Effect of removal of an invasive species, *Acacia mearnsii,* on plant species diversity in a shola-grassland ecosystem

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Certificate

This is to certify that this dissertation entitled “Effect of removal of an invasive species, *Acacia mearnsii,* on plant species diversity in a Shola-grassland ecosystem” towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents original research carried out by Ms. Mithila Unkule at the National Centre for Biological Sciences, Bangalore under the supervision of Dr. Mahesh Sankaran, Associate Professor, Ecology and Evolution during the academic year 2016-2017.

Mithila Unkule

Dr. Mahesh Sankaran

Declaration

I hereby declare that the matter embodied in the report entitled “Effect of removal of an invasive species, *Acacia mearnsii* on the plant diversity in a Shola-grassland ecosystem” are the results of the investigations carried out by me at the National Centre for Biological Sciences, Bangalore under the supervision of Dr. Mahesh Sankaran and the same has not been submitted elsewhere for any other degree.

Mithila Unkule

Dr. Mahesh Sankaran

Abstract

Species invasions have become a global threat to native biodiversity in the past couple of centuries. Getting rid of invasive species from an ecosystem is a difficult task, owing to their aggressive nature; but there are studies being carried out throughout the world for the restoration of invaded spaces. The most common method used to restore native ecosystems is the manual removal of invasive species.

Acacia mearnsii, or black wattle, is one such invasive tree species which has invaded the high-altitude grasslands of the shola-grassland ecosystem in the Nilgiris, and the Tamil Nadu Forest Department has been taking efforts to restore these grasslands by clearing wattle trees (cutting them down one site at a time, revisiting it every 2-3 years). This study attempted to quantify changes in plant species richness and cover in grasslands over time, as well as changes in soil carbon and nitrogen content, following the clearing of wattle. This was done by sampling (a) species richness, (b) vegetation cover, and (c) soil carbon and (d) nitrogen of sites that have been cleared of wattle over the past five years.

It is seen that the vegetation cover of grassland species in wattle cleared areas is higher than that in intact wattle sites. However, there is not much change in the species richness across different sites, wattle cleared, or intact. This suggests that the wattle patches support most grassland species, but do not give it a conducive environment to spread. Once wattle is removed, grassland species spread and occupy the cleared areas. The richness and cover of grassland species in all wattle cleared sites is much higher than richness and cover of shola or invasive species, indicating that the regeneration of flora after wattle removal is dominated by native grassland species. The soil carbon and nitrogen has not change across years since wattle removal. However, there seems to be an unexpected change in species richness, cover as well as carbon and nitrogen across the two elevations which were sampled. This could be due to factors that were unaccounted for, and needs to be investigated further to get a better understanding of the system.

Acknowledgements

I would like to extend my heartfelt gratitude to Dr. Mahesh Sankaran for giving me an opportunity to work in his lab. This project has been an immense learning experience, and a fun one. BEER lab has been extremely warm, and every member of the lab has been available at my first cry for help. Atul has been very helpful since day one, when I entered the lab and was clueless about what I was supposed to do. He has been a constant support since then. I did my first trip to field with Yadugiri, and she gave me a lot of much-needed advice while I was on the field. Chandan, Manaswi and Anand MO have been my go-to people whenever I had doubts in statistical analysis. Thank God for your statistical skills! Asmita and Joyshree have done a great job helping me with random doubts, clarifying my concepts so well, and peer reviewing my thesis. I have troubled Karthik, Lalitha, Siddharth, Rasika, Manju and Dharmendra on multiple occasions to discuss my study design, analyses, and interpretations. Thanks to Nandita and Chengappa for help with soil sample analysis. Thank you all for your patience with me. I would like to thank Dr. Kavita Isvaran from IISc for clearing my concepts in statistics and guiding me about data analysis.

I would like to thank the Tamil Nadu Forest Department for giving me the permit to work in the Reserve Forest of Kundah. My field work could not have been completed without the help of my hardworking field assistants- Selvakumar, Kamal, Vishu, and Painter. The Tamil Nadu Forest Department staff, Mr. Pandiya Raj and Mr. Rajesh, who were the RFOs of Avalanchi and Korakundah ranges respectively, provided a lot of help despite the language barrier.

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A big thank you to Aseem, who gave me interesting insights on various topics, and patiently listened to my rants about the project when things were not going very smoothly. Lastly, I would like to thank my mother, sister, and all my friends who believed in me at every step and encouraged me to do my best. They have been a pillar of support in everything that I do.

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Introduction:

Exotic species are species that are introduced to regions where they do not occur naturally. This introduction can be intentional- for industrial, aesthetic or any other defined purpose, or unintentional. Many a times these species establish themselves in the new region, spread in the ecosystem and alter it permanently. Such species are called invasive species (Bullard; Eiswerth and Johnson, 2002; Hulme, 2009; McNeely, 2001, 2006; Richardson). Recently, a lot of invasive species, plants and animals, have found their way into different ecosystems due to globalization and the dissolution of geographical boundaries because of increase in trade and transport (Hulme, 2009; McNeely, 2006; Richardson, 2013). For example, water hyacinth (*Eichhornia crassipes*), a native of South America, is one of the worst aquatic invasive in the world (Villamagna and Murphy, 2010). The strawberry guava (*Psidium cattleyanum*) is a native plant of Brazil and was introduced to new areas for its edible fruit. It has now successfully invaded Florida, Hawaii, tropical Polynesia, Norfolk Island and Mauritius (Foster Huenneke and Vitousek, 1990). *Lantana camara*, an invasive ornamental shrub, that was brought in from the American tropics, has invaded and taken over vast ranges of forests not just in India, but also in Australia and South Africa (Bhagwat et al., 2012; Ramaswami and Sukumar, 2013). These, and innumerable other introductions of plants and animals in new places have resulted in invasions that are now tough to mend.

Most intentional introductions in the world are based on the attractiveness of the species to humans. This attraction could be aesthetic, or commercial. Several hypotheses have been proposed by researchers to explain invasion mechanisms. Invasive plants typically have wider niches, higher growth rates, extended flowering period, and phenotypic plasticity, all of which may result in higher survival rates. This leads invasive species to outcompete native plants, and thereby decrease the species richness and diversity of the area (Allendorf and Lundquist, 2003; Pyšek and Richardson, 2007; Sakai et al., 2001; Wilson et al., 2011).

The presence of an invasive species in an ecosystem is known to change water and fire regimes, and bring about economic damage (Pyšek and Richardson, 2007). The available data suggests that they also increase overall biomass and net productivity of the ecosystem, increase nitrogen availability, and hence bring about a change in carbon and nitrogen levels in the soil (Ehrenfeld, 2003). They also modify soil properties such as soil pH, moisture, salinity and degree of soil erosion (Waal et al., 2012).

Thus, the ecosystem dynamics depends to a great extent, on the biodiversity, species composition and soil conditions of a region (Hooper et al., 2005; Loreau and de Mazancourt, 2013; Sankaran and McNaughton, 1999; Tilman, 1999; Tilman et al., 2006). In order to maintain ecosystem stability, it is necessary to maintain the native biodiversity of the ecosystem, which becomes difficult with the presence of other exotic and invasive species. While there are a few studies that have reported facilitation of native species by invasive species (D’Antonio et al., 1998; Bernard-Verdier and Hulme, 2015; Eldridge et al., 2011; Rodriguez, 2006), most studies observe adverse effects of invasive species on native biodiversity (D’Antonio et al., 1998; Bhagwat et al., 2012; D’Antonio and Meyerson, 2002; Eiswerth and Johnson, 2002; Hejda et al., 2009; Hulme and Bremner, 2006; Ramaswami and Sukumar, 2011; Srinivasan et al., 2007, 2012). Invasion has become a global ecological problem, and several researchers are trying to address it by studying invasive species, invasions, their removal, and as a result restoration of the native ecosystem.

The most common approach to restore biodiversity of an invaded ecosystem is removal of invasive species. This is done in a variety of ways including cutting down plants, setting fire, and introduction of biocontrols which selectively feed on the invasive plants (D’Antonio et al., 1998; Bergstrom et al., 2009; Marchante et al., 2009; Pollen-Bankhead et al., 2009; Srinivasan et al., 2015a; Zavaleta et al., 2001).

Removal of exotic species from ecosystems can lead to a variety of cascading effects affecting both floral and faunal diversity as well as soil characteristics of the area (Zavaleta et al., 2001). These effects depend on the method of removal, the susceptibility of the ecosystem to other invasive species, and the recovering ability of native species. Also, the types of species being removed, the degree of their removal, the presence of other exotic and native species influence the effects of removal of these species. The impact of the removal of invasive flora may also change with time (Zavaleta et al., 2001). Barring a few studies which show negative effects (Bergstrom et al., 2009; Pollen-Bankhead et al., 2009), removal of exotic species has most often been reported to help in restoration of the plant and soil composition in native ecosystems (Marchante et al., 2009; Muller et al., 1998; Tessema et al., 2016; Tong et al., 2017).

With this background, we investigated the effect of removal of an invasive woody tree species, *Acacia mearnsii*, on plant species diversity and soil carbon and nitrogen of the invaded region. We studied this in a shola-grassland ecosystem, in the Upper Nilgiris, a part of the Nilgiri Biosphere Reserve in the Western Ghats biodiversity hotspot in India.

Figure 1: Dense wattle patches surrounding a shola patch. *Acacia mearnsii* has not been able to invade shola patches, and has invaded only the grasslands.

Acacia mearnsii, or black wattle, is a native of Australia, and one of the 100 most invasive species in the world (Lowe S., Browne M., Boudjelas S., 2000). This species has invaded several places like India, South Africa, Hawaii and China (Kull et al., 2011;

Richardson et al., 2013; Srinivasan, 2011; Waal et al., 2012). Wattle has invaded many parts of India including the grasslands of the Shola-grassland ecosystem in the higher altitudes of the Nilgiris (Srinivasan, 2011).

The 'shola-grassland' ecosystem, found in the upper elevations of the Nilgiris is a forest-grassland mosaic, characterized by vast grasslands, interspersed with tropical montane tree patches (Bunyan et al., 2012). The grasslands in this ecosystem have been colonized by a variety of invasive species like *Acacia mearnsii* (black wattle)*, Ulex europaeus* (gorse) *and Cytisus scoparius* (scotch broom). Wattle patches alter not only the foraging availability for grazers, but also the soil quality, making the soil unacceptable for the growth of many other species (Waal et al., 2012). Even though a lot of research has been conducted in the Nilgiris Biosphere Reserve, and the Western Ghats in general (Bunyan et al., 2015; Ghats, 2007; Hiremath and Sundaram, 2013; Ramaswami and Sukumar, 2011; Richardson; Robin and Nandini, 2012; Srinivasan et al., 2012; Srinivasan, 2011, 2012; Sukumar, 2014), the invasion ecology of *Acacia mearnsii* remains largely understudied in India (Bullard; Kull and Rangan, 2008; Rangan et al., 2010; Srinivasan et al., 2015b). This was the motivation behind the study of consequences of wattle clearing in a shola-grassland ecosystem in South India.

The Tamil Nadu Forest Department (TNFD) has been cutting down wattle as a part of development plans since the past five years, with the intention of restoring the grasslands. We expected this step was to lead to a variety of effects depending on the method used for removal, the susceptibility of the ecosystem to other invasive species, recovering ability of native species, and the condition of soil after invasion. Also, the presence of other exotic and native species can influence the effect of the removal of *A. mearnsii*. There are a number of other exotic and invasive species (e.g. Scotch broom (*Cytisus scoparius*), Gorse (*Ulex europaeous*), *Eupatorium glandulosum* and bracken (*Pteridium esculentum*) present near wattle cleared areas, which can potentially take over the areas (Bunyan et al., 2012). Nevertheless, there will be an effect on the plant diversity as well as soil quality of that area after removal of the species. This impact may change with time once the species is removed (Zavaleta et. al., 2001) *A. mearnsii* is a nitrogen fixing species, and its removal can decrease amount of fixed nitrogen in the soil. The organic matter present in the system due to wattle will also reduce, thus reducing the carbon content of the soil. Soil chemical and physical properties may change with time after *A. mearnsii* removal, facilitating soil for growth and establishment of various plant species. Also, several factors like elevation, slope, aspect and other micro- climatic factors may play a role in the determination of vegetation structure (Chen et al., 1999). These factors will also govern the direction of recovery of plant diversity after clearing of *A. mearnsii*

Based on this background, this study addressed five major questions:

1. Does removal of wattle increase surface area and number, of grassland species in the wattle cleared areas?
2. How does time since removal of wattle influence regeneration of plant species in wattle cleared areas?
3. Is there an effect of elevation on the regeneration of plant species after wattle removal?
4. Does regeneration of plant species depend on density of wattle before removal?
5. Is there a change in soil carbon and nitrogen following wattle removal?

In this regard, I tested the following predictions:

1. Species richness and vegetation cover will be higher in wattle cleared areas compared to wattle intact areas.
2. Removal of wattle will increase the area covered by native grassland species over time after wattle removal.
3. The area occupied by regenerated wattle will be positively correlated with the initial wattle basal area in the site.
4. Species composition in low and high elevation sites will be different.
5. The percentage soil carbon, as well as nitrogen, will decrease with time after wattle removal.

Materials and methods

The focus of the study was to find out if the wattle clearing program helped in the restoration of grasslands. For this, I looked at various factors that could contribute to the regeneration of species after removal of wattle, and observed them in different wattle cleared sites in chronological order with space substituted for time (predictor 1). I observed the species richness and cover of different vegetation types in plots that were cleared of wattle one, two, three, four and five years ago respectively. Since wattle cleared sites were present at two different ranges separated by an elevation of 100-400 m, I sampled at two different elevations (predictor 2), which gave me an insight into the role of elevation in the restoration of grasslands. The initial density of wattle (predictor 3) was considered an important predictor, as the wattle seed bank would be higher in wattle cut areas, and would help in the regeneration of wattle. The major responses that would help me in determining the success of restoration were (1) species richness, (2) native grassland species richness, (3) total percentage vegetation cover, (4) percentage cover occupied by native grassland species, (5) percentage cover of regenerated wattle, (6) soil carbon percentage, (7) soil nitrogen percentage, and (8) soil carbon: nitrogen ratio.

Study Area

The Nilgiri Biosphere Reserve, which was set up in 1986 under UNESCO's Man and Biosphere program, was the first Biosphere Reserve in India (Daniels.R. J, 1996). It covers an elevational range from 80 m to 2600 masl (meters above sea level), and a mean annual rainfall of 500-7000 mm (2015). Owing to the diversity of climatic gradients, it supports all kinds of ecosystems including the scrubs (eastern plains), dry and moist deciduous forests (Bandipur and Madhumalai), evergreen forests (Silent Valley), and shola-grasslands (Nilgiri plateau) (Anandan, 2016; Baskaran et al., 2012; Daniels.R. J, 1996).

My study sites were situated in the upper elevations of the Nilgiri Biosphere Reserve, in the shola-grassland ecosystem. The ‘shola-grassland’ ecosystem consists of forest-grassland mosaics, characterized by vast grasslands, interspersed with tropical montane tree patches [Figure 1]. The word ‘shola’ means tropical montane forests in the local language, and hence the name ‘shola-grassland’. The shola-grasslands are situated at an elevation gradient of about 500 masl (metres above sea level) – 2500 masl, and many of the abundant species in the grasslands show mutually exclusive elevational ranges (Srinivasan et al., 2015). These include several endangered species of flora and fauna (Bunyan et al., 2012). During the 1800s, when grasslands were considered as 'wastelands', a variety of exotic species such as *Eucalyptus globulus*, *Pinus patula*, *Camellia sinensis* (tea), *Acacia mearnsii* (black wattle) were planted over grasslands for timber, paper industry and other industrial as well as domestic benefits. A few of these exotic species gradually spread and invaded remaining grasslands, thus changing the species composition of the area (Bunyan et al., 2012; Daniels.R. J, 1996).

Figure 2: A typical view from a hill top in a shola grassland ecosystem in the Nilgiris.

Acacia *mearnsii* which was introduced to provided firewood for industrial as well as domestic use, spread across the grasslands rapidly, invading them and converting majority of the grasslands to wattle patches (Bunyan et al., 2012; Daniels.R.J, 1996)

Efforts are now being made to restore the grasslands by removal of wattle. Under two such schemes of the Tamil Nadu Forest Department, a minimum of ten hectares of black wattle have been cut down every year since 2011 as close to the ground as possible, with the intention of restoring the grasslands. The wood is then dried and sold to various contractors [Figure 3]. All wattle cleared sites are revisited at regular intervals (~2-3 years) to cut down any wattle that has resprouted or germinated.

My study sites were based in the wattle cleared areas, as well as a few intact wattle areas and grasslands. They are situated in the Avalanchi and Korakundah ranges of the Nilgiris South Division, in the Udhagamandalam District of Tamil Nadu. The ranges are separated by an elevation of 100-400 m. My field sites ranged from Latitude

Figure 3: A wattle cleared area with stacks of wattle barks kept for drying

11°18'17.80"N to 11°13'42.66"N, Longitude 76°36'27.92"E to 76°32'40.03"E and elevation of 2000m to 2500 m.

Figure 4: Google Earth images of the study site in the Nilgiris in Tamil Nadu.

The temperature in my study sites in the upper Nilgiris remains low throughout the year, with an average minimum of 5 ºC during December and maximum of 25 ºC during April. The Nilgiris South Division receives rain from the Southwest as North East Monsoon winds. The amount of rainfall received varies across the year as well as in different part of the Nilgiris. Average annual rainfall ranges between 1500-3000 mm.

Study species

Acacia mearnsii (Black Wattle)

Acacia mearnsii is an evergreen tree species native to Australia. It can grow up to 25 m in height, and can generally have a basal diameter up to 100 cm. The trees have beautiful yellow flowers, which bloom during winter (Orwa, 2009). It grows well in temperatures ranging from 8-20°C, with a mean annual rainfall of 500-2050 mm, and altitudes 300-2500 masl (Booth and Jovanovic, 1988; Orwa, 2009), demonstrating its wide range and tolerance.

Acacia mearnsii has a variety of uses —twigs as fuel, timber for furniture, and bark as a source of tannin for leather. Because of this, it has historically been introduced to several places throughout the world as plantations for industrial use (Booth and Jovanovic, 1988; Kull and Rangan, 2008; Orwa, 2009). This introduction for industrial and domestic purposes turned out to be undesirable when the Acacia started invading all the areas in which it was introduced, such as India, Africa, South America, Hawaii and China. It has become a serious threat to native biodiversity, and is now one of the 100 worst invasive species in the world (Bosch and Saioa Fernández-Beaskoetxea, 2010). Efforts are being taken to remove *Acacia mearnsii* from many of ecosystems, with little success (Bennett, 2011; Kull et al., 2011; Thomas and Palmer, 2007; Waal, 2009; Van Wilgen et al., 2011; Wilson et al., 2011).

Figure 5: Image of a mature, flowering *Acacia mearnsii* tree.

Data collection

Floral biodiversity measurement and soil collection

Sampling sites were selected in which wattle had been removed one, two, three, four and five years ago (in 2015, 2014, 2013, 2012 and 2011 respectively), and these sites were located at two different elevations separated by 100-400 m. Uninvaded grasslands and intact wattle were also sampled as control plots [Table 1].

At each site, ten transects were established, each 50 m long along which systematic measurements of vegetation cover, species richness; and sampling of soil was done. All transects were parallel to each other, and were separated by a distance of at least 20 m. Factors considered while selecting the transect locations were:

1. No sampling in the valleys, as some of them have streams, which could alter the micro-conditions in the area.
2. Care was taken that sampling was done at least 10 m away from the road boundaries.
3. All transects were done in the east-west direction.

Table 1: Study design used for sampling.

Elevation	Year of removal	Years since removal	Number of transects
Low	2015	1	10
Low	2014	2	10
Low	2013	3	10
Low	2012	4	10
Low	2011	5	10
High	2015	1	10
High	2014	2	10
High	2013	3	10
High	2012	4	10
High	2011	5	10
Mid	-	Intact wattle	10
Mid	-	Uninvaded grassland	10

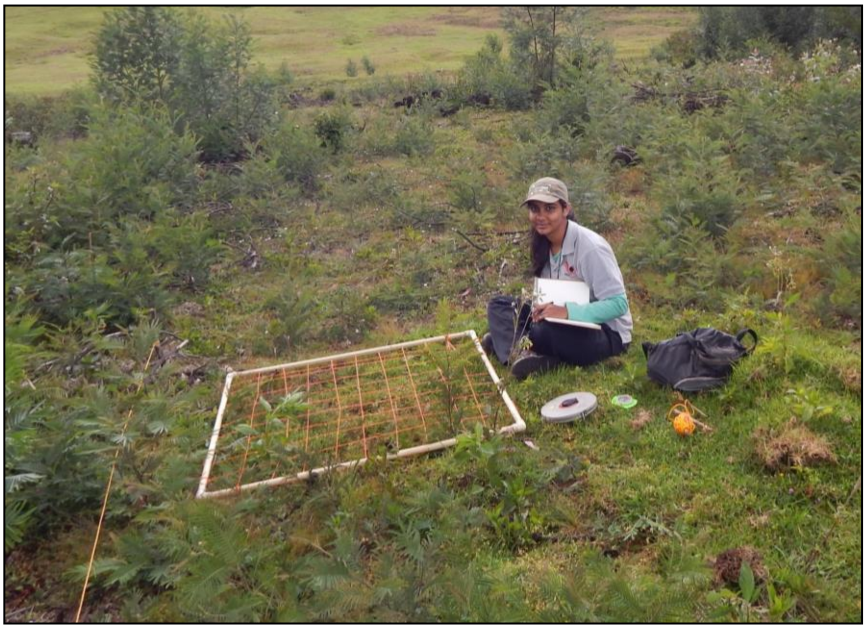

Figure 6: Herbaceous cover readings being taken by me in the field.

Each 50 m transect had five evenly spaced $1m^2$ (1m*1m) plots and two evenly spaced $25m^2$ (5m*5m) plots [Figure 7]. Percentage cover of all vegetation below 1 m height was measured in the 1 m^2 plots. This was done using a 1m*1m large grid, that was further divided into 100 parts, each part corresponding to 1% cover [Figure 6]. The percentage cover of each species present in the $1m^2$ area was visually estimated. In the $25m^2$ (5m*5m) plots, the basal circumference of all wattle trees that had been cut down was measured using a measuring tape. In addition, one soil sample to a depth of 20 cm was collected from each transect using a soil auger [Figure 8].

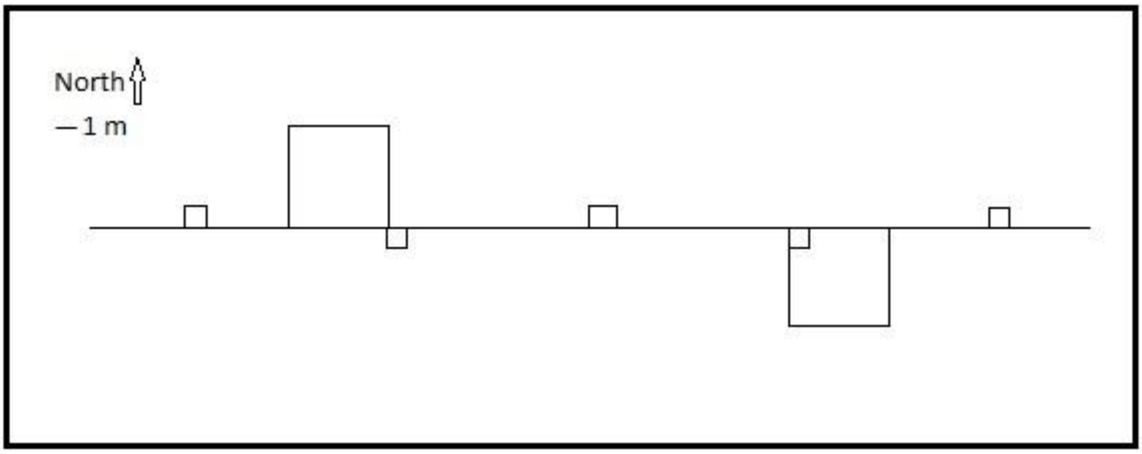

Figure 7: A schematic representation of transects laid for sampling.

Figure 8: A soil auger (left) with soil samples collected in zip lock bags lined up next to it.

Soil processing

The carbon and nitrogen content of the collected soil samples were measured in the laboratory using LECO Corporation’s TruSpec CN analyser. The following soil processing protocol was used to prepare the soil samples before analysis: Soil samples were air dried for about 8-10 days, until most of the moisture from the soil evaporated. The dried samples were ground and passed through a 0.2 mm sieve to remove any large particles of soil, rock or roots. The sieved samples were oven-dried at 60 ºC for 72 hours, and it was ensured that all moisture from the samples evaporated. The samples were then passed through a 0.05 mm sieve. Following these steps, the processed samples were analyzed in TruSpec Micro.

Carbon and nitrogen content measurement

TruSpec Micro is connected to an external computer, and uses a software program to control the system operation and data management [Figure 9]. From each soil sample,

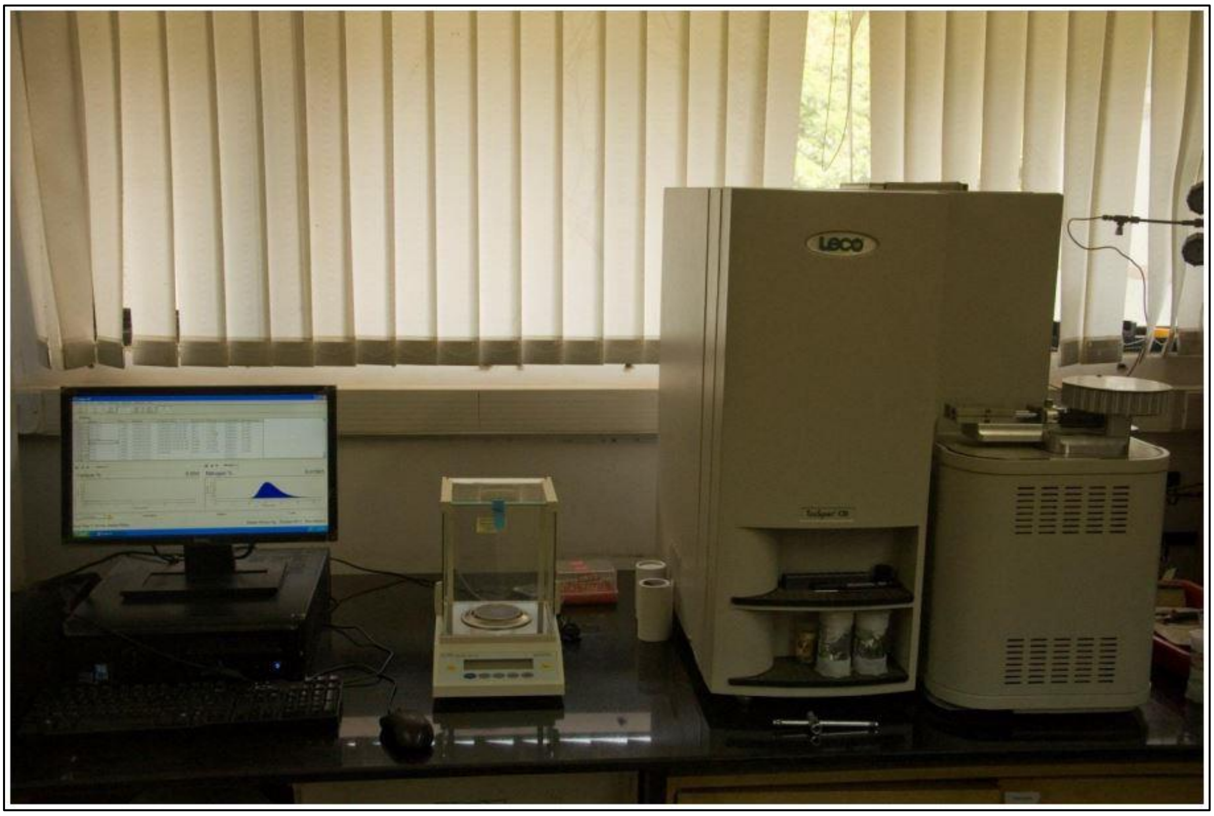

Figure 9: LECO Corporation’s TruSpec Micro used for analyzing soil samples to find their carbon and nitrogen content.

0.11 grams was used for analysis in TruSpec Micro. Each sample was weighed and loaded in a separate loading well. Once the sample is loaded in the loading head, the rest of the procedure is automated, and the result is the reading in percent by weight of the carbon and nitrogen in the soil.

Statistical Analysis

All analyses were done using R version 3.3.3 (R Core Team 2016).

The data obtained from the 1 m^2 plots and 25 m^2 plots was averaged for each transect to get one data point per transect, which was then used for all analyses.

Generalized Linear Mixed Models (GLMM) were used to determine the effects of time after removal of wattle, elevation and initial density of wattle before removal (predictor variables) on plant species richness, cover, species richness of native grassland species and cover of native grassland species, regenerated wattle cover and soil carbon and nitrogen contents (response variables). In these models, different combinations of predictors were the fixed effects, and each plot (each consisting of ten transects) was used as the random effect. GLMMs were run using the package lme4 (Bates et. al, 2015) with the command *lmer*. Multiple models were run [Appendix], and their AIC (Akaike Information Criterion) values and weights were compared, along with the coefficients of the models.

AIC, or Akaike Information Criterion is a measure of the quality of each model, and the lowest AIC value gives the best fit model for the given data. Akaike weights (ω(AIC)) of models were also calculated, which give the relative likelihoods of the model fit to data, among all the models. Δ AIC, relative likelihood, and the Akaike weights of the models were calculated to decide the best fit model, as per the following formulae:

$\Delta AIC_i = AIC_i - \min(AIC)$

Relative Likelihood (RL_i) = $EXP(-0.5 * \Delta AIC_i)$

$\omega(AIC)_i = (RL_i) / \Sigma(RL)$

Ten models were run for each of the responses [Appendix]. The ten models were selected based on backward deletion of variables. The models with delta AIC (Akaike Information Criterion) values between 0-2 were chosen as the best models. A model averaging was done in cases where there were multiple models using the package MuMIN in R (Barton, 2016). Then, the p-value of each parameter was observed to determine the significance ($p<0.1$) of the predictor.

A one-way ANOVA followed by posthoc HSD Tukey's test was carried out to compare the difference between percentage cover and species richness of the grassland, shola and invasive species at different time points (one year, two years, three years, four years, five years) and elevations (high and low).

Results

Species richness in wattle cleared areas

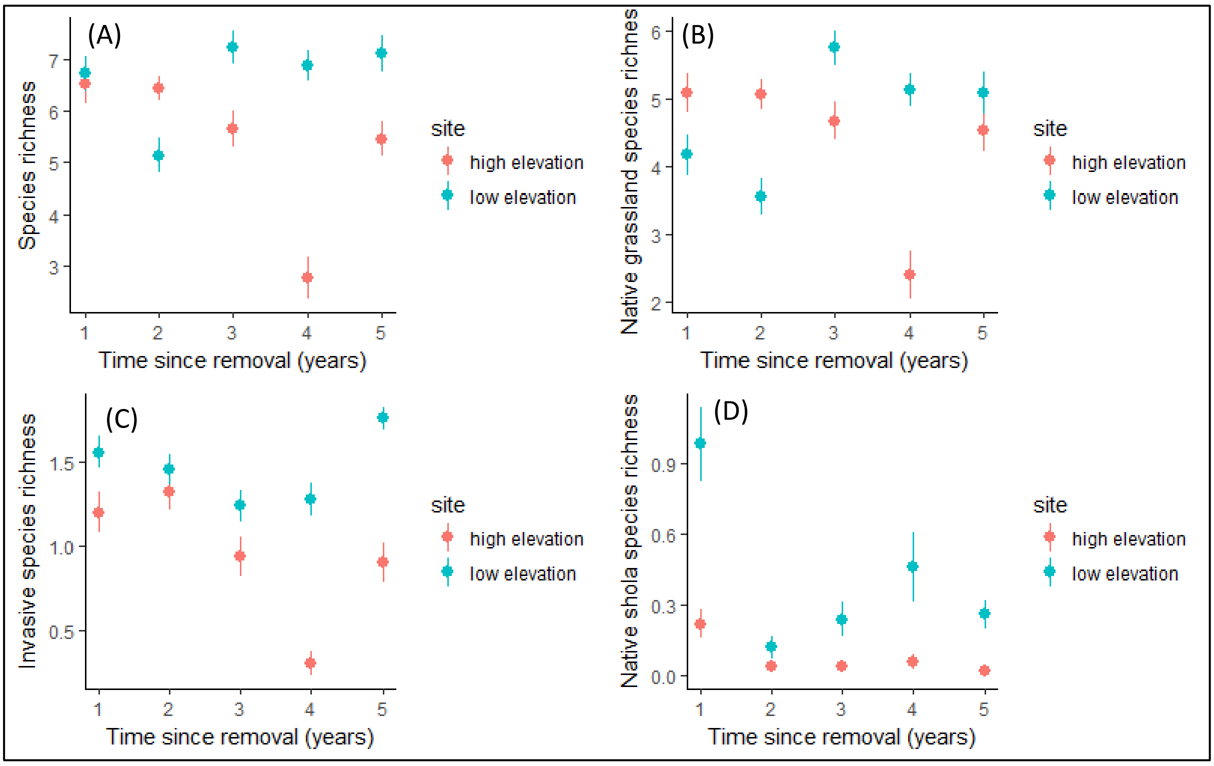

Figure 10: Patterns of species richness of different vegetation types (A) total species richness, (B) native grassland species richness, (C) invasive species richness and (D) native shola species richness, across time since wattle removal and elevations

There is no effect of time or elevation on the total species richness, native grassland species richness, invasive species richness, as well as the native shola species richness (GLMM results) ($p>0.05$) [Figure 11, Appendix].

Percentage vegetation cover in wattle removed areas

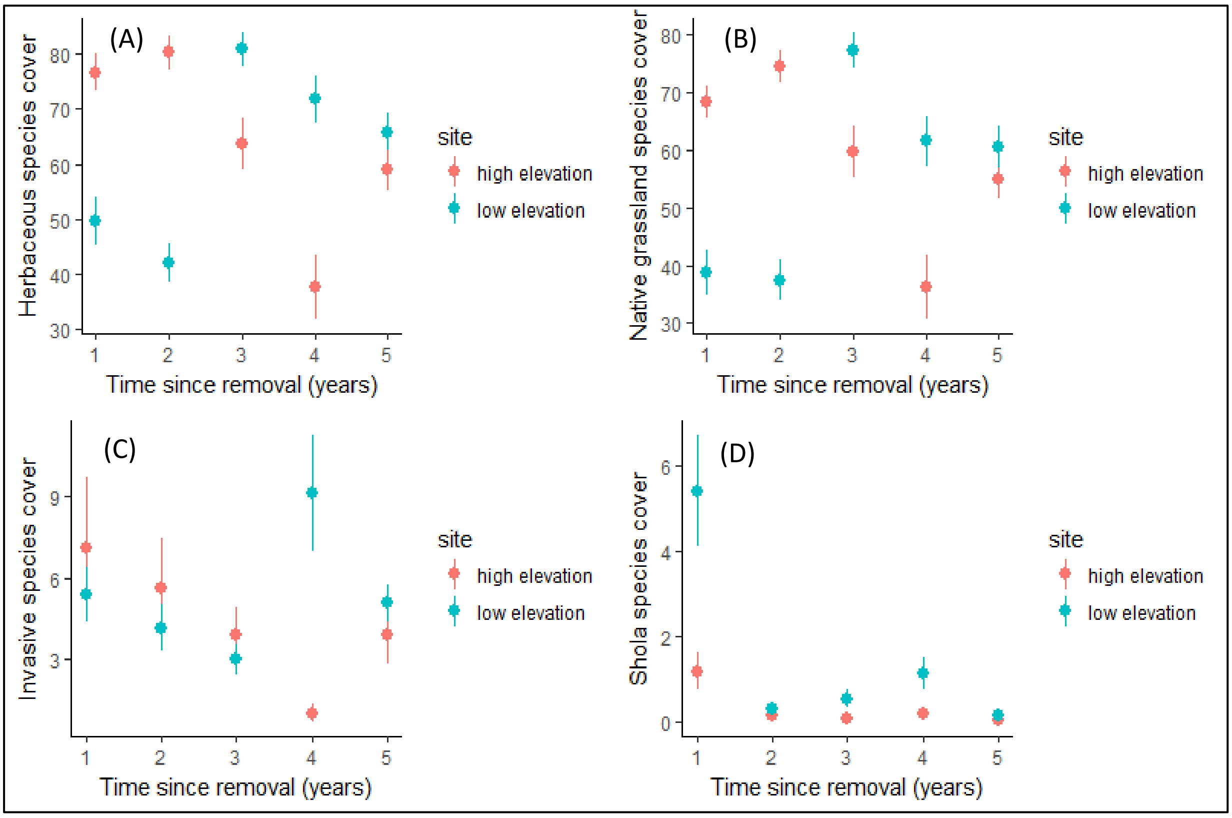

Figure 11: Patterns of percentage cover of different vegetation types (A) total vegetative cover (%), (B) native grassland species cover, (C) invasive species cover and (D) native shola species cover, across time since wattle removal and across elevations

There is no effect of time or elevation on the total species cover, native grassland species cover, invasive species cover, or the native shola species cover (GLMM results) ($p>0.05$) [Figure 12, Appendix].

Summarising GLMM results for different responses:

Response- Total vegetation cover: Out of the ten component models that were run, the model including elevation, time, and their interaction effect was the best fit to the total percentage cover as a response. Even though this model shows some significance ($p=0.06$), the response of total vegetation percentage cover is different at different years and elevations, and does not show any particular trend. The data available is insufficient to conclude the response of total vegetation cover to any of the predictors.

Response- Native grassland species cover: Out of the ten models, three had delta AIC values between zero and two [Table 2]. The three component models were then averaged to get better parameter estimates, however, none of the parameters correlated significantly with native grassland species cover ($p>0.05$).

Response- Total species richness: Out of ten component models, four had delta AIC between zero and two [Table 2]. These four models were averaged to get better parameter estimates. It was observed that total species richness is negatively correlated with the initial density of wattle ($p=0.08$). Also, even though there was no trend seen in species richness across the years, total species richness was higher in the low elevation sites compared to high elevation sites for all years ($p=0.04$).

Response- Native grassland species richness: Four out of ten models gave a delta AIC value less than two [Table 2]. Model averaging was done for these four models to get better parameter estimates. None of the predictors showed any trend with the native grassland species richness. However, the grassland species richness was higher in the lower elevation sites compared to high elevation sites for all years ($p=0.09$).

Table 2: Summary of GLMM results for species richness and cover. (* indicates p<0.05)

Response variable	Fixed effects	Random effects	Df	delta AIC	relative likelihood	W
Total percentage cover	Elevation + Time since wattle removal + **(Elevation x Time since wattle removal)***	Plots	6	0	1	0.838
Native grassland species cover	Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	Plots	6	0	1	0.476
	Elevation + Initial wattle density + (Elevation x Initial wattle density)	Plots	6	1.907	0.386	0.184
	Initial wattle density + Elevation + Time since wattle removal	Plots	6	1.924	0.383	0.182
Total species richness	Elevation	Plots	4	0	1	0.266
	Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	Plots	6	0.021	0.99	0.263
	Elevation + Initial wattle density + **(Elevation x Initial wattle density)***	Plots	6	0.714	0.7	0.186
Native grassland species richness	Elevation	Plots	4	0	1	0.296
	Elevation + Time since wattle removal + **(Elevation x Time since wattle removal)***	Plots	6	0.885	0.643	0.191
	Time since wattle removal	Plots	4	1.734	0.421	0.125

The results of one-way ANOVA followed by a post-hoc HSD Tukey's test showed that the native grassland species richness as well as percentage cover was significantly higher than invasive or shola species, across all years, at both elevations (p<0.05) [Figure 12,13]. The cover occupied by shola species and invasive species was not different in any of the sites (p>0.05) [Figure 12,13], suggesting that the dominant vegetation type in the wattle cleared sites was native grassland species.

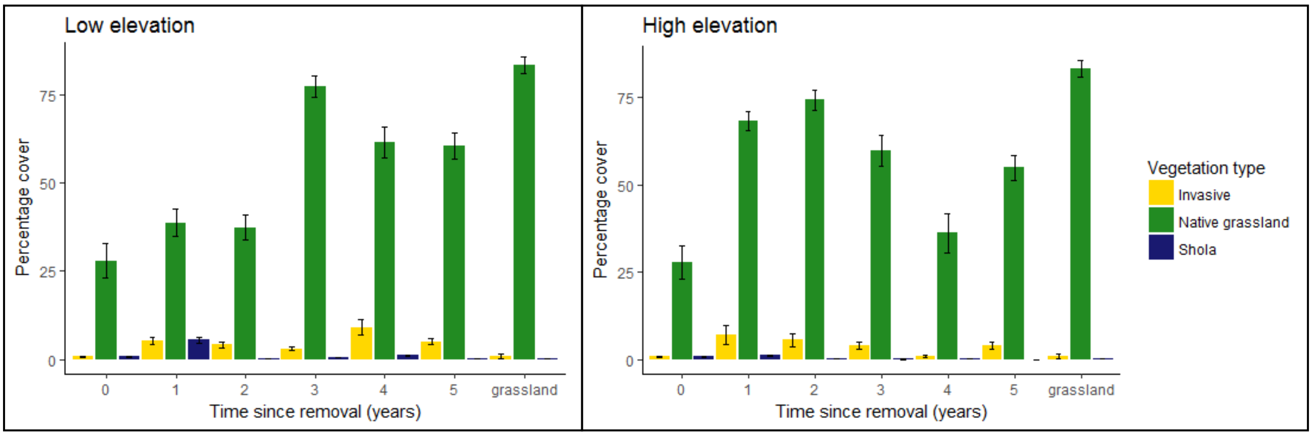

Figure 12: The figure shows time since wattle removal on the X-axis and percentage cover on the Y-axis. The three colors show different vegetation types, namely, invasive species, native grassland species, and native shola species. Figures (A) and (B) show different elevations

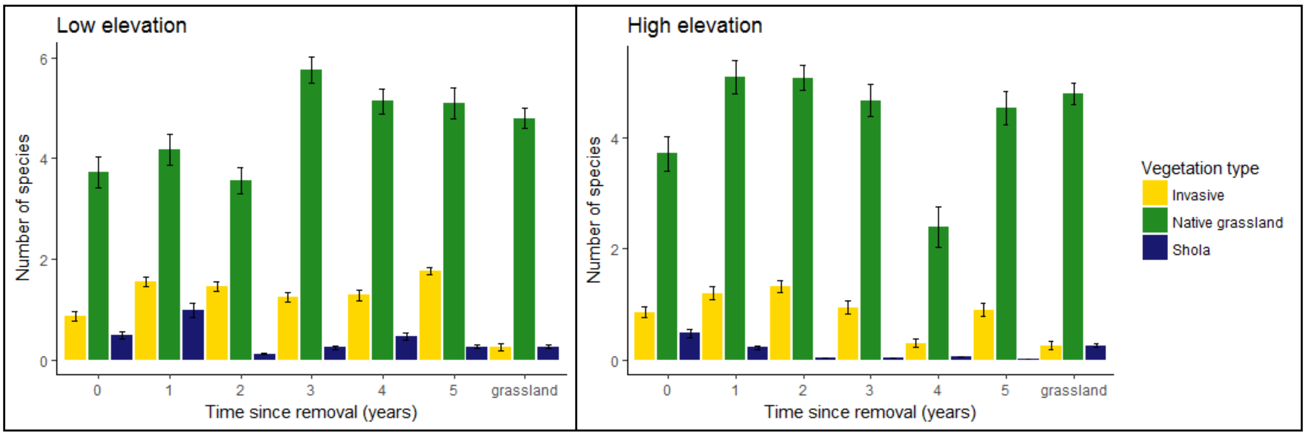

Figure 13: The figure shows time since wattle removal on the X-axis and number of species on the Y-axis. The three colors show different vegetation types, namely, invasive species, native grassland species, and native shola species. Figures (A) and (B) show different elevations

Effect of initial density of wattle on regenerated wattle cover

The results of the GLMM run with regenerated wattle as the response showed that Regenerated wattle cover is best explained by the interaction effect of elevation and initial wattle density (p=0.038) [Figure 14].

The high elevation sites have low initial wattle density, as well as low regeneration of wattle, implying that no conclusion can be made about the correlation of these two parameters in the high elevation sites. The low elevation sites do show a positive correlation between initial wattle density and percentage regeneration of wattle. However, there is too much variation in the data to strongly conclude anything.

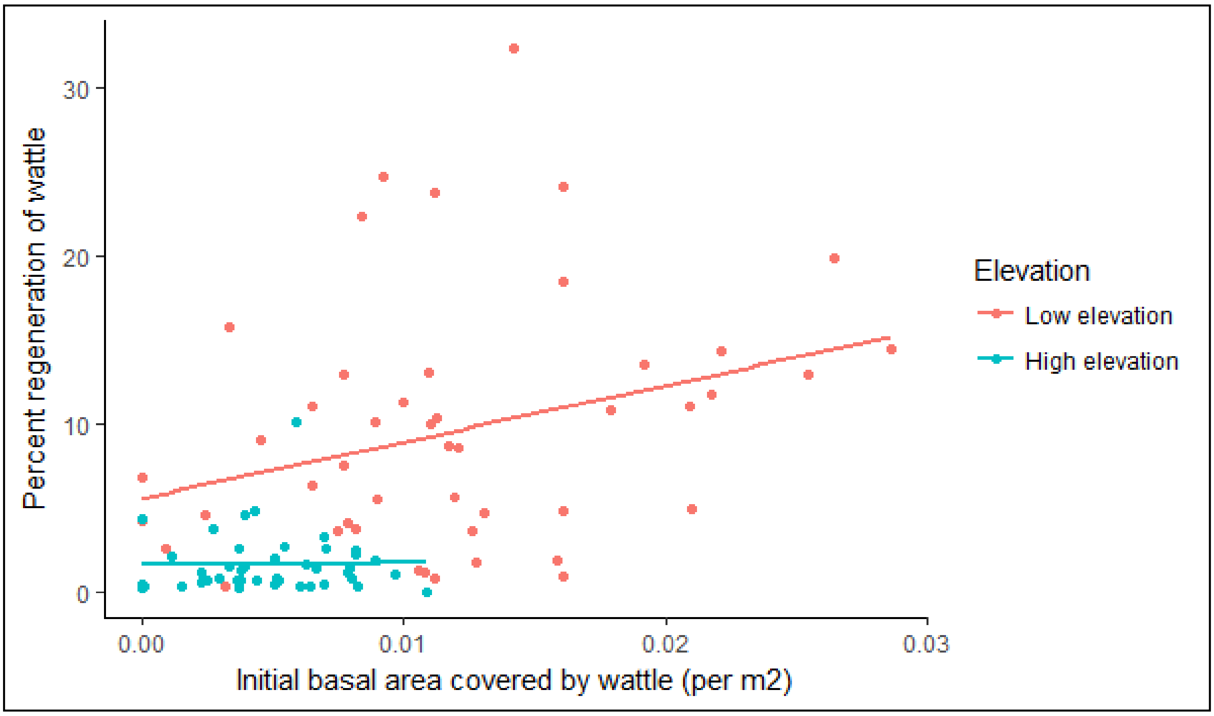

Figure 14: Linear regression of initial basal area cover by wattle on the X-axis plotted against percent regeneration of wattle on the Y-axis.

Effect of time since wattle removal and elevation on soil carbon, nitrogen, and C: N ratio

Summarising GLMM results for different responses:

Response- Soil carbon: Three out of the ten component models gave delta AIC between zero and two [Table 3]. A summary of the models averaging indicates that none of the observed factors significantly explain the percentage carbon in the soil. [Figure 17(A)].

Response- Soil nitrogen: Two out of the ten models had delta AICs between zero and two [Table 3]. Hence, these models were averaged to get better parameter estimates. Based on model averaging, only elevation has a significant effect (0.003) on the percentage nitrogen in the soil. It is seen to be higher at high elevation sites compared to low elevation sites [Figure 17(B)].

Response- Soil C: N: Out of the ten models, the best fit model indicates that the soil C:N ratio is higher at high elevation sites compared to low elevation sites (p=0.019) [Table 3, Figure 16].

Table 3: Summary of GLMM results for soil carbon and nitrogen content

Response	Fixed effects	Random effects	df	Δ AIC	Relative likelihood	ω(AIC)
soil C	Initial wattle density + Time since wattle removal + Elevation	Plots	6	0	1	0.295
	Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	Plots	6	0.024	0.989	0.292
	Elevation + Initial wattle density + (Elevation x Initial wattle density)	Plots	6	0.355	0.838	0.247
Soil N	**Elevation** + Initial wattle density + (Elevation x Initial wattle density)	Plots	6	0	1	0.629
	Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	Plots	6	1.871	0.393	0.247
Soil C: N	**Elevation**	Plots	4	0	1	0.464

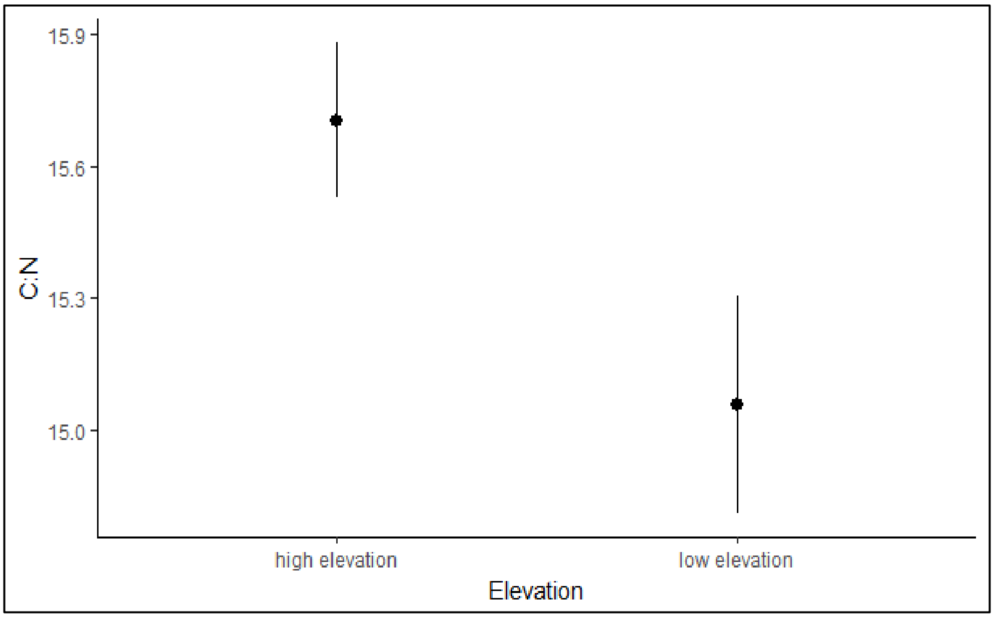

Figure 15: Soil Carbon: Nitrogen ratio at high and low elevations

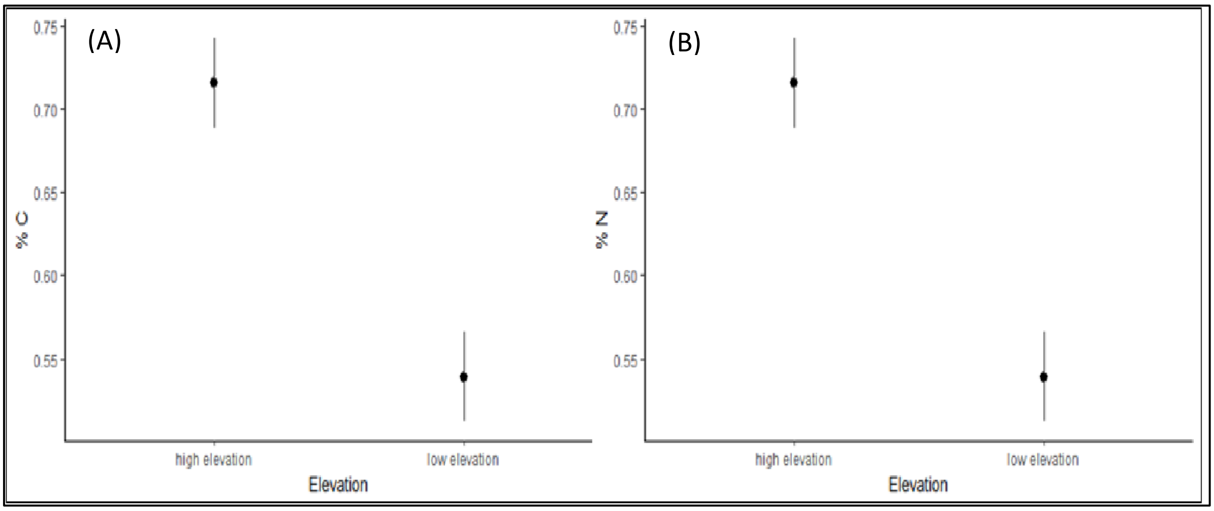

Figure 16: Soil carbon(A) and nitrogen(B) percentage at high and low elevations.

Discussion

The results of this study indicate that removal of wattle did recover the percentage cover of grasses that was lost due to the presence of dense patches of wattle. Most of this recovery happened in the first year post wattle removal. Also, number of species (specifically native grassland species) remained same across all wattle cleared and uncleared sites. There was no particular pattern seen in plant species richness or vegetation cover in the sites which were cleared of wattle chronologically. The soil carbon and nitrogen also did not show any difference across sites that were cleared of wattle at different time points. Another interesting outcome showed that regeneration of wattle correlated positively with the initial density of wattle present in a site before its removal. Also, there was a clear difference in patterns of recovery of plant species richness, vegetation cover, soil carbon and nitrogen, as well as regeneration of wattle at the two sampled elevations.

Previous studies on invasions have shown that invasive species reduce the species richness of the invaded area (Gerber et al., 2008; Hejda et al., 2009; McNeely, 2001; Brown and Sax, 2004). It was expected that removal of an invasive species will increase the species richness in the cleared area. No significant difference was seen in species richness in the wattle cleared sites compared to intact wattle sites. However, the number of grassland species in all wattle cleared and intact sites was lower than uninvaded grasslands. This implied that wattle patches harboured a variety of grassland species, but the fraction of area occupied by wattle was so large, that the grassland species did not have a conducive environment to grow and spread. There was also no significant difference between the sites sampled at different time points after wattle removal. Neither presence or removal of wattle, nor elevation, nor time after removal played a role in determining the species richness of a site. The independence of species richness with time could be because the time scale at which this study took place is too small to detect a trend. Also, the elevational difference of 100-400 m could be too small to see a difference in species richness across the two sampled elevations.

Along with species richness, the total vegetative cover was also expected to go up with time after wattle removal, as the removal of wattle creates a lot of space for other species to grow. The nutrient uptake by wattle also stops, and may allow other species to grow better and faster. There was a clear increase in total vegetative cover between wattle intact and cleared sites. However, there was no trend seen between sites at different time points after wattle removal; nor was there a difference seen in vegetative cover at different elevations. The lack of relationship between total vegetative cover and all the predictors could be attributed to factors that were not observed. These include elements such as slope, aspect, soil erosion and the presence of herbivory. They may be able to explain the patterns shown by the total herbaceous cover, and further investigation is required for the same.

The aim of wattle clearing was the restoration of grasslands, and hence I expected to see an increase in native grassland species richness as well as cover of grassland species compared to other species after clearing of wattle.

As expected, native grassland species richness, as well as cover was higher than invasive or shola species richness or cover at all time point sites at both elevations. However, there was no correlation of percentage cover occupied by grassland species with either time since wattle removal, elevation, or initial wattle density. Species richness of native grassland species was positively correlated with the time since wattle removal; and the correlation was stronger at low elevation sites than high elevation sites. This meant that the correlation between grassland species richness and time depended on the elevation. The factors that could differ across the two elevations include rainfall, temperature, and micro climatic variables, that were not accounted for. It may have been possible to come to better conclusions in the presence of more data.

One important aspect that determined the success of wattle clearing was the percentage cover of regenerated wattle. The percentage regeneration of wattle was lower at high elevation sites compared to low elevation sites. Also, it was positively correlated with the initial density of wattle. However, the positive correlation was stronger at low elevation sites compared to high elevation sites. This indicated that the higher initial density of wattle may have left behind a higher wattle seed bank. Despite the removal of wattle, the sites with higher initial wattle density gave rise to higher percentage of wattle regeneration. The data collected gave information of sites that were cleared of wattle only up to five years back. The species dynamics in different sites could change with time. Thus, there are higher chances of re-invasion of wattle in sites with higher initial wattle density. It is necessary to monitor these sites specifically, to prevent re-invasion by wattle.

Wattle is a nitrogen fixing tree, and contributes to the soil nitrogen. Hence, it was expected that once wattle is removed from an ecosystem, the percentage nitrogen in the soil would go down. Also, the carbon in the soil is contributed by the organic matter, which is higher in wattle intact sites than wattle cleared sites. And so, it was expected that soil carbon percentage would also go down after removal of wattle. It was also expected that soil nitrogen and carbon percentage would depend on the initial wattle density. However, contrary to expectations there is no effect of time since wattle removal or initial wattle density on the soil percentage carbon or nitrogen. Surprisingly, the soil carbon percentage does not depend on any of the tree factors that were considered (time since wattle removal, elevation, initial wattle density). However, soil percentage nitrogen as well as carbon: nitrogen ratio was higher at high elevations than low elevations. This leads us to infer that the time of five years is too small to see a change in soil carbon and nitrogen. However, there is direct dependence of soil carbon and nitrogen on elevation. The soil carbon and nitrogen may be different at the two different elevations due to other factors that are elevation specific and were not considered. It is possible that higher elevation sites have an increased soil microbial activity of nitrogen fixers, thus increasing the nitrogen content in the soil. It is also possible that the low elevation sites had higher slopes, leading to higher soil erosion in those sites.

Overall, even though there is direct recovery of grassland cover in the wattle cleared areas, the recovery depends on a variety of other factors, which need to be studied. Also, there needs to be long term monitoring of these sites to eliminate the variation arisen due to space for time substitution.

Management implications:

Wattle invasion has been an ecological problem in multiple areas for more than a decade. But very few studies have been done on the invasion ecology of wattle in India, and its management implications. Informal interviews with the forest department staff led me to believe that the current approach followed by the forest department for wattle removal is very random, and not well documented. There is no involvement of researchers working on invasion and restoration ecology in any of these practices. It is crucial to have a scientific basis to any large-scale ecological project. Hence, it is necessary that more studies be carried out in these areas to find out the most significant factors responsible for invasions, and the factors that need to be considered while deciding on a restoration strategy. Based on the increase in grassland species richness and cover compared to wattle intact sites, the current practice of wattle clearing by the TNFD seems to be working up till now, but a long-term plan must be chalked out to prevent the re-invasion of wattle or invasion by any other invasive species. Monitoring of all sites should be robust and should also take care of other invasive species growing in the wattle cleared sites. The follow-ups done currently allow the removal of only wattle from the sites.

The data collected, as well as field observations suggest that the wattle invasions have taken place across sites spanning a whole range of elevations, temperatures, rainfall, slopes, aspects and degree of herbivory. It is necessary to explore the reasons that let wattle invasion succeed, to restore the grasslands. There needs to be more enquiry about other methods that can be used to restoration programs. Also, the most important step in this process is documentation of all studies that have been carried out. A scientific approach, as well as proper long-term planning might help restore the grasslands faster.

Conclusions:

The results of this study indicate that the most important factor determining the species richness and percentage cover of herbaceous species, native grassland species, as well as soil carbon and nitrogen is elevation. It was predicted that the most important parameter determining species richness as well as cover would be time since wattle removal, followed by initial density of wattle. Even though this study shows a clear increase in grassland species cover across all sites after wattle clearing, there is no effect of time since wattle removal on either total species richness, total vegetative cover, grassland species richness, percentage cover of grassland species, as well as with soil carbon or nitrogen.

The possible reason behind this could be that the time scale is too small to see an effect. Also, my sampling sites had space substituted for time, which could have led to a lot of unexpected variation due to factors beyond control. In a similar study conducted by Van Der Waal et. al. in Kouga mountains in South Africa, the temporal effects of wattle clearing in terms of plant species diversity and soil properties were seen in sites only 13 years after clearing of wattle (Waal et al., 2012). Also, other important factors can affect the restoration of grasslands. For example, the slope of the site and its aspect determine the amount of soil erosion at a site, which could affect the regeneration of vegetation after wattle is cleared. Temperature of the area, presence or absence of frost and fire, as well as amount of rainfall received can determine seed viability, germination and survival of plant species. Vegetation in the surrounding area, as well as presence of herbivory can lead to increased competition, increasing the chances of regeneration of particular species. These parameters could not be accounted for due to unavailability of sites as well as time constraint. Further studies need to be carried out to come to better conclusions, and understand the grassland restoration ecology in the wattle invaded grasslands of the Upper Nilgiris.

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Appendix

1. Results of posthoc HSD Tukey's test to test the difference between different vegetation types across time and elevations.

A) High elevation, Cover

Time since wattle removal (years)	vegetation	Difference in cover	Confidence Interval (95%)		p adj
			lower	upper	
1	native: invasive*	61.265	49.293	73.238	0
1	shola: invasive	-5.885	-17.858	6.088	0.941
1	shola: native*	-67.15	-79.123	-55.178	0
2	native: invasive*	68.88	56.908	80.853	0
2	shola: invasive	-5.43	-17.403	6.543	0.97
2	shola: native*	-74.31	-86.283	-62.338	0
3	native: invasive*	55.902	43.93	67.875	0
3	shola: invasive	-3.8	-15.773	8.173	1
3	shola: native*	-59.702	-71.675	-47.73	0
4	native: invasive*	35.25	23.278	47.223	0
4	shola: invasive	-0.82	-12.793	11.153	1
4	shola: native*	-36.07	-48.043	-24.098	0
5	native: invasive*	51.03	39.058	63.003	0
5	shola: invasive	-3.83	-15.803	8.143	1
5	shola: native*	-54.86	-66.833	-42.888	0

Results of posthoc HSD Tukey's test for percent cover in high elevation sites

B) Low elevation, Cover

time since wattle removal (years)	Vegetation	Difference in cover	confidence interval (95%)		p adj
			lower	upper	
1	shola: invasive	0.05	-10.826	10.926	1
1	shola: native*	-33.32	-44.196	-22.445	0
2	native: invasive*	33.28	22.405	44.156	0
2	shola: invasive	-3.82	-14.696	7.056	0.998
2	shola: native*	-37.1	-47.976	-26.225	0
3	native: invasive*	74.305	63.43	85.181	0
3	shola: invasive	-2.425	-13.301	8.451	1
3	shola: native*	-76.73	-87.606	-65.855	0
4	native: invasive*	52.395	41.52	63.271	0
4	shola: invasive	-7.97	-18.846	2.906	0.447
4	shola: native*	-60.365	-71.241	-49.49	0
5	native: invasive*	55.53	44.655	66.406	0
5	shola: invasive	-4.91	-15.786	5.966	0.971
5	shola: native*	-60.44	-71.316	-49.565	0

Results of posthoc HSD Tukey's test for percent cover in low elevation sites

C) High elevation, species richness

time since wattle removal (years)	Vegetation	Difference in species richness	confidence interval (95%)		p adj
			lower	upper	
1	native: invasive*	3.90	3.02	4.78	0.00
1	shola: invasive*	-0.98	-1.86	-0.10	0.01
1	shola: native*	3.76	2.88	4.64	0.00
2	native: invasive*	-1.28	-2.16	-0.40	0.00
2	shola: invasive*	3.74	2.86	4.62	0.00
2	shola: native*	-0.90	-1.78	-0.02	0.04
3	native: invasive	-0.24	-1.12	0.64	1.00
3	shola: invasive*	3.64	2.76	4.52	0.00
3	shola: native*	-0.88	-1.76	0.00	0.05
4	shola: invasive*	-4.88	-5.76	-4.00	0.00
4	shola: native*	-5.04	-5.92	-4.16	0.00
4	native: invasive*	2.10	1.22	2.98	0.00
5	native: invasive*	-2.34	-3.22	-1.46	0.00
5	shola: invasive*	-4.52	-5.40	-3.64	0.00
5	shola: native*	0.00	0.00	0.00	0.00

Results of posthoc HSD Tukey's test for species richness in high elevation sites

D) Low elevation, species richness

time since wattle removal (years)	Vegetation	difference in species richness	confidence interval (95%)		p adj
			lower	upper	
1	native: invasive*	2.62	1.757	3.484	0
1	shola: invasive	-0.58	-1.444	0.284	0.603
1	shola: native*	2.1	1.237	2.964	0
2	native: invasive*	-1.34	-2.204	-0.477	0.001
2	shola: invasive*	4.52	3.657	5.384	0
2	shola: native*	-1	-1.864	-0.137	0.008
3	native: invasive*	3.86	2.997	4.724	0
3	shola: invasive	-0.82	-1.684	0.044	0.084
3	shola: native*	3.34	2.477	4.204	0
4	native: invasive*	-1.5	-2.364	-0.637	0.001
4	shola: invasive*	-3.2	-4.064	-2.337	0
4	shola: native*	-3.44	-4.304	-2.577	0
5	native: invasive*	-5.52	-6.384	-4.657	0
5	shola: invasive*	-4.68	-5.544	-3.817	0
5	shola: native*	-4.84	-5.704	-3.977	0

Results of posthoc HSD Tukey's test for species richness in low elevation sites

2. Generalized Linear Mixed Models

Summary of GLMMs that were run for each of the responses is given in the form of tables.

(A)

Total percentage cover	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation + Time since wattle removal + **(Elevation x Time since wattle removal)***	6	912.931	**0***	1	0.838
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	918.528	5.598	0.061	0.052
Initial wattle density + Elevation + Time since wattle removal	6	918.568	5.638	0.06	0.051
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	919.645	6.715	0.035	0.03
Elevation + Time since wattle removal	5	921.339	8.408	0.015	0.013
Initial wattle density + Elevation	5	921.831	8.9	0.012	0.01
Time since wattle removal + Initial wattle density	5	923.203	10.272	0.006	0.005
Elevation	4	924.595	11.665	0.003	0.003
Time since wattle removal	4	925.943	13.013	0.002	0.002
Initial wattle density	4	926.354	13.424	0.002	0.002

Summary of GLMM results for ten component models with response variable as total percentage cover. The model that best explains the total cover data includes elevation, time since wattle removal and the interaction between them.

(B)

Native grassland species cover	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	900.439	**0**	1	0.476
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	902.346	**1.907**	0.386	0.184
Initial wattle density + Elevation + Time since wattle removal	6	902.363	**1.924**	0.383	0.182
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	904.196	3.757	0.153	0.073
Initial wattle density + Elevation	5	905.463	5.025	0.082	0.039
Time since wattle removal + Initial wattle density	5	906.826	6.388	0.042	0.02
Elevation + Time since wattle removal	5	906.862	6.424	0.041	0.02
Initial wattle density	4	909.819	9.38	0.01	0.005
Elevation	4	909.953	9.515	0.009	0.005
Time since wattle removal	4	911.534	11.096	0.004	0.002

Summary of GLMM results for ten component models with response variable as percentage cover of native grassland species. Multiple models give a delta AIC between zero and two, but none of the parameters are significant enough to explain the data.

(C)

Wattle cover	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation* + Initial wattle density + **(Elevation x Initial wattle density)***	6	524.893	**0**	1	0.599
Initial wattle density + Elevation	5	528.303	3.41	0.182	0.109
Initial wattle density + Elevation + Time since wattle removal	6	528.627	3.735	0.155	0.093
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	529.458	4.565	0.103	0.062
Elevation	4	529.549	4.656	0.098	0.059
Elevation + Time since wattle removal	5	530.029	5.136	0.077	0.046
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	531.466	6.573	0.038	0.023
Initial wattle density	4	534.095	9.203	0.011	0.007
Time since wattle removal + Initial wattle density	5	534.192	9.299	0.01	0.006
Time since wattle removal	4	537.794	12.901	0.002	0.001

Summary of GLMM results for ten component models with response variable as percentage cover of regenerated wattle. The model that best explains the total cover data includes elevation, initial density of wattle, and the interaction between them. The interaction term is the most significant followed by elevation.

(D)

Species richness	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation	4	430.561	**0**	1	0.266
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	430.581	**0.021**	0.99	0.263
Elevation + **Initial wattle density*** + **(Elevation x Initial wattle density)***	6	431.275	**0.714**	0.7	0.186
Elevation + Time since wattle removal	5	432.212	**1.652**	0.438	0.117
Initial wattle density + Elevation	5	433.591	3.031	0.22	0.059
Time since wattle removal	4	433.887	3.326	0.19	0.051
Initial wattle density + Elevation + Initial wattle density	6	435.22	4.66	0.098	0.026
Initial wattle density	4	435.543	4.983	0.083	0.022
Time since wattle removal + Initial wattle density	5	437.073	6.513	0.039	0.011
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	439.045	8.484	0.015	0.004

Summary of GLMM results for ten component models with response variable as species richness. Multiple models fit the criteria for choosing the best fit model for the given data. However, the most significant parameters are the initial wattle density and the interaction between elevation and initial wattle density.

(E)

Native grassland species richness	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation	4	396.818	**0**	1	0.296
Elevation + Time since wattle removal + **(Elevation x Time since wattle removal)***	6	397.702	**0.885**	0.643	0.191
Time since wattle removal	4	398.552	**1.734**	0.421	0.125
Elevation + Time since wattle removal	5	399.191	2.374	0.306	0.091
Initial wattle density	4	399.285	2.467	0.292	0.087
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	399.431	2.613	0.271	0.081
Initial wattle density + Elevation	5	399.667	2.849	0.241	0.072
Time since wattle removal + Initial wattle density	5	401.689	4.871	0.088	0.026
Initial wattle density + Elevation + Initial wattle density	6	402.019	5.202	0.075	0.022
Initial wattle density + Time since wattle removal + (Initial wattle density * Time since wattle removal)	6	402.985	6.168	0.046	0.014

Summary of GLMM results for ten component models with response variable as the number of native grassland species. Multiple models fit the criteria for choosing the best fit models. However, the significant parameter in these models is the interaction effect between elevation and time since wattle removal.

(F)

Soil C	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Initial wattle density + Time since wattle removal + Elevation	6	966.062	**0**	1	0.295
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	966.085	**0.024**	0.989	0.292
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	966.417	**0.355**	0.838	0.247
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	968.593	2.531	0.283	0.084
Initial wattle density + Elevation	5	970.445	4.383	0.112	0.033
Elevation + Time since wattle removal	5	970.639	4.577	0.102	0.03
Initial wattle density + Time since wattle removal	5	972.142	6.08	0.048	0.015
Elevation	4	975.185	9.123	0.011	0.004
Time since wattle removal	4	975.646	9.584	0.009	0.003
Initial wattle density	4	976.53	10.468	0.006	0.002

Summary of GLMM results for ten component models with response variable as percentage by weight of soil carbon content. Multiple models fit into the criteria of choosing the best fit model. However, none of the parameters significantly explain the data. The most important parameter among all predictors in the elevation.

(G)

Soil N	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	932.262	**0**	1	0.629
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	934.133	**1.871**	0.393	0.247
Initial wattle density + Time since wattle removal + Elevation	6	936.515	4.254	0.12	0.075
Elevation + Time since wattle removal	5	938.666	6.404	0.041	0.026
Initial wattle density + Elevation	5	939.542	7.281	0.027	0.017
Elevation	4	941.675	9.413	0.01	0.006
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	944.489	12.227	0.003	0.002
Initial wattle density + Time since wattle removal	5	947.396	15.134	0.001	0.001
Time since wattle removal	4	949.462	17.2	0.001	0.001
Initial wattle density	4	951.073	18.811	0.001	0.001

Summary of GLMM results for ten component models with response variable as percentage by weight of soil nitrogen content. Multiple models fit the criteria for choosing the best fit model. However, the only elevation significantly explains the data.

(H)

Soil C: N	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation*	4	457.02	**0**	1	0.464
Elevation + Time since wattle removal	5	459.345	2.325	0.313	0.146
Initial wattle density + Elevation	5	459.821	2.802	0.247	0.115
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	459.901	2.881	0.237	0.11
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	460.055	3.036	0.22	0.102
Initial wattle density + Time since wattle removal + Elevation	6	462.147	5.128	0.078	0.036
Time since wattle removal	4	464.12	7.101	0.029	0.014
Initial wattle density	4	464.59	7.57	0.023	0.011
Initial wattle density + Time since wattle removal	5	466.473	9.454	0.009	0.005
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	468.712	11.692	0.003	0.002

Summary of GLMM results for ten component models with response variable as soil carbon: nitrogen ratio. Elevation is the only parameter that significantly explains the C: N data.

(I)

Invasive species cover	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation + Time since wattle removal + **(Elevation x Time since wattle removal)***	6	721.812	**0**	1	0.567
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	724.951	3.14	0.209	0.118
Initial wattle density + Elevation + Time since wattle removal	6	725.467	3.656	0.161	0.092
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	725.952	4.141	0.127	0.072
Initial wattle density + Elevation	5	726.262	4.451	0.109	0.062
Elevation + Time since wattle removal	5	727.892	6.081	0.048	0.028
Time since wattle removal + Initial wattle density	5	728.099	6.288	0.044	0.025
Elevation	4	728.673	6.862	0.033	0.019
Initial wattle density	4	728.825	7.014	0.03	0.017
Time since wattle removal	4	731.208	9.397	0.01	0.006

Summary of GLMM results for ten component models with response variable as percentage cover of all invasive species. The model that best explains the invasive cover data includes elevation, time since wattle removal and the interaction between them.

(J)

Shola species cover	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Initial wattle density* + Time since wattle removal + (**Initial wattle density x Time since wattle removal**)*	6	406.903	**0**	1	0.287
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	408.035	**1.132**	0.568	0.163
Initial wattle density* + Elevation + Time since wattle removal	6	408.848	**1.946**	0.379	0.109
Elevation + Time since wattle removal	5	409.103	2.2	0.333	0.096
Time since wattle removal + Initial wattle density	5	409.38	2.478	0.29	0.084
Elevation + Initial wattle density + (Elevation x Initial wattle density)	6	409.597	2.694	0.261	0.075
Initial wattle density + Elevation	5	410.218	3.315	0.191	0.055
Time since wattle removal	4	410.451	3.549	0.17	0.049
Elevation	4	410.656	3.753	0.154	0.044
Initial wattle density	4	410.785	3.882	0.144	0.042

Summary of GLMM results for ten component models with response variable as percentage cover of shola species. Multiple models fit the criteria that give the best fit models. However, the parameters that are significantly important to explain the data are, the interaction effect of initial wattle density and time since wattle removal, as well as just the initial density of wattle.

(K)

Invasive species richness	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Elevation*	4	148.078	**0**	1	0.729
Elevation + Time since wattle removal	5	151.855	3.778	0.152	0.111
Elevation + Time since wattle removal + (Elevation * Time since wattle removal)	6	153.497	5.42	0.067	0.049
Initial wattle density + Elevation	5	153.749	5.672	0.059	0.043
Time since wattle removal	4	153.909	5.832	0.055	0.04
Initial wattle density	4	156.215	8.138	0.018	0.013
Elevation + Initial wattle density + (Elevation * Initial wattle density)	6	156.792	8.715	0.013	0.01
Initial wattle density + Elevation + Initial wattle density	6	157.485	9.408	0.01	0.007
Time since wattle removal + Initial wattle density	5	159.831	11.754	0.003	0.003
Initial wattle density + Time since wattle removal + (Initial wattle density * Time since wattle removal)	6	165.399	17.322	0.001	0.001

Summary of GLMM results for ten component models with response variable as invasive species richness. The model that best explains the total cover data includes elevation as the predictor and the significant variable.

(L)

Native shola species richness	df	AIC	Δ AIC	relative likelihood	ω(AIC)
Initial wattle density	4	102.31	**0**	1	0.366
Elevation*	4	103.798	**1.489**	0.476	0.174
Initial wattle density + **Elevation***	5	103.927	**1.618**	0.446	0.163
Elevation* + Initial wattle density + **(Elevation x Initial wattle density)***	6	104.127	**1.818**	0.404	0.148
Time since wattle removal + Initial wattle density	5	106.068	3.759	0.153	0.056
Elevation + Time since wattle removal	5	107.208	4.899	0.087	0.032
Time since wattle removal	4	107.591	5.282	0.072	0.027
Initial wattle density + Elevation + Initial wattle density	6	107.596	5.287	0.072	0.027
Elevation + Time since wattle removal + (Elevation x Time since wattle removal)	6	110.691	8.382	0.016	0.006
Initial wattle density + Time since wattle removal + (Initial wattle density x Time since wattle removal)	6	110.783	8.474	0.015	0.006

Summary of GLMM results for ten component models with response variable as total percentage cover. Multiple models fit the criteria to choose the best fit models for the data. However, the significant parameters include elevation and the interaction effect of elevation and initial wattle density.