Exploring the concept of applied nucleation as a restoration tool in a previously invaded Mediterranean climate vegetation type

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Declaration

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Date: April 2022

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Summary

There is a need to scale-up ecological restoration efforts. The urgency to restore degraded habitats means that we, as researchers, need to be at the forefront of new and innovative restoration techniques. Sometimes this means assessing the efficacy of techniques which are not commonly employed in the vegetation type in need of restoration. In the case of this study, it involved exploring the concept of applied nucleation as a restoration tool in Cape Flats Sand Fynbos (CFSF). Applied nucleation involves establishing clusters of vegetation (nuclei) either by sowing or planting, and these clusters then produce and set seed into the surrounding area, facilitating nucleation. Colonization is further facilitated when the clusters of vegetation establish and are able to capture seed from other species (Corbin & Holl, 2012). This thesis assessed whether applied nucleation would be an effective restoration method in a vegetation type where it has not been employed before. This was done by resurveying previously restored plots to assess whether sown species had begun to set seed and nucleate into the surrounding environment (Chapter 2), and by designing a simulation model to assess which invasion management regimes and Cape Flats Sand Fynbos Species would most effectively facilitate nucleation (Chapter 3). The management regimes were fell & stack whereby felled *Acacia* biomass was stacked into brushpiles and fell & burn involved burning the felled *Acacia* biomass.

A resurvey of active restoration plots established in 2013 through sowing indigenous Cape Flats Sand Fynbos investigated which species had established and persisted, as well as determined which species had set seed outside the initial 10m x 5m sowed plot. Fourteen plots were resurveyed in 2019 by determining species presence and abundance. This information was then compared to survey data from 2014 and 2017 to assess how the restored plots were faring. Of the 30 species sown in 2013, only 11 were observed to still be persisting in 2019.

By establishing a larger 20m x 20m plot around the initial sowing plot, young plants of the species inside in sowing plot were identified, and these species were assumed to be nucleating species. The size (volume) of these young plants as well as their distance to the sowing plot was measured. This was to determine whether there was a significant difference between plant size inside the plot as opposed to outside, as well as to determine the distribution of plants of different ages. Plant size was used as a surrogate for plant age. Four species were seen to have consistently set seed outside the initial sowing plots, and these were *Anthospermum aethiopicum, Ifloga repens, Dimorphotheca pluvialis,* and *Pelargonium capitatum*.

A practical simulation model was designed to assess which management regimes and species would facilitate nucleation the most effectively. The model was designed using the principles of inverse modelling, which is a modelling technique commonly used when certain model parameters are not

available, as it makes use of model outputs to infer the values of model parameters. Management regimes were simulated by arranging theoretical felled *Acacia* brush piles in different patterns and distances around the initial sowed plot as seed traps. Furthermore, the dispersal and colonization of the four nucleating species identified in Chapter 2 was simulated to determine which species possessed the highest colonization and nucleation potential by manipulating certain biological parameters.

The models showed that a fell and stack management regime where brush piles were arranged in a radial pattern facilitated nucleation the best, as this obstacle arrangement initially allowed for long distance dispersal, whereafter seed was trapped when it reached the *Acacia* brushpiles. This resulted in new sources of seed to continue to facilitate nucleation. The *Acacia* reinvasion simulation resulted in the poorest nucleation, as seed was trapped nearby the sowing plot and not allowed to disperse further. The species which displayed the highest nucleation potential was *Dimorphotheca pluvialis*, as this species had a high dispersal distance and reproductive rate.

By analysing and interpreting the results from this study, certain management recommendations and recommendations for future research are proposed to provide a more in-depth understanding of using applied nucleation as a restoration tool in Cape Flats Sand Fynbos. It was concluded that this technique shows promise, but that further research is needed, particularly on the nucleation potential of species that require fire for seed germination.

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Preface

This thesis is presented as a compilation of four chapters. Each chapter is introduced separately and written according to the style of the journal Restoration Ecology. The data chapters have been written as stand-alone papers, and therefore have some overlap of content and information between them.

Chapter 1 – Introduction of the study, aims, and key findings.

Chapter 2 – Entitled "Are previously restored plots nucleating? An assessment of applied nucleation in a Mediterranean climate shrubland", provides an assessment of previously restored plots to determine whether nucleation has occurred.

Chapter 3 – Entitled "Designing a simulation model to test the impacts of different management regimes on the effectiveness of applied nucleation in restoring a degraded, fire-driven Fynbos ecosystem", simulates nucleation under different management regimes and of different species.

Chapter 4 – Entitled "Synthesis of findings and implications for management", provides a synthesis of findings, suggestions for future research, and implications for management.

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Chapter 1: Introduction and key components of the study

1.1 Background context

1.1.1 Ecological restoration

Ecological restoration can be defined as the process of assisting the recovery of a degraded habitat or ecosystem (Gann et al., 2019), or "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". (SER, 2002). As a result of global ecosystem degradation there is a need to scale up ecological restoration efforts. This includes identifying new restoration techniques to trial and implement, because although marginal success has been achieved with traditional methods, there is still room for improvement. Several challenges exist in scaling up restoration efforts, particularly with regard to limited resources. This means that restoration efforts need to effective, and simultaneously not resource intensive. Habitats which possess high biodiversity are of particular concern and require urgent intervention.

1.1.2 Threatened Cape Flats Sand Fynbos

Cape Flats Sand Fynbos (CFSF) occurs in the coastal lowlands of the southwestern portion of the Greater Cape Floristic Region (GCFR). According to Rebelo et al., (2006), CFSF is a vegetation type which is sclerophyllous in nature and dominated by shrubs, and which occurs at lower altitudes on acidic sandy soils. CFSF has incredibly high species biodiversity, and according to Cowling et al. (1996), also has high narrow-range endemism, and low-level growth form diversity. This indicates that many species are closely related or have experienced convergent evolution. Vegetation structure is typically comprised of ericoid and graminoid shrubs, geophytes, and an overstorey component of serotinous proteoid shrubs. These form a mix of non-sprouting (reseeding), and resprouting species (Hall, 2018).

Cape Flats Sand Fynbos is critically endangered, and only about 2% of the remaining habitat is protected, with much of the protected area degraded by invasive alien species (Hall et al., 2021). The vegetation type occurs in an area of less than 40km diameter, between Macassar and Kraaifontein to the east, Lakeside to the south, and the suburb of Blouberg to the north (Rebelo et al., 2006). The Strandveld vegetation type on the Atlantic Ocean coastline buffers CFSF on the seaward side to the west. This vegetation type has 16 endemic as well as 108 Red List threatened plant species (Raimondo et al., 2009), and the conservation of the remaining habitat and restoration of degraded habitat is crucial in ensuring the persistence of what is in actual fact a treasure trove of rare and endemic species.

There have been several restoration initiatives undertaken to restore the remaining areas of CFSF. These have largely involved clearing of alien vegetation and replanting and seed sowing of species indigenous to the area, by volunteers, students, as well as City of Cape Town (CoCT) Biodiversity Management officials (Hall, 2018; Holmes, 2002; Holmes & Cowling, 1997; Holmes et al., 2012). One of the more recent initiatives was that undertaken by Hall (2018) for his PhD. This study included a field trial where plots were both actively and passively restored. Passive restoration involved allowing natural succession to occur without any intervention, whereas active restoration involved sowing seed of native CFSF species in restoration plots. The larger ecological restoration project is being run by the Biodiversity Management Branch of the City of Cape Town Municipality at Blaauwberg Nature Reserve (BBNR). There has been some success with these initiatives, and a partnership with Stellenbosch University has enabled ongoing restoration ecology research in the nature reserve to investigate optimal treatments (City of Cape Town, 2018).

There is still a need to scale up restoration efforts in threatened ecosystems if biodiversity loss is to be slowed down (Hall et al., 2021). However, restoration is expensive and time consuming. A method to restore ecosystems as efficiently as possible is vital to scaling up restoration and thus preventing biodiversity loss.

1.1.3 History of invasion in CFSF

Invasive alien plants have been categorised as one of the largest threats to global biodiversity, after direct habitat destruction, with alien legacy effects persisting long after they have been eradicated (Holmes et al., 2020; Richardson & Van Wilgen, 2004). Invasive alien plants are considered a threat to the livelihoods of humans, as well as a threat to biodiversity (Henderson, 2007; Morris et al., 2020).

The Fynbos biome tends to be invaded relatively easily by fire-adapted alien trees, with two thirds of the protected areas in the Western Cape province invaded (van Wilgen et al., 2016). This poses a major threat to Fynbos species as the alien species are often able to outcompete native vegetation for resources (van Wilgen & Richardson, 1985). Species such as the Australian acacias grow rapidly and are much taller than Fynbos species which are typically shrubs, and thus outcompete native species for water, nutrients and light (Yelenik et al., 2004).

Acacia saligna is a well-known invasive alien species and is the primary invader in the BBNR and in the CFSF lowlands as a whole (Cowell, 2014; Hall et al., 2021; Mukundamago, 2016). Small-scale experiments using *A. saligna* have shown that they greatly reduce the seed banks of native Fynbos species, as well as reducing species richness and cover (Holmes, 2002). This may suggest large-scale

extinctions if the invasives are left unmanaged and are allowed to expand their infestation range, and if restoration initiatives are not implemented in an effort to curb the effects that alien vegetation has not only on biodiversity but on the landscape as a whole (Holmes & Cowling, 1997; Holmes et al., 2020; Morris et al., 2020).

While restoration efforts have been successful (Cowell, 2014; Hall et al., 2020; Mostert et al., 2015), much remains to be desired in terms of scaling up restoration in the most cost and labour efficient manner possible. The BBNR contains a critical portion (400 ha) of the last remaining CFSF remnants, and the conservation and restoration thereof are vital. One method which may be useful in scaling up restoration in the reserve is applied nucleation (Corbin et al., 2016). This is a restoration technique which relies on birds and/or other dispersers to facilitate dispersal in a radial pattern from the original nucleus (Corbin & Holl, 2012). This however may prove difficult in CFSF as frugivory is not a major seed dispersal vector in this vegetation type, while wind dispersal is, particularly for pioneering species such as *Anthospermum aethiopicum* L. and *Passerina corymbosa* Eckl. ex C.H.Wright, two species commonly observed in early stages of succession. The concept can be expanded to encompass wind dispersal, as applied nucleation involves establishing a restored nucleus which then radiates outwards.

1.1.4 Methods of ecological restoration

There are three broad contrasting approaches considered as ecological restoration, and these are passive restoration, broadcast active planting or seeding, and applied nucleation; the latter two being active restoration techniques (Corbin & Holl, 2012). These methods are most employed in forest vegetation types (Elliott et al., 2019). Passive restoration involves the termination of the cause of degradation, such as removal of alien vegetation, cessation of grazing by livestock, or ploughing (Morrison & Lindell, 2011). Applied nucleation and active planting are both successful active restoration techniques, both being the preferred restoration techniques in forest-type vegetation (Zahawi et al.,2013). In shrubland and prairie (Rowe, 2010), such as the Great Plains in the USA, and the Kwongan in Western Australia (Coates et al., 2014), restoration may apply a more agricultural approach, where large-scale broadcast seed sowing is done using agricultural machinery. This latter method is generally not used in forest restoration.

Below are the three primary restoration methods and how they work in ecosystem restoration.
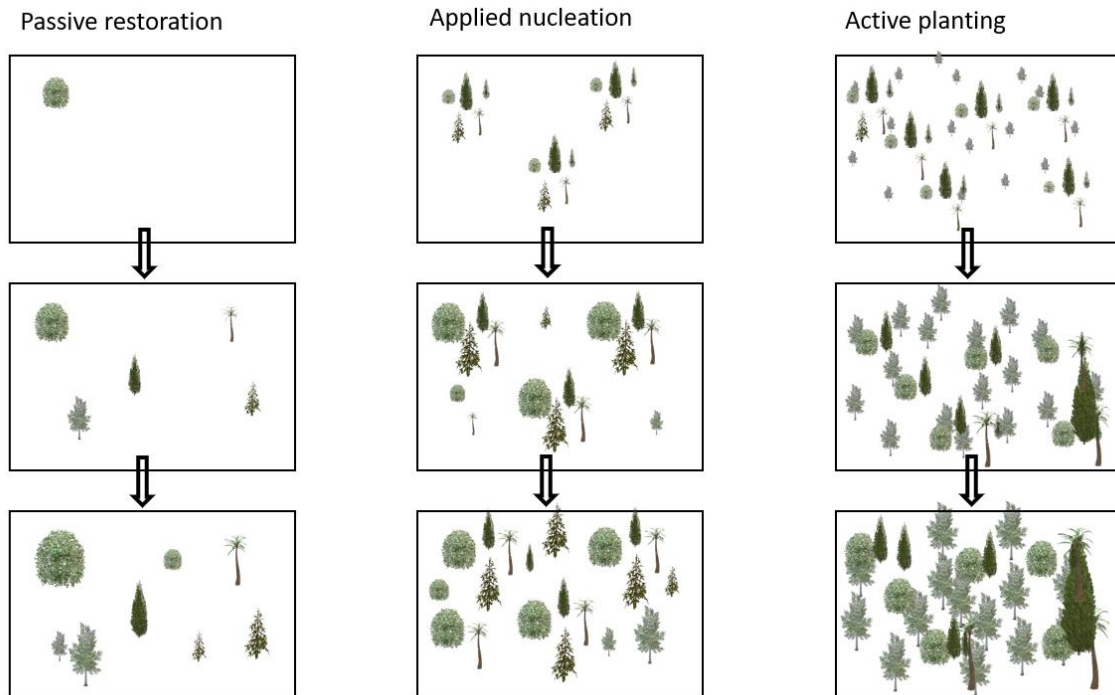
Figure 1.1 Three different restoration methods in forest restoration. The arrows indicate the passing of time.

Passive restoration in forest-type vegetation is arguably the cheapest option of the three, but its effectiveness is questionable unless natural remnants persist nearby as seed sources (Corbin & Holl, 2012). Active planting in this context can be very effective, but planting a large number of diverse indigenous trees could prove to be rather expensive (Bechara et al., 2021; Holl et al, 2011), and if not enough species are used this method can result in plant communities which lack diversity. Plantation establishment of rootstock in the Fynbos biome however would be challenging as many Fynbos species are difficult to establish in the field without irrigation through the first summer, which is simply not feasible in a nature conservation context. Even if the plants establish, it is an expensive and labour-intensive process which is not viable when intending on restoring large areas. An analogous approach here however may be to sow economically valuable species which can be harvested later in an attempt to offset costs (Gaertner et al., 2012). This may also not always be a viable option. In the Fynbos biome the most commonly used method is seed sowing. This however has its limitations as seed supply is limited (P.M Holmes, personal communication).

Applied nucleation however offers the best balance between cost and effectiveness in tropical forests specifically (Corbin & Holl, 2012). Holl & Aide (2011) found that an applied nucleation design which they created would cost up to a quarter of the cost of a typical plantation restoration effort (although

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this would certainly differ from site to site). Applied nucleation has also been found to be more similar to reference site vegetation conditions than large scale planting (Bechara et al., 2021). The effectiveness of applied nucleation in the Fynbos biome, or any dryland ecosystem for that matter, remains unknown, as no research on the efficacy of applied nucleation has been done here.

1.2 Introduction to applied nucleation

1.2.1 What is applied nucleation?

Applied nucleation involves the establishment of clusters of vegetation either by planting individual plants together or by sowing seed in patches, which act as nuclei. After the clusters are established, they expand outwards into the surrounding area and begin to colonise areas still requiring restoration, and this is termed nucleation (Schlawin & Zahawi, 2008). The established nuclei further facilitate colonization as they attract frugivorous species, or trap seed from nearby native vegetation (Corbin et al., 2016). The nuclei are placed in strategic locations and are designed to facilitate or "kick start" nucleation cost-effectively, utilising as few resources as possible, and "attracting" other species as well (Hulvey et al., 2017). As previously mentioned, applied nucleation has been successful in the Forest biome in particular (Corbin & Holl, 2012; Corbin et al., 2016) and this is largely because natural forest recovery occurs in a similar pattern as applied nucleation, whereby after disturbance (such as clearing or fire), pioneer species establish themselves in clumps (nuclei). Other species then establish around these nuclei and spontaneous succession duly occurs. Establishing nuclei is also known to reduce the risk of competition by other species such as grasses, to reduce the effects of harsh microclimates (Corbin & Holl, 2012), and due to a higher plant diversity can stabilise soil (Pohl et al., 2009). This may be beneficial when trying to establish species which are sensitive by nature, and which are difficult to establish.

According to Corbin & Holl (2012), once pioneers and other species colonise an area, further colonization can be facilitated. However, the nucleation concept has largely been applied to forest-type vegetation where frugivory is one of the main mechanisms of seed dispersal. Fynbos recruitment on the other hand is different, as seeds are dispersed passively, ballistically, by wind or ants, and fire is the primary recruitment trigger (Cowling et al., 1996; Mostert et al., 2015). Some inter-fire recruitment does however take place, and this is largely by pioneer shrub species such as *Anthospermum aethiopicum* L. which is dispersed passively.

The establishment of recruitment nuclei has already occurred in the BBNR, when Hall et al., (2021) stablished nuclei by sowing seed mixes of various CFSF plant species under various treatments in a plot in each of thirty two one-hectare blocks within the reserve after *A. saligna* was cleared by the Fell

& Burn method. This was to understand the effectiveness of passive and active restoration techniques. The research of Hall et al., (2021) found that active restoration techniques were necessary in areas which had severe *Acacia* invasion but postulated that passive restoration would be sufficient if some remnant species stayed behind after clearing, and if the native seedbank was still intact.

1.2.2 Factors influencing the success of applied nucleation

There are several factors which are known to influence the success of applied nucleation. According to Corbin & Holl (2012) one of the most influencial factors is the proximity of the nuclei to natural areas as this influences the availability of seeds as well as seed dispersers. This observation was made in forest vegetation types where frugivory is a major mechanism of seed dispersal (Muscarella & Fleming, 2007). Although this may be important in forest vegetation types, frugivory is not a prominent seed dispersal method of CFSF species, or any Fynbos vegetation type for that matter, barring a few species. The closest vegetation type to CFSF where frugivory is important is in the Strandveld along the coast where a thicket component is present (Cowling et al., 1997) as well as in the invaded areas of the reserve where the seeds of *A. saligna* are consumed by animals and may encourage frugivores to import species (Holmes & Cowling, 1997). According to Corbin et al., (2016) the size and number of nuclei are also a factor which influence the success of applied nucleation. Logically, the larger the nuclei are and the more of them there are, the higher the chances are of restoration being successful. This however is sometimes not viable as it may be labour intensive and require an unsustainable amount of resources. The intensity and extent of disturbance before restoration is also a factor to consider, because if the disturbance was too intense, restoration may not be a viable option (Holl & Howarth, 2000).

1.2.3 The ideal species to use for applied nucleation

According to the literature, the number and diversity of recruits may be affected by species which are planted as overstorey (Eccles et al., 2001). Nurse plants are effective in aiding establishment in semi-arid environments (Schurr et al., 2004) and using some nurse plant species may be useful when establishing nuclei in the future. These could typically be larger ericoid or proteoid shrubs (Vlok & Yeaton, 2000). This would also lead to better representation of a typical CFSF vegetation community, and ultimately result in increased resilience (Holmes & Richardson, 1999).

It is important to remember however that the area around the restored nucleus may initially have low species richness, as some species may take longer than others to disperse and/or establish

themselves. For example, many Fynbos species are dependent on fire for germination, and those dispersing from a nucleus will only emerge in the landscape after a future fire event (Hoffman et al., 1987). Such an event has not occurred in the study area since restoration sowing took place in 2013, as fire return intervals in Fynbos generally occur every 10 to 13 years (van Wilgen et al., 2010). Fire intervals in restored vegetation might even be longer as biomass accumulation is slower (K.J Esler, personal communication).

1.2.4 Applied nucleation in a Mediterranean-type ecosystem

Experiments to test the effectiveness of applied nucleation have been conducted previously such as that by Zahawi et al. (2013), Corbin & Holl (2012), Corbin et al. (2016), Bechara et al. (2016), and Bechara et al (2021). However, none have been conducted in the Fynbos biome and at present it has been difficult to determine whether it is applicable to CFSF. A study by Corbin & Holl (2012) found that when revisiting a site where applied nucleation was implemented, seed dispersal and seedling establishment were higher within the planted nuclei, and that species density was also higher inside the nuclei than in the immediate surrounding, suggesting that the plants growing in the surroundings around the nuclei are offspring from the plants in the nuclei. Applied nucleation as a restoration tool relies more on the ability of the nuclei to act as a source of activation to begin restoration rather than on the ability of the initial nuclei expanding (Corbin et al., 2016).

1.3 Rationale for this study

The Fynbos biome is one of the most biodiverse biomes on the planet, boasting extremely high endemism for the rather small area which it covers. The Fynbos biome forms the Core of the Greater Cape Floristic Region (GCFR) (Manning & Goldblatt, 2012). This is a recognised global biodiversity hotspot owing to its high level of endemism, species richness, and high threat of extinction. However, this critical biome has been largely degraded because of anthropogenic activity including habitat destruction for urban development or agriculture, and the introduction and spread of invasive alien plants. This has had a severe negative impact on the biodiversity of the region.

The Fynbos biome in its entirety is comprised of various types of Fynbos and renosterveld vegetation (Rebelo et al., 2006) one of which being Cape Flats Sand Fynbos (CFSF) which is the subject of this project. More than 89% of what was once the most common vegetation type within the Cape Town city area has been lost. This leaves a mere 11% (City of Cape Town, 2018), which falls woefully short of the 30% national conservation target (Rouget et al., 2004). According to Rebelo et al. (2006), CFSF

occurs at lower altitudes, primarily on sandy soils with a low pH. Species here are mostly sclerophyllous shrubs and have a very high degree of endemism, containing a mix of resprouting and reseeding species. Typical vegetation components here generally include restioid, ericoid and proteoid shrubs, with some Ericaceae species occurring in wetter regions.

Some efforts have been made to conserve the last remaining remnants of CFSF. These "conserved" areas however also face an array of challenges, including but not limited to heavy infestation by invasive alien species such as *Acacia saligna* (Labill.) H.L.Wendl (Port Jackson Willow) and *Leptospermum laevigatum* F.Muell. (Australian Myrtle)*.* It is therefore crucial that conservation and restoration efforts be maximised in these conserved areas to successfully conserve what is left of the CFSF.

The Blaauwberg Nature Reserve (BBNR) is one of the few conservation areas left where CFSF is still prominent. The BBNR is located behind the suburb of Bloubergstrand, approximately 25km north of the city of Cape Town between Saldanha Bay and Table Bay (Cowell, 2014). The reserve, as well as the entire Cape region experiences a Mediterranean-type climate characterised by hot, dry summers, and cold, wet winters with rain predominantly falling between the months of May and August (Rebelo et al., 2006). At BBNR annual rainfall averages >500mm per annum (Cowell, 2014). The dominant geology underlying the reserve consists of Malmesbury Shale, however Aeolian, nutrient-poor acidic sands overlie this. Older sands which have been leached of nutrients support Fynbos, and younger sands still containing calcium carbonate support Strandveld (Boucher, 1983).
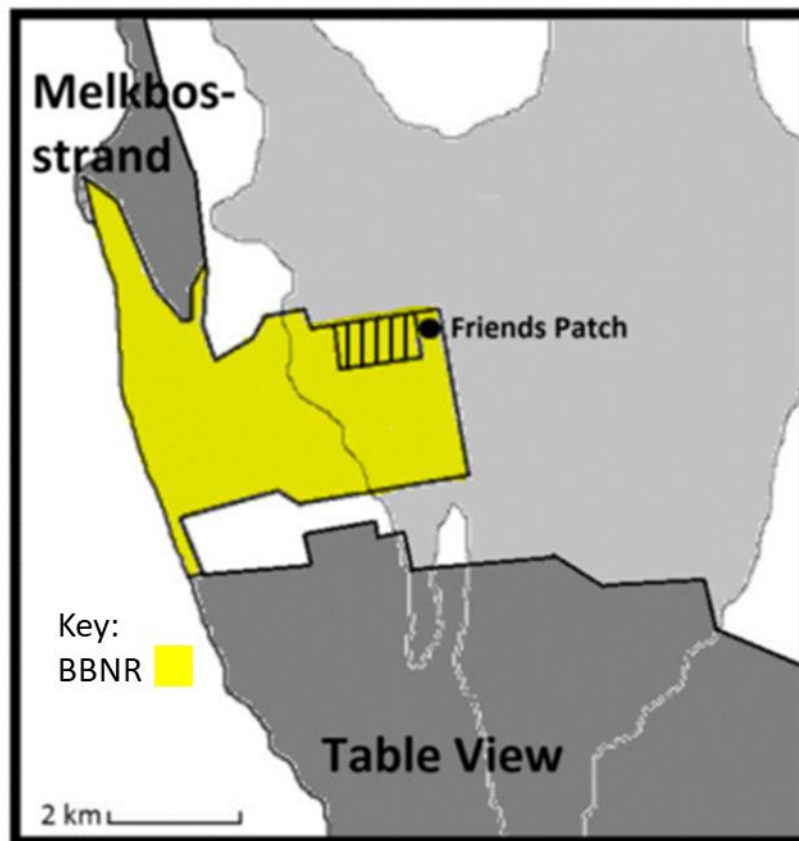
Figure 1.2 The location of the Blaauwberg Nature Reserve (highlighted) in relation to the Cape Town suburbs of Table View and Melkbosstrand (adapted from Hall, 2021).

There are three major vegetation types in the BBNR. On the ocean side of Blaauwberg, Hill Cape Flats Dune Strandveld is dominant, while Swartland Shale Renosterveld is dominant on the hill itself. On the landward side of the hill Cape Flats Sand Fynbos is the dominant vegetation type, interspersed with some thicket clumps comprising species such as *Searsia laevigata* (L.) F.A Barkley. The Sand Fynbos and the Renosterveld are considered to be critically endangered (Hall et al., 2021), while the Strandveld is endangered according to the National Spatial Biodiversity Assessment (Skowno et al., 2019).

Various restoration techniques have been investigated in the BBNR, including but not limited to the removal of alien vegetation by either 'fell and burn' (FB) or 'fell, stack (FS) and burn stack' treatments (i.e. passive restoration), and followed by active restoration by seed sowing in plots and planting rootstock after alien clearing (Hall et al., 2021). The FB and FS management regimes are important for Chapter 3 of this thesis. The implementation of these initiatives has had varied success, with areas being classified as having higher restoration potential being restored most readily to 'near natural' condition. The re-introduction of reseeder overstorey proteoids, which store seeds in the canopy and

not the soil, is one essential growth form to re-introduce after dense alien tree invasion (Mostert et al., 2017).

This research project aimed to provide useful information for implementing applied nucleation in ecological restoration not only in CFSF, also applicable to other lowland Fynbos vegetation types. It is important to trial different techniques and research different restoration methods which could be used to scale up restoration in what is being called the United Nations "decade on ecological restoration" (Nash & Vidal, 2019, https://www.iucn.org/news/forests/201903/un-elevates-action-ecosystem-restoration-iucn-ready).

The success of applied nucleation as a restoration tool is well-documented in forest vegetation types (Corbin et al., 2016). However, the efficacy of applied nucleation in dryland ecosystems remains largely unexplored and unknown, Fynbos being an example. A review paper by Corbin et al., (2016) in fact stated that applied nucleation would not be successful in a dryland ecosystem as frugivory, an important dispersal mechanism for successful nucleation in forests, is seldom a major seed dispersal vector in dryland habitats. By definition applied nucleation involves establishing clusters of vegetation either by direct planting or sowing of seed (Corbin & Holl, 2012), which are then considered nuclei (Corbin et al., 2012). Over time the nuclei begin to nucleate outwards as a result of natural plant colonization and succession (Corbin & Holl, 2012).

For the purposes of this MSc thesis the plots where active restoration was conducted were re-evaluated. This was to ascertain whether these plots/nuclei have begun to nucleate – i.e., whether succession had begun in the areas surrounding the nuclei. Many CFSF species require fire as a cue for germination (Hall, 2018), and since this area has not burnt since restoration sowing, the only species expected to be seen growing in the areas surrounding the restored plots were those species that do not require a direct fire-related germination cue, and which are generally wind-dispersed or disperse passively.

A predictive model was also designed using various rules and parameters to predict whether applied nucleation was a feasible restoration technique to use in CFSF, and if so, to give an indication of which management regimes would best facilitate nucleation and which species possess the highest nucleation potential. This model has the potential to be used as a conservation tool in furthering restoration efforts in the reserve and elsewhere. Presently, establishing nuclei is the only practical approach which can be taken, as there are insufficient seed resources as well as available funding to broadcast sow the entire reserve with the same level of restoration effort.

Overall, the MSc addressed the following question: "Can the concept of applied nucleation be applied to the restoration of Cape Flats Sand Fynbos, and to fire-driven systems in general?" The thesis is composed of two data chapters. The title of the first data chapter is: "Are previously restored plots nucleating? An assessment of applied nucleation in a Mediterranean climate shrubland"; the second chapter title is: "Designing a model: simulating the impacts of different management regimes on the effectiveness of applied nucleation for restoring a degraded, fire-driven ecosystem.", or in other words, by using a model can one predict the efficiency and success of applied nucleation in the BBNR?

1.4 The objectives for this study

The overall aim of this study was to determine whether applied nucleation and the use of restoration nuclei are effective in scaling up restoration in Sand Fynbos at the BBNR.

1. Determine whether previously restored plots have acted as nuclei of restoration and whether they have nucleated outward – Chapter 2

This involved revisiting the plots in which Hall (2018) sowed CFSF species seeds in 2013, to determine which species were present and compared to what he initially observed. Furthermore, the area surrounding the plots was assessed to determine whether these plants had successfully dispersed seed and recruited.

2. Design a practical model to inform role players on optimal management scenarios as well as to aid in selecting species to use for future restoration initiatives – Chapter 3

The model was designed using an inverse model as used by (Schurr et al., 2008) to model plant fecundity and seed dispersal distances. Inverse modelling is a modelling technique commonly used when certain model parameters are not available, as it makes use of model outputs to infer the values of model parameters (Migliavacca et al., 2008).

This model made use of certain parameters which were manipulated to simulate certain management conditions. To model the effects of different management conditions, the size and arrangement of certain obstacles were manipulated. This alters the path that a seed would theoretically pass through the environment. To model nucleation potential for different species I altered biological parameters such as reproductive rate, carrying capacity, and dispersal kernel.

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Chapter 2: Are previously restored plots nucleating? An assessment of applied nucleation in a Mediterranean climate shrubland

2.1 Abstract

There is a need to fast track the recovery of indigenous vegetation after the clearing of invasive alien species. While previous restoration efforts have been relatively successful, room remains for an effective, yet sustainable ecological restoration technique. This study investigated the concept of applied nucleation as an ecological restoration tool in previously invaded Cape Flats Sand Fynbos, a critically endangered vegetation type found in the lowlands of the greater Cape Town city area. Restoration plots established in 2013 were revisited and surveyed to determine species composition as well as to assess whether any species had begun to nucleate and colonise the area surrounding the restoration plots. A larger 20m x 20m plot was set up around the initial 5m x 10m sowed plot and young plants of the species growing within the sowed plot were identified, measured (volume), and distance to the plot edge recorded. Of the 30 species originally sown in 2013, 11 species were found to be persisting in the sowed plots. Of the 11, four species (*Anthospermum aethiopicum, Ifloga repens, Dimorphotheca pluvialis, Pelargonium capitatum*) were observed to be colonising the habitat surrounding the initial sowed plots. These species were deemed to be nucleating species. This study showed that using applied nucleation as an ecological restoration tool is feasible in a dryland ecosystem and gives an indication of which species to use for future restoration efforts. This will enable managers and practitioners to make more informed decisions in the future.

Keywords: applied nucleation, ecological restoration, Cape Flats Sand Fynbos.

2.2 Introduction

The Fynbos biome is one of the most biodiverse on the planet, boasting extremely high endemism for the rather small area which it covers (Rebelo et al., 2006). The Fynbos biome falls within the Core of the Greater Cape Floristic Region (GCFR; Manning & Goldblatt 2012), with over 70% of species being endemic. However, this biome has been largely degraded as a result of anthropogenic activity including habitat destruction for urban development or agriculture, and the introduction and spread of invasive alien species (Mostert et al., 2017). These factors have had a severe negative impact on the biodiversity of the Fynbos biome and this has led to large-scale restoration and conservation initiatives throughout the Western (Holmes et al., 2020) and Eastern Cape (Hosking & Du Preez, 1999).

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Many of these initiatives have involved restoring already protected areas in addition to conserving more areas. One of these areas is the City of Cape Town-managed Blaauwberg Nature Reserve (BBNR), which spans an area of 1500ha from the coast near the town of Melkbosstrand and inland over Blaauwberg Hill to encompass some of the sand plain (33.75°S, 18.48°E). The sand plain supports a special type of Fynbos called Cape Flats Sand Fynbos (from here on CFSF). This Fynbos vegetation type is considered critically endangered, with a mere 11% left of what was once the city's most common vegetation type (City of Cape Town, 2018), but the majority of which is highly degraded. An even scarier statistic is that less than 2% of the remaining vegetation occurs within protected areas (Hall et al., 2017; Raimondo et al., 2009). There is a need to scale up restoration in CFSF, and the BBNR has been the selected location for several restoration efforts conducted by the City of Cape Town Biodiversity Management Branch, often in collaboration with research initiatives by local universities. These initiatives largely include alien clearing followed by active ecological restoration interventions, both of which have received a parallel research focus.

By definition, ecological restoration is initiating or assisting the recovery of an ecosystem or landscape that has been destroyed, altered, or damaged in one or another way (Gann et al., 2019). There are a number of active ecological restoration techniques, all of which involve the planting of indigenous species or the sowing of their seed (Corbin & Holl, 2012). One of these, applied nucleation, is a tried and tested technique in some grasslands (Corbin & Holl, 2012; Corbin et al., 2016), but particularly in forest vegetation types (Corbin & Holl, 2011, 2012; Corbin et al., 2016; Holl & Aide, 2011), especially those where frugivory is a mechanism for seed dispersal. Applied nucleation involves the establishment of clusters of vegetation either by planting individual plants together or by sowing seed; the nuclei. After the clusters have established, they expand outwards into the surrounding area and begin to colonise areas still requiring restoration; nucleation (Schlawin & Zahawi, 2008). The nuclei are placed in strategic locations and are designed to facilitate or "kick start" nucleation cost-effectively, utilising as few resources as possible (Hulvey et al., 2017).

Frugivory is said to be the basis of applied nucleation, without which it simply will not occur (Corbin et al., 2016). This is because frugivores are attracted to the restored nuclei and bring with them the seed of plants from intact vegetation; they also ingest the fruit and seed from plants within the clumps and spread them into the surrounding area to facilitate nucleation and introduce new species to the nuclei and nucleation area. In the case of forest restoration, Corbin et al. (2016) believe that without frugivory, applied nucleation is not a viable restoration option.

Despite the perceived limitations of nucleation in systems where frugivory is not a dominant mode of seed dispersal, the need to optimise limited resources such as funding and native species' propagules,

motivates an investigation of such processes in CFSF in which frugivory is a rare mode of dispersal. The absence of frugivores however is not the only limiting factor when it comes to the success (or lack thereof) of applied nucleation in dryland ecosystems (Hulvey et al., 2017). Dryland ecosystems generally possess harsh conditions for plant establishment, including soils low in nutrients, and low rainfall (Maestre et al., 2016). These are both conditions experienced in the region in which Cape Flats Sand Fynbos occurs. A further challenge faced by CFSF and thus simultaneously faced by those trying to restore degraded areas containing CFSF, is the susceptibility of these areas to become invaded (or re-invaded) by alien vegetation which easily outcompetes native vegetation (Hall et al., 2021; Holmes et al., 2020; Mostert et al., 2017).

A major limiting factor for restoration in Fynbos in particular, would be the absence of fire. Fire is the key driver in determining species composition, community structure, as well as patterns of succession in the Fynbos biome (Hoffman et al., 1987; Kraaij & van Wilgen, 2014). Fire regimes in Fynbos date back about 15Ma to the Middle Miocene, and have played a crucial role in the evolution of the biome as a whole, leading to the diversity observed in "modern" Fynbos (Kraaij & van Wilgen, 2014). Fire is the major natural disturbance in Fynbos today and plays a vital role in Fynbos regeneration and thus is a key management tool (Kraaij & van Wilgen, 2014). The importance of fire in Fynbos, while crucial to the survival of many Fynbos guilds, can result in complications when it comes to restoration, especially where invasive alien trees dominate.

Applied nucleation in forest vegetation types for example is straightforward, as clusters of vegetation are established and over time these begin to nucleate. The only complication that nucleation here might face is competition from other species such as grasses as secondary invaders (Nsikani et al., 2019). Fynbos systems, however, have added complexities. After clearing of invasive alien trees, clusters of vegetation can be established to initiate succession and nucleation. Seed germination by some of the species in these clumps require fire and thus a periodic post-restoration prescribed burn is required (Holmes et al., 2000). This fire, however, will raze any aboveground biomass of the established nuclei, contradicting the fundamental first step of applied nucleation which is to establish a cluster of vegetation from which nucleation can be based (Corbin & Holl, 2012). In fynbos, only a few species recruit naturally in inter-fire periods, with most requiring fire to complete their life cycles (Kraaij & van Wilgen, 2014). A fire will therefore temporarily eliminate competition and induce germination of remnant native species, but also of the invasive alien species which were cleared in the first place, since these species can accumulate long-lived seed banks. This regrowth, if not carefully monitored and managed, may result in severe re-infestation. Even though razing of aboveground biomass contradicts the nucleation fundamentals, establishment of several Fynbos guilds will only be evident after a burn as the dispersed seeds require the effects of fire to germinate. Thus, the true

extent of colonization and nucleation will only be evident after 10-15 years which is the average inter-fire period in Fynbos; in contrast, nucleation in a forest habitat can occur continually, or on an annual basis (Holl et al, 2000; Zahawi & Augspurger, 2006). Most Fynbos species also have short-distance dispersal modes, barring a few wind-dispersed species. The implications thereof are that nucleation, if it can take place in Fynbos, will be much slower than in other vegetation types.

It is complexities such as these that require carefully planned management regimes in the Fynbos biome, and which potentially make restoration initiatives here more nuanced than in other biomes. The overall aim of this research was to determine whether previously restored plots in highly degraded CFSF have nucleated in the absence of fire, and if so to what extent. Applied nucleation has been shown to be an effective method of restoration in the forest biome (Bechara et al., 2021; Corbin & Holl, 2012; Corbin et al., 2016; Zahawi et al., 2013), however it is not understood how effective it will be in the CFSF vegetation type, or in a fire-driven system where frugivory is not an important mechanism for seed dispersal.

2.2.1 Study objectives

Based on preliminary field observations, this study seeks to test the hypothesis that certain CFSF pioneer species, which are not dependent on fire for germination, are able to disperse into matrix areas surrounding the active restoration plots, which represent restored nuclei. Here, plant size is used as a proxy for plant age, where evidence of movement beyond the plot would be assumed if plant size in the restored plot is larger than the plants of the same species observed in the surrounding areas. While frugivory is largely absent as a seed dispersal mechanism in CFSF (P.M Holmes, personal communication), it is postulated that other mechanisms such as wind and passive dispersal, may be sufficient to facilitate nucleation (in this case movement beyond previously seeded restoration plots). While fire is the key driver of regeneration in Fynbos, species without strong fire-related germination cues, located in degraded habitat with open spaces and low levels of competition from vegetation, may be expected to establish.

In addition, future research topics which could be beneficial in further exploring the efficacy of applied nucleation and could potentially improve the effectiveness of future restoration management plans are suggested.

2.3 Methods

2.3.1 Study site

Since 2012 the BBNR has been the site for ecological restoration initiatives by the City of Cape Town Biodiversity Management Branch and has been the study site for restoration ecology research in collaboration with Stellenbosch University and the Cape Peninsula University of Technology. In 2013 and 2014 for his PhD study, Stuart Hall actively restored 50m^2 (10m x 5 m) plots that were cleared of alien *Acacia saligna,* by the "Fell & Burn" method by sowing seed mixes of 30 indigenous CFSF species (Hall et al., 2021). Six years later, fourteen of these plots were revisited and data collected (Figure 2.1).
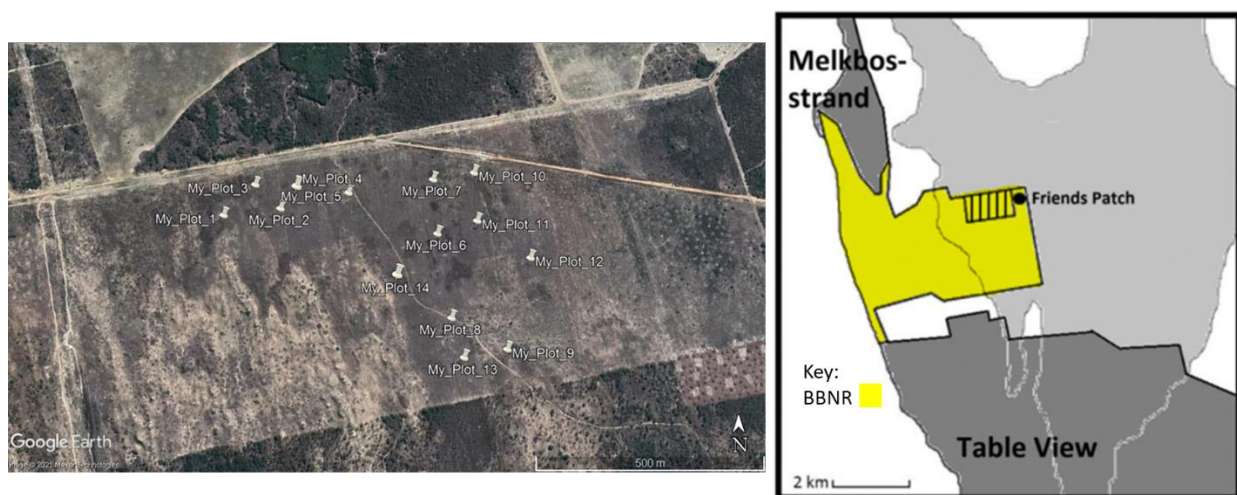
Figure 2.1 The location of the restoration plots located within the BBNR (left) that were revisited in this study, and the location of the Blaauwberg Nature Reserve (highlighted) in relation to the Cape Town suburbs of Table View and Melkbosstrand (adapted from Hall, 2021).

The BBNR is one of the few conservation areas left where CFSF is still prominent and where restoration efforts are still being undertaken. The reserve was used for livestock grazing and crop sowing between the 1960s and 1980s, after which it was left fallow (Cowell, 2014). An analysis of aerial photographs of the reserve between 1926 and 2011 by Wotsitsa & Mgese (2012) indicated that invasion by *Acacia saligna* started becoming visible from 1944, whereafter it became progressively worse.

2.3.2 Re-survey of 2013-sown plots

When the restoration plots were first established in 2013, a seed mix comprising 30 species was sown in a total of 32 plots (Hall et al. 2021). This mix consisted of common CFSF species and included eight geophytic species. Ericoid and proteoid shrubs as well as forbs and graminoids were sown to represent the important perennial structural guilds which make up a typical CFSF plant community. Six years later, in the Spring of 2019 a subset of 14 plots were re-surveyed to determine species' presence and

abundance. Time constraints resulted in 14 plots being sampled, and these plots were chosen at random throughout the landscape to ensure representivity.

The original 10m x 5m plots were located using GPS co-ordinates, and each species' identity and abundance was noted. Individuals of all plants in the plot were counted. A total of 11 species were observed in the plot survey in 2019.

These data were then compared to the list of species which were used in the initial sowing and establishment of the sowed plots, as well as to the data from surveys conducted in 2014 and 2017 (Table 2.1, Results). These surveys did not form a part of the PhD but were done by Stuart Hall (Hall, unpublished data) to assess how the plots were faring.

It is important to note that only a subset of 14 of the 32 restoration plots were surveyed, and one cannot say for certain whether species that were not recorded in the surveyed plots are not present in the unsurveyed plots.

2.3.3 Understanding population dynamics of restored plots and surrounds of nucleating species

The number of young plants per nucleating species was counted within the initial 50m^2 sowed plot as well as within the larger 350m^2 plot surrounding this one (400m^2 − 50m^2 = 350 m^2). These data (comprising means and standard deviations of counts per species) were then plotted on a bar chart. A nucleating species was defined as a species which was included in the initial sowing, and which had young plants growing beyond the borders of the initial sowing plot.

2.3.4 Assessment of dispersal modes

The two main modes of dispersal of the species sown in 2013 were passive and wind dispersal as determined from Holmes & Cowling (1997) and personal communication with P.M Holmes, with some species being ant and ballistically dispersed. The distances from the initial sowed plot at which young plants of the four nucleating species were found was used as a surrogate for seed dispersal distance. The species were then grouped based on their dispersal mode and compared.

2.3.5 Seed drop velocity and dispersal distance

Seed drop velocity was measured by dropping 10 seeds of each species from a distance of 2.5m and the velocity (m/s) calculated. The data were then compared to the maximum distance that young plants of *Anthospermum aethiopicum, Ifloga repens, Dimorphotheca pluvialis,* and *Pelargonium capitatum* were found from the initial sowed plots to determine whether there was a relationship between the two variables.

2.3.6 Determining dispersal distribution of different plant ages

Plant volume measurements (height x diameter 1 x diameter 2) were taken from 10 plants for each species which had set seed outside the initial sowed plot (*Anthospermum aethiopicum, Ifloga repens, Dimorphotheca pluvialis,* and *Pelargonium capitatum*) within the borders of the larger 20m x 20m sampling plot. This made a total of 140 plant volume measurements per species across the 14 plots. Furthermore, the distance from each of these ten plants to the edge of the initial sowed plot was measured as a surrogate for dispersal distance from what is essentially a "nucleus" of facilitation and colonization (Corbin & Holl, 2012; Corbin et al., 2016; Holl et al., 2011; Schlawin & Zahawi, 2008; Zahawi & Augspurger, 2006). The 20m x 20m plot was split into four quadrants (Figure 2.3), and while moving in an arcing motion, the number of plants encountered was counted, and the distance to the edge of the sowed plot was taken for ten of these plants. The quadrants were only used to make data collection more manageable, and to allow for a standardised search plan. If a young plant was observed outside the 20 x 20m plot, the distance to the nearest adult plant in the initial sowed plot was measured as well so as not to limit the maximum possible dispersal distance.

Furthermore, plant size was used as a surrogate for plant age. Large plants which were deemed to have grown from the initial 2013 sowing were considered adult plants, and small plants of the same species were considered young, dispersed plants (or offspring). Size cut offs were not implemented here as there were clear differences in the sizes of the plants within the initial sowed plots as opposed to the plants outside. Sampling was conducted in the months of September and October 2019 which is in Spring in the Southern Hemisphere.

2.3.7 Relative frequency of nucleation distance

Relative nucleation distance frequency was determined by counting the number of times a plant was observed at a certain distance. The larger 20m x 20m plot was split into four quadrants. The data were recorded radially starting from each of the four edges of the initial sowed plot and moving away from the plot boundary. Within these quadrants, the number of individuals per species was recorded, and 10 of these plants' distances from the initial sowed plot measured in metres. Subsequently for each species, relative frequency was determined by recording how many times a young plant was observed at one metre-interval distances from the initial sowed plot. The quadrants were merely used to make data capturing more manageable.
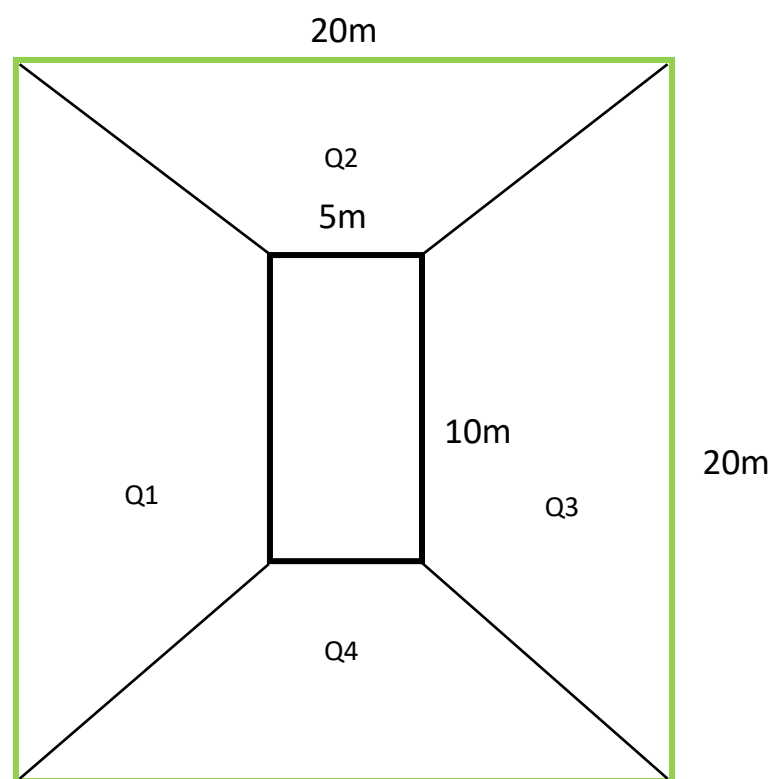
Figure 2.2 The larger 20m x 20m plot surrounding the initial 10m x 5m restoration plot established by Hall (2018). The quadrants were simply used to make sampling and data capture more manageable.

2.3.8 Statistical analyses

After plotting raw residuals, it was seen that the data for all species except *Dimorphotheca pluvialis* were not normally distributed. A simple test for correlation was done and then a linear regression to determine the relationship between plant size and distance from the plot edge. The log-transformed data was then plotted as a scatter plot.

Dispersal distances were shown to not be normally distributed and thus a Kruskal-Wallis one-way analysis was done to determine whether there was a significant difference in dispersal distances among species.

A regression was run on the distribution of different plant ages. All statistical analyses were done on Rstudio (Rstudio Team, 2020).

2.4 Results

2.4.1 Survey data

Of the 30 species sown in 2013, 13 CFSF fynbos mix species and one geophyte had established from the initial sowing when Hall (2018) resurveyed the plots in 2014, and this number increased to 18 CFSF species and one geophyte in 2017. A further two years later in 2019 when I resurveyed the plots, only 10 of the 18 species were recorded in the subset of 14 plots sampled (Table 2.1), and the one geophyte (*Watsonia meriana*) remained, making a total of 11 species: *Anthospermum aethiopicum*, *Dicerothamnus rhinocerotus*, *Dimorphotheca pluvialis, Erica mammos*a*, Ifloga repens, Leucadendron salignum, Metalasia densa, Pelargonium capitatum, Passerina corymbosa*, *Protea repens, Thamnochortus punctatus*, and *Watsonia meriana*. Some species such as *Erica plumosa, Agathosma imbricata* and *Stoebe plumosa* were not observed in the first survey in 2014 but were recorded in 2017 and were not observed in the subset of 14 plots in 2019. *Erica mammosa* was not observed 2014 but seen in the 2017 and 2019 surveys.

2.4.2 Growth form

The initial sowing contained 14 ericoid shrubs, three proteoid shrubs, one forb, one annual forb, and three graminoid species (Table 2.1). The life forms which persisted through to the most recent survey were the ericoid shrubs (five), the proteoid shrubs (two), annual forbs (one), forbs (one), and geophytes (one).

2.4.3 Regeneration modes

There were 14 resprouting and 16 reseeding species in the initial sowing in 2013 (Table 2.1). In 2014, ten reseeding species were observed, 12 in 2017, and eight in 2019. In 2014, four resprouting species were observed, seven resprouting species observed in 2017, and three in 2019.

2.4.4 Dispersal modes

The initial sowing contained 13 passively dispersed species, 13 wind dispersed, three ant-dispersed, and one ballistically dispersed. By the final survey in 2019, six of the 11 remaining species were passively dispersed and five were wind dispersed (Table 2.1).

2.4.5 Nucleation and nucleus development

Of the 11 species observed at the last survey in 2019, only six were found to have set seed that resulted in new recruitment in and around the sowed plots (Table 2.1). Four of these species were wind dispersed and two were passively dispersed. The species were *A. aethiopicum* (ericoid shrub, reseeder, passively dispersed); *D. rhinocerotus* (ericoid shrub, reseeder, wind dispersed); *D. pluvialis* (annual forb, reseeder, wind dispersed); *I. repens* (ericoid shrub, reseeder, wind dispersed); *M. densa* (ericoid shrub, reseeder, wind dispersed); *P. capitatum* (forb, reseeder, passively dispersed). For the purposes of this study however, *D. rhinocerotus* and *M. densa* were excluded as these species were observed to be growing naturally within the reserve and thus one could not say for certain whether the young plants in the study area came from these naturally occurring individuals or from the initial sowed plots.

Table 2.1 A comparison of species sown in 2013 (Hall et al. 2021), follow up survey in 2014 and 2017, and the most recent survey in 2019 for the 14 plots resampled in this study (note that most geophytes are ephemerals that are dormant in summer). The species observed to be spreading beyond the nucleus are underlined.

Original sowing species (2013)	Family	Life form	Regeneration mode	Dispersal mode	Present 2014	Present 2017	Present 2019	Are they nucleating?
Agathosma imbricata	Rutaceae	Ericoid shrub	Resprouter	Ballistic, ant	No	Yes	No	No
Anthospermum aethiopicum	Rubiaceae	Ericoid shrub	Reseeder	Passive	Yes	Yes	Yes	Yes
Dicerothamnus rhinocerotus	Asteraceae	Ericoid shrub	Reseeder	Wind	Yes	Yes	Yes	Yes
Dimorphotheca pluvialis	Asteraceae	Annual forb	Reseeder	Wind	Yes	Yes	Yes	Yes
Diosma oppostifolia	Rutaceae	Ericoid shrub	Resprouter	Ant	No	Yes	No	No
Erica ferrea	Ericaceae	Ericoid shrub	Reseeder	Passive	No	No	No	No
Erica mammosa	Ericaceae	Ericoid shrub	Resprouter	Passive	No	Yes	Yes	No
Erica plumosa	Ericaceae	Ericoid shrub	Reseeder	Passive	No	Yes	No	No
Ifloga repens	Asteraceae	Ericoid shrub	Reseeder	Wind	Yes	Yes	Yes	Yes
Leucadendron salignum	Proteaceae	Proteoid shrub	Resprouter	Passive	Yes	Yes	Yes	No
Metalasia densa	Asteraceae	Ericoid Shrub	Reseeder	Wind	Yes	Yes	Yes	Yes
Passerina corymbosa	Thymelaeaceae	Ericoid shrub	Reseeder	Passive	Yes	Yes	No	No
Pelargonium capitatum	Geraniaceae	Forb	Reseeder	Passive	Yes	Yes	Yes	Yes
Phyllica cephalantha	Rhamnaceae	Ericoid shrub	Resprouter	Ant	Yes	Yes	No	No
Protea repens	Proteaceae	Proteoid shrub	Reseeder	Passive	Yes	Yes	Yes	No
Protea scolymocephala	Proteaceae	Proteoid shrub	Reseeder	Passive	Yes	Yes	No	No
Restio praecutus	Restionaceae	Graminoid	Reseeder	Passive	Yes	No	No	No
Seriphium incanum	Asteraceae	Ericoid Shrub	Reseeder	Wind	No	No	No	No
Stoebe plumosa	Asteraceae	Ericoid Shrub	Reseeder	Wind	No	Yes	No	No
Thamnochortus punctatus	Restionaceae	Graminoid	Reseeder	Passive	No	Yes	Yes	No
Trichocephalus stipularis	Rhamnaceae	Ericoid shrub	Resprouter	Wind	Yes	Yes	No	No
Willdenowia incurvata	Restionaceae	Graminoid	Reseeder	Ant	No	No	No	No
Total 22					13	18	10	6
Geophytes								
Albuca sp1	Hyacinthaceae	Geophyte	Resprouter	Wind	No	No	No	No
Albuca sp2	Hyacinthaceae	Geophyte	Resprouter	Wind	No	No	No	No
Gladiolus sp	Iridaceae	Geophyte	Resprouter	Wind	No	No	No	No
Moraea neglecta	Iridaceae	Geophyte	Resprouter	Wind	No	No	No	No
Wachendorfia paniculata	Haemodoraceae	Geophyte	Resprouter	Passive	No	No	No	No
Watsonia meriana	Iridaceae	Geophyte	Resprouter	Wind	Yes	Yes	Yes	No
Watsonia sp	Iridaceae	Geophyte	Resprouter	Wind	No	No	No	No
Wurmbea spicata	Colchicaceae	Geophyte	Resprouter	Passive	No	No	No	No
Total 8					1	1	1	0

The average sizes of plants inside the initial sowing plot as opposed to outside. *Anthospermum aethiopicum* had the largest plants both inside and outside the initial sowing plots.
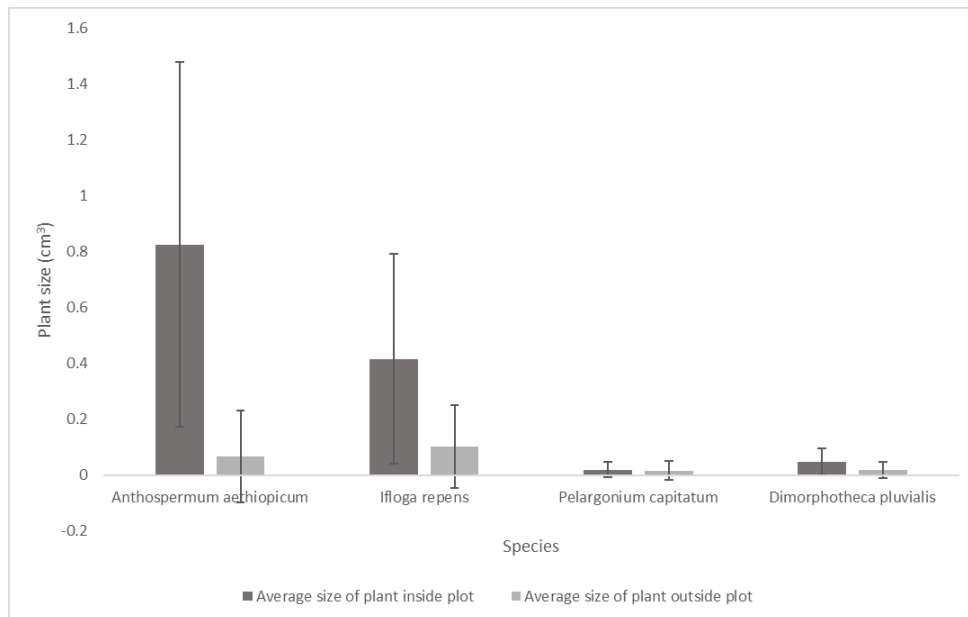
Figure 2.3 Means and standard deviations comparing the mean volumes ($\pm$ SD) of the four species seen to have set seed outside the initial sowed plot.

2.4.6 Nucleating species

The four main nucleating species were *A. aethiopicum, I. repens, P. capitatum,* and *D. pluvialis. Anthospermum aethiopicum* had more plants per metre squared than the other three species, both within the initial 50m^2 sowed plot, as well as outside in the larger 350m^2 plot.
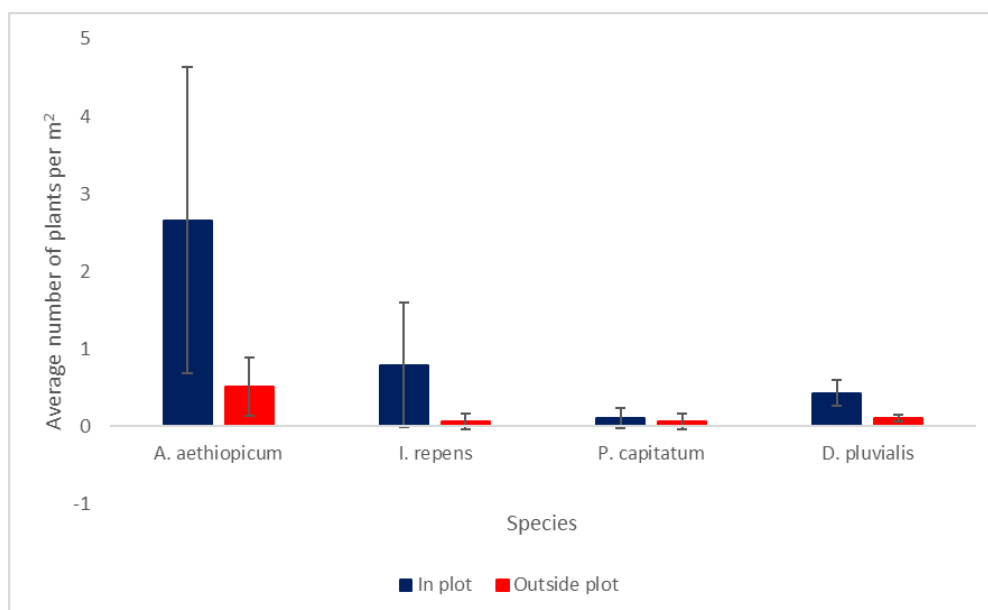
Figure 2.4 Number of young plants per m^2 (mean $\pm$ SD) within and outside the sowed plots.

<u>2.4.7 Seed drop velocity and dispersal distance</u>

Pelargonium capitatum was the species which had the lowest seed drop velocity (Table 2.2), while *A. aethiopicum* had the highest seed drop velocity.

Table 2.2 Seed drop velocity of the 4 nucleating species. R = replicate seed drop.

Species	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	Average seed drop velocity (m/s)
Anthospermum aethiopicum	0.75	0.65	0.77	0.55	0.83	0.68	0.65	0.7	0.63	0.73	0.360231
Dimorphotheca pluvialis	1.82	1.92	2.11	1.86	1.84	1.6	1.42	1.6	1.65	1.86	0.141403
Ifloga repens	1.45	1.8	1.62	1.47	1.53	1.37	1.45	1.32	1.38	1.37	0.169377
Pelargonium capitatum	2.51	4.63	3.14	6.28	3.54	5.36	4.45	4.03	3.12	7.76	0.055779

On average, wind dispersed species were observed at further distances away from the initial sowed plot (Figure 2.6), with *D. pluvialis* having an average distance of 8.56m.
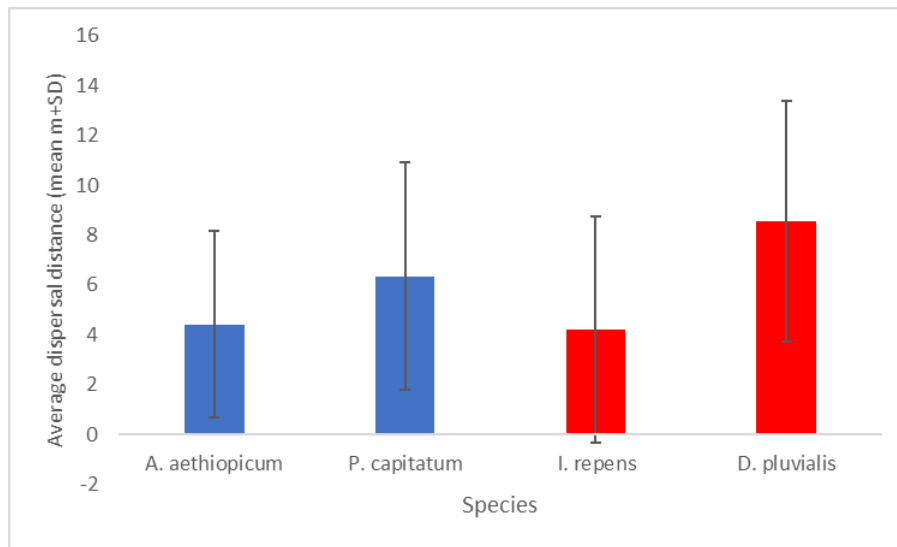
Figure 2.5 The average dispersal distance of the two primary dispersal modes (mean m+ SD). Passive dispersal in blue and wind dispersal in red.

2.4.8 Correlation between dispersal distance and seed drop velocity

When doing a test for correlation between the average dispersal distance of the 4 nucleating species and their speed drop velocity (Table 2.3), the correlation was seen to be significant (t > 0.05, p-value = 3.651e-06, correlation coefficient = 0.31).

Table 2.3 Dispersal distance and seed drop velocity of the nucleating species.

Species	Dispersal distance (m ± SD)	Seed drop velocity (m/s ± SD)
A. aethiopicum	4.42 ± 3.75	0.36 ± 0.8
P. capitatum	6.34 ± 4.53	0.06 ± 1.6
I. repens	4.22 ± 4.57	0.17 ± 0.14
D. pluvialis	5.56 ± 4.84	0.14 ± 0.2

2.4.9 Relative frequency of nucleation distance

All species followed a similar trend where there is a high relative frequency of nucleation distance nearest the edge of the initial sowed plot, all within approximately the first 2 metres (Figure 2.6). *Anthospermum aethiopicum, I. repens,* and *P. capitatum* then all display a decrease in relative frequency with distance from the sowed plot. *D. pluvialis* on the other hand behaves slightly differently with spikes in relative frequency, particularly at 11m away.
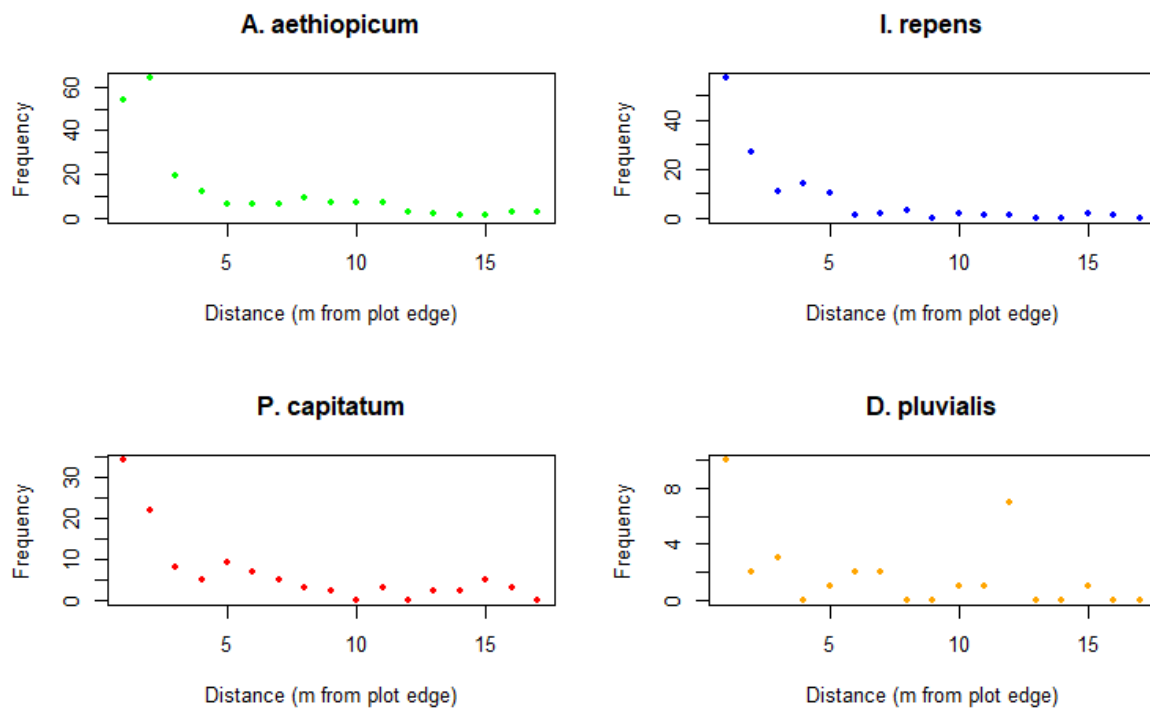
Figure 2.6 The relative frequency of young plants per metre of the four species encountered with distance away from the starting point at the edge of the initial sowed plot.

2.4.10 Distribution of different plant ages

The highest concentration of young *A. aethiopicum* plants was found within the first 3m of the initial sowed plots (across all plots), and thereafter the concentration decreased, and plants became more sparsely distributed. Each point represents an individual plant.

Much like *A. aethiopicum*, the concentration of young *I. repens* plants is highest within the first five metres of the initial sowed plots. The density and concentration of the young plants decreases with distance from the sowed plots until a few plants are observed at 15m. Again, as in the case of *A. aethiopicum* there is a general upward trend regarding the size of the young plants with increased distance from the initial sowed plots, with the plants of the highest volume being observed furthest away from the sowed plots.

Although there is an overall increasing trend in the sizes of young *P. capitatum* plants with distance from the sowed plot, it is far more varied than the species above. There was a greater range of sizes within 8m of the sowed plots, after which the presence of smaller plants became scarce.

As the only annual species studied, *D. pluvialis* displayed the highest variation and spread of plants of all species considered. All plants observed would be derived from seeds dispersed from the original 2013 established plants as well as from subsequent years' seed production from annually establishing plants. The highest concentration of smaller plants was within the first 2m from the sowed plot, although just under 12m there was a relatively high concentration as well. The sizes (volume) varied greatly, and plants of all sizes were found both near the sowed plot and further away.
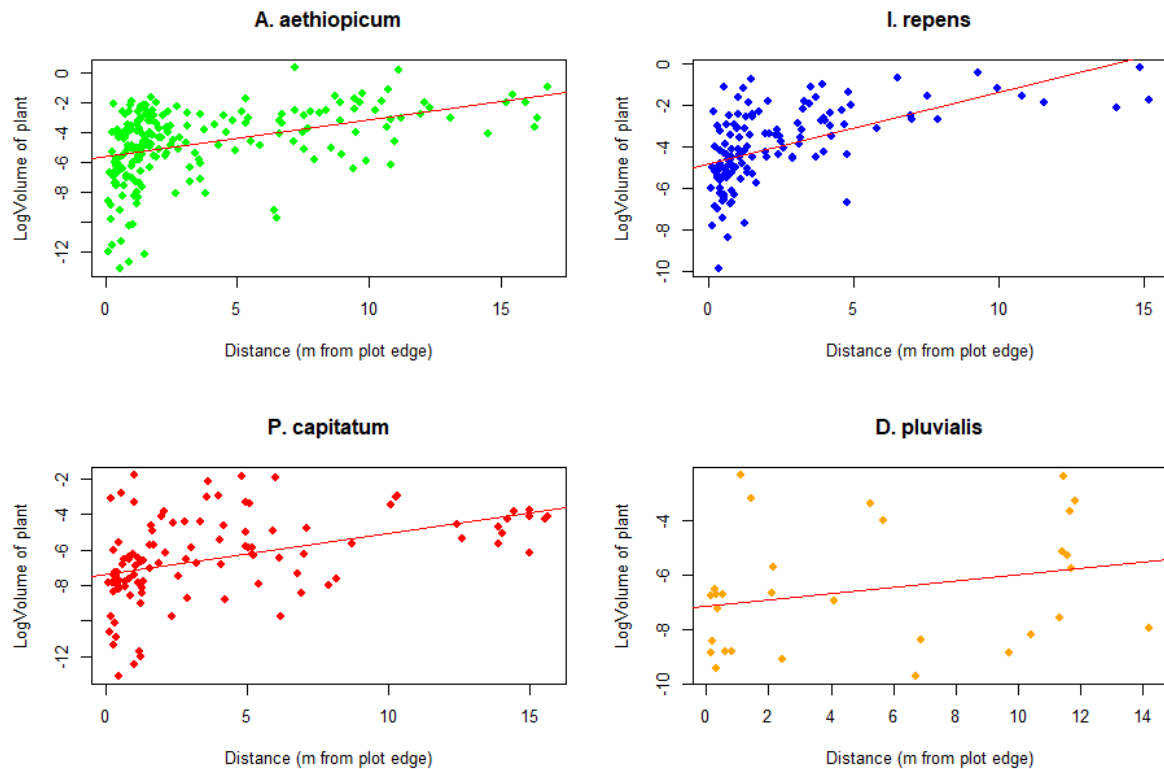
Figure 2.7 The differences in size (m) of young plants with distance (m) from the initial sowed plot. Each point represents an individual plant. Slope of regression was significant for all species (F>0.05 for all species). Regression lines fitted.

2.5 Discussion

The main aims of this research were firstly to determine whether previously restored plots (nuclei) had begun to spread into the surrounding area and begin the process of nucleation, and secondly to determine whether applied nucleation is a feasible restoration technique in a dryland, fire-driven ecosystem such as Cape Flats Sand Fynbos.

2.5.1 Plot survey

While 11 species were recorded as still present six years after their initial sowed in plots, only the species which were found to have young plants both inside and outside the sowed plots were considered further. These were *Anthospermum aethiopicum, Ifloga repens, Pelargonium capitatum, Dicerothamnus rhinocerotus,* and *Metalasia densa*. *Dicerothamnus rhinocerotus* and *M. densa* however occur naturally in the reserve and adult plants can be found growing across the site, thus they were excluded from the study as it could not be confirmed whether young plants found inside

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and outside the plots dispersed from the plants inside the initial sowed plots, or from naturally occurring plants outside. Nevertheless, observations of young plants of these species suggests that those species would also succeed in spreading into the nearby matrix and facilitate nucleation. *Anthospermum aethiopicum* was by far the most prolific of the sown species.

The above mentioned are all reseeding species, and no young resprouting plants were observed in and around the initial sowed plots. These results are to be expected as these species are not fire-dependent for seed germination (except for *P. capitatum* in which germination is optimized following heat shock treatment) (Brown, 1993; Hall et al., 2017), and are thus able to recruit during inter-fire periods. *Anthospermum aethiopicum, I. repens,* and *P. capitatum* were the only species which had young plants that had noticeably grown from seed set by the adult plants within the sowed plots. These, along with *D. pluvialis*, were dubbed the "nucleating species".

This leaves *D. pluvialis*, which is an annual and thus must establish from seed every year, meaning that the individuals which were observed could not be classed as young and old plants, but rather plants of the same age with varying sizes that resulted from the original restoration plots. Each year it has potential to disperse from both inside and outside the plots. This could well explain why there was such variation in the distribution of plants in the area surrounding the initial sowed plots. While one cannot call them young plants, this is still an indication that the original nuclei are expanding, and that nucleation has begun to take place, as they either germinated from seeds produced from plants in the initial restoration plots, or from seed sown in the initial plots but which were blown out by wind. This would be an example of secondary dispersal (Schurr et al., 2005). *Dimorphotheca pluvialis* was not observed on the reserve before the restoration plots were established, making it highly likely that any individuals observed arose from the initial sowing.

Fire is the most important driver for germination in the Fynbos biome, where many species use the fire cues, such as heat pulse or post-fire change in diurnal temperature amplitude or exposure to smoke as germination cues (Holmes & Richardson, 1999; Hall et al., 2017; Mukundamago, 2016). Some of the species Hall (2018) sowed in his restoration plots were either directly or indirectly fire dependent, and therefore would require fire or conditions mimicking fire to induce seed germination. Some of the seed sown during the initial sowing and establishment of the restoration plots was heat or smoke treated including species which were observed in at least one of the three surveys such as *Erica mammosa, Metalasia densa, Passerina corymbosa, Thamnochortus punctatus, Tricocephalus stipularis, Diosma oppositifolia, Phyllica cephalantha, Watsonia meriana, Agathosma imbricata* and one of the nucleating species *Anthospermum aethiopicum*. Thus, species which are dependent on either direct or indirect fire cues for germination were able to germinate. It would therefore be

expected that fire-dependent plants which established from the initial sowing would not yet have been able to produce offspring until a fire occurred in the reserve, as there would be a lack of germination cues, since a fire event has not yet occurred since the establishment of the initial sowed plots. However, *P. capitatum*, which is directly dependent on fire for germination (Hall et al., 2017), was noted to have produced seed that germinated in the inter-fire period. Soil temperatures are known to reach between 50°C and 60°C during hot summer days (Hall et al., 2017), and this may have been sufficient to induce some germination in species which require heat shock, as may be the case with *P. capitatum* being able to recruit in the absence of fire. This suggests that species cued to higher temperatures may well work in the applied nucleation context, as site conditions (hot soil surface conditions) in the absence of fire may allow such fast-growing species to recruit and spread in inter-fire periods before vegetation cover insulates the soil surface. While fire management will ultimately need to be applied in this system, identifying species which can be used to "kickstart" restoration and which can grow from seed without a fire event, is important for initiating vegetation recovery in restoration and management initiatives.

Species such as *A. aethiopicum, I. repens, D. pluvialis,* and *P. capitatum* noted in this study to have recruited without fire, are effective and important species to include in seed mixes for restoration efforts especially where sites cannot be uniformly broadcast sown. Of the species originally sown in restoration trials, they were the most effective in further setting seed, subsequently expanding the nucleus, and beginning to facilitate nucleation. Although not particularly diverse, they may offer a base upon which further restoration can occur. Applied nucleation also involves the initial clusters/nuclei capturing seed from other species and increasing the diversity of the nucleus (Corbin & Holl, 2012), and it is debatable as to whether this has begun here yet. Other species such as the proteas, restios and geophytes would also have to be included to ensure structural representivity. Serotinous proteoids disperse seeds from open cones after fires (Newton et al., 2021) and most geophytes flower most prolifically after fire and then immediately disperse their seeds, hence these species spread mainly post-fire. By contrast, restioids release seeds during the inter-fire period and as with many Fynbos species any dispersal will be evident only after the following fire cycle. The overstorey proteoid component is an important growth form in the structural make-up of a CFSF plant community (Holmes & Cowling, 1997), and once a future fire has been through the reserve young proteas are likely to disperse and establish beyond the location of the original sowed plots.

2.5.2 Young plant establishment

The study to determine whether the initial sowed plots had begun to nucleate yielded both expected as well as unexpected results. The frequency of plants decreased with distance away from the plots as expected, since nucleation begins as clumps of pioneering species, and plants gradually begin to colonise the surrounding areas in a roughly radial pattern (Schlawin & Zahawi, 2008).

At all plots, and for all species the number of plants decreased with distance away from the sowed plots; a similar pattern was observed in applied nucleation in the forest biome (Corbin & Holl, 2012; Corbin et al., 2016; Zahawi et al., 2013) where the initial plantings acted as a seed source and the immediate area was colonised first. Nucleation success here is, however, being judged in a dryland ecosystem, and in that case, the observed nucleus development and nucleation by four species was quite unexpected. However, while nucleus development was observed, it was limited to a few reseeding species that do not possess strong fire-related germination cues, rather than a complete range of fynbos guilds.

Corbin et al. (2016) stated that applied nucleation would not be successful in dryland ecosystems and even advised against using it as a restoration technique. This was largely because frugivory is seen as a vital mechanism for seed dispersal within forest vegetation types (Corbin et al., 2012), and less so in dryland ecosystems (Corbin et al., 2016). Frugivory is an uncommon seed dispersal mechanism in Cape Flats Sand Fynbos and Fynbos as a whole, being restricted to subtropical thicket species which make up a small percentage of the Fynbos biome (Holmes & Richardson, 1999). Of all the species sown by Hall et al., (2021) in the initial sowed plots, none were reliant on vertebrate dispersal. Of the species found to be colonising the surrounding area, all were either wind or passively dispersed. This may indicate that frugivory is not necessarily the key driver for applied nucleation as a whole, as proposed by Corbin & Holl (2012). The findings here indicate that dispersal by other mechanisms may be sufficient, particularly in dryland ecosystems where frugivory may be rare. One of the main reasons for establishing clusters of vegetation for applied nucleation is to attract frugivores and dispersers (Corbin & Holl, 2012). While this may not be the case in CFSF, these clusters of vegetation will attract pollinators which would ultimately facilitate nucleation, in combination with passive and wind dispersal, albeit over several fire cycles. The established nuclei would also act as seed traps to capture seed from other species (Corbin et al., 2016).

Young plants of the nucleating species were found up to 15m away, and one can thus assume that this is how far some of these seeds can be dispersed. This is to be expected as wind dispersed species are known to disperse even beyond these distances (Bond, 1988; Schurr et al., 2005). What was unexpected was the inter-fire recruitment where species established even without a fire to clear

competing vegetation and inducing germination, particularly in the case *of P. capitatum* which requires strong fire-related cues for germination (Brown, 1993; Hall et al., 2017).

Mainly larger plants of each species were observed at greater distances from the initial sowed plot which is not what one would expect. One would expect the plants furthest from the sowed plot to be smaller (Corbin et al., 2016). The pattern being observed could be because of a good initial dispersal event when the species in the sowed plots seeded for the first time in year two to three after they had established. These nucleated plants would have then matured, and in the interim the area between the sowed plot and these plants became colonised by weedy forbs, grasses, or *Acacia* seedlings, trapping any further dispersed seed and making the area immediately surrounding the plot denser, resulting in smaller plants being confined to the area nearest the sowed plot. This could explain why more young plants were observed nearer the plot, and this ties in with the seed-trap hypothesis in Chapter 3 of this thesis. Perhaps our idea of nucleus development and nucleation here is not what one would usually expect where plant size decreases with distance from the nucleus, but rather you have one good dispersal event in the beginning when conditions are favourable, resulting in another nucleus from where seed can originate. The area between these two nuclei then gradually becomes colonised and so nucleation continues.

Dimorphotheca pluvialis did not display the same pattern as the other species and had plants of various sizes at several distances. This species is an annual however and a random establishment pattern can be expected as new seedlings track and establish on bare ground.

Figure 2.8 Young *A. aethiopicum* growing amongst young alien *Acacia* trees.

Figure 2.9 Original sowing plot with dense *A. aethiopicum* growth.

2.5.3 Dispersal distribution

The concentration and total number of young plants was high (each dot on the graphs in Figure 2.8 represents an individual plant), indicating facilitation and the successful initiation of nucleation of these four species. The highest concentration of plants is within the first few metres, after which the numbers decrease. This is the general trend when it comes to applied nucleation. What was not expected however was that the average size of the plants outside the plots increased slightly with distance from the initial sowed plots. This was evident for all four species as regression analyses were significant. This was the opposite of what others such as Schlawin & Zahawi (2008) found. In their study based in neotropical wet forests, plants decreased in size with distance from the original clumps which is generally what one would expect. As previously mentioned, the Fynbos site experienced mass recruitment of *Acacia* seedlings immediately after clearing, making the area surrounding the plots unsuitable for establishment. Follow up *Acacia* clearing was conducted in 2015, coinciding with the plants in the sowed plots being at an age where they could produce seed. The larger plants observed further away from the sowed plots is likely because of seed being able to disperse at greater distances

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while the surrounding area was bare after the *Acacia* clearing, and suitable for establishment. After that it is likely that new seed was trapped closer to the restoration plots as vegetation established around the plots and became denser. More of this is mentioned in chapter 3 of this thesis where the role of obstacles as seed traps is discussed.

2.6 Conclusion and implications for management

The study supported the hypothesis that previously restored plots would be observed to be spreading and colonizing the surrounding area, initiating the nucleation process, but that only a subset of wind-dispersed species would be responsible for it. It can be concluded that applied nucleation has the potential to be used as an effective restoration tool in Cape Flats Sand Fynbos to initiate ecological restoration of degraded areas, even though frugivory isn't a mechanism for dispersal in this vegetation type. Wind dispersal is sufficient as a dispersal mechanism to facilitate applied nucleation in this case. For nucleation to occur, the species which begin to spread from the original nucleus need to create an environment which will trap seed from other species and facilitate further colonisation in that manner. This however is difficult in this context as the native CFSF seedbank has been severely depleted as a result of prolonged *Acacia* invasion (Hall et al., 2021), and thus the introduction of propagules naturally is unlikely unless there is a patch of native vegetation nearby which could act as a seed source.

These species are also prolific seeders (P.M Holmes, personal communication), which is particularly useful information as indigenous Fynbos seed is not always readily available, while the seed of *Anthospermum aethiopicum* and *Ifloga repens* for example are easier to collect in larger volumes. Even though this approach may result in very low species richness, nucleus establishment would be an effective method of establishing a vegetation base, or structural framework (Corbin & Holl, 2012), upon which further restoration efforts can be built. If one were to solely rely on applied nucleation as a restoration technique, the vegetation base would be shrubs, ericoid shrubs, and forbs, with the overstorey proteoid and restioid components missing outside the plots in the first restoration cycle. These missing components could however establish naturally if their seed is trapped by the nuclei (Corbin & Holl, 2012). The complication in this scenario however is that there are very little remnants of indigenous CFSF species in the BBNR where seed could originate (Hall et al., 2021), and the native seedbank has also been severely degraded as a result of the prolonged *Acacia* invasion (Hall et al., 2017).

After disturbance, in forest regeneration at least, pioneer species establish in clumps and this is what applied nucleation is designed to replicate (Corbin & Holl, 2012). These clumps initially have low

species diversity which gradually increases as frugivorous dispersers are attracted, bringing with them the seeds of other species from intact indigenous vegetation which then increases the species diversity within and around the clumps (Holl et al., 2011). These clumps then begin to nucleate into the surrounding area via natural forest successional processes (Corbin et al., 2016). A comparison can be drawn here between natural forest recovery and the restored plots in the BBNR, the only missing aspect being seeds being brought in by frugivorous dispersers. The clumps in both instances are initially species-poor, and while forest clumps increase in species diversity naturally via dispersers, the clumps in Fynbos would have to trap seed from nearby intact vegetation, or have this process replicated by certain species being planted in the plots so as not to rely on sowing alone, as this has already proven to not be very effective, with less than 50% of species originally sown being present in the surveyed plots.

For the first time, this study provides an indication of CFSF species with the ability to initiate nucleation, and their dispersal distances, as well as suggests species to use for further restoration sowing efforts. Future research could consider other species able to recruit in inter-fire periods, and also to monitor plots after the first prescribed burn to determine whether any fire-dependent species were able to set seed and recruit seedlings. Furthermore, the remaining plots which were not surveyed should be surveyed to ascertain whether nucleation has started. This study was only able to focus on wind and passively dispersed species as no fire occurred during the study period. These species are ideal as their seed is readily available, they are prolific seeders and annuals such as *D. pluvialis* generally track gaps/bare ground in the vegetation in which to establish free of competition.

Since all the species seen to be spreading were wind dispersed, future research should consider wind direction when assessing and determining the nucleation success of restored plots. Fynbos occurs on the western and southern coast of South Africa, and these areas experience wind for much of the year. Prevailing wind directions may aid restoration design, with nuclei strategically placed in areas where dispersal distances could be maximised. A distinct dispersal pattern correlating to prevailing wind direction was not determined, as this was not measured consistently across plots, and thus a precise decision about the influence that wind direction may have on seed dispersal cannot be made. However, it is known that northwesterly winds dominate in winter and southeasterly winds in summer. Analysing seed maturation and dispersal times for key species would help to determine which wind direction to harness in the placing of sowing plots. Future research could keep the larger sampling quadrants consistent in direction, so that one could determine if prevailing wind patterns influence the outcome of the results.

The ideal outcome of restoration initiatives would be a near-natural community comprised of all the major guilds of that specific habitat type. The applied nucleation restoration technique allows the establishment of a vegetation base upon which further restoration efforts can be built albeit a rather species-poor base. Reintroductions of under-represented guilds are recommended after the next fire cycle, particularly those which are fire dependent. It is important that guilds are well-represented as increased species richness results in improved community resilience and successful restoration in the long run (Holmes et al., 2020).

Fire is undoubtedly the most important driver for recruitment in the Fynbos biome (Brown, 1993; Cilliers et al., 2004; Kraaij & van Wilgen, 2014; Pierce & Cowling, 1991; van Wilgen et al., 2010), but as a result of management regimes, regulations, and the planning that goes into organising a prescribed burn, they are resource-intensive, and in fragmented remnants seldom occur naturally anymore. The importance of a burning schedule in management is critical, and if applied nucleation is to be incorporated into management regimes, it should be done so with an understanding of how a prescribed burn could impact the nuclei and influence recruitment.

Overall, applied nucleation has the potential to be used as a cost-effective restoration tool in Cape Flats Sand Fynbos, and potentially in other dryland ecosystems where seed sources are limiting, even those dependent on fire for succession. While the efficacy thereof is evident in the data and results, nucleation dynamics are still not fully understood, particularly for those guilds which were under-represented. Further research is thus crucial in the face of drastic habitat destruction, particularly for a concept which has the potential to be an effective restoration tool moving forward. Disadvantages of this approach are that data are limited, one is restricted to initially using a handful of species in the restoration plots, and these species do not truly represent a typical CFSF community. Furthermore, one has to wait for a fire event to determine whether other species are moving beyond the original plots and nucleating. Establishing restoration plots means that only a section of a cleared area is being colonised with plants. This leaves large areas of bare ground which are susceptible to invasion by invasive alien plants. In this situation monitoring and ongoing alien clearing are of the utmost importance.

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Chapter 3: Designing a simulation model to test the impacts of different management regimes on the effectiveness of applied nucleation in restoring a degraded, fire-driven Fynbos ecosystem

3.1 Abstract

Being able to predict the outcomes and consequences of ecological management alternatives is vital. Ecological restoration after the clearing of invasive alien species is important to ensure that indigenous species can establish to help prevent reinvasion. Several post-invasive alien clearing restoration initiatives have been undertaken in Cape Flats Sand Fynbos, a critically endangered vegetation type in the Cape Floristic Region of South Africa. While in some situations these have been successful, in other situations there is a need for effective post-clearing ecological restoration techniques. In this study, a model was designed for managers and practitioners to aid in making future management decisions. The model simulated the efficacy of applied nucleation under different management regimes, pertaining particularly to the arrangement of brush piles of felled alien *Acacia* biomass, referred to as obstacles. The study gave insight into the nucleation potential of four Cape Flats Sand Fynbos perennial species. The model simulations showed that a radial pattern of obstacles, 40m^2 in size, and 7m apart resulted in the highest facilitation of nucleation. The model also highlighted the importance that biological parameters such as reproductive rate and dispersal kernel can have on the nucleation potential of species. Species with a high reproductive rate and a dispersal kernel which allows for long distance dispersal have the highest nucleation potential.

Key words

Ecological restoration, Cape Flats Sand Fynbos, applied nucleation, nucleation potential, reproductive rate, dispersal kernel.

3.2 Introduction

It is well-documented that biological invasions negatively impact on biodiversity, and invasive alien plants have been categorised as one of the largest threats to global biodiversity, second only to direct habitat destruction (Richardson & van Wilgen, 2004). Invasive alien plants result in decreased biodiversity over time, and this can translate into considerable social and economic impacts (Henderson, 2007). Invasive alien plants can permanently and irreversibly alter the structure and functioning of ecosystems (Gaertner et al., 2012) and also pose a major environmental threat to South Africa's freshwater and terrestrial ecosystems (Le Maitre et al., 2002). One such invader is *Acacia*

saligna, a prevalent invader in the Fynbos biome. This species is fast-growing and able to outcompete indigenous Fynbos species for light, nutrients, and water (Gaertner et al., 2014). They are known to result in the depletion of native seed banks (Holmes, 2002) which can severely reduce the chance of passive vegetation recovery (Hall et al., 2021). This effect is not isolated to Fynbos, but has been seen in other Mediterranean climate vegetation types as well, such as in the *Acacia* invaded dune ecosystems in Portugal (Marchante et al., 2011). The depletion of native seed banks to the point where they cannot result in any germination and growth indicates that a threshold may have been crossed and intervention is required. When this is the case active restoration initiatives need to be implemented and this is where the introduction of seed into the environment by sowing is required (Hall et al., 2021; Holmes et al., 2020).

Fire is arguably the most important driver in Fynbos, and is key to the persistence and longevity of the biome as a whole (Kraaij & van Wilgen, 2014; Marais, 2012). While fire is an important management intervention in Fynbos (Kraaij & van Wilgen, 2014), control of invasive alien plants is equally important (Holmes et al., 2020). In many Fynbos ecosystems, invasive alien species easily outcompete the indigenous Fynbos for water, light and nutrients and some species are able to alter soil chemistry to the benefit of themselves i.e., by creating a positive feedback loop (Gaertner et al., 2014; Weidenhamer & Callaway, 2010). It is estimated that up to two thirds of the protected area of the Western Cape (where Fynbos is most prevalent) is invaded by invasive alien plants (van Wilgen et al., 2016), and thus the control of invasive alien plants within protected areas is important in ensuring the persistence of indigenous Fynbos species. Their ability to alter their habitat to such an extent means that they are "ecosystem engineers" (van Wilgen et al., 2008). The Fynbos biome is particularly susceptible to plant invasions and is subject to invasion by an array of alien species. One of the most widespread invasive alien plants in the Fynbos biome lowlands is the Port Jackson Willow (*Acacia saligna*), which is native to Australia and is an aggressive invader that produces copious quantities of long-lived seeds and can also resprout after fires (Hall et al., 2021). Dense stands of *Acacia* can deplete indigenous seed banks over time, meaning that seed sowing would be needed to re-establish certain species when restoring vegetation (Holmes, 2002).

It has been postulated that ecological restoration may protect biodiversity, ultimately improving the livelihoods of people as well contributing positively to the economic sector (Gann et al., 2019). Implementing ecological restoration is a multidisciplinary endeavour and involves the collaboration of scientists, politicians, land managers, and the community at large to ensure that it is undertaken correctly and ultimately results in the repair of degraded ecosystems. It is critical that informed management decisions are taken to ensure successful restoration.

In the Blaauwberg Nature Reserve (BBNR), a protected area undergoing ecological restoration after dense alien invasion (Hall et al., 2021), several clearing methods have been tested. These include the stacking of felled *Acacia* trees into brush piles, leaving them to decompose, or to burn piles during the wet winter season when negative impacts on the soil are minimized. These brush piles have unnaturally high fuel loads and thus burn at higher intensities. This has the potential to alter soil chemistry, reduce seedling density, and loss of species (Blanchard & Holmes, 2008). In both abovementioned techniques, it is important to stack as tightly as possible to minimize the negative impacts of the brush piles and maximize the area open for restoration (Cilliers et al., 2004). It is important to note that this may not always be possible as the teams contracted out to carry out the work often make the brush piles too large to minimize effort. Remaining brush piles may not be strategically placed but should allow enough space among them for passive (spontaneous succession) or active restoration. Since the decomposing brush piles may be a part of the restorative landscape, the question is posed as to whether they could be deployed to promote restoration as seed-trapping obstacles, or if their spatial arrangement could influence restoration outcomes.

In 2013 and 2014 seeded restoration plots were established in the recently cleared areas in the reserve as part of a PhD project (Hall et al., 2021) and these plots have been revisited to determine whether actively sown species have begun to colonise the surrounding habitat (Chapter 2 of this thesis). The process of the spread and establishment of species from an original nucleus of established vegetation is known as nucleation, and when used as a restoration technique, is called "applied nucleation" (Corbin et al., 2016). Applied nucleation is a method of ecological restoration whereby clusters of vegetation are established either by sowing or by planting, and then over time and through dispersal and spontaneous succession they begin to nucleate into the surrounding area, facilitating the introduction of other species as nucleation progresses (Corbin et al., 2016). However this method of restoration is more commonly used in forest vegetation types where frugivory is the primary mechanism for seed dispersal (Corbin & Holl, 2012) and is touted as the main driver of applied nucleation (Corbin et al., 2016). Frugivory is uncommon in Fynbos however, as most species have short-distance dispersal modes by ants, ballistic or passive mechanisms. Some Fynbos species are dispersed further by wind and such species potentially may nucleate from original restoration plots. In addition, most Fynbos species are either directly or indirectly dependent on fire for germination and establishment and dispersed seeds of such species will not germinate until after a subsequent fire (Brown, 1993; Cilliers et al., 2004; Hall et al., 2017).

Being able to predict the impacts of different management regimes is useful for management decision-making (van Wilgen et al., 2016). The use of ecological models in deciding which management regimes will be most effective is well-documented (Cuddington et al., 2013; Hall et al., 2020; Jopp et

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al., 2011; Rödder & Lötters, 2010; Sagnard et al., 2007; Schurr et al., 2005; Sutherland, 2006; Tackenberg, 2003) and the use of a predictive model in the context of different applied nucleation scenarios is feasible. Model outputs need to be synonymous with the overall goal of the management regime, which is to accelerate the process of ecological restoration, and inputs must be reflective of environmental factors. Modelling ecosystem dynamics is an important tool in predicting outcomes and making management decisions (Le Maitre et al., 2011).

Applied nucleation models have traditionally been done by means of mixed linear models (Rojas-Botero et al., 2020; Camargo et al., 2020) and general linear models (GLM) (Bechara et al., 2021). Both techniques make use of ecological data which has been collected, and using that information nucleation predictions are made. These are standard methods of ecological modelling (Cuddington et al., 2013; Hall et al., 2020; Jopp et al., 2011; Rödder & Lötters, 2010; Sagnard et al., 2007; Schurr et al., 2005; Sutherland, 2006; Tackenberg, 2003), and their importance in modelling nucleation and thus restoration trajectories is vital in determining restoration feasibility and efficacy as they offer insight into how nuclei might develop and expand under a number of conditions.

The theme of the research currently being conducted in the BBNR involves fast-tracking and scaling up the process of ecological restoration. Applied nucleation and appropriate spatial placement (e.g., position of nuclei and position of alien brush piles) has the potential to contribute to this theme. The assumption is that where only a few small areas are actively restored through active seed sowing, nucleation over time will result in the entire area being colonised.

While active restoration efforts have been partially successful, much remains to be desired in terms of scaling up restoration in the most cost and labour efficient manner possible. The BBNR contains a large portion of the last remaining Cape Flats Sand Fynbos (CFSF) remnants and the conservation and restoration thereof is a high national priority.

This chapter presents a practical and robust model which can be used by scientists, practitioners, and managers alike in making management decisions for planning future ecological restoration interventions. This is achieved by modelling the arrangement and size of brush piles to act as seed traps, while simultaneously modelling the different management regimes which employ this tactic. The model is used to test the nucleation potential of the four nucleating species identified in Chapter 2 of this thesis. The model was designed using the Inverse Modelling (IM) technique. This is a common modelling technique which makes use of model outputs to infer input data when data or input parameters are limited (Migliavacca et al., 2008). It is believed that this study will provide effective guidelines for management decision-making regarding the use of obstacles after *Acacia* clearing, as well as provide insight into the restoration potential of the four nucleating species (Chapter 2).

3.3 Methods

3.3.1 Study site

The study site was located in the Blaauwberg Nature Reserve (BBNR) which spans an area of 1500ha from the coast near the town of Melkbosstrand and inland over Blaauwberg Hill to encompass some of the sand plain (33.75°S, 18.48°E). This reserve has been the subject of multiple ecological restoration initiatives for over a decade by the City of Cape Town Biodiversity Management Branch in collaboration with various entities and universities. One of these initiatives involved establishing 50m^2 restoration plots for the PhD research of Stuart Hall (Hall et al., 2017, 2020, 2021). These plots were revisited for chapter 2 of this thesis, and the idea of modelling applied nucleation in this study arose from assessing whether these plots had begun to nucleate.

3.3.2 Sampling strategy

Fourteen of the thirty two active restoration plots established by Hall et al., (2021) were re-surveyed. In 2013, active restoration was conducted by sowing a seed mix of indigenous Cape Flats Sand Fynbos (CFSF) species into 10m x 5m plots (Hall et al. 2021). Field observations in 2019 showed that the plants which had grown from the initial sowing had started producing and dispersing their own seed, resulting in the emergence of several young plants both within the initial sowed plots and also beyond the plot perimeters (Chapter 2 of this thesis). Four plant species were nucleating from initial sowed plots and thus were able to germinate without direct fire-related cues. The number of adult plants per species was counted in the initial sowed plots, as well as the number of young plants of that species. A larger plot was then marked off around this initial sowed plot (see Chapter 2 methods), and the number of young plants per species also counted. There is no published research on plant fecundity and reproductive rates for these species, so the ratio between the number of adult plants and young plants within the plot was used as a surrogate for plant fecundity / reproductive rate. This seedling per parent ratio was also used by Midgley et al., (1998); however, it cannot be ascertained which seedling came from which parent plant.

To model applied nucleation, the techniques and principles used by Schurr et al., (2008) were applied, where modelling was centred around two major parameters: source effects and path effects. Source effects refer to variations in plant fecundity and dispersal kernels as influenced by the plants' immediate surroundings as well as their specific dispersal adaptations. Path effects are dependent on the environmental conditions a seed may encounter along its dispersal kernel. It is important to note that source and path effects do not necessarily refer to distinct variables, but rather describe how environmental variables affect dispersal (Schurr et al., 2008). In their 2008 paper Schurr et al. (2008)

transformed the physical space a seed will travel through in such a way that areas which have a low permeability (i.e., an environment where a seed may not pass through very easily) are enlarged in comparison to areas where a seed may pass through more easily. The "enlarged" space results in more seeds being trapped and can be referred to as being "sticky". An effective way of describing the enlargement of this movement space is to use a hiking analogy, whereby distances are often expressed in terms of hike duration rather than actual units of distance (Schurr et al., 2008). This is because time taken is often indicative of the roughness of terrain or the steepness of the hike. In the model, movement space was enlarged by increasing the number of obstacles (in this case brush piles) and decreasing the permeability of the area, which in turn increased seed trapping potential. Movement space is enlarged when certain parameters such as permeability of the environment are reduced.

Source effects were taken by estimating plant fecundity which was determined by calculating the ratio of seedlings per adult plant in the initial sowed plots. The young plants outside the sowed plot were omitted in this calculation as they may have not grown from seed originating from the plants within the initial sowed plot. Path effects were modelled by using different types of obstacles and arrangements of obstacles, in this case brush piles, around the initial restoration plots in the BBNR. The arrangement and size of brush piles was modelled to simulate different management regimes; including those which have been implemented before and some which have not yet been conceptualised or implemented.

3.3.3 Management regimes

Two of the management regimes currently implemented in the BBNR were modelled: Fell & Stack (FS) where felled *Acacia* trees are stacked into large brush piles and Fell & Burn (FB) where the felled *Acacia* biomass is spread and then burnt (Figure 3.2 A, B, C, D). Variations of these two management regimes were modelled using different scenarios (Figure 3.1). These included: for FS – grid and radial patterns of stacked *Acacia* brush piles. For FB – random obstacle arrangement, which simulated *Acacia* seedling regrowth or random obstacle placement, and a bare ground scenario simulating substrate completely devoid of any vegetation or obstacles. *Acacia* seedling regrowth was simulated here and not in the FS treatment as large *Acacia* seed banks are stimulated to germinate after fire, resulting in dense seedling establishment in the FB treatment (Hall, 2018). Brush pile sizes in the BBNR were measured using Google Earth measuring tools, and the average brush pile size came to $42.5m^2 \pm 8m^2$ (n=10). An example of brush piles can be seen in Figure 2B, C and D. The burn stack option was not considered for this study (Appendix 1.7).
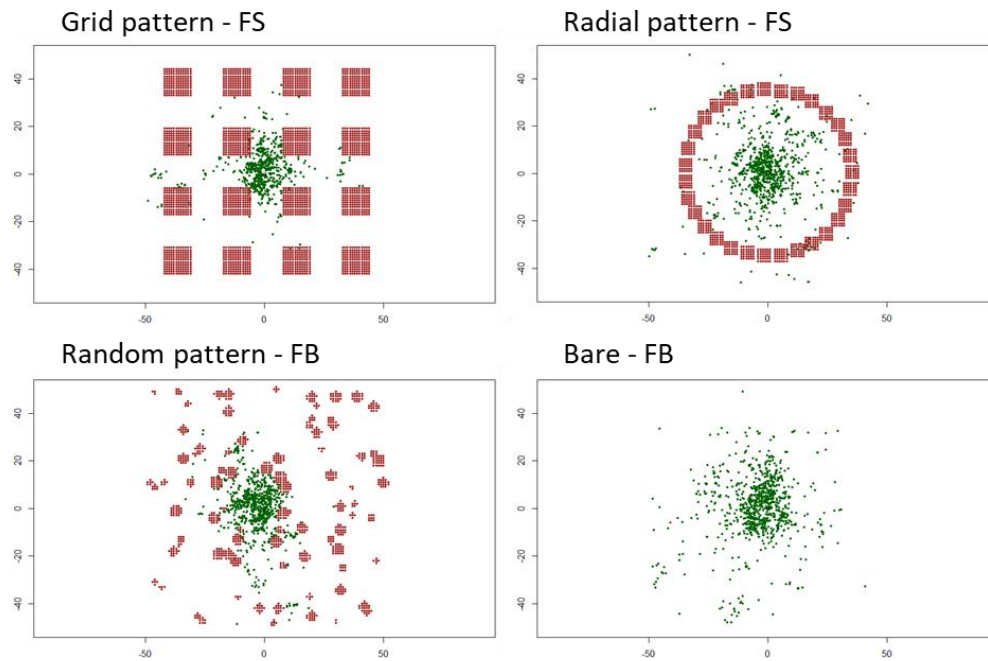
Figure 3.1 Conceptual diagrams of the various obstacle arrangements and management regimes modelled in this study. (Brown points are obstacles, green points are plants. FS – Fell & stack, FB – Fell & burn).
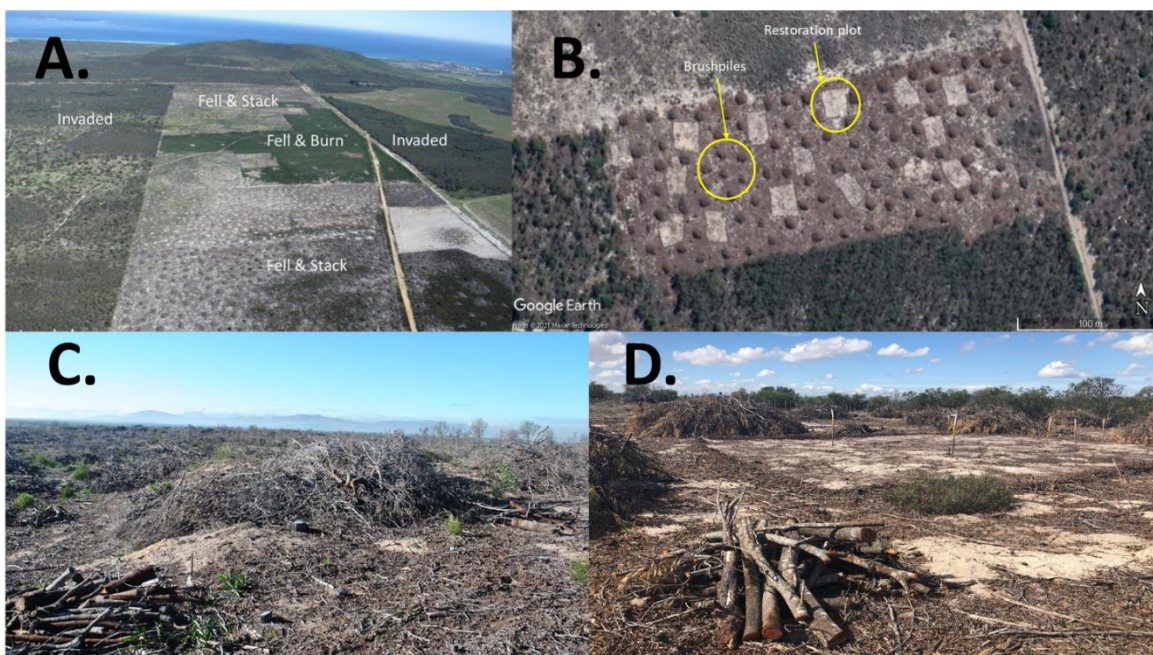
Figure 3.2. A. Fell & Stack (FS) and Fell & Burn (FB) within the Blaauwberg Nature Reserve; Blaauwberg Hill in the background (Image: City of Cape Town & PM Holmes, 2014). **B.** Brush piles surrounding the sowed plots in a recent study at the Blaauwberg Nature Reserve site (2019). The bare patches in this image are restoration plots in the study of a PhD student. **C.** Brush pile after felling *Acacia* trees (Photo credit: Stuart Hall); firewood logs are removed from site. **D.** Brush piles surrounding sowed plots; the occasional indigenous shrub has persisted; (Photo credit: K.J Esler).

3.3.4 Model conceptualization

The modelling strategy used an Inverse Model (Schurr et al., 2008). Inverse modelling is a modelling technique commonly used when certain model parameters are not available, as it makes use of model outputs to infer the values of model parameters (Migliavacca et al., 2008). The model code (Appendix 3) was obtained from Prof. Dr Frank Schurr from the Institute of Landscape and Plant Ecology at the University of Hohenheim in Stuttgart Germany. Several model codes were changed to suit the particular needs of this applied nucleation simulation model. The model was developed to simulate the effects that different management regimes had on applied nucleation and to indicate how an area subject to different regimes would be colonised by Fynbos plants over time. The model was also developed to assess the nucleation potential of the nucleating species observed in Chapter 2 of this thesis (Appendix 1.2). Using RStudio (Rstudio Team, 2020) the management regimes were simulated by having obstacles arranged in certain patterns around a theoretical restoration plot. By manipulating these parameters, variations of the abovementioned management regimes could be simulated. Furthermore, by manipulating certain biological parameters the nucleation potential of certain species could be simulated. The aim was to be develop the model as a practical, robust, and user-friendly tool, of use to scientists, practitioners, and managers for making future management decisions relating to ecological restoration.

After running simulations, the model produced a graph per timestep, meaning that if Tmax was four, four graphs were produced. The simulation results were stored in objects in the R Environment and could be extracted and analysed, as there is code in the model which extracts simulation data and tabulates it.

In terms of practical application, the model has a relatively small number of simple settings and parameters that can be manipulated. There are some general settings which would likely stay the same for different simulation scenarios. The biological parameters may be changed, depending on the species being considered, or on the nature of the environment surrounding the original restoration nucleus. The obstacle parameters can be changed to simulate different placement arrangements and sizes.

Finally, the "plants.start" setting enables specific co-ordinates to be specified (using x and y values) of the plants, which are identified as the "parent" plants. This is read into RStudio programme via a table; these values may be changed. For this study, a random number generator in MS Excel was used to generate starting points. For the x-value it was specified that the coordinate must be between -5 and 5, and the y-value between -10 and 10 for a 50m^2 initial sowing plot. One could essentially place nuclei

anywhere on the plot and simulate nucleation from multiple nuclei, however this was not done in this study. The table of starting points used in this simulation are in Appendix 1.8 attached.

The image in Plate 1 depicts the exact scenario this model is designed to simulate. Sown plots can clearly be seen, surrounded by a grid or random pattern of *Acacia* brush piles. If one knows the size of the brush piles, restoration plots, and species used in the sowing, the nucleation potential of this management scenario can be modelled.

3.3.5 Model settings

There are four general settings in the model (Table 3.1) which can be modified, but for the purposes of this chapter they were kept constant. The extent refers to the length of the sides of the simulation area. This was kept at 100m as this allowed for accurate assessment of the efficacy of the simulation. If any points fell outside this area, there was a rule in the model which disregarded these points. The length of the sides of each grid cell is 'd', measured in metres. Tmax is the total number of dispersal events being simulated and is essentially the number of years over which the simulation runs.

Nsim refers to the number of simulations run and can be manipulated to increase the number of replications. It was kept at one for the purpose of this study.

Table 3.1 General model settings.

Setting	Description
Extent	The side length of the simulation area in m
d	The side length of each grid cell in m
Tmax	The total number of dispersal events simulated
Nsim	The number of replicate simulations

The biological parameters (Table 3.2) may be modified depending on species characteristics: i.e., fecundity, dispersal kernel and carrying capacity. The reproductive rate or fecundity is 'R0'. As the literature on the fecundity of these Fynbos species is scarce, fecundity was measured as the ratio of young plants to adult plants in the sowed plots (Midgley et al., 1998), or the ratio between plants found within the sowing plot to plants found outside the sowing plots for the annual *D. pluvialis.* This was done as there was no data for the parent plants which would have been alive in the previous season. Carrying capacity per m^2 (K) may be altered depending on the state of vegetation cover or the stage of vegetation recovery. It was decided that a carrying capacity of three perennial plants per m^2 would be sufficient to use in all simulations as this is an appropriate density to aim for during initial

vegetation recovery (P.M Holmes, personal communication). For maximum carrying capacity this value could be changed to ten for example. The value "u" is the log-scale mean of lognormal dispersal kernel and determines the distance which the seed can travel based on its morphology. A higher u-value means a seed can travel further. A u-value of 1.2 was used for the passively-dispersed species *Anthospermum aethiopicum* which disperses further by tumbling after initial seed drop (Frank Schurr, personal communication, 2020). However, wind-dispersed species may have different dispersal kernels. With 1.2 as a benchmark value, seed drop velocity data (Appendix 1.9) were used to calculate u-values for the other species (Appendix 1.1). The seed drop velocity (0.36m/s) and u-value (1.2) for *A. aethiopicum* were known and using the ratio between them (1:3.33) it was possible to produce u-values for the other species (Appendix 1.9). This was done by subtracting the species' seed drop velocity from that of *A. aethiopicum* and multiplying this value by 3.33 (ratio mentioned above). The value obtained from this was then added to the original u-value of *A. aethiopicum* (1.2) to provide the u-value of the species in question.

The log-scale standard deviation of the lognormal dispersal kernel is represented by p, and beta_w is the parameter which determines the strength ("stickiness") of path effects. Beta_w represents how physical space is projected onto movement space. For 1 plant per m^2, space is stretched by a factor of beta_w. This value must be greater than or equal to 0, and for a value of 0 there is no path effect i.e., there is no "stickiness".

Seed drop velocity (Appendix 1.1) was determined by dropping 10 seeds per species from a height of 2.5m in a controlled environment and measuring the time it took for the seed to reach the ground.

Table 3.2 Biological parameters of the applied nucleation simulation model.

Biological parameter	Description	Comments
R0	Reproductive rate	The number of offspring per adult.
K	Carrying capacity	The maximum number of individuals per m^2.
u	log-scale mean of lognormal dispersal kernel	This value determines the distance which the seed can travel. The benchmark value is 1.2 for *A. aethiopicum* (Frank Schurr, personal communication, 2020). This value is suitable for tumble dispersal following seed drop. Using seed drop velocity data values for the other species were calculated. A higher number results in a larger dispersal kernel.
p	log-scale standard deviation of lognormal dispersal kernel	Standard deviation of the dispersal kernel
beta_w	Parameter determining strength of path effects	The parameter determining the strength of path effects. It describes how physical space is projected onto movement space. For 1 plant/m^2, the space stretched increases by beta_w. beta_w must be >=0, for beta_w = 0, there is no path effect i.e., there is no "stickiness".

The obstacle parameters may be changed to fit different management scenarios (Appendix 1.2). The "shape" refers to the way the obstacles are arranged. The "n" value is the number of obstacles which fit in the total obstacle area. Obstacle size is the size in m^2 of the obstacle and "distance" is the distance between the obstacles. Total obstacle area refers to the combined size of all the obstacles in the simulation.

3.3.6 Management scenario parameters

Several management scenarios were modelled, comprising five fell and stack scenarios, two of which were in a grid pattern, two in a radial pattern and one random (Appendix 1.3). The obstacle arrangement and sizes varied, but the first scenario simulated the current arrangement of *Acacia* stacks in the BBNR. The parameters were then changed to test the effects that different obstacle

arrangements and sizes may have on nucleation. Biological parameters were kept constant so as not to influence these data and are general values for a typical CFSF pioneer shrub species such as *A. aethiopicum*. Scenarios 1, 2, and 3 were designed to simulate a FS management regime where felled *Acacia* is stacked into brush piles in a regular grid pattern and left to decay over time. Given the same quantity of slash material from alien clearing, in an area of $2304m^2$, Scenario 1 had an n-value of 4 meaning there were 16 obstacles, Scenario 2 had an n-value of 8 or 64 obstacles and Scenario 3 had an n-value of 12 or 144 obstacles. The different n-values simulate management scenarios where there are fewer, large brush piles, or a higher number of smaller piles. The number 2304 was chosen as it allows one to have proportional square-shaped obstacles. For example, if n=4, you have a total of 16 obstacles (4x4=16), then $2304m^2/16=144m^2$, which is the size of a single brush pile whose dimensions are 12m x 12m.

Scenarios 4 and 5 simulated a FS management regime where stacks were arranged in a radial pattern around the sowed plot. Scenario 4 simulated brush piles which were 7m away from one another and an obstacle size of $40m^2$, and Scenario 5 simulated stacks 14m away from one another with an obstacle size of $60m^2$.

Scenarios 6 and 7 simulated the FB management regime where *Acacia* biomass is spread and burnt. Scenario 6 was designed to simulate *Acacia* regrowth if follow-up clearing was not done. The obstacle size ranged from $1m^2$ to $25m^2$ to simulate individual saplings as well as larger stands of *Acacia* saplings. This scenario can also be used to simulate various sizes of felled *Acacia* stacks randomly in the area. Scenario 7 was designed to simulate an area that was completely bare of any form of obstacle, be it biotic or abiotic. This would be the case if the area was burnt after felling, removing both dead and living biomass, and if follow up clearing was conducted timeously and effectively.

3.3.7 Nucleation potential parameters

The nucleation potential of species was also modelled to give an indication of which species would be beneficial to use in future restoration efforts (Appendix 1.5). The only parameters which were changed here were the biological parameters, whereas the general settings and obstacle parameters were kept constant. The two main values which were manipulated were the R0 and u-values, which are the reproductive rate/ fecundity, and the log-scale mean of lognormal dispersal kernel, representing the ability of the species to disperse seed. *Anthospermum aethiopicum* had an R0 value of 6.2 and u-value of 1.2. This species had a high young plant/parent ratio resulting in the high R0 value, and the u-value is typical of a species which relies more on tumble after seed drop (Table 3.2). *Ifloga repens* had an R0 value of 2.9 and a u-value of 1.93, *P. capitatum* had an R0 value of 1.83. *Dimorphotheca pluvialis* had

a very high R0 which can be attributed to the high young plant/adult ratio. It is important to remember that *D. pluvialis* is an annual and thus all plants observed are deemed to be the same age (Chapter 2). Thus, to compensate for this and to produce an R0 value for this species, the plants found within the initial sowed plots were used to surrogate adult plants, and the plants found outside the sowing plots used to surrogate young plants in order to determine the R0 value. In order to determine true R0 one would need to use the number of plants in the previous season as adult plants, and this was not possible in this case. *Dimorphotheca pluvialis* also had a high u-value meaning that it has high dispersal distance ability, given effect by its very slow seed drop velocity.

3.3.8 Data processing

The results from running the model were stored in objects in the R environment and these were tabulated in such a way as to compare the different management scenarios and to compare the nucleation potential of each species. Results were given for Timesteps 1 to 4.

3.3.9 Expected outputs of the simulation

The expected outputs from simulating different management scenarios were: the area colonised in m^2 for all timesteps, plant population size for all timesteps, the total number of plants, and the colonization distance in metres. The assessment of success of the different management scenarios was based on the area colonised and population size at the final timestep, as well as the colonization distance.

The outputs expected from simulating the nucleation potential of four species remain the same as above, with differences relating to changing biological parameters while keeping obstacle parameters constant.

3.4 Results

<u>3.4.1 Management scenarios</u>

Of all the management scenarios modelled (Table 3.3), the radial grid pattern under FS management of Scenario 4 (Appendix 2.4) was the most successful as it resulted in the greatest area colonised (935m^2), the highest population size of a typical CFSF shrub species such as *A. aethiopicum* by T4 (1619 plants) and had a maximum colonization distance of over 70m. All the scenarios start out with very similar values at T1 for all simulation results. Thereafter the effects of the obstacle parameters become apparent as the results begin to diverge from T2 onwards. Results from the grid patterns of Scenarios 1 to 3 were different (Table 3.3). In Scenario 1, with a lower number of large stacks, colonization was more widespread and the area colonised was 580m^2, with the population being 1144 plants. Colonization and nucleation were significantly stifled in Scenario 3 which was characterised by a high number of closely stacked small brush piles. The area colonised here was only 288m^2 and the population size being 612 plants.

The random obstacle pattern in Scenario 6 (Table 3.3 & Appendix 2.6) in the FB management regime simulated *Acacia* regrowth, and had a colonization area of 418m^2 at T4, a population size of 841 plants at T4, and a colonization distance of 60.8m. The other scenario under the FB management regime, Scenario 7, simulated a bare ground situation devoid of any obstacles. It had the highest area colonised of any of the scenarios at T2 (115m^2) and had the second highest at T4 (903m^2). It also had the second highest population size (1608 plants).

<u>3.4.2 Species nucleation</u>

Dimorphotheca pluvialis had the highest nucleation results of all the species assessed (Table 3.4 & Appendix 2.8). The area colonised was 4724m^2 with a population of 8801 plants. As is seen in Appendix 1.2 and Appendix 2.9, *D. pluvialis* displayed intensive colonization of the habitat. This species had the highest R0 value (reproductive rate) in the simulation. *Anthospermum aethiopicum* had the second highest nucleation results with 1761 m^2 of area colonised, and a population of 3314 plants at T4. All species had a colonization distance exceeding 70m. *P. capitatum* had the lowest R0 value of the four species and did not display intensive colonization like the other species did (Table 3.4 & Appendix 2.11)

Table 3.3 Simulation results obtained from RStudio after running simulations on various management scenarios (variations in scenario parameters can be found in Appendix 1.3).

Scenario	Management scenario	Obstacle pattern	Obstacle type	T1 area colonised (m²)	T2 area colonised (m²)	T3 area colonised (m²)	T4 area colonised (m²)	T1 population size	T2 population size	T3 population size	T4 population size	Total no. of young plants	Colonization distance (m)
Scenario 1	Fell & stack	Grid	Slash stack	34	105	266	580	40	165	491	1144	1144	>70
Scenario 2	Fell & stack	Grid	Slash stack	32	87	206	406	40	148	398	829	829	41.9
Scenario 3	Fell & stack	Grid	Slash stack	25	66	153	288	38	122	305	612	612	39.2
Scenario 4	Fell & stack	Radial	Slash stack	33	114	356	935	40	172	561	1619	1619	>70
Scenario 5	Fell & stack	Radial	Slash stack	32	106	309	776	40	168	511	1352	1352	>70
Scenario 6	Fell & burn	Random	*Acacia* regrowth	33	75	200	418	40	140	362	841	841	60.8
Scenario 7	Fell & burn	Bare	No indigenous regrowth and no invasion due to follow up clearing.	33	115	349	903	39	166	573	1608	1608	>70

Table 3.4 Results of nucleation potential simulation.

Key:

- R0 – reproductive rate
- K – carrying capacity
- u – log-scale mean of lognormal dispersal kernel
- p - log-scale standard deviation of lognormal dispersal kernel
- beta_w - parameter determining strength of path effects

Species	Obstacle pattern	Obstacle type	Actual R0	Used R0	K	u	p	beta_w	T1 area colonised (m²)	T2 area colonised (m²)	T3 area colonised (m²)	T4 area colonised (m²)	Total no. of obstacles	T1 population size	T2 population size	T3 population size	T4 population size	Total no. of young plants	Dispersal distance (m)
Anthospermum aethiopicum	Grid	Slash stack	6.2	6	3	1.2	1.2	3	48	209	660	1761	1113	56	319	1171	3314	3314	>70
Ifloga repens	Grid	Slash stack	2.9	3	3	1.93	1.2	3	23	73	220	591	1113	27	93	290	836	836	>70
Pelargonium capitatum	Grid	Slash stack	0.4	1	3	1.83	1.2	3	15	24	46	85	1113	16	30	57	109	109	52
Dimorphotheca pluvialis	Grid	Slash stack	8.6	9	3	2.2	1.2	3	51	285	1399	4724	1113	64	391	2106	8801	8801	>70

3.4.3 Obstacle arrangements

The results describing optimal nucleation are: area colonised, population size, and colonization distance. The obstacle arrangement which produced the lowest nucleation results was Scenario 3, where obstacles were arranged in a grid pattern. The grid pattern scenarios (Table 3.3) had a maximum area colonised of 580m^2 in Scenario 1, and a minimum of 288 m^2 in Scenario 3. The largest population was in Scenario 1 with 1144 plants, and the lowest in Scenario 3 with 612 plants. Scenario 1 had the greatest colonization distance of >70m, and Scenario 3 the lowest with 39.2m. The n-value here was 12, meaning that there was a total of 144 obstacles around the nucleus. The total area colonised in this simulation was 288 m^2, population size of 612 plants, and a colonization distance of 39.2m.

The radial obstacle arrangements produced some of the highest nucleation outcomes of all the scenarios. Scenario 4 (Appendix 2.4) which was a radial pattern with obstacles 40m^2 in size and 7m apart had a colonised area of 935m^2, final population size of 1619 plants, and a colonization distance of >70m.

The random obstacle arrangement (Appendix 2.6) produced a colonised area of 418m^2, population of 841 plants, and a colonization distance of 60.8m. The bare ground scenario (Table 3.3) produced a colonised area of 903m^2, population of 1608 plants, and a colonization distance of >70m.

3.5 Discussion

3.5.1 Obstacle arrangement simulating alternative management regimes

Ecological models have the ability to support role-players in making management decisions which will benefit ecological restoration (Bastos et al., 2018). All the obstacle arrangements that were modelled facilitated nucleation and colonization, with some being better than others.

When assessing the results obtained from running the simulations, parameters which would indicate optimal nucleation were: area colonised, population size, and colonization distance. Based on these, the radial pattern of obstacles performed well with the two radial scenarios placed first and third. The scenario which displayed the highest optimal nucleation results was Scenario 4, which was a radial pattern where obstacles were 40m^2 in size and 7m apart. When measuring the site using Google Earth Images, these values are close to the size of and distance between the stacks in the BBNR. However, they are not arranged in a radial pattern. The radial obstacle patterns provide sufficient area for a high rate of colonization after T1 (timestep 1) and T2 and seem to initially inhibit long distance dispersal. This is evident in T2 of Appendix 2.5 where the points at the top of the graph "stop" just before the obstacles. This is part of model design, whereby obstacles act as seed traps, results in a congregation of seed to potentially form a new nucleus. This was one of the considerations made by Schurr et al., (2008). It is only at T3 and T4 when plants start colonising the area beyond the obstacle ring. The high rate of colonization inside the ring before nucleation spreads beyond its boundary may be an advantage as it potentially allows the plant community to establish and build resilience through a seed bank. Corbin et al. (2016) state that as a plant community becomes more diverse, resilience increases, ultimately increasing the efficacy of nucleation (Corbin & Holl, 2012).

The grid patterns had some of the lowest nucleation results, Scenario 3 in particular. This scenario had a total of 144 obstacles surrounding the nucleus, and since the goal of the obstacles was to trap seed, it may indicate why the area colonised and colonization distances were lower than any of the other scenarios. What was unexpected however was that the population size in this scenario was lower than the rest, as the biological parameters including reproductive rate and carrying capacity was kept constant to avoid any compounding effects. This obstacle pattern facilitated dense recruitment close to the nucleus, which may not necessarily be a negative trajectory given that the expanded plant nucleus may establish successfully before nucleating further. The only difference between Scenarios 1 to 3 was the n-value, and this gives insight into the influence that the size, number, and spacing of obstacles can have on nucleation and colonization. Nucleation tended to penetrate the open gaps between the obstacles at first, after which they started to congregate around them, forming dense clusters of vegetation. This accurately simulates the natural environment as species will first colonise an area with the least competition from other species. This is typical for annuals such as *D.* pluvialis,

as they generally track gaps/bare ground in the vegetation in which to establish (P.M Holmes, personal communication).

The random pattern scenario following clearing of A*cacia* by FB most closely resembled the management implemented on site following sowing of the original restoration plots (i.e., nuclei) from which nucleation of Fynbos species were measured (Chapter 2). Obstacles here ranging from 1m^2 to 25m^2 were designed to simulate *Acacia* seedling growth. This scenario highlighted the impact that *Acacia* regrowth can have on nucleation, which was intense trapping, resulting in plants being unable to disperse as far as in other scenarios. The effects of *A. saligna* are well documented in CFSF and the Fynbos biome as a whole (Holmes & Cowling, 1997; Holmes, 2002; Holmes et al., 2020; Le Maitre et al., 2011; Yelenik et al., 2004). This species has the ability to affect both the biophysical environment as well as the ecosystem services of the habitat in which they persist (Le Maitre et al., 2011). The FB management regime has the potential to result in mass *Acacia* seedling recruitment due to a combination of two things: *A. saligna* is fire adapted, and the seeds responds well to heat, and the fact that they possess large, persistent seed banks (Cohen et al., 2018). While the burning of *Acacia* biomass would also result in the prime habitat for CFSF seeds to germinate, this habitat would be rapidly colonised by *Acacia* seedlings which would just outcompete the native vegetation. On the other hand, Hall et al., (2021) found that the FS management regime resulted in an increase in shrub cover of reseeding species which were not reliant on fire for germination. They also found that there may not be an increase in species richness over time, even after a fire has passed through, which should theoretically have resulted in the germination of fire-dependant species. While this may be the case, the argument can be made that at least one has a restoration base of native species from which to work, and future restoration initiatives can focus on introducing these species back into this environment either by sowing seed which has been pre-treated with smoke or heat, or by strategic planting of these species amongst existing reseeding species.

The above argument also can be made for the bare ground scenario. However, the model indicated that a bare ground scenario would result in long distance dispersal and a large colonised area. While this would be the case in the short term, *Acacia* seedlings would fast colonise the bare area, and any isolated native seed that had dispersed and germinated would quickly be outcompeted. This further advocates for the use of obstacles to act as seed traps. The accumulation and germination of native seed would increase resilience and improve the chances of successful restoration (Corbin et al., 2016). It also highlights the importance of follow-up alien clearing. If the native seed is given a chance to germinate and grow to a certain size, it has a better chance of surviving and producing seed to replenish the Fynbos seedbank. While bare ground might provide optimal nucleation conditions, it also provides ideal conditions for pioneer and secondary invasive species to colonise (Hall et al., 2021).

The lack of obstacles acting as seed traps here might result in longer distance dispersal, but on the other hand might result in the seed simply being blown away and not having the chance to establish along with other seeds (P.M Holmes, personal communication). The accumulation of seeds can result in the formation of a small community where the seeds are able to germinate and establish. This ultimately leads to a higher chance of survival (Corbin et al., 2016), and formation of a new nucleus from which seed can be sown and the process of nucleation can continue.

3.5.2 Assessment of simulated nucleation potential

Plant reproductive rate (fecundity) and dispersal kernels have a large impact on modelled nucleation potential. According to Schurr et al., (2008), these parameters would be considered source effects. These source effects are linked to the management conditions under which the simulation was run, by using aspects from generalized linear models (Mccullagh & Nelder, 1989). An assessment of the simulation graphs as well as the model results informs us that, using the different species' key biological parameters, all four species possess some nucleation potential.

While carrying capacity was kept constant for the purposes of this study, manipulating this value could aid in determining nucleation trajectories at various stages of the ecological restoration process. *Dimorphotheca pluvialis* displayed the highest nucleation potential of the four species. This can be attributed to its high reproductive rate and dispersal kernel adapted to long distance nucleation. This is however an annual species which must grow from seed every year, and thus all plants observed would have been the same age. It therefore cannot be said for certain whether this species has a high R_0 value, as one would need to know how many individuals there were in the previous season to determine this value. To surrogate for this, the ratio between plants outside the initial sowing plot per plant within the initial sowing plot was used. *Pelargonium capitatum* had a dispersal kernel adapted to long distance dispersal, but because of its lower reproductive rate, had low nucleation potential in comparison to the three other species. This is likely due to the fact *P. capitatum* requires a heat pulse to germinate (Hall et al ., 2017), and its full colonization potential will only be evident after the next fire. Once a fire has passed through the area one may be able to observe the true extent of the nucleation of this species. *Anthospermum aethiopicum* only had a slightly lower reproductive rate and u-value yet did not display anything close to the colonization and dispersal seen in *D. pluvialis*. As mentioned above however, *D. pluvialis* is an annual, and has effectively had six generations to spread, while *A. aethiopicum* (perennial) has had two to three at most. This highlights the importance of understanding biological parameters and the impact they can have on vegetation recovery. Selecting species for future restoration initiatives is crucial in scaling up restoration efforts. Prolific seeders

which are known to establish and persist are the best species to choose to initiate ecological restoration. The four nucleation species were sown in 2013 (Chapter 2) and have persisted through severe drought to still be present at the most recent plot survey in 2019.

While many of these scenarios displayed good results, they are being run in a simulation under potentially over-simplified conditions. In the field situation there are several factors which would significantly decrease the potential for successful nucleation including competition from other species such as *Acacia* seedlings, invasive grasses, and other native perennials. Furthermore, factors such as loss of seeds to granivory and failure of seedling establishment owing to drought could negatively impact on outcomes (P.M Holmes, personal communication).

3.5.3 Assessment of the model as a whole

While this model was designed to simulate applied nucleation, the settings and ability to link the changeable variables and model outputs (Mccullagh & Nelder, 1989; Schurr et al., 2008) make it flexible enough to model a variety of scenarios. The model could be used to: (1) simulate the restoration trajectory of individual species to determine their potential in restoration initiatives. This would include species with short distance dispersal modes such as myrmecochorous and resprouting species (2) simulate colonization from a variety of starting points across a landscape over time as well as indicate how many nuclei should be used, and (3) model the extent and intensity of invasion by secondary invaders (Nsikani et al., 2019) after initial *Acacia* clearing.

3.6 Conclusions

The model was able to indicate the obstacle dimensions and arrangement that would best facilitate nucleation and colonization of pioneer Fynbos species and has given valuable insights into how to plan for future management regimes.

This research has shown that instead of being barriers to dispersal, obstacles such as *Acacia* brush piles may be viewed as seed traps, potentially resulting in an accumulation of seed. Over time this gives the potential to form new nuclei from which future nucleation and colonization can occur.

The work done by Hall et al., (2021) has highlighted the importance of seed sowing to accelerate ecological restoration, particularly in an area as heavily invaded as the BBNR where the native seed bank has been depleted by years and years of alien *Acacia* infestation. While this is a given, the question remains as to how best to spatially arrange the sowing. Applied nucleation offers a

combination of being less labour intensive than broadscale sowing and more effective than passive restoration.

The model has given insight into which species would be most effective in future sowing, and other prolific seeders such as *Passerina corymbosa* (Pierce & Cowling, 1991) and *Metalasia densa* (Pierce & Moll, 1994) are recommended for future seed mixes.

Based on the results from running simulations in the model the following management actions are recommended:

1. Arrange felled *Acacia* brush piles in a radial pattern around the proposed restoration plots and ensure that follow up clearing is carried out regularly. The brush pile size can stay the same as that currently used ($42.5m^2$).
2. Include the four nucleating species (*A. aethiopicum, D. pluvialis, I. repens, P. capitatum*), and similar pioneer Fynbos species in any future active restoration initiatives, as they persist over time and have a high nucleation potential.

The above recommendations should be tested for efficacy against current methods to verify the results of the model. For future research it is recommended that factors such as competition from other species be included in such a model, to assess the true nucleation potential of species. The research of other key CFSF guilds to initiate restoration is also important. This includes the nucleation potential of restioids species such as *Thamnochortus punctatus*, which theoretically should be a key candidate as it is wind dispersed and germinates without fire, responding to a temperature regime of 20°C/40°C. These are temperatures which bare soil reaches in summer (Hall et al., 2017). Another important guild is the overstorey proteoid growth form, which are serotinous and do not drop seed until they are killed by fire. A prescribed burn which creates bare ground conditions may result in the dispersal of protea seed by tumbling as explained by Bond (1988).

At sites long-invaded by *Acacia*, management regimes employing the FS treatment in combination with actively sown restoration plots are recommended, as this results in sufficient native vegetation recovery, particularly those not requiring fire-related cues for germination. They result in less *Acacia* regrowth, and the stacks can be used in aiding applied nucleation and restoration by acting as seed traps.

3.7 References

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Chapter 4: Synthesis of findings and implications for management

4.1 Main conclusions

This study has provided some insights into a restoration strategy not previously studied in Cape Flats Sand Fynbos (CFSF), or any dryland ecosystem: namely, applied nucleation. The research outcomes indicate that applied nucleation does have a place in our arsenal of restoration tools, especially in threatened ecosystems where seed and rootstock resources for active restoration are limited. However, in a fire-driven ecosystem such as Fynbos in which most species recruit only after fires, it was anticipated that not many species would recruit during the inter-fire period. This study indicated that a few pioneer species did nucleate. These are species not entirely limited by fire-related germination cues and are dispersed either passively (with tumbling) or by wind. It is now known which types of species to include in future active restoration initiatives in Cape Flats Sand Fynbos (CFSF) to accelerate applied nucleation (Chapter 2). Four species (*Anthospermum aethiopicum, Ifloga repens, Dimorphotheca pluvialis, Pelargonium capitatum*) showed the best potential for nucleation, as these species persisted from the time of the original restoration plot establishment in 2013, and young plants of the same species were subsequently recorded in the immediate surrounding area. The study also suggests optimal ways to utilize felled alien *Acacia* biomass to promote vegetation and ecosystem recovery (Chapter 3); this was achieved by analysing the efficacy of different management regimes relating to the arrangement of felled *Acacia* brushpiles and simulating dispersal and colonization trajectories of the above-mentioned species to model their nucleation potential by using their reproductive rate and dispersal kernel information.

4.2 Making science-based management decisions

Decisions on any aspect of environmental management should be based on the most recent state of scientific knowledge (Schuwirth et al., 2019). While research can inform best practise, a gap still exists between recommendation and implementation (Hall et al., 2020). Recommendations are not always practical and often require the excessive use of resources. It is for this reason that researchers working in a field such as restoration ecology need to make management recommendations that are practical, and which are not resource intensive (King & Hobbs, 2006). Development and implementation of feasible recommendations are vitally important, and this can be achieved through collaboration between researchers and managers. All those who are involved in restoration initiatives in the Blaauwberg Nature Reserve (BBNR) are at the forefront in this regard, as managers and researchers work closely in the planning of restoration ecology research and the incorporation of research findings into management practises. Managers act as the interface between recommendations given by

researchers, and the implementation of said recommendations. It goes without saying that their role in ecological restoration is vital.

4.3 Implications for future restoration initiatives

Ecological restoration is considered to be one of the fastest growing fields in applied ecology (Choi, 2004). The need to actively restore degraded habitats is going to become increasingly necessary in years to come, particularly because of rapid human population growth, and in the face of a changing climate. A number of ecological assessments on a global scale since 2010 resulted in the United Nations declaring the "Decade on Ecosystem Restoration" for the years 2021 to 2030 (Aronson et al., 2021). The decade dedicated to ecological restoration aims to scale up restoration of degraded habitats to combat climate change, to improve food security and water supply, and increase biodiversity (Young & Schwartz, 2019). Ecosystem degradation is accelerating and it is for this reason that developing improved restoration techniques is important (Dickson et al., 2021). By using applied nucleation as a restoration tool, fewer resources are utilised than in broadscale sowing, and it is more effective than passive restoration (Corbin et al., 2016). This is a key necessity for scaling up restoration. By utilising the alien *Acacia* brushpiles as seed traps, their size and spatial configuration may be manipulated to optimise nucleation and colonization from the initial restored nuclei or sown plots.

Restoration goals must be realistic (Ehrenfeld, 2000), and this may include initially accepting a poorly represented structural composition, as this is the base upon which further restoration can be built. For Fynbos species which would not nucleate during an inter-fire period, restoration may only occur in "pulses" every 10 to 20 years following fire events (P.M Holmes, personal communication). The target for ecological restoration is generally based on a reference version of the habitat, and this pertains to vegetation structure, species richness and community composition, among others (Nunes et al., 2016). While most restoration plots did not achieve all such outcomes within six years, they may be on a trajectory to reach them (Hall et al., 2020). This could occur naturally after subsequent fires, or by the additional sowing or planting of rootstock of the missing elements. By first establishing a community of hardy, prolific seeder species, there is potential to create a more suitable environment for those species that struggle to establish directly from initial sowing by stabilising the environment and providing a window for practitioners and managers to introduce more diversity into the system over a longer period. This native cover is also able to act as a seed trap, and does not carry the legacy effects possessed by *Acacia* cover (Nsikani et al., 2018). The four pioneer species studied are important to include in any seed mix for future ecological restoration projects in highly degraded Cape Flats Sand Fynbos vegetation. Additional species with similar life forms, dispersal modes and reproductive rates

may be added to increase the diversity of the species which nucleate during the inter-fire period. It is however still important to include the seed of other functional types and guilds, as some will only be seen to be nucleating after a future fire event.

Corbin et al. (2016) maintain that frugivory is the driver of applied nucleation. While this may be the case in forest vegetation types where their research is based, it is not entirely the case here, or in any other Fynbos vegetation types. Frugivory is rare mechanism of dispersal in CFSF, and yet nucleation was still observed in a subset of species. This indicates that modes of dispersal such as passive and wind dispersal are sufficient in facilitating nucleation, and that this restoration technique has potential in dryland and fire-driven vegetation types where previously it was assumed it would be ineffective.

4.4 The use of models to guide ecological restoration

The use of ecological models (Chapter 3) in restoration allows researchers, practitioners, and managers to ask "what-if" questions and to predict restoration and invasion trajectories. Models allow us to understand complex systems and can help to predict certain environmental or ecological outcomes under a variety of conditions, especially where empirical experimentation is impractical, too risky or too expensive. Management which receives insufficient support can have negative and potentially irreversible effects on the environment they are trying to restore (Getz et al., 2018). Being able to simulate the responses of individual species and plant communities alike to different management scenarios or environmental conditions may be the most effective way to understand conservation outcomes. To do this, however, one needs information on population dynamics and individual species traits such as dispersal ability and fecundity.

Burning highly degraded Fynbos after clearing alien *Acacia* results in mass *Acacia* seedling recruitment, and this management regime is not recommended unless stringent follow up clearing is carried out (Hall et al., 2021). By using the predictive inverse model *Acacia* regrowth was simulated, and this was seen to stifle nucleation by not allowing seed to disperse far (Chapter 3). In the Fell & Stack alien clearing treatment, the use of obstacles in the form of *Acacia* brushpiles was more effective, as it resulted in higher dispersal and colonization by Fynbos species and lower follow up alien clearing intensity and costs than that associated with a burn (Hall et al., 2021). By clearing the standing *Acacia* biomass, seed movement was facilitated, and by strategically placing *Acacia* brushpiles, seed was trapped, and recruitment could occur.

4.5 Suggestions for future research

To determine the best restoration technique for a certain area, one has to fully comprehend the limitations one might encounter in terms of restoration outcomes (Kimball et al., 2015). Applied nucleation in a habitat such as CFSF has not been explored until now, and there is scope for further research on this restoration technique in this vegetation type and those like it. To fully grasp the nucleation potential of CFSF species, the nature of competition both from indigenous species as well as invasive grasses, and *Acacia* must be well understood. For example, if nucleating species are highly competitive, they might prevent other species from establishing, thereby disrupting future re-introduction of a diversity of species; alternatively, nucleating species might be able to competitively exclude invasive alien seedlings. This study has, however, provided a starting point from which to plan future studies. The nucleation potential of species from other guilds could be assessed to determine whether they would be valuable inclusions in seed mixes for future sowing. Studying the non-nucleating species in the sowed plots after the next fire event would help in determining how far they have dispersed during the inter-fire period and whether they possess nucleation potential. This may offer insight into how to spatially arrange future sowing and planting nuclei for such species. The use of pre-treated seed and the planting of rootstock in active restoration allows for the initial re-introduction of a range of species, but one has to plan and facilitate their dispersal and broader establishment in a fire-driven system over the long-term.

Hall et al., (2021) suggest delaying active seed sowing by a period of at least two years in areas which have a substantial alien *Acacia* seedbank, as this results in a hypothesised reduction of the seedbank by granivory after clearing the *Acacia* stands and thus lower mass recruitment. Under these conditions, focusing on those species that can nucleate without fire, by sowing post-fire, might well be strategic and complement any Fynbos species spontaneously recruiting from the seedbank.

The importance of fire is well researched (Kraaij & van Wilgen, 2011; Kraaij & van Wilgen, 2014; van Wilgen & Richardson, 1985) as the key driver of recruitment in Fynbos, and makes restoration in Fynbos more complex than in non-fire driven vegetation types. Incorporating fire into future applied nucleation models is thus an important aspect in understanding recruitment under post-fire conditions as well as during inter-fire periods.

There is scope for further research into the use of brushpiles as seed traps. The obstacle arrangements in Chapter 3 can be trialled in the BBNR and their potential as seed traps assessed. The spatial arrangement of restoration plots is another aspect to be considered, particularly about the optimal size of plots, the distance between plots, and their spatial arrangement within a landscape. Furthermore, one can test the results of the model under field work conditions to determine whether

nucleation and restoration are facilitated. The model can be tested in other South African vegetation types, and after clearing of other species invasives such as the *Eucalyptus* and *Pinus* species.

4.6 Concluding remarks

Applied nucleation is a viable option to trial in scaling up ecological restoration in CFSF. There are several species which should be used; generally, these species are considered pioneers and are resilient and prolific seeder species that may disperse moderate distances and recruit without fire. While this may not initially result in a diverse plant community, it can act as a base upon which further restoration can be built, especially after alien clearing where propagation material is limited. It is recommended that further field research be done on the arrangement of brushpiles as seed traps, to verify the model outputs of the three optimal patterns under the Fell & Stack management regime. Apart from understanding impacts of management regimes, understanding the biological parameters of each species and the impact this can have on vegetation recovery is also key; the selection of species to use is paramount in scaling up restoration efforts.

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Appendices

Appendix 1.

Appendix 1.1 Average seed drop velocity (n=10) and calculated u-values based on the u-value of *Anthospermum aethiopicum*.

Species	Seed drop velocity (m/s)	u-value
Anthospermum aethiopicum	0.36	1.2
Ifloga repens	0.14	1.93
Dimorphotheca pluvialis	0.17	1.83
Pelargonium capitatum	0.06	2.2

Appendix 1.2. Obstacle parameters of the model.

Obstacle parameter	Description	Comments
Shape	Obstacle arrangement.	For this study the obstacles were arranged in radial, grid, and random patterns.
N	The number of obstacles, when squared, within the total obstacle area. I.e., if the n-value is 4, there are 14 obstacles in the area.	This actually determines the size of the obstacles. The higher the n-value, the smaller the obstacles. By changing this value, one can change the number of obstacles which can fit into the total obstacle area.
Total obstacle area	The size (m²) of the entire area in which obstacles are placed.	Total obstacle area refers to the sum of the sizes (m²) of all the obstacles in the simulation combined.
Obstacle size	The size (m²) of the individual obstacles.	This is only applied to radial and random obstacle patterns but is determined by "n" and total obstacle area for the grid pattern.
Distance between obstacles	The distance between obstacles. Can be constant or random.	The distance between obstacles can be changed to suit management scenarios. This applies only to random and radial patterns.

Appendix 1.3 Parameters simulating different management scenarios in the applied nucleation model.

Scenario	Management scenario	Obstacle pattern	Obstacle type	Distance between obstacles (m)	Obstacle size (m²)	Total obstacle area (m²)	n	Extent	d	Tmax	Nsim	R0	K	u	p	beta_w
Scenario 1	Fell & stack	Grid	Slash stack	15	144	2304	4	100	1	4	1	6	3	1.2	1.2	3
Scenario 2	Fell & stack	Grid	Slash stack	10	36	2304	8	100	1	4	1	6	3	1.2	1.2	3
Scenario 3	Fell & stack	Grid	Slash stack	5	16	2304	12	100	1	4	1	6	3	1.2	1.2	3
Scenario 4	Fell & stack	Radial	Slash stack	7	40	1240	0	100	1	4	1	6	3	1.2	1.2	3
Scenario 5	Fell & stack	Radial	Slash stack	14	60	960	0	100	1	4	1	6	3	1.2	1.2	3
Scenario 6	Fell & burn	Random	*Acacia* regrowth	Random distances	Random between 1 and 25	1000	0	100	1	4	1	6	3	1.2	1.2	3
Scenario 7	Fell & burn	Bare	No indigenous regrowth and no invasion due to follow up clearing	Bare	0	0	0	100	1	4	1	6	3	1.2	1.2	0

Appendix 1.4. Description of parameters mentioned above.

Setting	Description
Extent	The side length of the simulation area in m
d	The side length of each grid cell in m
Tmax	The total number of dispersal events simulated
Nsim	The number of replicate simulations

Appendix 1.5. Parameters used to determine the nucleation potential of four Fynbos species in the applied nucleation simulation model.

Species	Obstacle pattern	Obstacle type	Average distance between obstacles in BBNR	Average obstacle size in BBNR	Extent	d	Tmax	Nsim	R0	K	u	p	beta_w
Anthospermum aethiopicum	Radial	Slash stack	7m between stacks	40m^2	200	1	4	1	6.2	3	1.2	1.2	3
Ifloga repens	Radial	Slash stack	7m between stacks	40m^2	200	1	4	1	2.9	3	1.93	1.93	3
Pelargonium capitatum	Radial	Slash stack	7m between stacks	40m^2	200	1	4	1	0.4	3	1.83	1.83	3
Dimorphotheca pluvialis	Radial	Slash stack	7m between stacks	40m^2	200	1	4	1	8.6	3	2.2	2.2	3

Appendix 1.6. Description of parameters in Appendix 1.5

Biological parameter	Description
R0	Reproductive rate
K	Carrying capacity
u	log-scale mean of lognormal dispersal kernel
p	log-scale standard deviation of lognormal dispersal kernel
beta_w	Parameter determining strength of path effects

Appendix 1.7. Measurements of brush piles in the BBNR using Google Earth.

Brush pile	Radius (m)	$A = \pi r^2$
1	8.46	58.63m²
2	8.32	54.37 m²
3	6.81	36.62 m²
4	7.38	42.78 m²
5	6.79	36.32 m²
6	6.39	32.17 m²
7	6.8	36.32 m²
8	7.48	43.94 m²
9	6.78	36.1 m²
10	7.82	48.03 m²
Average		42.5 m²

Appendix 1.8. Starting points of simulated nucleation. Created using random number function on MS Excel.

x	y
1	3
-5	3
0	4
-4	4
2	7
2	-3
-2	2
-4	-5

Appendix 1.9. Seed drop velocity data.

Species	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	Average seed drop velocity (m/s)
Anthospermum aethiopicum	0.75	0.65	0.77	0.55	0.83	0.68	0.65	0.7	0.63	0.73	0.360231
Dimorphotheca pluvialis	1.82	1.92	2.11	1.86	1.84	1.6	1.42	1.6	1.65	1.86	0.141403
Ifloga repens	1.45	1.8	1.62	1.47	1.53	1.37	1.45	1.32	1.38	1.37	0.169377
Pelargonium capitatum	2.51	4.63	3.14	6.28	3.54	5.36	4.45	4.03	3.12	7.76	0.055779

Appendix 2. Model simulation results
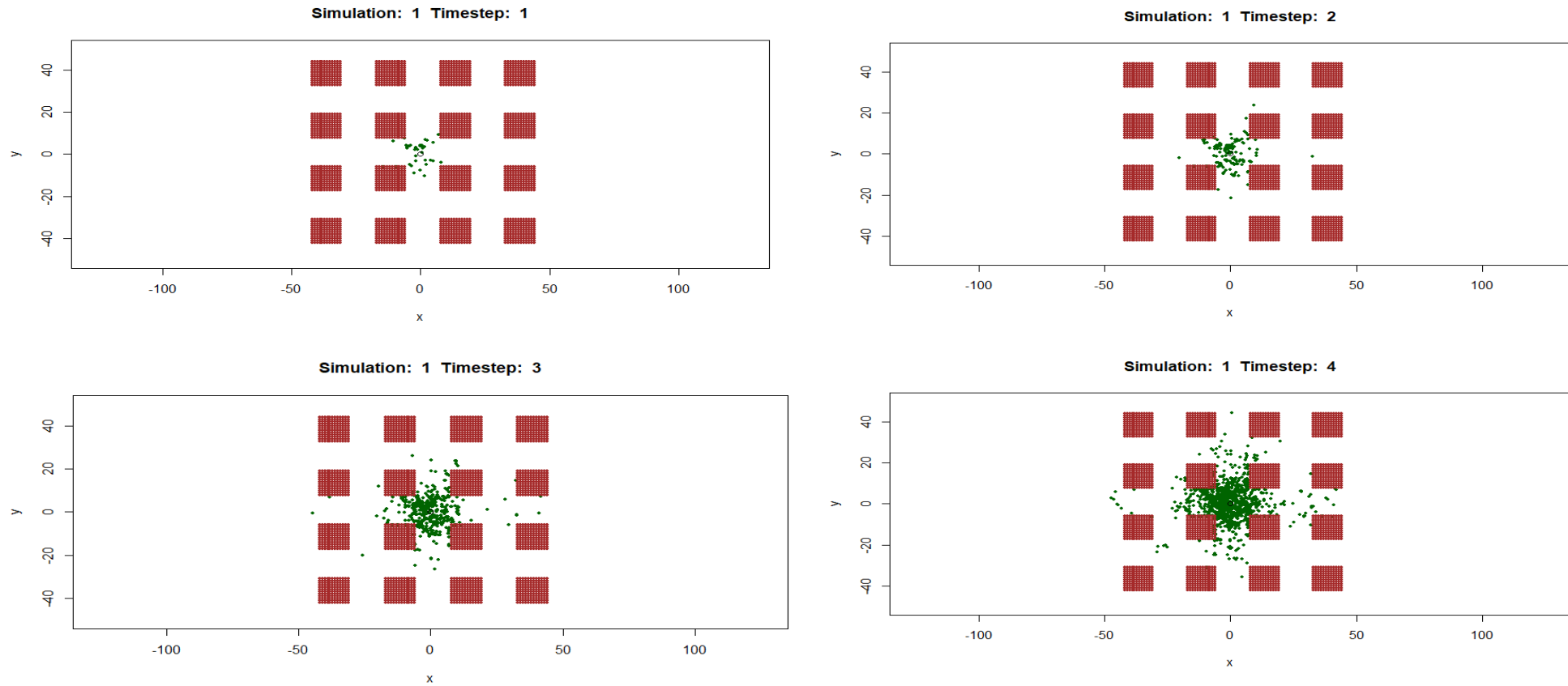
Appendix 2.1. Plant colonization and nucleation after Scenario 1 where a Fell & stack management regime was simulated over a hectare (100m x100m), and 16 brush piles simulated in a <u>grid</u> pattern. Stacked *Acacia* biomass was simulated in the form of obstacles. The green points represent individual plants.
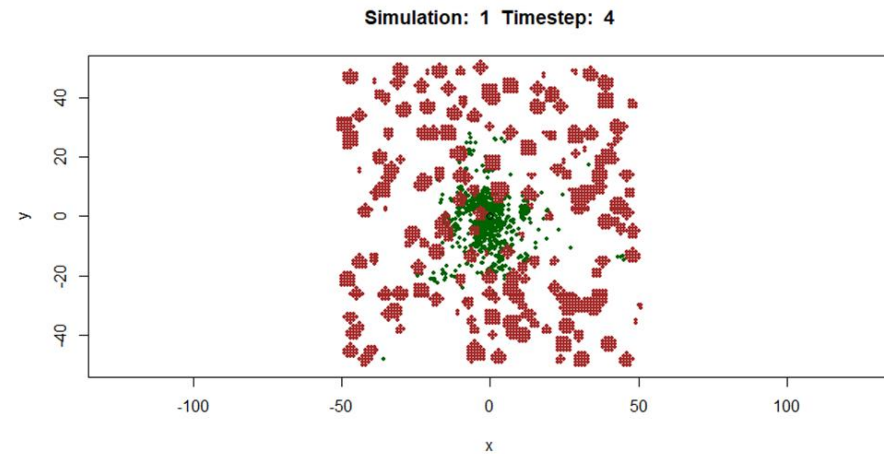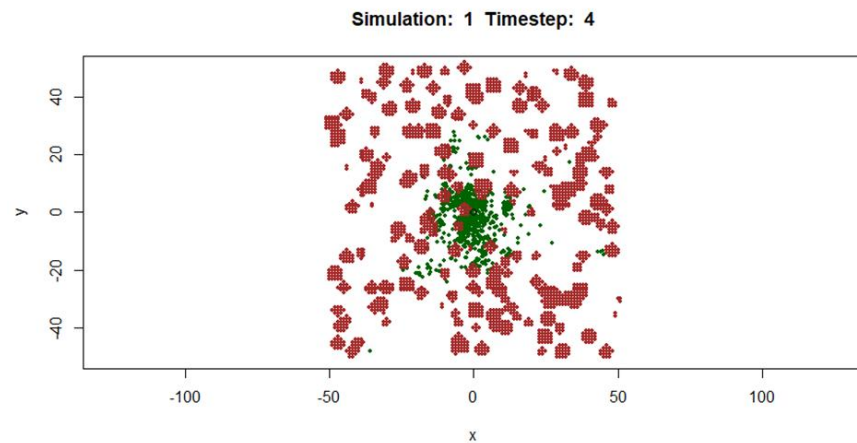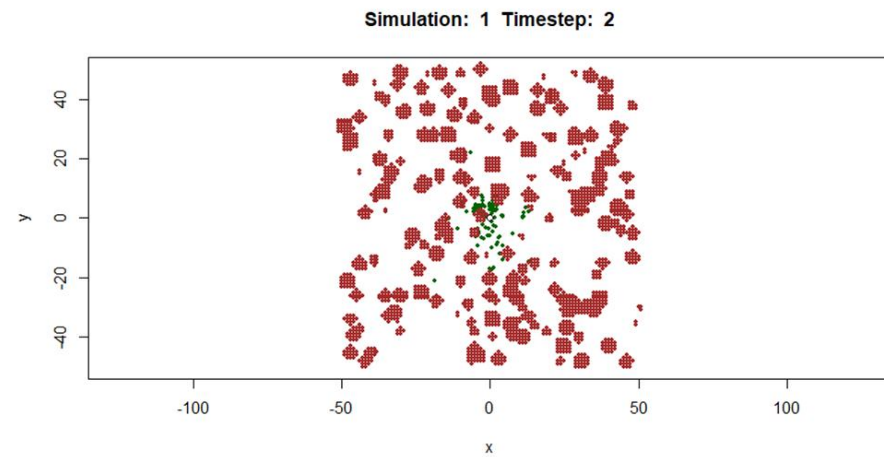
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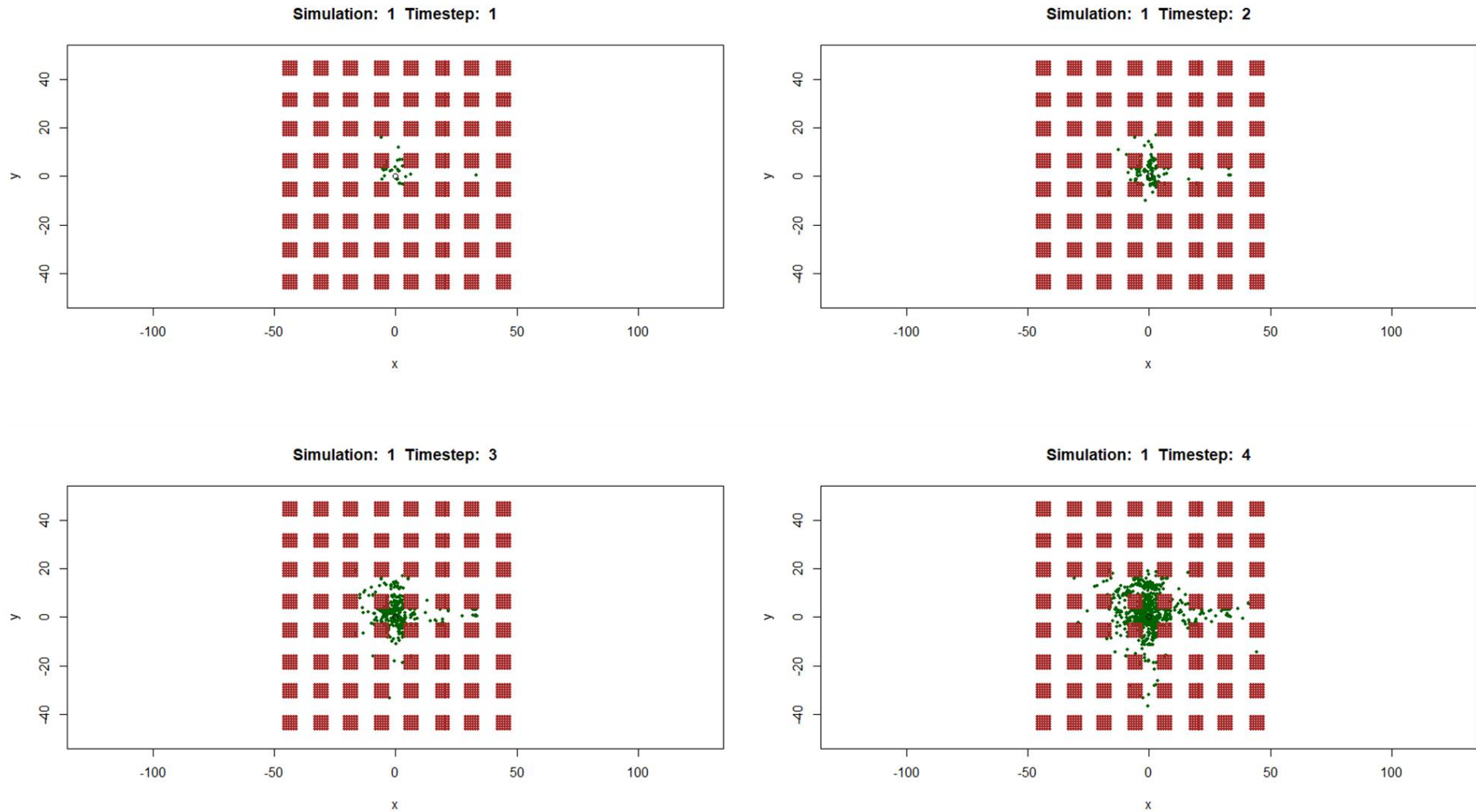
Appendix 2.2. Plant colonization and nucleation after Scenario 2 where a Fell & stack management regime was simulated over a hectare (100m x100m), and 64 brush piles simulated in a <u>grid</u> pattern. Stacked *Acacia* biomass was simulated in the form of obstacles. The green points represent plants.
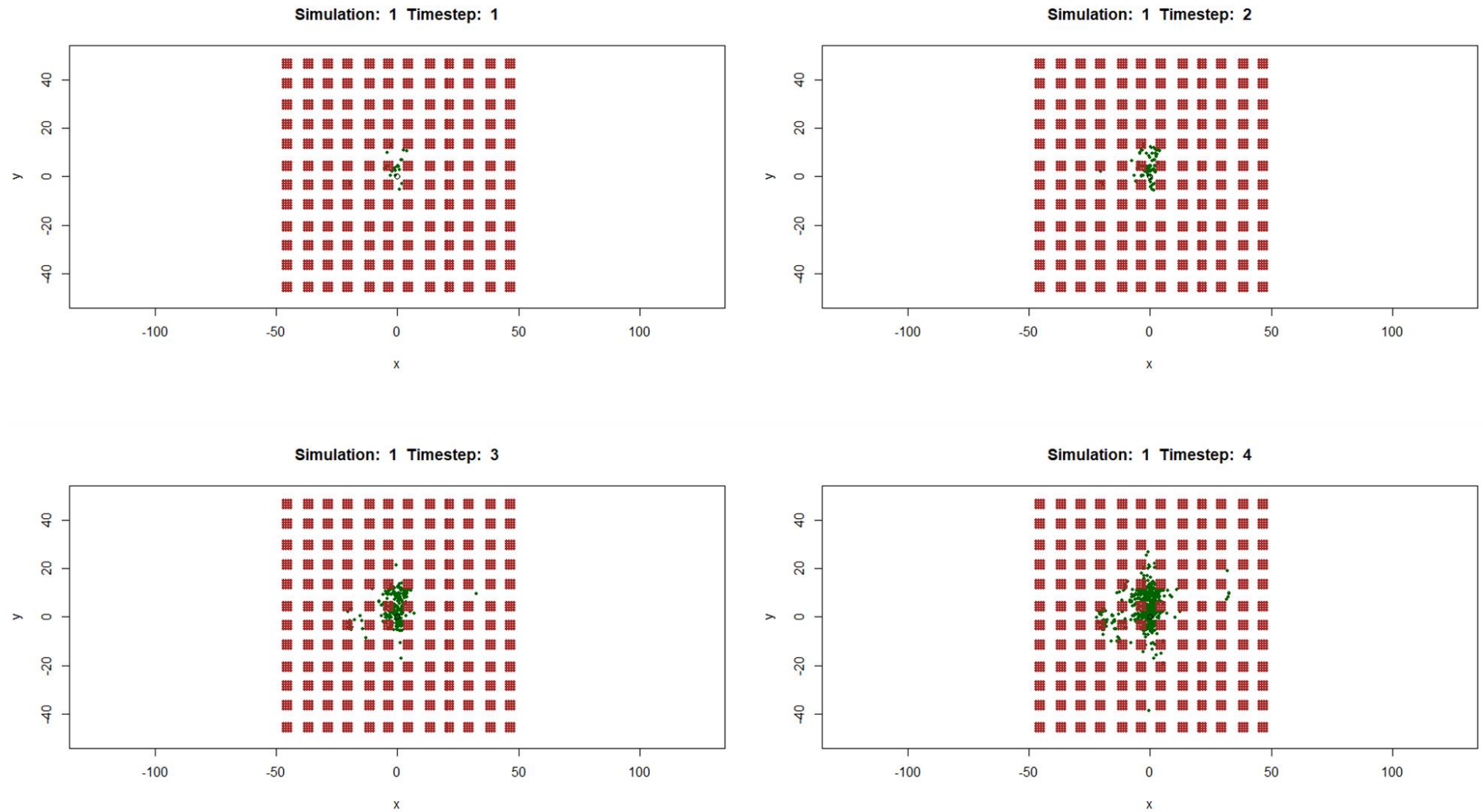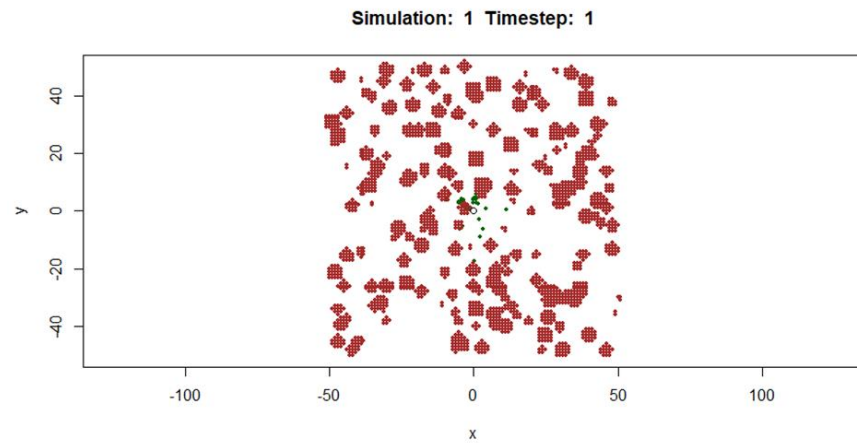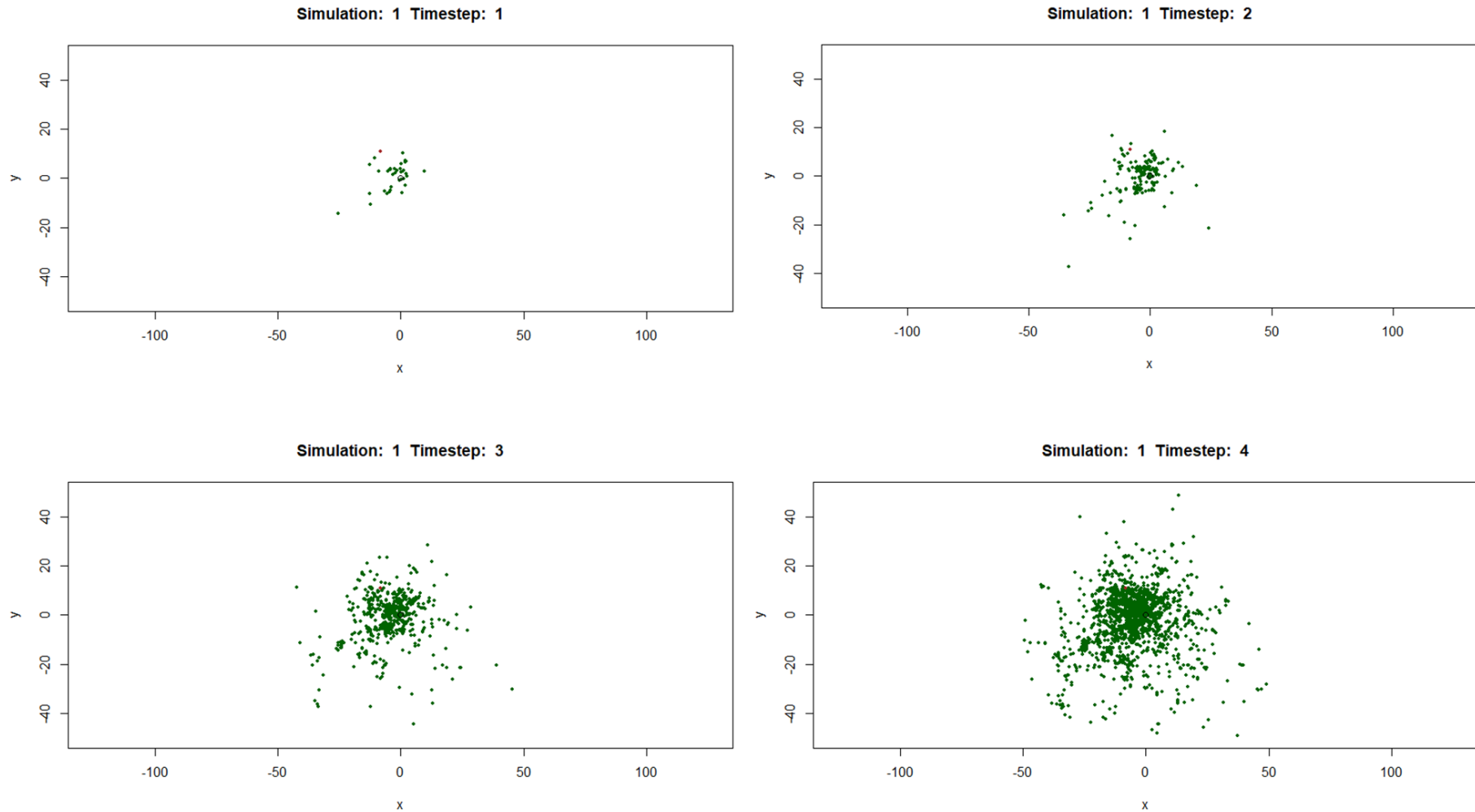
Appendix 2.3. Plant colonization and nucleation after Scenario 3 where a Fell & stack management regime was simulated over a hectare (100m x100m), and 144 brush piles simulated in a <u>grid</u> pattern. Stacked *Acacia* biomass was simulated in the form of obstacles. The green points represent plants.

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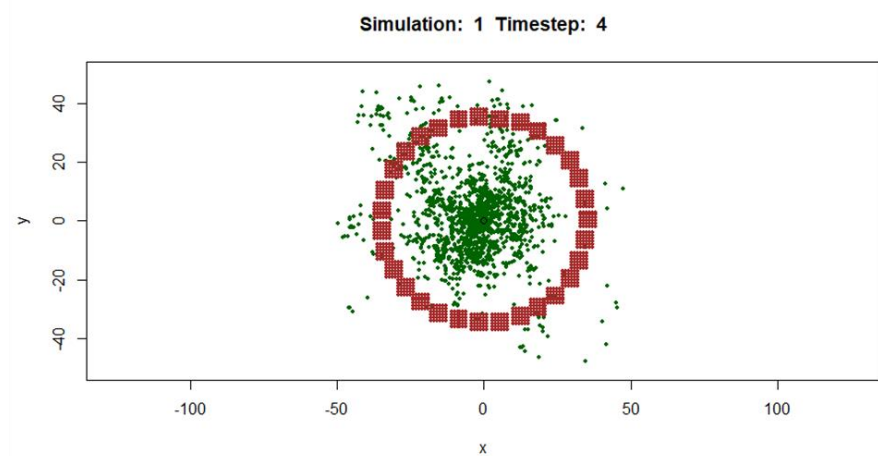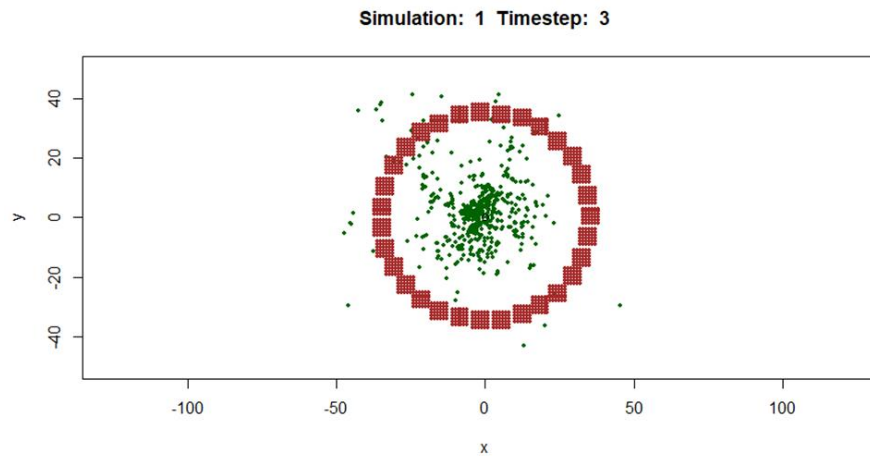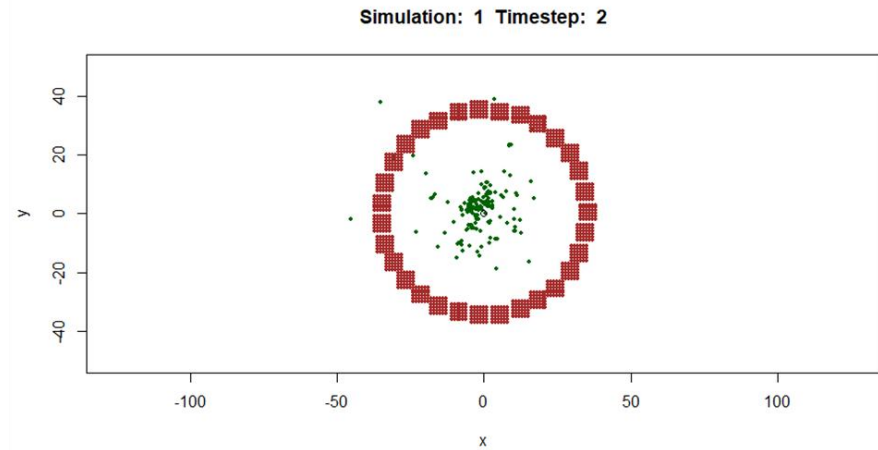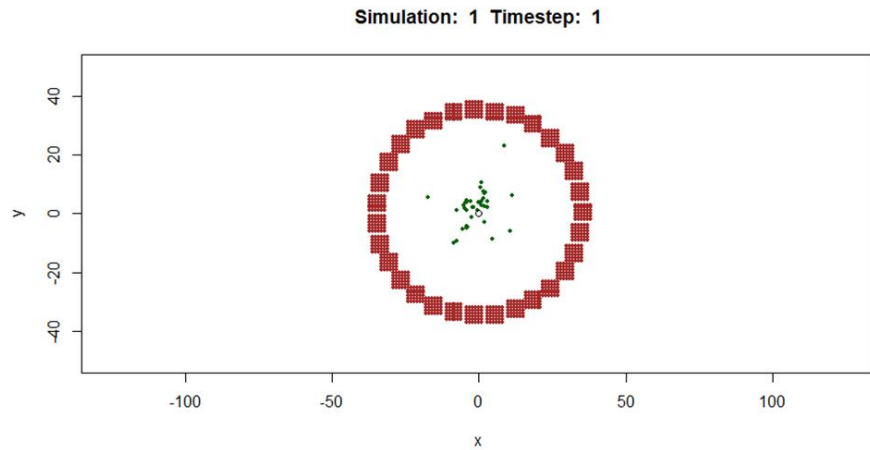
Appendix 2.4. Plant colonization and nucleation after Scenario 4 where a Fell & stack management regime was simulated over a hectare (100m x100m), and brush piles arranged <u>radially</u> around the sowed plot. Obstacles were 7m apart, and 40m² in size. Stacked *Acacia* biomass was simulated in the form of obstacles. The green points represent plants.
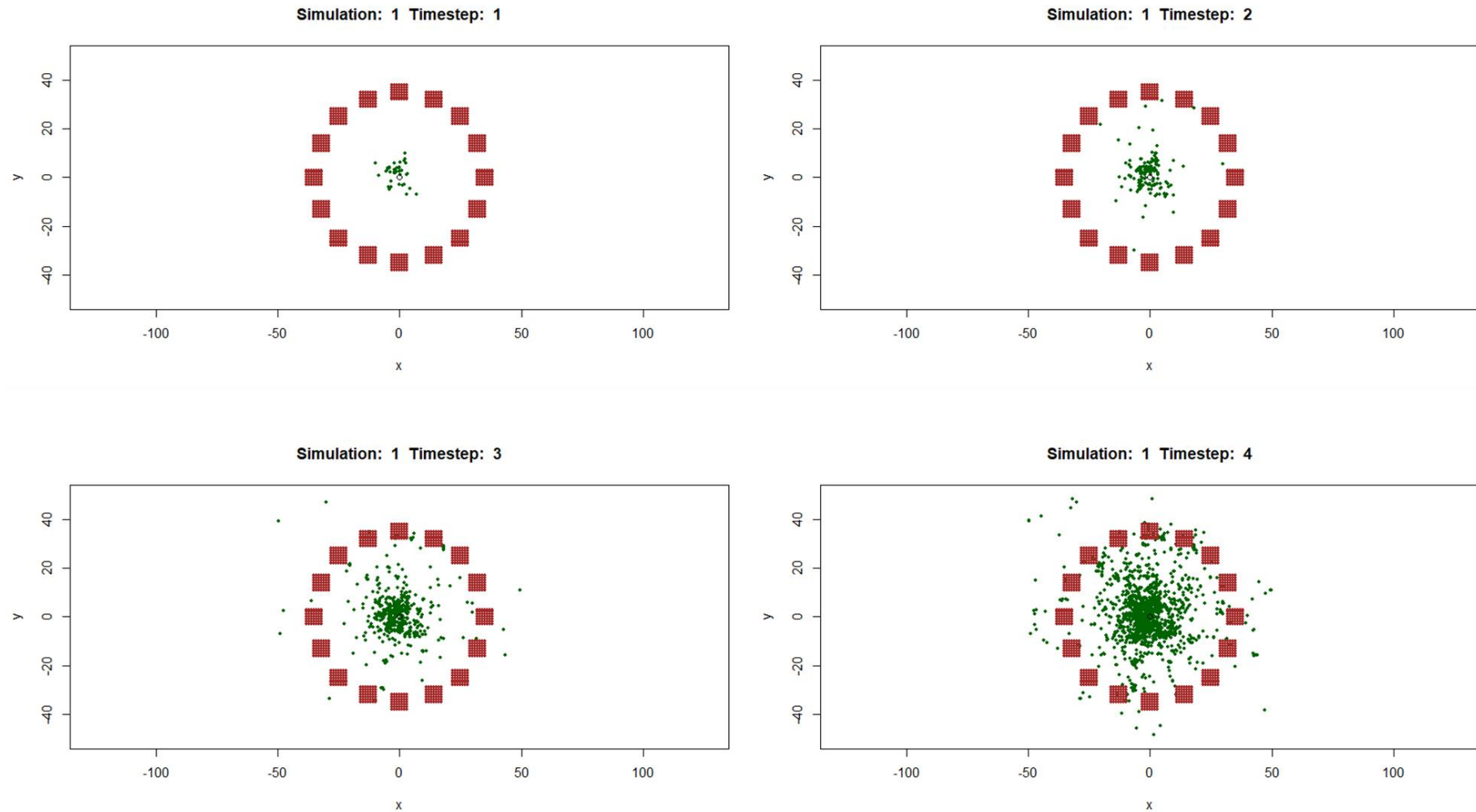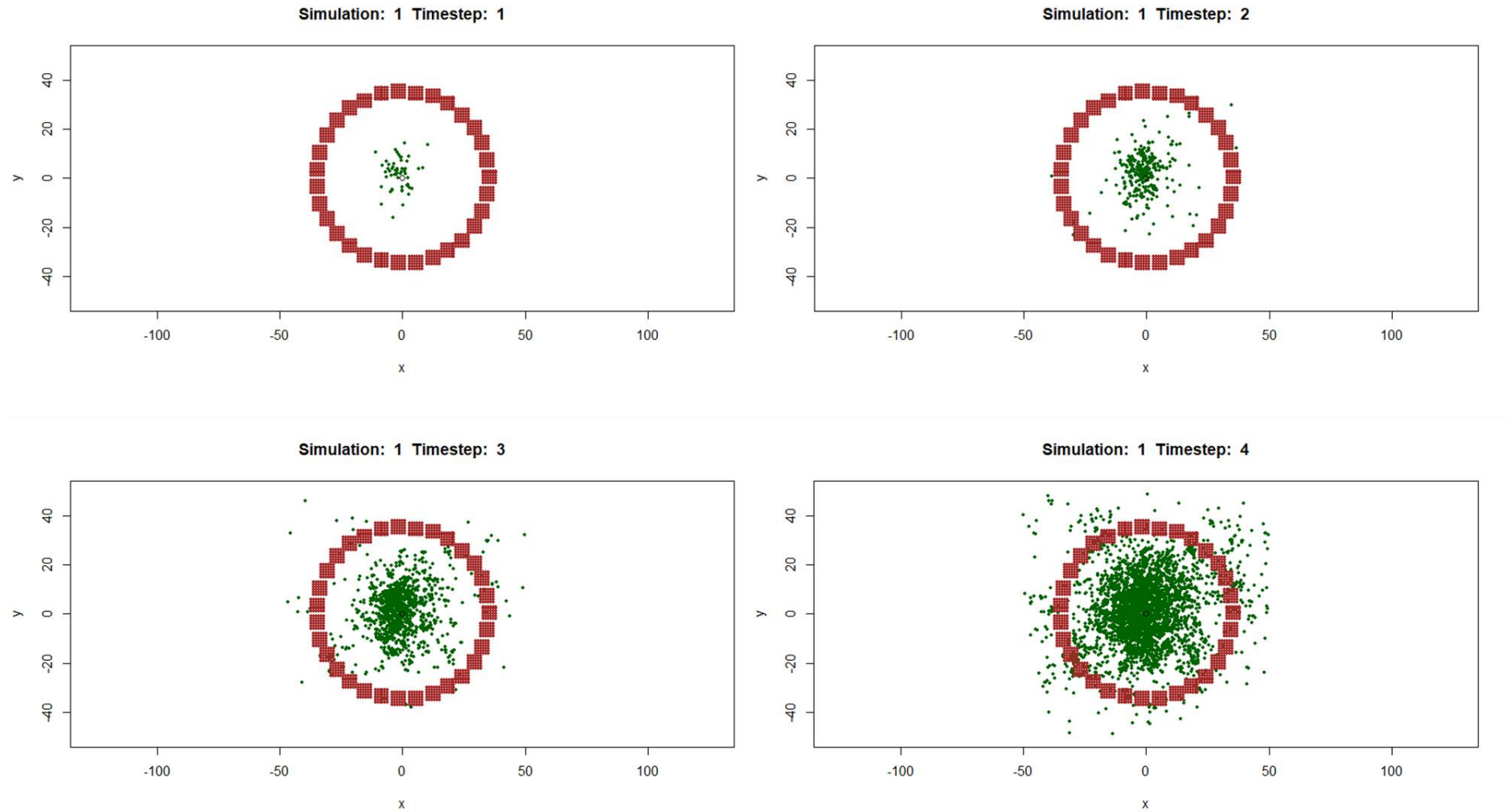
Appendix 2.5. Plant colonization and nucleation after Scenario 5 where a Fell & stack management regime was simulated over a hectare (100m x100m), and brush piles arranged <u>radially</u> around the sowed plot. Obstacles were 14m apart, and 60m^2 in size. Stacked *Acacia* biomass was simulated in the form of obstacles. The green points represent plants.
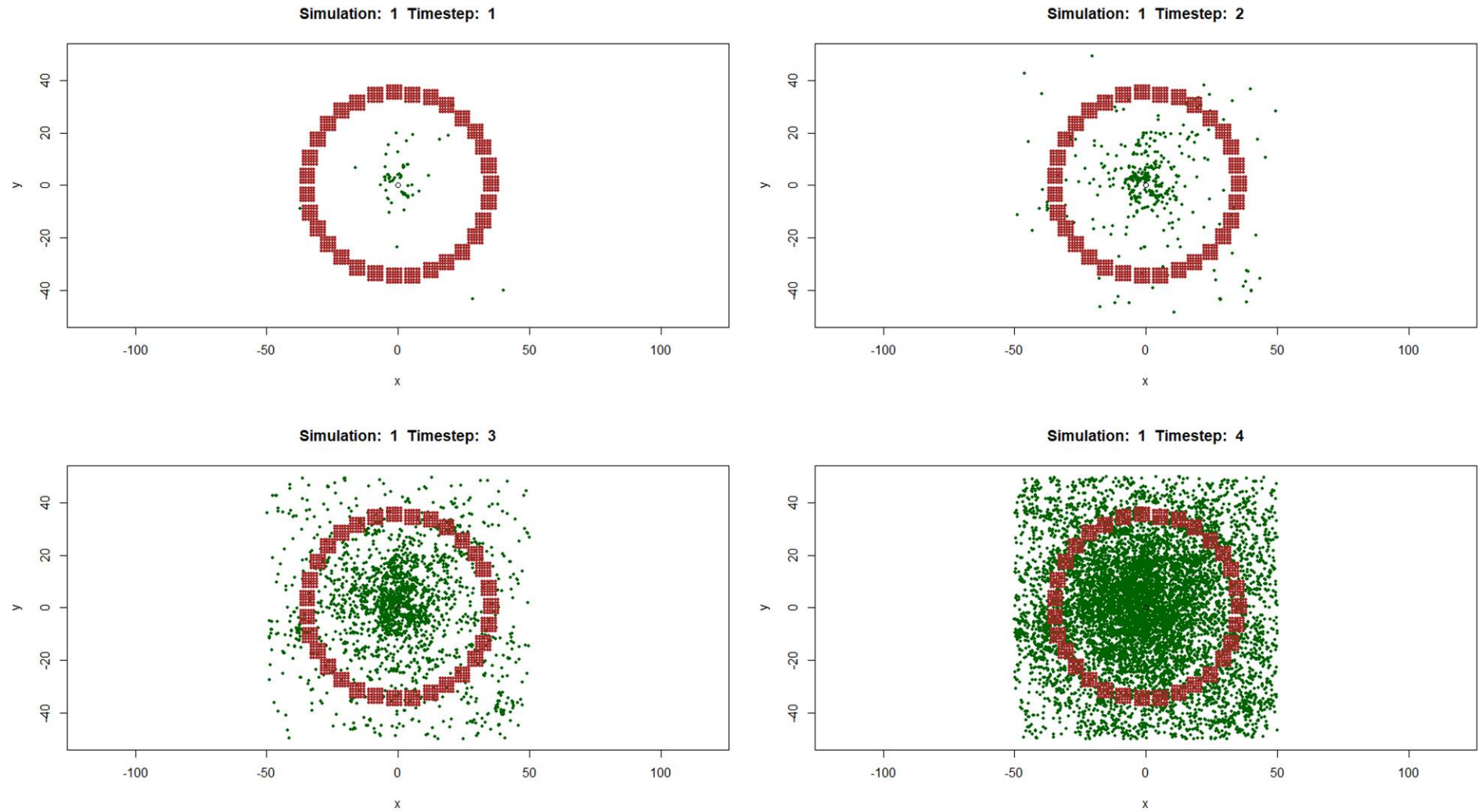
Appendix 2.6. Plant colonization and nucleation after Scenario 6 where a Fell & burn management regime was simulated over a hectare (100m x100m), and randomly arranged. Random sizes between 1m^2 and 25m^2 were assigned to simulate individual *Acacia* saplings as well as stands of *Acacia*. The green points represent plants.
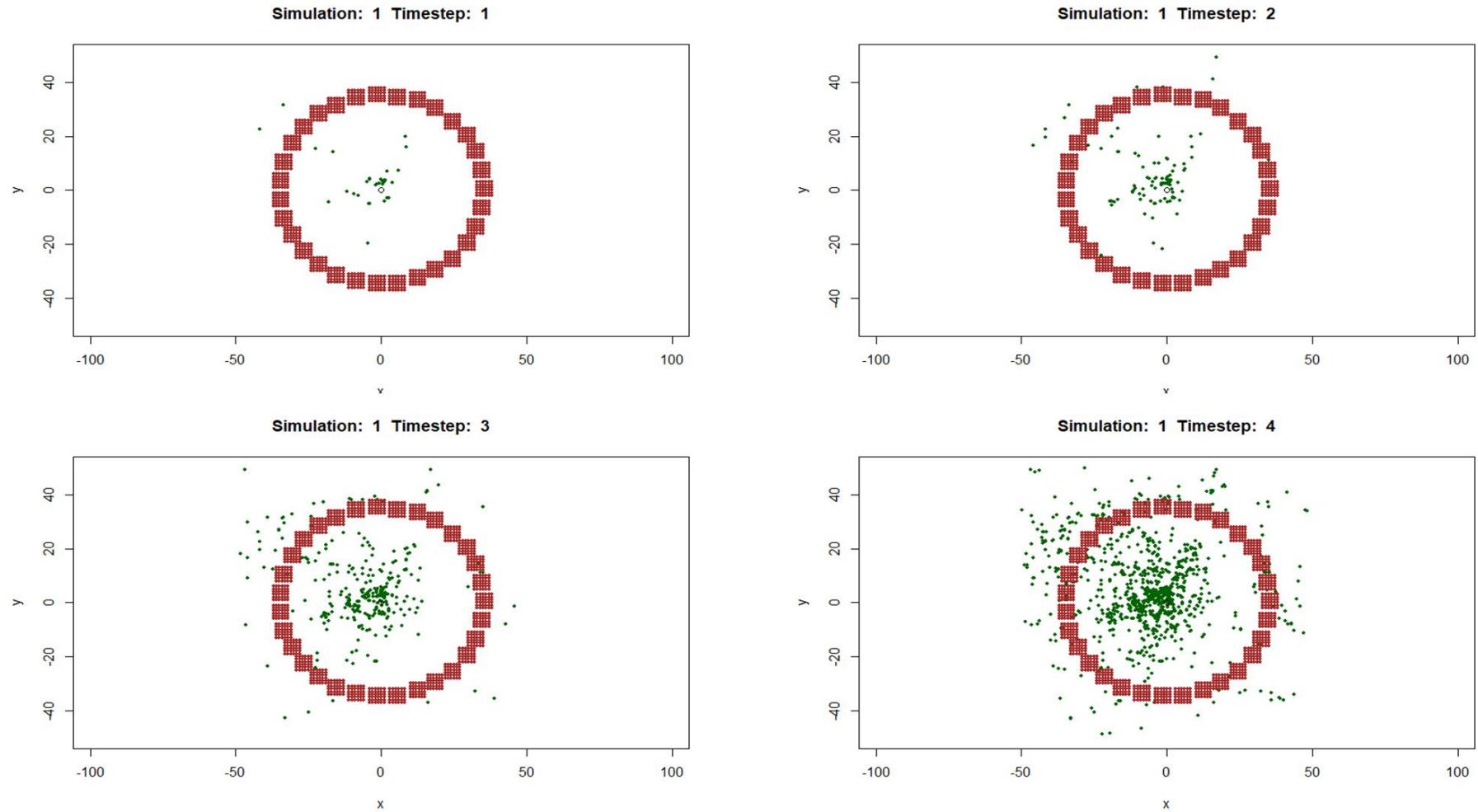
Appendix 2.7. Plant colonization and nucleation after Scenario 7 where a Fell & burn management regime was simulated over a hectare (100m x100m), and no obstacles were present. This would be the period immediately after a burn and when follow up Acacia clearing is done. The green points represent plants.
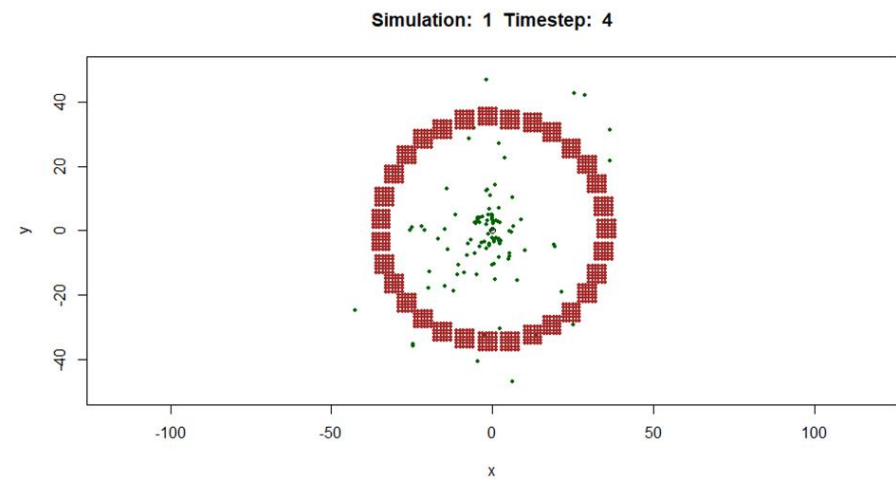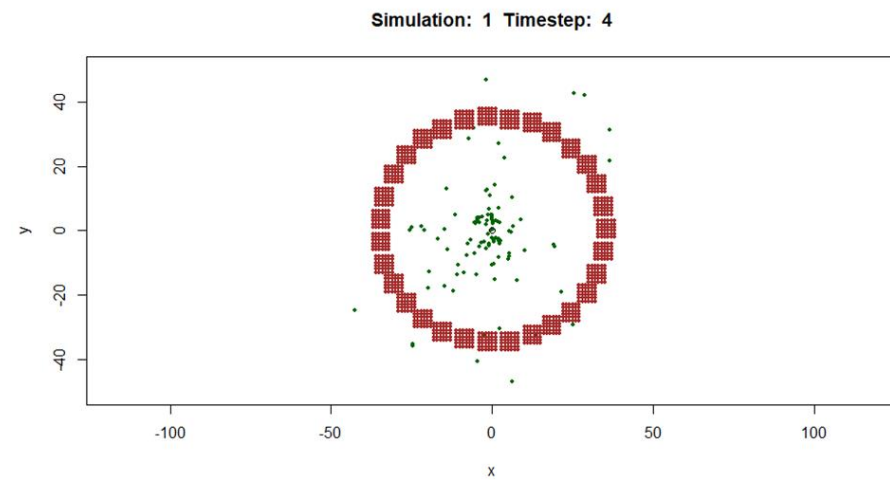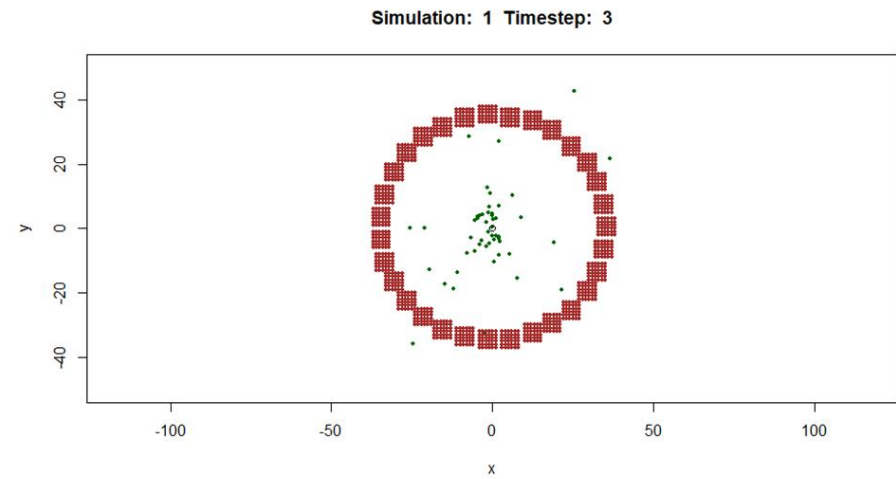
Appendix 2.8. Simulation of plant colonization and nucleation of *A. aethiopicum* over a hectare (100m x100m), over a 4-year period. The green points represent plants.

Appendix 2.9. Simulation of plant colonization and nucleation of *D. pluvialis* over a hectare (100m x100m), over a 4-year period. The green points represent plants.

Appendix 2.10. Simulation of plant colonization and nucleation of *I. repens* over a hectare (100m x100m), over a 4-year period. The green points represent plants.
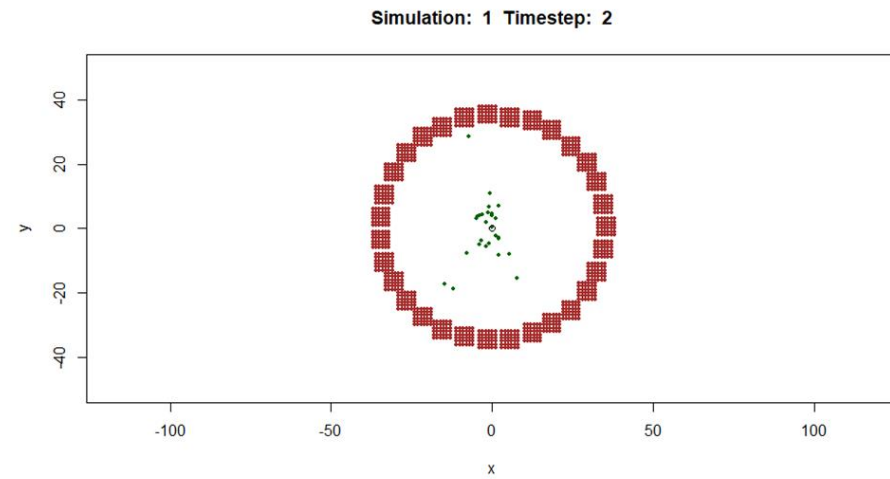
Appendix 2.11. Simulation of plant colonization and nucleation of *P. capitatum* over a hectare (100m x100m), over a 4-year period. The green points represent plants.

Appendix 3. Model code (Source: Prof. Dr. Frank Schurr, personal communication, Schurr et al., (2008)).

```
rm(list=ls())

gc()

#set your working directory - this is the directory in which file "spread functions.R" must be save

setwd("C:/R/Rscripts/")

#read in functions for simulating spread and path-dependent dispersal (from Schurr et al. 2008)

source("spread functions 202011.R")

############################################################################

#general settings (you may not need to change those)

extent <- 100 #side length of the simulation area (in m)

d<-1 #side length of each grid cell (in m)

Tmax<-4 #total number of dispersal events simulated (essentially the number of years)

Nsim<-1 #number of replicate simulations

############################################################################

############################################################################

#biological parameters

R0 <- 3 #reproductive rate: number of offspring per adult in each reproductive (NB: so far, adults
don't survive so we're looking at annuals/monocarpic species)

K <- 3 #carrying capacity: maximum number of individuals per m2

u <- 1.2 #log-scale mean of lognormal dispersal kernel; NB: previously I had suggested 0.8 but for
tumble dispersal you may want a larger value

p <- 1.2 #log-scale standard deviation of lognormal dispersal kernel

beta_w <- 3 #parameter determining the strength of path effects

        #(how physical space is projected onto movement space)
```

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#for 1 plant / m2 space stretched increases by beta_w

#beta_w must be >=0, for beta_w = 0, there is no path effect

###

##
##########

#THE ACTUAL SIMULATION CODE STARTS HERE

##
##########

#objects in which simulation results will be stored

area<-matrix(nrow=Tmax,ncol=Nsim)

dist<-matrix(nrow=Tmax,ncol=Nsim)

maxdens<-matrix(nrow=Tmax,ncol=Nsim)

popsize<-matrix(nrow=Tmax,ncol=Nsim)

maxphysdist<-maxmovedist<-matrix(nrow=Tmax,ncol=Nsim)

setwd("C:/R/Rdata")

#initial positions of plants (they could also be read in via read.table)

#plants.start<-data.frame(x=0.001,y=0.001)

plants.start<-read.csv("PlantsStart.csv")

#Read in the x and y co-ordinates of plant positions

x<-(plants.start$x)

y<-(plants.start$y)

#creating a data frame from x and y

xy<-data.frame(x,y)

Kcell <- K*d^2 #calculate carrying capacity at the grid cell level

for (s in 1:Nsim)

```
{

  noquote(paste("Simulation ",s))

  #Simulate obstacle pattern

  #NB: ONLY EVER USE ONE OF THE THREE SCENARIOS - THE OUTERS MUST BE OUTCOMMENTED

  #I) regular grid

  #obsttab <-
obstacle.simulation(scenario="grid",extent=extent,d=d,obstacle.permeability=100,n=4,total.obstacle
.area = 2304)

  #II) random pattern

  #obsttab <-
obstacle.simulation(scenario="random",extent=extent,d=d,obstacle.permeability=100,total.obstacle
.area=1000,min.obstacle.area=1,max.obstacle.area =25)

  #III) circle

  obsttab <-
obstacle.simulation(scenario="circle",extent=extent,d=d,obstacle.permeability=0,circle.radius=35,ob
stacle.distance=7,obstacle.area=40)


  plants<-plants.start

  celldens<-cell.density(plants,d) #calculate initial plant density per cell

  for (g in 1:Tmax)

  {

    print(g)

    #reproduction

    Noffspring<-rep(R0,times=nrow(plants)) #deterministic reproduction

    Nseeds<-sum(Noffspring)

    #seed dispersal

    #dispersal distance in movement space
```

100

```
r.dist<-rlnorm(n=Nseeds,meanlog=u,sdlog=p)

#dispersal angle

r.angle<-runif(n=Nseeds,min=0,max=2*pi)

startpos<-cbind(rep(plants[,1],times=Noffspring),

        rep(plants[,2],times=Noffspring))

disp.move<-cbind(startpos[,1]+r.dist*cos(r.angle),

        startpos[,2]+r.dist*sin(r.angle))

#calculation of environmental conditions (total obstacle density in each cell)

planttab <- cell.density(plants,d)

envtab <- combine.tabs(obsttab,planttab)


#projection from movement space to physical space

envtab$w<-beta_w*envtab$x/d^2 + 1

plantsnew<-matrix(NA,nrow=Nseeds,ncol=2)

for (i in 1:Nseeds)

{

 dist.phys<-dist.physical4(startpos[i,],disp.move[i,],envtab,d)

 plantsnew[i,]<-startpos[i,]+dist.phys*c(cos(r.angle[i]),sin(r.angle[i]))

}

plantsnew<-as.data.frame(plantsnew)

names(plantsnew)<-c("x","y")

  plants<-rbind(plants,plantsnew)

#plants outside the simulation area (defined by extent) are ignored

plants<-plants[abs(plants$x)<(extent/2)&abs(plants$y)<(extent/2),]

#density dependent mortality (competition)
```

```
plants<-mortality(plants,Kcell,d)

#statistics summarizing simulation results

celldens<-cell.density(plants,d)

area[g,s]<-nrow(celldens) #area covered: total number of cells with plants

popsize[g,s]<-nrow(plants) #population size (total number of plants)

#clean up memory

rm(plantsnew,envtab,celldens)

gc()

#graphics

#(commenting this out will make the simulation faster)

plot(plants,main=paste("Simulation: ",s," Timestep: ",g),xlim=c(-extent/2,extent/2),ylim=c(-extent/2,extent/2),asp=1,col="darkgreen",cex=0.5,pch=19)

points(ycell~xcell,data=obsttab,col="brown",cex=0.5,pch=19)

points(0,0)

 }

}
```