



# SHOULD I STAY OR SHOULD I GO? SURVIVING VARIABLE ENVIRONMENTS THROUGH DORMANCY AND DISPERSAL

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## ABSTRACT

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Seed dispersal and seed dormancy are considered survival traits for plants living in unfavourable conditions. The roles they play have been discussed for the last half century and many general models have been produced but due to their generalist nature, many of these models have been unable to explore the adaptive role of dispersal and dormancy in more complex environments. In this thesis, I aim to explore the roles of dispersal and dormancy in highly variable environments in four ways: (1) exploring adaptive site-specific dispersal, in habitats with sub-habitats that are have a similar average quality over time but differ in variability, using *Aethionema arabicum* as a model system, (2) discussing the long-distance dispersal and long-term dormancy strategy observed in many plant species, and how it is adaptive in environments with correlated variability with long periods of unfavourable sub-habitats, such as agricultural landscapes, (3) exploring dormancy and longevity as two evolutionary strategies that fulfil different purposes in variable environments, using empirical evidence collected from *Aethionema arabicum*, and (4) designing a model to describe the interaction between dormancy and dispersal of heteromorphic species in highly variable environments, using *Aethionema arabicum* as a model system. Understanding such strategies is key for generating impactful approaches to conservation and pest control, as well as understanding how species living in complex environments will be affected by environmental and land use changes.

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## INTRODUCTION

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### BACKGROUND

In highly variable environments, the conditions fluctuate daily, monthly or yearly. When the conditions in these environments become too poor for survival, many species are able to move away to find better conditions. Plants do not have this luxury, and those that germinate into such conditions often die before reproduction. They instead have additional strategies to “skip” bad years. While adult plants are unable to leave a poor environment, they are instead able to produce offspring that can, which is achieved by temporal (in time) or spatial (in space) dispersal. Temporal dispersal, which will here be referred to as dormancy, occurs when a seed postpones germination beyond a specified time period, under its “normal” conditions (Bewley, 1997). Germination can be defined as the uptake of water by imbibition, and then the expansion of the embryo (Finch-Savage & Leubner-Metzger, 2006). Spatial dispersal, which will here be referred to as dispersal, can be defined as the movement of an individual from its natal site to site of reproduction, or successive sites of reproduction (Matthysen, 2012).

There are three stages of dispersal: Emigration, which is the departure from the natal site, Transfer, during which the individual is vagrant, and Immigration, in which the individual settles in a site for reproduction (Clobert *et al.*, 2001, 2012). Active dispersal is defined by being, in some way, controlled by the organism (van Dyck & Baguette, 2005). On the other hand, passive dispersal is out of the control of the organism. In plants, dispersal is largely passive. This is because it is the seeds that disperse and they rely on the environment to move them to their reproductive site. However, not all plant dispersal is passive (Donohue, 1998;



Clarke, 2009). In some species, the parent plant has some control over the ratio of dispersing to non-dispersing offspring they produce (Lenser *et al.*, 2016; Nichols, Leubner-Metzger & Jansen, 2020). In this way, they have little control over where they will disperse to, but more control over the amount of dispersal performed by their offspring. Dispersal is adaptive for species surviving globally, while locally the species is at risk of becoming extinct. Therefore, dispersal can help to escape extinction, mitigate drift and reduce the mutation load of small populations (Ronce, 2007). The organism can be dispersed in many ways, including wind (anemochory), water (hydrochory or rafting), or by animals (zoochory) (Matthysen, 2012).

Dispersal is multicausal in nature. The causality can be investigated at individual level and environmental level (Matthysen, 2012), where dispersal mechanisms are driven by a combination of these factors (Lambin, 2001). The costs and benefits of dispersal differ between individuals, and so each has to have a different response, depending on the environmental cues available to them and their own individual cues. Individual causalities are based on variation in morphology, physiology or behavioural traits, all of which are largely genetically determined (Eriksson & Jakobsson, 1999). Environmental conditions and genetic variations have been shown to interact. For example, Sinervo demonstrated the interaction between the conditions the maternal organism experiences, and the resulting offspring genotype in lizard dispersal (Sinervo *et al.*, 2006).

Environmental causalities are complex and have a marked effect on dispersal. Dispersal is increased by many factors, including overcrowding, poor mate quality, kin selection, predation, shortage of resources, and deteriorating habitats (Bengtsson, 1978; Wolff, Lundy

& Baccus, 1988; Perrin & Mazalov, 1999; Ronce, 2007; Matthysen, 2012; Hidalgo, de Casas & Muñoz, 2016). One example of this in plants is the impact of environmental conditions on plant architecture (branching). Branching is a response to environmental conditions, which in turn influences the dispersing seed-type ratio. Fewer branches leads to fewer dispersing diaspores (Olivieri & Gouyon, 1997; de Casas *et al.*, 2015; Lenser *et al.*, 2016). Therefore, in plants, fitness is determined by parental characteristics, and so is under the control of the parentally determined diaspore and environmental factors.

Plants can produce seeds that germinate quickly and yield more seeds, or produce seeds that enter into a “seed bank” in which they will remain dormant (Cohen, 1966). While non-dormant seeds can germinate under a wide range of “normal” conditions, dormancy can be classified as when a seed does not have the capacity to germinate within a specified time period under its “normal” conditions (Bewley, 1997). Dormant seeds are sometimes confused with seeds undergoing longevity. Longevity occurs when a seed has active mechanisms to repair the damage of ageing. Where light induces germination in seeds undergoing longevity in the soil, light terminates dormancy in dormant seeds (Finch-Savage & Leubner-Metzger, 2006).

The widely accepted classification system for dormancy was first developed by Marianna G. Nikolaeva (Nikolaeva, 1969, 1977, 1999, 2004; Nikolaeva, Gladkova & Razumova, 1985), and later adapted by Baskin and Baskin (Baskin & Baskin, 1998, 2004). The hierarchical classification system is three-tiered and comprised of classes, then levels, and finally types. In total, there are 5 classes of dormancy. Physiological Dormancy (PD), Morphological Dormancy

(MD), Morphophysiological Dormancy (MPD), Physical Dormancy (PY) and Combinational Dormancy (PY+PD). Most angiosperms that undergo dormancy are categorised as PD of the non-deep level.

*Aethionema arabicum* is an annual brassica that lives on steep, stony slopes and in steppe environments, such as those found across the Anatolian mountainside (Bhattacharya *et al.*, 2019). They can be found growing from 0-3000 masl and use adaptive sensing and plasticity in their seed morph ratio to survive across highly variable environments (Nichols, Leubner-Metzger & Jansen, 2020). *Aethionema arabicum* is dimorphic and produces two fruit morphs, each containing a different seed morph (Lenser *et al.*, 2016). The larger fruits are called Dehiscent (DEH) and they contain two to six M+ seeds. The fruit dehisces while on the plant and the seeds disperse locally where they immediately germinate. M+ seeds are so named because of the mucilaginous layer they produce. Indehiscent fruits (IND) are comparatively small and contain one M- seed. The fruit abscises from the plant and is adapted for long-distance dispersal in two ways: with wings to aid with wind-dispersal and are buoyant to aid with water dispersal (Arshad *et al.*, 2019). Upon completing dispersal, M- seeds undergo dormancy within their IND fruit coat.

*Aethionema arabicum* has been shown to alter the ratio of its fruits plastically, in response to the temperature at which the parent plant is grown (Lenser *et al.*, 2016). In their natural environment, *Ae. arabicum* plants grow at different elevations and the temperature at the top of the elevation can be quite different to the elevation lower down (Bhattacharya *et al.*, 2019). The parent plants can therefore sense where along the elevation they have landed and

plastically alter their fruit morph ratio to produce more or less dispersing and dormant seed types. The initial idea for this thesis was to design a model to investigate this plastic dispersal behaviour and describe its adaptive properties. As I progressed, this idea flourished and three further models were designed to describe this response with the addition of dormancy in both annual and perennial species and finally in heteromorphic species such as *Ae. arabicum*.

## THESIS LAYOUT

When I first started working on this thesis, I began by investigating models designed to explain the evolution and function of dispersal and dormancy, both together and separately. For Chapter One, I start by exploring the key models featured in this thesis in a literature review and discuss how they work and what they show. I also provide a critical analysis of each, discuss their limitations, and present how the models presented in this project add novel insight into the evolution of dormancy and dispersal. Many of the models that investigated the adaptive function of seed dispersal were based on desert annuals. It was assumed that *Aethionema arabicum* behaved in a similar manner because the species had been described as a desert annual. However, after further investigation into the species I discovered that it grew on steep, steppe environments and so the conditions these plants face are considerably different to those found by desert annuals. Mountainous, steppe environments can be roughly divided into two sub-habitats, which I describe as sub-habitat 1 and sub-habitat 2. Sub-habitat 1 is at the top of the mountain, where the environment is dry, exposed and has limited access to nutrients and water. Sub-habitat 2 is at the bottom of the mountain, where the environment is more constant, but there is much greater crowding and competition.

Compared to a desert annual, that only has to compete in one fairly undesirable environment, *Ae. arabicum* must have evolved to survive in both of these sub-habitats.

This discovery was discussed in a paper that I was a contributing author of in 2019 (Appendix I; Arshad *et al.*, 2019). In the paper my hypothesis was that *Ae. arabicum* has site-specific dispersal rates in order to survive between the two sub-habitats. To further support the findings of the paper, I developed a model with my supervisor, Vincent Jansen. The model is described in Chapter Two and investigates an annual species in an environment with two sub-habitats. Seeds disperse between the sub-habitats simultaneously, mimicking the environment experienced by *Ae. arabicum*. This allowed us to get an insight into the effect of surviving between two poor quality sub-habitats, and how dispersing between them allows a species to survive in two sub-habitats in which they would otherwise go extinct. These insights from this chapter were published in Ecology Letters in 2020 (Nichols, Leubner-Metzger & Jansen, 2020). On completion of this model, there was a Cambrian Explosion of ideas for ways in which I could investigate the adaptive roles of dormancy and dispersal in complex environments, expanding on the findings from Chapter Two.

Interestingly, a comment from a reviewer of the Arshad paper inspired the creation of Chapter Three. The reviewer remarked that dispersal and dormancy have a negative relationship and that it was unusual that *Ae. arabicum* has a diascore type with both high dispersal and high dormancy. I did not find this unusual but rather I found it surprising that a positive relationship had not been investigated thus far. Therefore for Chapter Three, I decided to investigate possible reasons for why a high dispersal and high dormancy rate could

be found in some seed-types. It was an analysis of plants where high dormancy and high dispersal rates were found that led to the creation of a model. It was interesting to discover that many of them existed in similar sub-habitats, within managed landscapes or landscapes that rhythmically fluctuate in quality. This model was further adapted to investigate this behaviour in perennial species, as many of the species found to exhibit both high dormancy and high dispersal rates were perennials.

Having explored the relationship between dormancy and dispersal in Chapter Three, I found there was a gap of knowledge in terms of dispersal and dormancy in heteromorphic species such as *Ae. arabicum*. Chapter Two addressed the dispersal mechanism of *Ae. arabicum* using life history data, however, little was known about the dormancy effect of the dispersing IND fruit. Therefore, for Chapter Four, I undertook artificial ageing experiments to investigate the resilience of IND fruits, and M+ and M- seeds, and how dormancy interacts with diaspore resilience. Using the information gathered from these experiments, a final model was designed for Chapter Five, to look at the life history of *Ae. arabicum* in its entirety. This model brings together the models designed in Chapters Two and Three, and represents a heteromorphic species that can undergo site-specific and diaspore-type dormancy and dispersal rates across two sub-habitats. This model was then used to investigate the adaptations of longevity and dormancy discovered from Chapter Four and their roles in aiding the survival of *Aethionema arabicum* in its natural habitat.

This thesis was completed in three years with three months out for a mandatory Professional Internship for PhD Students (PIPS). The final write-up was carried out during the COVID-19

pandemic between March and August 2020, without access to university and with reduced interactions with supervisors.

## CHAPTER ONE: LITERATURE REVIEW

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### INTRODUCTION

Several models describing dormancy and dispersal have been designed over the last half century. Such models generally describe the evolution of these two traits either independently or together, within an environment or environments, with low levels of environment variability. Here, I will review the dormancy, dispersal, and dormancy and dispersal models that feature in this thesis. Many reviews exist for dormancy (Bewley, 1997; Baskin & Baskin, 1998, 2004; Koornneef, Bentsink & Hilhorst, 2002; Finch-Savage & Leubner-Metzger, 2006), dispersal (Willson & Traveset, 2000; Clobert *et al.*, 2001, 2012; Levin *et al.*, 2003; Ronce, 2007; Matthysen, 2012), and for the relationship between dormancy and dispersal (Buoro & Carlson, 2014; de Casas *et al.*, 2015), all of which provide a thorough background into their associated research.

I will also discuss the limitations surrounding each and present the novelty of the models consequently developed in this thesis. Results from these models generally predict a small window in which dormancy or dispersal will evolve. For models that investigate the relationship between the two traits, a trade-off is predicted. This is because they both assist an individual in avoiding years of poor conditions. Of these models, most are based on the bet-hedging strategy. The definition of 'bet-hedging' is different across fields and in 1987 there were five definitions in common use. Seger and Brockmann (1987) reviewed these and summarised bet-hedging as "adaptive coin-flipping". Individuals are able to sacrifice their immediate fitness so that the probability of their fitness long-term is increased. When this sacrifice is made, a trade-off between mean and variance of a measured variable occurs, such



as population growth rate or Darwinian fitness (Cooper & Kaplan, 1982). Fitness in this sense is measured as a geometric mean of reproductive output, which is the fitness used for many bet-hedging models (Venable, 2007).

## DORMANCY MODELS

Seed banks are useful in case of an unfavourable year, as seeds that immediately germinate may do so during an unfavourable year and therefore fail to survive before yielding more seeds (Venable & Pake, 1999). Having a seed bank means seeds will germinate over a number of years, and so the probability that no offspring will survive before reproduction is reduced. Dormancy can therefore be described as an example of bet-hedging, as it is adaptive if it increases the geometric mean fitness (Clausen & Venable, 2000). Models investigating dormancy have largely focused on desert annuals. The first model designed to describe seed dormancy in randomly varying environments was by Cohen (1966). In this model, the optimal germination fraction was derived from the yield of seeds per germinating seeds and the viability of seeds. To simulate environmental variability, a fraction of years were “good” where fecundity is high and the rest are “bad” where fecundity is low. From this, and with later alterations to the model by MacArthur (1972), it was shown that the fraction of good years is approximately equal to the germination rate. This remains true, even when mortality of dormant seeds is high. This was attributed to bet-hedging. Instead of germinating 100% of the seeds when mortality of the seed bank is high, maintaining a small number of seeds in the seed bank allows the population to avoid subsequent bad years.

Bulmer (1984) adapted the model. Bulmer first adapted the model to include density-dependency by using the Lottery Model by Chesson and Warner, in which they assume that there is always a sufficient proportion of dispersing offspring to fill available spaces within an environment (Bulmer, 1984; Chesson, 1984; Warner & Chesson, 1985). As with the previous model by Cohen, germination rate is approximately equal to the fraction of good years. As the models had been working on an “all-or-nothing” basis, where fecundity in good and bad years is either high or low. Bulmer then altered the model to include continuous environmental variability, in which fecundity is the average number of seeds produced by a surviving plant in any given year. With this addition, it was once again concluded that dormancy rate is dependent on the fraction of good years. The model was re-summarised by Leon (1985) and showed germination rate is high when fecundity is high and that dormancy evolves when yields are substantially affected by the environment.

Bet-hedging models of this nature largely assume that the fraction of seeds entering the seed bank is fixed. More recent research has demonstrated that plant species are able to alter the number of seeds entering the seedbank, dependent on environmental cues (Lenser *et al.*, 2016). *Aethionema arabicum* alters the proportion of dormant and non-dormant seeds depending on temperature cues from the environment. *Aethionema arabicum* is an example of a heteromorphic species, because it produces “seeds of different form or behaviour” (Venable, 1985). Seed heteromorphism is associated with bet-hedging strategies, as the production of a seed-type capable of avoiding temporal or spatial variance increases long-term success (Harper, 1977). In 1985, Venable produced a model to describe the life history of a heteromorphic, annual plant. In this model, fitness is determined by the survival of its

two seed-types which are better adapted to different environments. It is assumed that one seed-type is adapted for one year type and the other seed-type is adapted for the other year type. In order to evolve heteromorphism, each of the two seed-types should outperform the other in one of the year types and underperform them in the other.

Venable's model assumes that seeds are better adapted for one year type or the other. In the case of species such as *Aethionema arabicum*, the environment is unpredictable, and so growing seeds of one type or the other to suit the year-type would be inefficient. Instead, species are able to sense their location through environmental clues, such as temperature, and alter the ratio of the two morphs plastically in response (Lenser *et al.*, 2016; Nichols, Leubner-Metzger & Jansen, 2020). In this way, seeds aren't adapted to one year type, but rather have a function within the sub-habitat. The adaptive significance of sensing in plasticity becomes clear when the environmental variability is high and differs between multiple sub-habitats (Nichols, Leubner-Metzger & Jansen, 2020). Because of the generality of the models presented here, they are unable to investigate such environmental conditions. Dormancy is also often confused with longevity, a process by which seeds actively repair the damage of ageing. One key difference in the two is that light induces germination in seeds that are persisting in the soil with longevity, where light terminates dormancy in dormant seeds (Finch-Savage & Leubner-Metzger, 2006). None of the models presented have considered the difference between longevity and dormancy or investigated the relationship between the two traits.

## DISPERSAL MODELS

In environments with spatial variability, dispersal enables an individual to spread the chance of successful germination across a landscape, colonise new sub-habitats and reduce competition (Cohen & Levin, 1991). Dispersal can be described as an example of bet-hedging, as it is adaptive if it increases the geometric mean fitness (Krug, 2001). Fretwell and Lucas proposed the Ideal Free Distribution (IFD) theory, which predicts that if a population exists in an environment with multiple, different sub-habitats, the population will spread across the environment so that mean individual fitness is equalised and the local population sizes will differ (Fretwell & Lucas, 1970; Fretwell, 1972). A study by Cressman *et al.* went on to demonstrate that this IFD theory is an evolutionary stable strategy (ESS) and is stable under single species systems but can become unstable with the introduction of a second species (Cressman, Křivan & Garay, 2004). This model was built to describe the dispersal of birds foraging, and so individuals are assumed to be able to sense the environment into which they disperse. In the case of seed dispersal, it has to be assumed that the seed cannot make an informed choice about the sub-habitat that it will land in. The model also doesn't account for individuals dispersing out of sub-habitats simultaneously, but rather into or out of single sub-habitats.

Hasting (1983) developed a model to investigate the impact of populations existing within sub-habitats with constant temporal conditions, with differing spatial quality. Under these conditions, a non-dispersal strategy is optimal. This is due to the fact that dispersing out of the natal sub-habitat will mean encountering sub-habitats of lower quality more often than sub-habitats of higher quality. Therefore, the risk does not outweigh the reward. Two-patch

dispersal models were developed by Holt (1984), which were used to investigate a population dispersing passively between two sub-habitats. The first model is used to describe an environment with a single population, dispersing between two density-dependent sub-habitats. The second is used to describe an environment with a source sub-habitat and a sink sub-habitat. The models are used to demonstrate that dispersal reduces population fitness when environments are spatially different but temporally the same. These models demonstrate that not only is it crucial for the environment to be heterogenous spatially, but also that in environments with temporal homogeneity, dispersal will not evolve.

McPeck and Holt (1992) later went on to develop a model to show that if the environmental conditions in sub-habitats fluctuate and their quality is overall statistically different, it is possible that dispersal rates are specific to each sub-habitat. This raises the question, what strategies could evolve if the sub-habitats are of similar spatial quality, but differ in variability temporally? In environments where the population could go extinct if it was to remain within one of these sub-habitats, a population can survive by balancing between multiple sink sub-habitats (Jansen & Yoshimura, 1998; Nichols, Leubner-Metzger & Jansen, 2020). Distributing offspring across such sub-habitats can increase fitness and allows population survival in environments where they could not without dispersal.

## DISPERSAL AND DORMANCY MODELS

Dispersal and dormancy are both methods of travel, either through space or time. The relationship between dispersal and dormancy in seeds has been described through many

models. Results from models described in this review largely point to a negative relationship or trade-off between dormancy and dispersal. However, species producing seeds with both dispersal and dormancy capabilities are commonly cited in the literature (Den Boer, 1968). The relationship between dormancy and dispersal of annual plants was investigated by Venable and Lawlor (1980). The results from this model suggest that a range of dormancy strategies can be achieved with different dispersal rates and a trade-off between dormancy and dispersal occurs under temporal uncertainty. The model is built on the assumption that the surrounding sub-habitats are uncorrelated in space. Venable and Brown (1988) further discuss the function of seed size, dispersal and dormancy as traits to reduce risk and escape competition. Results from this model suggest selective trade-offs between the three traits and any environment favourability for one of the traits will lead to a reduction in the other two.

Cohen and Levin investigated the selection for dispersal and dormancy in environments with multiple sub-habitats and developed several models to describe them (Levin et al, 1984; Cohen and Levin, 1987). Overall, results from these models suggested that an increase in either dormancy or dispersal would decrease the other. These results were based on environmental homogeneity. In 1991, Cohen and Levin investigated dispersal between sub-habitats that had the same temporal correlation but had spatial heterogeneity. Again, under these conditions dormancy and dispersal showed negative correlation. Increased temporal correlation also decreased the dispersal and dormancy rates of the populations. This model was more recently revisited by Siewert and Tielbörger (2010). They performed an experimental study to test the negative-relationship model predictions and found no convincing evidence

for a negative relationship, but that dormancy and dispersal are different risk-reducing strategies. The results also suggest there is little evidence for bet-hedging through dormancy. Results from this study were further supported by Buoro and Carlson in their 2014 review of dispersal and dormancy models. They noted the discrepancies between theoretical and empirical evidence, with theoretical evidence pointing towards a negative relationship, but experimental evidence only weakly supporting this.

In 2013, Vitalis *et al.* investigated the joint evolution of dispersal and dormancy by designing a metapopulation model with a particular look at the impact of kin competition. Their model predicts that both dormancy and dispersal evolve when population sizes are low and extinction rates are low. They suggest that because the cost of dormancy is lower than the cost of dispersal, dormancy becomes the preferred escape from crowding in larger populations. They further predict that if the cost of dispersal and dormancy differs between environments then a negative correlation between dispersal and dormancy will emerge, so that only non-dispersing seeds should undergo dormancy. This model is built on the assumption that environmental variability is uncorrelated in time and space. However, it has been suggested that correlations in space and time can lead to a positive covariation between dormancy and dispersal (Cohen & Levin, 1987; Venable & Brown, 1988; Cohen & Levin, 1991).

## MODELS IN THIS THESIS

Models designed in this thesis are based on the Cohen model (1966). In this way, they investigate environmental variability by altering the order and number of “good” and “bad” years. Good years are defined by years of high fecundity or a large number of offspring, and

bad years are defined by low fecundity or few to no offspring. The severity of good and bad years can also be manipulated in these models by increasing or decreasing the fecundity. The models are made up of sub-habitats 1 and 2, and are able to track dispersal out of and into both sub-habitats simultaneously. The model tracks the number of individuals that will be in each sub-habitat in the following generation. Because these models are largely used to investigate plant populations, dispersal and dormancy are not cognitive decisions, but can be informed by environmental clues. Model simulations were run in R 3.5.0 (R Core Team, 2018), using packages cowplot (Wilke, 2019) and reshape2 (Wickham, 2007) Simulations were run for 1000 iterations, and the fitness ( $Q$ ) of the two sub-habitats was calculated at the end:

$$Q = \frac{\Delta N_x}{\Delta t_x}. \quad (1)$$

Fitness was determined by the average growth rate of the population which was calculated by the change in population size ( $\Delta N_x$ ) divided by the run time ( $\Delta t_x$ ). The log of the average growth rate ( $\log(Q)$ ) was then calculated.  $\log(Q)$  was then compared with changes in different variables, dependent on the purpose of the model in each chapter, and the relationship between the changing variable and fitness was investigated.

## CONCLUSION

Reviewing both independent and relational dispersal and dormancy models demonstrated some areas in which they could be further developed. Dispersal models reviewed here have largely focused on a population dispersing into or out of a single habitat surrounded by a



number of sub-habitats. They have not investigated the effect of seeds moving from multiple sub-habitats simultaneously. Further to this, the environments tend to contain a favourable sub-habitat. In Chapter Two, I present a model that investigates simultaneous dispersal from two sub-habitats of similar poor quality, but with differing environmental variability. Dormancy and longevity have been used interchangeably in the literature until recently. In Chapter Five, I present a model that investigates the relationship of the two traits in a heteromorphic species and present experimental evidence in Chapter Four to support the model. Models designed to investigate the relationship between dormancy and dispersal have not considered environments with sub-habitats that are correlated in time and space, with either the same or different patterns of correlation. They have also not considered perennial species exhibiting high-dormancy high-dispersal traits. In Chapter Three, I present a model that investigates the relationship between dispersal and dormancy in annual and perennial species surviving in highly correlated, managed landscapes.

## CHAPTER TWO: BETWEEN A ROCK AND A HARD PLACE

### ADAPTIVE SENSING AND SITE-SPECIFIC DISPERSAL

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Bethany S. Nichols, Gerhard Leubner-Metzger & Vincent A. A. Jansen

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#### ABSTRACT

*Environmental variability can lead to dispersal: why stay put if it is better elsewhere? Without clues about local conditions, the optimal strategy is often to disperse a set fraction of offspring. Many habitats contain environmentally differing sub-habitats. Is it adaptive for individuals to sense in which sub-habitat they find themselves, using environmental clues, and respond plastically by altering the dispersal rates? This appears to be done by some plants which produce dimorphic seeds with differential dispersal properties in response to ambient temperature. Here we develop a mathematical model to show, that in highly variable environments, not only does sensing promote plasticity of dispersal morph ratio, individuals who can sense their sub-habitat and respond in this way have an adaptive advantage over those who cannot. With a rise in environmental variability due to climate change, our understanding of how natural populations persist and respond to changes has become crucially important.*

## INTRODUCTION

Environmental conditions are ever-changing, temporally and spatially. Trying to survive amid a change in conditions within a local habitat requires species to adapt and develop specialised mechanisms. In many cases, however, the changes are to such an extent that it is better to leave, be it for one or more generations, or altogether. In these cases, many species have adapted to disperse. Dispersal can be defined as the movement of an individual from site of birth to site of reproduction. If better sites can be reached via dispersal, this drives evolution as organisms escape unfavourable conditions (Matthysen, 2012). Dispersal can be divided into three phases: emigration, inter-patch movement and immigration. During emigration, the individual can obtain clues from both biotic and abiotic factors in the local sub-habitat. Using these clues, the individual can then either disperse or not. If they do, they enter the transfer phase or movement through the habitat, where many species require clues from the environment in order to choose a new location to settle in (Clobert *et al.*, 2001, 2012). The successful settlement into a new sub-habitat is the immigrant phase. Many species disperse passively, and so are unable to make informed choices about the final sub-habitat in which they find themselves.

Dispersal and emigration can reduce the likelihood of competition with kin, and mitigate against drift and inbreeding (Bengtsson, 1978; Wolff, Lundy & Baccus, 1988; Perrin & Mazalov, 1999; Ronce, 2007; Hidalgo, de Casas & Muñoz, 2016). However, environmental variability is arguably the most important driver for dispersal evolution (Poethke & Hovestadt, 2002). Many species have offspring that either can or cannot disperse. Experimental research has demonstrated that the ratio of dispersing to non-dispersing offspring changes in response

to the environment. For example, Sinervo et al. demonstrated that maternal environmental conditions affected the offspring dispersal ratio in lizards (Sinervo *et al.*, 2006). Dispersal plasticity is taxonomically widespread and similar results are seen in animals, insects and plants (Harrison, 1980; Fox & Mousseau, 1998; Dingle, 2006; King & Roff, 2010; Steiner *et al.*, 2012; Arendt, 2015; Duckworth, Belloni & Anderson, 2015). The ability to alter offspring dispersal ratio is a selective advantage when persisting in highly variable environments (Arendt, 2015).

Within a habitat, there are often several sub-habitats. These sub-habitats can differ in biotic and abiotic factors. Environmental variability is determined by how much and how frequently these factors fluctuate. When environmental conditions within sub-habitats are constant, but the sub-habitats differ in quality, a non-dispersal strategy is optimal. This is because offspring dispersing from the native sub-habitat will encounter lower quality sub-habitats more often than higher quality sub-habitats (Hastings, 1983). However, in bet-hedging scenarios, if the environment fluctuates, with sites of differing quality across time, but statistically the same overall quality, then producing some dispersing offspring is optimal (Harper, 1977; Den Boer, 1981; Venable & Brown, 1993; Baskin & Baskin, 1998; Starrfelt & Kokko, 2012). If the environmental conditions in sub-habitats fluctuate and their quality is overall statistically different, it is possible that dispersal rates are sub-habitat specific (McPeck & Holt, 1992). But when sub-habitats are of more or less equal quality, yet differ in variability, what dispersal strategies will evolve? Will dispersal be adaptive, and if so, will the dispersal rates be habitat specific (Seale & Nakayama, 2019)?

In mountainous habitats, the sub-habitat at the top of the mountain can be considerably different from the sub-habitat at the bottom of the mountain. If neither sub-habitat is of substantially higher quality, and environmental variability is different within each, is sensing and site-specific dispersal adaptive? Here, we use the term “site-specific dispersal” to describe altering the ratio of dispersing to non-dispersing offspring produced by an individual, in response to the environment that they experience during their lifetime. An example of such site-specific dispersal is given by the plant *Aethionema arabicum*. *Aethionema arabicum* is an annual which grows along the steep stony slopes of the Anatolian Mountains, at a range of 0-3000 meters above sea level (Bhattacharya *et al.*, 2019). *Aethionema arabicum* exhibits fruit and seed dispersal dimorphism and is able to undergo site-specific dispersal between sub-habitats of similar quality but different variability by sensing its location through temperature (Figure 1) (Lenser *et al.*, 2016; Mohammadin *et al.*, 2017; Arshad *et al.*, 2019; Seale & Nakayama, 2019).

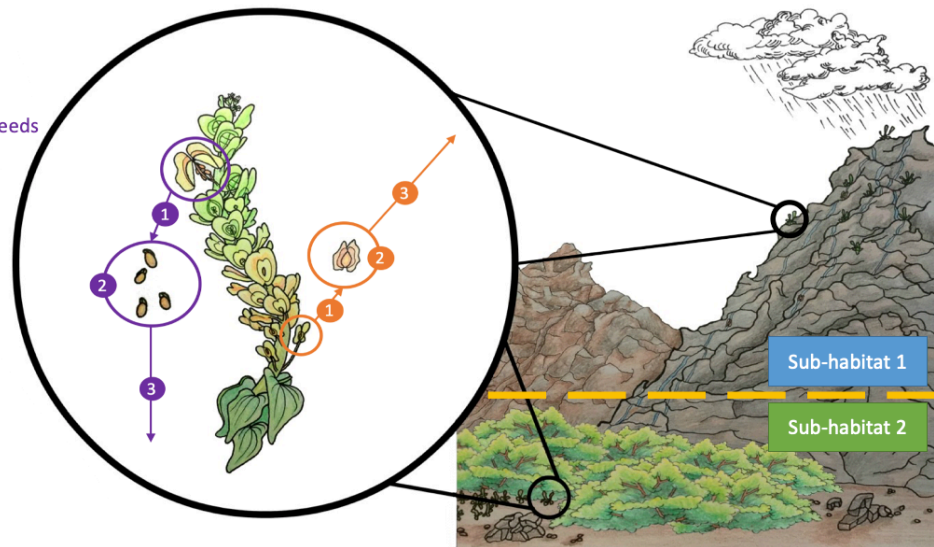
Mountainous habitats, including the Anatolian Mountains, can be roughly divided into two sub-habitats: high elevation, and low elevation (Velchev, 1984; Mohammadin *et al.*, 2017). Neither sub-habitat is favourable, neither are optimal. The higher elevation is dry, exposed, and rocky, making the abiotic conditions unfavourable, however, there is little to no competition. At low elevation, the environment is overcrowded, shaded and highly competitive, providing many biotic stresses. However, there is a constant supply of water and nutrients (Atalay, 2006). One sub-habitat is environmentally variable in terms of abiotic stresses but with few competition stresses, while the other is environmentally constant but much more over-crowded, making them of both low quality and differing in variability.

**Dehiscent fruits:**

- Larger fruit
- Contains 2-6 seeds
- 1 Fruit dehisces
- 2 Diaspore: mucilaginous seeds
- 3 Local dispersal

**Indehiscent fruits:**

- Smaller fruit
- Contains 1 seed
- 1 Fruit abscises
- 2 Diaspore: seed in fruit
- 3 Long-distance dispersal



**Figure 1: *Aethionema arabicum* sub-habitats and dimorphic dispersal strategy (not to scale).** *Aethionema arabicum* is a dimorphic plant species that grows along steep stony slopes in the Anatolian Mountains and produces a ratio of dispersing and non-dispersing offspring, dependent on the ambient temperature of the native sub-habitat (Lenser et al., 2016).

Distributing offspring across sub-habitats can increase fitness and allows population survival in environments where they could not without dispersal (Jansen & Yoshimura, 1998). If an organism can sense which sub-habitat it resides in, is it adaptive to have dispersal strategies that are contingent on the sub-habitat? Here we show theoretically how individuals altering their dispersal ratio in response to localised environmental variability could be aided through sensing. We develop a theoretical approach for sub-habitats that differ in their environmental variability. We show that site-specific dispersal ratios, aided by sensing, are adaptive in response to differences between sub-habitats, and therefore there is selection for traits that possess this ability.

## MATERIAL AND METHODS

The model (2) is comprised of four variables: number of plants in a site ( $N_x$ ), fecundity ( $S_x$ ) determined by how many offspring are produced by an individual, dispersal rate ( $d_x$ ), and death rate ( $\mu$ ). The number of individuals in a site in the following year ( $N'_x$ ) is determined by the number of offspring that do not disperse ( $((1 - d_x(1 - c))S_x N_x)$ ) plus the number of offspring that survive dispersal from the other site ( $((1 - \mu)d_x(1 - c)S_x N_x)$ ). The individuals are presumed to be annuals, and therefore do not survive into the following year. A proportion of offspring that disperse fail to do so and remain in the native sub-habitat. This percentage is denoted by  $c$ .

$$N'_1 = (1 - d_1(1 - c))S_1 N_1 + (1 - \mu)d_2(1 - c)S_2 N_2 \tag{2}$$

$$N'_2 = (1 - \mu)d_1(1 - c)S_1 N_1 + (1 - d_2(1 - c))S_2 N_2$$

The model was then arranged to form a vector-matrix multiplication (3 and 4). Sub-habitat 2, is a constant environment so only experiences good years. Sub-habitat 1 fluctuates in environmental condition and the frequency of which it experiences a bad year is  $\frac{1}{f}$ . The proportion of  $S_1$  that survive, or the severity of the year, is  $v$ . In good years (3), the fecundity is increased by  $\frac{v}{f}$  and in bad years (4), the fecundity is decreased by  $(1 - \frac{1}{f})v$ .

Good Year:

$$N' = \begin{bmatrix} (1 - d_1(1 - c)) \left( S_1 + \frac{v}{f} \right) & (1 - \mu) d_2 S_2 (1 - c) \\ (1 - \mu) d_1 \left( S_1 + \frac{v}{f} \right) (1 - c) & (1 - d_2(1 - c)) S_2 \end{bmatrix} N \quad (3)$$

Bad Year:

$$N' = \begin{bmatrix} (1 - d_1(1 - c)) \left( S_1 - \left( 1 - \frac{1}{f} \right) v \right) & (1 - \mu) d_2 S_2 (1 - c) \\ (1 - \mu) d_1 \left( S_1 - \left( 1 - \frac{1}{f} \right) v \right) (1 - c) & (1 - d_2(1 - c)) S_2 \end{bmatrix} N \quad (4)$$

This model contains two variables for dispersal,  $d_1$  and  $d_2$ . This is to allow for the dispersal rates between the two sub-habitats to be altered independently. The model was run for 1000 iterations in R, and the fitness ( $Q$ ) of the two sub-habitats was calculated at the end (5). Fitness was determined by the average growth rate of the population which was calculated by the change in population size divided by the number of simulations run.

$$Q = \frac{\Delta N_x}{\Delta t_x} \quad (5)$$

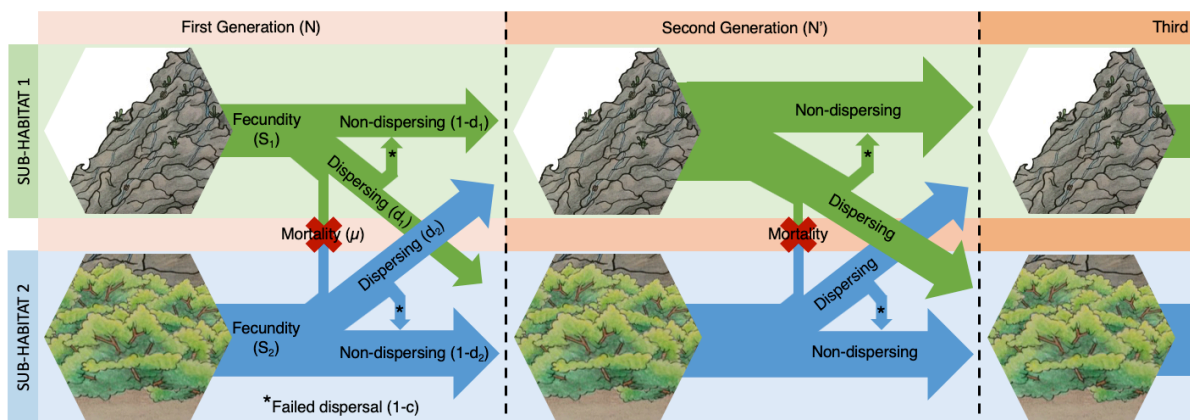
The log of the average growth rate ( $\log Q$ ) was then calculated. ( $\log Q$ ) was then compared at different dispersal rates ( $d_1$  and  $d_2$ ), and the relationship between the two investigated. For a detailed description of the model see the supplementary material from Nichols, Leubner-Metzger and Jansen (Supplementary Material; 2020)



## RESULTS

### *The model*

Dispersal models have been used to describe the implications of dispersal on the fitness of species that persist within a single habitat (Cohen, 1966, 1967; Fretwell & Lucas, 1970; Bulmer, 1984; Cohen & Levin, 1991), and dispersal ratios have been fixed (Hastings, 1983). Although, in some of these models, multiple sub-habitats are considered through the dispersal into or out of the stated sub-habitat, the models are not equipped to investigate the impact of dispersing into and out of multiple sub-habitats at once.



**Figure 2: Mathematical model of dispersal across two sub-habitats of differing environmental variability.** The model is divided into two sub-habitats: 1 and 2. Each sub-habitat has a starting population of either the same or different sizes. The arrows branch-off to demonstrate the fate of the offspring: a proportion will not disperse, and the rest will. Of those that disperse, some will fail to disperse, and some will die before reaching the other sub-habitat. The width of the arrows is representative of the proportion of seeds performing each action. In each generation, sub-habitat 2 remains constant in the number of offspring

produced and therefore, the dispersing to non-dispersing ratio is constant. Sub-habitat 1, on the other hand, experiences environmental variability.

Here, we constructed a matrix model to describe dispersal in two sub-habitats: 1 and 2 (Figure 2). The model gives the number of individuals that will be in each sub-habitat in the following generation. The model describes an annual plant, and so there will be no overlapping generations, and that dispersal is not a cognitive decision, but it can be informed by environmental clues. The number of offspring/fecundity of each plant can be the same or different in each sub-habitat. There are two variables for dispersal, one for each habitat. This allows for the rate at which the offspring disperse from either sub-habitat to be altered (Figure 2). The diagrammatic model in Figure 2 is representative of the matrix model (3, 4) used in this paper.

The model is divided into sub-habitats 1 and 2, each starting with a population of size  $N_x$ . The arrows branch-off to demonstrate the fate of the offspring ( $S_1$ ): a proportion will not disperse ( $1-d_x$ ), and the rest will ( $d_x$ ). Of those that disperse, some will fail to disperse and remain in the native sub-habitat ( $1-c$ ), where they will attempt to leave the native sub-habitat but remain in the native sub-habitat, and some will die before reaching the other sub-habitat ( $\mu$ ). In each generation, sub-habitat 2 remains constant in the number of offspring produced and therefore, the dispersing to non-dispersing ratio is constant. Sub-habitat 1, on the other hand, experiences environmental variability, with a severity ( $v$ ), which fluctuates the number of offspring produced (fecundity) depending on whether the environment is good or bad in that year, and the frequency in which there are bad years ( $\frac{1}{f}$ ), and so the number of offspring differ

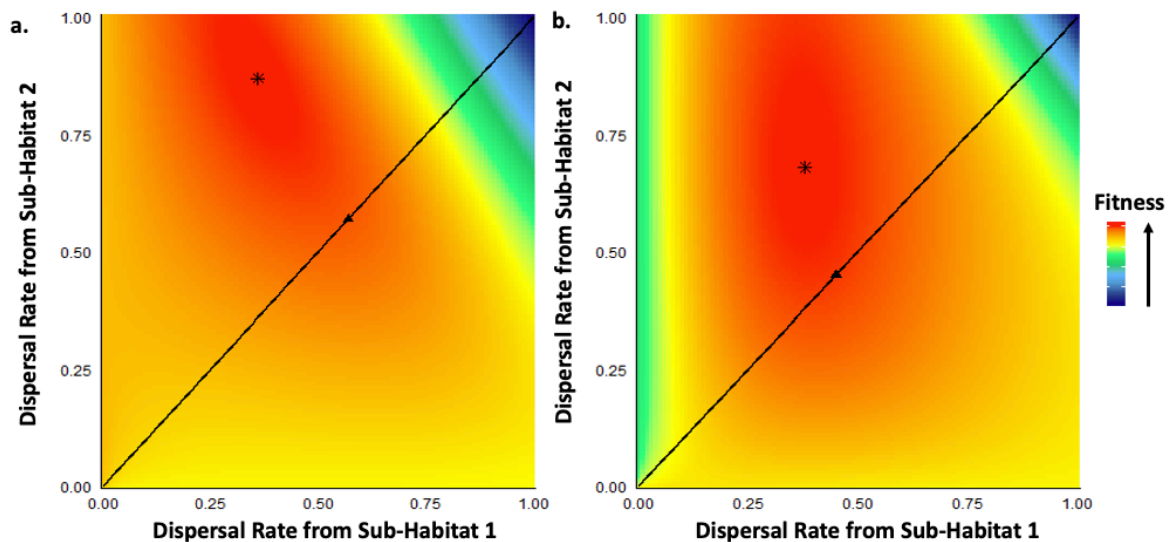
year-on-year. The matrix demonstrated above is for good years. In bad years, the fecundity is  $\left(S_1 - \left(1 - \frac{1}{f}\right)v\right)$ . This is represented by the width of the arrows. The pattern of variability is changed for each simulation. The fitness of the population was measured as the long-term average population growth rate.

We assume that sub-habitat 2 has a constant, homogenous environment. Sub-habitat 1 experiences a range of differently variable environments. We define environmental variability by 2 variables: frequency and severity of “bad years”. Productive years, when fecundity is high, are noted as “good years”. Frequency is measured by the number of good years between bad years. In a bad year, only a percentage of the offspring produced in a good year will survive. This percentage is determined by the severity variable.

### *Sensing and site-specific dispersal rates*

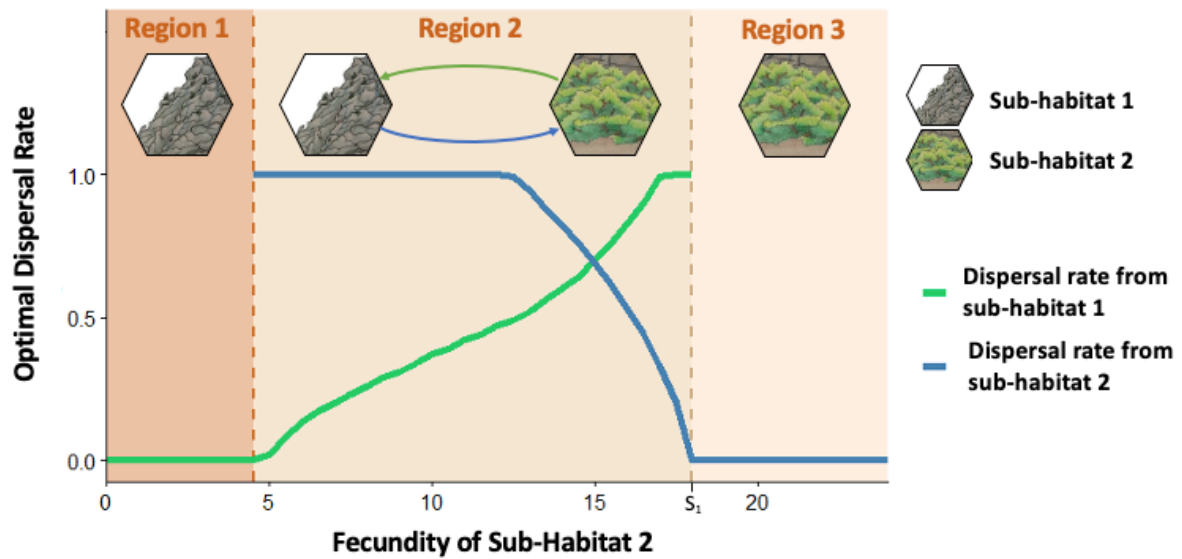
When the environment fluctuates within a sub-habitat, and environmental variability is sufficiently high, the optimal dispersal strategy is to produce a proportion of dispersing and non-dispersing seeds (Figure 3). If individuals do not have clues about which habitat they are in, then the only way to do this is disperse from all habitats at the same rate (combinations of dispersal rates that are the same in both sub-habitats sit on the diagonal in Figures 3a and b). However, when such clues are available and individuals can get a sense as to where they are, they adjust the dispersal rate to each habitat. The optimal dispersal strategy in both examples is then away from the diagonal, providing selection for site-specific dispersal rates, and, in this way, there is selection for sensing and adapting the dispersal rate to the native

habitat. Which dispersal rates are selected for depends on the details, such as changes in frequency of environmental variability. Here we show the difference when there is a change in the frequency of the good years.



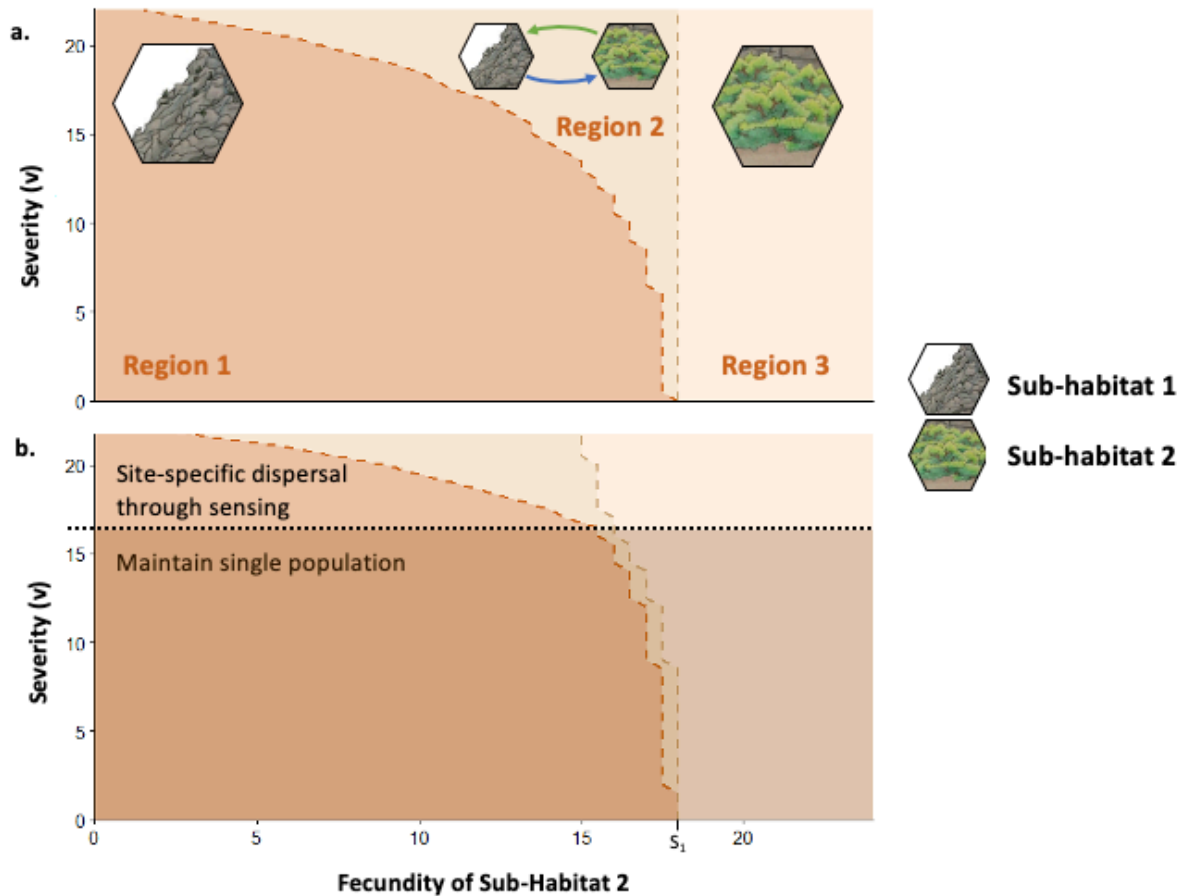
**Figure 3: Optimising dispersal strategy with changing frequency of bad years.** Figures 3a and 3b differ in frequency of bad years. 3a has a frequency of  $\frac{1}{3}$  and 3b has a frequency of  $\frac{1}{5}$ . The heat maps demonstrate the fitness (growth rate) of the population at different dispersal ratios. \* indicates the optimal dispersal ratio to maximise fitness. It is mostly assumed in dispersal models that sub-habitats have used the same dispersal rate for all habitats, and so this is indicated by the black line where the dispersal rate from sub-habitat 1 is equal to the dispersal rate from sub-habitat 2. ▲ indicates the optimal dispersal ratio along this line. In both, there is additional fitness when you move away from the black line and have a dispersal rate dependent on the sub-habitat and the frequency of variability. Variables used to generate graphs:  $v = 20$ ,  $S_1 = 18$ ,  $S_2 = 14$ ,  $f$  in 3a = 3,  $f$  in 3b = 5.

By how much the two sub-habitats differ in fecundity is critical for contingent dispersal strategies to evolve. Consider two sub-habitats. In sub-habitat 1, the environment is highly variable, with fecundity being high in intermittently good years, and low in bad years. Sub-habitat 2 has a constant environment. In Figure 4, the fecundity in sub-habitat 2 is put on a sliding scale. If the average in sub-habitat 2 is higher than that of sub-habitat 1, then the dispersal rate from sub-habitat 2 will be 0 and sub-habitat 1 will be left empty. The optimal dispersal rate from sub-habitat 1 can then take any value (Figure 4, region 3, Supplementary Material; Nichols, Leubner-Metzger and Jansen, 2020). If the average fecundity in sub-habitat 1 is much higher than sub-habitat 2 the reverse happens and the dispersal rate from sub-habitat 1 is zero and sub-habitat 2 is left empty. When, however, fecundity in the sub-habitats are roughly the same, the optimum strategy is to have contingent dispersal rates so that the offspring is distributed over the two sub-habitats: one with high variability and is very productive in good years, and one with low variability but is lowly productive, causing both to be of similar fitness. There is no obvious best location, and in some years one sub-habitat will be better, in other years the other. In environments such as this, site-specific, non-zero dispersal rates will evolve. In order to demonstrate this, we completed a sensitivity analysis which modulated the model parameters. Figure 5 shows the result of modulating the parameter  $\mu$ . Further results can be found in the supplementary material of Nichols, Leubner-Metzger and Jansen (Supplementary Material; 2020).



**Figure 4: Optimising dispersal strategy for changes in fecundity.** The optimal dispersal rate from sub-habitats 1 and 2 is dependent on the relationship between the average fecundity of sub-habitats 1 and 2. The regions represent areas of the graph where one or both sub-habitat is favourable and so in region 2, where both are favourable, dispersal between the two sub-habitats is likely to occur. In the other regions, the populations will be maintained in one sub-habitat and will go extinct in the other. At low average fecundities of sub-habitat 2, the optimal sub-habitat is sub-habitat 1 and so dispersal will favour remaining in sub-habitat 1. The converse is true at high average fecundities of sub-habitat 2. When the average fecundities of sub-habitats 1 and 2 are about equal, mixed dispersal ratios are seen. Under these conditions, there is additional fitness in sensing the environment in which the individual has grown and producing site-specific dispersal ratios in response. Variables used:  $v = 21, S_1 = 18, S_2 = 0 - 23, f = 5, \mu = 0, c = 0$ .

When the severity ( $v$ ) of the fluctuations in sub-habitat 1 is low, the region in which sensing is adaptive is small, however, as  $v$  increases, the region widens (Figure 5a). By plotting the width of region 2 from Figure 4 with an increase of  $v$ , the effect of the severity of fluctuations in sub-habitat 1 can be seen. With an increase in  $v$  comes an increase in the width of region 2. The more severe the fluctuations, the bigger the scope for site-specific dispersal rates. In this way, as the fluctuations become more severe, there is a greater potential for site-specific dispersal rates to evolve. When the fluctuations are small, the effect is negligible. This is more apparent with an increase in dispersal mortality (Figure 5b). At low severity, there is no scope for site-specific dispersal. With high severity, site-specific dispersal creates additional fitness and in order to produce site-specific rates, a mechanism for sensing will evolve. This demonstrates the importance of severity as a driver for the evolution of sensing and site-specific dispersal.



**Figure 5: Evolution of sensing and site-specific dispersal with increasingly severe environmental variability.** The regions represent areas of the graph where one or both sub-habitat is favourable and so in region 2, where both are favourable, dispersal between the two sub-habitats is likely to occur. In the other regions, the populations will be maintained in one sub-habitat and will go extinct in the other. By mapping the size of the regions in Figure 4 with a change in severity ( $v$ ), it is apparent that with an increase in  $v$ , there is greater potential for site-specific dispersal to evolve. With an increase in dispersal associated mortality rate ( $\mu$ ) (Figure 5b), the potential for site-specific dispersal to evolve is limited to high values of  $v$ , demonstrating the importance of  $v$  as a driver for this effect. Variables used:  $v = 0 - 23$ ,  $S_1 = 18$ ,  $S_2 = 0 - 23$ ,  $f = 5$ ,  $c = 0$ ,  $\mu$  in 5a = 0,  $\mu$  in 5b = 0.1.



## DISCUSSION

MacArthur asks, “Why would any individual ever migrate to a less favourable area? Why not stay put if it is better at home?” (MacArthur, 1972). Often times the environmental variability of each sub-habitat is unique and different from the others within the habitat. When this is the case, there is additional fitness if individuals have the ability to alter the dispersal rate from each habitat. This means that having site-specific dispersal rates is adaptive (Figure 3). When environmental variability within each sub-habitat is considered, and individuals who are able to sense their location have an additional fitness, they benefit from the ability to alter their dispersal ratio in accordance with where they find themselves.

Populations existing within a widespread habitat will be subjected to different environmental conditions depending on where within that habitat they find themselves. To what degree can organisms have information about where they find themselves? Across some habitats, there are likely to be differences in environmental conditions, which will have a bearing on the fitness of a population. For instance, differences in temperature or rainfall will vary and can be used as clues to which sub-habitat an organism finds itself in. Plants and seeds, for instance, sense changes in temperature through the seasons and use these as cues to define their timing of flowering, germination and seedling emergence (Linkies *et al.*, 2010). Germination timing is controlled via dormancy cycling for which temperature and moisture are the two most important environmental cues (Finch-Savage & Footitt, 2017). A typical plant has over 600 receptor-like kinases (RLKs) involved in sensing specific molecules including from the environment; animals evolved only about 1% of this (Shiu & Bleecker, 2001). Although plants do not have a nervous system, they can sense their environment

extremely well and integrate the environmental factors both long-term and short-term. Similar cues are used by the individual seed or plant to determine where they might find themselves within their habitat. Using these cues, individuals are able to produce site-specific offspring ratios, such as the example of *Ae. arabicum* (Lenser *et al.*, 2016).

Many species, including plant species, are limited to sensing in the emigration phase of dispersal where other species are able to also sense their environment during the transfer phase. In this way, they cannot sense the surrounding sub-habitats and make informed dispersal choices about the sub-habitat into which they ultimately immigrate. As a result, many species depend on the environmental clues in the emigration phase and so the risk of dispersing is much higher, because they cannot make an informed decision once they have dispersed. For this reason, it is crucial to sense the condition of the local environment to determine if the risk of entering a potentially worse sub-habitat is worth taking the chance. Adding the interactions between dispersal mechanisms and environmental conditions into models, such as the one presented in this paper, gives a fuller, more in-depth understanding into population dynamics and the consequences of the environment on dispersal (Seale & Nakayama, 2019).

If the future quality of the entire environment is highly predictable, it is possible to use cues to determine the next future state. In terms of dispersal, the best strategy is then to somehow disperse offspring to the best sub-habitat. Often times, the future is uncertain and information about possible future states is unavailable. What we show here, theoretically, is that even if this is the case, systematic differences in either the average quality or variability

between sub-habitats can lead to adaptations that favour site-specific dispersal. However, an adaptation favouring site-specific dispersal relies on an organism being able to get clues as to which sub-habitat they find themselves in. How an organism can sense the environment is unimportant, so long as it provides information to help them determine in which sub-habitat they are in. In the case of *Ae arabicum*, for instance, the key difference between the high and low altitude environments might be in terms of competition and severity and unpredictability. There is no need to sense these factors directly; temperature, for example, gives a clue as to the likely altitude the organism finds itself at (Arshad *et al.*, 2019). Sensing provides the individual with enough information about the local environment to determine where they are, and site-specific dispersal allows the individual to alter their dispersal ratio in order to maximise the likelihood of the offspring surviving to the following year.

The importance of dispersal plasticity in response to local environmental variability is something seen across the kingdoms (Arendt, 2015). *Poa alpina* is an alpine species that persists in a highly variable environment. The species adopts a seed-reproduction strategy at lower elevations, and bulbil-reproduction strategy at higher elevations (Steiner *et al.*, 2012). This allows it to occupy a large ecological niche so that it can persist in multiple sub-habitats in case one or more of these sub-habitats become unfavourable. In many insect species, wing polymorphism dictates dispersal rates. In aphids, offspring are either winged or wingless, making them dispersing or non-dispersing. Competition, crowding and host condition appear to be the driving forces for the ratio of offspring dimorphism, all of which the maternal aphid is able to sense and respond to by producing wingless or winged offspring (Harrison, 1980). Cycles of bluebird species have been shown to be driven by maternal effects. Following the

creation of a new environment by a wildfire, the area is colonised by mountain bluebirds (*Sialia currucoides*). To compete with the mountain bluebirds, maternal western bluebirds (*Sialia mexicana*) produce aggressive, dispersing offspring. Once the area is colonised by western bluebirds, nonaggressive, non-dispersing offspring are produced. Population density, resource limitations and competitive interactions all appear to be cues for maternal western bluebirds (Duckworth, Belloni & Anderson, 2015).

The habitat in which *Ae. arabicum* exists in the Anatolian Mountains can be roughly divided into two sub-habitats: high elevation, and low elevation (Velchev, 1984; Mohammadin *et al.*, 2017). At high elevation, the environment is dry, exposed, and rocky, with little to no competition. The exposure makes it prone to extreme weather conditions, and so the environmental variability is considered to be higher. At low elevation, the environment is overcrowded, shaded and highly competitive, with better availability of a steady water supply and nutrients. At this elevation, the environment is more competitive but generally sheltered, making the environment less variable year on year (Atalay, 2006). As well as this, there is also a temperature gradient along the elevation, as there is a drop of 3°C for each 300 metres above sea level (masl) climbed. *Aethionema arabicum* has been found growing between 0-3000 masl (Bhattacharya *et al.*, 2019). By sensing the environment into which the dispersing, indehiscent fruits (IND) disperse through this temperature gradient, the resultant plant grows and produces different ratios of dispersing to non-dispersing offspring (Lenser *et al.*, 2016; Arshad *et al.*, 2019).

The life-history of *Ae. arabicum* fits with the strategy observed in the model. There is a dramatic temperature difference along the elevation of the slopes on which they grow (Figure 1 in Arshad *et al.*, 2019). *Aethionema arabicum* has been shown to alter the ratio of IND and non-dispersing, dehiscent fruits (DEH) that it produces when the mother plant is grown at different temperatures during reproduction (Lenser *et al.*, 2016). In this way, the germination timing due to temperature differences (season, elevation) and the consequently distinct temperature during plant growth and reproduction both influence the final offspring ratio of the plant (Lenser *et al.*, 2016; Arshad *et al.*, 2019).

In a lower temperature regime during reproduction, the plant produces more IND fruits. Therefore, it can be suggested that at higher altitudes, *Ae. arabicum* plants will produce more of the dispersing morphs. This would mean they are able to take advantage of the dispersing adaptations of the IND fruit: its buoyant nature for water-mediated dispersal and wings for wind dispersal. This would allow them to spread out across the mountain side in greater numbers and take advantage of wherever most is accommodating in the following year. At lower elevations, *Ae. arabicum* reduces the proportion of dispersal-type offspring with higher temperature and competition stress. However, in response to nutrient stress, *Ae. arabicum* increases the proportion of dispersal-type offspring (Bhattacharya *et al.*, 2019). Whether a plant emerges from an IND or DEH fruit does not seem to predict the ratio of dispersing to non-dispersing seeds that it will, in turn, produce. The plasticity is a response to the environmental conditions in which the plants are grown (Lenser *et al.*, 2016).

One way to efficiently alter the dispersal ratio is through heteromorphism. Heteromorphism was first described by Venable as “the production by single individuals of seeds of different form or behaviour” (Venable, 1985). In this context, behaviour refers to their ecological traits such as their dispersal mechanism. There is a fitness advantage of being able to detect location and therefore, evolving a method to respond by dispersing out of or remaining within the environment is crucial for many species. The main method of doing so for many species is heteromorphism: producing two or more offspring phenotypes that have no, or different methods of dispersal (Imbert, 2002).

One such model to describe the evolution of dispersal heteromorphism is by Venable (Venable, 1985). In this model, the production of two seed morphs in different year types is investigated. The two morphs have different mean and variance based on evolutionary constraints. Offspring morphs are adapted to perform in particular year types, causing more of one to be produced in its favourable year and more of the other to be produced in the opposing years. Evolutionary constraints between years lead to heteromorphism, which produce two offspring morphs that are better adapted to the evolutionary constraints. This is the generalised model used to describe the evolution of dispersal heteromorphism. Our model is an alternative that allows for severely fluctuating, multi-habitat environments. Furthermore, the model gives an explanation for the purpose of sensing in dispersal heteromorphism. Each individual produces two offspring morphs; neither is better adapted for a particular year type, but rather one type is able to disperse and the other is not. How much more or less the offspring disperse out of the sub-habitat is determined by where they are. In this way, our model shows the impact of difference in variability between multiple

environments and how this leads to the evolution of sensing and site-specific dispersal plasticity.

Another method of responding to the environment is through responsive phenotype switching (Moxon *et al.*, 1994; Metzgar & Wills, 2000; Jansen & Stumpf, 2005; Kussell & Leibler, 2005). This is where the individual senses an ambient environmental cue and switches its phenotype. However, this is costly because it relies on developing and maintaining machinery to detect environmental conditions. For organisms with a fast turnover rate, such as bacteria, switching rates that mimic the infrequent environmental variability can be favourable over sensing. Kussell and Leibler (2005) call this spontaneous stochastic switching. In environments where there is higher environmental variability, there is an additional benefit to responsive switching. On the other hand, if the environment is fairly constant and variability is infrequent or less, then the stochastic switching method is favoured, as the cost of sensory machinery is too high (Kussell & Leibler, 2005). This pattern mimics closely the pattern observed in our model.

In bet-hedging theory, geometric mean is used to describe fitness. Existing theories on bet-hedging assume that organisms respond to a single environmental variable, so that therefore the geometric mean of this variable can be used as a proxy for fitness. In an environment consisting of two distinct sub-habitats this is not possible as the growth rate of a population cannot be expressed as a simple geometric mean (Tuljapurkar, 1990). In this scenario, sensing doesn't evolve, because no one sub-habitat is better than any other, as they are all statistically identical, and therefore having site-specific dispersal rates gives no advantage. However,

when the environments are statistically variable across the years, and multiple variables for population growth rate are introduced, as in our model, the need to sense location and produce site-specific dispersal rates is adaptive. Although bet-hedging within our model is possible, the results from our model go beyond bet-hedging theory (Supplementary Material; Nichols, Leubner-Metzger and Jansen, 2020).

Results from the model show that the dispersal strategy best adopted by individuals differs dramatically depending on the environmental variability between multiple sub-habitats. Previous models of dispersal have overlooked the importance of altering the dispersal ratio, depending on the many sub-habitats in which an individual may find itself. This “one size fits all” approach should be reconsidered, as it does not match the life history of species persisting in highly variable environments. Although it has been suggested that climate variability influences aphid reproduction being sexual or asexual by parthenogenesis, this has largely been overlooked in most other species (Halkett *et al.*, 2004).

A higher incidence of extreme weather conditions are on the rise as a result of climate change. Droughts, heatwaves, flash flooding, heavy downpour and hurricanes are just some of the unpredictable weather phenomena putting species at risk. Especially species that have evolved in lowly variable, temperate climates (Michener *et al.*, 1997; Watson *et al.*, 1998; Easterling *et al.*, 2000; McLaughlin *et al.*, 2002). In the case of *Ae. Arabicum*, in a mountainous habitat, the two sub-habitats will experience climate change differently, due to their size and topography. Higher up mountains and on mountaintops, the environment is more exposed, and so will be more affected by windstorms and precipitation, where further down, the plains



are generally sheltered, but prone to flooding and erosion (Barry, 1992; Beniston, 2006). Sub-habitats experiencing differing environmental stresses like this is also common in coastal areas (Keddy, 1981).

Invasive species also put ecosystems at risk. Phenotypic plasticity is an important adaptation to invasive species, as it allows them to occur in a wide range of environments (Richards *et al.*, 2006). Environmental change brings new opportunities for invasive species, which disperse into those environments and outcompete native species. Dispersal strategies responding plastically to environmental changes are commonly researched in animals, but rarely are for plants (Imbert & Ronce, 2001). This is because plants have been widely regarded as passive organisms to those outside of plant sciences. However, it has been recognised that plants are able to undergo site-specific dispersal and can manipulate the dispersal phenotypes of their offspring in response to their environment (Seale & Nakayama, 2019). With little knowledge on how plasticity or lack thereof will affect plant populations in the wake of environmental unpredictability, this could put many species at risk.

Individuals alter the dispersal ratio of their offspring in response to localised environmental variability to an evolutionary advantage. When a species is dispersing between a rock and a hard place, the optimal strategy is to sense the environment and alter the dispersal ratio of their offspring in response. In this way, the population is balanced within a highly variable environment with multiple differing sub-habitats, where they would otherwise go extinct if the population was restricted to one sub-habitat. With increasingly severe fluctuations in environmental variability comes an increase for the scope of this dispersal strategy. Species

adopting this lifestyle are able to thrive in otherwise challenging environments. However, dispersal plasticity is widely under researched and underappreciated across all kingdoms and with a rapid increase in environmental variability, one can only speculate the impact on the natural world.

## CHAPTER THREE: MAKE HAY WHILE THE SUN SHINES

### SEED DISPERSAL AND DORMANCY IN MANAGED LANDSCAPES

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Bethany S. Nichols & Vincent A. A. Jansen

*Prepared for submission*

#### ABSTRACT

*The agricultural landscape is a fluid mosaic of different environments, changing through space and time. Management systems, designed to secure agricultural productivity, can be to the detriment of some wild plants and the relief of others. Plants adapt their dispersal and dormancy characteristics to their environments. Generally, dispersal and dormancy tend to be negatively correlated: high dormancy rates tend to correlate with low dispersal rates and vice versa. In environments with temporal and spatial variability, some species have adopted a positive dispersal and dormancy strategy; dispersing to cope with spatial variability and only germinating in years of optimal conditions. Management systems with periods of recovery through coppicing or fallow land, provide a window of opportunity, and appear to lead to adaptations where dispersal correlates with dormancy. Here we show, through theoretical modelling, that in environments with differing, long-term periods of spatial and temporal variability, positive dispersal and dormancy strategies can be adaptive.*

## INTRODUCTION

Seed dispersal and seed dormancy are two adaptations that plants can use to spread the chance of successful reproduction across time and space in variable environments. Seed dispersal is categorised by relocating an individual from their natal site to a site for reproduction. The relocation process is divided into three phases: emigration, transfer and immigration (Clobert *et al.*, 2001, 2012). In the case of seed dispersal, the individual seeds cannot make informed choices about the site they ultimately disperse into, so there is an associated risk that they will end up in a worse location than their natal site. Seed dispersal allows a population to escape spatially variable environments, where Sub-habitats within the environment differ in variability. In this case, the population could go extinct if it remained within one of these sub-habitats, but by balancing between multiple sub-habitats it is able to be maintained (Jansen & Yoshimura, 1998; Nichols, Leubner-Metzger & Jansen, 2020).

Seed dormancy is a delay in germination and can be interpreted as escaping current conditions through dispersal in time. A seed is considered dormant when it does not have the capacity to germinate within a set timeframe, under normal abiotic factors such as temperature and light intensity (Bewley, 1997). There are a variety of mechanisms for dormancy, which have been classified into a system of levels and types (Baskin & Baskin, 2004). Breaking dormancy requires specific physical factors, which differ between species. These can include temperature, light and physical or chemical scarification. Dormancy can be risky too, as the ideal environmental conditions for breaking dormancy may not occur before the seed perishes due to death or predation. Dormant seeds build up in a seedbank, maintaining a population, should years of poor fecundity arise. Adopting dormancy allows a

species to escape temporally variable environments, in which they may encounter viable years between some or many undesirable years (Venable & Brown, 1988).

Dispersal and dormancy in seeds can both be perceived as methods by which an individual can escape unfavourable environments: dispersal as an escape through space, and dormancy as an escape through time. The relationship between dispersal and dormancy has been hotly contested in plant ecology for the last half decade (Buoro and Carlson, 2014). As dispersal and dormancy are both methods of travel, either through space or time, it has been suggested that there is a trade-off between the two; if a species opts for one, it would be unnecessary to also adopt the other (Buoro and Carlson, 2014). This would lead to a negative correlation between the two (Siewert & Tielbörger, 2010; de Casas *et al.*, 2015). If environmental conditions are not largely independent over space or time, the effects of dispersal and dormancy for a plant are similar and the two traits have effects that are interchangeable. High dispersal would then correlate with low dormancy, and vice versa. Also effects of kin competition reinforce this pattern: only non-dispersing seeds should enter dormancy (Vitalis *et al.*, 2013). While the majority of plants demonstrate a negative correlation between rate of dispersal and rate of dormancy, there are pockets of species across the families, with either annual or perennial lifestyles, performing the opposite (Table 1; full details can be found in Appendix II); producing seeds that undergo both long-term dormancy and long-distance dispersal.

**Table 1:** Species exhibiting long-distance dispersal and long-term dormancy, with information about their lifestyle and natural habitat.

Family	Species	Lifestyle	Habitat
Amaranthaceae	<i>Chenopodium album</i>	Annual	Wasteland and arable land
Asteraceae	<i>Cirsium palustre</i>	Perennial	Wetland, grassland and woodland
	<i>Galinsoga parviflora</i>	Annual	Disturbed habitats and arable land
	<i>Senecio paludosus</i>	Perennial	Wetland
	<i>Senecio palustris</i>	Annual	Wetland
Brassicaceae	<i>Aethionema arabicum</i>	Annual	Stony slopes, steppe
	<i>Chorispora sibirica</i>	Annual	Steppe and gravel desert
	<i>Crambe maritima</i> L.	Perennial	Coastal
	<i>Goldbachia laevigata</i>	Annual	Desert and grassland
	<i>Rapistrum rugosum</i>	Annual	Wasteland, disturbed land and grassland

	<i>Spirorrhynchus sabulosus</i>	Annual	Stationary and semi-stationary sand dunes
	<i>Sterigmostemum fuhaiense</i>	Annual	Gravel desert
	<i>Tauscheria lasiocarpa</i>	Annual	Desert
Caryophyllaceae	<i>Lynchnis flos-cuculi</i>	Perennial	Disturbed land, wetland and arable land
Cyperaceae	<i>Carex panicea</i>	Perennial	Wetland and grassland
	<i>Carex pilulifera</i>	Perennial	Woodland and grassland
Fabaceae	<i>Prosopis juliflora</i>	Perennial	Sandy, rocky and poor soil and arable land
Hypericaceae	<i>Hypericum tetrapterum</i>	Perennial	Wetland
Juncaceae	<i>Juncus bufonius</i>	Annual	Wetland and riparian woodland
	<i>Juncus effusus</i>	Perennial	Wetland, riparian woodland and grassland
	<i>Juncus filiformis</i>	Perennial	Wetland

Lamiaceae	<i>Lycopus europaeus</i>	Perennial	Wetland
	<i>Mentha aquatica</i>	Perennial	Wetland and grassland
	<i>Stachys palustris</i>	Perennial	Wetland, disturbed and arable land, and grassland
Plantaginaceae	<i>Plantago major</i>	Perennial	Disturbed land and grassland
	<i>Veronica chamaedrys</i>	Perennial	Disturbed land and grassland
	<i>Veronica officinalis</i>	Perennial	Grassland and woodland
	<i>Veronica serpyllifolia</i>	Perennial	Disturbed land, grassland and woodland
Poaceae	<i>Amphicarpum purshii</i>	Perennial	Disturbed land and sandy coastal areas
	<i>Anthoxanthum odoratum</i>	Perennial	Grassland
Polygonaceae	<i>Polygonum aviculare</i>	Annual	Disturbed and arable land
	<i>Rumex acetosa</i>	Perennial	Grassland and arable land
	<i>Rumex obtusifolius</i>	Perennial	Arable land, grassland, waste land, wetland and woodland



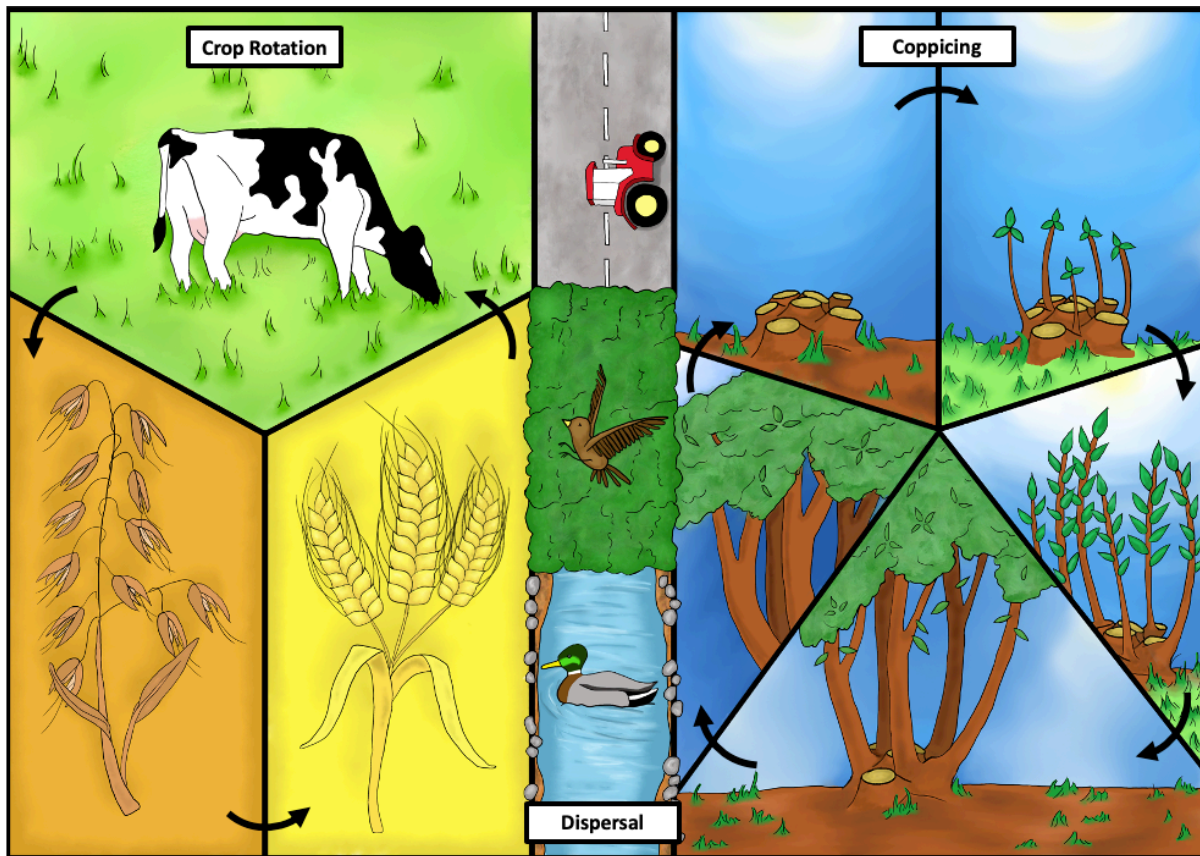
Ranunculaceae	<i>Ranunculus repens</i>	Perennial	Arable land, wetland and grassland
Rosaceae	<i>Potentilla palustris</i>	Perennial	Wetland
	<i>Prunus serotina</i>	Perennial	Grassland, disturbed land and woodland
Solanaceae	<i>Solanum nigrum</i>	Perennial	Woodland and disturbed land
Sparganiaceae	<i>Sparganium erectum</i>	Perennial	Wetland
Violaceae	<i>Viola palustris</i>	Perennial	Wetland, woodland and disturbed land

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Den Boer (1968) suggested dispersal and dormancy are alternative risk spreading strategies. It has been argued that dispersal and dormancy cannot be substituted for one another and that they evolve to fulfil differing roles (Den Boer, 1968; Frisch, 2002). In this way, there would not simply be a negative correlation between dormancy and dispersal, but instead other strategies would emerge. Dormancy is an important risk reducing trait in temporally variable environments, therefore, dispersal cannot substitute risk reduction by dormancy. Equally, dispersal is an important risk reducing trait in spatially variable environments and therefore cannot be substituted by dormancy. In order for seeds to adopt both dormancy and dispersal

traits, there would have to be environments that varied both temporally and spatially and by adopting both traits there would need to be an adaptive advantage.

Landscapes are shaped by the way humans have managed them. When you fly over the countryside, you do not see one monotonous patch of greenspace but instead a rich tapestry of farms, fields, woodland, grassland, wetland and settlement (Rackham, 2000). All of these sub-habitats are also connected by roads, rivers, hedges, power cables and trainlines. This tapestry is not stagnant, but instead changes over the years between and within sub-habitats. It is moved and managed by human activity (Figure 6). The impact of human activity on the natural world has been widely documented for centuries. Habitat declines, species extinction and biodiversity loss are among the issues that have arisen since people first started cultivating the land (Chase & Bengtsson, 2010). However, some species have found ways to thrive in an ever-changing landscape. Transportation of material, crop rotation, coppicing and the building of ponds and ditches mean the same patch of land can look quite different every few years and with each alteration, new environments will emerge. Ecological studies often focus on species interactions with environmental conditions within habitats. However, more recently, the importance of the role of temporal and spatial variability within and between those habitats has been recognised and researched. In this paper we will show, theoretically, that adapting to a lifestyle with both long-term dormancy and long-distance dispersal has an advantage in regularly cultivated environments.



**Figure 6: Managed landscapes are temporally and spatially variable.** Crop rotation and coppicing are two examples of management strategies that vary the environmental conditions year-on-year. Human disturbance, agricultural machinery, animals and waterways provide mechanisms for dispersal. In highly variable landscapes such as these, adopting strategies for both dispersal and dormancy are adaptive; dispersal as a mechanism for spatial variation and dormancy as a mechanism for temporal variation. For example, if a seed should disperse out of a fallow field into woodland, it might find itself in a year where the canopy is full and light is poor, and so adopting dormancy will allow it to persist in the soil until the coppicing year.

Species found to have both long-distance dispersing and long-term dormant seeds exist in a variety of environments; habitats disrupted by wildfires and human interference, habitats managed through farming and coppicing, and freshwater habitats such as streams, ditches and damp meadows (Table 1). In all of these environments, there is a pattern of temporal and spatial variability that spans over several years. Here I will show that annual and perennial species that thrive under these conditions rely on dispersal to distribute themselves across a spatially variable environment, and dormancy in order to germinate at specific periods during these cycles. For example, in species that rely on the coppicing cycle, they may not have the light requirements to grow during the years that the canopy is allowed to grow, and so they remain dormant until the coppicing year, during which the canopy is removed (Brown & Oosterhuist, 1981).

We produced two models to investigate the covariance between dormancy and dispersal: one for annual and one for perennial plants. The models focus on environments with two sub-habitats, which differ in their spatial and temporal environmental conditions. Both sub-habitats will have cycles of environmental variability that differ but that both span over several years. In such environments, it could be possible that dormancy and dispersal are adaptive for different reasons and by adopting both dispersal and dormancy, the population can take advantage of environments managed by human activity. Here we will show, theoretically, that the relationship between dormancy and dispersal is not a “one size fits all” scenario. Instead, the relationship between dormancy and dispersal is dependent on variability between the sub-habitats in both time and space.

## MATERIAL AND METHODS

### *Annual model*

Models designed to investigate the relationship between seed dispersal and dormancy have largely focussed on the individual level, whereas, empirical data has often been collected at a species level (Buoro & Carlson, 2014). Empirical evidence has suggested that the relationship could fluctuate from positive to null, where these models have not been equipped to investigate these relationships (de Casas *et al.*, 2015). We therefore designed a model to investigate the relationship at a species level, using the fitness of two populations, measured as the rate of population growth, as an indicator for the optimum strategy. The model (6, 7) is used to investigate the rate of dormancy and dispersal of an annual species in two sub-habitats:

$$N' = \begin{bmatrix} (1 - g_1)(1 - r) + (1 - d_1(1 - c))S_1g_1 & (1 - \mu)d_2(1 - c)S_2g_2 \\ (1 - \mu)d_1(1 - c)S_1g_1 & (1 - g_2)(1 - r) + (1 - d_2(1 - c))S_2g_2 \end{bmatrix} \cdot N. \quad (6)$$

$$N = \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} \quad (7)$$

The model is divided into two sub-habitats ( $N_1$  and  $N_2$ ). Each sub-habitat has a fecundity ( $S_1$  and  $S_2$  respectively) that each has its own rate of dispersal ( $d_1$  and  $d_2$ ) and rate of germination ( $g_1$  and  $g_2$ ), with dormancy being the failure to germinate ( $1-g_1$  and  $1-g_2$ ). Of the seeds that disperse, a proportion fail to disperse, and fall back to the natal sub-habitat ( $c$ ) and there is a mortality rate associated with dispersal ( $1-\mu$ ). There is also a mortality rate associated with dormancy ( $1-r$ ).

This model reflects the annual lifestyle, in which plants die at the end of the year, and therefore do not survive into the following year. For the sake of simplicity, we assumed that the dispersal rate and the dormancy rate from each sub-habitat was the same ( $d_1 = d_2$  and  $g_1 = g_2$ ). Although this model is, of course, a caricature of the complexity encountered in the real world, it is sufficient to demonstrate the correlations that emerge between dispersal and dormancy. The optimal strategy was determined by the population with the greatest fitness ( $Q$ ) (1), and the associated dispersal and dormancy rates associated with this fitness were recorded.

To alter variability of the environments, the two sub-habitats experienced “good” and “bad” years in differing random or alternating patterns, where the frequency of bad years ( $f$ ) and the severity of the year ( $v$ ) can be manipulated. The severity of the year ( $v$ ) is how much additional or reduced fecundity the population has. Good years were categorised by high fecundity (8) and bad years were categorised by low fecundity (9).

*Good year:*

$$S_x = S_x + \frac{v}{f} \tag{8}$$

*Bad year:*

$$S_x = S_x - \left(1 - \frac{1}{f}\right)v \tag{9}$$

### *Perennial model*

The perennial model (10, 11) is an expansion of the annual model (6, 7) and describes two sub-habitats in which vegetative plants and seeds in a seed bank are calculated year on year. The model is used to investigate the rate of dormancy and dispersal of the seeds under different environmental conditions. In the annual model, only the number of seeds in the seed banks of the two sub-habitats are tracked. In the perennial model, the two seed banks and the number of vegetative plants after over-wintering in each sub-habitat are tracked, to simulate the plants re-emerging:

$$N' = \begin{bmatrix} (1-g_1)(1-r) + (1-d_1)g_1S_{1,t} & (1-d_1)S_{1,t} & (1-\mu)d_2g_2S_{2,t} & (1-\mu)d_2S_{2,t} \\ g_1\pi_1 & \pi_1 & 0 & 0 \\ (1-\mu)d_1g_1S_{1,t} & (1-\mu)d_1S_{1,t} & (1-g_2)(1-r) + (1-d_2)g_2S_{2,t} & (1-d_2)S_{2,t} \\ 0 & 0 & g_2\pi_2 & \pi_2 \end{bmatrix} \cdot N. \quad (10)$$

$$N = \begin{pmatrix} N_1 \\ P_1 \\ N_2 \\ P_2 \end{pmatrix} \quad (11)$$

The number of vegetative plants is dependent on the over-winter survival rate ( $\pi_x$ ). This means that the population of a sub-habitat is now made up of seeds that germinate from the seed bank, seeds that disperse in from the other sub-habitat and plants that survive winter. In bad years,  $\pi = 0$ , because we assume that farming techniques or overcrowding will inhibit the survival of the vegetative plants. In good years,  $\pi = 1$ , as the land is left undisturbed and will allow for the perennial lifestyle. A detailed description of the perennial model can be found in Appendix III.

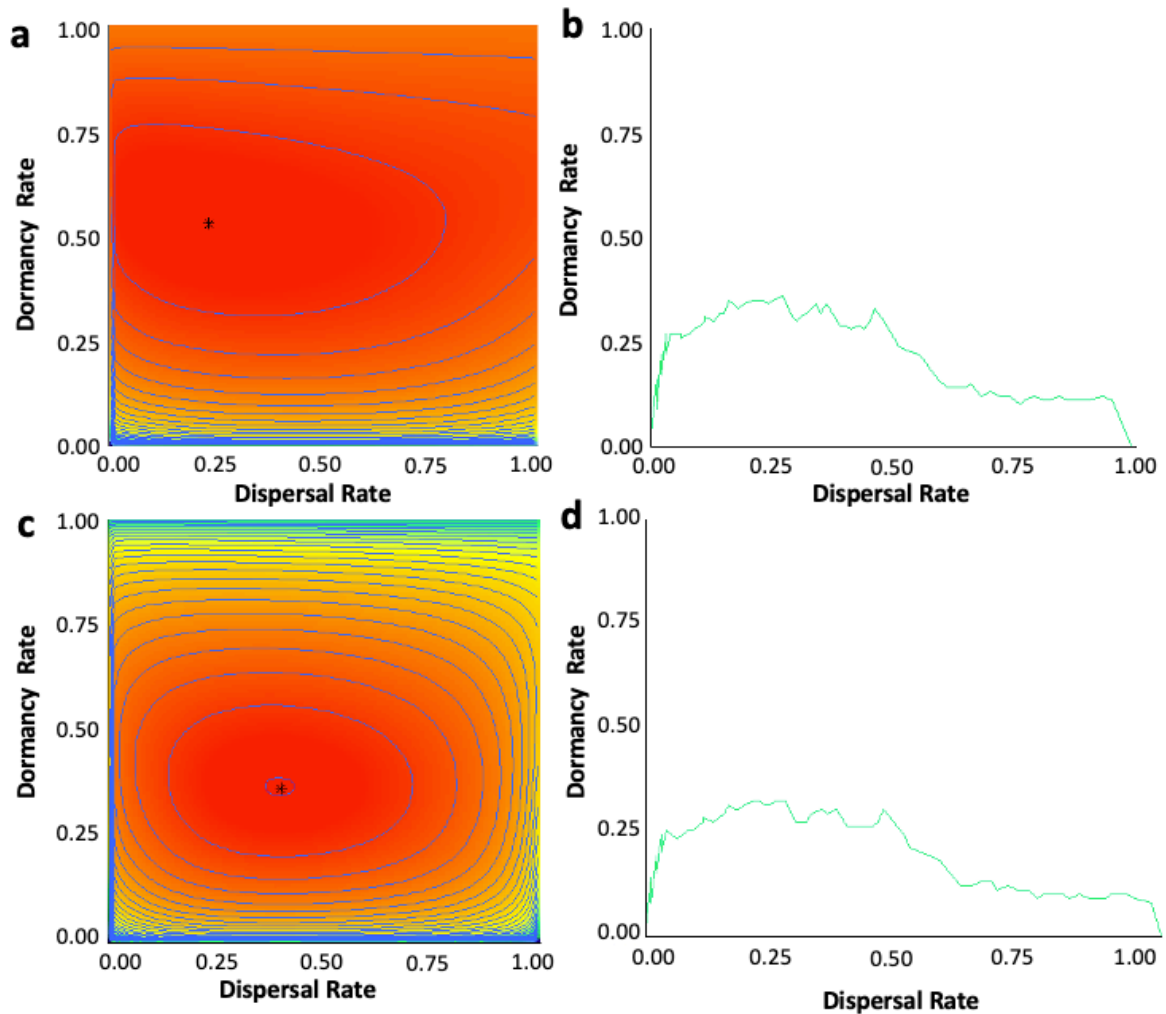
To investigate the models, we simulated an environment in which both the spatial and temporal variability differed in the two sub-habitats. The optimal strategy was determined by the population with the greatest fitness ( $Q$ ) calculated in the same way as the annual model (6), and the associated dispersal and dormancy rates associated with this fitness were recorded. This set of variables can be clearly seen in figures 7a and c, 8a and c, and 9a and c as the \* symbol. By mapping the optimal dormancy and dispersal rates associated with  $Q$  (1), it is possible to look at the relationship between these two strategies with a change in parameters.

## RESULTS

### *Randomly ordered year types*

The annual and perennial models were first investigated with the sub-habitats experiencing different, randomly ordered year types (Figure 7). Different good year percentages require different relationships between dispersal and dormancy. Under random conditions, the interaction between the two strategies is much more complex than simply negative or positive. There are negative, positive and null relationships between the two. Environments with increasingly sparser good years have optimally positive relationships between dispersal and dormancy rate. When over-wintering survival is equal to zero for both good and bad years, the perennials adopt an annual lifestyle and rely on dormancy (Figure 7d).



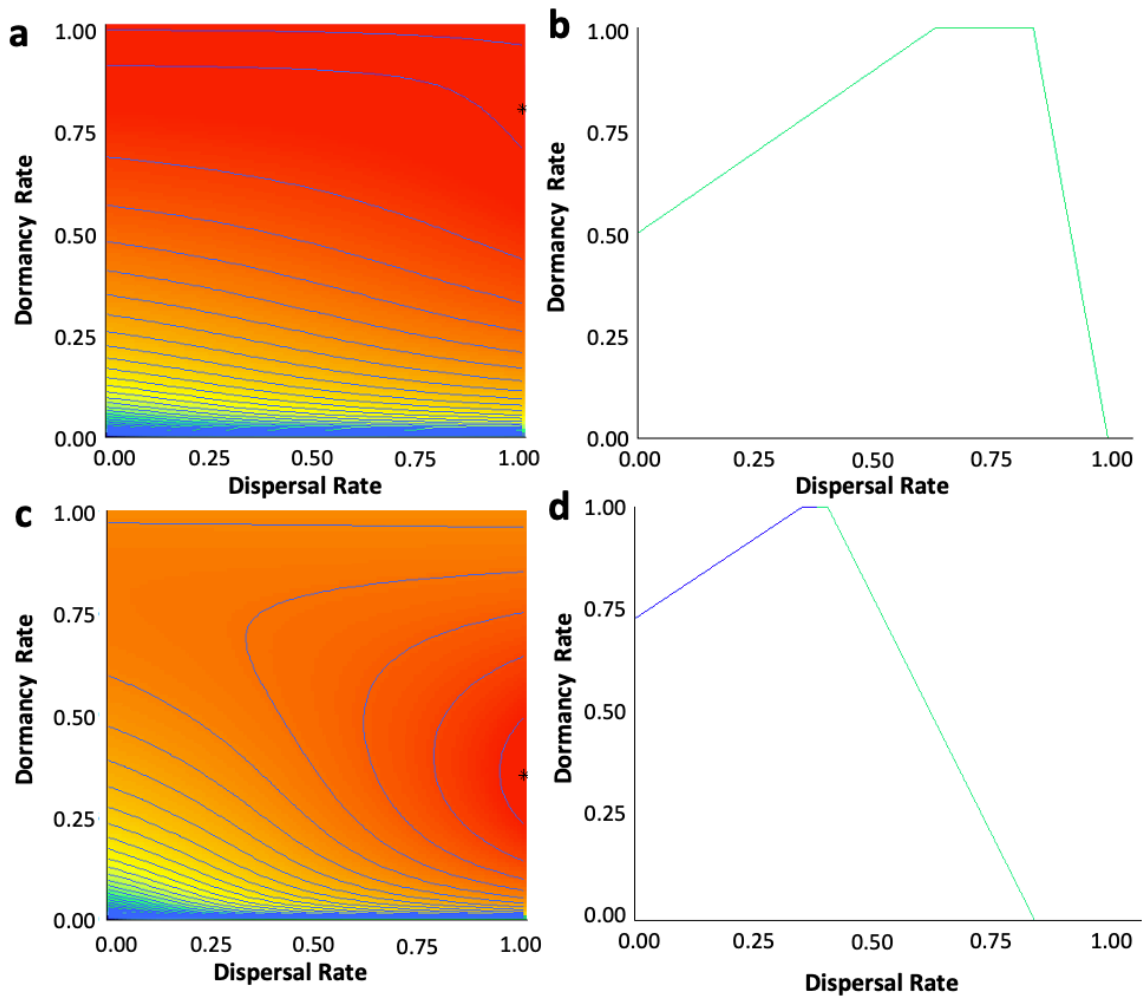


**Figure 7: Changing the year order patterns affects the relationship between dispersal and dormancy in annual plants.** \* indicates the optimal dispersal and dormancy ratios to maximise fitness. The annual model (a and b) and the perennial model (c and d) behave very similarly when winter survival for perennials is equal to zero. The heat gradients (a and c) demonstrate this change in fitness under different combinations of dispersal and dormancy rates. The following variables were used to generate this graph: percentage of good years = 40%,  $\mu = 0.2$ ,  $r = 0.2$  and  $c = 0.1$ . (b and d) By tracking the change in percentage of good years against dispersal and dormancy rate, it is possible to see the range of relationships between dormancy and dispersal. There is little difference between annual and perennial species experiencing a random environment under these conditions.

### *Managed environments with the same cycle pattern*

To investigate the effects of controlled environments, such as those in managed landscapes, the year type order experienced by the two sub-habitats in the annual and perennial model were set to mimic this (Figures 8a and b). Each sub-habitat experienced a good year every three years. These good years were out of sync with each other, with one sub-habitat experiencing a good year in the year after the other sub-habitat. Under these conditions, a positive relationship, a null relationship and a negative relationship between dispersal and dormancy emerges when the sub-habitats experience a range of dormancy related mortality.

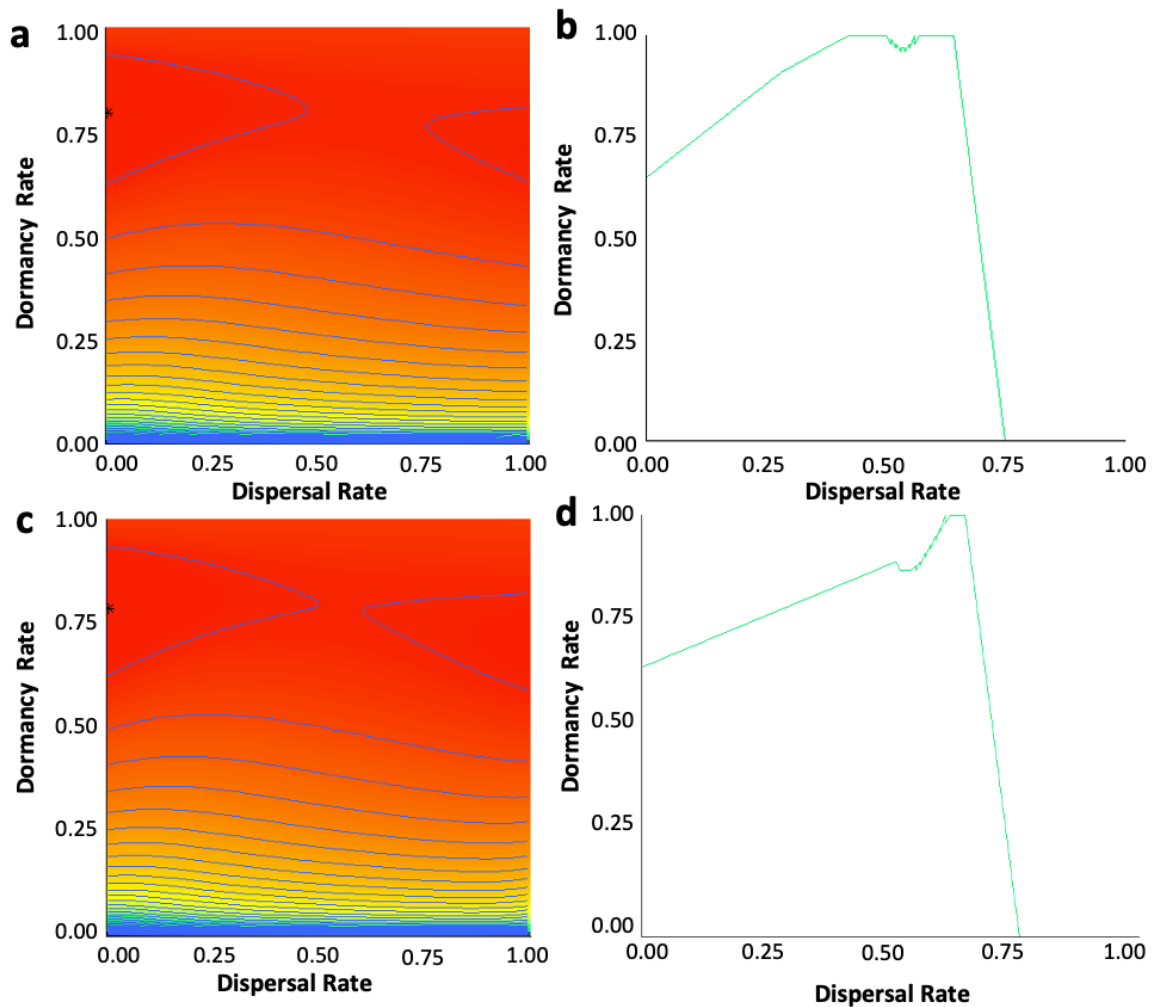
Interestingly, under these conditions, the optimal dormancy rate rises to 1 with some dispersal rates, suggesting that the optimal behaviour is to remain dormant indefinitely instead of germinating. This suggests that existing in a dormant state and dying out gradually is preferable over germinating immediately to produce more offspring. This is due to the simplistic nature of the model, as there isn't a limit on how many years the seeds will remain dormant for. In these cases, the term optimal doesn't seem appropriate because in nature it wouldn't be deemed optimal to remain dormant and slowly go extinct in the place of germinating and continuing the population. Therefore, a future model should account for this and a finite number of years of dormancy applied.



**Figure 8: Cycling the year type pattern every three years promotes a positive relationship between dormancy and dispersal rates in both annual and perennial species.** (a and c) The heat gradients demonstrate this change in fitness under different combinations of dispersal and dormancy rates. \* indicates the optimal dispersal and dormancy ratios to maximise fitness. The following variables were used to generate these graphs:  $\mu = 0.2$ ,  $r = 0.2$ ,  $c = 0.1$ ,  $\pi$  in good years = 1 and in bad years 0. (b) By tracking the change in  $r$  against dispersal and dormancy rate, it is possible to see the range of relationships between dormancy and dispersal. (d) For the perennial model, this same pattern appears, but with a change in  $\mu$  (green) and  $r$  (blue).

### *Managed environments with differing cycle patterns*

In an environment, such as a coppice or arable land, there would be an out of sync, correlated pattern across several years. To mimic this, we simulated one sub-habitat to mimic the three field system, with a good year every three years, and the other sub-habitat to mimic a chestnut coppicing schedule (Rackham, 2000), with a good year every 5 years (Figure 9). Under these conditions, a mixture of positive, null and negative strategies evolved. The results from this simulation suggest that strategies with both strong negative and positive relationships between dormancy and dispersal can evolve when the environment is temporally correlated. Taking this further, even if this pattern is unsynchronised and lasting many years, this pattern still occurs.



**Figure 9: Sub-habitat one had a cycle length of 1/3 good years and sub-habitat two had a cycle length of 1/5 good years for the annual model (a and b) and the perennial model (c and d).** \* indicates the optimal dispersal and dormancy ratios to maximise fitness. (a and c) The heat gradient demonstrates this change in fitness under different combinations of dispersal and dormancy rates, under the following variables:  $\mu = 0.2$ ,  $r = 0.2$ ,  $c = 0.1$ ,  $\pi$  in good years = 1 and in bad years 0. (b and d) By tracking the change in  $r$  against dispersal and dormancy rate, it is possible to see the range of relationships between dormancy and dispersal.

## DISCUSSION

In environments with spatial and temporal variability, dispersal and dormancy in annuals and perennials can both evolve and the two strategies have two clear, differing purposes. Dispersal allows colonisation in new environments, rescuing species from extinction in the current location and will therefore affect meta-population dynamics. Dormancy allows survival in sub-habitats during unfavourable years and requires the population to already be established in the location in order to build up a seedbank, leading to recolonization of disturbed sub-habitats (Buoro & Carlson, 2014). A well-documented invertebrate example of this is the Colorado potato beetle (*Leptinotarsa decemlineata*) which undergoes dispersal to colonise new sub-habitats but also dormancy in order to survive pest control management techniques (Alyokhin *et al.*, 2008). This behaviour is mirrored in our model analysis; adopting both high rates of dormancy and dispersal can be adaptive in environments with regular, managed environmental variability.

In perennial species, if over-wintering survival is inefficient, an annual lifestyle is adopted. If over-wintering survival is possible in good years, a range of dispersal and dormancy strategies are still seen. In annuals, this wide range is only seen with a change in dormancy related mortality, however in perennials, this range is seen with a change in both dormancy related mortality and dispersal related mortality. This suggests that in such environments, perennials adopting dispersal and dormancy are more equipped to survive in a greater range of environments than annual species, which could explain why there is a larger number of perennial species listed as exhibiting both dormancy and dispersal (Table 1). Perennial species

are often excluded from dispersal and dormancy models, so the impact of winter survival on dispersal and dormancy strategy has not been investigated in this way.

In environments with randomly occurring spatial and temporal environmental variability, a range of strategies emerge (Figure 7b). With increasing rates of bad years, the rate of dormancy increases. This is to be expected, as dormancy acts as a risk reduction strategy across time. As the interval between good years emerges, so does the need for seeds to undergo dormancy to survive long periods without ideal germination conditions. Dispersal is also adaptive between the sub-habitats because the variation of each is different. Therefore, it is adaptive to disperse some seeds between sub-habitats for years when the environmental conditions are good in one sub-habitat and not the other. However, there comes a point when the environmental variability is too high, both temporally and spatially, and so the optimal strategy is to stay put and undergo dormancy to minimise risk.

When the environmental variability is correlated, adopting high rates of dormancy and dispersal becomes adaptive (Figure 8b). Even when the sub-habitats are not correlated, but instead they have differing, repeating patterns of management, adopting high rates of dormancy and dispersal becomes adaptive (Figure 9b). Dispersing between sub-habitats that are correlated in spatial environmental variability allows the population to take advantage of the best quality sub-habitats in any given year. Dormancy allows those that disperse into environments that are not yet at that level of quality to wait until an optimal year arises. How realistic is this strategy and do such environments exist?

When discussing the positive relationship that occurs between dormancy and dispersal in some plant species, it has been suggested that this is caused by pleiotropy between the two traits. Larger seeds have a lower dispersal rate because of weight (Fenner, 1985; Martinez-Ghersa *et al.*, 2000). Smaller seeds are more likely to become dormant because of physical constraints caused by deep burial (Thompson & Grime, 1979; Baskin & Baskin, 1998). Therefore, having smaller seeds may lead to a plant adopting both traits, rather than the two evolving in the same species. It has also been found that genes controlling dispersal traits have some control over dormancy as well (Groszmann *et al.*, 2010; De Casas *et al.*, 2015; Nguyen *et al.*, 2015). However, if this was solely the case, it might be expected that the majority of plants with small seeds would exhibit both high rates of dormancy and dispersal.

From theoretical models and empirical evidence, a positive relationship seems to be the exception rather than the rule, as both have pointed towards a negative relationship between rate of dispersal and rate of dormancy. Perhaps there is an adaptive advantage to adopting both traits in certain environments, and this could explain why it has evolved in some species and not others. In this paper, we have compiled a list of 37 species, from 17 different families, all with dispersal and dormancy capabilities (Table 1). In each of these species, they persist across several sub-habitats that are disturbed by environmental factors or human management, in regular intervals, occurring in intervals that last more than 2 years.

Coppicing and pollarding are woodland management strategies. In coppicing, trees are cut down to the ground and many stems grow from the cut trunk. In pollarding, the trunk is cut high enough to prevent browsing by animals (Freethy, 1986). Different species require



different amounts of time between coppicing. For example, the Romans would coppice chestnut trees every five years and oak every seven (Rackham, 2000). Coppicing opens up the canopy and provides sunlight to the woodland floor. For species that are light-demanding, this is an essential time for them to germinate and establish themselves before the canopy regrows. When the process of coppicing is stopped, species reliant on the regular source of sunlight cannot grow and become limited to woodland edges and small clearings (Freethy, 1986). Many species of plants disperse into woodlands from surrounding cropland, mainly by attaching themselves to the hair or feathers of vertebrate animals (epizoochory) (Devlaeminck, Bossuyt & Hermy, 2005). In riparian woodland, rivers provide a watercourse through dense vegetation in which both species adapted for water dispersal and those that are not are able to disperse long-distance (Calçada *et al.*, 2015).

The importance of light has been noted for germination post-dispersal. One such example is *Cirsium palustre*, which disperses into ash coppices and will remain dormant until a coppicing year (Pons, 1984). In a study by Brown (1981), soil samples were taken from five neglected coppiced woodlands in East Anglia and the seeds found in each sample were germinated and identified (Brown, 1981). 68 species germinated, 87% of them were light-demanding and majority were not representative of the flora found in the coppices at the time of collection. Many of these species are capable of both dormancy and dispersal. In the case of *Chenopodium album*, *Cirsium palustre*, *Rumex obtusifolius* and *Jucus effuses*, these species were found to have the ability to disperse into woodlands from croplands and go dormant in coppiced woods (Brown, 1981; Devlaeminck, Bossuyt & Hermy, 2005). This strategy allows species to move between sub-habitats that differ in their environmental variability, but

should they find themselves in a sub-habitat of unfavourable conditions, go dormant until the optimal conditions occur.

Coppicing is not the only management strategy spanning several years over a regular pattern. Crop rotation is a cropland management strategy where a series of different crop-types are grown in succession over a number of years. This strategy can be traced back to the Roman occupation, sometime between 43 and 410 AD (Knox *et al.*, 2013). Across Europe, the three field system was commonplace; a strategy in which the land was divided into three areas and, in each, a different type of crop or fallow land was grown in each year. A winter corn, a summer corn and fallow land, where livestock were kept overnight, would be rotated between each area on each successive year. This was increased to the Norfolk Four-Course Rotation in the 18<sup>th</sup> century, where an additional area was added to the rotational system. This provides a correlated, regular cycle, spanning over many years, providing temporal variability for dormancy.

In an agricultural landscape, the presence of different crop areas on rotation, surrounded by hedgerows, woodland and ponds provides spatial variability for dispersal (Kristensen, Thenail & Kristensen, 2001). If a species were to disperse into this landscape and find themselves in a cropland area, burial from ploughing or lack of sunlight from crop cover could mean they enter the seedbank and remain dormant. Once this area becomes fallow land and is trampled and grazed, it becomes optimal for germination (MacDougall *et al.*, 2018). This provides another ideal environment in which a strategy of dispersal and dormancy could be adaptive. Non-deep physical dormancy is common in buried weed seeds, as they require light exposure

during their non-dormant cycle to germinate (Baskin & Baskin, 1998). There are many opportunities for dispersal in an agricultural landscape, many of which have been found to be successful: during manure spreading, by farm animals internally and externally, through transportation on farm machinery and vehicles, along hedgerows by nesting birds and by ants (Kjellsson, 1985; Schmidt, 1989; Hodkinson & Thompson, 1997; Strykstra, Verweij & Bakker, 1997; Jensen & Meyer, 2001; Cosyns *et al.*, 2005; Deckers *et al.*, 2005; b, Mountford & Hughes, 2012; Bravo *et al.*, 2014). Dispersal by birds has been found to be higher in cropped areas than in field boundaries (Holmes & Froud-Williams, 2005).

From prehistoric pollen and plant remains, it has been confirmed that grassland species were rare across the British Isles before colonisation (Rackham, 2000). Grassland herbs did not appear until the Neolithic era, roughly 6500 years ago, and evidence of organised farming and land management has been found predating the Romans. Could a strategy of dormancy and dispersal evolve in this time span, or could this strategy predate land management? A positive correlation between dispersal and dormancy is very common in crop plants, such as cereals and pulses. Artificial selection against dormancy and dispersal led to a loss of seed shattering before harvest and promotion of germination in crops (Larson *et al.*, 2014). This also demonstrated the speed at which selection works on dispersal and dormancy (De Casas *et al.*, 2015).

There is also evidence that a positive strategy could be selected for in natural environments. The domestication of plants can be traced back to the Holocene, 11,700 years ago. In these areas, the deltas provided fertile land with steady water supplies in often dry and arid

environments. While the area directly beside the rivers is lush and fertile, the surrounding area is often sand, steppe or desert, providing spatial variability. Rivers and deltas are also subject to regular flooding and droughts. Records of Nile flow levels have been documented from the 7<sup>th</sup> to early 20<sup>th</sup> century and suggest the river has periodic cycles of 64, 19, 12 and 7 years (Macklin & Lewin, 2015). The Nile basin also appears to have drought/flood cycles lasting 18.6 years and a weaker cycle lasting 10-11 years, induced by periodic lunar nodal tides (Hameed & Currie, 1985; Currie, 1987). This is further supported by the fact that many species with positive dispersal and dormancy strategies survive in wetlands at the edges of lakes (Cosyns *et al.*, 2005). Lake water levels cycle through the year, but can also have long-term changes due to sediment build up and break down (Reading, 1978).

European Neolithic-derived grasslands are becoming rarer. Changes to land management and the impact of human activity are cited as being one of the driving forces for their decline (MacDougall *et al.*, 2018). While what it is about changes to land management that could be affecting this decline have been discussed, the potential importance of the positive dispersal and dormancy strategy found in these species, and others, has not yet been explored. Understanding the positive correlation between dispersal and dormancy will help with biodiversity conservation, pest management and disease outbreak (Buoro & Carlson, 2014). In order to thrive in landscapes designed for the mass production of specific species, and reduction in all others, the best strategy is to remain on the run and undercover. Adopting a positive dispersal and dormancy strategy makes a species resistant to spatial changes and long periods of poor conditions. However, it can also make them weak. Relying on regular, diverse methods of land management has meant that with a rise in industrial farming and

decline in traditional methods, many plant species are now at risk. In order to create successful conservation strategies, the role and adaptation of positive dormancy and dispersal strategies in these species needs to be better understood.

## CHAPTER FOUR: GROWING OLD GRACEFULLY

### ARTIFICIAL AGEING RESILIENCE OF LONGEVITY AND DORMANCY IN *AETHIONEMA ARABICUM*

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*Draft paper*

#### ABSTRACT

*Seed dormancy and seed longevity are two traits that maintain seed viability from dispersal to germination. Until recently, dormancy has been considered a method by which a seed undergoes longevity, and so an increase in one leads to the increase in the other. *Aethionema arabicum* is a dimorphic species that alters the ratio of its two diaspore types in response to environmental conditions. One of these diaspores is able to undergo dormancy, while the other does not, but instead persists via longevity. Here we will show, that in *Ae. arabicum*, dormancy reduces resilience against artificial ageing compared to longevity. This is an unusual finding, as longevity has previously been shown to be susceptible to high relative humidities and temperatures. This suggests dormancy and longevity are separate traits with different ecological purposes for persistence in the seed bank. We discuss the implications of this finding in relation to the highly variable environment in which *Ae. arabicum* is found. Better understanding the ecological roles for longevity and dormancy could have important implications for seed storage in conservation and agriculture.*

## INTRODUCTION

Seed persistence is the ability of mature seeds to survive in an environment (Long *et al.*, 2014). This ability is particularly adaptive in highly variable environments, as it allows them to postpone germination in environments when the conditions are unfavourable and where failure to reproduce is high (Cohen, 1966). One way of persisting in the soil is through dormancy. Dormancy is the prevention of seed germination within a set timeframe, under normal abiotic factors (Bewley, 1997). There has previously been confusion in the literature about the relationship between dormancy and persistence, where some studies have suggested that dormancy is necessary for persistence, and in others, that dormancy and persistence are synonymous (Thompson *et al.*, 2003). It is now recognised that persistence is the combined effect of dormancy, longevity and resistance (Long *et al.*, 2014). In this paper, we will be focusing on longevity and dormancy as two mechanisms for persistence.

Dormancy and longevity are two separate traits in seeds that maintain viability from seed dispersal to germination (Nguyen & Bentsink, 2015). Dormancy allows a seed to escape an environment temporally, by delaying germination until optimal conditions arise. Dormancy has been shown to be adaptive in environments with reduced access to water, or aridity (Barazani *et al.*, 2012). Longevity is seed viability following storage and aids in seed survival through protection, degradation renewal and detoxification (Rajjou & Debeaujon, 2008). Longevity maintains seed vigour upon germination, preventing the seed from ageing and becoming sensitive to germination conditions. It has been shown to be susceptible to storage under high relative humidity and high temperatures, because these lead to protein denaturation which prevents the seed from repairing damage to DNA, RNA and proteins

(Sano *et al.*, 2016). Both dormancy and longevity have been described as persistence mechanisms and both have been shown to protect seeds in the face of extreme temperatures, freezing and desiccation (Sano *et al.*, 2016).

A positive correlation between dormancy and longevity has been recorded, with dormancy being cited as a method by which seeds achieve longevity (Lubzens, Cerda & Clark, 2010). In this way, a seed that can undergo dormancy should have increased longevity under ageing conditions compared to one without dormancy. However, recent experimental research cites a negative relationship between dormancy and longevity in *Arabidopsis* (*Arabidopsis thaliana*), with each being an adaptive mechanism for seed survival under differing environments (Nguyen *et al.*, 2012). This research investigated the genetic regulators for dormancy and longevity in *Arabidopsis* and identified that the *DOG1*- Cape Verde Islands allele that increases dormancy decreases longevity. While the mechanisms behind dormancy have been thoroughly researched and reviewed (Bewley, 1997; Baskin & Baskin, 1998, 2004; Koornneef, Bentsink & Hilhorst, 2002; Finch-Savage & Leubner-Metzger, 2006), longevity is still widely under researched. Research into the protection and repair traits of longevity have shown the importance of embryo viability and seed coat structure in longevity processes (Sano *et al.*, 2016). However, it still remains unclear where the same mechanisms used during dormancy are similar to those of longevity.

*Aethionema arabicum* is an annual brassica that grows along the steppe environment across the Anatolian Mountains (Mohammadin *et al.*, 2017). *Aethionema arabicum* exhibits seed and fruit dimorphism, producing two fruit types, each containing a different seed-type



(Lenser *et al.*, 2016). These two fruit types are called dehiscent and indehiscent. Dehiscent fruits (DEH) are the larger of the two, containing 2-6 seeds (M+) which disperse locally and produce a mucilaginous layer. Indehiscent fruits (IND) are smaller and contain 1 seed (M-) each. The fruit abscises from the plant and is adapted to undergo long-distance dispersal by wind or water (Arshad *et al.*, 2019). The ratio of IND to DEH fruits is different depending on the temperature at which the parental plant is grown (Lenser *et al.*, 2016). Sensing and altering the dispersal offspring ratio in this way allows *Ae. arabicum* to undergo site-specific dispersal, by using temperature as a clue to location along the slope and producing a different dispersal ratio. This is adaptive in highly variable environments, as it allows a species to balance between sub-habitats in which they would otherwise go extinct (Nichols, Leubner-Metzger & Jansen, 2020).

Of the two morphs, the dispersing IND fruits containing M- seeds are able to undergo dormancy, while the M+ seeds of DEH fruits germinate immediately (Lenser *et al.*, 2016). The dimorphic lifestyle of *Ae. arabicum* makes it a good candidate for investigating the ecological purposes of dormancy and longevity. The differing dispersal mechanisms adopted by each diaspore is adaptive for surviving in a harsh environment. Could having differing dormancy and longevity mechanisms also be adaptive in this way? If dormancy and longevity use similar mechanisms, will the different diaspores respond similarly to artificial ageing, or will one be more resilient to a wider range of conditions? Here we will investigate the resilience of M+ and M- seeds and IND fruits in *Ae. arabicum* using artificial ageing experiments, and discuss how longevity of M+ seeds and dormancy of IND fruits affects their resilience. In this chapter, M+ and M- seeds and IND fruits will be referred to as 'diaspore types'.

Artificial or accelerated ageing of seeds can be achieved in the laboratory by exposing them to high humidities and temperatures (Delouche and Baskin, 1973). In this chapter, I used a range of humidities for varying lengths of time to see the impact of different ageing treatments on the different diaspore types. To ensure that ageing had killed the diaspores, I repeated the treatments with reduced germination with a hormone treatment. This was to ensure diaspores were dead and not dormant. As a final precaution, I also used Tetrazolium dye to stain seeds. Tetrazolium dye stains active, living seeds red while leaving dead seeds unstained. In this way, I was able to determine the resilience of each to a range of treatments by calculating the final germination percentage of each diaspore. As well as comparing the two diaspores, I also investigated the purpose of the pericarp of IND fruits by removing M- seeds and ageing them outside of the endocarp. Therefore, the three diaspore types to be compared were IND fruits, M- seeds and M+ seeds. IND fruits were compared to M+ seeds as these are the two diaspore types in the natural environment. IND fruits were also compared to M- seeds to investigate the purpose of the pericarp. Comparing this to existing knowledge about the dormancy of these diaspore types, I will discuss how longevity and dormancy possibly aid to the resilience of the seeds under different environmental conditions, such as those experienced in the Anatolian Mountains.

## MATERIAL AND METHODS

### *Diaspore preparation*

*Aethionema arabicum* diaspores were originally harvested from greenhouse grown plants, which were harvested from M+ seeds from a Turkish assession. I sowed the seeds in July 2018

and harvested in December 2018. Following harvesting, M+ seeds were manually removed from the DEH pericarps. IND pericarps were separated into two groups. In the first group, M- seeds which were manually removed from the IND pericarp and in the second group IND fruits remained intact. M+ and M- seeds and IND fruits are here referred to as diaspore types. Diaspore types were stored at room temperature for four months before the ageing experiments began. A pilot study was conducted to ascertain the lengths of time needed for seeds to be aged, and the germination conditions required following the ageing treatment.

### *Ageing treatment*

Diaspores were aged at humidities of 50%, 60%, 70% or 80%, for a period of 2, 7 or 29 days in an incubating chamber set to 42°C. Ageing chambers were prepared with 500 ml solution of autoclaved water with lithium chloride in the following quantities: 185 g lithium chloride for 50% humidity, 150 g lithium chloride for 60% humidity, 125 g lithium chloride for 70% humidity and 85 g lithium chloride for 80% humidity. The chambers were placed in an incubator at 42°C for 48 hrs prior to ageing. A total of 36 treatments were conducted (Table 2). Three replicates of approximately 30 diaspores were used for each treatment. For each replicate, the diaspores were placed into 0.2 ml PCR tubes with three, 2 mm holes punched through the lid. All replicates were kept in a silica gel drying chamber at room temperature for 48 hrs prior to ageing. Controls of each diaspore type were kept in the drying chamber for the duration of the ageing experiment. For each control there were also three replicates. All experimental replicates were moved into their respective ageing chambers at the same time, and placed back into the drying chamber at the end of their incubation period. Once the 29-

day treatments were placed into the drying chamber, all replicates were kept for a further 48 hours prior to germination.

**Table 2:** Ageing treatments for *Aethionema arabicum* diaspores M+, M- and IND over varying ageing times and humidity. For each treatment there were three replicates.

Ageing time (days)	Humidity (%)	Diaspore type
2	50	M+
2	50	M-
2	50	IND
2	60	M+
2	60	M-
2	60	IND
2	70	M+
2	70	M-
2	70	IND
2	80	M+

2	80	M-
2	80	IND
7	50	M+
7	50	M-
7	50	IND
7	60	M+
7	60	M-
7	60	IND
7	70	M+
7	70	M-
7	70	IND
7	80	M+
7	80	M-
7	80	IND

29	50	M+
29	50	M-
29	50	IND
29	60	M+
29	60	M-
29	60	IND
29	70	M+
29	70	M-
29	70	IND
29	80	M+
29	80	M-
29	80	IND

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To germinate the seeds, each replicate was transferred into a petri dish containing 3 ml of 0.1% Plant Preservation Mixture™ (PPM) (Plant Cell Technology). The petri dishes were kept in black boxes at 12°C temperature. The number of seeds with a visible radicle were counted once or twice daily, until no further germination had taken place over three days. The percentage germination, mean and standard deviation was calculated across each of the three replicates. Treatments that did not reach an average final germination were marked and carried forward into the hormone treatment experiment to ensure the seeds in these treatments were dead and not dormant.

#### *Ageing and hormone treatment*

The ageing process was repeated with treatments with a final average germination percentage of less than 80% (Table 3). During a pilot study of the three diaspores germination rates, all three diaspore types reached an average germination percentage of at least 80%. 80% was therefore chosen as a threshold, over which the diaspores were expected to germinate in order to be within a normal range. Three replicates of each treatment were prepared and aged as above and stored in the drying chamber for 48 hours prior to the hormone treatment. A pilot study was conducted to determine the more effective combination of hormones for germination with all three diaspores. A combination of 0.1% gibberellin (GA) and 0.1% dimethyl sulfoxide (DMSO) was found to be the most effective and was selected for the follow up experiment, with 0.1% PPM.

**Table 3:** Ageing treatments for *Aethionema arabicum* diaspores M+, M- and IND over varying ageing times and humidity to be repeated with gibberellins. For each treatment there were three replicates.

Ageing time (days)	Humidity (%)	Diaspore type
2	50	IND
2	60	IND
2	70	IND
2	80	IND
2	80	M-
7	50	IND
7	60	IND
7	60	M-
7	70	M-
7	80	M+
7	80	M-



7	80	IND
29	50	IND
29	60	IND
29	60	M-
29	70	M+
29	70	M-
29	70	IND
29	80	M+
29	80	M-
29	80	IND

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The percentage germination, mean and standard deviation was calculated each of the three replicates. Treatments that did not reach an average final germination percentage were marked and carried forward into the staining experiment, to ensure the seeds in these treatments were dead and not dormant.

### *Staining assays*

Five seeds from each replicate where 80% average final germination was not reached were transferred to new plates (Table 4). For the IND fruits, the pericarp was removed before being transferred. Tetrazolium dye was added to the seeds and they were left to develop in a black box at 25°C for 24 hours. A positive and a negative control for M+ and M- seeds was also prepared and stained. For the positive control, three replicates of five seeds of each type were imbibed in a black box for 24 hours at 25°C. The dye was then added and the seeds left to develop. For the negative control, three replicates of five seeds of each type were placed in the 80% relative humidity ageing chamber at 42°C for 48 hours before being heated twice in a Moisture Analyzer (Mettler Toledo HB43-S). The negative control replicates were then imbibed and stained. Positive control seeds stained a bright red colour and negative control seeds did not. The experimental seeds were assessed beside the negative and positive controls, and the number of seeds that stained were counted and recorded.

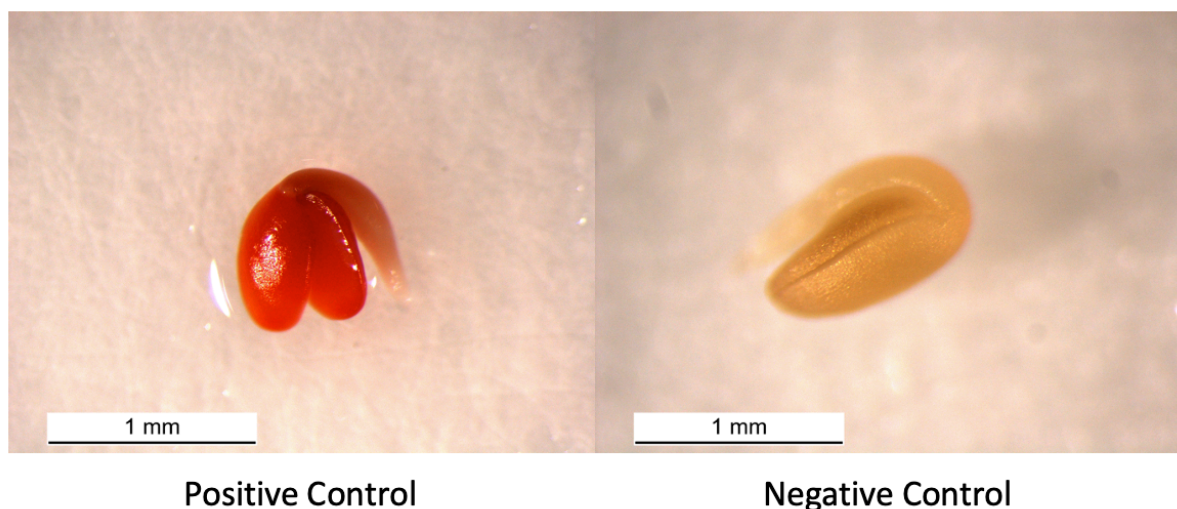
**Table 4:** Aged and hormone germinated treatments for *Aethionema arabicum* diaspores M+, M- and IND, stained with Tetrazolium dye.

Days in Chamber	Humidity	Diaspore
2	80	M-
2	80	IND
7	70	M-

7	70	IND
7	80	M+
7	80	M-
7	80	IND
29	80	IND
29	60	M-
29	60	IND
29	70	M+
29	70	M-
29	70	IND
29	80	M+
29	80	M-



After being aged and germinated in a GA hormone treatment, none of the M- seeds removed from IND fruits, M- seeds, or M+ seeds stained positively with Tetrazolium dye, compared to 100% of the positive control seeds, indicating that 100% of the seeds that failed to germinate under these conditions had died (Fig. 10).



**Figure 10: *Aethionema arabicum* control M+ seeds stained with Tetrazolium dye.** On the left is the positive, alive control and on the right is the negative, dead control. The positive control has successfully dyed red and the negative control has not.

### *Statistical analysis*

A one-way ANOVA analysis of variance with Tukey HSD test was performed in R 3.5.0 (R Core Team, 2018) using the dplyr package (Wickham *et al.*, 2020). The treatments were divided up by seed-type and humidity, and compared the three ageing times against the control results. The response variable was the final germination percentage of each replicate and the normality assumption was based on the Shapiro-Wilk Test ( $\alpha=0.05$ ). Table 5 shows the

treatments that have a statistically significant p-value when compared to the control results. In Figure 10, these results are indicated by a \*. The results for the seed-type M+ at humidity 80 group couldn't be processed because the test resulted in infinity.

**Table 5:** Final average germination percentage of *Aethionema arabicum* diaspores M+, M- and IND treated with artificial ageing that are statistically significant when compared to the control final average germination percentage for each diaspore type. A one-way ANOVA analysis of variance with Tukey HSD test was performed with a Shapiro-Wilk Test assumption ( $\alpha=0.05$ ) on each treatment against the control diaspore type. p-values for each treatment are listed.

Diaspore type	Humidity (%)	Ageing time (days)	p-value
I	60	29	3.7E-04
I	70	7	4.0E-02
I	70	29	5.4E-07
I	80	2	7.9E-03
I	80	7	3.8E-08
I	80	29	3.8E-08
M	50	29	5.4E-02

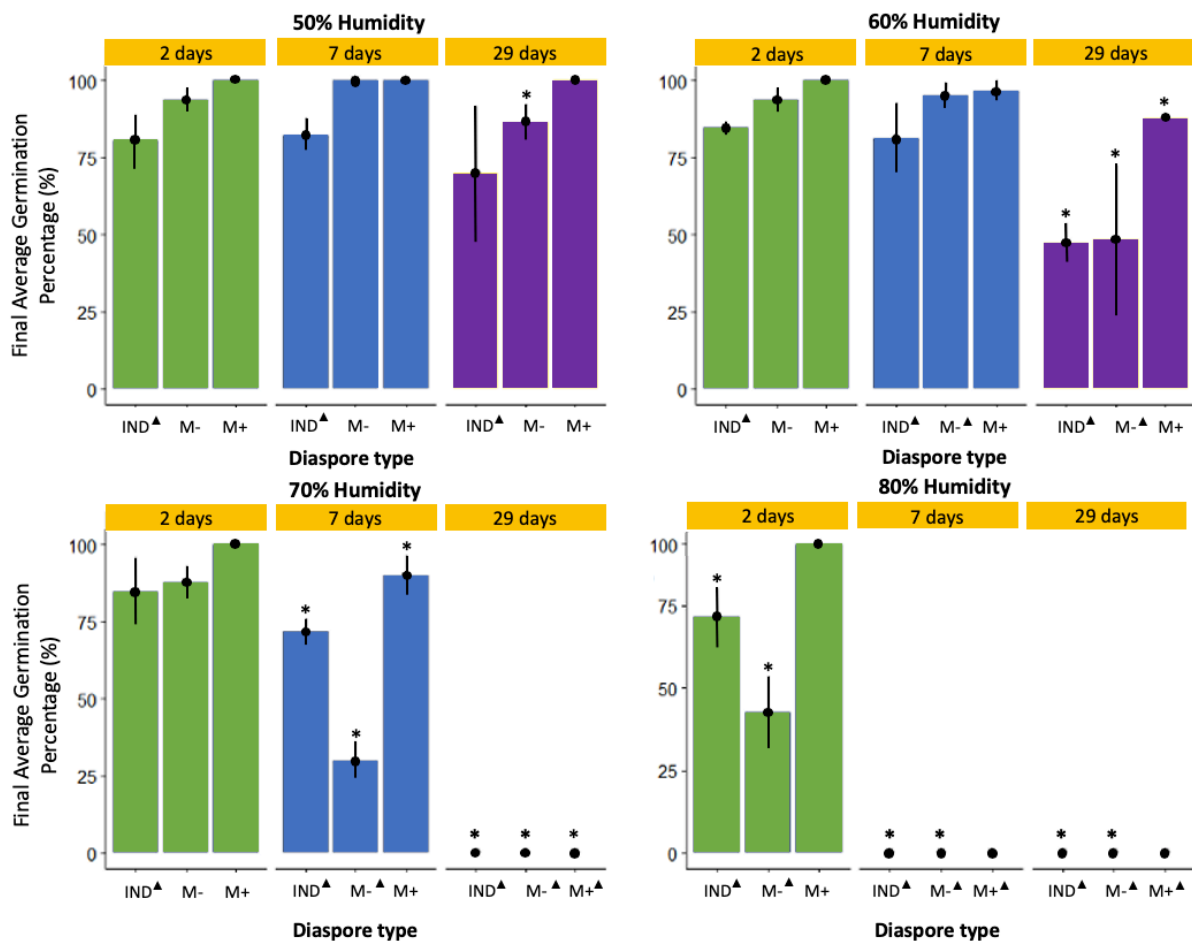
M	60	29	6.2E-03
M	70	7	3.3E-07
M	70	29	1.9E-08
M	80	2	1.6E-05
M	80	7	1.6E-07
M	80	29	1.6E-07
P	60	29	2.1E-04
P	70	7	2.7E-02
P	70	29	3.3E-09

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## RESULTS

As diaspores were left at each humidity for an increasing amount of time, the final germination percentage reduced (Fig. 11). Out of the three diaspores, IND took the longest time to start germinating and had the slowest germination rates (Appendix IV). Without the addition of hormones, none of the IND treatments or control reached 100% germination rate, so it was difficult to assess the effect of the ageing treatment on final germination percentage. With the removal of the pericarp, the M- seeds germinated at a much higher and faster rate

than the IND fruits. However, at higher humidities and longer ageing times, the final germination percentage of M- seeds was lower than IND fruits. Removing the pericarp increases germination rate under optimal conditions, but reduces resilience against ageing.

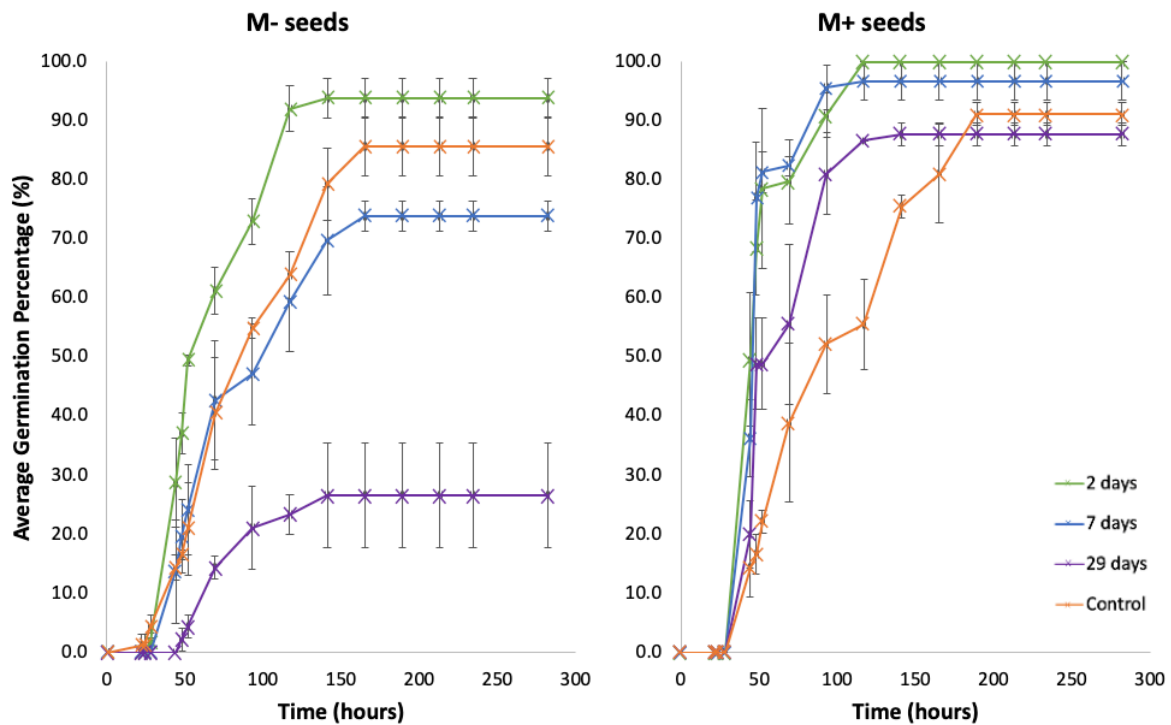


**Figure 11: Final germination percentages of M+ and M- seeds and IND fruits of *Aethionema arabicum* across all treatments.** Treatments with the addition of hormones will be indicated with a <sup>▲</sup>. M+ seeds were more resistant to a wider range of ageing treatments than IND fruits or M- seeds. IND fruits were also more resistant to some ageing treatments than M- seeds. \* indicates that this result is statistically significant when compared to the control for this diaspore type.

### *M+ seeds and M- seeds resilience to ageing*

M+ seeds were more resilient to a wider range of ageing treatments than M- seeds (Fig. 12). Only three of the treatments halted germination in M+ seeds, compared to M- seeds which had reduced or halted germination in 7 treatments. M+ seeds also either reached complete germination or did not germinate at all. They did not show a reduction in germination like M- seeds. Compared to the control M+ seeds, M+ seeds that had been aged had an increase in germination rate. They began germinating at the same time but the germination rate was slower in the control seeds. M- seeds generally had a lower final germination percentage compared to the control seeds. Where the addition of hormones increased the final germination percentage in some M- seed treatments, repeating the ageing experiment with M+ seeds that did not germinate had no effect (Appendix IV).

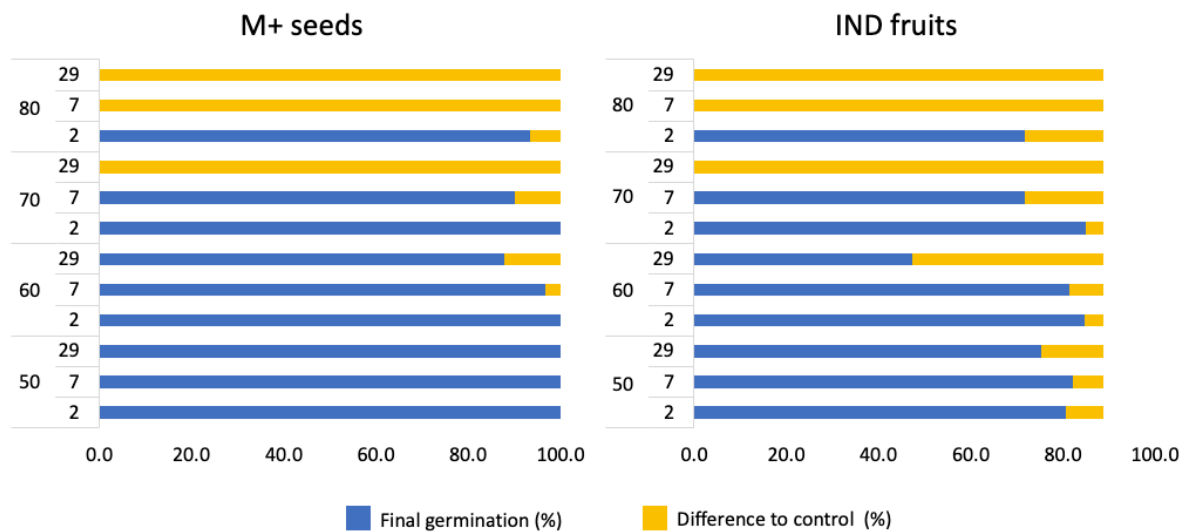




**Figure 12: Average germination curves for M+ and M- seeds of *Aethionema arabicum* at 60% humidity with standard deviations.** Germination rates for M+ seeds are faster than M- seeds at each ageing time and final germination percentages are higher. M+ seeds are less affected by the 60% humidity ageing treatment at all ageing times.

#### *M+ seeds and IND fruit resilience to ageing*

The natural diaspores of *Ae. arabicum* are M+ seeds, which dehisce from DEH fruits and do not undergo dormancy, and IND fruits, which abscise and show dormancy. M+ control seeds reached 100% average final germination, where control IND fruits reached only 88.7% average final germination (Fig. 13). M+ seeds showed resilience to a wider range of ageing treatments than IND fruits. As well as this, M+ seeds showed greater resilience to some of the ageing treatments than IND fruits. Of the two diaspores, M+ seeds are more resilient to artificial ageing than IND fruits.



**Figure 13: Final average germination of M+ seeds and IND fruits of *Aethionema arabicum* compared to their controls.** Final germination percentage of M+ seeds is overall higher than IND fruits across all treatments, and M+ seeds showed greater resilience to artificial ageing than IND fruits.

## DISCUSSION

When comparing the naturally occurring diaspores of *Ae. arabicum*, IND fruits were found to be less resilient to artificial ageing than M+ seeds (Fig. 11). If dormancy was a strategy for ensuring longevity, as previous literature had assumed, it should be the case that the dormant seeds are more resilient to ageing than non-dormant seeds. This is not the case in *Ae. arabicum* and suggests that instead, longevity in M+ seeds serves a different function to dormancy in IND fruits. Both could be traits to ensure resilience of the seeds in the seed bank, but where M+ seeds are equipped to cope with a wider range of environmental pressures, IND fruits are less so. The removal of the pericarp of IND fruits removed the dormancy

potential, demonstrating that it is the pericarp of IND fruits that is involved in dormancy of this diaspore, supporting previous literature (Lenser *et al.*, 2016; Arshad *et al.*, 2019). The pericarp also allowed for greater resilience against artificial ageing, with IND fruits being resilient to a wider range of artificial ageing treatments than M- seeds alone.

M+ seeds and M- seeds had similar germination patterns, but M+ seeds were more resilient to a wider range of artificial ageing treatments than M- seeds. M+ seeds also demonstrated an all-or-nothing response to artificial ageing treatments. They appear to be able to withstand certain artificial ageing treatments or fail to germinate altogether. This is different to the IND fruits and M- seeds, which showed reduced germination and final germination percentage in response to higher humidity for greater ageing times (Fig. 11). This could potentially be explained by their longevity mechanisms, as these mechanisms could be involved in repairing the damage caused by artificial ageing. However, at greater humidities and for longer ageing times, if these mechanisms are then damaged, that would cause the seed to fail to repair itself and therefore fail to germinate. This could go part of the way to explaining why there is such a drastic difference in whether the M+ seed is able to germinate or not.

Previous studies have demonstrated the susceptibility of seeds persisting with longevity to high relative humidity and high temperature (Walters, 2008; Groot *et al.*, 2012; Sano *et al.*, 2016). This can lead to problems when storing seeds, as high seed moisture levels cause loss of vigour. However, results from these artificial ageing experiments suggest that longevity makes *Ae. arabicum* seeds more resilient to a wider range of relative humidities, including higher relative humidities, than dormancy. As shown by previous studies, very high relative

humidities did cause a dramatic decrease in germination, the range of humidities at which the M+ seeds were able to withstand were wider than IND fruits. M+ seeds and IND fruits of *Ae. arabicum* would therefore be a good candidate for determining and researching longevity mechanisms. M+ seeds are able to produce a mucilaginous layer where M- seeds are not. It would be interesting to see the effect of removing the mucilaginous layer of M+ seeds and seeing how this impacts their resilience to ageing. This mucilage has previously been suggested to assist in embryo DNA damage and promote seedling growth in harsh desert environments (Yang *et al.*, 2011; Yang *et al.*, 2012).

While artificial ageing is limited in the information it can provide about the response of seeds and fruits to natural ageing in the native environment, it can reveal important insight into the relative tolerance of different diaspore types to environmental pressures. Using this, it is possible to gauge the potential for a seed to survive in different environments. It also allows for insights, such as those presented in this chapter, about the kind of mechanisms in place for different seed-types. While it is not possible to gauge the length of time a seed can persist for in the seed bank, what the ageing experiment can reveal is the different mechanisms used to persist. This allows us to better understand why a plant may exhibit heteromorphism and produce two different fruit and seed types. If there is a different evolutionary advantage to adopting longevity or dormancy, then these two mechanisms could allow for the survival of seeds and fruits in different environments.

If a seed disperses into a sub-habitat where fixing damage by ageing leads to increased persistence, longevity would be the more advantageous mechanism. Alternatively if the

environment required a seed to go dormant, having another seed-type with this capability would be more adaptive. In the case of *Ae. arabicum*, there are two distinct environments in which these seeds persist. Across the Anatolian mountains the environment can be roughly separated into two distinct sub-habitats: the top of the mountain, which is more exposed and has limited nutrients and water access, and the bottom of the mountain, which has greater nutrient and water access but is more competitive. As well as this, there is a temperature gradient from the bottom to the top of the mountain. *Ae. arabicum* is known to grow between 0-3000 metres above sea level, and is able to sense the sub-habitat into which it has dispersed and respond by producing a different ratio of IND and DEH fruits in response to this (Lenser *et al.*, 2016; Arshad *et al.*, 2019; Bhattacharya *et al.*, 2019; Nichols, Leubner-Metzger & Jansen, 2020). Having two seed-types that are able to use different mechanisms for persistence in the seed bank could be adaptive in such an environment with two different sub-habitats.

A negative correlation between longevity and dormancy was recently discovered in *Arabidopsis* (Nguyen *et al.*, 2012). This negative correlation had a genetic basis, in which genes promoting seed dormancy decreased seed longevity. Seeds are able to either extend lifespan through dormancy or active longevity mechanisms. It was suggested that this could be because the two mechanisms are adapted for different environmental pressures. Increased dormancy has been linked to reduced access to water, or aridity (Barazani *et al.*, 2012). This, in part, could explain the increased ratio of dormant IND seeds of *Ae. arabicum* at the top of the mountains, where there is reduced water access. *Aethionema arabicum* has been shown to alter the ratio of its two fruit types in response to temperature as a clue to location

(Nichols, Leubner-Metzger & Jansen, 2020). It could also be possible, therefore, that they are able to respond similarly to a reduction in water supply and produce a greater ratio in IND fruits.

Until recently, empirical studies have mainly focussed on seed dormancy (Nguyen *et al.*, 2012). This could be because dormancy has been misrepresented in the literature (Finch-Savage & Leubner-Metzger, 2006). Dormancy requires a mechanical or physiological mechanism that prevents germination from taking place. Some instances of dormancy have been seeds failing to germinate due to environmental conditions and have had no mechanical mechanism associated, making these a passive form of dormancy which, in recent literature, has been dismissed as true dormancy. Research into longevity is limited. Especially research with a focus on longevity as an active repair mechanisms that cause it. Understanding these mechanisms and the contribution they have to seed persistence are required for greater ecological understanding (Nguyen & Bentsink, 2015). Future work should investigate these longevity mechanisms and their adaptive advantages, because understanding them could have important implications for conservation and agriculture.

## CHAPTER FIVE: HORSES FOR COURSES

### SEED PERSISTENCE TRAITS IN HETEROMORPHIC SPECIES *AETHIONEMA ARABICUM*

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Bethany S. Nichols & Vincent A. A. Jansen

*Draft paper*

#### ABSTRACT

*Heteromorphism can evolve in response to highly variable environment in which intermediate forms have low fitness. *Aethionema arabicum* is a heteromorphic species that alters the ratio of its two diaspore types in response to environmental conditions. One of the diaspores can undergo dormancy to avoid unfavourable years, while the other does not disperse and actively repairs the damage of ageing through longevity. The ratio of these diaspores can be plastically altered in response to the environment in which the parental plant grows and this has been shown to be adaptive for dispersing in a highly variable environment. Here we will show through mathematical modelling that altering the rate of longevity and dormancy is also adaptive under different environmental conditions. Using life history data from this species, we will also show that under conditions similar to those found in their natural habitat, having plasticity between the diaspore types is optimal and discuss the possible reasons for this. Understanding the ecological differences between dormancy and longevity could be essential for seed storage, and conservation and management of plants.*

## INTRODUCTION

Seed heteromorphism was described in 1985 by Venable as, “the production by single individuals of seeds of different form or behaviour” (Venable, 1985). Spatial and temporal variability within an environment can lead to heteromorphism, where a plant can produce two offspring morphs that are adapted to cope with different evolutionary constraints. Heteromorphism has been shown to evolve as a bet-hedging strategy in environments where temporal or spatial variability are high (Harper, 1977; Schoen & Lloyd, 1984). However, heteromorphism has also been shown to evolve in response to extreme environmental variation, when intermediate forms have a relatively low fitness (Venable, 1985). Heteromorphism can lead to structural differences such as in the size and shape of seeds and fruits, or behavioural traits, including dispersal and dormancy capabilities. In this chapter, we will focus on *Aethionema arabicum*, a heteromorphic, or more specifically a dimorphic species, which produces two different fruits and seeds which have different structures, and dispersal and dormancy traits (Lenser *et al.*, 2016; Arshad *et al.*, 2019).

*Aethionema arabicum* is a heteromorphic, annual species from the Brassicaceae family and has two fruit types, each containing different seed-types (Lenser *et al.*, 2016). The larger of the two fruits are called dehiscent fruits (DEH) and they contain 2-6 seeds (M+). Indehiscent fruits (IND) are smaller and contain only 1 seed (M-). The fruits and seeds have different dispersal and dormancy mechanisms. IND fruits are capable of dispersal, and have evolved traits to aid their movement. The fruits are winged to aid with wind dispersal and buoyant to aid with water dispersal (Arshad *et al.*, 2019). The M- seeds contained within IND fruits lack a mucilaginous layer, and undergo dormancy when inside the IND pericarp. DEH fruits dehisce



while on the plant and drop their seeds into the local environment. The M+ seeds they contain produce a mucilaginous layer and do not go dormant but germinate under optimal conditions.

Results from Chapter Four indicate that the seeds also differ in their resistance to ageing. M+ seeds appear to be more resistant to artificial ageing than M- seeds, suggesting that they could be undergoing longevity and have active repair mechanisms. Previous literature has often confused longevity with dormancy (Thompson *et al.*, 2003). However, more recently, dormancy and longevity have been described as two separate traits that maintain viability in seeds until germination (Nguyen & Bentsink, 2015). Dormancy is temporal dispersal, and allows a seed to delay germination until the environmental conditions are optimal. Whereas, longevity maintains seed vigour, preventing the seed from ageing and becoming sensitive to environmental conditions (Rajjou & Debeaujon, 2008). As dormancy and longevity have different roles in persistence, they are each an adaptive mechanism for seed survival (Nguyen *et al.*, 2012). Both persistence mechanisms have been shown to protect seeds in the face of extreme temperatures, freezing and desiccation (Sano *et al.*, 2016).

Venable produced a generalised model to describe the evolution of dispersal heteromorphism, where each morph is better adapted to a different year type (Venable, 1985). We produced an alternative model with Gerhard Leubner-Metzger (2020) in Chapter Two that allows for severely fluctuating, multi-habitat environments, where neither offspring morph is better adapted for a particular year type, but rather one type is capable of dispersal and the other is not (Nichols, Leubner-Metzger & Jansen, 2020). The model shows the importance of sensing and site-specific dispersal plasticity when there is a difference in

variability between multiple environments. However, in this model dispersal rates are not directly linked to morph types and so can be used to investigate other strategies such as phenotype switching (Moxon *et al.*, 1994; Metzgar & Wills, 2000; Jansen & Stumpf, 2005; Kussell & Leibler, 2005). Phenotype switching is the ability of an individual to sense an ambient environmental cue and switch phenotype.

In the wild, *Ae. arabicum* can be found along steep slopes and stony steppe in the Anatolian mountains. The plants are able to sense their location through temperature as an environmental clue and alter the diaspore ratio in response. This response is plastic and is dependent on the environment that the offspring disperses into (Lenser *et al.*, 2016; Arshad *et al.*, 2019; Nichols, Leubner-Metzger & Jansen, 2020). In Chapter Two, we discussed how optimal dispersal ratios differed depending on the sub-habitat the plant grew in. As *Ae. arabicum* is a heteromorphic species that exhibits plasticity in its seed and fruit morph ratios, it is an ideal candidate for investigating the effect of the environment on the relative fraction of diaspore morphs (Nichols, Leubner-Metzger & Jansen, 2020). It is also a good candidate to investigate the optimal dormancy rates in response to environmental variability. Here, I will show theoretically that in environments of high environmental variability, longevity and dormancy have different ecological functions. I will do this by investigating the fractions of seed morphs produced under different environmental conditions. In this way, it is possible to investigate how the morph associated traits will perform under different environmental conditions. These roles help the plant to survive in environments with multiple sub-habitats, such as those along the Anatolian Mountains.

## MATERIAL AND METHODS

### *The model*

The model (12) is an expansion of the dispersal model from Chapter Two (Nichols, Leubner-Metzger & Jansen, 2020) and describes an annual, heteromorphic plant population living between two sub-habitats:

$$\dot{N} = \begin{bmatrix} (1-g_{11})(1-r_1) + (1-d_1(1-c))j_1s_1g_{11} & (1-d_1(1-c))j_1s_1g_{12} & (1-)d_2(1-c)j_2s_2g_{21} & (1-)d_2(1-c)j_2s_2g_{22} \\ (1-j_1)s_1g_{11} & (1-g_{11})(1-r_1) + (1-j_1)s_1g_{12} & 0 & 0 \\ (1-)d_1(1-c)j_1s_1g_{11} & (1-)d_1(1-c)j_1s_1g_{12} & (1-g_{21})(1-r_1) + (1-d_1(1-c))j_2s_2g_{21} & (1-d_2(1-c))j_2s_2g_{22} \\ 0 & 0 & (1-j_2)s_2g_{21} & (1-g_{22})(1-r_2) + (1-j_2)s_2g_{22} \end{bmatrix} N. \quad (12)$$

Within each sub-habitat, the population ( $N$ ) is a vector of four variables ( $N_1, P_1, N_2, P_2$ ): IND fruit seed bank in sub-habitats 1 and 2 ( $N_1$  and  $N_2$ ) and M+ seed banks in sub-habitats 1 and 2 ( $P_1$  and  $P_2$ ). There is a fecundity for each sub-habitat ( $S_1$  and  $S_2$ ). Plants that grow from M-seeds in IND fruits or M+ seeds can produce both IND and DEH fruits, so a fraction of this fecundity is IND fruits ( $j_1$  and  $j_2$ ) and the remaining fraction is DEH seeds ( $1-j_1$  and  $1-j_2$ ). The fraction of the two diaspores is dependent on whether the parental plant was grown in sub-habitat 1 or 2. IND fruits disperse at a rate depending on the sub-habitat that it was grown in ( $d_1$  and  $d_2$ ). A fraction of IND fruits will die before reaching the other sub-habitat ( $\mu$ ). Another fraction will disperse from the sub-habitat but will fail to disperse and fall back into the native sub-habitat ( $c$ ). M+ seeds do not disperse.

The two diaspores also have differing germination rates (Chapter Four). This is because the IND fruits undergo dormancy, whereas the M+ seeds undergo longevity. There are four

germination rates: germination in sub-habitat 1 of IND fruits ( $g_{11}$ ), germination in sub-habitat 1 of M+ seeds ( $g_{12}$ ), germination in sub-habitat 2 of IND fruits ( $g_{21}$ ) and germination in sub-habitat 2 of M+ seeds ( $g_{22}$ ). This model simplifies the variables of dormancy and longevity. In this way, longevity in M+ seeds is defined by  $g_{12}$  and  $g_{22}$ , and dormancy in IND fruits is defined as  $1-g_{11}$  and  $1-g_{21}$ . The two diaspore types also have associated germination mortality rates, depending on whether they undergo dormancy or longevity ( $r_1$  and  $r_2$ ). Fitness ( $Q$ ) was determined by the average growth rate of the population which was calculated by the change in population size divided by the number of simulations run (1).

### *Environmental conditions*

There are two types of environmental conditions used in these simulations. The first is random. In the random conditions, both sub-habitats are exposed to the same percentage of good years, in which fecundity is 5, and bad years in which fecundity is 0.0005. The order of good and bad years is different in the two sub-habitats, but the percentage is the same. The second set of environmental conditions are more complex and are based on the environmental conditions used in Chapter Two (Nichols, Leubner-Metzger and Jansen, 2020). These conditions are designed to mirror the environment experienced in the Anatolian Mountains, which *Ae. arabicum* experiences under normal conditions. In sub-habitat 1, fecundity is  $S_1 + \frac{v}{f}$  in good years, where  $v$  is the severity of the year and  $f$  is the frequency of bad years. In bad years, fecundity is  $S_1 - \left(1 - \frac{1}{f}\right)v$ . In sub-habitat 2, the environment is constant and so fecundity is calculated as half way between the fecundity of sub-habitat 1 in good and bad years. The frequency of bad years experienced in sub-habitat 1 is  $\frac{1}{f}$ , and so the

fecundity of sub-habitat 1 is higher than the fecundity of sub-habitat 2 in good years, and every few years the fecundity of sub-habitat 1 will drop below the fecundity of sub-habitat 2.

### *Life history data*

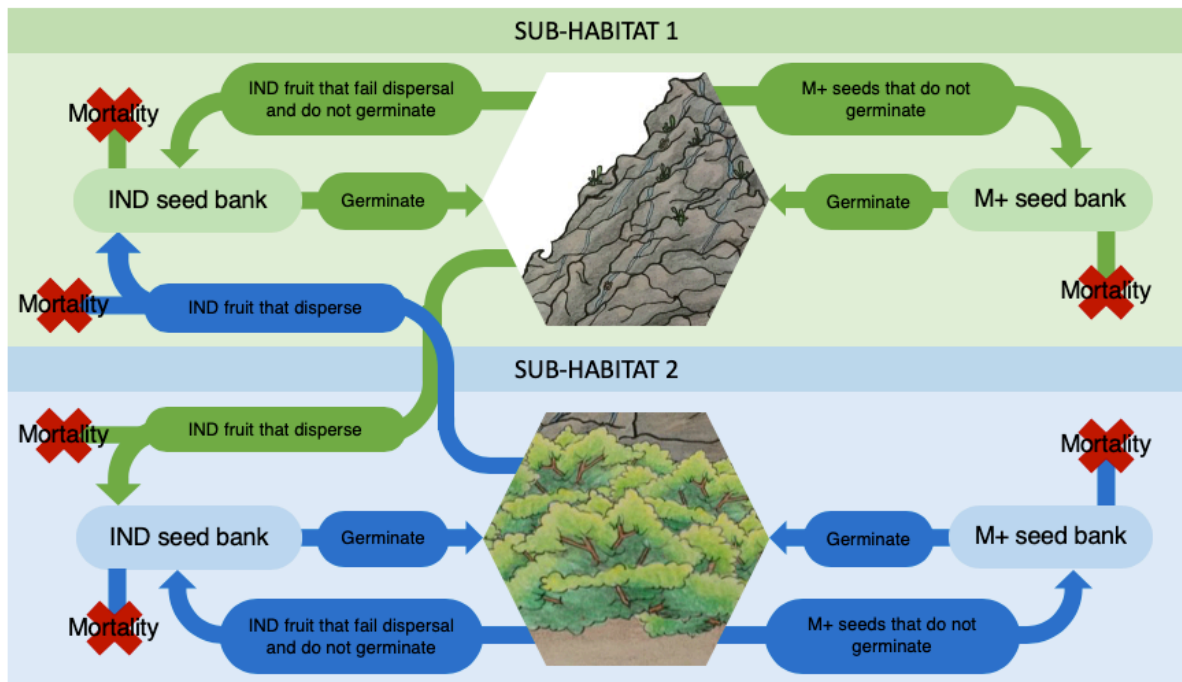
For the purpose of making the model specific to *Aethionema arabicum*, some life history data was used for the variables. The fractions of IND fruits ( $j_1$  and  $j_2$ ) were taken from the results from Lenser *et al.* (Fig. 10C; Lenser *et al.*, 2016). The results showed that at a higher temperature, the fraction of IND fruits was approximately 0.2 and at the lower temperature, the fraction was approximately 0.55. In this model, the higher temperature would be expected to be at the bottom of the mountain in sub-habitat 2, and therefore  $j_2$  was set to 0.55.  $j_1$  was then set to 0.2, as the lower temperature was expected to be at the top of the mountain in sub-habitat 1.

For the differently variable sub-habitat conditions, the germination rates for DEH fruits and M+ seeds were taken from Chapter Four. I do not have information about germination rates of either diaspore type under natural conditions. Therefore, germination rates of IND fruits ( $g_{11}$  and  $g_{21}$ ) were both set to the final average germination percentage of the control IND fruit without hormones, which was 0.16. Likewise, germination rates of M+ seeds ( $g_{12}$  and  $g_{22}$ ) were both set to the final average germination percentage of the control M+ without hormones, which was 0.91 (Appendix IV).

## RESULTS

### *The model*

The model (Fig. 14) tracks the number of seeds in two seed banks in each sub-habitat in any given year. One seed bank contained IND fruits and the other contains M+ seeds. Every year, each sub-habitat produces a number of M+ seeds and IND fruits. A proportion of M+ seeds that do not germinate enter the M+ seed bank. M+ seeds already in the seed bank germinate at a given rate and also have a mortality rate. IND fruits disperse into the other sub-habitat at a given rate. Of the IND fruits that disperse, they're exposed to a mortality rate and a rate of dispersal failure, meaning they land back in their natal sub-habitat. IND fruits that survive dispersal either enter the seed bank of the other sub-habitat or germinate immediately. IND fruits that fail to disperse enter the natal seed bank. In both seed banks, they are then exposed to a mortality rate and a germination rate. The model tracks only the seeds in the seed banks and so does not include seeds that immediately germinate in either sub-habitat.

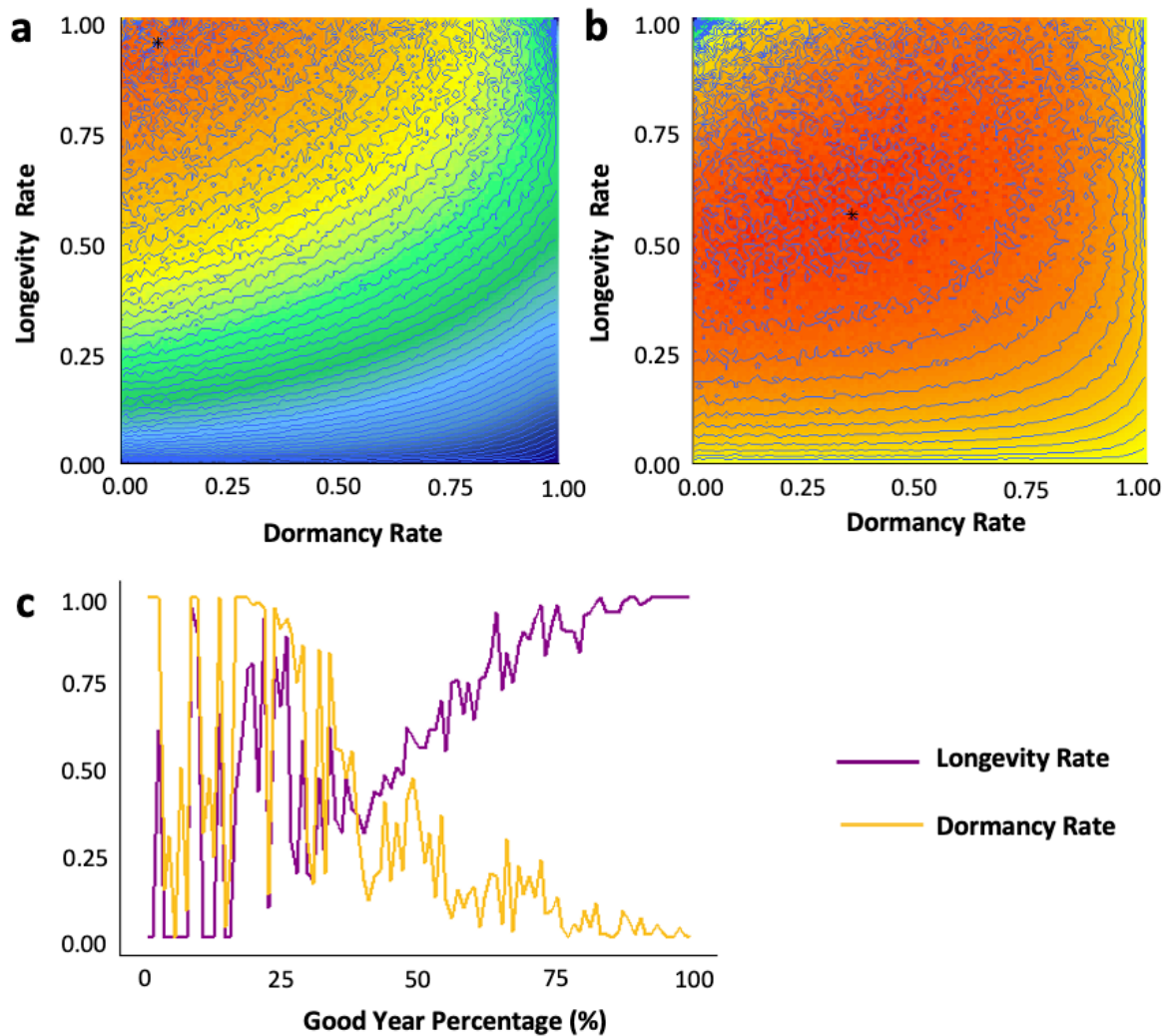


**Figure 14: The model represents the heteromorphic lifestyle of *Aethionema arabicum* and tracks the movement of the two diaspores *M+* seeds and *IND* fruits between two sub-habitats. The model is divided into four seed banks: two *IND* fruit seed banks with one in either sub-habitat and two *M+* seed banks with one in either sub-habitat. *M+* seeds that do not germinate enter the seed bank. *M+* seeds already in the seed bank are exposed to a germination rate and a mortality rate. *IND* fruits are dispersing diaspores and so a proportion of these will enter the *IND* seed bank of the other sub-habitat and are exposed to a mortality rate. Some *IND* fruits will fail to disperse and will fall back into the natal sub-habitat seed bank. *IND* fruits already in either *IND* seed bank are exposed to a germination rate and a mortality rate.**

### *Longevity and dormancy in increasingly variable environments*

When the environment is assigned a percentage of good years, randomly spread among bad years, the results suggest that the relationship between dormancy and longevity is negative (Figs. 15a and b). The optimal dormancy and longevity rates are indicated by the \*. When the percentage of good years is decreased from 90% (Fig. 15a) to 50% (Fig. 15b), and so from less variable to more variable, the corresponding dormancy rate increases and longevity rate decreases. Looking at this relationship across a range of randomly variable environments, where the optimal longevity rate increases with an increase in good years, the optimal dormancy rate decreases (Fig. 15c).

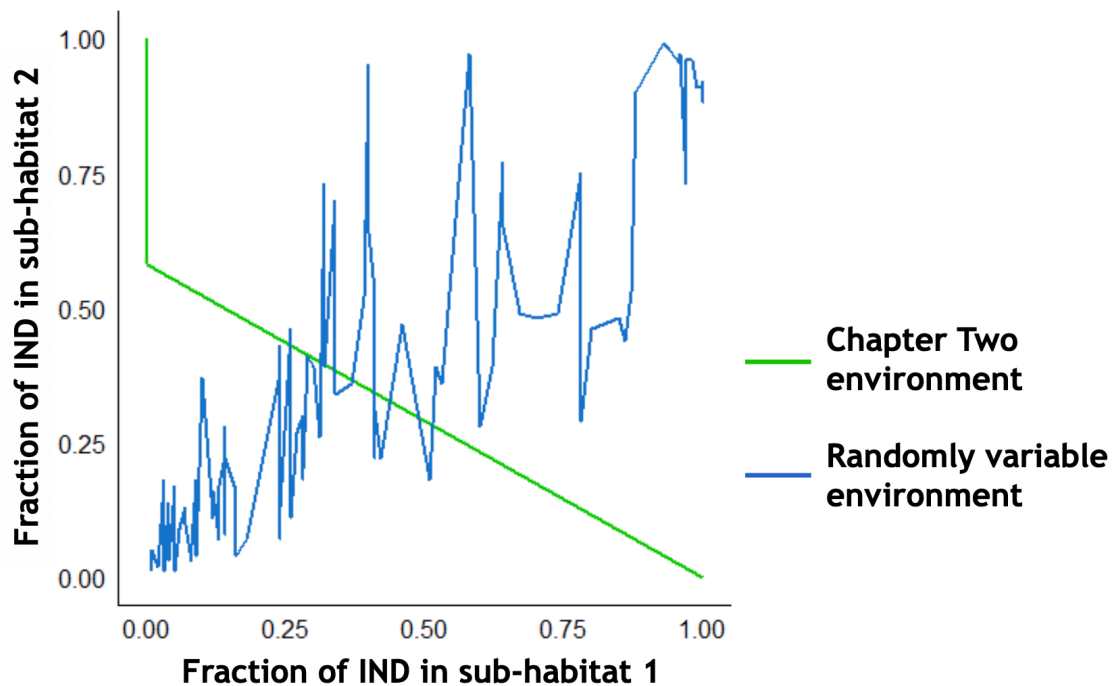




**Figure 15: Under randomly variable environments, longevity and dormancy are negatively correlated.** (a and b) The heat maps show a negative relationship between longevity and dormancy rate. The optimal longevity and dormancy rate is indicated by the \*. (a) percentage of good years = 90% and (b) percentage of good years = 50%. (c) Tracking the optimal longevity and dormancy rate at each good year percentage reveals the trade-off between the two traits under the following variables were used:  $d_1 = 0.99$ ,  $d_2 = 0.99$ ,  $\mu = 0$ ,  $r_1 = 0$  and  $r_2 = 0$  and  $c = 0$ .

### *Heteromorphism under different environmental conditions*

When the heteromorphic model is exposed to an environment in which the two sub-habitats experience the same percentage of randomly ordered good and bad years, the fraction of IND fruits in both sub-habitats is approximately the same. However, when the model is exposed to an environment where one sub-habitat is constant but low and the other variable, the opposite relationship is seen. Under these conditions, as the frequency of bad years is altered, the fraction of IND fruits in sub-habitat 1 is negatively related to the fraction of IND fruits in sub-habitat 2 (Fig. 16). A higher fraction of IND fruits in sub-habitat 1 is optimal when the frequency of bad years is higher in sub-habitat 1 and a higher fraction of IND fruits in sub-habitat 2 is optimal when the frequency of bad years is lower in sub-habitat 1.



**Figure 16: Optimal fractions of IND fruits in sub-habitats 1 and 2 are different under different environmental conditions.** Under randomly variable environments, there is a positive relationship between the fractions of IND fruits in sub-habitats and 1 and 2. In an environment where one sub-habitat experiences constant conditions and the other experiences conditions that fluctuate above and below the other, specifically the environment from Chapter Two (Nichols, Leubner-Metzger & Jansen, 2020), a negative relationship between the two is seen. The following variables were used:  $S_1 = 180$ ,  $v = 200$ ,  $d_1 = 0.99$ ,  $d_2 = 0.99$ ,  $\mu = 0$ ,  $r_1 = 0$  and  $r_2 = 0$  and  $c = 0$ . Good year percentage was altered from 0-100% in the randomly variable environment and the frequency of bad years experienced in the Chapter Two environment was altered between 1 to  $\frac{1}{9}$ .

## DISCUSSION

Results from this model suggest that a heteromorphic lifestyle is not optimal under randomly variable environments, but also in environments with different environmental variability, but of similar low quality. In two sub-habitat environments with one constant, but low yielding sub-habitat and one fluctuating sub-habitat, adopting different fractions for dormant IND fruits in either sub-habitat is optimal (Fig. 16). A higher fraction of dormant seeds is optimal in one sub-habitat whereas it is lower in the other. Having two diaspore types, one that can undergo dormancy and the other that can undergo longevity, allows for survival in environments that are both temporally and spatially varying. Furthermore, in an environment with two sub-habitats where conditions are randomly variable, there is a negative relationship between dormancy and longevity (Fig. 15). Longevity appears to be more adaptive under less variable conditions and dormancy appears to be more adaptive under strongly variable environmental conditions. In Chapter Four, I suggested that a greater ratio of IND fruits are produced in sub-habitat 1, higher up in the mountainous landscape because increased dormancy has been linked to limited access to water (Barazani *et al.*, 2012; Lenser *et al.*, 2016; Arshad *et al.*, 2019). This was because at the top of the mountains, where there is reduced water access, dormant IND seeds of *Ae. arabicum* would perhaps perform better. Results from this chapter support this hypothesis, as dormancy was found to be favoured in sub-habitats with higher variability (Fig. 15).

By using the environmental conditions from Chapter Two, it was possible to begin investigating the aspect of plasticity in *Ae. arabicum*, in relation to dispersal (Nichols, Leubner-Metzger & Jansen, 2020). Plasticity of the diaspore-types allows for additional fitness, when

investigating dispersal as a trait for survival in differently variable environments. In this Chapter, we were able to show that this also relates to heteromorphism and dormancy, and that plasticity between M+ seeds and IND fruits is optimal between the sub-habitats under similar environmental conditions as those from Chapter Two (Fig. 16). I would like to take this investigation further and look at the breadth of environmental conditions for which this is true. In Chapter Two, I was able to do this by altering both severity and frequency of environmental variable in sub-habitat 1 (Fig. 5). If a similar method was applied to the heteromorphic model presented in this chapter, I think it would reveal the scope for this model in assessing heteromorphic plant responses to environmental variability.

With extreme weather conditions such as droughts, flooding and storms on the rise due to climate change, species that have evolved in lowly variable, temperate climates are more at risk (Michener *et al.*, 1997; Watson *et al.*, 1998; Easterling *et al.*, 2000; McLaughlin *et al.*, 2002). *Aethionema arabicum* populates mountainous environments where the two sub-habitats will experience climate change differently. At higher elevations and on mountaintops, will be more affected by windstorms and precipitation due to being more exposed. Whereas, at lower elevations and on the plains, they will be more sheltered but prone to flooding and erosion (Barry, 1992; Beniston, 2006). Understanding how heteromorphic species could respond to increases or changes in environmental variability is key for conservation and management programs. In Chapter Two, we produced a model to describe populations dispersing within such environments and in Chapter Three we produced a model to describe annual and perennial populations dispersing and undergoing dormancy in such environments. In this Chapter, we produced a model that describes annual,

heteromorphic species that undergo dormancy and dispersal. This is important, because in heteromorphic species, dispersal and dormancy rates are now linked to seed types, and so these rates are now constrained by what fraction of seed types are produced.

Having a heteromorphic model such as the one presented in this chapter also allows for the exploration of dispersal and dormancy traits within a species such as *Ae. arabicum*. While empirical data has often been collected at a species level, seed dispersal and dormancy models have largely focussed on the individual level (Buoro & Carlson, 2014). Results from such empirical studies has suggested that the relationship between dormancy and dispersal could fluctuate from positive to null. However, these models have not been equipped to investigate these relationships (de Casas *et al.*, 2015). In Chapter Three, we designed a species level model and were able to investigate positive and null dispersal and dormancy strategies in managed landscapes in annual and perennial species. In this chapter, results from the heteromorphic model again suggest that responding plastically in sub-habitats with different environmental variability is optimal. Because such environments are temporally and spatially variable, having plasticity in a trait that aids against temporal variability (dormancy) and a trait that aids against spatial variability (dispersal) can be adaptive (Den Boer, 1968; Frisch, 2002).

Seed dormancy and longevity have previously been misrepresented in the literature (Finch-Savage & Leubner-Metzger, 2006; Long *et al.*, 2014). Dormancy has been seen to be mechanism by which a seed gains longevity. However, a recent study has shown a negative relationship between longevity and dormancy at a genetic level in *Arabidopsis* (Nguyen &

Bentsink, 2015). The *DOG1*-Cape Verde Islands allele responsible for reducing longevity promoted dormancy. The evolution and adaptive qualities of dormancy have been discussed and reviewed, but as of yet, no review of longevity or persistence exists (Bewley, 1997; Baskin & Baskin, 1998, 2004; Koornneef, Bentsink & Hlhorst, 2002; Finch-Savage & Leubner-Metzger, 2006). As more evidence emerges about the differences between dormancy and longevity, there needs to be better clarity in the field of seed ecology to separate these traits and determine their adaptive qualities. Understanding these could assist in the conservation and management of plants adopting these different traits when persisting in the soil.

The model is equipped to investigate the relationship between longevity and dormancy within the micro-environment within each sub-habitat using the parameters of  $r_1$  and  $r_2$ .  $r_1$  and  $r_2$  are the mortality rates and are therefore associated with longevity and dormancy. By manipulating these variables it would be possible to see the impact on longevity and dormancy rates associated with each micro-environment. This is something that I would like to investigate following this project, as I believe it will provide further theoretical evidence as to the function of longevity and dormancy as two different traits for seed persistence in the soil. In this chapter we have been able to show how longevity and dormancy could be different persistence mechanisms as the two traits were found to be optimal under different environments (Figs. 15 and 16). With further investigation, it may be possible to describe the adaptive function they have within the sub-habitats and discuss the range of environments in which they are optimal.

Another element that could be explored using this model is longevity and dormancy and their relationship with seed depth. Because both diaspores of *Ae. arabicum* can disperse into or remain in either sub-habitat, it could be that neither are specifically adapted to a sub-habitat, but rather the seed bank they fall into within that sub-habitat. Seeds of different shapes and sizes can end up in different levels within the soil, where they experience different conditions (Harper, 1977; Brown & Oosterhuis, 1981; Bekker *et al.*, 1998; Chambers, 2000). If the two diaspore types of *Ae. arabicum* are buried at different depths, dormancy or longevity could be adaptive for the environment at that depth. For example, greater proportions of high-dormancy phenotypes of Canola (*Brassica napus* L.) were found in deeper seed banks where soil temperatures were higher during Spring (Gulden, Thomas & Shirtliffe, 2004). By replicating the seed banks that M+ seeds and IND fruits disperse into in this model, this could provide insight into the adaptation of dormancy and longevity of the two diaspores in a natural environment. A potential next step for research into dormancy and longevity in *Ae. arabicum* could investigate the burial potential of IND fruits and M+ seeds. There could be some adaptive benefit to becoming dormant or undergoing longevity dependent on how buried the diaspores are in either sub-habitat.

Adopting both seed dispersal and dormancy can make a species resistant to spatial changes and long periods of poor conditions. In such environments, it is a question of horses for courses; producing diaspores of different form and behaviour in order to increase the chance of survival in an environment with highly variable spatial and temporal conditions. Understanding seed dispersal and dormancy strategies will help with biodiversity conservation, pest management and disease outbreak (Buoro & Carlson, 2014). In



heteromorphic species, these traits are tied to diaspore type, and so the effect of the additional constraints of this need to be explored. When it comes to understanding dormancy, much of the previous literature has mistaken longevity for dormancy (Finch-Savage & Leubner-Metzger, 2006) and as a result, research into longevity is limited (Nguyen *et al.*, 2012). Understanding longevity as a different persistence mechanism to dormancy is required for greater ecological understanding (Nguyen & Bentsink, 2015). Future work should investigate the scope for the evolution of heteromorphism in highly variable environments, and the adaptive potential of longevity because understanding them could have important implications for seed storage, conservation strategies and agriculture.

## DISCUSSION

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In this thesis, I investigate seed dormancy and dispersal as two survival strategies, both together and separately. Understanding such strategies is key for generating impactful approaches to conservation and pest control, as well as understanding how species living in complex environments will be affected by environmental and land use changes. However, existing models based in bet-hedging theory were incapable of exploring more complex environments to the extent that the models presented in this thesis have been able to do. Being able to investigate more complex environments allows us to understand how plants are surviving in the harshest and most difficult of conditions.

In Chapter Two, I explored how adopting a plastic offspring dispersal rate is an evolutionary advantage, in response to localised environmental variability. This ability is aided by sensing, as sensing the environment into which an individual has dispersed allows the plant to alter their dispersal rate to best fit the environment they are in. This model is not limited to plant dispersal, but is also able to investigate the dispersibility of animals who have a similar mechanism. This trait allows individuals to survive in otherwise challenging environments and demonstrates the importance of plastic dispersal mechanisms. Dispersal in plants has largely been considered passive, with plants having no control over their fate. This model demonstrates that plasticity allows plants to alter their dispersal rate and so gives them an active role. Plasticity of this nature in plants is under-researched, and should be explored empirically to better understand its role.

This opinion was also aired by DeAngelis and Zhang in their recommendation of the Chapter Two published paper on Faculty Opinions, and its relevance for both animal and plant species existing in highly varying environments was discussed (DeAngelis & Zhang, 2020). In particular, they cited how the model demonstrates the impact of having a severely fluctuating high-elevation sub-habitat, how that promotes the evolution of long-distance dispersal and the importance of being able to sense the relative quality of the sub-habitat in order to determine the offspring dispersal rate.

The model in Chapter Two was adapted for Chapter Three to include dormancy so that the relationship between dormancy and dispersal could be explored. Many plant species have been found to have a positive relationship between dormancy and dispersal, but this had largely been dismissed to pleiotropy. Using the model, I was able to recreate a crude version of the environments in which many of these plants exist, and demonstrated how a positive relationship between dormancy and dispersal is possible. I then adapted the model for a perennial lifestyle, as many of the species exhibiting high dormancy and dispersal rates are perennial, and showed that this behaviour is even stronger in perennials. Environments, such as those managed by human activity, have seasonal and multi-year rotations that provide both the spatial and temporal variability required for both dormancy and dispersal to become adaptive. As land management changes, this could massively impact species evolved to survive in fluctuating landscapes such as these (MacDougall *et al.*, 2018). Understanding the role of both dispersal and dormancy in such species is key in building strong, appropriate conservation plans (Buoro & Carlson, 2014).

In order to produce a model that wholly represents the life-history of *Ae. arabicum*, I wanted to better understand dormancy in this species. I performed an ageing experiment to understand the resilience of the two seed-types, M+ and M- and the impact of the IND fruit coat, so as to better understand their role in the survival of *Ae. arabicum* within its native environment. The results showed that the two seed-types have different persistence mechanisms, with M+ seeds being more resilient and undergoing longevity, and IND fruits controlling dormancy of the less resilient M- seeds. The IND fruit also provides additional resilience to M- seeds. In the literature, dormancy has been cited as being a mechanism of longevity. However, recent research has suggested that an increase in dormancy can lead to a decrease in longevity within a species. Results from Chapter Four support the theory that these traits are separate and so have different roles. Little research has been conducted into longevity as a mechanism for persistence, however, its role could be key to understanding how some species seeds are adapted for existing in certain environments (Sano *et al.*, 2016).

The purpose of Chapter Five was to design a model to explain the lifestyle of the heteromorphic species *Ae. arabicum*, with two seed-types, each possessing different dispersal and dormancy mechanisms and traits for persisting in the soil. This model was used to demonstrate that longevity and dormancy are two separate traits that are differently optimal within different environments. The results showed that under randomly variable environments, longevity and dormancy may be adaptive under different conditions to one another. Further to this, under the simulated natural environmental in which *Ae. arabicum* grows, there is plasticity in the diaspore types, with IND seeds adapted to dispersal and dormancy performing better under more variable environments. I would like to continue this

research to investigate the scope for the plasticity observed and the adaptive benefits of both longevity and dormancy in this species and others. Additionally, I would like to explore whether there is an adaptive benefit to both diaspores persisting in different micro-environments within the sub-habitat, such as different burial depths in the seedbank.

Throughout this thesis, I have shown that limiting a model to one sub-habitat prevents you from seeing why complex traits like dormancy and dispersal evolve. The relationship between the two environments and how they interact is key to understanding such behaviours. Models built on bet-hedging theory are limiting because they don't allow for differing conditions in multiple environments (Supplementary Material; Nichols, Leubner-Metzger & Nichols, 2020). The models presented in this thesis are required to look at more complex, highly variable environments. It is possible to manipulate the models from this thesis to recreate bet-hedging, but the environments discussed in this thesis are outside the operational capacity of bet-hedging.

Extreme weather conditions such as droughts, flooding and storms are becoming more frequent climate change, and it puts pressure on species evolved to life in more temperate conditions (Michener *et al.*, 1997; Watson *et al.*, 1998; Easterling *et al.*, 2000; McLaughlin *et al.*, 2002). Species such as *Aethionema arabicum* survive in environments with multiple sub-habitats where they experience climate change differently depending on which sub-habitat they disperse into. In the Anatolian Mountains for example, higher elevations and mountaintops are becoming more affected by windstorms and precipitation due to being exposed. At low elevations and on the plains, there is greater shelter but these areas are

prone to flooding and erosion (Barry, 1992; Beniston, 2006). With a change in environmental conditions due to climate change, it will become essential to understand the relationship between dispersal and the environments within which it is taking place. By building dispersal-environment relationships into models it will help us to anticipate the impact of climate change on such species (Seale and Nakayama, 2020). How these changes to species will alter community composition is yet to be explored by these models. As many species adapted to life in highly variable environments are invasive or highly competitive, it would be beneficial to anticipate the impact they will have on communities (Richards *et al.*, 2006).

When an individual disperses into a complex, highly variable environment, it asks the question, “Should I stay or should I go?”. By producing seeds that disperse or go dormant, it has two mechanisms by which to do this. Dormancy and dispersal have two different adaptive roles, each important to survive different environmental constraints. Some species exist on the very edge of habitable by relying on these mechanisms and taking advantage of multiple, poor sub-habitats. Seale and Nakayama stress the importance of building ecological models designed to investigate dispersal-environment interactions that go beyond the simplistic characteristics that have previously been produced (Seale & Nakayama, 2020). In this thesis, I have developed and discussed three that go beyond bet-hedging and are capable of looking at more complex dispersal- and dormancy-environment interactions (Tuljapurkar, 1990; Nichols, Leubner-Metzger & Jansen, 2020). By understanding the roles of dormancy and dispersal in complex, highly variable environments, it is possible to design more appropriate conservation and management strategies for both at risk, and highly invasive species.

## APPENDICES

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### APPENDIX I

Publication in *The New Phytologist* on which I am a co-author and formulated the hypothesis that temperature provides the cue for elevation, leading to adaptive plasticity of diaspora ratio (Arshad *et al.*, 2019).

### APPENDIX II

Supplementary material for Chapter Three. Detailed information about species exhibiting both long-term dormancy and long-distance dispersal, with references.

### APPENDIX III

Supplementary material for Chapter Three. Working for the perennial model.

### APPENDIX IV

Artificial ageing data for Chapter Four. The data is separated into three sheets, named (1) Germination with hormones: germination data following artificial ageing, (2) Germination without hormones: germination data with a gibberellin hormone treatment following artificial ageing and, (3) Staining: staining data following artificial ageing and germination with a hormone treatment.

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