‘A Fine Balance’: Exploring the Interplay of Reproductive Strategies and Growth Dynamics in Trees

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1 Introduction

The fundamental processes in a plant’s life cycle—growth, reproduction, defense, and storage—all compete for the same resources. Plants must apply trade-offs to maximize their fitness when resources are limited. One of the most significant of these is the growth-reproduction trade-off, which is influenced by both environmental conditions and a plant’s life history strategy (Grime, 1977; Stearns, 1998). In resource-rich environments, plants are able to allocate resources both to rapid growth and reproduction, while in resource-poor environments, plants often face a decision: they can either allocate resources to growth, ensuring their long-term survival, or they can invest in reproduction, which may come at the expense of growth (Bazzaz, 1997). This trade-off leads to high variability in reproduction across years, which is manifested as mast seeding, an important reproductive strategy for many plant species. (Pearse *et al.*, 2016).

Mast seeding is the phenomenon of synchronized and variable seed production within plant populations; it is closely related to ecosystem-level functions influencing processes such as seed dispersal, predation and plant recruitment, since seeds can be food resources for many mammals or hosts for pathogens (Davies & MacPherson, 2024; Janzen, 1971; Kelly, 1994), and also determines regeneration within a population. Mast seeding is widely observed in wind-pollinated tree species, but also occurs in *Poaceae* as well as *Diperocarpaceae* (Kelly & Sork, 2002). Although there are several hypotheses explaining the potential mechanism of mast seeding (e.g., predator satiation, resource matching, *etc.*) (Koenig, 2021), the exact factors triggering it in different species and ecosystems are not fully understood. The best supported hypotheses, given current data, suggest that it is mainly driven by specific climatic conditions that makes masting a successful strategy for the species at population level (Pearse *et al.*, 2016). The major hypotheses either try to explain the mechanism from the environmental perspective, such as the resource matching hypothesis, or from an adaptive perspective to ensure reproductive success, such as the predator satiation hypothesis and the pollination coupling hypothesis. These hypotheses are closely related to the inter-annual and annual reproductive variability.

All of these hypotheses build on unique features of masting, which makes it distinct from annual fluctuations in seed production of non-masting species, especially its interannual variation, synchrony, temporal autocorrelation, and frequency (Hacket-Pain & Bogdziewicz, 2021). Interannual variation in masting is not entirely random or caused by immediate environmental conditions, but are part of a population-level strategy, with synchrony occurring across large spatial areas, which can extend hundreds of kilometers (Kelly, 1994). Temporal autocorrelation describes the pattern in which a mast year is typically followed by several years of low or no seed production, which distinguishes masting from annual fluctuations. Finally, frequency refers to how often mast years occur, with some species exhibiting a more fixed interval (e.g., every 2-3 years) and others a more irregular pattern (e.g., 2-5 years). Annual fluctuations in seed production, by contrast, are more closely tied to short-term environmental factors and do not exhibit this kind of regularity.

Masting plays an important ecological role by influencing seed dynamics and broader ecosystem processes. According to the predator satiation hypothesis, mast years overwhelm seed predators by producing abundant seeds, ensuring that some seeds will survive and germinate. In this way, plants can regulate predator populations and enhance seedling establishment. Mast seeding contributes to the creation of seed banks, which provide a reserve of seeds that help the population buffer against environmental variability, allowing seeds to wait for favorable conditions to germinate (Venable, 1989). This strategy not only improves seedling survival in the short term but also promotes long-term regeneration, helping to maintain a plant population over time.

With the ongoing climate change, causing the change of growing season and precipitation patterns, the environmental variability is likely becoming more unpredictable. These changes may influence the balance of the growth-reproduction trade-off through altered plant resource availability and consequently, masting behavior, which will not only affect the forest population dynamics itself, but also the seed predator community that relies on the forests. Understanding how these dynamics function, and how climate plays the role, is critical for predicting future forest composition and regeneration. Currently, there is no comprehensive model to predict how climate change will affect masting considering the relationship between growth and reproduction across different species and ecosystems, due to the complex and variable nature of mast seeding.

The aim of my thesis is to investigate how masting as a reproductive strategy, is related to the growth dynamics of tree species and their role in forest ecosystems, particularly in the context of climate change. Using Mount Rainier as a case study, my proposed research will address three key questions: (1) Which reproductive traits are associated with masting? This help us potentially understand what might trigger the behavior of masting in different environments. (2) Is there a detectable trade-off between mast seeding events and tree growth? (3) How will changing climate conditions affect seed dynamics at Mount Rainier? Answering these questions will contribute to our understanding of how masting shapes the growth and regeneration dynamics of coniferous forests in Mount Rainier, with inference on how masting dynamics might be related to growth and environmental changes in other coniferous forests globally.

2 Explore which reproductive traits are relevant to masting

Masting is widely observed across different plant lineages in different biomes, with many hypotheses for how masting could yield fitness benefits compared to reproducing every year (Koenig, 2021; Waller, 1979). The most commonly accepted hypothesis is the predator satiation hypothesis, which suggests that masting species overwhelm seed predators with a large seed crop, then starve the seed predators during years with a low seed crop (Janzen, 1971). By manipulating the seed predator population, masting plants increase the likelihood that their seeds will survive to germinate. Another widely accepted hypothesis, the pollination coupling hypothesis, suggests that environmental conditions and resource availability together determine the flowering effort of plants (Crone & Rapp, 2014). Highly synchronized flowering improves pollination success and results in more seeds. The third major hypothesis, resource matching hypothesis, suggests that a fixed fraction of resources is allocated to reproduction every year (Kelly, 1994). The amount of resources available for reproductive output depends on the total resources available to the plants. Closely related to all these hypotheses is the environmental cues hypothesis, which suggests that certain environmental events trigger masting (Pearse *et al.*, 2016). These hypotheses are not mutually exclusive and may hold true for different species in different environments.

Based on these hypotheses, we can link specific traits to the phenomenon of masting. Since masting is a reproductive event, the most relevant traits are likely related to seed reproduction, which occurs through at least three critical stages: pollination, seed maturation and seed dispersal (Satake & Kelly, 2021). Each stage presents unique opportunities that can influence the overall success of mast seeding. During pollination, traits like whether a plant is monoecious or dioecious can be linked to the pollination coupling hypothesis, as dioecious plants require separate genders for reproduction, which may reduce pollination success in low-density populations (Bawa, 1980). This predicts that masting species are more likely to be monoecious. Another important trait is duration of flowering, since a longer flowering period might increase pollination success (Knight *et al.*, 2005). Masting species are also most likely to be wind-pollinated, so pollination is not restricted by the number of pollinators when large numbers of flowers bloom simultaneously (Bogdziewicz *et al.*, 2017, 2020).

After pollination, fertilized seeds enter the maturation stage, which is more related to the resource matching hypothesis. Traits such as leaf longevity and determinacy, which influence the timing of seed development and a plant's ability to invest in reproduction, are thus likely important at this stage. Determinacy defines whether the leaf material is prebuilt or not (Lechowicz, 1984), may influence how much resources plants can allocate to reproduction. Longer leaf longevity facilitates more carbon fixation, which could enhance the resources available for reproduction (Adler *et al.*, 2014).

When seeds mature and are ready for dispersal, the role of seed predators becomes crucial. According to the predator satiation hypothesis, in masting years, plants overwhelm seed predators by producing large numbers of seeds. Masting species, however, may also rely on seed dispersers to carry seeds away from the parent tree, increasing the chances of seedling survival (Janzen, 1971; Silvertown, 1980). In this context, seed traits such as seed size, nutrient content, dispersal mode, seed dormancy and seed longevity all can play important roles. Larger seeds with higher nutrient content might be more attractive to seed predators, so they are more likely to benefit from masting events. Seed dormancy and seed longevity help ensure that seeds do not germinate immediately after dispersal, allowing them to wait for better conditions to establish in a more favorable environment since mast events only occur once every few years.

There are several preliminary studies explored the relationship between some traits with inter-annual variability in seed production, which provided some evidences for different hypotheses

(Fernández-Martínez *et al.*, 2019; Journé *et al.*, 2023; Pearse *et al.*, 2020), but did not explain how different environmental conditions might directly linked to which reproductive traits might be more critical. In this meta-analysis, I will include reproductive traits associated with different hypotheses to investigate how these traits are related to a species' tendency to mast in different forest types and biomes.

2.1 Research Question and Objectives

Which seed traits are related to masting, and more specifically, whether hypotheses explaining the mechanisms vary by species or environment?

– **Investigate Trait Associations:** Analyze the relationships between specific reproductive traits and masting event and frequency to determine which traits are more important in masting for different species.

– **Compare across Different Environments:** Compare the most critical traits across different forest types and biomes to determine if they vary.

2.2 Methods

This chapter aims to explore the relationship between reproductive traits and the tendency of a species to mast in various environments through a meta-analysis.

Data collection

Data for this meta-analysis will be primarily sourced from following resources:

– **Silvics of North America:** Provides a comprehensive database of tree species and their reproductive characteristics in North America, will be our main dataset. It includes flowering traits, seed dispersal traits, mast cycles and forest types I am interested in. For biomes, I will use the information in the distributional map provided by the book and categorized into temperate, subtropical and tropical. For forest type, I will extract information from the section of associated forest cover, and try to categorize it according to North American forest cover types.

– **MASTREE+:** This is a specialized database focused on tree species' mast seeding behavior, which will be a supplemental source for identifying species tendencies for mast seeding and interannual variability.

- **Kew Seed Dataset, Worldwide Seed Mass Dataset, USDA Seed Manual:** These sources will offer supplementary information on seed mass and other reproductive traits.

Statistical Analysis and Model Development

The main analysis will involve logistic regression to determine the likelihood of mast seeding based on the selected reproductive traits and environmental variables. The response variables, whether a species mast or not and the coefficient of variation (CV) of the mean annual seed crop which is widely used in masting related research to describe the highly variable year-to-year production of seeds will be analyzed separately to evaluate the occurrence and variability of mast seeding behavior (Kelly & Sork, 2002).

2.3 Significance

Studying the reproductive traits related to masting can provide valuable insights into reproductive strategies and the broader ecological impacts on forest ecosystems. First, it can help explain the potential mechanisms that drive this complex reproductive strategy, shedding light on why certain species mast while others do not in different environments. By examining traits such as seed size, nutrient content, dormancy, and longevity, researchers can gain insights into how these characteristics influence the success of seed production and dispersal during mast years, and how this is related to seed predators' population dynamics.

Additionally, understanding these relationships can help us to predict how environmental factors, such as climate change, may impact masting behavior in the future. For example, knowing which seed traits are most relevant to masting behavior in specific ecological contexts can help us anticipate how shifts in temperature, precipitation, and other environmental cues might change masting patterns. By answering the question of what causes masting through looking at seed traits, we can better understand the dynamics of forest ecosystems.

3 Understanding the relationship between masting and growth

The growth-reproduction trade-off suggests that increased investment in one process often comes at the expense of the other (Grime, 1977; Stearns, 1998). For trees, the decision to allocate resources to a large seed crop during a masting year can significantly affect overall growth dynamics (Hacket-Pain *et al.*, 2016a). This relationship between growth and reproduction can be complex, as the years leading up to a masting event may involve resource accumulation for reproductive efforts, while the years following masting could exhibit a different pattern, influenced by less demand for reproduction (Kelly, 1994).

With anthropogenic climate change, tree growth in generally expected to increase, as warmer temperatures increase growth rates and provide trees with more time to growth each year with extended growing season (Keenan *et al.*, 2014; Finzi *et al.*, 2020). Most climate models predict a positive relationship between temperature and growth (Friedlingstein *et al.*, 2022; Ito *et al.*, 2020). However, recent studies have questioned whether the extending of growing seasons due to warming has actually led to increased tree growth (Dow *et al.*, 2022; Green & Keenan, 2022). Studies have suggested that biotic factors, such as intrinsic species differences and how plants allocate the additional carbon gained during warmer seasons, also play a significant role (Hacket-Pain *et al.*, 2016b). In the context of masting, these dynamics become even more complex, underscoring the importance of understanding how different tree species will behave in future climates.

While many studies have examined how climate influences both growth and reproduction, often comparing responses to various climate factors (Bajocco *et al.*, 2021; Koenig *et al.*, 2020; Redmond *et al.*, 2019; Sánchez-Humanes *et al.*, 2011), only a few have directly investigated the growth-reproduction trade-off in the context of masting. The majority of these studies have focused on oak and pine species. Research on oaks, for example, found little evidence of a strong, consistent trade-off between radial growth and seed production (Koenig *et al.*, 2020; Patterson *et al.*, 2023). However, this lack of evidence may be due to biomass allocation to roots, as oaks generally have deep root systems and tend to allocate more resources to root development from youth to maturity (Burns, 1990). In contrast, the species I will use in this study, either have shallow roots or do not develop resources-expansive taproots, thus exhibit a different response, leading to potentially different conclusions.

Masting and growth responses could differ across elevations, where resource availability and environmental stresses fluctuate. Trees at higher elevations may experience a more pronounced trade-off between growth and reproduction due to these resource limitations and harsher environmental conditions (Figure. 3). By examining different species at varying elevations, we can gain a better understanding of the complex relationship among resources, growth, and reproduction.

With Mount Rainier's unique elevational gradient and utilizing long-term tree growth data from tree rings, this chapter explores the relationship among resource availability, growth and reproduction in six common coniferous species. It emphasizes the trade-offs that shape reproductive strategies and how these strategies might differ across varying ecological conditions.

3.1 Research Question and Objectives

Is there a detectable trade-off between mast seeding events and growth?

- **Assess Growth Patterns:** Test for a trade-off by analyzing historical annual growth of selected tree species in relation to their masting events.

- **Compare Species Responses:** Evaluate the differences in masting and growth responses among various tree species across different elevations with various resources allocation strategies.

3.2 Methods

This chapter aims to examine the growth-reproduction trade-off in relation to mast seeding for six common conifer species at Mount Rainier across different elevations. To explore this relationship, I will incorporate long-term seed trap data with historical growth data derived from tree core samples, and use statistical approaches to analyze their relationship.

Study site and sample collection

I will conduct this study in Mount Rainier National Park, Washington, USA. I will focus on six common conifer species that exhibit varying masting behaviors and occur across different elevations in the park (Figure. 2). The data I am going to use in this chapter include two components:

- **Long-term seed data:** Our collaborator Dr. Janneke Hille Ris Lambers, has been collecting stand-level seed production data using seed traps since 2008, which will provide a valuable record of masting events across different stands and elevations at Mount Rainier (Figure. 4).

- **Tree growth data:** To assess the historical growth of individual trees, I will collect cores from targeted species in Table. 1 in each stand with long-term seed data. Within each stand, there are at least two targeted species, and each species appears in at least four stands. I plan to collect tree cores from 25 individuals per species per stand, covering a size gradient. To make sure the trees we core were mature enough to reproduce at least 10 years ago, I will only collect from trees with DBH greater than 25 cm. Additionally, I will prioritize individuals that are close to seed traps to better correlate with seed data. I will core trees at breast height using increment borers, taking two tree cores from the opposite sides of the tree while avoiding slopes. To account for at least 15 years of growth and for cross-dating purposes, I will collect long cores of 25 cm from larger trees with a DBH above 50 cm, while for smaller trees, I will core to the center if possible.

Tree core processing

I will prepare the cores for analysis by sanding them with fine grit sandpaper (up to 2000 grit depending on the visibility of rings) to ensure a smooth, clear surface. For cores with rings that are difficult to distinguish, I will use a microtome to further enhance the visibility of the rings, creating a clear surface for better quality.

After preparation, I will scan the cores using a high-resolution camera to capture detailed images of the growth rings, then I will analyzed the images with CooRecorder, a software used to measure tree ring width. I will also double check the cross-dating results with COFECHA Cook & Kairiukstis (2013); Speer (2010).

Statistical analysis

This model investigates the trade-offs between growth and reproduction by modeling seed production and radial growth. I treat species and stand effects with partial pooling to allow for variation while sharing information between groups.

Likelihood for Seed Production

The seed count $\text{Seed}_{i,k,y}$ for stand i, species k, and year y follows a Poisson distribution with mean $\lambda_{i,k,y}$:

$$\text{Seed}_{i,k,y} \sim \text{Poisson}(\lambda_{i,k,y})$$

The seed count $\lambda_{i,k,y}$ for stand i, species k, and year y is then modeled as:

$$\text{Seed}_{i,k,y} = \beta_0^{\text{sp}[k]} + \beta_1^{\text{sp}[k]} \cdot \text{Growth}_y + \beta_2^{\text{sp}[k]} \cdot \text{Growth}_{y-1} + \beta_3 \cdot \text{Elevation}_i + \beta_4^{\text{stand}[i]} + \beta_5^{\text{stand}[i]} \cdot \text{Growth}_y$$

Where:
$\alpha_1^{\text{sp}[k]}$ is the species-specific intercept for species$k$,
$\beta_1^{\text{sp}[k]}$ is the slope for the relationship between current-year growth and seed production for species k,
$\beta_2^{\text{sp}[k]}$ is the slope for the relationship between previous-year growth and seed production as the lag effect for species k,
β_3 is the effect of elevation on seed production),
$\beta_4^{\text{stand}[i]}$ is the change in intercept caused by stand effects i,
$\beta_5^{\text{stand}[i]}$ is the change in slope for the relationship between current-year growth and seed production for stand i.

Likelihood for Radial Growth

The radial growth Growth_y for year y in stand i and species k follows a normal distribution with mean μ_y and standard deviation σ_{growth}:

$$\text{Growth}_y \sim \mathcal{N}(\mu_y, \sigma_{\text{growth}})$$

Where the mean μ_y is:

$$\mu_y = \alpha_2^{\text{sp}[k]} + \beta_6^{\text{sp}[k]} \cdot \text{Elevation}_i + \beta_7^{\text{stand}[i]} + \beta_8^{\text{stand}[i]} \cdot \text{Elevation}_i$$

Where:
$\alpha_2^{\text{sp}[k]}$is the species-specific intercept k,
$\beta_6^{\text{sp}[k]}$ is the slope for the relationship between elevation and growth for species k,
$\beta_7^{\text{stand}[i]}$ is the change in intercept caused by stand effects i,
$\beta_8^{\text{stand}[i]}$ is the change in slope for the relationship between elevation and growth for stand i.

3.3 Significance

Understanding the relationship between masting and growth is important for predicting how tree species will respond to changing environmental factors, particularly in the context of extending growing season, how trees might allocate additional carbon. By examining how these processes interact, we can gain insights into the adaptive strategies of different species and their potential resilience or vulnerability to future climate changes. This knowledge allows us to make more informed predictions about future forest dynamics, including shifts in species composition, regeneration, and ecosystem health. As climate conditions continue to fluctuate, understanding the masting behavior and growth responses will be essential for effective forest management and conservation efforts, helping us to anticipate changes and make management plans that will support the sustainability and resilience of forest ecosystems.

4 Investigate how changing climate affect masting dynamics

Plants need to assimilate enough resources to produce seeds, a process that requires a combination of environmental conditions such as light, water, nutrients and suitable temperature. These factors can directly influence mast seeding by affecting seed development process or affect it indirectly by regulating flowering or growth. Flowering, for instance, is regulated by day length, and light plays a key role by influencing the production of hormones which control both flowering and growth (Lau & Deng, 2010). Light is also a critical element for photosynthesis, which supports healthy plant growth. Water is another essential element for both flowering and fruiting. It helps maintain optimal turgor pressure, which is necessary for proper flower development, while also facilitating nutrient transport and supporting cell expansion (Taiz & Zeiger, 2002). When water availability is limited, plants may conserve energy, leading to fewer or smaller flowers, reduced pollination success, or even shedding flowers before maturation. After fertilization, water continues to play a crucial role in the expansion and maturation of seeds. Beside its direct effects on reproduction, water stress also inhibits growth, limiting the resources available for reproduction (Hsiao, 1973; Anjum *et al.*, 2011). Nutrients, both macronutrients and micronutrients, are essential for both energy transfer and storage, playing a significant role in the formation of flowers and seed development. Nutrient availability influences the timing of lowering and seed formation, with well-nourished plants more likely to flower at the appropriate time and set seeds successfully. One of the most widely studied climatic factors linked to masting events is temperature (Bajocco *et al.*, 2021; Moreira *et al.*, 2015; Schauber *et al.*, 2002; Bogdziewicz *et al.*, 2024), especially spring temperature, which is crucial period for the meiosis of pollen and ovules.

To understand how climate change may impact masting events, it is important to explore the relationship between environmental factors and mast seeding behavior first. Mast seeding is characterized by four main features: interannual variation, synchrony, temporal autocorrelation, and frequency. These characteristics are all likely to be affected by climate change in different ways (Hacket-Pain & Bogdziewicz, 2021). Once we have a sense of how different environmental factors are manipulating different aspects of masting, we can make better prediction of how future changing climate might shape the seed dynamics in this region. One significant change expected with climate change is the extension of the growing season, which may allow trees to allocate more carbon to growth and reproduction (Keenan *et al.*, 2014). This shift could have profound implications for the frequency and intensity of masting events. Additionally, warmer temperatures could increase the frequency of droughts, which would limit water supply. On the other hand, in areas with year-round snow cover, temperature changes may alter water dynamics, affecting the timing and availability of water. Another critical factor in the flowering and fruiting process is environmental vetoes, which refer to conditions where weather events or environmental factors prevent certain processes in a plant, even when the plant has sufficient resources (Bogdziewicz, 2022) . Environmental vetoes can take two forms: (1) a lack of weather cues, such as when specific weather conditions required to trigger flowering or fruit maturation are not met, preventing reproduction despite adequate resources; and (2) extreme weather events, such as frost, drought, or heavy rainfall, which can directly damage plant tissues, including shoots, flowers and fruits, thereby preventing successful reproduction. With climate change, it is likely that environmental vetoes will become more frequent, which is generally considered detrimental to plants. However, studies have shown that environmental vetoes preventing seed production in certain years can actually facilitate masting, allowing for higher regeneration success (Bogdziewicz *et al.*, 2018, 2019). Therefore, understanding how environmental vetoes influence seed production in different species and regions is critical for predicting future forest dynamics.

Elevation is closely linked to a variety of climatic factors, particularly temperature and water availability, and has long been used as a proxy for climate change in ecological studies. It provides a natural system to study the long-term, large-scale effects of climate change on communities and ecosystems which cannot be accomplished by experiments (Sundqvist *et al.*, 2013). By using elevation as a proxy for climate change, we can better understand how plant populations at different elevations respond to environmental factors and refine predictive models that incorporate shifting climatic variables at finer spatial resolutions. This approach also helps us understand ecosystem and vegetation shifts within a region.

Mount Rainier provides an ideal location for studying how climate change may impact forest dynamics, as it features a distinct elevation la gradient and diverse snowmelt patterns. The rain shadow effect on different sides of the mountain also creates varying water availability. The climate in this region has already undergone significant changes in recent decades, and by combining historical seed data with climate data, we can explore the relationship between climatic variables and various aspects of mast seeding. This will allow us to make more accurate predictive models. This chapter aims to identify common patterns in masting influenced by environmental factors. By investigating the large variance in interannual masting patterns, and exploring the relationship between spatial as well as temporal changes in masting across elevational gradients, we can better understand how climate change will impact seed dynamics in this area.

4.1 Research Question and Objectives

How does changing climate affect seed dynamics at Mount Rainier?

- **Identify Environmental Influences:** Investigate how key environmental factors (e.g., temperature, precipitation) are related to masting events at Mount Rainier.
- **Climate change proxy:** Use the elevational gradient at Mount Rainier as a proxy for changing climate conditions to compare how masting behavior varies across different elevations.
- **Develop Predictive Models:** Develop predictive models of masting behavior across elevations to forecast future seed dynamics under changing climate conditions.

4.2 Methods

This chapter aims to investigate how climate change influences seed dynamics at Mount Rainier, focusing on the relationship between mast seeding patterns adapted to local climatic conditions across different elevations for the same species. By using long-term seed trap data and corresponding climate data, I will assess how seed production synchrony and variability change along the elevation, which is used as a proxy for climate change for same species we used in last chapter. **Data collection**

- **Long-term seed data:** The same long-term seed trap data from last chapter.

– **Local climate data:**

Statistical Analysis and Model Development

– **Time series model, mixed-effect models:**

– **Predictive modeling:** I will develop predictive models to forecast future trends in masting behaviours at Mount Rainier under projected climate scenarios. These models will use climate projections for this retion to predict how seed dynamics might shift in response to future climate change.

4.3 Significance

Changes in masting behavior can have cascading effects on forest dynamics, including seed predator interactions and the regeneration success of tree species. Since masting events can provide a large food source drives population dynamics of lots of mammals in the forest, changes of masting patterns will alter these ecological relationships, and further the overall structure of ecosystems. Fore example, if climate change causes masting events to be less synchronized across species or elevations, it will affect seed availability for animals that rely on them as food source, potentially impacting their survival and reproduction. Masting will also affect the regeneration of tree species itself. Many tree species rely on mast seeding years to establish successful new seedlings in the face of competition and predation. If climate change affects the frequency or intensity of mast seeding events, the successful regeneration of some tree species might be adversely affected. Thus, understanding how these characteristics of masting might be influenced by climate change is essential for predicting the resilience of forest ecosystems.

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Table 1: Targeted species

Tree species	Common name
Abies amabilis	Pacific silver fir
Pseudotsuga menziesii	Douglas fir
Tsuga heterophylla	Western hemlock
Tsuga mertensiana	Mountain hemlock
Thuja plicata	Western redcedar
Callitropsis nootkatensis	Yellow cedar

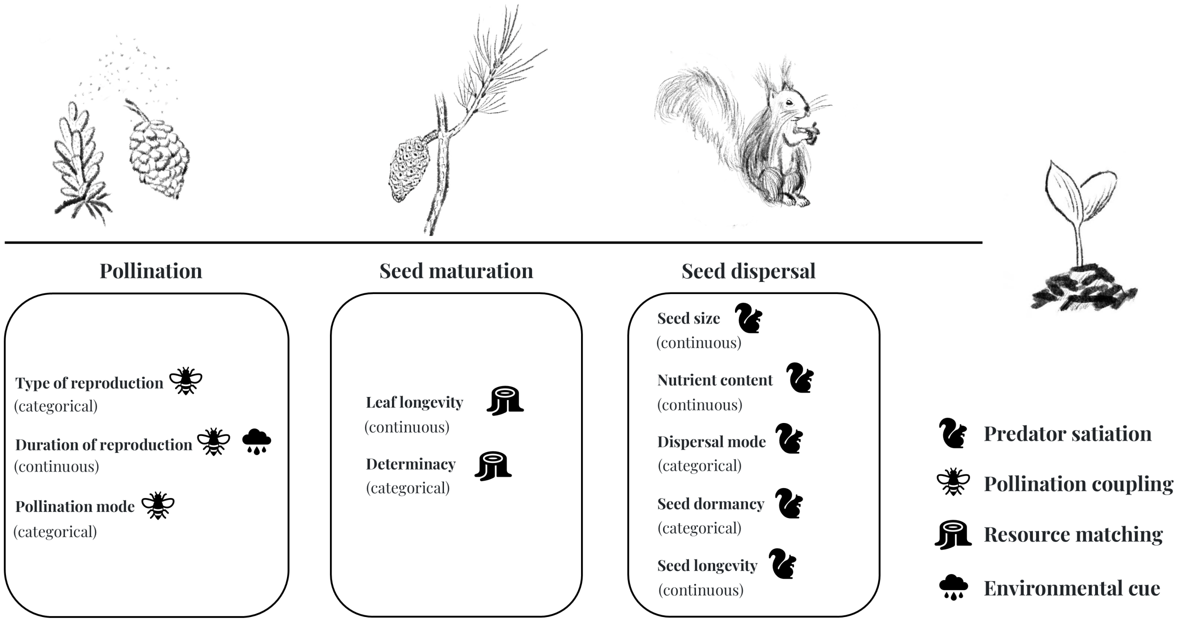
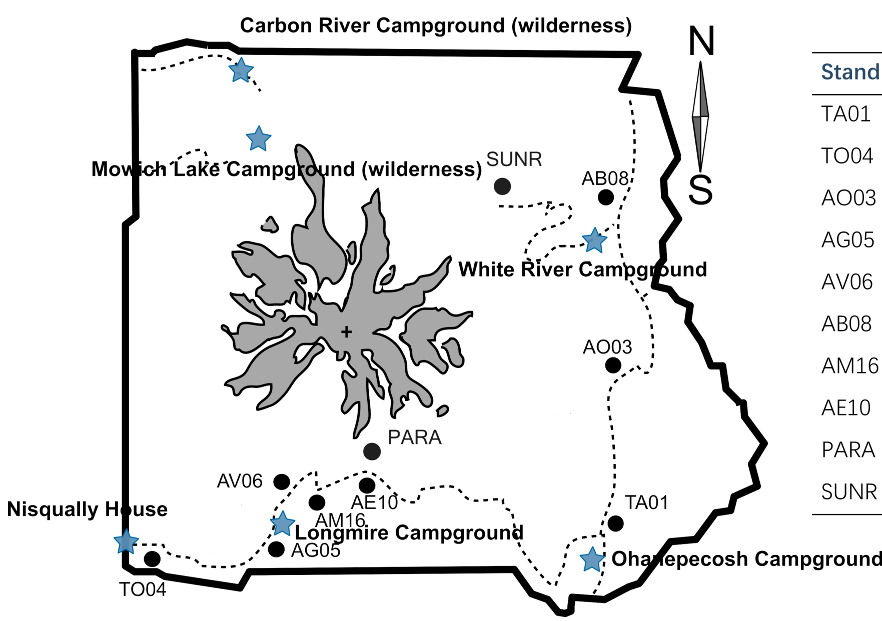


Figure 1: Conceptual framework linking reproductive traits to the phenomenon of masting across critical stages of seed reproduction. The symbols indicate different hypotheses. I include the information on whether the traits is categorical or continuous below each traits.



Stand	Elevation
TA01	~700m
TO04	~700m
AO03	~900m
AG05	~950m
AV06	~1060m
AB08	~1100m
AM16	~1200m
AE10	~1450m
PARA	~1600m
SUNR	~1800m

Figure 2: A map of Mount Rainier with all the sampling stands for this study and the elevation of each stand. The black dots are the standsand the blue starts are the campgrounds

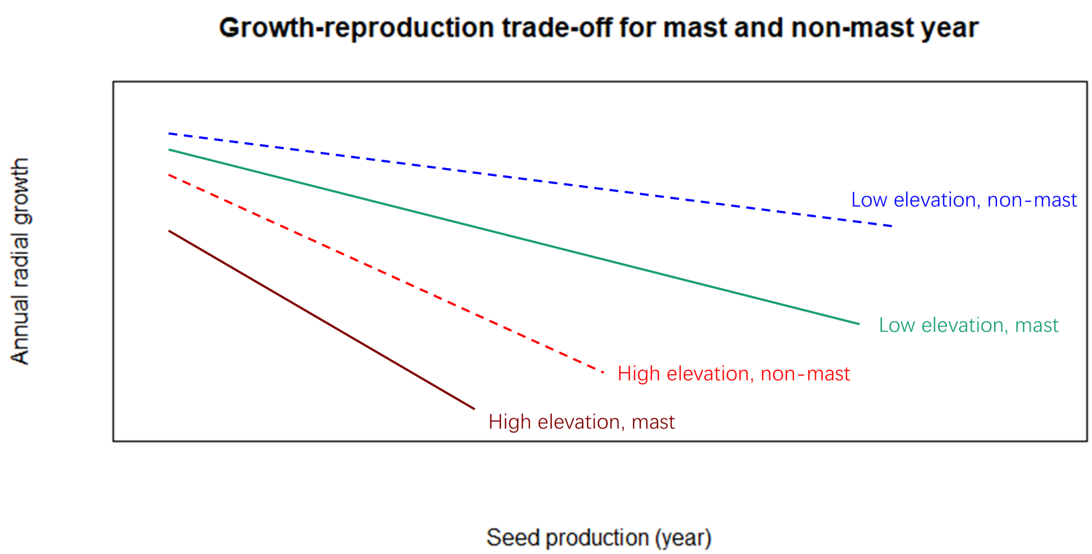


Figure 3: A conceptual figure showing the expected trend of growth-reproduction trade-off in masting year and non-masting year at different elevations. I would expect that the trade-off is more pronounced in masting years compared to non-masting years in general and individuals at higher elevation would experience a higher trade-off

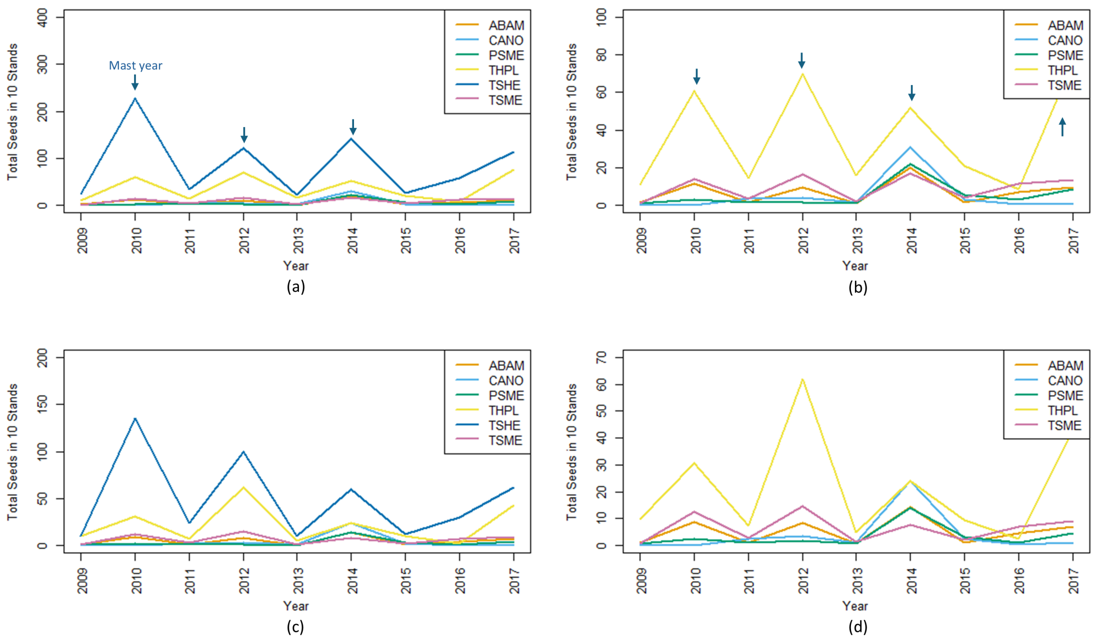


Figure 4: Seed data across all 10 stands collected by seed traps from 2009-2017 at Mount Rainier. (a) total seeds (sum of filled and empty seeds) for all six species; (b) total seeds for only five species excluding TSHE in finer resolution; (c) filled seeds for all six species; (d) filled seeds for only five species exluding TSHE in finer resolution. Short blue arrows indicate potential masting years. ABAM: *Abies amabilis*, CANO: *Callitropsis nootkatensis*, PSME: *Pseudotsuga menziesii*, THPL: *Thuja plicata*, TSHE: *Tsuga heterophylla*, TSME: *Tsuga mertensiana*