Distribution patterns of fleshy-fruited woody plants at local and regional scales

Matilda Arnell
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Abstract

Fleshy-fruited woody plants share a long history with humans, providing us with food and wood material. Because of this relation, we have actively moved some of these plants across landscapes and continents. In Sweden, these species are often found in open and semi-open habitats such as forest edges, their fruits are most often dispersed by birds and their flowers are, with some exceptions, pollinated by insects.

In this thesis my overall aim was to map and analyse distribution patterns of fleshy-fruited woody plants in Sweden to expand our knowledge on the mechanisms governing their distributions. First, I mapped a population of the early flowering, fleshy-fruited shrub *Daphne mezereum* (common mezereum, tibast) and surveyed the reproduction and fruit removal of all individuals (chapter I). My main aim was to investigate to what extent reproduction and fruit removal was affected by local distribution patterns. Secondly, I mapped local distribution patterns of fleshy-fruited woody species and analysed spatial associations between life stages and species (chapter II). My main aim was to relate these spatial associations to predictions of how bird dispersal would shape the local distribution patterns and the hypothesis that birds create ‘wild orchards’. Thirdly, I digitized historical maps and surveyed fleshy-fruited woody species along transects across landscapes (chapter III). My aim was to examine the hypothesis that these species accumulate in open and semi open habitats created by human land use. Fourthly, I estimated range filling of woody plants in Sweden at a 1 km\(^2\) resolution (chapter IV). My aim was to compare these estimates among species with different dispersal systems to understand the effect of dispersal on the occupancy of woody species at regional scales.

I found the distribution patterns of these species to be affected by past and present land use, supporting the hypothesis that these plants accumulate in open habitats. Occurrences of species in this guild in todays’ forest are positively related to past human land use (chapter III) and the density of *D. mezereum* increases with decreasing distances to forest edges (chapter I). This accumulation may in part be explained by the positive effect of forest edges on reproduction and fruit removal (chapter I). I further found local distribution patterns of this guild and the individual species to be aggregated (chapter I and II), and spatial associations between saplings and reproductive individuals to support the ‘orchard’ hypothesis (chapter II). The aggregated pattern of fruit-bearing individuals was positively related to fruit removal whereas aggregated flowering individuals was negatively related to fruit set (chapter I). On the regional scale, I found these species to occupy climatically suitable areas, or fill their potential ranges, to a less extent that wind dispersed trees and shrubs (chapter IV), which may indicate dispersal limitation.

In conclusion, the behaviour of birds and humans have shaped, and still shape the current distribution of fleshy-fruited trees and shrubs in Sweden, resulting in accumulation in open habitats and locally aggregated distribution patterns. Changing land-use practices and potential mismatches between fruit maturation and bird dispersal with a changing climate may thus result in even lower chances of these species to fill their potential ranges, due to habitat losses and dispersal limitations at local and regional scales.

Keywords: Fleshy fruits, woody plants, dispersal, distribution patterns, range filling, dispersal limitation, historical land use, spatial associations, point-pattern analysis, recruitment, reproduction, pollination, fruit set, fruit-removal, *Daphne mezereum*.
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“Soutenus des découvertes déjà faites, nous pouvons nous élancer dans l’avenir, et, pressentant les conséquences des phénomènes, fixer à jamais les lois auxquelles la nature s’est assujettie. C’est au milieu de ces recherches que nous nous préparons une jouissance intellectuelle, une liberté morale qui nous fortifie contre les coups de la destinée, et à laquelle aucun pouvoir extérieur ne sauroit porter atteinte.”

“Sustained by previous discoveries, we can go forth into the future, and by foreseeing the consequences of phenomena, we can understand once and for all the laws to which nature subjects itself. In the midst of this research, we can achieve an intellectual pleasure, a moral freedom that fortifies us against the blows of faith and which no external power can ever reach.”


Translated by Sylvie Romanowski
This thesis is based on the following chapters, which are referred to in the text by their Roman numerals.


## Contributions

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**OE** = Ove Eriksson  
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Field assistants: Malin Borg, Anna Lundell, Frida Sjösten and Ebba Tamm
Abstract

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In conclusion, the behaviour of birds and humans have shaped, and still shape the current distribution of fleshy-fruited trees and shrubs in Sweden, resulting in accumulation in open habitats and locally aggregated distribution patterns. Changing land-use practices and potential mismatches between fruit maturation and bird dispersal with a changing climate may thus result in even lower chances of these species to fill their potential ranges, due to habitat losses and dispersal limitations at local and regional scales.

Keywords: Fleshy fruits, woody plants, dispersal, distribution patterns, range filling, dispersal limitation, historical land use, spatial associations, point-pattern analysis, recruitment, reproduction, pollination, fruit set, fruit-removal, Daphne mezereum
Svensk sammanfattning

Fruktbärande träd och buskar är vedartade växter med frön som omges av olika typer av fruktkött. Dessa köttiga vävnader, som kan vara bildade från olika delar av blomman, går i dagligt tal under samlingsnamnen 'bär' eller 'frukter'. I denna avhandling har jag fokuserat på utbredningsmönster hos vilda och naturaliserade fruktträd och buskar inom den boreo-nemorala vegetationszonen i Sverige, som sträcker sig från lövskogsbältet i södra Sverige till ekens nordliga utbredningsgräns i höjd med Gästrikland. Jag förlade mina fältstudier till Södermanland och delar av Roslagen i Stockholms skärgård.

Utbredningen av dessa arter är ofta kopplad till öppna och halvöppna habitat såsom igenväxande ängmark, lundar och skogsbyn. Till de vanligaste och kanske mest igenkända arterna inom denna grupp hör rönn, hallon, en, hägg, slån och fågelbär samt olika arter av vilda nyponrosor. Till de vanliga men kanske mer förbisedda arterna hör måbär, skogstry och brakved. Bär och frukter med tillhörande frön från dessa växter sprids främst av fåglar och, med undantag av barrväxterna en och idegran som är vindpollinerade, pollinersas alla arter i denna grupp av insekter.

Målet med denna avhandling var att kartlägga och analysera utbredningsmönster hos denna grupp av arter på olika rumsliga skalar för öka våra kunskaper om de underliggande mekanismer som styr deras förekomster. I mitt första kapitel (kapitel I) kartlade jag en population av den tidigblommande, fruktbärande busken tibast (Daphne mezereum) i Roslagen och samlade in data över antalet producerade blommor och frukter samt andelen upptagna frukter, för varje individ. Målet med denna studie var att undersöka hur artens lokala utbredningsmönster påverkade reproduktionen och fåglarnas fröspridning genom att relatera antalet blommor, fruktödlning och upptagna frukter med avstånd till skogsbyn och den samlade blomningen och fruktödlningen hos närväxande individer. I mitt andra kapitel (kapitel II) kartlade jag lokala utbredningsmönster för alla fruktbärande träd och buskar i detalj på flera platser i ett studieområde i Södermanland och analyserade avstånd mellan individer av olika arter och livsstadien. Målet var att utröna om dessa mönster stämde överens med teorier och resultat från tidigare studier som förutsår att fågelspridning mellan fruktätande träd av olika arter med tiden skapar aggregerade lokala utbredningsmönster som...
poetiskt har kallats för 'fågelskapade fruktträdgårdar'. I mitt tredje kapitel (kapitel III) utvecklade jag och testade hypotesen att den historiska markanvändning i form av inägor och utmarker som skapade öppna marker och bibehöll dem på samma plats under långa tidsperioder skapade förutsättningar för fruktbärande arter att ackumuleras i och omkring dessa öppna marker. För att testa denna hypotes digitaliserade jag historiska häradskartor från början av förra seklet och kartlade alla fruktbärande träd och buskar längs med transekter på olika platser i Södermanland och Roslagen. I mitt fjärde kapitel (kapitel IV) tog jag fram ett mått på i vilken utsträckning träd och buskar i Sverige återfinns på platser där de rådande klimatmässiga förutsättningarna är fördelaktiga för dem. Därefter jämförde jag i vilken utsträckning detta mått skilde sig åt mellan arter med olika spridningsanpassningar varav en spridningsanpassning är utvecklandet av bär och frukter anpassade för djurspridning.

Jag kom fram till att dagens förekomst av dessa arter påverkas positivt av öppna marker då och nu, vilket stödjer hypotesen att dessa arter ackumuleras i och omkring öppna marker (kapitel III). I dagens skogar är förekomsten av dessa arter vanligare där det har skett en övergång från öppna marker till skog (kapitel III) och antalet individer av tibast ökar med minskande avstånd till skogsbyrin (kapitel I). Mina resultat visar att denna ackumulation till viss del kan förklaras av en ökad produktion av blommor och frukter i skogsbyrin samt av en ökad spridning i dessa habitat (kapitel I).

Vidare kom jag fram till att denna grupp av arter samt de ingående arterna uppvisar lokala förekomstmönster där individer är aggregerade i grupper (kapitel I och II). I dessa grupper förekommer små busk- och trädplantor oftare i närheten av reproduktiva individer av andra arter än vad som kan förklaras av slumpen, vilket stödjer hypotesen att fågelspridning är upphovet till dessa ’fruktträdgårdar’ (kapitel II). Aggregerade utbredningsmönster kan i sin tur påverka hur många frukter som sprids från varje planta, eftersom fåglar påverkas positivt av den totala fruktsättningen hos grupper av närväxande individer när dom väljer vilka frukter att åta (kapitel I). Däremot kan själva fruktsättningen hos insektspollinerade arter påverkas negativt, eftersom insekter ofta besöker färre blommor när det finns många andra blommor i närheten (kapitel I). När jag undersökte träd och buskars utbredningsmönster i boreo-nemoral Sverige, med en kvadratkilometers upplösning, så fann jag att fruktbärande träd och buskar i lägre utsträckning förekommer i
klimatmässigt lämpliga områden än vindspridda träd och buskar (kapitel IV). Detta antyder att fruktbärande arter generellt är mer spridningsbegränsade på den här skalan.

Fruktbärande träd och buskars utbredningsmönster i Sverige har påverkats, och fortsätter att påverkas av fåglars och människors beteenden. Detta har resulterat i att grupper av olika arter har ackumulerats i och omkring öppna marker. Förändrad markanvändning med färre öppna marker som följd riskerar därför att påverka dessa arter negativt. Pågående förändringar i vårt klimat riskerar även att skapa en sämre passning mellan när frukter mognar och fåglars rörelsemönster, vilket skulle kunna påverka fruktbärande arters chanser att nå lämpliga habitat.

Denna avhandling visar att vi genom att studera fruktbärande träd och buskars förekomster kan öka vår förståelse av de mekanismer som styr arternas utbredningsmönster. Detta kommer att öka våra chanser att trygga deras överlevnad, till glädje för kommande generationer av insekter, fåglar och människor.
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1. Introduction

The relationship between humankind and plants with fleshy fruits extends back to times before we evolved into *Homo sapiens* (Teaford & Ungar, 2000). Since then, humans have enjoyed eating and cultivating fruits, and we have even made sure to preserve them across seasons and centuries by painting them on our walls (FIG. 1).

FIGURE 1. A fresco of birds and fruits from a townhouse in Pompeii, dating to the 1st century AD. According to Strocka (1984) the fruits are cherries and Mirabelle plums belonging to the *Prunus* genus. The work depicted is in the public domain and obtained from https://commons.wikimedia.org/.
Our interest in how we, and other animals, have shaped the distribution of these fruit-bearing plants extends back to the 18th and 19th century and the early days of the field of biogeography (Linnaeus, 1781; von Humboldt & Bonpland, 1805). In their *Essay on the geography of plants*, von Humboldt and Bonpland (1805) marvel over the way plants like strawberries and cherry trees have accompanied us from one end of the planet to the other.

These days we know that plants in fact have evolved fleshy fruits as a dispersal strategy (Eriksson, 2008; Herrera, 1982). By enticing animals to swallow the pulp including the seeds, plants facilitate the movement of their otherwise immobile seeds. This movement of seeds forms the template on which factors regulating the establishment and survival act, which ultimately determines plant distributions (Schupp, 1995). Animal dispersal differs from dispersal by abiotic vectors like wind or water, since animal behaviour and habitat choice will affect the movement of seeds across the landscape and across continents (Jordano, 2000).

Throughout this thesis, for the sake of simplicity, the term ‘fruit’ includes all fleshy tissues surrounding plant seeds, whether formed from the ovary or from other parts of the plant. I have chosen to focus my attention on fruit-bearing trees and shrubs since they, apart from sharing dispersal system, also share growth form. From here on, I will refer to this guild of plants as fleshy-fruited woody plants. Not included in this definition are woody dwarf shrubs with fleshy fruits, e.g. *Vaccinium myrtillus* (blueberry, blåbär) or woody vines, e.g. *Hedera helix* (common ivy, murgröna). Further, I restricted the spatial extent of the analyses to Sweden, focusing on the boreo-nemoral vegetation zone (Sjörs, 1999) as this is an area where studies on the distribution of fleshy-fruited woody plants remain scarce.

1.1 Dispersal and distribution patterns

As mentioned above, their fleshy fruits have allowed some woody plants, like *Prunus avium* (wild cherry, fågelbär), to spread across and between continents by the aid of humans. Apart from this intentional favouring (Haeggström, 1998; Smith, 2011), many fleshy-fruited woody plants are found in semi-open habitats like forest edges and open woodlands (Kollmann & Schneider, 1999; Plieninger et al., 2015) and may thus have been unintentionally favoured by agricultural practices creating such habitats.
The main dispersal strategy however is dispersal by wild vertebrates. In temperate Europe, the main dispersers are generalist frugivorous birds like *Turdus merula* (blackbird, *koltrast*), although some mammals like *Vulpes vulpes* (red fox, *räv*) also include fruits in their diets (Herrera, 1989; Snow & Snow, 1988).

When compared to wind dispersal, vertebrate dispersal has been found to have both higher mean and maximum dispersal distances (Thomson et al., 2011). Unlike capricious winds, birds and other animals may also direct dispersal to suitable habitats (Breitbach et al., 2012; García et al., 2005).

In the light of this knowledge, one interesting question is how interactions with animal dispersers have shaped the ranges of these species, and whether they are limited by dispersal. If a species is limited by dispersal, there exists areas with suitable habitats which have not yet been reached by any seeds. On large geographical scales, suitable habitats are usually defined as the climatic conditions under which a species may establish and reproduce. These conditions can be modelled using occurrence records and climate variables. On this scale, dispersal limitation may lead to entire suitable regions being unoccupied by a species. Dispersal limitation can be estimated by calculating a species’ range filling. This is done by relating a species modelled potential range with the range actually occupied by the species, the realized range (Svenning & Skov, 2004).

On local scales, dispersal limitation may be defined as patches of suitable habitats being unoccupied in regions where the species is present. On this scale, factors like vegetation and land use are more commonly included when defining suitable habitats. One way of testing if species are limited by dispersal is by performing seedling recruitment experiments in the field. If seeds germinate and grow in previously unoccupied patches their recruitment is limited by dispersal (Eriksson & Ehrlén, 1992).

Another related question is how their dispersal system have shaped the joint distribution pattern of this entire guild of species and what we can learn from studying these. Since the fruits of many of these species are ripe at the same time, they may be eaten and dispersed together. If the seeds are dropped under the canopies of fruit-bearing individuals (García et al., 2007; Kwit et al., 2004) this may lead to aggregations of wild fruit trees and shrubs which have been termed ‘bird-made fruit orchards’ (Lázaro et al., 2005). By mapping local distribution patterns of this entire guild in detail, we may gain...
insights on how dispersal shaped the spatial relationships between species and life stages.

1.2 Fleshy-fruited woody plants in Sweden

In Sweden, the guild of fleshy-fruited woody species consists of 104 species from 28 different genera following the nomenclature in Mossberg & Stenberg (2018) (TABLE 1). *Rubus* is the most species-rich genus (34 species of which 32 are apomictic blackberry species) followed by *Rosa*, *Cotoneaster* and *Prunus*. None of the trees included in the guild form forest stands. Like in the rest of temperate Europe, the species are often associated with forest edges and other semi-open habitats (Jonsell, 2010; Rydberg & Wanntorp, 2001). Only two of the species are wind pollinated, *Juniperus communis* (*common juniper, en*) and *Taxus baccata* (*common yew, idegran*), while the rest of the species are pollinated by insects.

1.2.1 Land-use history and distribution

Historically, fleshy-fruited woody plants were common on meadows managed for leaf-hay close to human settlements (Palmgren, 1916). Their fruits were valued as food and livestock fodder (Plieninger et al., 2015; Smith, 2011) and their hardy wood provided good material for different wood-works (Haeggström, 1992). Meadows and the associated agricultural system of infields and outlands dates back to the Iron Age, around 2000 years ago (Eriksson & Arnell, 2017).

Today, due to the modernization of agriculture, most meadows are no longer managed (Cousins et al., 2015). In the cases when they were not turned into forest plantations but left without management, these meadows have been overgrown with deciduous trees and shrubs. In these habitats, which we in Sweden refer to as ‘lund’-habitats, fleshy-fruited trees and shrubs are still often found. Given this knowledge, one interesting question to resolve is to what extent the present distribution of fleshy-fruited woody species is a legacy of past land use.
TABLE 1. Fleshy-fruited woody plants in Sweden listed in Mossberg & Stenberg (2018). The list includes native trees and shrubs excluding a few native species with very limited ranges (e.g. species of whitebeam in the Aria and Hedlundia genera. The list also includes common naturalized and non-native species, indicated with an asterisk (*).

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<td>hagtorn</td>
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<tr>
<td>Family</td>
<td>Common Name</td>
<td>Latin Name</td>
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<td>slän</td>
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<tr>
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<td>European plumm</td>
<td>plomon</td>
</tr>
<tr>
<td>Prunus avium</td>
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<td>fågelbär</td>
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<tr>
<td>Prunus cerasus*</td>
<td>sour cherry</td>
<td>surkörsbär</td>
</tr>
<tr>
<td>Prunus padus</td>
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<td>hägg</td>
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<td>havtorn</td>
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<td>olvon</td>
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<td>red elderberry</td>
<td>druvfläder</td>
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<tr>
<td>Sambucus nigra*</td>
<td>elderberry</td>
<td>fläder</td>
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<td><strong>CAPRIFOLIAEAE</strong></td>
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<td>snöbär</td>
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<tr>
<td>Lonicera xylosteum</td>
<td>fly honeysuckle</td>
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1.3 Distribution patterns and reproductive success

As mentioned earlier, land use and patterns of seed dispersal together with other biotic and abiotic factors may shape the distributions of fleshy-fruited woody species. The resulting environmental context of individual plants, or in other words: in which habitat they end up, will affect how much resources the plant can allocate to producing flowers and fruits. The resulting flower and fruit production by the plant itself (Harder & Johnson, 2009; Jordano, 1987) and its neighbours (Carlo & Morales, 2008; Goulson, 2000) has the potential to feed back and affect the behaviour of pollinators and dispersers. The environmental context may also have a direct effect on pollinators and dispersers since also animals like birds and bees have habitat preferences (Albrecht et al., 2012; Grundel et al., 2010). Given that a plants’ spatial context has the potential to affect pollination and fruit removal, one interesting question to answer is if the patterns created by land use and dispersal positively affect pollination and fruit removal, thus acting reinforcing.
2. The aim of this thesis

The chapters included in this thesis aim to map and analyse distribution patterns of fleshy-fruited woody plants in Sweden to expand our knowledge on the mechanisms governing their distributions. My main focus was to investigate the effect of dispersal and land use on the distribution of these species at regional, landscape and local scales. FIGURE 2 gives an overview of the main topics and spatial scales of the four chapters.

In chapter I, my aim was to analyse the relationships between land use, local distribution patterns and species traits on the reproductive success and fruit removal of the fleshy-fruited, early flowering shrub *Daphne mezereum*.

In chapter II, my main aim was to describe local distribution patterns of fleshy-fruited woody plants in relation to predictions of how bird dispersal may shape spatial association between different species and life stages.

In chapter III, my aim was to analyse the effect of historical land use on the distributions of fleshy-fruited woody plants at a landscape scale.

In chapter IV, my aim was to analyse if woody plants with different dispersal systems differ in their abilities to occupy suitable habitats at a regional scale.
FIGURE 2. Overview of the main topics and spatial scales of the four chapters.
2.1 chapter I: aim and spatial scale

Reproductive success, fruit removal and local distribution patterns in the early-flowering shrub Daphne mezereum

Plants’ reproductive investment, the number of flowers produced, may vary across habitats (Obeso, 2002). Suitable habitats for Daphne mezereum in Sweden include forest edges and other semi-open habitats (Mossberg & Stenberg, 2018). The flowers and fruits produced may affect visits by pollinators (Harder & Johnson, 2009) and dispersers (Jordano, 1987), affecting the reproductive success and fruit removal. In various habitats, a plant’s position relative to other reproductive individuals may further affect pollination and removal rates since pollinators (Goulson, 2000) and dispersers (Carlo & Morales, 2008) are affected by resource patch size.

In chapter I, I describe local distribution patterns of D. mezereum and analyse the effect of land use, spatial associations and plant traits on reproductive success and fruit removal. My aim was to understand to what extent the potential effects of these variables feed back and explain local distribution patterns. The mapped population was located in south-eastern Sweden at a study site of approximately 4.8 hectares (FIG. 3).

Chapter 1 in summary: In this chapter, I map the local distribution patterns of *Daphne mezereum* (common mezereum, *tibast*) and investigate the relationships between plant traits, land use and spatial associations between individuals on the reproductive success and fruit removal. If the spatial context effects reproduction and dispersal this may explain how the local distribution pattern of this species was formed.
2.2 chapter II: aim and spatial scale

Local distribution patterns of fleshy-fruited woody plants – testing the orchard hypothesis

It has been suggested that bird dispersal of fleshy-fruited woody plants may result in ‘bird-made fruit orchards’ (Lázaro et al., 2005). When several species of wild or naturalized trees and shrubs are found in the same area and their fruiting seasons overlap, birds may disperse seeds between reproductive individuals (García et al., 2007; Kwit et al., 2004). This will then result in aggregated assemblages of different species, beautifully described as ‘orchards’.

In chapter II, with the aim to examine the formation of orchards, I mapped and analysed spatial associations between fruit-bearing individuals (reproductive individuals) and saplings of all fleshy-fruited woody plants at several sites in one area in south-eastern Sweden. I also performed a recruitment experiment to assess whether the recruitment of the species was limited by the availability of seeds. Local occurrences were mapped in circles with 50 m diameters (FIG. 4) and spatial associations were analysed at distances between 0 and 20 meters. In the recruitment experiment, seeds were sown in 50×50 cm quadrats.
Chapter II in summary: In this chapter, I test the hypothesis that bird dispersal patterns have created aggregated assemblages of fleshy-fruited woody plants of different species or ‘bird-made fruit orchards’. If these plants are distributed as ‘orchards’, saplings and fruit-bearing individuals of different species should be found closer together than expected by chance. In other words, there should be positive spatial associations between saplings and fruit-bearing individuals of different species.
2.3 chapter III: aim and spatial scale

*Does historical land use affect the regional distribution of fleshy-fruited woody plants?*

Legacy effects of historical land use have been extensively studied for some groups of plant species, notably forbs and grasses in semi-natural grasslands (Cousins & Eriksson, 2002; Gustavsson et al., 2007; Lindborg & Eriksson, 2004). Agricultural practices dating back around 2000 years created open habitats such as meadows, and stabilized them in space and time (Eriksson & Arnell, 2017). This spatio-temporal stabilization has been proposed to allow species to accumulate in these habitats (Eriksson, 2013) resulting in the very high plant species richness in today’s semi-natural grasslands. In chapter III, I develop the hypothesis that the same mechanisms resulted in an accumulation of fleshy-fruited woody species in these open and edge habitats created by human land-use practices.

With the aim to analyse the effect of historical land use on the distributions of fleshy-fruited woody plants I digitized historical land-use maps and related the occurrences of fleshy-fruited species to open habitats in 1900. Field studies were performed in two regions in Sweden, surveying all fleshy-fruited plants along 500 m transects at different sites in the landscape (FIG. 5).
Chapter III in summary: In this chapter, I develop and test the hypothesis that the distribution and richness of fleshy-fruited woody plants is a legacy of past land use. Individuals would have been dispersed and been able to establish and accumulate in, and at the edges of, open habitats created by agricultural practices. Given this, species may still be common in areas where there has been a transition from open habitats to forest, as illustrated by the sapling in the figure. On the historical maps (year 1900), open habitats are coloured light green (meadows) and orange (arable fields). In the present landscape (year 2015), open habitats are coloured light green (settlements and other open areas) and beige (arable fields).
2.4 *chapter IV*: aim and spatial scale

*Regional range filling and dispersal limitation of woody plants with different dispersal systems*

Range filling is estimated by comparing a species’ potential range with the range occupied by the species, the realized range (Seliger et al., 2020; Svenning & Skov, 2004). Range filling can be seen as a measure of a species ability to reach and occupy suitable habitats, where suitable but not occupied habitats may be evidence of dispersal limitation. Species with different dispersal systems may differ in their levels of range filling and dispersal limitation.

In *chapter IV*, with the aim to assess the effect of dispersal system on regional range filling I modelled the distributions of fleshy-fruited woody plants in Sweden and species belonging to the two other dispersal systems, vertebrate dispersal with acorns or nuts and abiotic dispersal. Species distribution models were performed by relating occurrences with climate and land-use data. I estimated regional range filling of one species per genus within the three dispersal systems. The estimates were restricted to areas with ten or more observations of woody plants (low ignorance areas) in the nemoral and boreo-nemoral vegetation zones in Sweden (FIG. 6) at a 1 km² resolution.

![FIGURE 6. Regional scale area for the estimations of range filling, including the nemoral and boreo-nemoral vegetation zones of Sweden. Redrawn from (Sjörs, 1999).](image-url)
Chapter IV in summary: In this chapter, I develop a method to downscale estimates of range filling to test the hypothesis that woody plants with different dispersal systems differ in the extent to which they are limited by dispersal. The three dispersal systems represented among woody species in Sweden are: 1) vertebrate dispersed with fleshy fruits, symbolised here by wild cherries, 2) vertebrate dispersal with acorns or nuts, symbolized by oak acorns and 3) species with abiotic dispersal, symbolized by the winged fruits of the wind-dispersed maple.
3. General methodology

The data underlying this thesis is to a large extent based on detailed mapping of species occurrences. Occurrence data was mapped during field surveys at different sites in south-eastern Sweden (chapter I, II and III), as well as obtained from the Global Biodiversity Information Facility (GBIF.org, 2021) (chapter IV).

3.1 Field surveys and experiments

Field surveys were performed in two regions in south-eastern Sweden (FIG. 7). These two regions were chosen to represent differences in past and present land-use practices, including the timing of the modernisation of agriculture (chapter III). In region A, hereafter referred to as Södermanland, continuous areas of soils suitable for crop production promoted a modernization process starting around the mid-19th century (Cousins et al., 2015). Region B, hereafter referred to as Stockholm archipelago, represents a more marginal agricultural area where traditional agriculture was practiced as late as the 1950s (Jerling & Nordin, 2007). Species in the two genera *Crataegus* and *Rosa*, were not identified to species level. *Rubus idaeus* was identified, but all *Rubus fruticosus* agg. species were counted as one taxon. The native *Ribes rubrum* ssp. *rubrum* and the cultivated and naturalized *Ribes rubrum* ssp. *spicatum* were counted as one species.

3.1.1 Transects surveys

To answer questions about the effect of historical land use (chapter III), I sampled the landscape in the two regions by surveying the occurrences of all fleshy-fruited woody plants along 500 m long and 50 m wide transects. 44 transects in Södermanland and 23 transects in region the Stockholm archipelago (FIG. 7). Transects were chosen as the survey method to capture as many transition between areas of different historical land use as possible. For every individual I estimated the surrounding forest cover.
FIGURE 7. The two study regions in south-eastern Sweden. A: Part of the County of Södermanland (referred to as Södermanland). B: The peninsula of Väddö and Björkön and the island of Singö (Referred to as Stockholm archipelago). Green circle, region A: field area of chapter II (referred to as Tullgarn). Green circle, region B: field area of chapter I (referred to as Väddö). Black dots: transect locations in the two study regions (chapter III).
3.1.2 Mapping spatial associations

To answer questions about spatial associations between individuals (chapter I and II) it is important to map species occurrences in large enough areas to capture spatial associations and potential small scale clustering, or aggregation, of individuals.

In chapter I, I mapped the occurrences of all individuals taller than 10 cm in one population of *Daphne mezereum* in an area of approximately 4.8 ha at Väddö in the Stockholm archipelago (FIG. 7). For every individual I recorded height as well as counted the number of buds, flowers and fruits on several occasions during the reproductive season for three consecutive years. In chapter II, I mapped the occurrences of all fleshy-fruited species at 15 sites at Tullgarn in the county of Södermanland (FIG. 7). At each site, all individuals of 10 cm or higher were mapped in a 50 diameter circle. The combined circle area was approximately 9 ha. For every individual I recorded height or diameter at breast height as well as their reproductive status. Saplings were defined as plants of 30 cm or less in height and fruit-bearing (reproductive) individuals as plants taller than 30 cm displaying flowers or fruits at the time of our mapping.

3.1.3 Recruitment experiment

To answer the question of whether the recruitment of fleshy-fruited species is limited by dispersal (chapter II) I set up three plots in and adjacent to each of the 15 circles in Tullgarn where I mapped species occurrences. In 50×50 cm subplots I sowed 50 seeds each of *Crataegus laevigata*, *Frangula alnus*, *Juniperus communis*, *Lonicera xylosteum*, *Prunus avium*, *Prunus padus*, *Prunus spinosa*, *Ribes alpinum*, *Rubus idaeus* and *Sorbus aucuparia* (please refer to TABLE 1 for common names in English and Swedish). I then followed the faith of the seeds for three seasons, recording seedlings and juveniles.

3.1.4 Pollination experiment

To answer the question of whether fruit set in *Daphne mezereum* is pollination limited (chapter I) I performed a hand pollination experiment assessing fruit set on hand pollinated branches compared with branches subjected to ambient pollination on the same individual.
3.2 Point pattern analyses

To answer questions about spatial associations between plant individuals (chapter I and II) I performed point pattern analyses. Point patterns analyses can be applied to any data that can be described as a point with a spatial location (Baddeley et al., 2015; Wiegand & Moloney, 2013), for example trees in a forest. A basic question that can be answered with point pattern analyses is if the observed pattern is clustered or more dispersed than random (chapter I and II). One way of comparing the observed pattern to patterns generated by a random process is the pair correlation function (Illian et al., 2008; Stoyan & Stoyan, 1994). To calculate the pair correlation function g(r), you start by drawing a band in a circle with radius r around every observed point and estimate the density of points falling within the bands (FIG. 8). This is repeated for values of r at constant intervals from zero up to a maximum value, roughly half of the width of the area where the pattern was recorded. In the pair correlation function g(r), the density of points at every value of r is then divided by the density of the total point pattern, to standardise the result. For a point pattern generated by a random process, the density at all values of r is close to the total density, hence

\[ g(r) \text{ of a random pattern: density (r) / total density } \approx 1 \]

For observed point patterns, values of g(r) larger than one indicate clustering or positive spatial associations, and values of g(r) smaller than one indicate dispersion or negative spatial associations. To test if the g(r) of the observed pattern is likely to have been generated by a random process or not, I compared the observed g(r) to the g(r) of a number of randomly generated point patterns, displayed as a confidence interval in the resulting graphs (FIG. 8).

The pair correlation function can also be used to answer questions regarding spatial associations between different types of points within the same area, such as the associations between fruit-bearing individuals and saplings (chapter III). In these bivariate pair correlation functions, g(r)_{12} was estimated by drawing the band with radius r around each fruit-bearing individual (pattern 2) estimating the density of saplings (pattern 1) divided by the total density of saplings (pattern 1). For the observed point patterns of saplings and fruit-bearing individuals, values of g(r)_{12} larger than one indicates positive spatial associations, and values of g(r)_{12} smaller than one indicates
FIGURE 8. Schematic illustration of how to calculate the pair correlation function $g(r)$. A band with circle radius $r$ is drawn around every observed point. The density of points falling within the bands is estimated and divided by the total density to standardize the result. In the bottom panel, the observed, standardized density at $r$, $g(r)$, is compared to the $g(r)$ of a number of randomly generated point patterns, displayed as a confidence interval (in green). In this example, the point pattern is more clustered than would have been expected by chance up to around six meters from any individual, and more dispersed at distances exceeding eight meters.
negative spatial associations between the two life stages. Positive spatial associations means that saplings are found closer to fruit-bearing individuals than would be expected by chance.

3.3 Historical land-use analyses
To assess the effect of historical land use on the landscape scale distribution of fleshy-fruited woody species (chapter III) I rectified and digitized District Economic Maps (Häradsekonomiska kartan) (FIG. 9) for the Stockholm archipelago region from around the year 1900 following the methodology in (Cousins et al., 2015), from where the digitized maps for the Södermanland region were obtained. Present-day land use was obtained from the Swedish Terrain Map (Terrängkartan). Only the parts of transects with present forest cover were included in the analyses in order to exclude the effects of present forest cover.

To compare the effect of historical land use on species richness I grouped transects into transects covering both open habitats and forests and transects covering only forest in 1900, where present forest cover was extracted from the Terrain map. To analyse the effect of historical land use on the probability of occurrence of individual species, I divided transects into 20×20 m segments and estimated the fraction historically open habitats per segment for

FIGURE 9. Historical land use in 1900 (left panel) and present land cover (right panel) at the location of one of the survey transect in the Stockholm archipelago region (modified from FIG. 2 in chapter II). On the historical map, open habitats are coloured light green (meadows) and orange (arable fields) and forests are light areas with asterisks and circles symbolizing trees. In the present landscape, open habitats are coloured light green (settlements and other open areas) and beige (arable fields) and forests are coloured dark green.
segments with present forest cover estimated from the field observations. Per species, segments containing occurrence records were classified as presences and segments lacking occurrence record were classified as absences.

3.4 Regional range filling estimates
To answer questions about differences in regional range filling between woody plants with different dispersal systems (chapter IV), I estimated range filling by comparing species’ potential ranges with the ranges occupied by the species, their realized ranges (Seliger et al., 2020; Svenning & Skov, 2004). A species’ potential range can be modelled and projected using species distribution models (SDMs). To estimate the ranges occupied by the species, most studies have used existing range maps produced by experts (Seliger et al., 2020; Svenning & Skov, 2004). However, these range maps often have a low resolution. In the above mentioned studies the resolution of the range maps ranged from 9 to 15 km².

In chapter IV, I wanted to estimate range filling at a higher resolution compared to previous studies since this may help finding and understanding differences between species with different dispersal systems. In Sweden, we unfortunately have no digitized, high resolution range maps. I therefore developed a method to estimate a species realized range at a 1 km² resolution (the pixel size of the range maps produced) based on occurrence records, resulting in an estimate I refer to as regional range filling. Since species from the same genus are likely to be more similar in their responses to biotic and abiotic factors compared to species from different genera, I chose to only include one species per genus, to avoid pseudo-replication. I restricted the range filling estimations to the nemoral and boreo-nemoral zones of Sweden, since they encompass the main distributions of most of the woody species in Sweden (Hultén, 1950).

3.4.1 Dispersal systems
Trees and shrubs in Sweden can be divided into three main dispersal systems: vertebrate-dispersed species with fleshy-fruits, vertebrate-dispersed species with nuts or acorns and species with seeds dispersed mainly by wind. I hereafter refer to these three systems as vertebrate dispersal with fleshy fruits, vertebrate-dispersal with nuts and wind dispersal. The two animal-dispersed systems differ in the way the
animals consume and disperse the seeds. Seeds covered by fleshy fruits are mainly dispersed by birds and are often consumed together with the pulp which are then dispersed to a perching site (Herrera & García, 2009; Jordano, 2000). Seeds enclosed in a hard shell, such as hazelnuts (Corylus avellana) and oak acorns (Quercus spp.), attract both birds and rodents who predate the seeds. The seeds are dispersed due to these animals’ scatter-hoarding behaviours where seeds are collected, stored and sometimes forgotten and thus allowed to germinate. The species which are mainly wind dispersed have fruits which lack adaptations that make them attractive to animals. Instead they may have fruits with wings or appendages to promote wind dispersal.

3.4.2 Database occurrence records
To estimate potential ranges and estimate regional range filling I obtained occurrence data for all genera of woody plants in Sweden, excluding the main forest forming species Picea abies and Pinus sylvestris, from the Global Biodiversity Information Facility (GBIF.org, 2021). After data cleaning, the dataset included over 1.8 million occurrence records from 44 genera.

3.4.3 Estimating realized ranges
I estimated each species realized range, the pixels actually occupied by a species, using occurrence records. However, occurrence records only allow me to estimate where a species is found and not where a species is absent, which is equally important when delimitating a species range. One way of generating a more reliable estimate of pixels where the species is absent is to produce a map where each pixel gets a value representing if it is well sampled or not, a low ignorance map (Ruete, 2015). I produced a low ignorance map using all the 1.8 million occurrence records of woody species where pixels with ten ore more species present represented well sampled areas (low ignorance areas) and pixels with fewer species recorded represented poorly sampled areas (FIG. 10). If a species is absent from a highly sampled, low ignorance area, the absence is more likely to be a ‘true’ absence and not a result of a low sampling effort. To reduce the number of ‘false’ absences, I thus restricted my regional range filling estimates to areas of low ignorance.
FIGURE 10. Producing a low ignorance map and modelling species’ potential ranges using occurrence records. Occurrence records of all woody species were used to produce a low ignorance map. If a species is absent from a highly sampled, low ignorance area, the absence is more likely to be a ‘true’ absence and not a result of a low sampling effort. For one species per genus, I employed species distribution models (SDMs) to produce potential range maps where each pixel gets assigned a suitability score. A subsample of the occurrence records falling within a subset of the low ignorance pixels were set aside for the regional range filling estimations.
Since the occurrence records form the basis for both the modelled potential ranges and the estimated realized ranges, I used a subset of the low ignorance area (5000 pixels) including the associated occurrence records to estimate the realized ranges and calculate the range filling estimates. The realized range was thus the occupied pixels within the low ignorance pixel subset (FIG. 10).

3.4.4 Modelling potential ranges

I modelled and projected potential ranges by relating species occurrence records to three bioclimatic variables and one land-use variable at a 1 km² resolution. The bioclimatic variables included precipitation of the driest quarter, temperature annual range and growing degree days base 5°C obtained from CHELSA version 1.2 (Karger et al., 2017, 2018). The land use variable open land was created to map the proportion open land in each 1 km² pixel, using data from the National Land Cover database (Swedish Environmental Protection Agency, 2020).

Ranges were modelled using an ensemble of four different SDMs to produce robust predictions of the species’ potential distributions (Marmion et al., 2009) using the biomod2 package (Thuiller et al., 2020) in R (R Core Team, 2021). The output from the SDMs was one (potential) range map per species, where each pixel was given a suitability score based on the model predictions. Low suitability scores are given to pixels where the species is likely to be absent given the data, and high scores are given to pixels where the species is likely to be present.

3.4.5 Estimating regional range filling

I estimated regional range filling for each species as the sum of all suitability scores within the realized range (all ‘presence’ pixels within the 5000 low ignorance subset) divided by the sum of all suitability scores within the potential range (all 5000 low ignorance pixels) (FIG. 11).
FIGURE 11. Estimating regional range filling. Suitability scores per pixel were estimated using species distribution models (SDMs) (FIG. 10). Within the low ignorance pixel subset, I estimated regional range filling per species by taking the sum of the suitability scores for the pixels with occurrences records (regional realized range) and dividing them by the sum of the suitability scores for all pixels (regional potential range).
4. Results and discussion

4.1 Boreo-nemoral fleshy-fruited woody species

The chapters included in this thesis has increased our knowledge on the distribution patterns of the boreo-nemoral guild of fleshy-fruited woody plants at various spatial scales.

In total, 31 species of fleshy-fruited woody species were found during the field surveys (chapter II and III) (FIG. 12), a number that would have increased somewhat if individuals in the Rosa and Crataegus genera as well in Rubus fruticosus agg. had been identified to species level. Overall, the species recorded during the field studies constitute a representative sample of the Swedish guild of fleshy-fruited species (c.f. TABLE 1).

I have found the composition and richness of these plants to vary between Swedish regions (chapter III) (FIG. 12 and 13). In both study regions, Sorbus aucuparia (rowan, rönn) was the most abundant species. The second most common species differed between regions, with Rubus idaeus (raspberry, hallon) and Ribes nigrum (alpine currant, måbär) being the second most common in Södermanland and Stockholm archipelago respectively. At a local scale, rowan was also the only species found at all of the plots in Tullgarn, Södermanland (chapter II).

Although abundance patterns vary between regions, species’ abundance patterns across spatial scales are similar. In general, species with high regional abundances (chapter III) also have high occupancy within transects and sites (chapter II and III) and rare species are both regionally and locally rare. At local scales, individuals of the boreo-nemoral guild of fleshy-fruited woody species have aggregated distribution patterns. Up to around 10 meters from any given individual, there are more neighbouring individuals than would be expected by chance (chapter I and II). I found the recruitment to be limited by seed availability for all ten species included in the seedling recruitment experiment, although the vast majority of seeds did not germinate or survive to be recorded (chapter II).
FIGURE 12. The abundance of fleshy-fruited woody species in Södermanland (pink), at the Tullgarn study site in Södermanland (gray) and in Stockholm archipelago (orange) (chapter II and III). Abundance: fraction of the total number of occurrences in each region and at the Tullgarn site. Dots: abundance <0.01 (fewer than 10 occurrences). Asterisks: absence.
4.2 Patterns of accumulation and aggregation

4.2.1 Accumulation, reproductive success and dispersal

In chapter III, I hypothesize that agricultural practices stabilizing open habitats in space and time, together with intentional favouring of fruit-bearing plants created conditions which allowed fleshy-fruited woody plants to accumulate in the landscape. My results from chapter I provides some insights into the details of this accumulation.

As hypothesized, I found that the density of *D. mezereum* to be highest close to forest edges, with declining numbers further in to the forest (chapter I). Since reproductive success and the subsequent dispersal of seeds form the template for plant distribution patterns, I investigated how flower and fruit production as well as fruit removal were effected by distance to forest edges. In insect-pollinated, vertebrate dispersed plants like *D. mezereum*, and most of the plants in this guild, the environmental context has the potential to affect the interaction between the plants and their pollinators as well as their dispersers, and the result of these interactions may in part explain their accumulation in forest edges. In chapter I, I found forest edges to
be suitable habitats for regeneration of *D. mezereum*, since flower and fruit production increased with closeness to forest edges (FIG. 14). Moreover, the fruit set (proportion of flowers producing fruits) increased, indicating that forest edges are also suitable habitats for the pollinators of this plant. Also fruit removal (proportion of fruits removed) increased, which increases the chances for seeds to be dispersed. These results show positive effects of edge habitats on the early stages of the regeneration process, supporting the hypothesis that fleshy-fruited species accumulate in edge habitats.

### 4.2.2 Aggregation, dispersal and reproductive success

In *chapter I*, I show local scale accumulation of individuals. Another local scale distribution pattern found in *chapter I* as well as in *chapter II*, is the aggregated pattern of plant individuals in this guild. In *chapter II* I test the hypothesis that this pattern is created by bird dispersal (Lázaro et al., 2005) by assessing spatial associations between saplings and reproductive individuals of different species. If birds disperse seeds among fleshy-fruited species with overlapping fruiting seasons, this would create positive spatial associations between these life stages. In line with this hypothesis, I found saplings to be closer to reproductive heterospecific individuals than would have been expected by chance (FIG. 15).

Like the environmental context, these aggregated pattern have the potential to affect pollinators and dispersers, and potentially reinforce the aggregated pattern. In *chapter I*, I show that reproductive success and fruit removal in *D. mezereum* is related to the spatial associations between reproductive individuals, measures as reproductive success and fruit production of neighbouring individuals within 10 m. Flower and fruit production was positively related to the flower production

![Diagram](image.png)

**FIGURE 14.** The effect of distance to forest edge on flower and fruit production as well as fruit set and fruit removal in *Daphne mezereum*. **32**
of neighbouring plants, which indicates that reproductive individuals aggregate in suitable habitats (FIG. 14). However, as hypothesized, the flower production of neighbouring individuals affected fruit set negatively (FIG. 16), probably because pollinators tend to visit fever flowers as the flower patch increases (Goulson, 2000). While the proportion flowers pollinated deceased with increasing numbers of neighbouring flowers, the opposite pattern was found for fruit removal. As the total fruit-crop of neighbouring plants increased, so did the proportion fruits removed on individual plants (FIG. 16). Aggregations of reproductive individuals thus may be reinforced by attracting dispersers and weakened by the negative effect on fruit set.

4.2.3 Landscape scale accumulation

In line with previous results and the hypnotized effect of land use and intentional favouring on this guild of species, I found the landscape scale distribution patterns to partly be a legacy of historical land use (chapter III). In the Stockholm archipelago, the species richness of fleshy-fruited woody plants in todays’ forest was higher on forest
FIGURE 16. The effect of number of flowers on neighbouring plants on flower production, fruit production and fruit set as well as the effect of number of fruits on neighbouring plants found for Daphne mezereum (chapter I).

transects which contained open habitats in the year 1900 compared to transects completely covered by forest according to the historical maps (FIG. 17). The reason behind the lack of effect of historical land use in the Södermanland region may be attributed to the timing of the modernization of agriculture which occurred earlier in this region.

In both regions I found an effect of historically open habitats on the occurrence of individual species. In the Stockholm archipelago the occurrence patterns of the majority of the species analysed was positively affected by past open habitats. In Södermanland, only a minority of the species were affected, which is in line with the landscape effects on species richness.

4.3 Regional scale dispersal limitation

The regional distribution patterns of fleshy-fruited woody plants in nemoral and boreo-nemoral Sweden are related to their dispersal system (chapter IV). At this scale, compared to woody plants dispersed mainly by wind, fleshy-fruited plants are absent in potentially suitable habitats to a higher extent. This results in lower values of regional range filling. Because this effect of dispersal system on range filling, I interpret the lower range filling values to reflect higher dispersal limitation in fleshy-fruited plants (FIG. 18).

However, also other factors could cause species to be absent in climatically suitable habitats. After being dispersed, seeds need to survive, germinate and establish, and failing to do so results in recruitment limitation. To my knowledge, few studies have compared recruitment limitation across species with these different dispersal
FIGURE 17. The effect of land use in 1900 on the species richness of fleshy-fruited woody plants in today’s forest (chapter III).

system, which makes it hard to assess the effect of recruitment limitation on range filling. On a local scale, my recruitment experiment confirmed both dispersal limitation and recruitment limitation for the fleshy-fruited species included (chapter II) since more seeds germinated in the plots where seeds were added (dispersal limitation) although a majority of the seeds failed to germinate (recruitment limitation). In Mediterranean landscapes, recruitment limitation has been found to be high for both fleshy-fruited and dry-fruited species (Mendoza et al., 2009). In the fleshy-fruited species, dispersal limitation was linked to the movement of birds within the landscape whereas dispersal limitation for dry-fruited, mainly wind dispersed species, decreased with increasing density of adult trees. On landscape scales, animal dispersal has been found to direct seeds to suitable habitats (Breitbach et al., 2012; García et al., 2005). This capacity for directed dispersal, as well as for long distance dispersal (Thomson et al., 2011), does not seem to translate into low values of dispersal limitation on regional scales. However, in chapter IV, I define suitable habitats based on climate variables and one estimate of
FIGURE 18. Illustration of differences in range filling in relation to dispersal system found for woody species in Sweden (chapter IV). Fleshy-fruited species (symbolised here by wild cherries) fill their predicted potential range to a less extent than wind dispersed species (symbolized by the winged maple fruit), potentially caused by higher dispersal limitation.

landscape openness at a 10 km² resolution, which correspond more to climate suitability than the classic definition of habitat suitability which typically includes vegetation cover. Fleshy-fruited species may thus have lower chances of tracing suitable climates than wind dispersed species, while still having high chances of ending up in suitable habitats on landscape and local scales. When birds deliver seeds under the canopies of fruit-bearing individuals (García et al., 2007; Kwit et al., 2004), accumulating species and plants in orchards (Lázaro et al., 2005, chapter II), they may concentrate the occurrences of this guild to some areas in the landscape leaving other suitable habitats empty. These distribution patterns may contribute to dispersal limitation at regional scales.
5. Future perspectives

I have devoted this thesis to studies of distribution patterns of fleshy fruited species in boreo-nemoral Sweden. However, many things remain to be discovered.

Concerning local distribution patterns, I would like nothing more than to resolve to what extent dispersal is responsible for the aggregated distribution patterns found and discussed throughout this thesis (chapter I and II). Given my result, I would argue that dispersal plays an important role in structuring the distribution of species as well as the joint distribution patterns of the entire guild. However, parts of the aggregated or patchy distributions found may also be local variations in suitable habitats. Given enough monetary resources, I believe it would be possible to get closer to an answer by mapping the distributions of all woody species, fleshy and non-fleshy in a larger area, similar to what has been done in other parts of the world (e.g. Anderson-Teixeira et al., 2015; Hubbell & Foster, 1983), and then follow the fate of newly recruited individuals. This detailed mapping would allow for comparisons among species with different dispersal systems. In combination with mapping of soil properties and field layer and their potential effects on local distributions, I think this would give us important new insights (FIG. 19). Given a large fully

FOREST PLOT

FIGURE 19. Potential future forest plot in which to collect data on spatial location of species, soil properties, vegetation cover, genetic relations as well as, among many things, variations in seed predation and dispersal in space and time.
mapped area it would also be interesting to collect information on the genetic relation between individuals (Godoy & Jordano, 2001) to better understand dispersal distances. I would also like to understand the role of post-dispersal seed predation (García et al., 2007; Webb & Willson, 1985; Whelan et al., 1991) and how this varies within the landscape in this region. Moreover, for most species of fleshy-fruited woody plants, we lack detailed information on the species of birds dispersing the seeds in Sweden (but see Bolmgren & Eriksson, 2015; Englund, 1993; Green et al., 2019) as well as the timing of peak dispersal. In combination with data on fruiting phenology (Eriksson & Ehrlén, 1991) this would allow us to understand and potentially predict mismatches between peak fruiting and peak dispersal (Bolmgren & Eriksson, 2015).

Concerning regional and Europe wide distribution patterns of this guild of species, as well as other groups of plants, I believe that we would gain important knowledge by taking advantage of already existing range data. In the mid-20th century, Erik Hultén performed work of paramount importance when he published his *Atlas of the distribution of vascular plants in NW. Europe* (Hultén, 1950) and *Atlas of North European vascular plants* (Hultén & Fries, 1986). The information in these publications is to this day confined to the pages of the printed books and remain to be made publicly available for modern analyses by georeferencing and digitizing the maps. This information would, together with existing occurrence records, improve species distribution models and range filling estimates (*chapter IV*, Seliger et al., 2020, Svening and Skov 2004) as well as increase our knowledge on plant climatic niches (De Frenne et al., 2013; Vangansbeke et al., 2021).

6. Concluding remarks

The behaviour of birds and humans have shaped, and still shape the current distribution of fruit-bearing trees and shrubs in Sweden, resulting in accumulation in open habitats and locally aggregated distribution patterns. Future changes in land-use practices resulting in fewer open habitats thus have the potential to affect distribution patterns in this guild of species. Since they are dependent on birds to carry their seeds across the landscape, changes in climate resulting in
mismatches between bird dispersal and fruit maturation would result in lowered chances of these species to track suitable habitats.

I show that by studying distribution patterns of fleshy-fruiting woody plants at different spatial scales, we may increase our understanding of the mechanisms governing their distributions. This will give us a chance to ensure their survival throughout coming centuries so that future generations of insects, birds and people may enjoy their flowers and fruits in nature, not only from paintings on our walls.
7. References


an open-forest gradient. *Ecological Applications*, 20(6), 1678–1692.


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Göran Tunström: *Juloratoriet*. 1983