A dynamic modelling tool to anticipate the effectiveness of invasive plant control and restoration recovery trajectories in South African Fynbos.

Running head: Modelling Fynbos restoration recovery trajectories

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Abstract

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Invasive alien plants negatively impact ecosystems, necessitating intricate management actions. In a critically endangered vegetation type within the fynbos biome of South Africa, a study was performed comparing different management interventions over plots invaded by *Acacia saligna*. A dynamic modelling approach was designed to analyze field data and simulate effectiveness of several restoration methods. Field data for vegetation recovery rates over the course of two years were fed into the model, which allowed the extrapolation of multiple recovery trajectories over a long time-span, not possible to obtain from traditional short-term field surveys. Our model simulations show that different treatments in similarly degraded states at the time of clearing can result in vastly different recovery trajectories. Active seed sowing was initially most expensive but resulted in most successful native shrub recovery, decreasing costs of longer-term follow-up acacia clearing. Clearing without burning was cheapest but resulted in limited establishment of both native and acacia cover, providing an opportunity for secondary invasion by alien forbs. In this case, biotic thresholds may have been crossed which prevented recovery of certain vegetation components. Active sowing can partially reverse thresholds by restoring shrub cover but not structural diversity. Therefore even applying this treatment did not resemble vegetation structure of the reference condition after an extended period of 30 years, but does show how restoration can be improved by native seed sowing compared to passive restoration alone. Our model simulations provide a useful tool to support decision-making by providing management recommendations for optimizing alien plant clearing protocols.

Keywords: Dynamic modelling, invasion biology, restoration, recovery trajectories, conservation management

Implications for practice:

- Presence and diversity of native vegetation cover post-clearing is dependent on species presence before initial clearing, and therefore clearing without burning is only advisable where all native vegetation components are still abundant.
- Areas of low native cover and diversity show poor recovery of vegetation components over the long term without further intervention regardless of clearing treatment; therefore although initially the most expensive option, active sowing is the best method to increase native plant diversity and cover as well as resilience to secondary invasions.
- Delaying seed sowing until after one follow-up clearing as well as seed pre-treatment facilitates establishment of increased diversity of vegetation components and at a decreased long term cost due to decreased alien acacia reestablishment.

Introduction

Invasive alien plants negatively impact natural ecosystems through a long term decrease in biodiversity and altered ecosystem functioning (Richardson et al. 2000; Ortega & Pearson 2005). Invasive alien plant species removal may mitigate some of these impacts, but this often fails to achieve a functional native ecosystem due to the lack of active intervention after the initial clearing (D'Antonio & Meyerson 2002; Hulme 2006; Reid et al. 2009). Most restoration initiatives are assessed through short-term vegetation recovery and these have shown varied results (Nsikani et al. 2018). It is therefore important to determine the likely long-term trajectories of plant community recovery, especially in ecosystems with high levels of species richness and local endemism such as the fire-adapted fynbos vegetation within the Cape Floristic Region of South Africa.

The most common practice for invasive alien plant management in fynbos currently involves clearing the primary invasive species alone. This may not stimulate germination of many native species which possess dormant seed requiring a range of different fire-related cues for germination (Hall et al. 2016). An alternative treatment is to burn the site after clearing to stimulate germination of dormant fynbos seed (Holmes & Cowling 1997), as well as reduce the dormant soil seed bank of the invasive species (e.g. acacias; Holmes et al. 1987), but this treatment has been poorly studied until now. *Acacia saligna* is a particularly problematic alien invasive species in the fynbos, as it produces copious seed and accumulates long-lived soil-stored seed banks that remain dormant until stimulated by heat from a fire (Holmes et al. 1987; see also Strydom et al. 2019). This species also resprouts after fires or cutting and is difficult to eradicate; it has a higher negative impact on fynbos recovery than other alien trees such as pines (Mostert et al. 2017). *Acacia saligna* alters soil chemistry through nitrogen deposition from leaf litter (Yelenik et al. 2004), and changes the fire regime through increased biomass (Van Wilgen & Richardson 1985). Fynbos recovery potential therefore declines with each fire cycle of dense invasion (Holmes & Cowling 1997), as native plant species are lost from the ecosystem (Holmes et al. 2000; Gaertner et al. 2012), and native seed banks are also likely to be depleted under dense invasions (Holmes 2002).

A biotic threshold is crossed when crucial components such as native seed banks are lost, along with the ability of the system to restore through spontaneous succession (i.e. passive restoration). Thresholds are seen as break-points between alternative states in the ecosystem, where the reinforcing feedbacks that maintain a system in a certain state change when the threshold is crossed. Active intervention involving sowing seed of appropriate native species would be necessary to pass the threshold for re-establishing a balance of the different structural components of fynbos vegetation. To date there has been limited work done to assess active restoration success in fynbos (Gaertner et al. 2012), and where this was done, it was only documented up to three years after initiating treatments. Short-term monitoring may not determine the most effective treatment in the long-term since different vegetation components dominate the community at different times during succession (Hoffman et al. 1987). Where longer-term data exist it has been shown that legacy effects induced by invasive species, such as altered soil chemistry, can persist for an extended period of time (Nsikani 2017). Therefore, it is valuable to determine the relationships between long-term vegetation recovery and potentially related variables such as soil chemistry, or vegetation richness and plant density to evaluate long-term success of the different treatments.

Ecological process-based modelling is a useful tool to better understand ecosystem properties and processes, by using key-components of a system (Jørgensen 1994). Dynamic modelling approaches can be developed and adapted to understand ecosystem responses to invasion (Le Maitre et al. 2011) and predict vegetation dynamic trends (Scheffer et al. 1993; Fernandes et al. 2013), while informing management actions for habitat or species conservation (Arosa et al. 2017).

Dynamic models can capture functional, structural and composition patterns in systems experiencing long-term environmental disturbances (Santos et al. 2011). Evaluating the success of restoration experiments can be improved by the use of ecological dynamic models that can simulate conditions that are difficult or impossible to understand otherwise (e.g. environmental conditions not present in the study area or alternative management practices) (Jørgensen & Bendoricchio 2001). In fact, they have been extensively used to support the design and evaluation of management strategies, as they allow incorporating the dynamic processes behind both the invasive species and control techniques (e.g., Krug & Richardson 2014; Portela et al. 2020). In our case of invasive plant control and restoration recovery, the invasive species and native vegetation functional groups represent key system components, and the incorporation of the dynamic processes and interactions between them under different scenarios are central to the model we have developed.

The objective of this study is to predict and evaluate the efficiency of several contrasting restoration treatments using a dynamic modelling tool to support decision-making, namely by: (1) determining whether dynamic simulations reproduce realistic fynbos vegetation recovery following invasive plant control; (2) simulating the impact of different restoration treatments on invasive and native vegetation recovery and cost in the long-term; and (3) detecting potential biotic thresholds as well as treatments that could facilitate the reversal of a threshold where it has been crossed.

These objectives were assessed through development of a dynamic model in order to predict long-term recovery of native vegetation following invasive *Acacia saligna* clearing at Blaauwberg Nature Reserve, located in the Cape Floristic Region of South Africa. The potential of the modelling approach and relevant simulation results are discussed in the context of future management of the Cape Flats Sand Fynbos and more broadly regarding alien plant clearing protocols.

Methods

Study area

Data were collected at a restoration study site at Blaauwberg Nature Reserve, which is located within the largest remaining area of critically endangered Cape Flats Sand Fynbos (Rebelo et al. 2006), just north of the city of Cape Town, South Africa (33.75°S, 18.48°E; Figure 1). This is a vegetation type confined to deep sandy soil of low pH at low altitudes, within a strongly Mediterranean climate region of hot dry summers and cool wet winters. Ericoid shrubs with reduced leaves, graminoid-like shrubs called restios of the family Restionaceae, and taller proteoid shrubs mostly of the family Proteaceae are the key vegetation structural components typical of fynbos. In a pristine state this vegetation contains an extremely high richness of narrow range endemic species. However, due to the extent and duration of invasion by *Acacia saligna* the native vegetation has been much degraded, with a reduction in shrub cover and structural diversity that are typical of this vegetation type. Examination of historical aerial imagery indicated that dense *Acacia saligna* invasions had been present at the site for more than 50 years (CoCT, unpublished data).

Restoration treatments

Two different initial clearing treatments (passive clearing) were applied. *Stack-block* involved cutting and stacking of acacias into brush piles. *Burn-block* involved cutting and spreading acacia biomass evenly across the site and burning it (Figure 2). Initial clearing was completed in March 2013, and the controlled burn was conducted on 4th April 2013 which is later than most wildfires in fynbos (January-March), since the felled acacia biomass burns at a higher intensity than would be experienced in a fynbos burn (Holmes et al. 1989; Van Wilgen et al. 1985). Follow-up clearing took place 12 months after initial clearing (Krupek et al. 2016) in order to control acacia recruitment. Within the *Burn-block* treatment, an active restoration intervention – sowing treatment – was conducted; this involved sowing seed of a mix of fynbos species representing different structural components and included competitive and fast-establishing shrub species (See Hall 2018 for further details of species sown). This procedure was performed initially a month after a managed burn, and again a year later. The delayed sowing treatment was divided into two sub-treatments, one with seed sown without pre-treatment (as in the initial sowing treatment) while the other had seed treated with an appropriate combination of heat pulse and smoke to stimulate seed germination (Hall et al. 2016). These treatments were compared with vegetation at two reference sites, one unburnt and one recovering following a wildfire within the same season as the managed burn at Blaauwberg.

Sampling strategy

Thirty-two plots of 5x10 meters were surveyed in each of the two passive treatments (Figure 2), as well as 32 additional plots adjacent to each *Burn-block* plot for the initial sowing active treatment. In the second year two additional plots were surveyed adjacent to each of 10 of the *Burn-block* plots for the delayed sowing active treatment, one with pre-treated seed and one with untreated seed. Five plots were surveyed in burnt and five in unburnt vegetation at the reference site. Data were collected for vegetation cover, species richness and plant density immediately before clearing, and at 6-month intervals up to two years after initiating each of the treatments. Soil chemistry data were sampled from each plot at the time of initiating treatments in March 2013 and again after one year in March 2014, and were analysed at Bemlab (Pty) Ltd. (Somerset West, South Africa) for available phosphorus (P, mg/kg, PBray II), mineral nitrogen (ammonium, NH4-N, mg/kg; and nitrate, NO3-N, mg/kg), percentage carbon (%C) and moisture (%$H_2$0). Other soil chemistry variables were collected from the field, but running a Generalised Linear Model as exploratory analyses showed only these 5 variables to be important in explaining the response variable (see Table 3). Plant species were grouped according to vegetation growth form (Non-sprouting Shrub, Resprouting Shrub, or Restio – Graminoid-like Shrub). The change in vegetation cover between each survey was used to determine rates of recovery of the different growth forms. The costs associated with each treatment were calculated, including: the initial clearing of the site and either stacking or spreading of slash, burning the stack piles versus block-burn, follow-up clearing of acacia recruits under different treatments, and costs of acquiring, treating and sowing seed.

Dynamic model conceptualization

Based on the System Dynamics fundamentals (Jørgensen & Bendoricchio 2001; Krug & Richardson 2014; Portela et al. 2020), a dynamic model was developed to simulate fynbos vegetation dynamics and capture the effects of different alien plant clearing treatments on expected long-term recovery of both acacia and fynbos vegetation cover. The dependent variables within the ecosystem – plant species richness and density, and soil chemistry – were estimated using models based on cover of different vegetation and life-form components (Fernandes et al. 2013), in order to determine how these are affected by different treatments and are predicted to change over long time periods. Therefore, four interactive sub-models were designed aiming to: a) recreate the vegetation dynamics based on different surface covers, b) estimate associated environmental parameters of community structure and soil chemistry and their correlation with vegetation cover, c) test different management scenarios, and d) calculate the associated economic costs based on initial and follow up invasive alien vegetation clearing effort, managed fire, as well as seed collection and sowing (Figure 3).

The month was chosen as the time unit and the simulation period was established for 360 months (i.e. 30 years), a robust period to test multiple follow-up clearing interventions and incorporating a suitable period in which fynbos vegetation could reach a climax community following disturbance (Kraaij & Van Wilgen 2014). All modelling procedures were performed using the software STELLA, version 10.0.5® (Isee Systems, Inc.). The original conceptual sub-models, all details and explanations (Supplement S1), including equations (Supplement S2) and parameters (Supplement S3) used in the model construction, are available in Supplementary Data.

Dynamic model implementation

Vegetation cover and life-form components

Six main vegetation covers were included in the model (Figure 3b): i) acacia, characterized by areas dominated by *Acacia saligna*, the dominant cover before clearing (greatest competition against fynbos reestablishment), ii) bare ground, characterized by areas lacking woody vegetation cover after acacia clearing in degraded sites, iii) burnt area, characterized by areas lacking woody vegetation cover as a result of fire, and iv) – vi) native perennial cover, characterized by areas of restios (E), resprouting shrubs (R) and non-sprouting shrubs (S) respectively, for which higher cover is a general goal of restoration.

Perennial growth forms were chosen based on Hoffman et al. (1987), except for the exclusion of Proteaceae and herbaceous cover from the model since Proteaceae were generally absent from the site while herbaceous species account for insignificant cover in mature pristine vegetation. Ericoid shrubs were divided into non-sprouting and resprouting shrub cover since these groups have different yet important life-history strategies in this system (Le Maitre 1992), and along with restios should make up the majority of mature vegetation cover.

Vegetation regeneration dynamics

In order to recreate the succession process between the main vegetation components considered, regeneration rates based on field sampling data (Hall 2018) were included as parameters in the model. Monthly growth rates (MGR) were calculated for all vegetation components by taking the average monthly fractional change in cover across all plots for each treatment separately, and since rates come from a temporal scale other than the month, these data were incorporated into the following formula: MGR = [(1 + ATGR)exp(1/ITIY)] - 1 (Chaves et al. 2000; see also Bastos et al. 2012):

ATGR is the total growth rate over a 6 month interval between field surveys, given by each vegetation components' current extent (the sum of all components making up the total fynbos cover; see Figure 3a for the four vegetation components) divided by their potential spread area (the total area of the study site not already occupied), and ITIY is the invasion time interval, given by the number of months during which time the rates were calculated from the collected data, (e.g. the period of time between initial clearing and follow-up clearing). See Supplementary Table S3 in Supplementary data for all rates used in parameterizing the model and a brief description of each parameter.

The interaction between the acacia control treatments (Figure 3c) and vegetation components (Figure 3a) represent the main influencing factor for forecasting treatment effectiveness. Combinations of treatment options (detailed in Table 1) were therefore implemented in the dynamic model for the different scenarios considered (Figure 3c), influencing the vegetation cover through different rates of increase in vegetation cover (as %). Specific settings of parameter activation within treatments are detailed in Table 2 based on site field data. Although a stochastic element was not included directly into the model, treatments were replicated across multiple plots which included inherent stochasticity for all growth and competition rates, from which the mean values were incorporated into the model.

Pristine vegetation is known to support higher diversity and larger seed banks of native vegetation components in comparison with vegetation degraded by acacia invasion (Le Maitre et al*.* 2011). This parameterization was included in the model as different growth rates of vegetation components, dependent on whether a site is invaded or not (Table 2 and Supplement S2). When initial and follow-up clearing took place, all acacia cover was converted to bare ground, while a managed fire resulted in all vegetation cover being converted to burnt area. This was colonized over time by vegetation components, with rates of increase in cover being dependent on the treatment selected (Table 2 and Supplement S2). Furthermore, fire stimulated germination of acacias from the seed bank (Jeffery et al. 1988), thus accelerating the rate of increase in percentage cover after a burn took place (based on the rate recorded following *Burn-block* treatment in the field).

Wildfires are typical and recurrent events that markedly shape fynbos ecosystems (Kraaij & Van Wilgen 2014). Fire effects were simulated for reference fynbos vegetation scenarios but not included directly in the restoration treatments since a restoration site would likely exclude wildfire due to limited biomass until native cover is successfully restored. Therefore, wildfires were included in the dynamic model as stochastic phenomena, and the average trends of wildfire impacts were measured by running 100 independent simulations. Wildfires were mediated by parameters that reproduce the random fire occurrences at the study region during dry summer months between November and March (Esler et al. 2014). The post-fire succession was included in the vegetation cover dynamics by using temporal growth rates of each vegetation component based on rates recorded after fire in reference fynbos plots in this study (Table 2 and Supplement S2).

Seed sowing can counter the effect of lower rates of increase in cover of native vegetation where native seed banks have been depleted, resulting in increased shrub cover after sowing seed in bare or burnt ground (Gaertner, Nottebrock, et al. 2012). Timing of sowing after clearing or burning, and whether or not seed is pre-treated, will affect subsequent vegetation growth rates. Therefore once the sowing treatment was activated in the model it influenced native vegetation growth rates accordingly (Table 2 and Supplement S2).

Management scenarios

In order to compare the effectiveness of the different combinations of restoration treatment options, five scenarios were implemented based on experiments tested in the field (for treatment options see Table 1, for parameter settings see Table 2). The five scenarios considered were: (0) *Reference condition* - Vegetation consisted of fynbos shrub components alone and stochastic wildfire events as the only disturbance, after which fynbos components recovered and experienced competitive interactions; (1) *Stack-block* - Invaded vegetation cleared of acacia without managed fire where the fynbos cover present at each clearing event exhibits a recovery process based on the recovery rates recorded for this treatment; (2) *Burn-block* - Invaded vegetation cleared of acacia followed by managed fire, after which the resulting burnt ground (occupying the entire site) was colonized by fynbos and acacia based on the recovery rates recorded for this treatment; (3) *Initial Seed Sowing* – The same initial path as *Burn-block treatment* but with rates of acacia and fynbos recovery changing immediately after managed fire; (4) *Delayed sowing with untreated seed* – The same initial path as *Burn-block treatment* but with vegetation recovery rates changing a year after managed fire to rates recorded for delayed sowing with un-treated seed; and (5) *Delayed sowing with pre-treated seed* – The same path as *Delayed sowing with untreated seed* but with growth rates recorded for delayed sowing with pre-treated seed.

Indicators of community structure and soil chemistry

In order to assess the long-term influence of different acacia clearing treatments on environmental (soil) factors and ecological indicators of community structure (Figure 3b), Generalized Linear Models (GLMs) were implemented to test the strength of relationships between independent and dependent variables. The independent variables tested were: bare ground, burnt area, acacia cover, restio cover, non-sprouting and resprouting cover (Figure 3a), while the dependent variables were: plant species richness and density, as well as soil chemistry (Figure 3b). For plant species richness and density GLMs, a Poisson variance distribution and a log link function were used, whereas for soil chemistry parameters, a Gaussian distribution and an identity link function were fitted to assess the best model supporting the data. All (valid) combinations of explanatory variables for the dependent variables were considered (Burnham & Anderson 2002) and the best model was selected among candidate models according to the lower value of the Akaike Information Criterion (AIC, Hurvich & Tsai 1989). The coefficient results were incorporated into the dynamic model construction, following the principles of the Stochastic Dynamic Methodology (StDM) (Santos et al. 2011). The statistical analyses were carried out using R software (R Core Team 2015). Most parameters perform higher than 20% goodness of fit value and thus are considered to be at least partially explained by the model vegetation components; parameters with lower than 20% correlation value are considered to be insufficiently well explained by modelled vegetation components and were excluded from further analysis.

Economic assessment

Costs of initial clearing, burning and sowing (for scenarios where these treatments were considered) were assumed as constant values based on costs estimated for these treatments in the field. Costs of follow-up clearing treatments were simulated as a function of acacia cover at each clearing time, applying an equation based on the known cost of follow-up clearing for the acacia cover recorded in the field for each treatment, which increased or decreased follow-up costs in the model depending on whether acacia cover in the simulation was higher or lower than that in field experiments. Rates of change in costs were dependent on the different scenarios carried out in the field (Figure 3c and Table 2), which were therefore incorporated into the model. For ease of applicability to large-scale clearing scenarios, costs were scaled up to South African Rands per hectare (1 USD = 14 ZAR as of 10 July 2019).

Results

Outcomes of management scenarios

Model simulations concerning each management scenario resulted in different recovery trajectories (Figure 4). However, in terms of fynbos structural recovery, neither the passive nor the active treatments resembled a reference state even after an extended period of time (30 years). A reference state is represented within the model by typical fluctuations marked by periods of higher vegetation covers, during the post-fire recovery, and periods of lower vegetation covers induced by wildfire burnt areas (Figure 4a). In terms of acacia reinvasion potential and total native perennial cover, the sowing treatments resembled an uninvaded state more closely with time.

Modelled vegetation covers are illustrated over the simulation period in Figure 4 and the percentage cover is shown in Table 4. In this perspective, the *Burn-block* treatment had the highest rate of increase in percentage of acacia cover, although decreasing over time (13.72% total cover after 360 months) (Figure 4c). The *delayed sowing* treatments both had lowest rates of increase in percentage acacia cover (0.31% for untreated and 1.51% for pre-treated seed). The rate of increase in percentage of non-sprouting shrub cover was highest in the *Initial sowing* treatment (80.79%) and, along with all other sowing treatments, was much higher even than the reference site (16.49%), while there was almost no recovery in the *Burn-block* treatment (0.49%). The rate of increase in percentage of resprouting shrub cover was lowest in the *Initial sowing* treatment (1.44%), but higher in the *Delayed pre-treated sowing* treatment (5.93%). Across all restoration treatments, *Burn-block* and *Stack-block* treatments had almost the same rates of increase in percentage of resprouting shrub cover (13.12% and 13.2%, respectively). The rate of increase in percentage of restio cover was highest within the *Delayed pre-treated sowing* treatment (3.97%), while in *Stack-block* the restio cover slowly decreased over time from 10% to 6.68%. Other scenarios showed almost no recovery of restio cover after burning (1.05% in *Burn-block*, 1.53% in *Initial sowing* and 0.9% in *Delayed untreated sowing* treatment). Both resprouting shrub and restio cover was much higher in the reference site (21 and 31% after 360 months respectively) than across all invaded scenarios tested.

Effects of Acacia control treatments on soil chemistry and plant community structure

Only soil ammonium increased while all other variables decreased with increasing overall vegetation cover. Apart from geophyte richness, species richness and plant density of all vegetation components showed a minimum goodness of fit value of 27% with cover of the modelled vegetation components.

Plant species richness and density and soil chemistry differed in all treatments from the reference vegetation, based on estimations of these variables from vegetation cover. The resulting estimated values of these variables at the end of the simulation are shown in Table 4. All treatments had lower richness of restios (maximum 2 vs. 3 species) and resprouters (maximum 2 vs. 5 species) than in reference sites. *Initial sowing* treatment had the highest richness (16 species) although mostly due to non-sprouting shrubs (9 species), while *Burn-block* treatment resulted in lowest richness overall (9 species), apart from graminoids (4 species). Lower shrub species richness was predicted in both *delayed sowing* treatments (8-10 vs. 12 spp.). The *Burn-block* treatment had lowest plant density per plot including all components (21 plants). Non-sprouting shrub density was comparable between *Stack-block* treatment (21 plants) and the reference site (20 plants), while all *sowing* treatments had much higher density than the reference site (31-54 vs. 20 plants). All *sowing treatments* also had increased restio and herbaceous density but not that of resprouters. For soil chemistry, C (2.07-2.17 vs. 1.88%), NO_3^- (4.49-5.81 vs. 2.65mg/kg) and P (3.37-4.81 vs. 1.56mg/kg) were similar for all invaded treatments but higher than the reference. NH_4^+ was lower in the *Burn-block treatment* (5.55mg/kg) but higher in all other treatments (42.95-83.34mg/kg) than the reference, especially in all *sowing treatments* (67.1-83.34mg/kg). Soil moisture content was higher for all treatments (0.32-1.10%) than the reference (0.15%), but particularly high for the *Burn-block treatment* (1.10%).

Economic assessment

Cost accumulation of different treatments under management scenarios is illustrated in Figure 5 and total costs are shown in Table 4. After the first clearing cycle *Stack-block treatment* was cheapest at R17,505 ($1,250) per ha (cost includes initial clearing and one follow-up clearing), followed by *Burn-block* at R44,536 ($3,181) per ha (cost includes initial clearing, burning and one follow-up clearing), and *sowing treatments* were most expensive at R52,546 ($3,751) per ha (cost includes initial clearing, burning, seed sowing and one follow-up clearing, the latter after sowing in initial sowing treatment and before sowing in delayed sowing treatment, hence a slight difference in costs between these treatments due to the effect of initial sowing on follow-up acacia clearing cost). However, the accumulated cost after three clearing cycles in *Stack-block* came to R24,277 ($1,734) per ha (39% increase from cost after first clearing), while the *Delayed sowing with pre-treated seed* came to R75,173 ($5,369) per ha (43% increase from cost after first clearing) and the *Burn-block treatment* was the most expensive treatment in the long term at R85,044 ($6,075) per ha (91% increase from cost after first clearing).

Discussion

Ecological dynamic models can be seen as useful tools to support decision making, since they allow not only to grasp the functioning of ecosystems under different sources of environmental change, but also to test alternative measures prior to their implementation at local scale where conservation planning and management actions usually take place (Bastos et al. 2018). In this perspective, our model was able to simulate a stable yet dynamic reference vegetation state and to predict vastly different outcomes for each restoration treatment. The sowing treatment with pre-treated seed was most effective in restoring structural diversity and high cover as well as achieving resilience against re-invasion, therefore improving intervention cost effectiveness. Depleted seed bank and competition from invasive plants, rather than altered soil chemistry, appears to be primarily responsible for a lack of autogenic recovery, therefore biotic rather than abiotic thresholds were crossed since sowing with pre-treated seed was able to shift the ecosystem to a pre-threshold state.

Simulated ecological succession and recovery after invasive plant control

Models of ecosystem dynamics must be developed in order to be useful to support management decision-making on a broader scale, as recommended by Le Maitre et al. (2011) and demonstrated for example by Rastetter et al. (2003). Our dynamic model simulations determined that the reference scenario was capable of realistically simulating the vegetation cover dynamics of pristine fynbos (Hall 2018) in terms of key structural components and their responses to periodic wildfires. Furthermore, the simulations of reference vegetation cover trends are in agreement with field observations recorded for mature fynbos plots in other studies (e.g., Hoffman et al. 1987). Community level richness of modelled plant components and soil chemistry were also predicted within the range expected based on plot data obtained in this study. However, plant density was not reliably predicted as compared to field observations, likely because of the large change in number of plants in the field over time i.e. many seedlings in early successional vegetation to fewer larger shrubs in mature vegetation (Hall 2018).

In acacia-invaded vegetation, the *Burn-block treatment* presented the highest rate of increase in acacia cover following clearing, which was expected since *Acacia saligna* is adapted to recruit after fire

(Richardson & Kluge 2008). In the *sowing treatments*, the high shrub cover provided competition against colonization by acacias or alien herbaceous weeds and combined with follow-up clearing resulted in low acacia growth rates. This agrees with studies from other systems which found that active revegetation can prevent further invasion episodes by other invasive species (Kettenring & Adams 2011; Vranjic et al. 2012).

Impact of restoration treatments on native vegetation recovery and costs of treatments

Restoration treatments have been compared in terms of vegetation recovery in several other studies (Wilson & Gerry 1995; Ruwanza et al. 2013; Daehler & Goergen 2005). However, studies very seldom compare treatments more than four years after treatment initiation; Ruwanza (2018) did a follow-up survey after more than 4 years, while in a longer-term study by Blanchard and Holmes (2008) no initial or early post-clearing data were collected. In this study, the *Stack-block treatment* resulted in highest percentage cover of restios and resprouting shrubs in the long-term, but this was due to persistence of plants that were present before clearing. Once these species disappear they will likely remain absent without fire, since fire is necessary for stimulating germination of many fynbos species from the persistent soil seed bank (Holmes & Cowling 1997). However, limited native vegetation recovery, especially of non-sprouting shrubs, after burning alone was likely due to a depleted native seed bank (Holmes 2002) as well as competition from acacias (Musil 1993). The high establishment of native shrub cover after sowing was sustained over the long-term, assuming follow-up clearing of acacia. Active seed sowing was also found to benefit restoration in other regions (Wilkerson et al. 2014), since propagule limitation was otherwise a barrier to ecosystem restoration following invasive alien plant removal (Kettenring & Adams 2011).

A key objective of our model was to determine the most ecologically- and cost-effective fynbos restoration treatment. Although the *Stack-block treatment* costs the least, a greater long-term investment would be required for secondary invader control (Blanchard & Holmes 2008) and to prevent reinvasion, as was found in numerous restoration studies in different sites by Pearson et al. (2016). Since cost of secondary invader control was not included, factoring in this aspect would likely make the *Stack-block* treatment significantly more expensive in reality (Loo et al. 2009). Although initially more expensive due to labour involved in collecting, processing and sowing seed, *sowing treatments* resulted in improved shrub cover and therefore decreased potential for acacia reestablishment, assuming this is in combination with follow up alien control. By the second follow-up clearing this treatment became cheaper than *Burn-block* alone due to the decreased resources required for follow up alien control. This agrees with Le Maitre et al. (2011) who indicate that longer-term cumulative costs following seed sowing could be lower than continued higher costs of removing invaders.

Anticipating biotic thresholds and using treatment simulation results in decision-making to facilitate their reversal

The low post-clearance recovery projected in the long-term for treatments without sowing shows that restoration is constrained by seed-limitation pointing to a biotic threshold having been crossed (Gaertner et al. 2012). In the *Stack-block* treatment, the lack of shrub cover left a niche of higher soil nitrogen availability and low competition in which secondary invasive species established (Nsikani et al. 2017). Secondary invaders accumulate biomass faster than native shrubs and increase the risk of too-frequent fires, negatively impacting native vegetation recovery (Vilà et al. 2001) and resulting in an alternative stable state of herbaceous rather than shrub cover.

Active sowing can overcome seed limitation and reverse the biotic threshold by restoring structural elements and diversity of the vegetation as well as decreasing acacia recovery potential. However, the *initial sowing treatment* resulted in poor recovery of resprouting shrub and restio cover while *delayed sowing* resulted in increased resprouting shrub cover and decreased acacia cover. Pre-treating seed using appropriate heat and smoke cues (Hall et al. 2016) further improved recovery of resprouting shrub and restio cover, but this was still not comparable to a reference site. Effectively restoring these components will likely require planting out rooted material in addition to seed, which is more costly but should improve establishment (Godefroid et al. 2011; Cole et al. 2011).

Abiotic, functional thresholds may also have been crossed due to the changes in soil chemistry which are sustained over the long-term as predicted by the model simulations. This was also found in the case of *Acacia longifolia* by Marchante et al. (2009) in spite of attempting to reduce excess soil C and N, which suggests a legacy effect of invasive plants on soil chemistry (Gaertner et al. 2012; Corbin & D'Antonio 2012). However, the fact that some diversity of shrub cover reestablished in sowing treatments, further improved by pre-treating seed, motivates that a biotic rather than an abiotic threshold was crossed.

It may not be feasible to expect to restore a degraded site to a reference condition, and perhaps the short-term goal should rather be to reinstate vegetation structure in support of key ecosystem functions (Gaertner et al. 2012). This will still provide habitat for species of conservation concern, as was done in a nearby restoration site for *Erica verticillata,* a species endemic to lowland fynbos which became extinct in the wild but is being reintroduced to habitats with restored vegetation structure (Hitchcock & Rebelo 2017).

The dynamic model as a tool to inform and optimise future management

Results from several modeling approaches have been used to inform management related to invasive alien plant clearing protocols (Higgins et al. 2000). Restoration treatments have also been compared using models to simulate long-term trends which were not evident over short time periods (Arosa et al. 2017). In this scope, after developing a dynamic model considering a real ecosystem with real problems, our modelling approach can provide valuable management recommendations by simulating longer-term trends of how vegetation will likely respond to different treatments, even when only short-term field data are available. Different site conditions (e.g. initial vegetation cover or rates of increase in cover) can be incorporated into this flexible model parameterization, in order to make assessments over a wider range of conditions, being adaptable to local management requirements (objectives and parameters) in specific contexts. Overall, the obtained simulation results are encouraging since they seem to demonstrate the reliability of our approach to predict the behavioural pattern for the key components selected under complex and variable environmental spatial scenarios. Nevertheless, validation is considered a fundamental process when showing the relative accuracy of the model response in relation to its applicability (Rykiel, 1996). However, since the available data did not allow for validation of this model, which can only be done after several years of collecting relevant site-specific information under well-known local environmental conditions (Glenz et al., 2001; Chaloupka, 2002), it is not likely to be used by restoration planners or scientific advisors at least in its current form. Future data collected from this restoration site and additional restoration experimentation will allow for validation of the model. Despite this limitation, inherent to a demonstrative study case in progress, the model in its current form is particularly helpful to capture these multi-factor influences under relevant management scenarios, which may be used to support protocols for specific management needs after validation with additional data.

In conclusion, this study highlights the interplay between dynamic model-based research, experimental field tests and ecological monitoring, which will make ecological models more instructive and credible to environmental managers. Predictive dynamic modelling tools can improve efficiency and usefulness of monitoring results, whereas strategic monitoring can provide robust datasets to validate models and improve their predictive power in anticipating the restoration treatment effectiveness to mitigate the impacts of invasive alien species.

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References

Arosa ML, Bastos R, Cabral JA, Freitas H, Costa SR, Santos M (2017) Long-term sustainability of cork oak agro-forests in the Iberian Peninsula: A model-based approach aimed at supporting the best management options for the montado conservation. Ecological Modelling 343: 68–79

Bastos R, Santos M, Ramos JA, Vicente J, Guerra C, Alonso J, Honrado J, Ceia RS, Timóteo S, Cabral JA (2012) Testing a novel spatially-explicit dynamic modelling approach in the scope of the laurel forest management for the endangered Azores bullfinch (*Pyrrhula murina*) conservation. Biological Conservation 147: 243-54

Bastos R, D'Amen M, Marcos B, Santos M, Braz L, Vicente J, Honrado J, Gonçalves J, Monteiro A & Cabral JA (2018) Towards functional biodiversity predictions: A hierarchical modelling framework from primary productivity to biomass of upper trophic levels. Landscape Ecology 33: 2221-2237

Blanchard R, Holmes PM (2008) Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. South African Journal of Botany 74: 421–431

Buchadas A, Vaz AS, Honrado JP, Alagador D, Bastos R, Cabral JA, Santos M, Vicente JR (2017) Dynamic models in research and management of biological invasions. Journal of Environmental Management 196: 594-606

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer

Chaves C, Maciel E, Guimarães P, Ribeiro JC (2000) Instrumentos estatísticos de apoio à economia: conceitos básicos. McGraw-Hill, Lisboa

Cole RJ, Holl KD, Keene CL, Zahawi RA (2011) Direct seeding of late-successional trees to restore tropical montane forest. Forest Ecology and Management. 261:1590-1597

Corbin JD, D'Antonio CM (2012) Gone but Not Forgotten? Invasive Plants' Legacies on Community and Ecosystem Properties. Invasive Plant Science Management 5: 117–124

D'Antonio C, Meyerson LA (2002) Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. Restoration Ecology 10: 703–713

Daehler CC, Goergen EM (2005) Experimental Restoration of an Indigenous Hawaiian Grassland after Invasion by Buffel Grass (*Cenchrus ciliaris*). Restoration Ecology 13: 380–389

Esler KJ, Pierce SM, De Villiers C (2014) Fynbos : ecology and management. Briza Publications, Pretoria.

Fernandes C, Cabral JA, Crespí AL, Hughes SJ, Santos M (2013) Converting simple vegetation surveys in functional dynamics. Acta Oecologica 48: 37-46

Gaertner M, Holmes PM, Richardson DM (2012) Biological invasions, resilience and restoration. Pages 265-280 In: Andel J, Aronson J (eds) Restoration Ecology: The new frontier. Wiley-Blackwell, Oxford

Gaertner M, Nottebrock H, Fourie H, Privett SDJ, Richardson DM (2012) Plant invasions, restoration, and economics: Perspectives from South African fynbos. Perspectives in Plant Ecology, Evolution and Systematics 14: 341–353

Godefroid S, Piazza C, Rossi G, Buord S, Stevens AD, Aguraiuja R, Cowell C, Weekley CW, Vogg G, Iriondo JM, Johnson I, Dixon B, Gordon D, Magnanon S, Valentin B, Bjureke K, Koopman R, Vicens M, Virevaire M, Vanderborght T (2011) How successful are plant species reintroductions? Biological Conservation 144: 672–682

Hall SA (2018) Restoration potential of alien-invaded Lowland Fynbos. PhD dissertation, Stellenbosch University, Stellenbosch

Hall SA, Newton RJ, Holmes PM, Gaertner M, Esler KJ (2016) Heat and smoke pre-treatment of seeds to improve restoration of an endangered Mediterranean climate vegetation type. Austral Ecology 42: 354–366

Higgins SI, Richardson DM, Cowling RM (2000) Using a dynamic landscape model for planning the management of alien plant invasions. Ecological Applications 10: 1833–1848

Hitchcock A, Rebelo AG (2017) The Restoration of *Erica verticillata* - a Case Study in Species and Habitat Restoration and Implications for the Cape Flora. Sibbaldia: the Journal of Botanic Garden Horticulture 15: 39-63

Hoffman MT, Moll EJ, Boucher C (1987) Post-fire succession at Pella, a South African lowland fynbos site. South African Journal of Botany 53: 370–374

Holmes PM (1989) Effects of different clearing treatments on the seed-bank dynamics of an invasive Australian shrub, *Acacia cyclops*, in the Southwestern Cape, South Africa. Forest Ecology and Management 28: 33–46

Holmes PM (2002) Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. Austral Ecology 27: 110–120

Holmes PM, Cowling RM (1997) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrubland. Journal of Applied Ecology 34: 317–332

Holmes PM, Macdonald IAW, Juritz J (1987) Effects of Clearing Treatment on Seed Banks of the Alien Invasive Shrubs *Acacia saligna* and *Acacia cyclops* in the Southern and South-Western Cape, South Africa. Journal of Applied Ecology 24: 1045–1051

Holmes PM, Richardson DM, Van Wilgen BW, Gelderblom C (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecology 25: 631–639

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835–847

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76: 297–307

Jeffery DJ, Holmes PM, Rebelo AG (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. South African Journal of Botany 54: 28–34

Jørgensen SE (1994) Models as instruments for combination of ecological theory and environmental practice. Ecological Modelling 75–76: 5–20

Jørgensen SE, Bendoricchio G (2001) Fundamentals of Ecological Modelling. 3rd edition. Elsevier, Amsterdam

Kandziora M, Burkhard B, Müller F (2013) Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators—A theoretical matrix exercise. Ecological Indicators 28: 54–78

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48: 970–979

Kraaij T, van Wilgen BW (2014) Drivers, ecology, and management of fire in fynbos. Pages 48-72 In: Allsopp N, Colville J, Verboom GA (eds) Fynbos: Ecology, evolution and conservation of a megadiverse region. Oxford University Press, Oxford

Krug RM, Richardson DM (2014) Modelling the effect of two biocontrol agents on the invasive alien tree *Acacia cyclops* - Flowering, seed production and agent survival. Ecological Modelling 278: 100-113.

Krupek A, Gaertner M, Holmes PM, Esler KJ (2016) Assessment of post-burn removal methods for *Acacia saligna* in Cape Flats Sand Fynbos, with consideration of indigenous plant recovery. South African Journal of Botany 105: 211–217

Loo SE, Mac Nally R, O'Dowd DJ, Lake PS (2009) Secondary Invasions: Implications of Riparian Restoration for In-Stream Invasion by an Aquatic Grass. Restoration Ecology 17: 378–385

Le Maitre DC (1992) The relative advantages of seeding and sprouting in fire-prone environments: a comparison of life histories of *Protea neriifolia* and *Protea nitida*. Pages 123-144 In: van Wilgen BW, Richardson DM, Kruger FJ, van Hensbergen HJ (eds) Fire in South African Mountain Fynbos. Springer-Verlag, Berlin

Le Maitre DC, Gaertner M, Marchante E, Ens EJ, Holmes PM, Pauchard A, O'Farrell PJ, Rogers AM, Blanchard R, Blignaut J, Richardson DM (2011) Impacts of invasive Australian acacias: implications for management and restoration. Diversity and Distributions 17: 1015–1029

Marchante E, Kjøller A, Struwe S, Freitas H (2009) Soil recovery after removal of the N_2-fixing invasive *Acacia longifolia*: Consequences for ecosystem restoration. Biological Invasions 11: 813–823

Mostert E, Gaertner M, Holmes PM, Rebelo AG, Richardson DM (2017) Impacts of invasive alien trees on threatened lowland vegetation types in the Cape Floristic Region, South Africa. South African Journal of Botany 108: 209-222

Musil CF (1993) Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. Journal of Applied Ecology 30: 361–372

Nsikani MM, Novoa A, Van Wilgen B, Keet J, Gaertner M (2017) *Acacia saligna's* soil legacy effects persist up to 10 years after clearing: Implications for ecological restoration. South African Journal of Botany 42: 880-889

Nsikani MM, van Wilgen B, Gaertner M (2018) Barriers to ecosystem restoration presented by soil legacy effects of invasive alien N_2-fixing woody species: Implications for ecological restoration. Restoration Ecology 26: 235-

244

Ortega YK, Pearson DE (2005) Weak vs. Strong Invaders of Natural Plant Communities: Assessing Invasibility and Impact. Ecological Society of America 15: 651–661

Pearson DE, Ortega YK, Runyon JB, Butler JL (2016) Secondary invasion: The bane of weed management. Biological Conservation 197: 8–17

Peterson G, Allen CR, Holling CS (1998) Ecological Resilience, Biodiversity, and Scale. Ecosystems 1: 6–18

Portela R, Vicente JR, Roiola SR & Cabral JA (2020) A dynamic model-based framework to test the effectiveness of biocontrol targeting a new plant invader- the case of *Alternanthera philoxeroides* in the Iberian Peninsula. Journal of Environmental Management 264 (in press). [doi: 10.1016/j.jenvman.2020.110349]

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rastetter EB, Aber JD, Peters DPC, Ojima DS, Burke IC (2003) Using Mechanistic Models to Scale Ecological Processes across Space and Time. Bioscience 53: 68–76

Rebelo AG, Boucher C, Helme N, Mucina L, Rutherford MC (2006) Fynbos Biome. Pages 52-219 In: Mucina L, Rutherford MC (eds) The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria

Reid AM, Morin L, Downey PO, French K, Virtue JG (2009) Does invasive plant management aid the restoration of natural ecosystems? Biological Conservation 142: 2342–2349

Richardson DM, Kluge RL (2008) Seed banks of invasive Australian *Acacia* species in South Africa: Role in invasiveness and options for management. Perspectives in Plant Ecology, Evolution and Systematics 10: 161–177

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93–107

Ruwanza S, Gaertner M, Esler KJ, Richardson DM (2013) The effectiveness of active and passive restoration on recovery of indigenous vegetation in riparian zones in the Western Cape, South Africa: A preliminary assessment. South African Journal of Botany 88: 132–141

Rykiel EJ (1996) Testing ecological models: the meaning of validation. Ecological modelling 90: 229-244

Santos M, Freitas R, Crespí AL, Hughes SJ, Cabral JA (2011) Predicting trends of invasive plants richness using local socio-economic data: an application in North Portugal. Environmental research 111: 960–966

Scheffer M, Bakema AH, Wortelboer FG (1993) MEGAPLANT: a simulation model of the dynamics of submerged plants. Aquatic Botany 45: 341–356

Strydom M, Veldtman R, Ngwenya MZ, Esler KJ (2019) Seed survival of Australian *Acacia* in the Western Cape of South Africa in the presence of biological control agents and given environmental variation. PeerJ 7: e6816

Van Wilgen BW, Le Maitre DC, Kruger FJ (1985) Fire behaviour in South African fynbos (macchia) vegetation and predictions from Rothermel's fire model. Journal of Applied Ecology 22: 207-216

Van Wilgen BW, Richardson DM (1985) The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. Journal of applied Ecology 22: 955-966

Vilà M, Lloret F, Ogheri E, Terradas J (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. Forest Ecology and Management 147: 3–14

Vranjic JA, Morin L, Reid AM, Groves RH (2012) Integrating revegetation with management methods to rehabilitate coastal vegetation invaded by Bitou bush (*Chrysanthemoides monilifera ssp. rotundata*) in Australia. Austral Ecology 37: 78–89

Wilkerson ML, Ward KL, Williams NM, Ullmann KS, Young TP (2014) Diminishing Returns from Higher Density Restoration Seedings Suggest Trade-offs in Pollinator Seed Mixes. Restoration Ecology 22: 782–789

Wilson SD, Gerry AK (1995) Strategies for Mixed-Grass Prairie Restoration: Herbicide, Tilling, and Nitrogen Manipulation. Restoration Ecology 3: 290–298

Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem Level Impacts of Invasive *Acacia saligna* in the South African Fynbos. Restoration Ecology 12: 44–51

Zurell D, Jeltsch F, Dormann CF, Schröder B (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? Ecography 32: 733–744

Figures and Tables

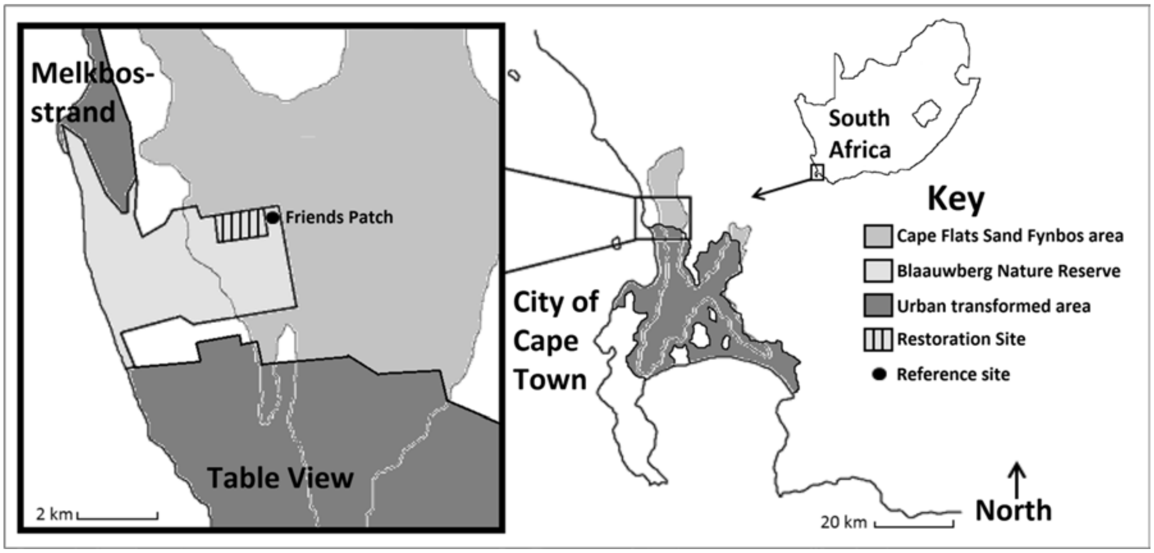

Figure 1. Location of the study area at Blaauwberg Nature Reserve north of the city of Cape Town, within the Western Cape province of South Africa.

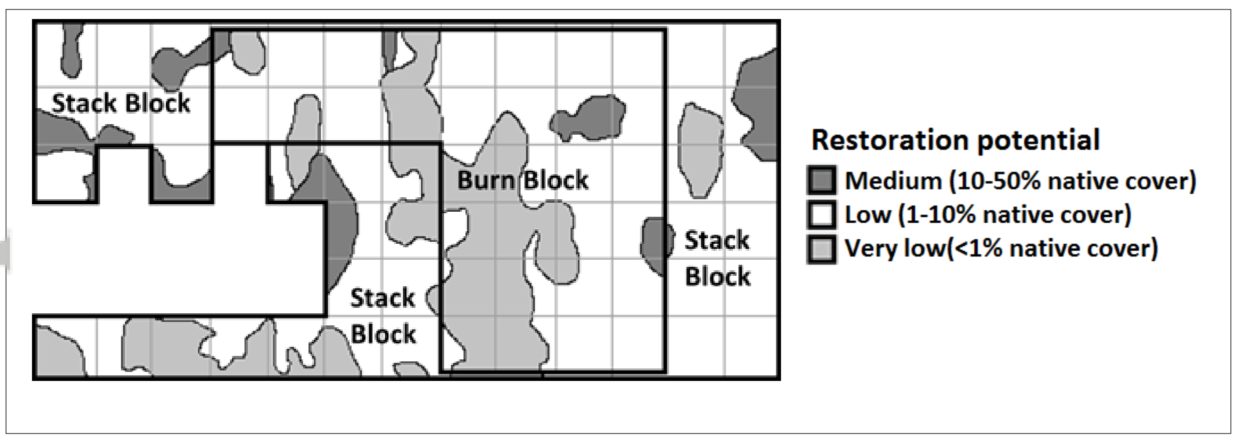

Figure 2. The treatment setup implemented at Blaauwberg Nature Reserve. Each small block is one hectare; 32ha *Burn-block treatment* was nested within the surrounding *Stack-block treatment*. Active *sowing treatments* were set up within *Burn-block* plots.

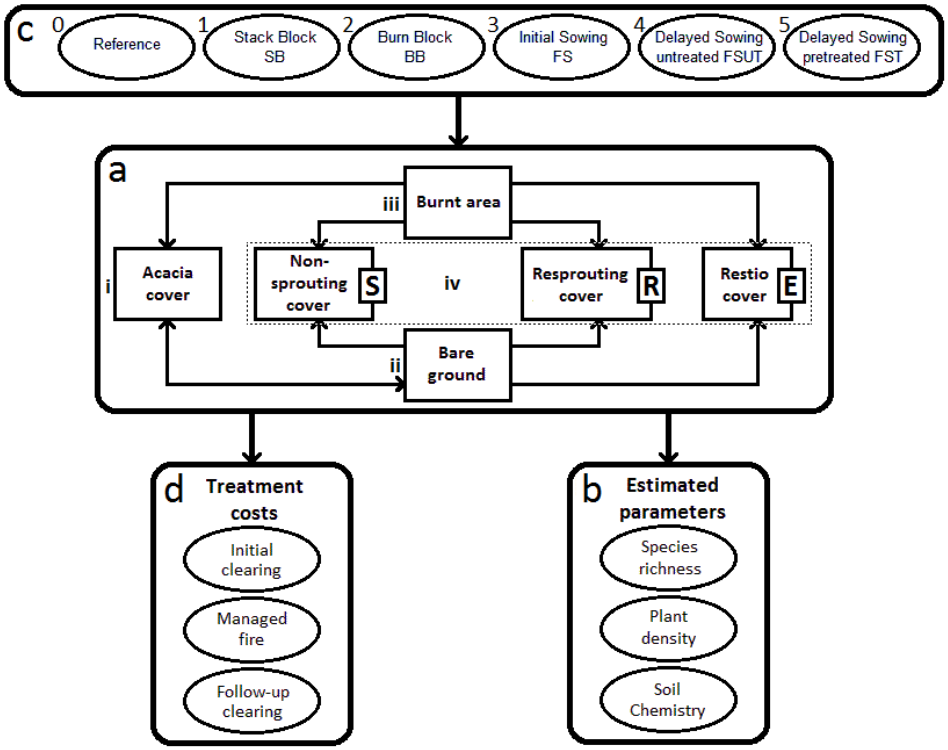

Figure 3. Conceptual diagram of the dynamic model used to simulate changes in vegetation cover under different alien clearing treatment scenarios. The sub-components of the model are grouped as follows: a) vegetation dynamics based on ground cover classes i-iv including vegetation components E, R and S, b) emergent indicators of community structure and soil chemistry, c) management scenario treatments 0-5 and d) associated management costs.

Table 1. Descriptions for the five modelled scenarios and reference state, showing which treatment options are activated in each scenario, as well as rationale behind testing each scenario.

Name of Scenario	Symbol	Wildfire option	Invaded site	First clearing	Fire management	Followup clearing	Sowing management	Delayed Sowing	Pre-treated seed	Rational	Reference
Stack-Block	SB		1	1		1				Limit disturbance to standing vegetation	Holmes 1989
Burn-Block	BB		1	1	1	1				Stimulate native seed to germinate and deplete Acacia seed	Holmes 1989
Initial Fynbos sowing	FS		1	1	1	1	1			Reintroduce lost native vegetation structural components	Ruwanza et al 2013
Delayed sowing untreated seed	FSUT		1	1	1	1		1		Wait until after most intense follow-up clearing to decrease potential disturbance	Harwayne et al 2008
Delayed sowing pretreated seed	FST		1	1	1	1		1	1	Treat seed to increase germination success of species requiring heat/smoke cues.	Hall 2016
Reference state	REF	1								Comparison with pristine vegetation after burning	

Table 2. The description of main parameters and the respective settings considered within the model simulations. Parameters are set at the values indicated depending on whether or not the treatment involves an invaded or a reference vegetation state. Further data for rates of vegetation growth and competition as well as equations and calculations included within the model are provided in Supplement S2. E = restio cover, R = resprouting shrub cover, S = non-sprouting shrub cover.

Parameters	Setting	Units of measurement	Set value in restoration treatments	Set value for reference state
Chances for fire to occur	Wildfire option	inverse probability	NA	10
Length of simulation without management	Invaded site	time duration (months)	NA	360
Initial Acacia cover	Invaded site	Percentage cover	70	0
Initial Bare cover	Invaded site	Percentage cover	0	0
Initial Burnt cover	Invaded site	Percentage cover	0	100
Initial E cover	Invaded site	Percentage cover	10	0
Initial R cover	Invaded site	Percentage cover	10	0
Initial S cover	Invaded site	Percentage cover	10	0
Clearing time after initial	First clearing	point in time (months)	2	NA
Clearing period	First clearing	time duration (months)	120	NA
Number of clearing cycles per simulation	First clearing	point in time (months)	3	NA
Management fire time after first clearing	Fire management	point in time (months)	2	NA
Followup clearing time after first clearing	Followup clearing	point in time (months)	12	NA

Table 3. Goodness of fit of models in estimating parameters based on cover of vegetation components, as well as effect on parameters of an increase in native or alien cover. Parameters with less than 20% goodness of fit are not included since they were not considered to be sufficiently explained by cover of vegetation components. For overall effect of vegetation cover on estimated parameters, N = negative effect, P = positive effect, X = neutral effect.

Parameter	model code	GLM model goodness of fit	AIC	acacia cover	native cover	total cover
log total carbon	log C	26%	-831.92	N	N	N
log soil moisture	log Moist	35%	-101.15	N	N	N
ammonium	NH_4^+	38%	1950.9	P	P	P
log nitrate	log NO_3^-	24%	-8.7583	N	N	N
log phosphate	log P	46%	-238.23	N	N	N
restio spp richness	ERich	54%	892.85	N	P	X
resprouting shrub spp richness	RRich	47%	1945.4	N	P	X
non-sprouting shrub spp richness	SRich	27%	2426.1	P	P	P
graminoid spp richness	GRich	30%	2507.2	N	N	N
herbaceous spp richness	HRich	38%	4327.8	P	X	P
restio plant density	EDens	74%	3960.8	N	P	X
resprouting shrub plant density	RDens	76%	4494.8	N	X	X
non-sprouting shrub plant density	SDens	42%	6977	P	P	P
geophyte plant density	BDens	43%	10321	X	P	P
graminoid plant density	GDens	31%	14125	P	X	P
herbaceous plant density	HDens	37%	18782	P	X	X

Table 4. Results of different treatments at the end of 360 months simulated. Cover is expressed by the percentage (%) of the plot area, richness is the average number of species per plot, plant density is number of plants per m^2, soil chemistry is expressed by % for C, P and moisture, and mg/kg for NH_4^+ and NO_3^-. Follow-up cost is calculated in South African Rands. E = restioid shrub, R = resprouting shrub, S = non-sprouting shrub, G = graminoid, H = herb, NH_4^+ = Soil nitrate, NO_3^- = soil ammonia, P = phosphorus, moist = effective soil moisture.

	Cover %				Species richness					Plant Density					Soil chemistry					Treatment cost in Rands	
Treatment	Acacia	S	R	E	E	R	S	G	H	E	R	S	G	H	C	NH_4^+	NO_3^-	P	moist	1 follow-up	3 follow-ups
Reference site	0	22	27	44	3	5	5	2	2	28	13	20	12	11	1.88	16.51	2.65	1.56	0.15	NA	NA
Stack-block SB	9.98	40.91	13.20	6.68	1	2	5	2	2	8	7	21	4	10	2.07	42.95	4.49	3.37	0.47	17505	24277
Burn-block BB	13.72	0.49	13.12	1.05	0	2	1	4	2	1	5	4	5	6	2.17	5.55	5.59	4.81	1.10	44536	85044
Fynbos-sown FS	3.06	80.79	1.44	1.53	2	1	9	1	3	12	5	54	3	19	2.10	83.34	5.38	4.11	0.32	52546	78497
Delayed sowing untreated FSUT	0.31	67.6	2.72	0.9	1	1	6	1	3	8	5	31	4	17	2.15	70.2	5.81	4.37	0.52	52520	73538
Delayed sowing pretreated FST	1.51	65.3	5.93	3.97	2	1	7	1	3	11	6	35	4	15	2.12	67.1	5.27	3.82	0.45	52520	75173

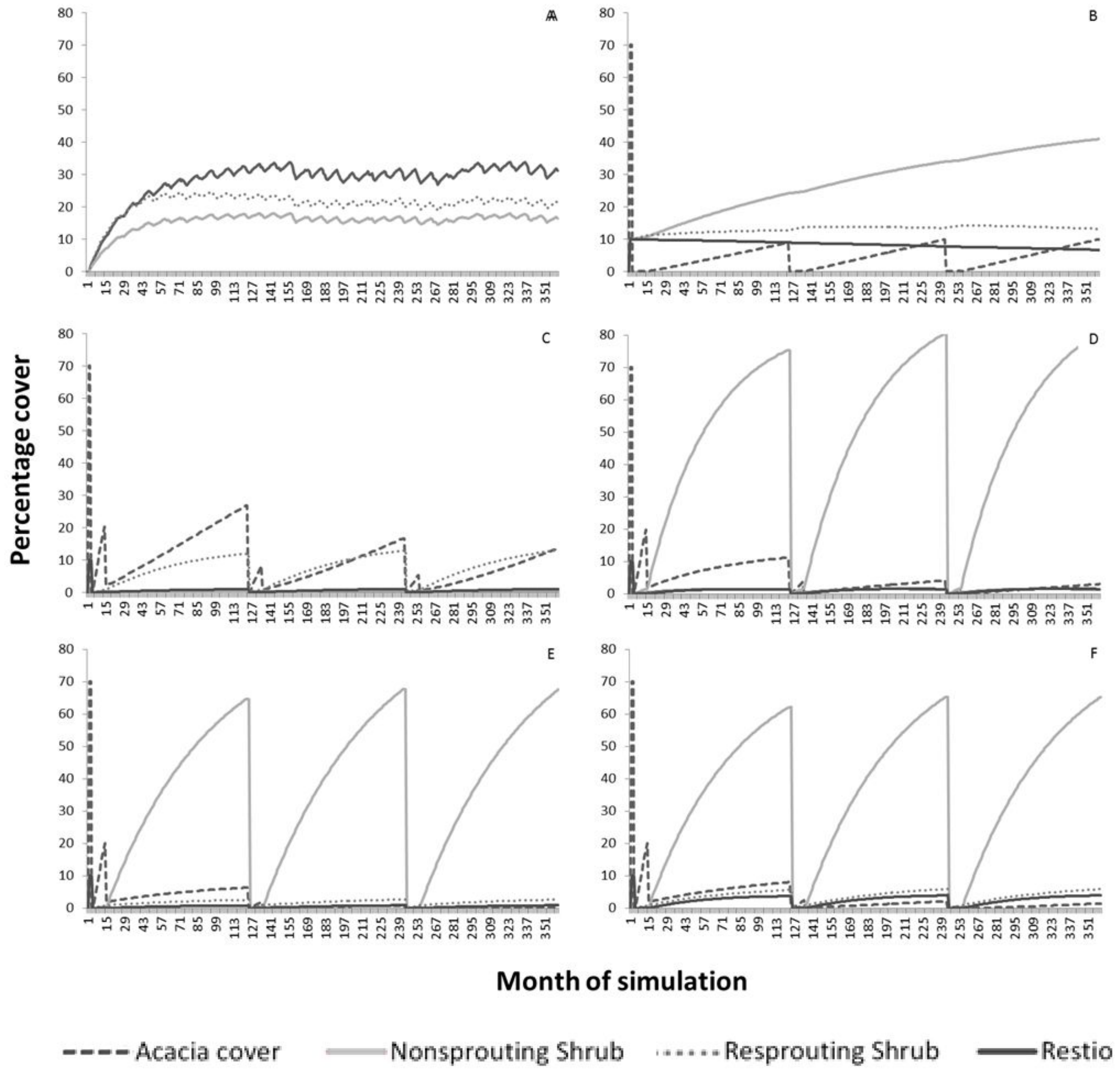

Figure 4. Model simulations of vegetation cover (acacia, non-sprouting shrub cover, resprout cover and restios) throughout 360 months of simulation, including the stochastic occurrence of fires in the reference scenario (simulation with 100 replications), as well as alien clearing and managed fire in relevant scenarios every 120 months. (A) Scenario 0: Reference. (B) Scenario 1: Stack-block. (C) Scenario 2: Burn-block. (D) Scenario 3: Initial Sowing. (E) Scenario 4: Delayed Sowing untreated seed. (F) Scenario 5: Delayed Sowing pre-treated seed.

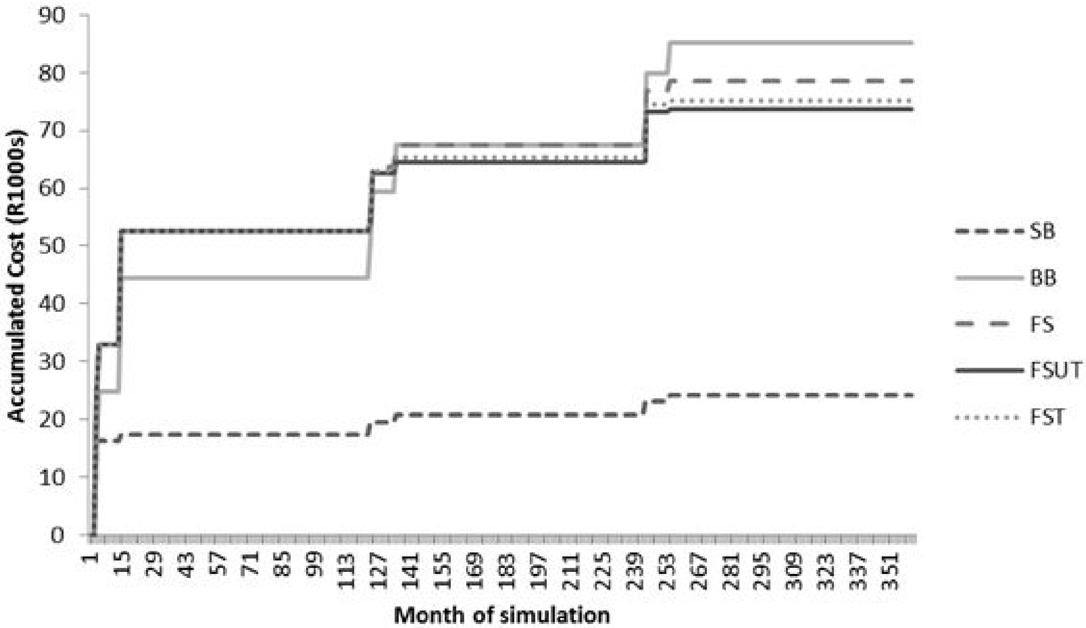

Figure 5. The average expenditure (R1000/ha) predicted for each scenario considered, throughout 360 months of simulation. SB – Stack-block treatment, BB – Burn-block treatment, FS – initial Fynbos-sowing, FSUT – follow-up untreated Fynbos-sowing, FST – follow-up pre-treated Fynbos-sowing.