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Guidelines for plant population offsetting

Improving the effectiveness of biodiversity offsetting

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Executive summary

Biodiversity offsetting is a policy tool used to compensate for impacts on biodiversity from development activities. Current biodiversity offsetting guidelines frequently lack scientific support for choice of appropriate plant population sizes needed to consistently maximise long-term population viability. Use of the ‘precautionary principle’, *i.e.* selecting a population size that is highly likely, but not certain, to be larger than adequate; can inflate the required number of individual plants to ensure population viability. Its current widespread use, however, is not underpinned by rigorous evaluation of plant demography and genetics. This offsetting practice: 1) is done without consideration of the *biology* and *ecology* of a given plant species and 2) risks investing either considerable effort far beyond the point of diminishing returns or, conversely, insufficient effort leading to offset failure. More generally, this practice decreases the effectiveness and success of offsets.

In this report, we have developed science-based guidelines of population offsetting for four different plant groups (eucalypts, *Acacia*, forbs and grasses) of the Brigalow area based on their life-history and ecology. We developed and analysed a demographic simulation model for each plant group. The simulation modelling analysis was specifically done to:

1. Identify key biological traits (traits essential for reproduction and survival) for each plant group.
2. Estimate offset sizes that maximise population viability under different scenarios.

Main outcomes of this study are:

I. Estimated offset ratios (this ratio varies between plant groups), specific recommendations and associated management actions for each plant group to maximise long-term population viability and reduce the possibility of over- or underestimating offset sizes.
II. Mitigating mortality factors (*e.g.* fire, inbreeding depression, weed competition) is as important as choosing appropriate offset sizes to increase offset success.
III. For all plant groups, maintaining population connectivity and gene flow is essential to decrease extinction risk.
IV. Combined management actions to increase spatial availability and genetic diversity increases up to 50 % population viability and population persistence. This is particularly important in short-lived species with self-incompatibility mating systems.

Based on our results, we suggest to:

- apply offset ratios and management actions tailored to each plant group as guidance to do population-offsetting planning
- use modelling and population viability analysis as complementary tools to predict extinction risk
- report demographic data and success rate from offset monitoring to inform future plant population offset planning

- implement research project offsets when levels of uncertainty (*i.e.* lack of biological knowledge of the targeted species) are high to maximise the success of the offset plan.

Biological differences are important considerations for biodiversity offsetting. Guidelines taking such differences into account can help to improve current population offsetting practices by making them more cost-effective as well as increasing the chances of success of plant population offsetting. More generally, science-based policies will help managers and government and state agencies to generate more effective and efficient regulations.

1 Introduction

1.1 Biodiversity offsetting: towards science-based offsetting guidelines

Biodiversity offsets aim to compensate for the losses due to the impact of development activities on biodiversity by generating equivalent ecological gains (Maron et al. 2016) However, the effectiveness of this tool to compensate the losses and generate quantifiable gains is still debatable (Maron et al. 2016; Lindenmayer et al. 2017; May et al. 2017). For example, 30 % of offsets between 2004 and 2015 in Western Australia were found be "*ineffective through non- or inadequate implementation*" (May et al. 2017). A nest-box program intending to offset the clearing of hollow-bearing trees in Southern Australia, which was targeting three threatened species of vertebrates, had low levels of use by targeted species and therefore indicated failure of the offsetting planning (Lindenmayer et al. 2017). There are multiple potential causes for the failure of an offset, however some of the major problems shown in the literature are: 1) poor project planning for offsets, 2) poor reporting and compliance with environmental conditions, 3) unreliable or deficient estimators of offset effectiveness and 4) general lack of realistic offset ratios (Maron et al. 2012, 2016; May et al. 2017). Most of the aforementioned problems are mainly related to technical issues and our inability to effectively restore habitats. In this report we will mainly address the two latter problems related to improving effectiveness of offsets and calculating more realistic offset ratios in plant population offsets.

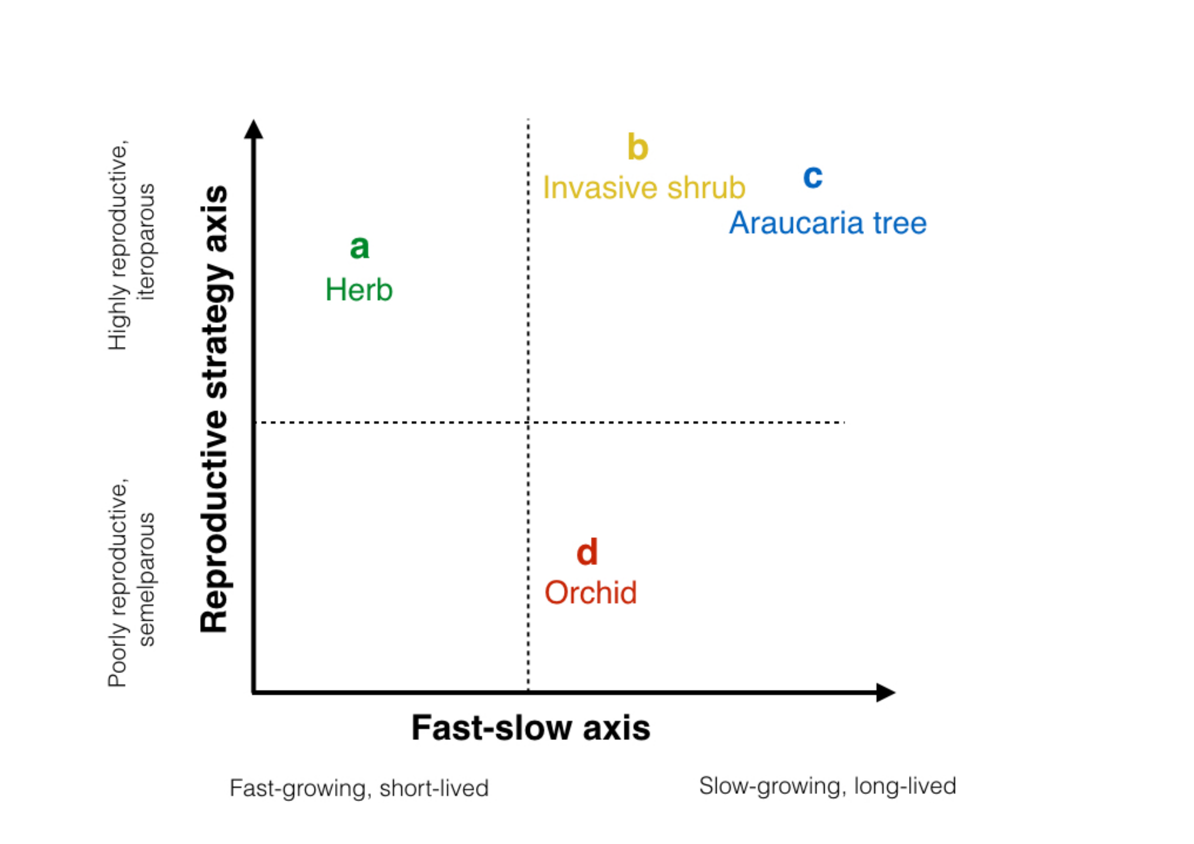
Bridging the gap between science and policy is important to ensure the balance of gains and losses. There are currently no science-based guidelines or adequate estimates for the size of plant populations needed to consistently maximise long-term population viability and local species persistence. Use of the 'precautionary principle' can inflate the required number of individual plants to ensure population viability. Therefore, offset multipliers in plant population offsetting are generally inflated to account for large uncertainty about future extinction probabilities that are not estimated under any rigorous scientific evaluation based on plant demography and genetics. This practice 1) is done without consideration of the biology and ecology of the target species and hence increases risk of extinction, 2) risks investing considerable effort far beyond the point of diminishing returns or on the contrary, it increases the probability of offset failure by underinvesting.

1.2 Population viability analysis and the importance of species biology

Population viability analysis (PVA) has been long used in conservation biology as a method to assess population extinction risk, identify key life-stages as management targets and/or determining likelihood of species persistence among other purposes (Morris and Doak 2002). A wealth of knowledge has been developed in conservation biology using PVAs over decades, which could be harnessed to improve current plant population offsetting practices.

Plant life-history strategy variation

Box 1. Plant life-history strategies can be largely explained across two main axes: 1) The *fast-slow continuum*: includes fast-growing, short-lived plant species (*e.g.* herbs **a**) at one end and slow-growing, long-lived species at the other (*e.g.* trees, **b**) and 2) The *reproductive strategy axis*: with semelparous, poorly reproductive plants at one extreme (**d**) and highly reproductive, iteroparous species at the other end (**a**, **b**) (Salguero-Gomez et al, 2016).



To estimate long-term population viability of any organism it is necessary to consider different factors related to the biology (*intrinsic* factors) and environment (*extrinsic* factors) of the targeted species (see Figure 1). The main biological factors determining average vital rates (birth, death and growth rates) in a population are: genetics, demographic stochasticity and life-history of the species. A lack of understanding of life-history and genetics in a targeted species unavoidably will generate spurious estimates of population viability and hence it will increase the chance extinction and failure of any conservation management program or offset plan. Therefore, to maximise our estimates of long-term population viability and apply more effective offset management plans we require a thorough understanding of the life-history, genetics and ecology of the species impacted.

Habitat quality and different sources of environmental variation (including catastrophes such as droughts and fires) are also crucial factors to consider in population viability analysis. These external factors create temporal variation of vital rates (i.e. survival, reproduction and growth rates) increasing uncertainty and decreasing long-term population viability. Thus, these factors need to be considered when estimating extinction risk based on a good understanding of the habitat and climatic requirements of the target species.

1.3 Grouping species based on their life-histories

Ideally, assessments of population viability would be done individually for each species targeted for population offsetting. This would provide highly specific recommendations to improve population growth and persistence. However, in Australia, as in other, similarly biodiverse regions of the world, information on the life-history traits and ecology of many native plant species remains limited. The resulting uncertainty creates a major problem for the success of plant population offsetting as this information is crucial to decrease extinction risk. To circumvent this problem we can use biological knowledge to group species based on their life-history traits besides incentivising through current policy frameworks to do more scientific research to decrease the knowledge gap. For example, plants can be broadly classified into different life-forms (*i.e.* trees, shrubs, forbs) that have inherent life-history traits associated with each life form (*e.g.* long time to reach maturity is characteristic of trees). It is also possible to quantitatively classify species into different groups according to their life-history strategies (see Box 1) (Salguero-Gómez et al. 2016).

Classifying plant species into groups for plant population offsetting allow us to: 1) make general predictions of extinction risk and population viability (using available demographic data), 2) provide more reliable estimates of offset-ratios and 3) improve offset planning and management actions for each plant group. While such predictions would be less exact than those based on species-specific analysis, they are more feasible given incomplete knowledge of species traits and ecological parameters.

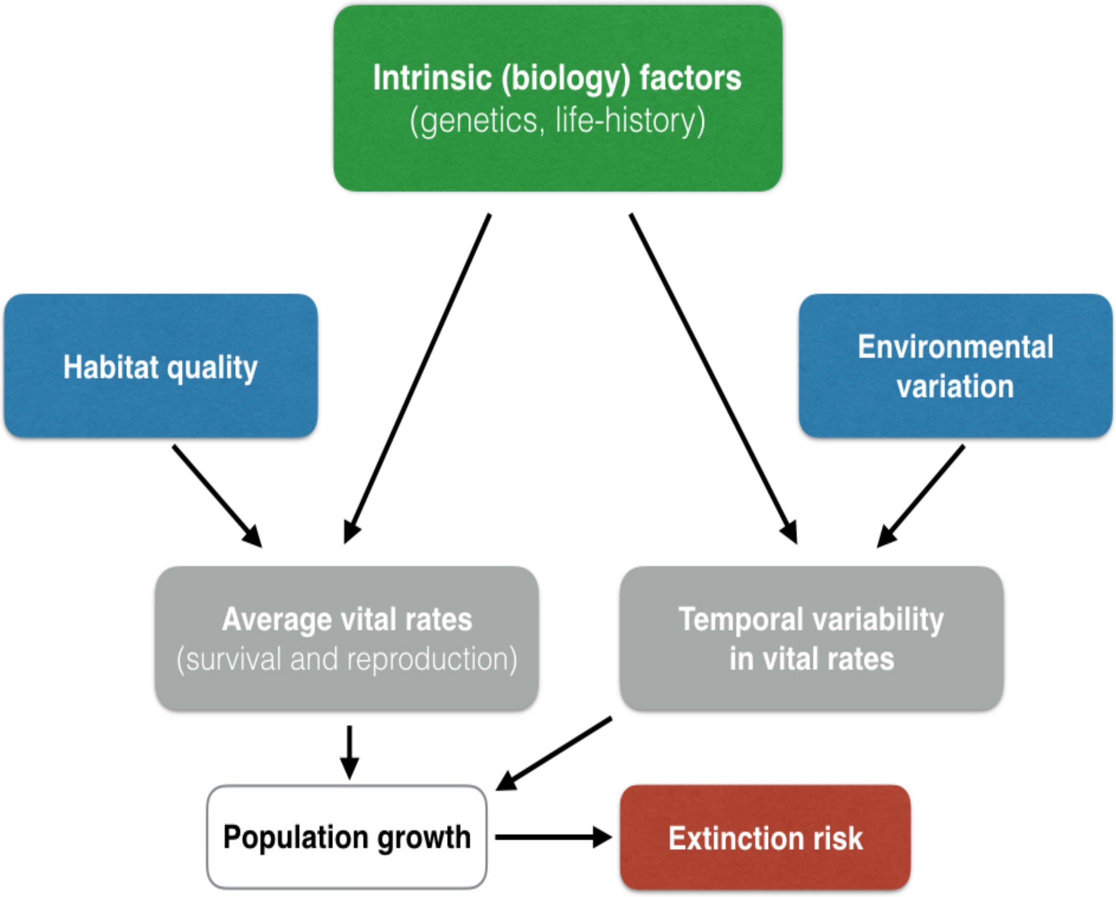


Figure 1 Factors affecting population viability. Intrinsic (green) and extrinsic (blue) factors are both determinant for viability.

2 Objectives

The main aim of the project was to deliver guidelines for several broad categories of plant species to improve the effectiveness of plant population offsetting, inform effective management operations and help developing science-based policies. Taking into account the biology of an individual species will enable more targeted and resource-efficient approaches to conservation management. The main potential benefit of this project aims to improve current practices for offset planting and habitat restoration in Queensland, and especially in CSG areas.

Two specific objectives to achieve the main aim of this project are:

1. **Classification of plant groups and identification of key life-history traits for the species studied**: more-accurate and pertinent estimations of population viability are only possible with good knowledge of the biology and ecology of the species studied. To be able to provide general guidelines we have compiled a list of species of potential concern for the Brigalow region and classified them into several categories based on their life-history traits. We identified which traits are most informative for modelling population viability.

2. **Estimations of population viability for multiple plant categories using the a simulation model**: population sizes, offset ratios and number of populations for biodiversity offsetting can be estimated using a simulation model that considers the ecology, genetics and the different life-history traits identified in the previous objective. Using realistic model parameter values collected from available data and literature, the simulation analysis aims to: 1) conduct a sensitivity analysis for the key life-history traits identified for each plant group 2) Explore the effects of environmental variation (*e.g.* stochastic temporal variation of vital rates).

3 Methods

3.1 Plant groups chosen

We mainly focused on native plant species from the Brigalow area (QLD) (see Table 2), which have been impacted by the CSG development and are either subject to offsetting work or potentially of concern in the future. A stakeholder workshop took place in Brisbane on 24 February 2017, allowing stakeholders from government, industry and the research community to nominate species of interest for population offsetting and classify them into groups of plants based on their biology and ecology. The groups selected by the seventeen participants of the workshop were: eucalypts, *Acacia*, forbs and grasses.

3.2 General population viability model

A spatially and genetically explicit model was developed for each plant group. We assume a spatial grid of 100 x 100 cells, with absorbing boundaries, and each cell (site) can only be occupied by one individual. Each individual has a genome composed of five unlinked neutral loci with five alleles each and, for acacias, forbs and grasses, a self-incompatible (SI) locus. The number of self-incompatible alleles (S alleles) was fixed to ten, except in cases where we studied the effect of S allele diversity. The model assumes diploid genetics and that individuals can act both as pollen donors and as females (Thrall *et al*, 2014). The fraction of sites suitable for occupancy can be varied. At the beginning of each run, genotypes were randomly assigned to each of individual. This means that we randomly chose an allele for each locus with the constraint that individuals must be heterozygous at the SI locus) (see Glossary). These were randomly placed in a subset of the available sites. In addition to site and genotype, the simulation also tracked individual ages. The model assumes no fitness consequences related to inbreeding (i.e. inbreeding depression).

Specific details of the demography and life-history of each plant group, such as presence of seed bank and self-incompatibility, were implemented on specific demographic models (see below). We assume individuals reproduce every year. The model was implemented in C++ using the GNU Scientific Library and is available from the first author on request.

Simulations following population dynamics were run for a period of 500 years. This period of time was considered long enough (much longer than 20 year time frame established in the current policy framework) to obtain more accurate estimations of long-term population viability. For all the analyses (including the sensitivity analysis and exploration of restoration-offset scenarios) we ran 500 replicates for each parameter combination.

The simulation analysis considered biologically sensible parameter values for each group based on published literature. Other parameters of the model were fixed across the different models (see Table 1). To estimate the probability of offset success and effectiveness we used two well-known metrics used in population viability analysis: *log stochastic growth rate* (**λ_s**) and *quasi-extinction probability* (Morris and Doak 2002) (see Glossary). To estimate quasi-extinction probability we fixed the quasi-extinction threshold value to fifty (50) individuals. Other indicators of population viability such as *population persistence* (measured as percentage of simulations that reached the end of the total generation time; i.e. % populations that did not become extinct), mate availability and genetic diversity were also used to evaluate the importance of key vital rates and restoration practices.

3.3 Specific life-history traits considered for demographic models of each plant group

3.3.1 Eucalypts demographic model

We considered the following life-history traits for this group based on available biological information and data: eucalypts are slow-growing, long-lived species with high mortality of early age classes and low mortality of adult reproductive classes. We sampled mortality rates for each age class from a negative exponential distribution: $f(i;\lambda) = \lambda e^{-\lambda i} + m$, where m_i is the mortality rate of age class i, λ is a constant called rate parameter and m is the minimum mortality rate for all age classes. For all simulations we assumed that $\lambda = 0.2$. This assumes that young age classes will have much higher mortality rates than adult reproductive classes. We also assumed that individuals older than 70 years have a higher mortality rate (30 % more) due to senescence. Reproductive maturity was reached at 12 years of age. Eucalypts are characterized as having short distance seed dispersal. We assumed that seeds could only be dispersed up to 4 sites (*i.e.* 400 m) from the parental tree. Mixed mating was assumed, as many eucalypt species are able to self as well. Specifically, we assumed a selfing rate of 30 % (therefore outcrossing of 70%) across the population. Fecundity was assumed to be relatively low ($f = 250$ seeds/individual) due to losses from multiple effects of inbreeding depression, seed insect predation, and seed shedding into unsuitable conditions. Therefore we assumed that eucalypts generally had a low number of viable seeds.

3.3.2 *Acacia* demographic model

We considered the following life-history traits for this group based on available biological information and data: We assumed that wattles generally can live up to 20-30 years and senescence occurs on individuals older than 20 years. Similar to eucalypts we assumed sampled mortality rates for each age class from a negative exponential distribution: $f(i;\lambda) = \lambda e^{-\lambda i} + m$, where m_i is the mortality rate of age class i, λ is a constant called rate parameter and m is the minimum mortality rate for all age classes. For all simulations we assumed that $\lambda = 0.2$. Intermediate levels of survival of early age classes were based on reported values. Reproductive age maturity was reached at 7 years. Wattles are known for having long-distance seed dispersal by animals (*e.g.* birds) and gametophytic self-incompatibility has been found in many species (Kenrick and Knox 1989). Thus, we assumed a gametophytic self-incompatibility mating system. We assumed the individuals could produce large number of viable seeds ($f = 400$ ovules/individual) as well as long seed longevity (i.e. presence of seed bank) (up to 10 years of seed longevity).

Serotiny was also assumed as many *Acacia* species of the Brigalow depend on fire or high temperatures to germinate or mechanical disturbance of the seed coat (Hodgkinson and Oxley 1990). Therefore, low intensity fire increased the probability of seed germination in the model.

3.3.3 Forb demographic model

This most heterogeneous group is composed of a mixture of species, some of which are phylogenetically very distantly related (Asteraceae and Solanaceae, *e.g. Rutidosis lanata*). However, most of them are short-lived but perennial forbs (3-5 years) with a sporophytic self-incompatibility system, meaning they are obligate outcrossers. They consequently require a certain genetic diversity of self-incompatible alleles to allow population persistence, with an absolute minimum of four alleles. We assumed that they have relatively long-distance seed dispersal of up to 40 sites from parental tree and moderate seed germination rates (0.03). We assumed that there is no seed bank, and reproductive age of maturity is reached at 2 years. We considered two different mortality rates between seedling/vegetative (age < 2) and adult reproductive individuals (age > 2).

3.3.4 Grass demographic model

We had to make some strong assumptions for this group given the limited available biological information. We assumed that they are short-lived perennial (5-7 years) species with a gametophytic self-incompatibility system (obligate outcrossers). We also assumed relatively long-distance seed dispersal and low values of seed germination rates (as mentioned by project stakeholders) with no seed bank. Vegetative reproduction and moderate adult survival was also considered because the most important mortality factors (*e.g.* grazing and weed competition) seem to mainly affect adults. Reproductive maturity was reached at 2 years.

3.4 Restoration offset scenarios

We evaluated plant population offset restoration practices used in impacted sites in the Brigalow area by the CSG development. These restoration practices are commonly used when offsets are required for a specific population(s) of a listed vulnerable or threatened plant species.

The main restoration practice is to offset the impacted population by augmenting a pre-existing population of the same species on a degraded site. Multipliers and offset ratios are calculated and applied according to state or federal legislation and current biodiversity offsetting guidelines (Australia. Department of Environment Heritage and the Arts 2009).

We evaluated these scenarios assuming different levels of offset ratios (i.e. offset sizes) on a pre-existing reproductive population in the area (this is particularly recommended for long-lived and/or slow-growing plant species, such as eucalypts and cycads).

3.5 Simulating the effects of genetic diversity and spatial availability in forbs

To test the importance of genetic diversity (*e.g.* sourcing seeds or individuals from multiple provenance) and spatial availability in population viability we peformed a set of simulations with different offset sizes, genetic diversity and spatial availability levels. These two effects were highly relevant to study because: 1) Many forbs are obligate outcrossers (i.e. self-incompatible) and hence these species require high within-population genetic diversity (and gene flow between populations) to ensure mate availability (Pickup and Young 2008; Thrall et al. 2014), and 2) Lack of available space for recruitment in short-lived species can be a serious constraint for population growth.

On one hand, we simulated the effect of increasing genetic diversity on an offset population by increasing the number of self-incompatible (S-alleles) and neutral alleles according to a specific probability. On the other hand, the spatial availability effect was studied by increasing the percentage of available sites in the model for plant recruitment.

3.6 Environmental disturbances

Major environmental disturbances can generate catastrophic events that will impact population viability. Therefore, besides considering demographic stochasticity (*i.e.* variability in population growth arising from sampling random births and deaths in a population of finite size) we also considered stochastic events of environmental disturbances that directly affect survival and long-term population viability, such as fire or competition for space with weeds (*e.g.* Buffel grass). Fire seems to be the most important since it is the Brigalow area is fire-prone. Therefore, we did extensive simulation modeling considering the effects of the fire severity or intensity (*i.e.* measured as percentage of increased mortality rate) and frequency.

Table 1 Default parameter values for simulation modeling analysis of all plant groups.

PARAMETER	VALUE
Lattice size (area)	100 x 100 cells (sites)
Number of alleles of neutral locus	5
Default number of alleles of SI locus	10
Number of generations	500 years
Default initial percentage of occupied cells	25%
Default fraction of safe sites	0.25
Pre-existing population size	250

4 Discussion and Results

4.1 Eucalypts

4.1.1 Sensitivity analysis

Population viability of long-lived species with slow growth is affected strongly by the mortality of early life-stages (i.e. seedlings, juveniles). Young age class individuals are highly susceptible to multiple external mortality factors, such as fires, pathogens, browsing or inter-specific (and intraspecific) competition. Our results show that seedling and juvenile mortalities were determinant for the long-term viability of eucalypt populations. Small changes of seedling and juvenile mortality (< 10%), but not fecundity (*i.e.* successful germinant recruits per individual) highly affected reproductive output, population persistence and growth (Figures 2 and 7). Another life-history trait that was important for viability of eucalypts, although less important than seedling/juvenile mortality rate, was seed establishment rates, which resulted in a greater than 20% reduction of the number of reproductive individuals at rate 0.02.

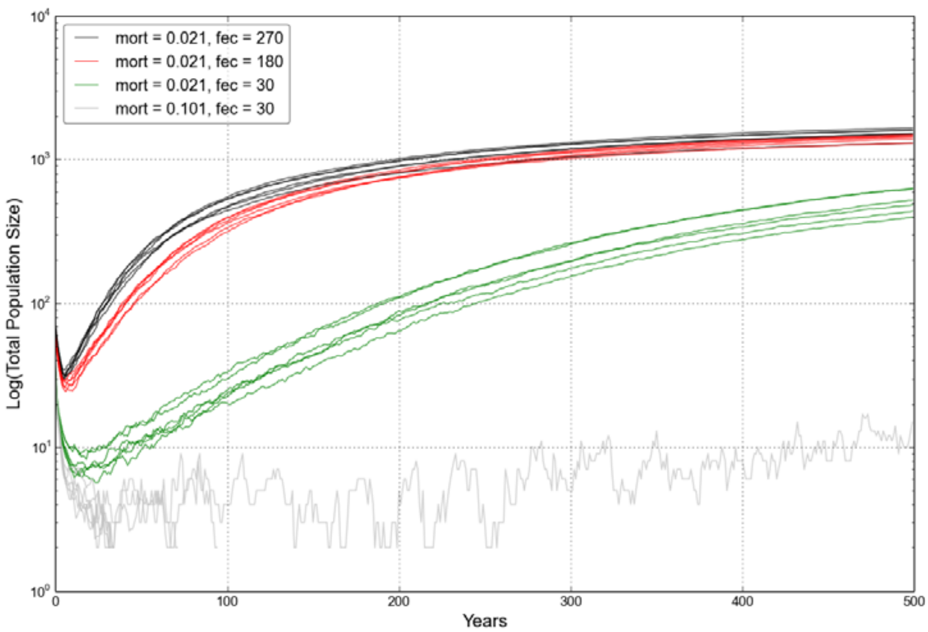


Figure 2 Temporal dynamics for different seedling mortality and fecundity rates in eucalypts. Coloured lines represent examples of temporal trajectories for each offset size- seedling mortality combination.

Inbreeding depression, a relatively common problem in eucalypts, which nearly always possess mixed-mating systems (Hardner & Tibbits, 1998), is also very likely to cause mortality of young age classes, as well as result in decreased fecundity (i.e. low seed viability). However, overall fecundity tends to be high in eucalypt species because they can produce, on average, thousands of seeds per year.

Offset sizes in a pre-existing population were not as important for decreasing extinction probabilities and increasing log stochastic population growth (**λ_s**) as seedling/juvenile mortality rates (see Figure 3). Importantly, only when seedling mortality rate was below 0.05 (< 77%) we observed a strong effect of offset size (Figure 3) and best results were found when offset ratio was ten times the size of the initial population (10:1).

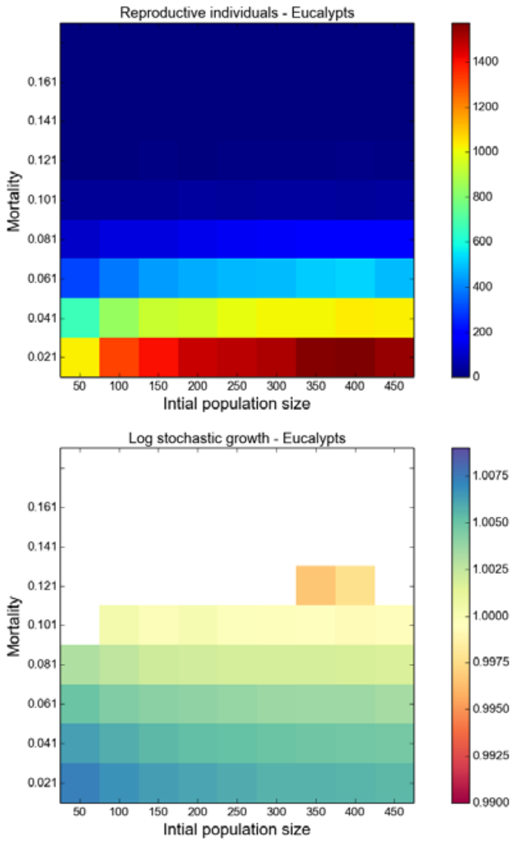


Figure 3 Effect of offset size and juvenile mortality rate on log stochastic population rates and total number of reproductive individuals. Top panel: average number of reproductive individuals. Bottom panel: Log stochastic growth rate (λ_s). Blank spaces on bottom panel represent simulations where most populations went extinct.

However, mitigating and controlling for mortality factors (*e.g.* fires, pathogens, inbreeding depression, weeds) might be more effective than using large offset ratios (*e.g.* 10:1).

4.1.2 Environmental disturbances – effects of fire on population viability

Disturbances (*e.g.* fire severity and frequency) had a dramatic effect on population viability of eucalypts; therefore they are an important management consideration. More specifically, we found that population extinction risk (based on low log stochastic population growth, $\lambda_s < 1$) (see Figure 4) is very high if fire severity (*i.e.* intensity of the fire potentially produced by, for example, high ground fuel loads from invasive weeds (Butler and Fairfax 2003)) is higher than 10-25% and the frequency of fire events is higher than 15-20 % per year. Although low to moderate levels of fire could be beneficial for seed germination of several plant species of the Brigalow area, the elevated presence of weeds such as Buffel grass could imperil the viability of eucalypts.

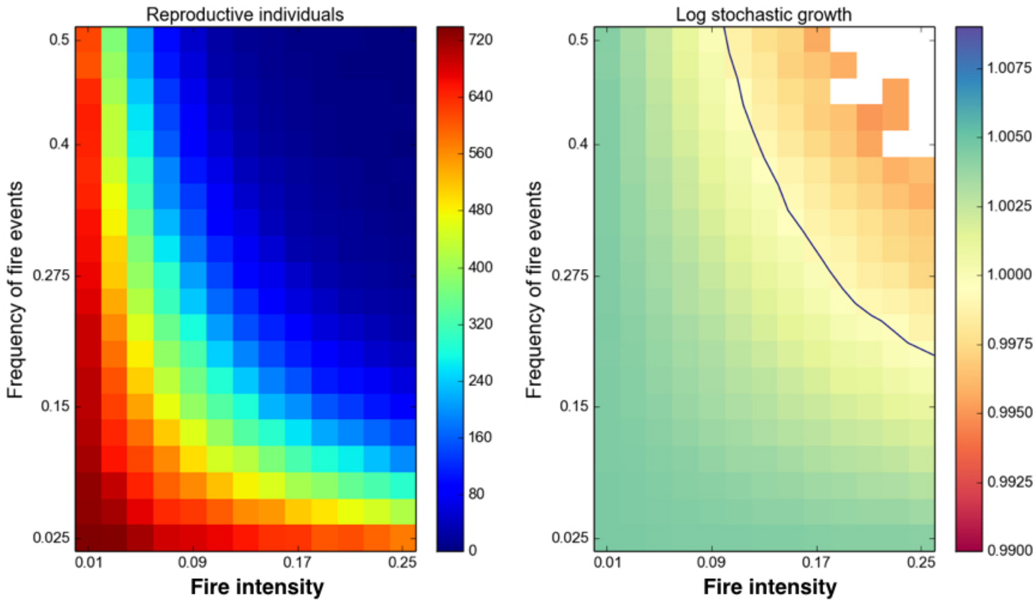


Figure 4 Effects of fire frequency and severity on eucalypt's population viability. Left panel shows average number of reproductive individuals and right panel shows log stochastic growth rate (λ_S). Extinction threshold line ($\lambda_S < 1$) is shown in dark blue (right panel). Blank spaces on right panel represent simulations where most populations went extinct.

4.1.3 Simulating offsets on pre-existing population

We simulated the offsetting of a eucalypt population on a pre-existing population under high seedling/juvenile mortality as reported from natural populations. Specifically, we used the following background seedling/juvenile mortality rates: m_s = 70, 75 and 78%. We also explored the effect of adding different offset sizes (N = 100, 300, 500, 700). We found that there was always a large positive effect of offsetting (adding new individuals to the population) on a pre-existing population composed of high number of reproductive individuals, particularly when mortality was 70% (Figure 5).

The short-term positive effect of offset size declined strongly if seedling mortality was higher than 70% (Figure 5). Large amounts of viable seeds are therefore necessary to ensure survival of the next cohort given that seedling mortality can be very high under natural conditions (Henry and Florence 1966), with fire and browsing some of the most important seedling mortality factors.

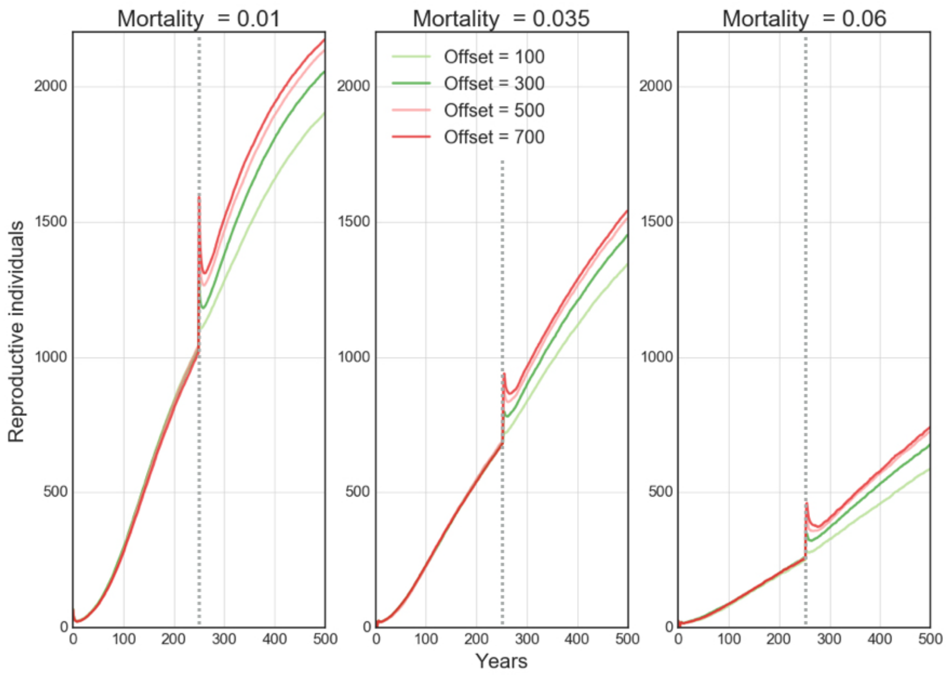


Figure 5 Simulations of offsets under different seedling mortality rates and offset sizes in eucalypts. Left panel: seedling/juvenile mortality rate m_s = 0.01 (70 %). Middle panel: seedling/juvenile mortality rate m_s = 0.035 (75%). Right panel: seedling/juvenile mortality rate m_s = 0.06 (78 %).

4.2 *Acacia*

4.2.1 Sensitivity analysis

Acacia species are characterised by their high fecundity (i.e. large number of viable seeds) and long seed longevity (*i.e.* presence of seed bank). We detected two key vital rates of acacias: adult mortality and seed establishment rates. The results show that adult mortality seems more sensitive than seed establishment rates indicating drastic decline of log stochastic growth rate when adult mortality rate is higher than 25 % (see Figure 6). However, maximum growth is reached when adult mortality is less than 10% for a wide range of seed establishment rates.

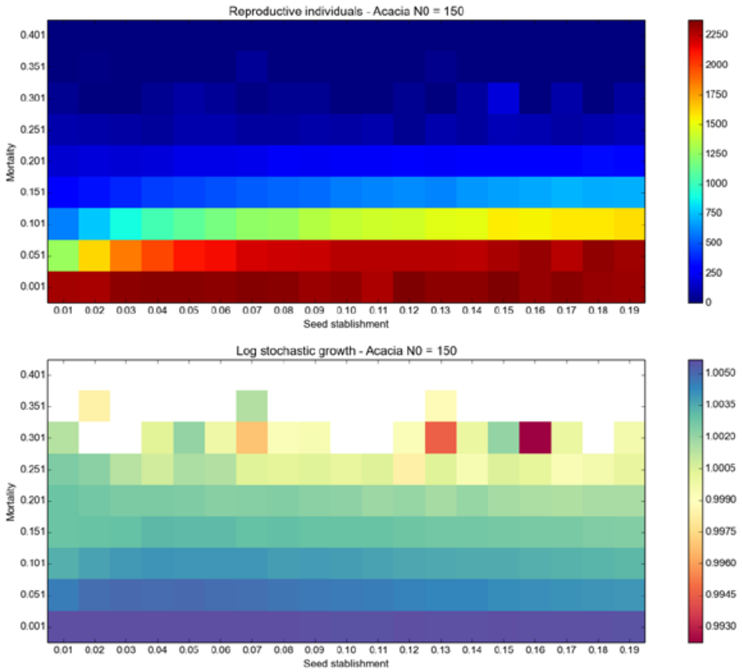


Figure 6 Relationship between *Acacia* adult mortality and seed establishment rate on number of reproductive individuals and log stochastic growth. Blank spaces on bottom panel represent simulations where most populations went extinct.

In simulated scenarios where *Acacia* seed longevity and adult survival rates are drastically reduced, long-term population growth can rapidly drop to critical extinction threshold levels if facing large environmental disturbances (*e.g.* high intensity fire). Offset size has a positive effect on the population viability; however, contrary to the eucalypt group, small increases of offset size already highly augmented the number of reproductive individuals and decreased the probability of quasi-extinction (Figure 7).

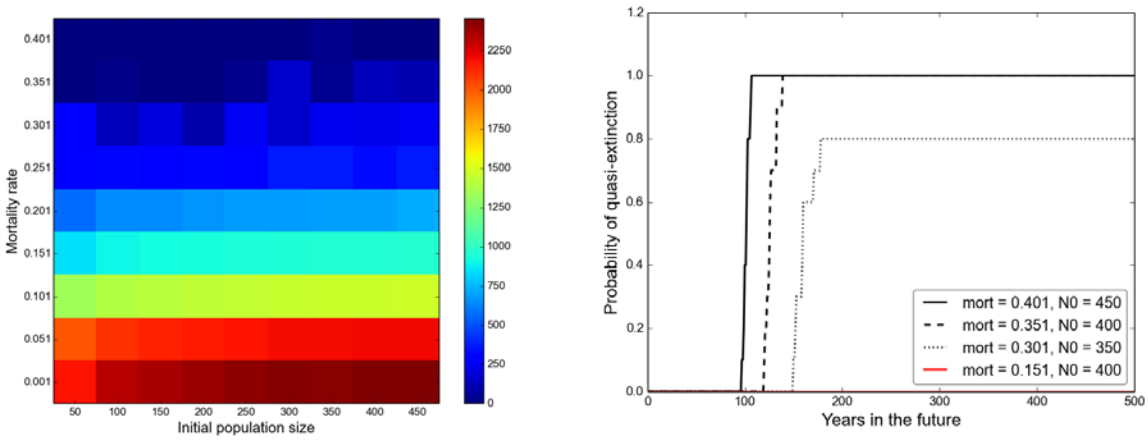


Figure 7 Effects of offset size (N0) and adult mortality rate (m) on the number of reproductive individuals and log stochastic growth rate in *Acacia*. Left panel: average number of reproductive individuals. Right panel: Probability of quasi-extinction probability. Each line describes the cumulative probability of quasi-extinction for different

mortality rates and offset sizes. Note that for m = 0.151 and N0 = 400 (red line) probability of quasi-extinction as zero.

Thus, similar to the findings of the eucalypt group, external mortality factors can have also serious consequences on population viability. However, the presence of seed banks and high fecundity make this group particularly resilient to disturbances and they are well known pioneer species. Offset ratios might not need to be as large as for eucalypt species if appropriate management is applied to the restored offset site (i.e. weed management, fire control) given the resilience of species with these characteristics to disturbances (offset size was not determinant for quasi-extinction probability). Therefore, according tot he analysis offset ratios of 4:1 or higher can already maximise long-term viability. Similarly to eucalypt species, mitigation and control of external mortality factors might be a more effective management action for population viability than propagating seedlings.

4.2.2 Environmental disturbances – Effects of fire on population viability

Serotiny was also considered (some *Acacia* species increase their seed germination rates in the presence of low intensity fires) and, as expected, it showed that for low levels of fire frequency and severity, there is a positive effect on population growth. Although fires with high severity and frequency had damaging effects on *Acacia* population viability, they did not decrease log stochastic growth rate to critical levels below the extinction threshold ($\lambda_s < 1$) (Figure 9). This indicates that fire management is a good option to manage restoration of *Acacia* serotinous species if applied with caution.

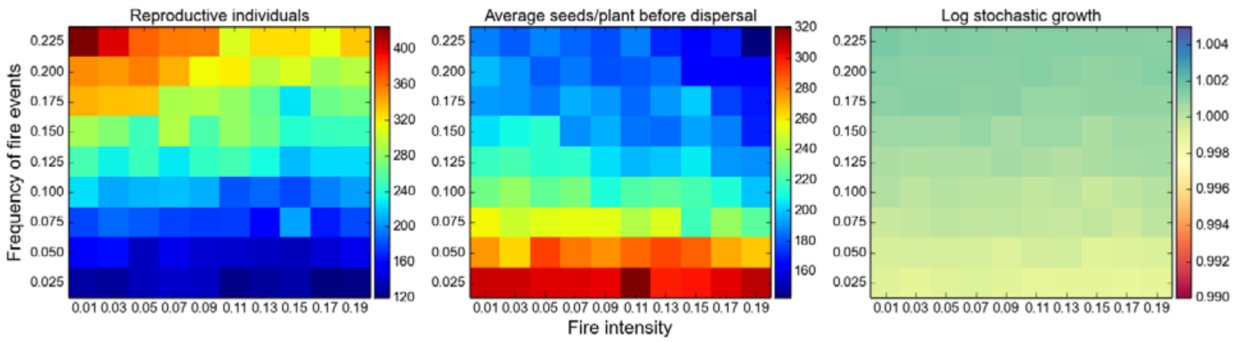


Figure 8 Effects of fire on reproductive individuals, average viable seeds and log stochastic growth rate in *Acacia*. Left panel: average number of reproductive individuals. Middle panel: average number of seeds per plant. Right panel: Log stochastic growth rate.

4.3 Forbs

4.3.1 Sensitivity analysis

Species with self-incompatibility systems, such as many species of the *Asteraceae* family, are highly sensitive to disturbances and habitat fragmentation. We found that adult mortality was the key vital rate driving long-term population growth of this group of short-lived species.

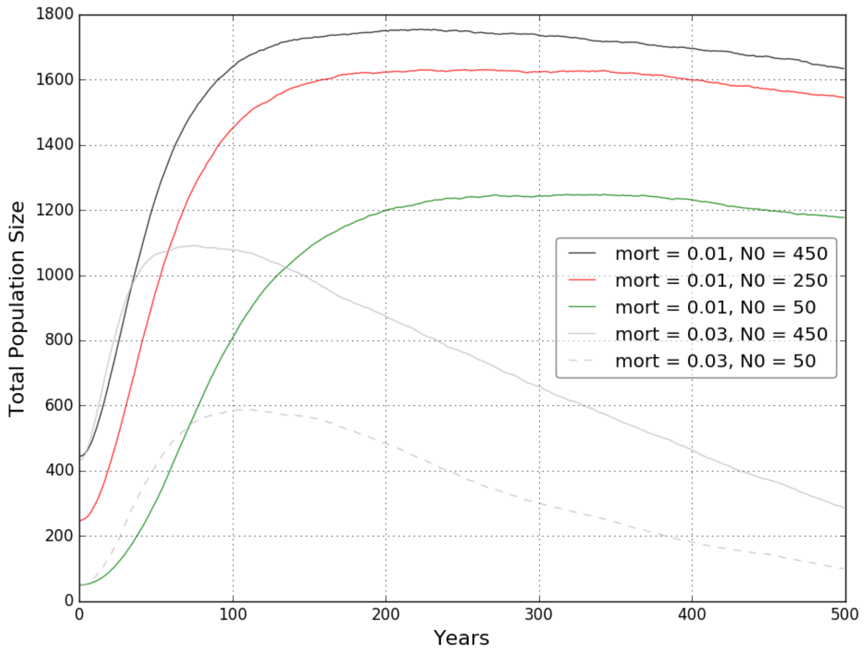


Figure 9 Temporal dynamics of average total population size of forbs under different adult mortality rates and offset sizes.

Contrary to eucalypts and *Acacias*, offset sizes (which determined initial population sizes) were more critical to obtain low quasi-extinction probabilities. More specifically, low offset sizes (lower than 300 individuals) had very low persistence and long-term growth, however gradual increases of offset sizes greatly improved population viability (Figure 9). Therefore, offset ratios for plants with these life-history characteristics will tend to be high (> 5:1) and propagation of seedlings seems a reasonable restoration strategy to offset impacted populations.

4.3.2 Environmental disturbances – Effects of fire on population viability

High levels of disturbances produced by fire can have serious effects on population viability by rapidly reaching extinction thresholds. We found that the effects of fire notably reduced population persistence even for low frequency fires (2.5 % / year), but more importantly the combination of moderate fire intensity (~ 0.09) and increased fire frequency (>25%) takes forb populations to the brink of extinction very rapidly (Figure 10). This shows that forbs are more sensitive to fire catastrophes than the eucalypt and *Acacia* groups.

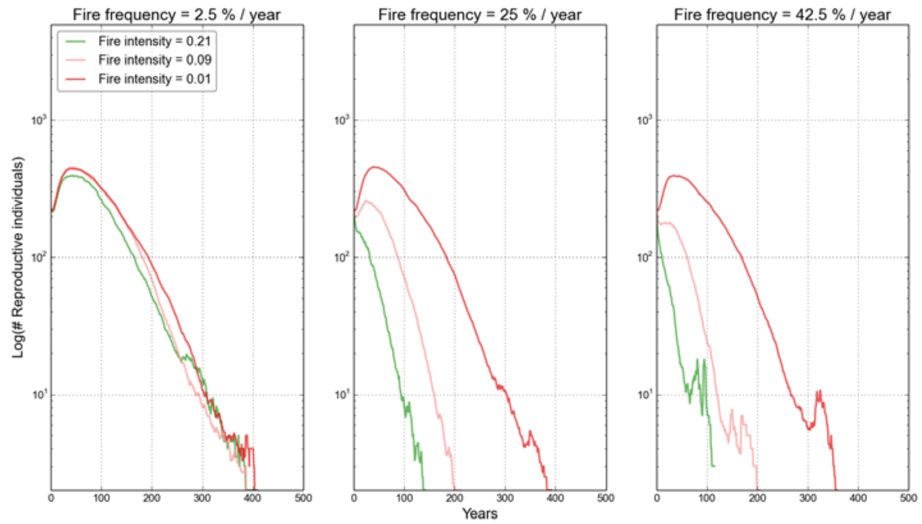


Figure 10 Effects of fire intensity and frequency on the average number of reproductive individuals in forbs. Left panel: fire frequency = 2.5%. Middle panel: fire frequency 25%. Right panel: fire frequency 42.5%. Each coloured line represents an average population trajectory for different fire intensity values (0.01, 0.09, 0.21).

4.3.3 The effects of increasing genetic diversity and spatial availability on viability of forbs

Results show that there was at least a 50% increase of total population size when we increased genetic diversity by 10%. This shows the importance of introducing genetically diverse individuals into offsets for self-incompatible species (Figure 11). The increase of genetic diversity also rapidly increased the average number of viable seeds per plant as a result of the increase of mate availability and this effect was greatly improved by large offset sizes (7:1) (Figure 12). Interestingly, increasing spatial availability (*e.g.* removing Buffel grass) proved to be very effective as well, it increased population persistence by 100 years (Figure 11).

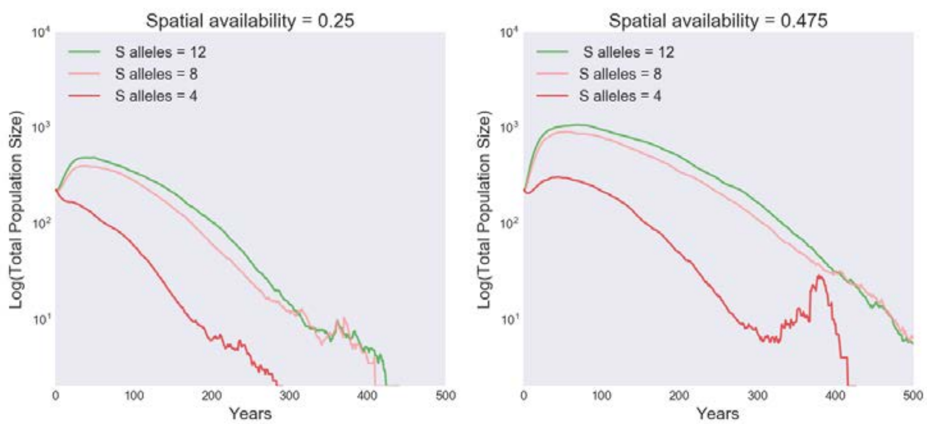


Figure 11 Effects of spatial availability and genetic diversity on average total population size in forbs. Left panel considers an increase of 25% of spatial availability and right panel a 47.5% increase of spatial availability. We also considered different levels (low, intermediate and high) of initial genetic diversity of SI alleles: S alleles = 4 (red), S alleles = 8 (pink) and S alleles = 12 (green).

We also simulated gene flow from other populations. It dramatically increased (>70 %) mate availability and persistence. For example, simulations have shown that assuming gene flow of self-incompatibilities (SI) alleles from other populations generated lower quasi-extinction probabilities than scenarios without gene flow. This corroborates previous findings demonstrating the importance of gene flow between populations of SI forbs (Thrall et al. 2014).

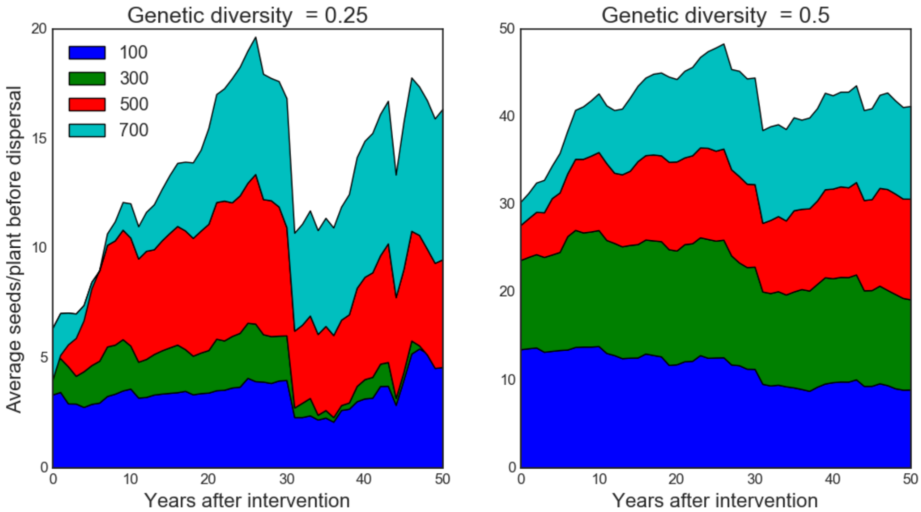


Figure 12 Effect of genetic diversity and offset size on average seed per plant before dispersal fifty years after implementing an offset on a pre-existing population of forbs. Left panel considers an increase of 25% and right panel of 50% of genetic diversity.

4.4 Grasses

4.4.1 Sensitivity analysis

The key vital rate for the grasses group was seed germination rates based on published studies and conversations with project stakeholders. However our results did not show that this trait was crucial, likely because of the lack of available biological information and demographic data. The analysis with the grass model showed very similar results as the forbs analysis. Changes to fecundity resulted in little changes to log stochastic population growth given the large amount of seeds produced, seed longevity and large role of vegetative reproduction. However, low rates of adult mortality rate and transition from seeds to seedlings largely impaired population growth according to our analysis. Offset size did not have a dramatic effect on population viability when seed germination and adult mortality rates were moderately high (> 0.1) (Figure 13). This means that controlling and mitigating the negative effects of fire and weeds or other potential competitors might be determinant for the persistence of offset populations.

This group proved to be problematic due to the lack of ecological and biological information about some of the targeted species (*e.g. Homopholis belsonii*). Therefore, our analysis has high uncertainty on our predictions of population viability and offset ratios, and therefore we recommend more research on this group to enable more precise predictions and recommendations.

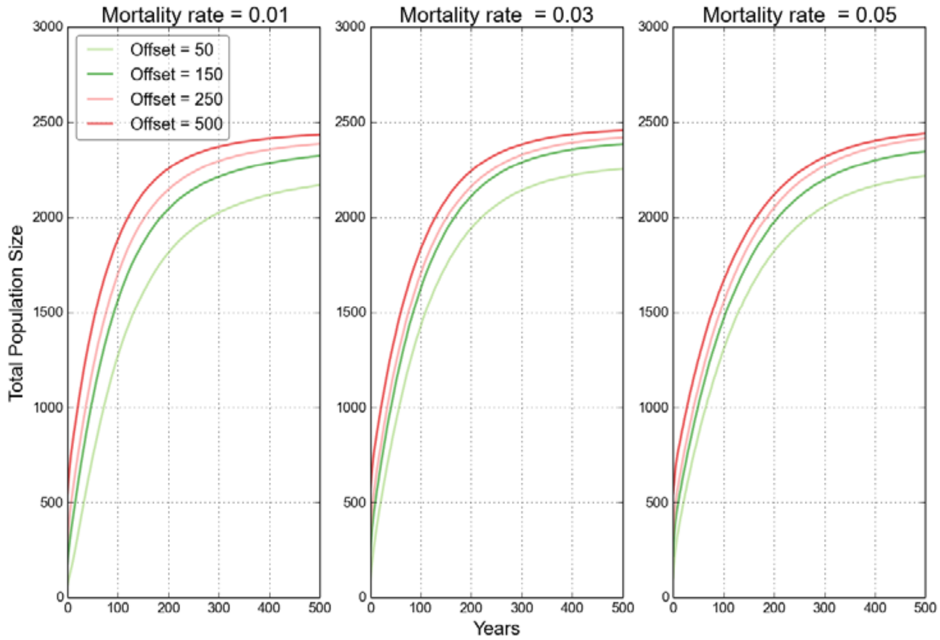


Figure 13 Temporal dynamics of total population size under different offset sizes and adult mortality rates in grasses. Left panel: adult mortality rate $m_s = 0.01$. Middle panel: adult mortality rate $m_s = 0.03$. Right panel: adult mortality rate $m_s = 0.05$. Each panel shows the trajectory of offset sizes (N0): 50, 150, 250 and 500.

5 Specific population offsetting recommendations for each group

Based on the simulation analysis and relevant ecological literature for each group we make these specific recommendations:

Eucalypts:

1. High levels of mitigation and control of external mortality factors (i.e. any factor that might decrease survival of young age classes, such as fire, weeds and/or browsing) on pre-existing populations present at offset sites might be more effective than using large offset ratios (*e.g.* 10:1). This means using large offset ratios are not effective restoration strategies for long-term viability; ensuring the survival of young age classes is more critical.
2. We recommend minimising impact on large populations with numerous reproductive individuals, if it can be avoided, because slow growing species and especially those susceptible to inbreeding depression might take hundreds of years to recover to their initial state if fragmented.
3. Restoration offset ratios equal to or higher than 4:1 might be sufficient to maximise viability considering previous recommendations (1,2).

Acacias:

1. Control and mitigation of weeds and highly frequent and severe fire events should be considered for management of restoration offsets of *Acacia* as these factors can directly decrease longevity of seeds and survival of reproductive age classes. However, moderate fire regimes are likely to be beneficial in serotinous species in augmenting seed germination.
2. Propagation of seedlings and juveniles on offset sites with pre-existing populations could be an effective restoration strategy generating positive results in a short-time scale (~ 10 years) assuming large seed-banks and high fecundity.
3. Restoration offset ratios equal to or higher than 3:1 might be sufficient to maximise viability considering previous recommendations (1,2).

Forbs:

1. Short-lived insect-pollinated herbs with a self-incompatibility system (obligate outcrossers) will benefit from having multiple offset sites (populations) that are spatially connected (relatively close) to improve gene flow among them. This will augment genetic diversity and mate availability, and hence decrease the probability of reaching extinction thresholds generated by positive density-dependence (Allee effects). We specifically recommend at least three offset sites connected spatially or closed to existing healthy populations.
2. Control and mitigation of weeds and fire should be considered for management of restoration offsets of insect-pollinated forbs as these factors decrease survival and reproduction of reproductive individuals.
3. Population offset sites located in highly fragmented landscapes might experience problems of poor pollination service which will have direct consequences on mate availability and

reproduction. Therefore, carefully selecting offset sites is a priority for a successful restoration offset in insect pollinated forbs.
4. Propagation of seedlings and juveniles on offset sites without pre-existing populations, but connected to other populations, could be an effective restoration strategy generating positive results in a short-time scale (~ 5 years) assuming low adult mortality.
5. Restoration offset ratios equal to or higher than 5:1 might be sufficient to maximise viability considering previous recommendations (1,2,3,4).

Grasses:

1. More research about the genetics, life-history and ecology of this group is needed to make effective recommendations for this group.
2. Control and mitigation of weeds and fire should be considered for management of restoration offsets of grasses as these factors decrease population growth. Assuming low seed germination rates, as reported by ecologist working with native grasses of the Brigalow area, more thorough understanding of their biology is necessary to inform successful restoration offsets.
3. Propagation of seedlings and juveniles on offset sites without pre-existing populations, could be an effective restoration strategy in a short-time scale (~ 5 years) assuming low impact of weeds and fire.
4. Restoration offset ratios equal to or higher than 5:1 could be sufficient to maximise viability considering previous recommendations (1,2), although uncertainty is high in this group and hence more research is needed.

Table 2 Main recommendations of plant population offsetting for each groups studied.

Plant group	Key vital rates	Main threats	Offset ratios	Main recommendation
Eucalypts	Mortality of early age classes	Fire, browsing, inbreeding if fragmentation is severe	≥ 10:1	Mitigation and control of external mortality factors on offset sites with pre-existing populations more important than propagation. This is particularly important for young age classes.
Acacia	Adult and seed mortality	High intensity fire	≥ 4:1	Fire regime controls are important for viability of this group. Offsets preferably close to other populations.
Forbs	Adult mortality	Habitat fragmentation, fire, weeds	≥ 7:1	Multiple offset sites with high connectivity are recommended as well as control for external mortality factors affecting reproductive individuals. Mixing provenance and removing weeds is highly recommended. Propagation can be effective.
Grasses	Seed germination rates and adult mortality	Weeds, fire	10:1	More research needed, high uncertainty. Weed and fire control and mitigation necessary to ensure population viability. Propagation could be effective, however uncertainty is large.

6 General recommendations for plant population offsetting

These are some general recommendations that we think should be considered before planning a plant population offset:

1. We always found better results when offsetting was done on a pre-existing reproductive population (also known as population augmentation). This was particularly important for slow-growing and longevous species (eucalypts).
2. Offset sites should be closely connected to other populations allowing gene flow between them. This is essential to avoid the negative effects of inbreeding and particularly important for obligate outcrossers.
3. Mixing provenances is, however, not always beneficial (*e.g*. *Solanum johnsonianum)* (Shapcott et al. 2017) in forbs. Although, mixing provenances is recommended under the assumptions made in our model, we recommend to obtain data on local adaptation, population genetics, outbreeding depression and polyploidy where possible.
4. Reporting demographic data and success rate from offset monitoring. We recommend making available whenever possible data related to the progress and status of plant population offsets. For example, a large database available across all Australia containing information about demographic data would be extremely valuable to improve the effectiveness of future offset projects (as implemented in Western Australia with the Environmental offset register).
5. Implementing research project offsets (as implemented in Western Australian Offset Guidelines) when levels of uncertainty are high (*e.g.* Ooline). This would be particularly useful when there is little available biological information for the targeted species and therefore the risk of offsetting failure is high.
6. We recommend demographic modelling and population viability analysis whenever possible to improve the effectiveness of offsetting planning. Modelling work could also help to evaluate counterfactual scenarios (what is likely to happen if no action is taken?) and alternative management strategies.

7 Future directions and limitations

Our models did not consider climate and other environmental variables (*e.g.* annual precipitation, soil nutrients) related to habitat quality (Figure 1) for plant population viability. This is because the focus of our analysis was to study the demography and genetics of the different plant groups. However, these ecological factors are important for plant population viability and they need to be evaluated and considered along with the suggested recommendations presented here. Similarly, due to complexity of the model, we ignored the effects of inbreeding depression on population viability. We think that including the effects of inbreeding depression on the models developed here should be the next step to improve our predictions, which can be particularly important for certain plant groups (*e.g.* eucalypts). The effects of inbreeding depression will be most marked for fragmented populations that produce predominantly inbred seed. In species such as eucalypts which are highly fecund, there would normally be enough outcrossed seed for losses of inbred individuals to not be limiting to population viability.

Another important and logical extension of this work would be to include other plant groups (*e.g. Proteaceae*) and specific case studies (*e.g.* Ooline or cycads) not consider here, to increase our knowledge and recommendations for plant restoration and population offsetting. Finally, the results of this work have an associated uncertainty and hence it is important to consider our recommendations with caution. To improve the estimations and predictions presented in this report future work will need to include more biological information and demographic data for each plant group, as well as data related to offset success.

8 Conclusions

To increase the effectiveness of restoration and offsetting practices it is necessary to increase our knowledge of the biology and ecology of plants and animals. Our analysis clearly shows that considering biological differences between plant groups produced different predictions and recommendations to maximise viability for population offsetting. We have simulated and analysed a broad range of conditions and environmental disturbances that might impact the population viability of the plant groups studied in the Brigalow area. The results and recommendations that we have obtained from the modelling work could be applied more generally to other plants from Australian semi-arid regions where fire or other mortality factors are prevalent (*e.g.* droughts, weed competition). In the future it would be necessary to include more plant groups and specific cases (*e.g.* orchids) to refine and expand our recommendations. The specific and general recommendations that we suggest here aim to improve the effectiveness of current plant population offsetting policies by maximising long-term population viability and making it more cost-effective. Population viability analysis and demographic modelling are recommended as powerful tools to evaluate the success of offsets and management actions. We think these guidelines are the first steps towards science-based policies that will help managers and government and state agencies to generate more effective and efficient regulations and targets for conservation.

Glossary

Life-history: is the pattern of survival and reproduction, along with the traits that directly affect survival and the timing or amount of reproduction.

Population viability analysis (PVA): is a range of tools to do species-specific risk assessment and probability of extinction, which is frequently used in conservation biology.

Log stochastic growth rate: the arithmetic mean of the log ratios of population sizes in adjacent years. It is used to predict long-term population growth.

Probability of quasi-extinction rate: probability that a population will fall under certain extinction threshold.

Inbreeding depression: is the reduction of biological fitness in a given population as a result of inbreeding, typically resulting in poor growth and survival. Many plants, including eucalypts, are capable of self-mating, which causes a particularly severe form of inbreeding.

Self-incompatibility: is a general term for several genetic mechanisms in angiosperms, which prevent self-fertilization and thus encourage outcrossing and allogamy.

S locus: is the gene that controls the self-incompatibility mating system. The S locus has many different alleles (S alleles).

Offset multipliers: are ratios between damaged and compensated amounts (areas) of biodiversity.

Semelparous: species characterized by a single reproductive episode before death.

Iteroparous: species characterized by multiple reproductive cycles over the course of its lifetime.

Absorbing boundaries: is a condition for the dispersal or movement of individuals across the landscape (lattice) of the model where individuals that go beyond the boundaries or limits of the lattice are lost from the model; *i.e.* beyond which propagules are essentially lost from the system.

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