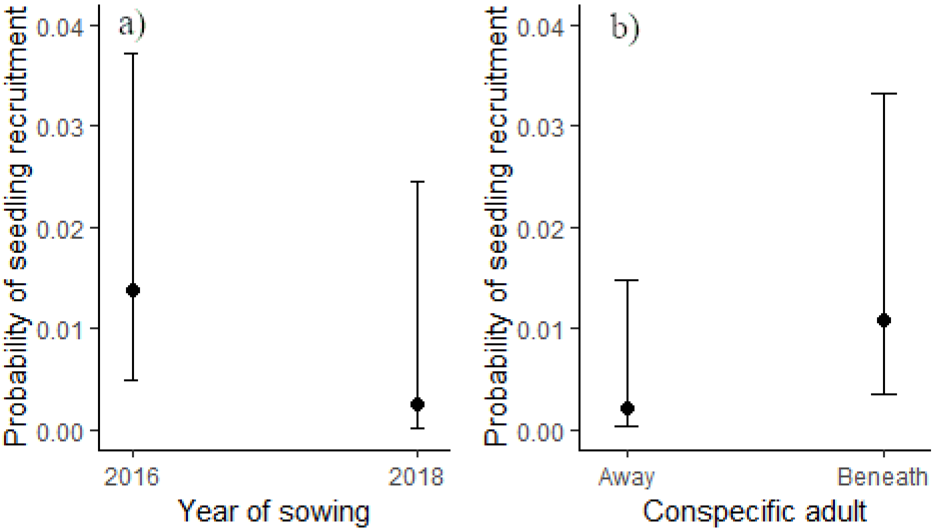
Apodemus flavicollis and *Sus scrofa* were only observed using camera trapping in a pilot study (Kohlbrecher 2015).



Supplementary figure 2: Life cycle diagram with a pre-reproductive census of the temperate tree *F. alnus*. Large and small circles display established individuals and new recruits.

Supplementary information text 1: Seedling recruitment of *Frangula alnus*

Peak recruitment of *F. alnus* was low in the Białowieża Forest and was only influenced by year (LRT, $\chi^2 = 4.12$, $p = 0.042$, Supplementary Fig 5), but not canopy closure (LRT, $\chi^2 = 0.21$, $p = 0.650$). No seedlings recruited from seeds sown in 2017. On average, the probability of recruitment of *F. alnus* was 0.844% in the first year, 0.002% in the second year and 0.041% in the third year after dispersal. Because seedling recruitment in the second and third year was negligible, we modelled seedling recruitment of *F. alnus* without persistent seed bank. In 2018, we additionally sowed out 250 seeds of *F. alnus* beneath 10 conspecific adults in each of the degraded and intact forest. After correcting for naturally occurring seedlings, the conspecific adults did not affect seedling recruitment of *F. alnus* in the next year (LRT, $\chi^2 = 2.45$, $p = 0.118$, Supplementary Fig. 5).



Supplementary figure 3: (a) Effects of the year of sowing and (b) conspecific adults on recruitment of seedlings of *Frangula alnus* in the Białowieża Forest. The results are shown for the year of peak recruitment of *F. alnus* (after one year). No seedlings recruited from seeds sown in 2017. Mean ± 95%CI.

Supplementary table 4: Summary of the rank selection of the most parsimonious model across the vital rates (survival, growth, fruiting probability and number of fruits) of *F. alnus* in Białowieża Forest.

Model	**Fixed factors**	**Survival**			**(log) Growth**			**Fruiting prob.**			**Number of fruits**			**Summed ranks**	**Mean dAICc**
		Rank	AICc	dAICc	Rank	AICc	dAICc	Rank	AICc	dAICc	Rank	AICc	dAICc		
1	Year (Y) + Canopy cover (C) + Diameter (D) + Diameter² (D²)	**1**	**687.4**	**0.0**	6	-1484.7	10.2	5	842.2	3.4	6	5660.4	32.4	18	11.5
2	Y * C + D + D²	2	689.3	1.9	7	-1483.6	11.3	7	843.4	4.6	7	5663.0	35.0	23	13.2
3	**C + Y * D + Y * D²**	4	690.7	3.4	**1**	**-1494.9**	**0.0**	**1**	**838.8**	**0.0**	**1**	**5628.0**	**0.0**	**7**	**0.8**
4	Y + C * D + C * D²	3	690.6	3.3	8	-1481.5	13.4	6	842.7	3.9	8	5663.8	35.8	25	14.1
5	Y * C + Y * D + Y * D²	5	692.7	5.4	2	-1493.8	1.0	3	839.9	1.1	2	5632.0	4.0	12	2.9
6	Y * D + Y * D² + C * D + C * D²	6	694.0	6.6	3	-1491.3	3.6	2	839.7	0.9	3	5636.2	8.2	14	4.8
7	Y * C + Y * D + Y * D² + C * D + C * D²	7	696.0	8.7	4	-1490.3	4.6	4	841.8	3.0	4	5636.2	8.2	19	6.1
8	Y * C * D + Y * C * D²	8	698.9	11.5	5	-1481.5	13.4	8	844.7	5.9	5	5663.8	35.8	26	16.6

AICc, Akaike's information criterion with a correction for small sample sizes.

The diameter of plant individuals was log10-transformed, and canopy cover as well as diameter were standardized before analyses.

All component models included a quadratic term of diameter (’Diameter²’) as a fixed factor and study site as a random factor. The number of fruits also included an observation-level random effect to account for overdispersion.

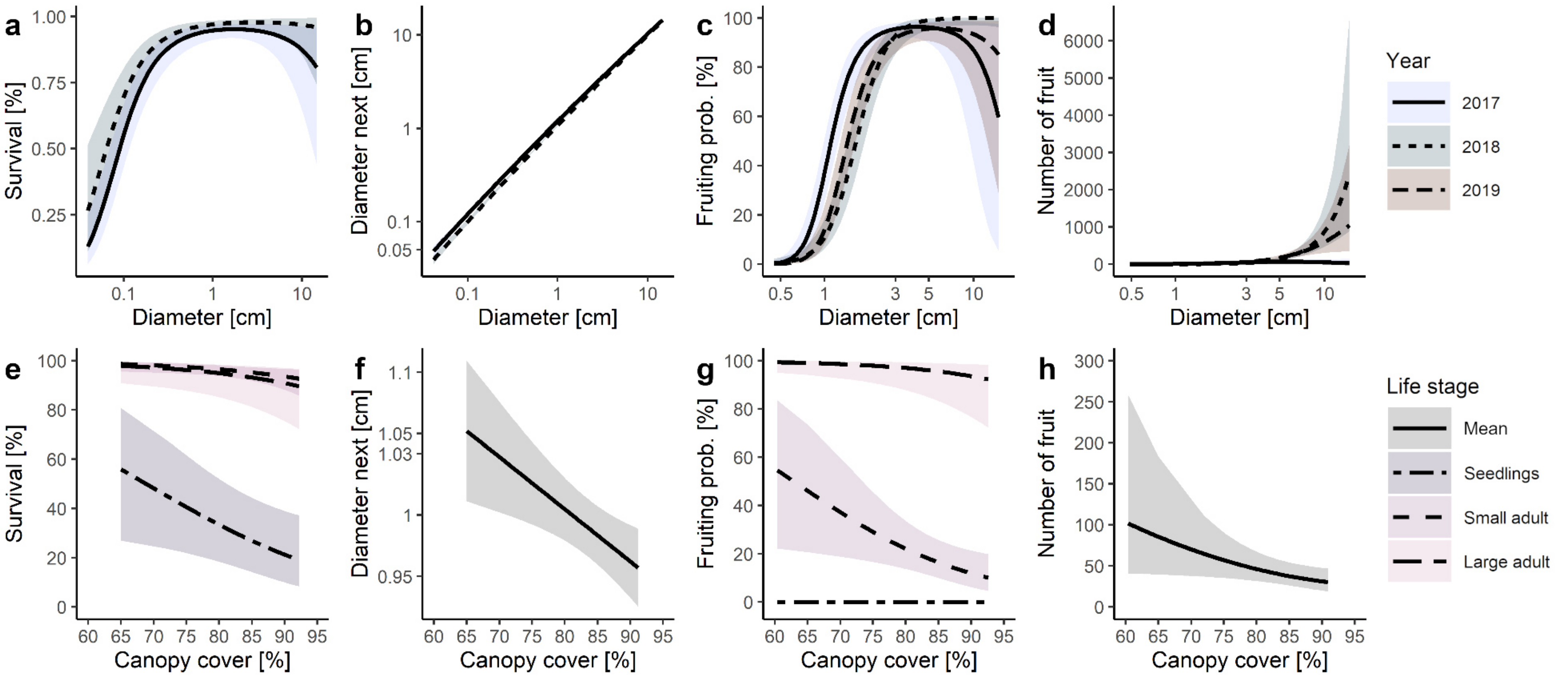
The best-ranked model of a vital rate based on AICc is bold.

Supplementary table 5: Analyses of variance of the effects of year, canopy and diameter on plant vital rates (survival probability, diameter next, fruiting probability, number of fruits, breakage probability and resprouting) of *F. alnus* in Bialowieza Forest, Poland.

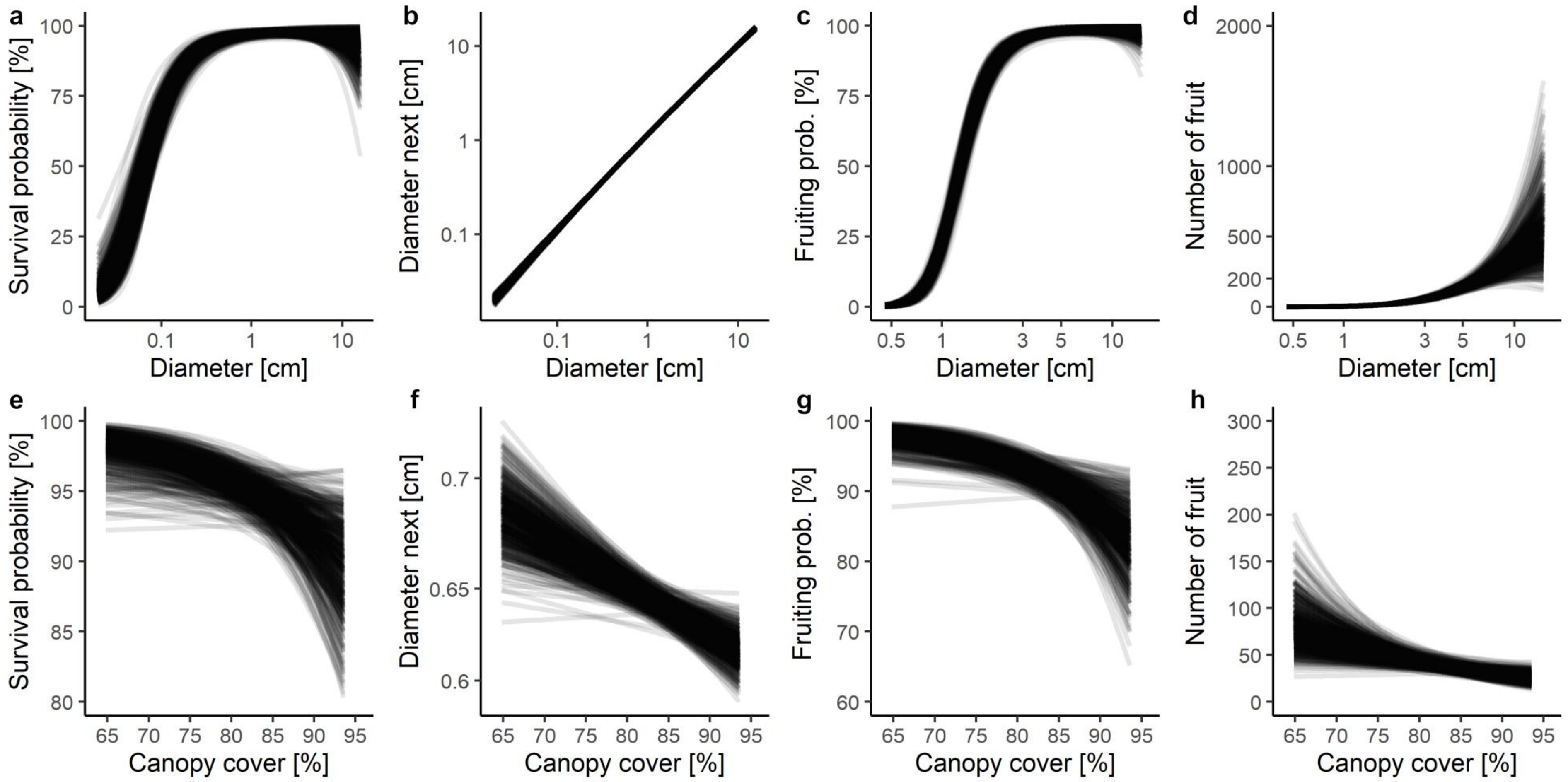
	Survival probability			**Diameter next**			**Fruiting probability**		
	df	Wald-χ^2	p	df	Wald-χ^2	p	df	Wald-χ^2	p
Canopy cover	1	5.2	**0.023**	1	8.8	**0.003**	1	6.0	**0.014**
Year	1	10.0	**0.002**	1	104.0	**< 0.001**	2	35.6	**< 0.001**
Diameter	1	38.4	**< 0.001**	1	25162.4	**< 0.001**	1	122.3	**< 0.001**
Diameter^2	1	27.2	**< 0.001**	1	18.1	**< 0.001**	1	31.2	**< 0.001**
Year * Diameter	1	0.5	0.464	1	7.5	**0.006**	2	3.9	0.144
Year * Diameter^2	1	0.5	0.476	1	< 0.1	0.996	2	7.2	**0.027**
Residual	1094			900			1786		

	Number of fruits			**Breakage probability**			**Resprouting next**		
	df	Wald-χ^2	p	df	Wald-χ^2	p	df	Wald-χ^2	p
Canopy cover	1	4.6	**0.031**						
Year	2	9.1	**0.011**						
Diameter	1	61.4	**< 0.001**	1	9.5	**< 0.001**	1	133.6	**< 0.001**
Diameter^2	1	5.5	**0.020**				1	28.1	**< 0.001**
Year * Diameter	2	0.6	0.736						
Year * Diameter^2	2	6.6	**0.038**						
Residual	514			1883			8		

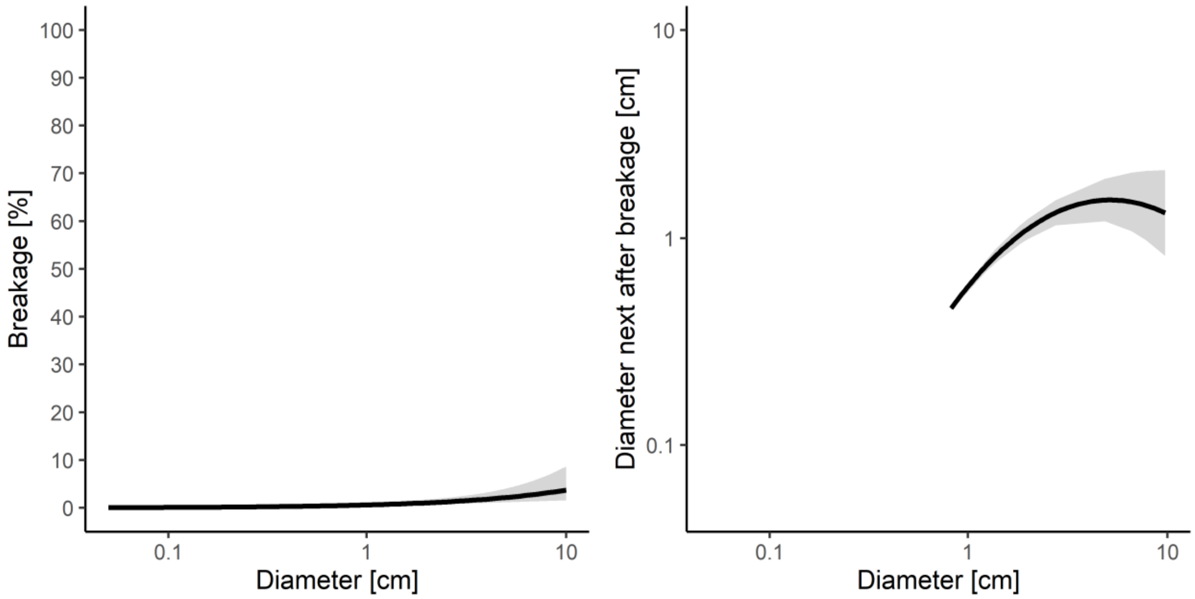
Diameter, diameter of plant individuals at time t; Diameter next, diameter of plant individuals at time t+1; Resprouting next, diameter of plant individuals after breakage.



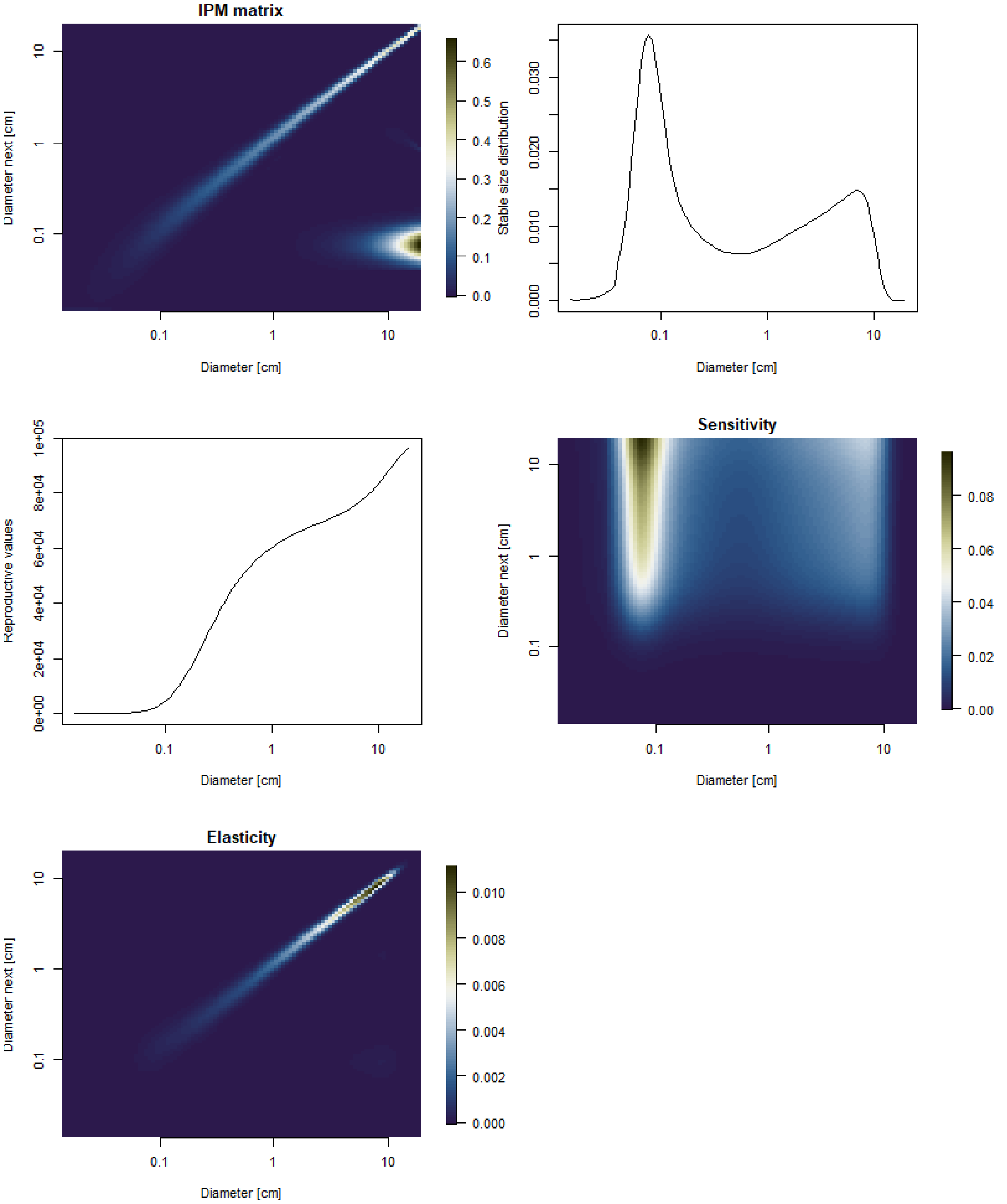
Supplementary figure 4: The effect of (a,b,c,d) diameter of plant individuals and study year (2017, 2018, 2019) and (e, f, g, h) canopy cover on the (a,d) probability to survive from time t to t+1, (b,f) next diameter at time t+1, (c,g) probability to fruit and (d,h) the number of fruit of *F. alnus* in Białowieża Forest, Eastern Poland. Due to the non-linear relationships, we illustrated the effect of canopy cover on survival and fruiting probability for three life stages (seedlings, small adult, large adult). Predicted mean ± 95%CI. Note the log-scale for diameter and diameter next.



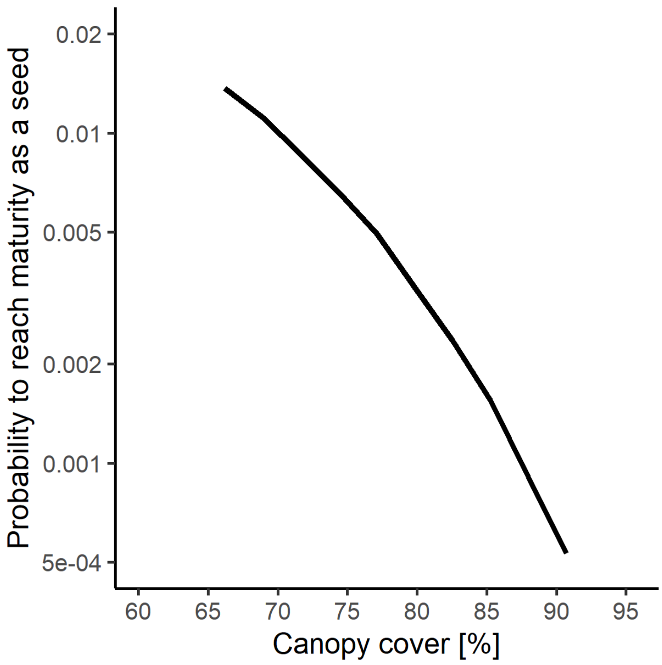
Supplementary figure 5: The effect of (a,b,c,d) diameter of plant individuals averaged across study years (2017, 2018, 2019) and (e, f, g, h) canopy cover on the (a,d) probability to survive from time t to t+1, (b,f) next diameter at time t+1, (c,g) probability to fruit and (d,h) the number of fruit of *F. alnus* in Białowieża Forest, Eastern Poland. Each grey line displays one of 500 draws from non-parametric bootstraps with replacement, collectively representing uncertainty in the vital rate regressions. Note the log-scale for diameter and diameter next.



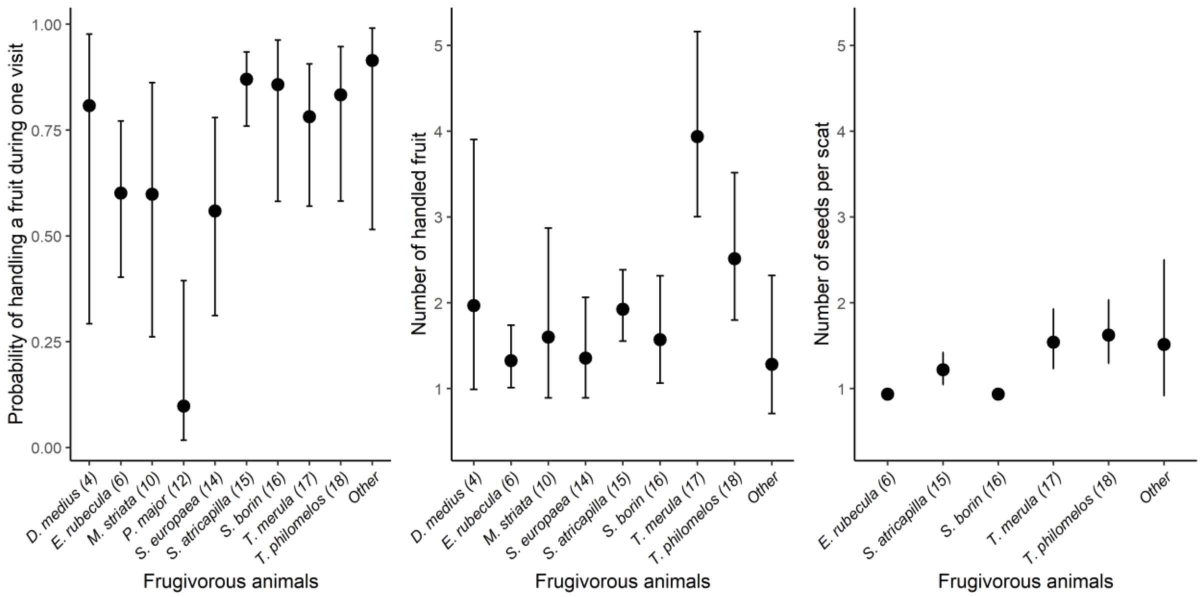
Supplementary figure 6: The effect of diameter of plant individuals on (a) the probability to break and survive from time t to t+1, (b) the diameter of individuals after breakage at time t+1 of *F. alnus* in Białowieża Forest, Eastern Poland. Predicted mean ± 95%CI. Note the log-scale for diameter and diameter next after breakage.



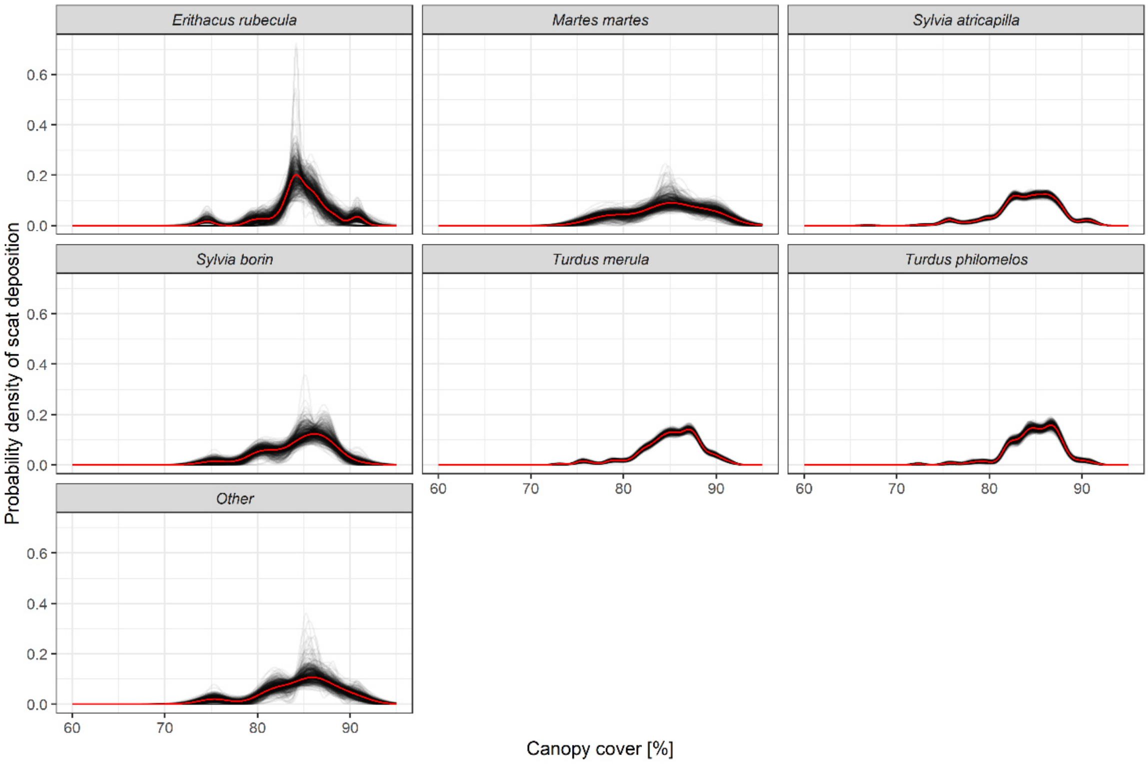
Supplementary figure 7: Basic model output of the meta-population of *F. alnus* with a fecundity kernel modelling gravity dispersal in Białowieża Forest, Eastern Poland. (a) IPM matrix, (b) stable size distribution, (c) reproductive value of individuals, (d) sensitivity and (e) elasticities of the IPM matrix. Note the log-scale for diameter and diameter next



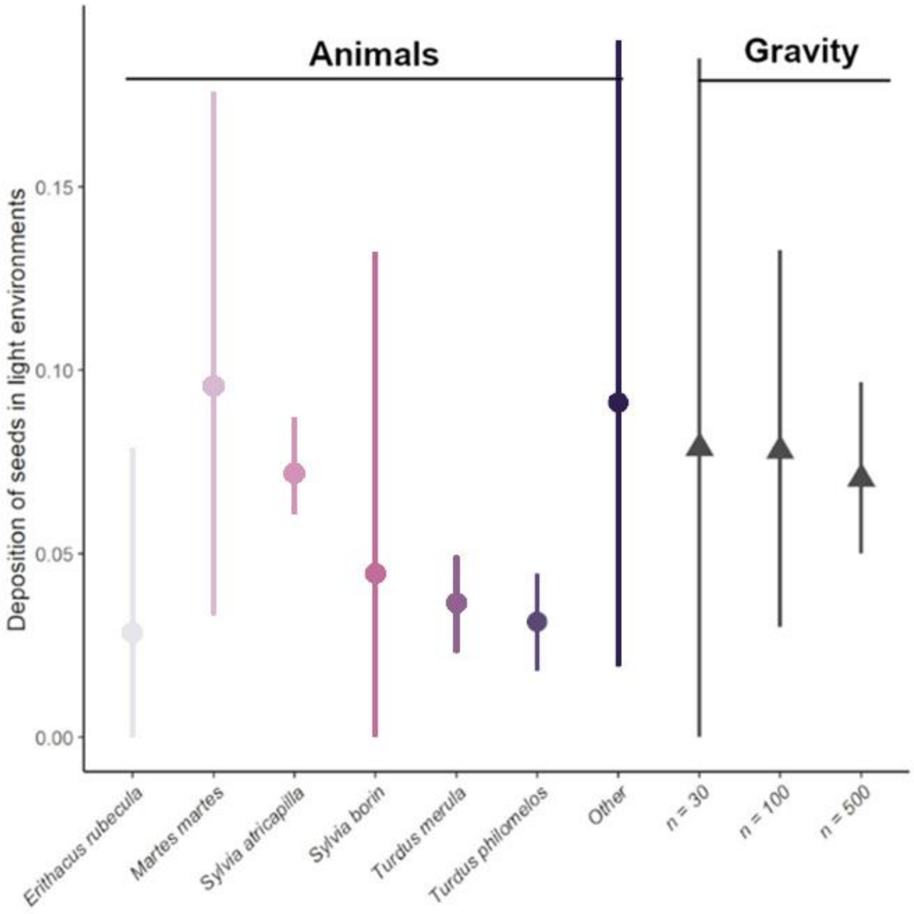
Supplementary figure 8: The probability of a seed of *F. alnus* to reach maturity in relation to the canopy cover in Białowieża Forest, Eastern Poland. Note the log-scale for the probability



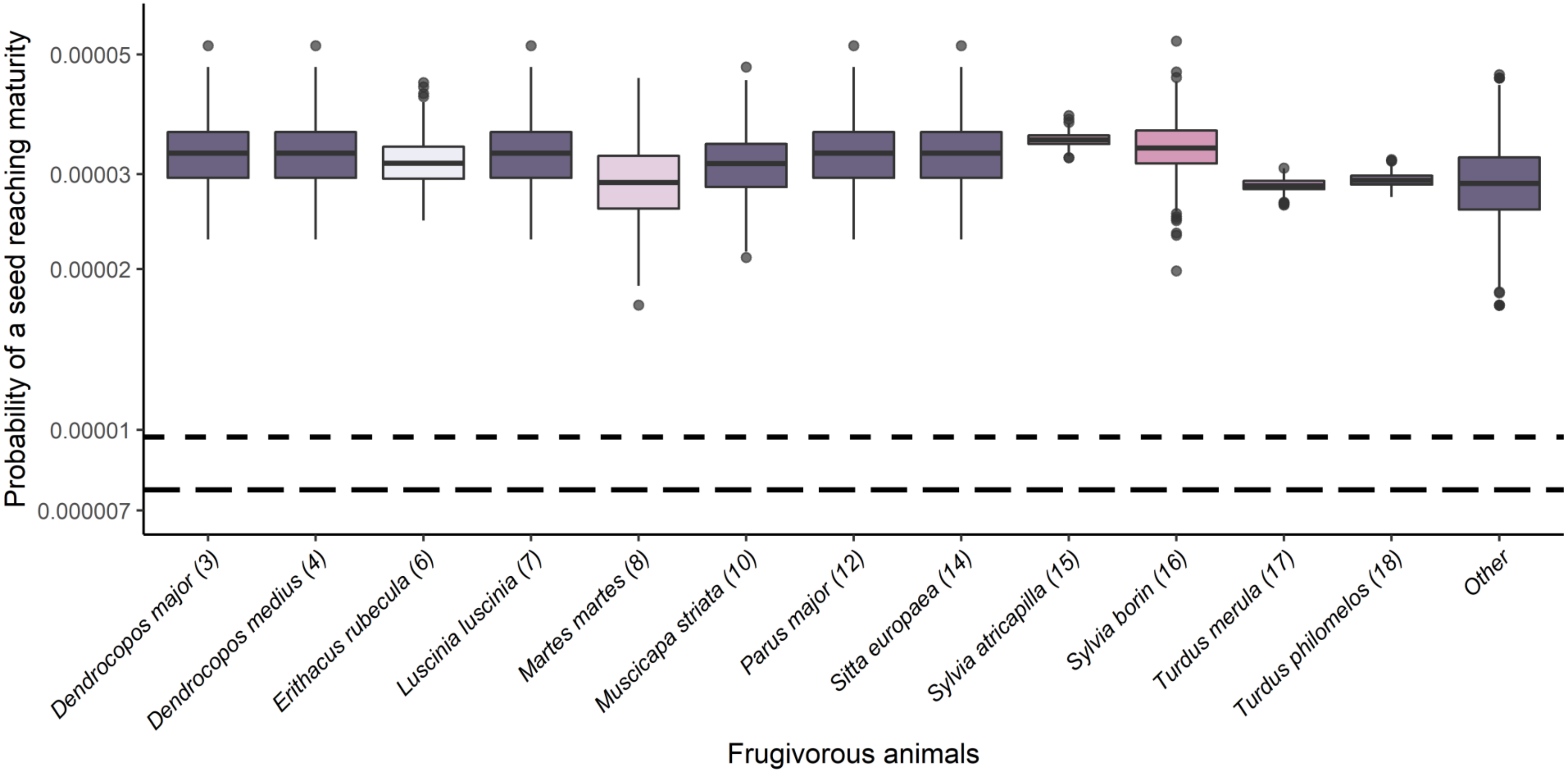
Supplementary figure 9: (a) The probability of handling a fruit, (b) the number of handled fruit during each visit and (c) the number of seeds per scat as an effect of animal species. The numbers in the brackets reflect the species labels in the interaction network (see manuscript, Figure 1). The data on fruit removal is from Albrecht et al. (2013) and on seed deposition from Schlautmann et al. (2021). The effect of animals on the probability of handling a fruit during one visit (Wald-$\chi^2 = 48.58$, $p < 0.001$), number of fruits (Wald-$\chi^2 = 78.69$, $p < 0.001$) was significant, and on number of seeds per scat (Wald-$\chi^2 = 10.63$, $p = 0.059$) marginally significant. Mean ± 95% CI.



Supplementary figure 10: Uncertainty in the relative deposition pattern of animal species along the canopy cover gradient in Białowieża Forest, Eastern Poland. Animal disperser species were *Erithacus rubecula, Martes martes, Sylvia atricapilla, Sylvia borin, Turdus merula, Turdus philomelos* and all remaining disperser species (‘Other’). The red solid line displays the mean deposition pattern. Each grey line displays one of 500 draws from non-parametric bootstraps with replacement.



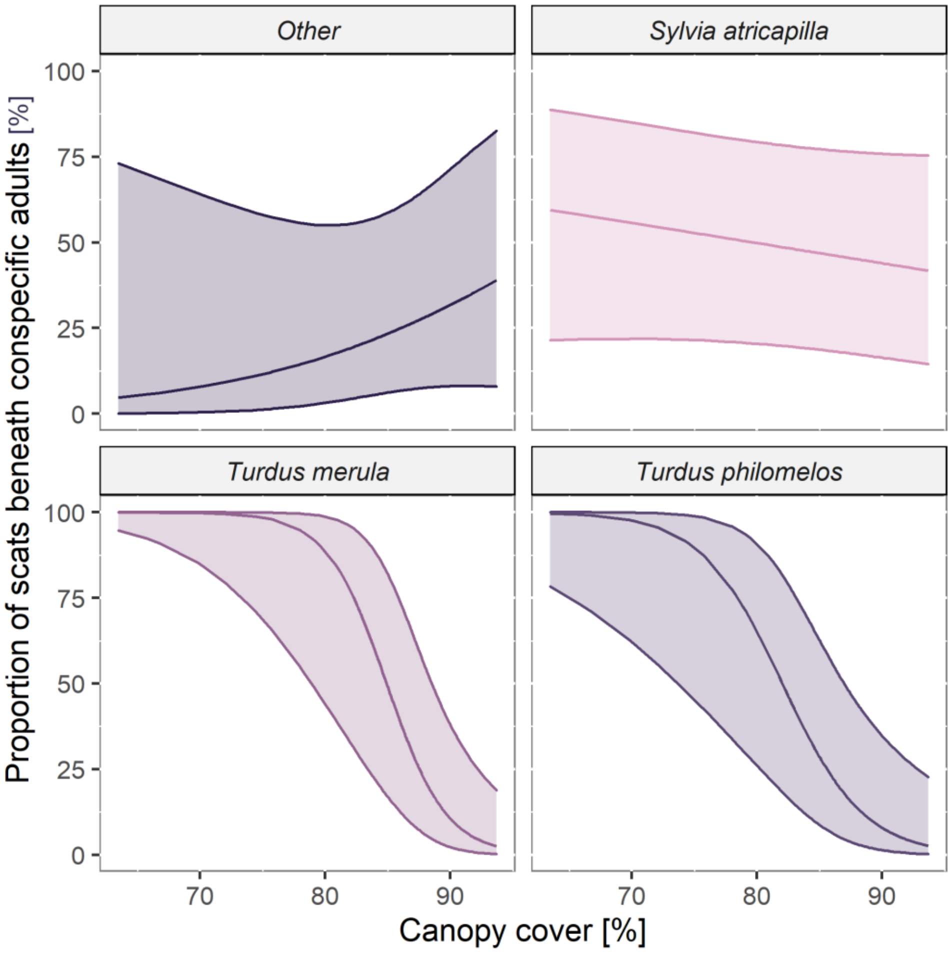
Supplementary figure 11: Uncertainty in the relative deposition pattern of seeds by animal species or gravity into the 50% lightest environments (forest gaps, edges) along the canopy cover gradient in Białowieża Forest, Eastern Poland. Animal disperser species were *Erithacus rubecula, Martes martes, Sylvia atricapilla, Sylvia borin, Turdus merula, Turdus philomelos* and all remaining disperser species ('Other'). Seed deposition of gravity dispersal was modelled as the relative abundance of microhabitats along the canopy gradient in the forest depending on the number of replicates for each bootstrap, with only 30 replicates (similar to *E. rubecula*, *Martes martes*, *Sylvia borin* and 'Other' disperser), 100 replicates and 500 replicates (similar to *S. atricapilla, T. merula* and *T. philomelos*). The results of gravity thus correspond to what we expected based on random deposition of seeds by animals. Mean ± 95% prediction intervals based on 500 non-parametric bootstraps.



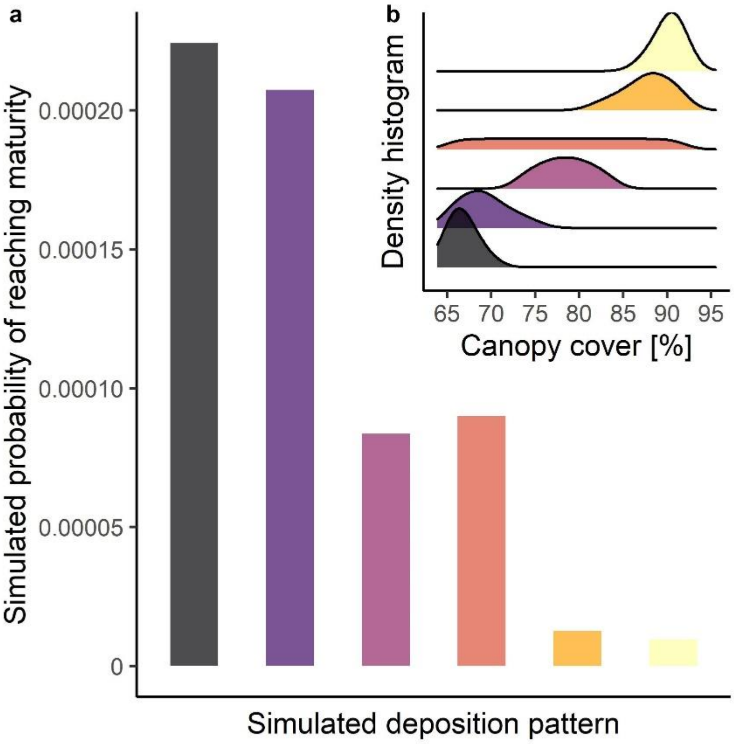
Supplementary figure 12: Boxplots of the effect of legitimate disperser species on the quality of seed dispersal (i.e. the probability of a seed reaching maturity) of *F. alnus* in Białowieża Forest, Eastern Poland. Uncertainty in the probability of a seed reaching maturity is based on 500 non-parametric bootstrap of only animal-related seed dispersal components; plant-related components of the model (e.g. uncertainty in vital rates or the effect of canopy cover on vital rates) were kept constant. Horizontal lines depict the quality of seed dispersal by gravity, when *F. alnus* is fully established along the entire canopy cover gradient in the forest (‘Gravity dispersal’), or is established only along the 50%-darkest part of the gradient, i.e. *F. alnus* depends on animal seed dispersal to forest gaps or edges (‘Gravity dispersal with disturbance events’). Please note the log-scale for the probability of a seed reaching maturity. While the reduced probability of a seed reaching maturity in *Martes martes* and the ‘other’ disperser (including small rodents) is due to low rates of seed predation (~ 5%, see Supplementary table 3), the reduced probability of a seed reaching maturity in *Turdus merula* and *T. philomelos* is due to the non-random deposition of seeds into dark environments (see Supplementary figure 7). The seed-predating bird species *Coccothraustes coccothraustes* was not included.

Supplementary information text 2: Seed deposition beneath conspecific adults

We found 62.15% of all scats with seeds of *Frangula alnus* beneath fruiting conspecific adults. However, there was an interaction between animal disperser and canopy cover (Wald-$\chi^2 = 19.1$, $p = 0.003$, Supplementary figure 4). In light environments, *T. merula* and *T. philomelos* almost exclusively deposited seeds beneath parental plants of *F. alnus*, but the probability of depositing seeds beneath conspecific adults decreased sharply at a canopy cover level of more than 80% (Supplementary figure 4). Seeds of *F. alnus* were deposited more often beneath conspecific adults by *Sylvia atricapilla* than by the remaining disperser ("other"), but the deposition of seeds beneath conspecific adults of these species did not change with canopy cover.



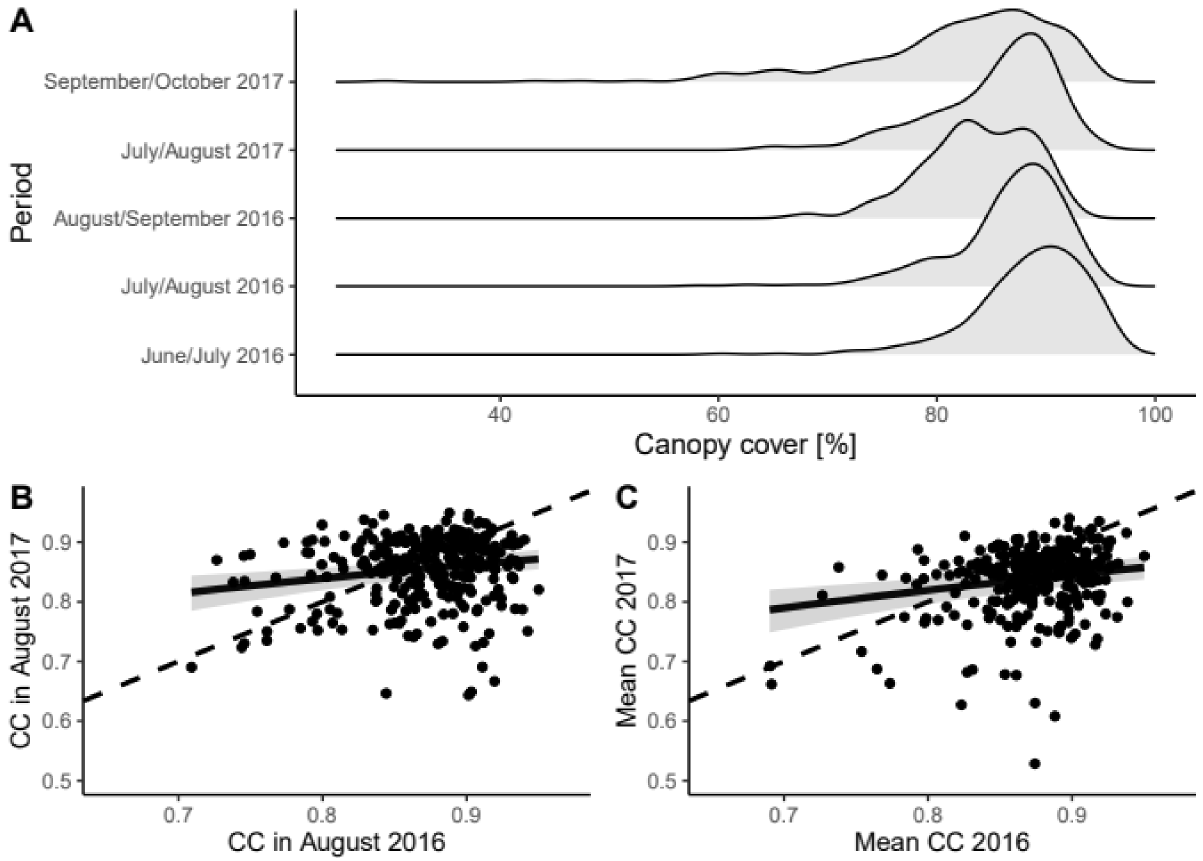
Supplementary figure 13: The effects of disperser on the proportion of scats with seeds of *Frangula alnus* deposited beneath fruiting conspecific adults along a canopy gradient in the Białowieża Forest. Mean ± 95%CI. Number of scats: Other: n = 30; *Sylvia atricapilla* n = 264; *Turdus merula* n = 53; *Turdus philomelos* n = 68.



Supplementary figure 14: Simulations of (a) probabilities for seeds of *F. alnus* to reach maturity, when all parameters are constant except the underlying (b) patterns of seed deposition. In (a) *S. atricapilla* was chosen as the baseline disperser.

Supplementary information text 3: No transition of canopy cover in the spatial IPM

The canopy cover gradient of forests is dynamic and changes from one year to the next in natural forests (Metcalf et al. 2009). We aimed at including natural changes in the canopy structure of the forest into the demographic models of *F. alnus*, but we were ultimately limited for two major reasons: firstly, the period when a hemispherical photo was taken affected the canopy cover of the forest (Wald- χ^2 = 211.14, $p < 0.001$; Supplementary Fig. 15a). In September/October, plants had already discarded some of the leaves why the forest was more open in September/October than in June/July. Secondly, uncertainties in the exact position where the hemispherical photo had been taken resulted in weak correlations of canopy covers over time due to local differences in the surrounding vegetation (Supplementary Fig. 15b/c). The relationship between canopy covers were always positive. This shows that light enviroments were on average lighter and dark environments on average darker despite the underlying variation. Therefore, we believe that the averaged values of canopy covers of up to six photos per transect segment is a good predictor for the actual light availability of a location at ground level.



Supplementary figure 15: (a) The distribution of canopy cover along the transects segments depending on the period of time when a hemispherical photo was taken in Białowieża Forest. (b/c) Canopy cover of the transect segments over time compared between (b) August in 2016 and 2017 or (c) the years 2016 and 2017 on average. CC = canopy cover. Mean ± 95%CI.

Supplementary information text 4: Calculating the survival probability of a seed until the age of first reproduction

To calculate the survival probability of a seed reaching maturity, we used a Markov chain, in which reproduction is an absorbing state in addition to mortality (Ellner et al. 2016):

$$P_0(z',z,c) = \int_L^U f_{repr}(z,c)S(z)\big(1-B(z)\big)G(z',z,c)n_t(z,c)dzdc + \int_L^U f_{repr}(z,c)S(z)B(z)R(z',z)n_t(z,c)dzdc \text{ (Eq 1).}$$

The kernel P_0 is a modified survival-growth kernel, in which reproduction can be interpreted as a second kind of 'death'. Similar to the manuscript, here, $P_0(z',z,c)$ growth is modelled for individuals that did and did not break: $S(z,c)$ models survival, $G(z',z,c)$ models growth of individuals that did not break with the probability $1-B(z)$, and the size distribution $R(z',z)$ of individuals that broke with the probability $B(z)$, conditional on individual plant size z and canopy c.

The fundamental operator N_0 of the modified reproduction-survival-growth Kernel is given by

$$N_0(z',z,c) = (I - P_0(z',z,c))^{-1} \text{ (Eq 2)}$$

and gives the distribution function for expected total time in state z' prior to either dying or reproducing, conditional on initial size z and canopy c. Now, we can calculate the probability that an individual reproduces at least once, which is

$$B(z',c) = f_{repr}(z,c)N_0(z',z,c) \text{ (Eq 3).}$$

The modified chain P_0 has two absorbing states, reproduction and death. To compute the mean age at reproduction (for those which reproduce), we computed the transition probability conditional on absorption into only reproduce. The conditional survival kernel is

$$P_{repr}(z',z,c) = P_0(z',z,c) * \frac{B(z',c)}{B(z,c)} \text{ (Eq 4).}$$

P_{repr} defines the 'lifetime' of an individual until it reproduces for the first time. The fundamental operator N_{repr} of the modified reproduction-growth Kernel is then given by

$$N_{repr} = (I - P_{repr})^{-1} \text{ (Eq 5),}$$

where I is an identity matrix with the same dimensions as P_{repr}. The dominant eigenvalue of the fundamental operator N_{repr} gives the mean number of censuses at which individuals appear before they have reproduced:

$$\bar{a}_{repr} = e(N_{repr})^{-1} - 1 \text{ (Eq 6)}$$

The survival probability of a seedling until the age of first reproduction $\bar{a}_{repr}$ is then given by

$$l_{(\bar{a}_{repr}-1)}(z_0, c) = (\int_L^U S(z_0, c)\big(1 - B(z_0)\big)G(z', z_0, c)dzdc + \int_L^U S(z_0, c)B(z_0)R(z', z_0)dzdc) \,\hat{}\,\bar{a}_{repr} - 1 \text{ (Eq 7)}$$

where z_0 is the relative size distribution of a initial cohort of seedlings of *F. alnus*. For more information on Markov chains in population models, we kindly refer to Caswell (2001) and Ellner et al. (2016, Chapter 3).

References Supplementary Material

Caswell, H. (2001). *Matrix popultion models: construction, analysis, and interpretation*. 2nd ed. Sunderland, Massachusetts: Sinauer Associates.

Ellner, S. P., Childs, D. Z., and Rees, M. (2016). *Data-driven Modelling of Structured Populations*. Cham: Springer International Publishing doi:10.1007/978-3-319-28893-2.

Metcalf, C. J. E., Horvitz, C. C., Tuljapurkar, S., and Clark, D. A. (2009). A time to grow and a time to die: A new way to analyze the dynamics of size, light, age, and death of tropical trees. *Ecology* 90, 2766–2778. doi:10.1890/08-1645.1.

Chapter 5: Synthesis

Ecological interactions build the backbone of biodiversity and ecosystems. Understanding how species interactions are structured across ecological scales, how they work, and how they are disrupted by anthropogenic pressure is important to predict and reverse the ongoing decline in biodiversity worldwide. In this thesis, I investigated the seed dispersal mutualism between a fleshy-fruited plant community and their associated animal dispersers in degraded and intact temperate forest in Białowieża Forest, Poland.

5.1. The large subindividual trait variation in small-fruited plants increases their connectedness with seed-dispersing animals

Gape-size limitations in seed dispersal can have negative consequences for the respective plants, when large-gaped animals go extinct and the remaining community is physically limited in the consumption of fruits (e.g. Wheelwright, 1985). These patterns have often been observed for large-fruited plants in the tropics and on islands (e.g. Wheelwright, 1985; Brodie, 2017), but little is known whether size limitations similarly occur in small-fruited plant species. In Chapter 2, I showed that size limitations occurred between small-fruited plant species and their associated small-gaped animals. However, because the plants varied to a considerable extent in fruit size at the subindividual level (i.e. within plant individuals), small-gaped animals were able to find size-compatible fruits at each plant individual in the community (except in one large-fruited species). In a second analysis, I further showed that large-gaped animals potentially dispersed fruits with more and larger seeds than small-gaped dispersers in four of nine plant species, because they were not limited by their size in fruit consumption.

My findings suggest that size limitations are common in seed dispersal of fleshy-fruited plant species. While size limitations in large-fruited plant species occur mainly at the species level, size limitations in small-fruited plants occur at the subindividual level (González-Varo and Traveset, 2016). The large subindividual trait variation in fruit size improves the connectedness of small-fruited plants with their dispersers (Herrera 2009). This makes their seed dispersal robust against strong interannual variations in the abundance of key species, or the loss of single animal species, promoting species persistence and richness of plant-frugivore communities (Emer et al., 2019; Peralta et al., 2020). Simultaneously, however, positive fruit-seed trait relationships are common in fleshy-fruited plant species, such that gape-size limitations potentially decrease the mass and the number of dispersed seeds in small-gaped dispersers (Herrera, 2009). As seed size can improve post-dispersal regeneration of plants, gape-size limitations might negatively affect the effectiveness of seed disperser species by constraining the efficiency of fruit handling (Schupp et al., 2010), even in small-fruited plant species.

5.2. Intact forest safeguards the complementarity of high-quality seed dispersal

More than 75% of the world's forests are degraded (Potapov et al., 2017), which can significantly impact the functions and services that forests provide to people. Seed dispersal by animals is an important ecological function, and has been shown to be quantitatively robust to forest degradation, because generalist dispersers can often take over the function of lost frugivores in degraded forest (Albrecht et al., 2014; Farwig et al., 2017). However, little is known about if and how forest degradation affects later stages of seed dispersal, i.e. the deposition of seeds by animals and plant recruitment in heterogenous microhabitats. In Chapter 3, Jan Schlautmann and I co-investigated the effect of forest degradation on the quality of animal seed dispersal of a species-rich plant-frugivore community. By combining extensive field observations, DNA barcoding and environmental niche modeling, we show that forest degradation reduces a three-dimensional niche space of forest microhabitats by half. Frugivores responded to the loss of microhabitats by depositing seeds more frequently in microhabitats of a similar type. Because the lost microhabitats were beneficial for plant recruitment, seed dispersal shifted from high-quality and partially complementary dispersal in intact forests to low-quality, redundant dispersal in degraded forests. It is important to note that animal species provided seed depositions differently along the three environmental gradients. This indicates that not only the functional complementarity of seed dispersal was increased in intact forest compared to degraded forest, but also the functional asynchrony of species during seed dispersal (Yachi and Loreau, 1999). Overall, these observations demonstrate that the maintenance of environmental heterogeneity preserves not only the diversity of species, but also their interactions (see also Thiel et al., 2021) and ultimately the high functionality of forest ecosystems.

5.3. Generalist birds are effective and redundant mutualists of fleshy-fruited plants

Linking the interactions between plants and animals with their functional outcomes, as well as assessing the complementarity of provided services among animals is needed to understand the relationship between the diversity of seed-dispersing animals and ecosystem functioning (Wang and Smith, 2002; Schupp et al., 2010; Winfree, 2020). In Chapter 4, I closed the seed dispersal loop for a fleshy-fruited temperate tree along the natural gradient of forest canopy cover, i.e. the animal behavior during fruit removal and seed deposition was linked to their later effects on plant population growth. I showed that the seed dispersal mutualism was beneficial for *F. alnus*, as population growth increased with the number of seeds dispersed. When population growth was modelled by assuming the absence of individuals of *F. alnus* from the 50%-lightest environments (7.3% of the absolute gradient), the effect of animal dispersal was increased by further c. 13.7%. This highlights the importance of animal seed dispersal for plant populations during forest succession and the colonization of favorable habitats. However, the environment of temperate forests was relatively benign and seed dispersal by gravity can result in population growth close to equilibrium in *F. alnus*. This indicates that animal-dispersed plants may be relatively independent of the seed dispersal mutualism. The effectiveness of animal species during seed dispersal was almost perfectly related to the quantity of removed fruits rather than the quality of dispersed seeds. Because recording fruit removal is easier than calculating the total effectiveness of pair-wise species interactions, taking fruit removal as a surrogate for total effectiveness could facilitate large-scale analyses of seed dispersal networks, and the identification of important species for ecosystem functioning (García-Callejas et al., 2018; Timoteo et al., *preprint*).

I then simulated the loss of seed dispersal with the loss of species under two different scenarios: animal interactions with *F. alnus* were (i) irrevocably lost or (ii) quantitatively compensated by the remaining animal community. These analyses showed that seed dispersal was relatively robust against species loss, when the quantitatively least important species were lost, or the remaining community compensated the lost interactions. However, when one of the four quantitatively most important species were lost without interaction compensation by the remaining animal community, seed dispersal was disrupted. This draws attention to generalist bird species such as *S. atricapilla* as main disperser of *F. alnus*, and shows that otherwise the frequency of interactions is more important than species identity for the function of seed dispersal.

5.4. Conclusion

The chapters of this thesis have three major implications: First, the mutualism with seed-dispersing animals has long-term positive effects on the regeneration of plant populations and communities. Nevertheless, gravity dispersal can lead to successful plant regeneration and to population growth close to equilibrium. This suggests that fleshy-fruited plants might be relatively independent of the seed dispersal mutualism (Chapter 4). Seed dispersal might therefore be a by-product mutualism (*sensu* Chomicki et al., 2020), i.e. plants do not necessarily need the seed dispersal by animals to persist over time, but benefit from a set of advantages coming along with the service, for instance the improved seed germination after dispersal (Rogers et al. *preprint*), seed dispersal to favorable habitats and the colonization of new habitats. From an evolutionary perspective, the low dependence of fleshy-fruited plants on animal seed dispersal and frugivory could also explain the low number of seed-predating animal species in seed dispersal networks (Farwig et al., 2017; Simmons et al., 2018, see also Perspectives).

Second, the loss of animal species alone is unlikely to result in co-extinctions of fleshy-fruited plant species in temperate forests, because (i) species loss will mostly not result in size mismatches during seed dispersal (although the loss of especially large species might induce selective pressures on plant traits), (ii) many species are not effective seed dispersers, (iii) seed dispersal is qualitatively redundant, and (iv) even seed dispersal without animal species can potentially lead to long-term stable population growth. However, changes in the abiotic and biotic environment that will ultimately lead to the loss of species, will lead to a loss of seed dispersal before (McConkey and O'Farrill, 2016), and influence fleshy-fruited plants directly (Jansen and Zuidema, 2001). Over the course of the project, we exemplified this by the correlated loss in disperser richness (Albrecht et al., 2013; Farwig et al., 2017), microhabitat availability and seed dispersal quality (Chapter 3), and changes in the population dynamics of fleshy-fruited plants (*master thesis* of Fassbender, 2020) between the degraded and intact forest of Białowieża Forest. Beyond, the forest degradation in Białowieża Forest interacted with the outbreak of a pest insect, severely impairing the regeneration of plant-animal communities after further human interventions (Lindenmayer et al., 2017). These so-called 'cryptic' effects (*sensu* McConkey & O'Farrill, 2015) on seed dispersal before species loss critically alter population persistence of plants and the effectiveness of seed dispersal (McConkey and O'Farrill, 2015, 2016), and similarly affect other functions of forest ecosystems (McConkey and O'Farrill, 2015; Both et al., 2019; Grass et al., 2020). Given the large scale of forest degradation worldwide, cryptic functional loss before biodiversity loss is potentially pervasive and a threat to forest ecosystems (Säterberg et al., 2013; McConkey & O'Farrill, 2015). My findings and those of our research group thus further highlight the exceptional values of intact forests for the biodiversity of plant-frugivore communities and high-quality ecosystems. Notably, the protection of intact forests was ineffective and partly overlooked by global environmental agreements (Mikusiński et al., 2018; Watson et al., 2018). Improving the conservation status and management of the Białowieża Forest (Mikusiński et al., 2018) and other intact forests

(Potapov et al., 2017; Sabatini et al., 2018) should thus be a central goal of proactive environmental strategies at global, national and sub-national scale (Watson et al., 2018).

Lastly, I conclude that in a species-rich community, the function of seed dispersal can be improved by maintaining plant-frugivore interactions, especially between plants and generalist birds such as *S. atricapilla* providing very efficient seed dispersal (i.e. high levels of fruit removal and high-quality seed dispersal). The direct relationship between the relative interaction frequency and the effectiveness of an ecological function is of particular interest for nature conservation. The populations of many bird species have declined, especially those of common and migratory birds (Hallmann et al., 2014; Gilroy et al., 2016; Rosenberg et al., 2019; Kamp et al., 2021; Kim et al., 2021). For example, over 1 million individuals of *S. atricapilla* and *T. merula* are illegally hunted in the Mediterranean area each year (Brochet et al., 2016) and a total of over 400 million bird individuals were lost in the last decades (Inger et al., 2015; populations of species belonging to the genus *Sylvia* decreased by 15%, Vickery et al., 2014). This must have led to a massive loss of interactions in various ecosystems (e.g. Boissier et al. 2020). If the importance of the frequency of interactions for ecological functions hold true for other types of interactions as well (Vázquez et al., 2005; Winfree et al., 2015; Timoteo et al. *preprint*), then stopping and reversing the ongoing decrease in the abundance of animal individuals should be the primary goal of nature conservation to reinforce multifunctionality and -services of ecosystems.

Final remarks

The rationale that ecological interactions needs to be protected because they contribute to a large set of ecological functions and services has become an increasingly important argument in biodiversity conservation (Harvey et al., 2017). This is perhaps due to the reason that economic and other benefits of ecological interactions are more likely to motivate people and institutions supporting nature conservation than inherent, moral arguments. However, this line of argumentation may not be without risk (Silvertown, 2015): It has been shown that a small number of common species contribute the most to pollination of crop species (Kleijn et al., 2015; Winfree et al. 2015). In this thesis (Chapter 4), the seed dispersal effectiveness of animal species might have also been related to their relative abundance in the community as common species were efficient seed dispersers, and rare species tended to be inefficient. This suggests that the maintenance of well-functioning ecosystems may be ensured by rather simple measures, such as protecting and supporting the populations of a few common species (Vázquez et al., 2005; Kleijn et al., 2015) and their interactions (Silva et al. 2020). However, the protection of common species and their interactions will unlikely lead to the protection of species that are not yet important for ecosystem functioning and never will be, simply because they are rare (Winfree, 2020). Ecologists need to highlight these differences more clearly in future debates to the public, policy makers and conservation organizations in order to improve the conservation of biodiversity and not just that of a few common species.

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Chapter 6: Perspectives

Chapters 2-5 outline several possibilities for future research, one of which I will discuss in detail below.

6.1. The mutualism-antagonism continuum of seed-predating animal disperser

During seed dispersal, the nutritious, fleshy fruits of plants are the reward for the frugivorous animals. A minority of granivorous species however feed not only on the fruit pulp, but also on the seed inside fruits which can be an additional important food source for animals (Vander Wall 1990). In addition, seeds can be stored and are long-lasting. A suite of granivorous animals has therefore developed the behaviour to not immediately consume all seeds, but instead collect and store them (Vander Wall 1990). If these stored seeds are not predated, they can contribute to plant regeneration (see reviews of Vander Wall, 1990; Hulme and Benkman, 2002; Lichti et al., 2017; Gómez et al., 2019; and references therein).

While seed dispersal by frugivores is beneficial to plants because it increases population growth compared to situations when seeds are dispersed by gravity (Chapter 4), seed dispersal by granivorous animals needs to exceed the costs of seed predation to be strictly beneficial (Zwolak and Crone, 2012). The mutualism-antagonism continuum framework provides a possibility to order the ecological interactions such as those between granivorous animals and plants (Perea et al., 2013; Montesinos-Navarro et al., 2017; Gómez et al., 2019), when partners have beneficial effects (i.e. effective seed dispersal, *sensu* Schupp et al., 2017*,* Vander Wall, 1993) and negative effects (i.e. predation) simultaneously. However, similar to the research on frugivory (Wang and Smith, 2002; Rogers et al., 2019), seed dispersal by granivorous animals is difficult to study in complex environments (Vander Wall et al., 2005; Zwolak et al., 2020). Due to this, most studies on granivorous animals probably had not been able to link the costs and benefits of their seed dispersal to their later effects on plant populations, although there are a few exceptions (e.g. Yang et al., 2011; Elwood et al., 2018). Thus, it is poorly understood when granivorous animals provide beneficial seed dispersal in plants, and when they deflect and exploit the seed dispersal mutualism (Bronstein, 2001). A better understanding of the role of granivorous animals for seed dispersal of fleshy-fruited trees will provide insights into whether and under which conditions exploitations of mutualistic interactions occur (Axelrod and Hamilton, 1981; Bronstein, 1994, 2001; Chomicki et al., 2020).

In **Chapter 4**, we closed the seed dispersal loop of the fleshy-fruited tree *Frangula alnus* and 20 animal species along the natural gradient of canopy cover in the Białowieża forest using spatial integral projection models, and found evidence for the benefits of the seed dispersal mutualism to plants (see **chapter 4** for more information). However, not each type of pair-wise species interaction was beneficial for *F. alnus*. For example, the hawfinch *Coccothraustes coccothraustes* predated 80% of the seeds it removed. Seed dispersal of the 20% non-predated seeds did not outweigh costs of seed predation, such that seed dispersal by *C. coccothraustes* affected the population growth of *F. alnus* negatively (λ = -0.0000105). Therefore, *C. coccothraustes* was the only animal species, whose dispersal was worse than gravity dispersal and whose simulated extinction increased population growth of *F. alnus* (**Chapter 4**, Fig. 3a). These results suggest that *C. coccothraustes* is a strict-sense granivore, antagonist of *F. alnus* and exploiter of the seed dispersal mutualism (Simmons et al., 2018).

In contrast, the two granivorous animal species *Apodemus flavicollis* and *Myodes glareolus* (Fig. 6.1) increased population growth of *F. alnus* (λ = 0.000116). However, *A. flavicollis* and

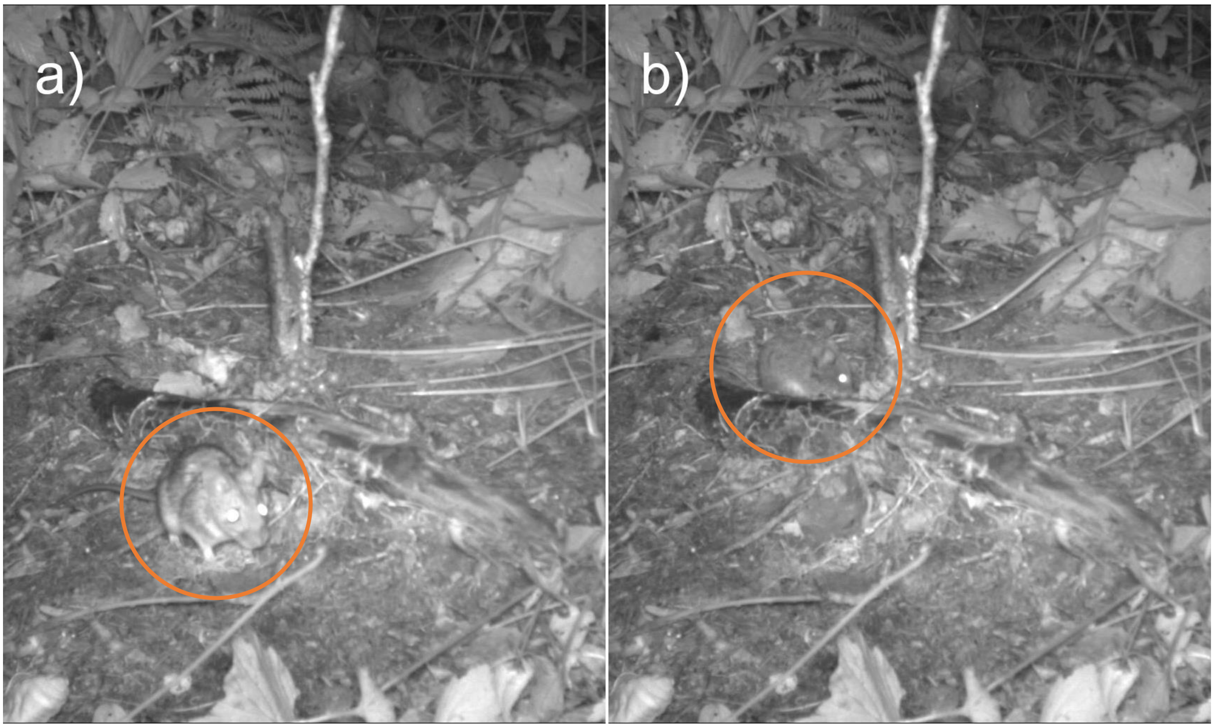

Fig. 6.1: Terminators or assistants? (a) *Apodemus falvicollis* and (b) *Myodes glareolus* as seed-caching, granivorous dispersers of *Frangula alnus*. By placing fruits in front of camera traps, a pilot study (Kohlbrecher 2015) found that *A. falvicollis* and *M. glareolus* accounted for 99% of ~2.000 ground removal events of 14 plant species in Białowieża forest.

M. glareolus were neither observed removing fruits, nor observed predating seeds of *F. alnus*. To keep the role of animal species separate in the spatial models, I estimated their fruit removal and seed predation by taking the mean of that of *C. coccothraustes* and other rare disperser species (e.g. seed predation = 5%, see **Chapter 4**, Supplement 3). These values are therefore only vague estimates for seed predation. This puts me in the rare position of having a good estimate for the quality of seed dispersal for non-predated seeds of animals, but a high uncertainty about the proportion of seed predation by granivorous animals, in contrast to the many studies on granivores before (but see Vander Wall et al., 2005). Investigating the effect of seed predation on the plant demography of *F. alnus* will allow me to describe the mutualism-antagonism continuum for the seed dispersal of a fleshy-fruited, temperate tree species. In the benign environments of temperate forests (Merges et al., 2020, **Chapter 4**), gravity and other types of secondary dispersal can lead to the successful regeneration of plant species typically dispersed by animals (Hampe, 2004, **Chapter 4**). Therefore, plant regeneration of *F. alnus* in Białowieża forest might be primarily limited by the number of dispersed seeds (Arnell et al., 2021). As seed predation is fatal, this could lead to a situation where only low levels of predation might result in beneficial seed dispersal. In this perspectives project, I raised the following questions: How many seeds can granivorous animals predate such that their overall contribution to plants is still beneficial? And how is the shift towards antagonism influenced by environmental factors, such as gap-dynamics in forest which improve the positive effects of animal seed dispersal?

Based on the spatial integral projection models in **Chapter 4**, I calculated the probability of a seed of *F. alnus* reaching maturity $f_{maturity}$ after seed predation, which is given by

$$f_{maturity}(z_0, c') =$$

$$\iint_L^U f_{nocrush}\, f_{consumed}\, f_{deposition}(c')\, f_{recruit1}\, l_{(\bar{a}_{repr}-1)}(z_0, c')\, dz_0 dc$$

(Eq 6.1a)

$$+$$

$$\iint_L^U f_{nocrush}\, f_{drop}(c')\, f_{recruit1}\, f_{recfruit}\, l_{(\bar{a}_{repr}-1)}(z_0, c')\, dz_0 dc$$

(Eq 6.1b).

This is the same formula as Eq. 4 in **Chapter 4** and is the sum of the probability of consumed fruits (Eq 6.1a) and dropped fruits (Eq 6.1b) reaching maturity conditional on seed dispersal (benefits) and seed predation (costs) of the granivore *M. glareolus*, the initial size of seedlings z_0 and the canopy cover c'. While all parameters were kept constant, $f_{nocrush}$, i.e. the probability of not being crushed and therefore not predated, varied between 0 and 1. If I assumed that all seeds were predated, then $f_{nocrush} = 0$ applies and $f_{maturity}$ equals zero. However, when the overall relative contribution of granivore dispersal increases up to a point where no seeds are predated ($f_{nocrush} = 1$), then $f_{maturity}$ increases, respectively. Please note, because information on seed dispersal of granivorous animals was rare (**Chapter 4**), I used the same parameters to calculate the quality of seed dispersal of non-predated seeds for different species, resulting in only one relationship between seed dispersal quality conditional on seed predation.

These results represent the continuum from mutualism to antagonism for seed dispersal and seed predation of granivorous animals in *F. alnus* (Fig. 6.2). In contrast to my expectation, even considerably high levels of seed predation (up to 65%, conditionally up to c. 75%) resulted in beneficial contributions of granivores to plant regeneration. This was possibly due to the strong

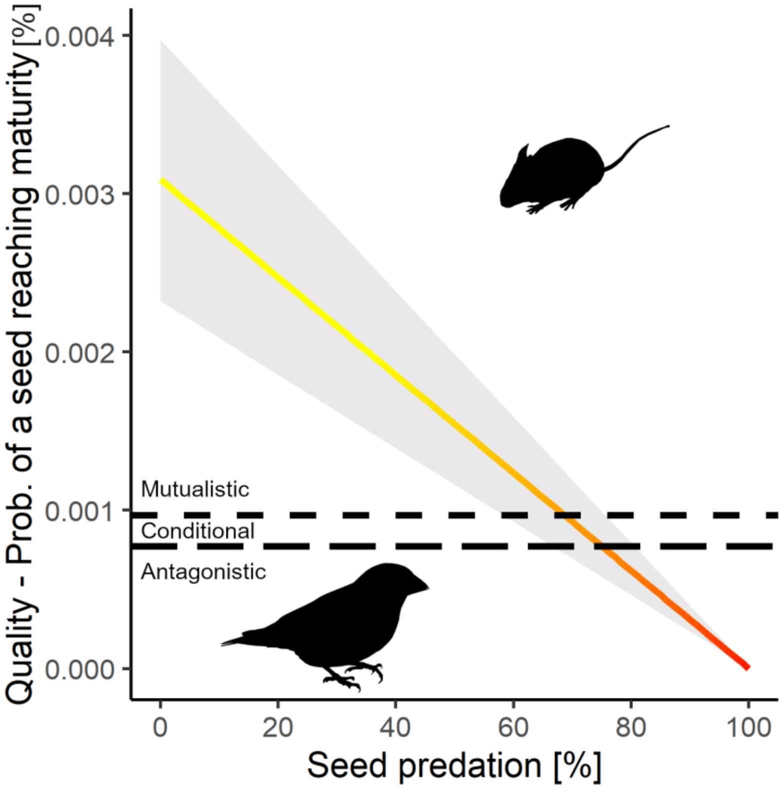

Fig. 6.2: The mutualism-antagonism continuum of granivorous animals in *F. alnus*. The vertical dashed lines display the quality of seed dispersal by gravity in plant populations of *F. alnus* that are either fully established along the natural canopy cover gradient in Białowieża forest (upper, short-dashed) or only occur in the closed forest and depend on animal seed dispersal to forest gaps (lower, long-dashed).

deinhibition effect of the pulp on seed germination when seeds were not dispersed (-70%, *sensu* Rogers et al. *preprint*), which strongly decreased the total effectiveness of gravity seed dispersal (**Chapter 4**). The intermediate, conditional state of granivore dispersal depended on whether individuals of *F. alnus* were already present in forest gaps (antagonistic) or not (beneficial), as the presence of individuals in forest gaps improved the quality of gravity dispersal through improved plant regeneration (**Chapter 4**). When > 75% of seeds were predated, the costs of seed predation always outweighed the benefits of dispersal of non-predated seeds by granivorous animals independent of forest succession and forest gap dynamics. These findings also explain, why interactions of *C. coccothraustes* (seed predation = 80%) negatively affected the plant population of *F. alnus* (**Chapter 4**).

By keeping seed dispersal constant and only varying the probability of seed predation, I show that moderate to high levels of seed predation in a fleshy-fruited plant species can change the direction and effectiveness of seed dispersal from mutualistic to antagonistic. This shift was conditional on the dependency of the plant population on animal dispersal to forest gaps (Brodie et al., 2009; Wenny & Levey, 1998, **Chapter 4**), and shows the context-dependency of this mutualism with respect to succession and gap-dynamics of forests (Bronstein, 1994). The mutualism-antagonism threshold of c. 65-75% seed predation was higher than previously expected (c. 40-60%, Perea et al., 2013). Large-bodied mammals that occasionally crush seeds (less than 40% of seeds in c. 76% of pair-wise species interactions, Perea et al., 2013), or the agouti (*Dasyprocta leporina*) in tropical forests (at least 50% seed predation, e.g. Mittelman et al. 2020) are thus beneficial for the plants they disperse. In contrast, many interactions between plants and strict granivores may be antagonistic, for instance between parrots and parana pine (*Araucaria angustifolia*, at least ~78.5%, Tella et al., 2016), between yellow pine chipmunks (*Tamias amoenus*) and Jeffrey pine (*Pinus jeffreyi*, 86%, Vander Wall & Joyner, 1998) or between nutcracker (*Nucifraga cayocatactes*) and Swiss pine (*Pinus cembra*, ~80%, referenced in Neuschulz et al., 2015). In line with this, a recent study found that the costs of seed predation by *Apodemus flavicollis* in two *Quercus* species outweighed the benefits of seed dispersal for early plant recruitment (Bogdziewicz et al., 2020) and seed dispersal by granivorous animals was antagonistic for a plant population of *Castanea dentata* when the proportion of predated seeds was modelled similar to field conditions (Elwood et al., 2018).

When exploiting the seed dispersal mutualism offers more benefits to seed-predating animals than to cooperating seed-dispersing animals, why are there so few seed-predating animal species? All things being equal, gravity dispersal led to population growth in *F. alnus* very close to equilibrium (**Chapter 4**). Thus, *F. alnus* does not strongly depend on animal dispersal and, technically, the seed dispersal mutualism may be a by-product (*sensu* Chomicki et al., 2020; Sachs et al., 2004). This means that providing fruit pulp is (theoretically) of no costs to *F. alnus*, because it could survive independently of animal dispersal, but having evolved fruits offers a suite of advantages coming along with animal dispersal, for instance improved seed germination (Rogers et al. *preprint*), seed dispersal to forest gaps (**Chapter 4**), long-distance dispersal (Nathan, 2006; Viana et al., 2016) and gene flow (Browne et al., 2018). In line with this, plant-frugivore interactions in temperate forests are relatively ‘loose’ and traits are only weakly co-evolved (Albrecht et al., 2018; Rehling et al., 2021). From an evolutionary perspective, there is no benefit in exploiting mutualisms with a low dependence and no costs (Chomicki et al., 2020). Because fruits are costly to plants to some extent, nevertheless, this might explain why seed predation infrequently occurs (1.6-8.3%) in fleshy-fruited plants in Białowieża Forest and throughout Europe (Farwig et al., 2017; Simmons et al., 2018).

I provided evidence for a mutualism-antagonism continuum based on interaction effectiveness (*sensu* Schupp et al., 2017), exemplified by the interactions between a fleshy-fruited, temperate tree population and associated, rare granivorous animals. In **Chapter 4**, we first showed that population growth of a fleshy-fruited plant in a temperate forest is largely independent of animal dispersal. Nonetheless, the benefits of animal dispersal were considerably large, even for fully established plant populations. Over the full life cycle of a plant, there is thus a large potential of mutualistic seed dispersal by seed-predating animals. However, whether seed-predating animals will ultimately be beneficial or antagonistic for the growth of plant populations will depend on two further factors: (i) the proportion of total fruit removal and (ii) the effectiveness of seed predation by strict granivores. When plants lack fruit removal, any dispersal of a seed-predating animal will improve the population growth of the respective plants. For example, unlike most other small-gaped animals, the agouti is able to disperse the large fruits of plants that have lost their associated large-gaped dispersers (e.g. Donatti et al. 2009; Mittelman et al. 2020). In contrast, if most fruits are removed during fruiting, it is more beneficial for a plant to be dispersed by a non-predating seed disperser than by a granivorous animal (**Chapter 4**). In addition, the findings of the previous studies suggest that many granivorous animals are very effective seed predators (e.g. *C. coccothraustes* in **Chapter 4**; Farwig et al. 2017; see also Vander Wall & Joyner, 1998; Tella et al., 2016). Seed-predating animals will thus often have negative effects on population growth of the plants they prey.

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Deutsche Zusammenfassung

Jedes Lebewesen auf der Erde trägt zu einem schier unendlichen Netzwerk an Interaktionen und damit zur Stabilität des Ökosystems und zum Erhalt der Biodiversität bei. Gleichzeitig leiden Ökosysteme und die Biodiversität unter dem zunehmenden Einfluss des Menschen auf die Natur. Landnutzungswandel, Klimawandel, Umweltverschmutzung und die Ausbreitung invasiver Arten werden zu einem Artenverlust führen, der bald fünfmal so hoch ist wie noch vor wenigen Jahrhunderten. Ein Hauptziel des globalen Naturschutzes ist es, diesen Verlust der Biodiversität zu verhindern. Die Feststellung, dass viele Ökosystemfunktionen und -dienstleistungen von Interaktionen abhängig sind, d.h. von den Interaktionen zwischen Individuen, die zur Zeit verloren gehen, führt zu einem Paradigmenwechsel im Naturschutz: der Erhalt der Biodiversität soll durch den Erhalt von Interaktionen und Ökosystemprozessen gewährleistet werden. Ein Problem ist allerdings, dass Ökolog:innen und Naturschützer:innen nur in bestimmten Fällen wissen, wie stark die Biodiversität von ihren Interaktionen abhängig ist, ob der Verlust von Arten zum Verlust weiterer Arten führt und welchen Einfluss der Mensch auf diese Prozesse hat.

Die Samenausbreitung von Pflanzen durch Tiere ist ein wichtiger Prozess von Ökosystemen: Pflanzen bieten Tieren wertvolle Ressourcen wie Früchte oder Nüsse an und die Tiere breiten im Gegenzug die Samen der Pflanzen aus. Ungefähr 50% der Pflanzen werden weltweit durch Tiere ausgebreitet. Damit ist die Samenausbreitung durch Tiere ein wesentlicher Faktor der Regeneration terrestrischer Ökosysteme. Der Mensch profitiert auf verschiedenen Wegen von der Samenausbreitung: direkt, durch die Produktion von Früchten als Nahrungsmittel und Holz und indirekt, durch den Beitrag der Samenausbreitung zur Speicherung von CO_2, zum Stickstoffkreislauf und zur Klimaregulierung.

Die Samenausbreitung von Pflanzen über Tiere gilt als Mutualismus, d.h. die beitragenden Partner haben einen Vorteil durch ihre Interaktion mit dem jeweils anderen. Während diese Vorteile (z.B. die Nahrungsaufnahme) für Tiere direkt sind, sind die Vorteile der Samenausbreitung für Pflanzen eher schwer zu fassen. Samenausbreitung verbessert die Keimung der Samen, trägt auf kleiner räumlicher Skala zur Ausbreitung in besonders günstige Habitate und zur Kolonisierung neuer Habitate bei und bestimmt die räumlichen Muster von Individuen. Auf großen räumlichen Skalen kann Samenausbreitung über weite Distanzen stattfinden sowie zum Genfluss innerhalb von und zwischen verschiedenen Populationen beitragen. Um zu untersuchen, wie Pflanzenpopulationen von einzelnen Tierarten beeinflusst werden, muss das Schicksal der von den Tieren ausgebreiteten Samen über den gesamten

Lebenszyklus der Pflanzen verfolgt werden. Es gilt zu verstehen, wie häufig Tiere Pflanzen aufsuchen und wie viele Früchte sie dabei fressen, wie Tiere Samen transportieren und währenddessen mit diesen umgehen, wo sie die Samen ablegen, wie die Samen in der neuen Umwelt keimen und zu einem adulten Individuum heranwachsen. Diese Prozesse sind isoliert für sich gut erforscht und die Samenausbreitung in der Theorie verstanden. Allerdings gibt es wenige Studien, die den Kreislauf eines Samens von der Entstehung bis zum adulten Individuum verfolgen. Dies limitiert unser Wissen über die Effektgröße der Samenausbreitung auf Pflanzenpopulationen und die Effektivität und Komplementarität der Samenausbreitung einzelner Tierarten.

Ein weiteres Problem ist, dass die Samenausbreitung durch Tiere sowie die Regeneration der Pflanzen durch Menschen beeinflusst wird. Zum Beispiel ist nachgewiesen, dass die Degradierung von Wäldern durch Holzschlag zum Verlust von Waldspezialisten (z.B. Spechte, Haselhühner) und großen Tieren (z.B. Wisente) führt. Der Verlust von wichtigen Samenausbreitern kann die Anzahl der gefressenen Samen verringern. Auch die Qualität der Samenausbreitung mag durch die Walddegradierung beeinflusst werden, wenn besonders günstige Habitate zur Rekrutierung von Pflanzenindividuen verschwinden oder Tiere ihr Verhalten ändern. Bisher gibt es allerdings kaum Studien über die langfristigen Folgen von Walddegradierung auf die Samenausbreitung durch Tiere und das Wachstum von Pflanzenpopulationen. Dadurch lässt sich schwer einschätzen, wie sich der globale Artenverlust auf Ökosystemfunktionen, wie die Samenausbreitung, auswirkt.

In dieser Dissertation habe ich die Langzeiteffekte der Samenausbreitung durch Tiere auf Pflanzenpopulationen, sowie den Einfluss des Menschen auf die zugrundeliegenden Prozesse untersucht. Das Studiensystem bestand aus einer Gemeinschaft mit 15 Pflanzenarten mit fleischigen Früchten (z.B. Eberesche, Johannisbeere, Schneeball) und ihren 42 assoziierten Samenausbreitern (z.B. Amsel, Mönchsgrasmücke, Rotkehlchen). Die Studie fand im letzten Tiefland-Urwald Europas in Białowieża (Polen) statt. Die Kernzone des Białowieża-Waldes ist seit mindestens 500 Jahren vor Abholzung geschützt. Der Wald, der rings um die Kernzone liegt, wurde hingegen seit dem ersten Weltkrieg teilweise abgeholzt. Die vom Staat gemanagten Teile des Waldes und die Kernzone stellen ein einzigartiges „natürliches“ Experiment dar, um den Einfluss von Degradierung durch Holzeinschlag auf die Samenausbreitung in temperierten Wäldern zu untersuchen.

In den Tropen und von Inselsystemen weiß man, dass Pflanzen mit großen Früchten in ihrer Samenausbreitung limitiert sind, wenn assoziierte, große Tiere aussterben und die verbliebenen, kleinen Tiere die großen Früchte nicht fressen können. In temperierten Wäldern sind die Früchte von Pflanzen vergleichsweise klein, können aber innerhalb von Arten relativ stark in ihrer Größe variieren. In Kapitel 2 habe ich deswegen untersucht, ob es zu Größenlimitierungen während der Samenausbreitung von kleinfrüchtigen Arten kommen kann. Die große Variation in der Größe der Früchte innerhalb und zwischen Arten führte dazu, dass Tiere in der Wahl der Früchte größenlimitiert waren. Weil die Größe der Früchte innerhalb ein und desselben Individuums stärker variierte als zwischen unterschiedlichen Individuen, konnten alle Hauptausbreiter an Pflanzenindividuen Früchte finden, die zu der Größe ihres Mauls passten (außer bei einer Pflanzenart). Gleichzeitig war die Fruchtgröße bei acht von neun Arten mit Merkmalen von Samen positiv korreliert. Dies führte dazu, dass Tiere mit kleinen Mäulern bei vier von neun Arten potentiell Früchte mit kleineren oder weniger Samen ausbreiten, weil sie große Früchte nicht fressen können. Diese Ergebnisse weisen darauf hin, dass die Größenlimitierungen kleinerer Tiere typisch sind für die Samenausbreitung von Pflanzen. Allerdings treten Größenlimitierungen bei kleinfrüchtigen Arten vor allem zwischen den Früchten desselben Individuums auf und nicht auf Artebene. Das macht die Samenausbreitung von Arten mit kleinen Früchten robust gegen das Aussterben einzelner großer Tierarten, kann aber auch zur Selektion von Fruchtmerkmalen führen, wenn nur noch Früchte mit kleinen oder weniger Samen ausgebracht werden.

Weltweit sind 75% der Wälder bereits in einem degradierten Zustand. Albrecht et al. (2013, 2014) und Farwig et al. (2017) konnten bereits in vorherigen Studien zeigen, dass die Degradierung des Białowieża-Waldes zu einem Verlust von Waldspezialisten und großen Ausbreitern führte. Der Verlust von bestimmten Ausbreiterarten führte jedoch nicht dazu, dass proportional weniger Früchte ausgebracht wurden, weil generalisierte Arten die Funktion der verlorenen Arten übernommen haben. In Kapitel 3 haben Jan Schlautmann und ich (mit anderen Kolleg:innen) zusammen untersucht, ob die Degradierung des Białowieża-Waldes stattdessen zu Veränderungen in der Qualität der Samenausbreitung führt, indem die Verfügbarkeit einzelner Mikrohabitate oder das Verhalten der Tiere die Muster der Samendeposition verändern. Dafür haben wir standardisiert über 3000 Kotproben im intakten und degradierten Teil des Białowieża-Waldes gesammelt, über DNA-Barcoding den Ausbreiter bestimmt und die Mikrohabitatstruktur aufgenommen. Bei den Mikrohabitaten haben wir besonderen Wert auf Faktoren wie Licht, Bodenvegetation und Totholz geachtet, weil entweder vorherige Studien oder eigene Aussaatexperimente und Langzeitbeobachtungen von Keimlingen gezeigt haben, dass helle Mikrohabitate, Mikrohabitate mit geringer Bodenvegetation oder mit viel Totholz gut für die Rekrutierung von neuen Pflanzen sind. Basierend auf Nischenanalysen zeigten wir, dass (i) die Walddegradierung die Verfügbarkeit von Mikrohabitaten um die Hälfte reduzierte, insbesondere qualitativ hochwertige Mikrohabitate mit viel Licht und Totholz, (ii) dass die Tiere auf den Mikrohabitatverlust reagierten, indem sie häufiger Samen in ähnliche Mikrohabitate brachten und (iii) insgesamt die Samenausbreitung der Tiere dadurch redundant und von geringerer Qualität war im Vergleich zur Samenausbreitung im intakten Wald. Diese Ergebnisse weisen darauf hin, dass die strukturelle Vielfalt intakter Wälder nicht nur die Biodiversität, sondern auch die Diversität von ökologischen Interaktionen gewährleistet, welche die Basis für qualitativ hochwertige Ökosysteme sind.

In Kapitel 4 habe ich mich mit den vermeintlich einfachen, aber methodisch anspruchsvollen Fragen beschäftigt: Ist die Ausbreitung der Samen über Tiere langfristig positiv für Pflanzenpopulationen? Und wenn ja, wie effektiv sind die einzelnen Tierarten in ihrer Samenausbreitung? Hierfür habe ich die Forschung unserer Arbeitsgruppe aus den letzten 10 Jahren in einem speziellen Populationsmodell (sog. „Integral projection models“) zusammengeführt, am Beispiel der Populationsdynamiken des Faulbaums (lat. *Frangula alnus*) und der Samenausbreitung durch die 20 assoziierten Tierarten entlang des natürlichen Lichtgradienten des Waldes. Mit anderen Worten, habe ich analysiert, welche Tierarten die Früchte des Faulbaums fraßen, wie sie die Samen handhabten, wo sie wie häufig die Samen entlang des Lichtgradienten deponierten und welchen Einfluss das spätere Mikrohabitat der Samendeposition auf die Rekrutierung und das langfristige Wachstum, Überleben und die Reproduktion von Faulbaumsamen hatte. Die Analysen zeigten, dass sich die Samenausbreitung der Tiere positiv auf das Populationswachstum des Faulbaums auswirkte. Auch wenn sich die positiven Effekte durch Samenausbreitung von Tieren erhöhten, wenn der Faulbaum theoretisch noch nicht in Waldlücken vorhanden war und von der Samenausbreitung dorthin abhängig war, waren Populationen langfristig relativ stabil, die sich nur durch Gravität verbreiteten (d.h. die Früchte sind vom Baum heruntergefallen und wurden nicht gefressen). Die Effektivität der Samenausbreitung durch eine Tierart hing stark mit der Anzahl der gefressenen Früchte und weniger mit der Qualität ihrer Samenausbreitung zusammen. Die vier effektivsten Arten waren die Mönchsgrasmücke (lat. *Sylvia atricapilla*), die Amsel (*Turdus merula*), die Singdrossel (*T. philomelos*) und das Rotkehlchen (*Erithacus rubecula*). Mit Hilfe von Simulationen zum Aussterben einzelner Arten zeigten wir, dass sich der positive Effekt der Samenausbreitung auf das Populationswachstum am stärksten verringerte, wenn die effektivsten Arten ausstarben, ohne dass die verbliebene Artengemeinschaft die Interaktionen quantitativ kompensierte. Wenn allerdings Arten ausstarben, die kaum Früchte fraßen oder die Interaktionen durch die Gemeinschaft kompensiert wurden, veränderten sich die positiven

Effekte der Samenausbreitung nur geringfügig. Diese Ergebnisse heben zunächst die Bedeutung generalistischer Vogelarten wie der Mönchsgrasmücke oder der Amsel für die Samenausbreitung fleischig-fruchtender Pflanzen in temperierten Wäldern hervor. Ansonsten scheint die Samenausbreitung durch Tiere vor allem dann an Effektivität einzubüßen, wenn Interaktionen verloren gehen (d.h. wenn weniger Früchte gefressen werden). Folglich ist für die Effektivität der Samenausbreitung die Anzahl der Samenausbreiter wichtiger als die Qualität der Samenausbreitung einzelner Tierarten. Dieser Zusammenhang wurde in ähnlicher Weise auch schon für andere Pflanze-Tier-Interaktionen, wie die Blütenbestäubung, gezeigt.

Aus meiner Dissertation lassen sich folgende Schlüsse ziehen: Die langgehegte Vermutung von Ökolog:innen, dass die Samenausbreitung durch die Tiere langfristig positiv für die ausgebrachten Pflanzen ist, hat sich bestätigt. Darüber hinaus wird das Aussterben einzelner Tierarten unwahrscheinlich zu einem starken Rückgang in Pflanzenpopulationen führen, aus vier Gründen: (i) die meisten Tierarten sind unbedeutend für das Populationswachstum (da sie wenige Früchte fressen), (ii) die verbliebene Artengemeinschaft könnte potentiell die Samenausbreitung der verlorenen Art kompensieren, (iii) die verbliebene Artengemeinschaft wird nicht größenlimitiert sein und (iv) die Ausbreitung durch andere Prozesse (z.B. Gravität) kann ebenfalls zur Regeneration von Populationen beitragen. Wenn allerdings das Aussterben einer Art eine Folge der Veränderung der abiotischen und biotischen Umwelt ist, z.B. durch die Degradierung des Waldes, geht der Verlust von Arten mit einem Verlust der Effektivität der Samenausbreitung einher. Der Verlust der Effektivität der Samenausbreitung wird besonders dann groß sein, wenn für die Pflanze qualitativ-hochwertige Mikrohabitate verschwinden (z.B. Waldlücken) oder das Aussterben einzelner Arten mit dem Rückgang anderer Arten einhergeht und insgesamt weniger Früchte gefressen werden.

In Europa geht durch Bemühungen des Naturschutzes die Anzahl der aussterbenden Tierarten zurück. Allerdings sind ein Großteil der verbliebenen Arten über die letzten 40 Jahre drastisch in ihrer Populationsgröße geschrumpft, insbesondere Vogel- und Insektenpopulationen. Diesen Rückgang in der Populationsgröße innerhalb von Arten aufzuhalten und umzukehren, muss ein Hauptziel des Naturschutzes sein, um Ökosysteme mit einer hohen Funktionalität zu gewährleisten.

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Here was originally a page on the author's curriculum vitae.

Declaration / Erklärung

Ich versichere, dass ich meine Dissertation mit dem Titel

Integrating animal seed dispersal into plant regeneration

selbstständig und ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe. Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, den 16.11.2021

Finn Rehling