The effect of introduced chital (*Axis axis*) on the structure, composition and functional traits of plant communities in the forests of the Andaman Islands

Thesis submitted towards the partial fulfilment of BS-MS Dual Degree Programme at

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Submitted by

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CERTIFICATE

This is to certify that this dissertation entitled "The effect of introduced chital (*Axis axis*) on the structure, composition and functional traits of plant communities in the forests of the Andaman Islands" 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 Krishna Anujan at the National Centre for Biological Sciences (NCBS), Bangalore, under the supervision of Dr. Jayashree Ratnam, Associate Director, Wildlife Biology and Conservation Programme, during the academic year 2014-2015.

JAYASHREE RATNAM   Date: 24TH MARCH 2015

DECLARATION

I hereby declare that the matter embodied in the report entitled "The effect of introduced chital (*Axis axis*) on the structure, composition and functional traits of plant communities in the forests of the Andaman Islands" are the results of the investigations carried out by me at the National Centre for Biological Sciences (NCBS), Bangalore, under the supervision of Dr. Jayashree Ratnam and the same has not been submitted elsewhere for any other degree.

Krishna Anujan   Date: 24th March, 2015

I dedicate this manuscript to that Ethiopian goatherd in the distant past, with his dancing goats, whose "magic beans" fuel research all over the world today.

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Abstract

Herbivory has been shown to have a major impact in driving community structure and species composition in various ecosystems around the world. Although ungulate-vegetation interactions have been prevalent for millennia, the last few centuries have seen rapid changes in ecosystems globally, due to human-mediated introductions and range expansions of ungulates. In the Andaman archipelago, an introduced mammalian herbivore, the spotted deer or chital (*Axis axis*) has been reported to cause extensive damage to vegetation. Chital, being browsers in this ecosystem with no native mammalian herbivores or predators, have the potential to alter successional trajectories and community and ecosystem dynamics. This study attempts to quantify the community-level effects of varying densities of this introduced ungulate on the evergreen forests in these islands. I predicted that, in response to increasing ungulate habitat use, plant communities would show shifts in a) the size class distribution of trees, b) the species composition, richness and relative species abundances of both understory and adult tree communities, and c) community-level leaf functional traits, such that modified communities would reflect a decrease in the abundances of species that are susceptible to herbivory and the functional traits that characterise such species.

Contrary to my expectations, I found no density-dependent effect of introduced chital on the size class distributions of trees or the abundances of understory and adult tree communities. However, intensity of habitat use by chital has a small but consistent negative effect on the species richness of the understory. A detrended correspondence analysis of community compositions, however suggests that understory community compositions are relatively similar across sites, while the compositions of adult tree species differ across sites. There appear to be community-wide shifts in SLA and leaf thickness along a gradient of increasing habitat use intensity by chital. Rather than resulting from shifts in species compositions, these shifts appear to result from within-species shifts in leaf functional traits along a gradient of herbivory. Species thus showed an unexpected degree of plasticity in these responses. Sampling needs to be done in islands with intermediate to high intensities of herbivory and more functional traits like leaf fibre and tannin content need to be quantified for a more robust understanding of the system.

Introduction

Mammalian herbivory plays a major role in determining the diversity, composition and structure of plant communities (Côté et al., 2004; Estes et al., 2014; Martin et al., 2011; Nuttle et al., 2014). Herbivores, through varied mechanisms like preferential browsing and physical disturbance, exert top-down control on ecosystems (Kardol et al., 2014). These mechanisms often act simultaneously to bring about net changes in community and ecosystem properties. They may heavily impact a few species but not others, increase heterogeneity in the environment by creating gaps and create novel and diverse microhabitats (Huntly, 1991). These effects can change, often non-linearly, with the intensity of herbivory (Estes et al., 2014; Senn and Haukiojat, 2014). At the population level, herbivory can alter selection pressure on various plant traits (Salgado-Luarte and Gianoli, 2012). At the community level, it can cause divergence of communities and shape meta-community structure (Suzuki et al., 2013) while at the ecosystem level, it can lead to alternative stable ecosystem states (Côté et al., 2004). Herbivores can also impact the trajectories of ecosystems by influencing terrestrial carbon cycling and carbon stocks (Tanentzap and Coomes, 2012).

Ungulate-vegetation interactions have had large-scale impacts on ecosystem trajectories for the past 500000 years (Bradshaw et al., 2003). With increased human migrations and colonisations in the nineteenth and twentieth century, several non-native ungulates have been introduced into ecosystems all over the world (Courchamp et al., 2003). There have also been several instances of human-mediated range expansions of ungulates into new territories (Waller and Alverson, 1997). The effects of these introductions are highly variable, difficult to evaluate and often delayed (Simberloff et al., 2013). Plant functional diversity has been shown to be an important determinant of the vulnerability of a community to herbivory, which feeds back into plant functional composition and diversity (Laliberté and Tylianakis, 2012; Schuldt et al., 2014). Functional traits of vegetation communities that are related to carbon balance, like specific leaf area (leaf area per unit mass, SLA), leaf toughness, leaf thickness and petiole length can come under direct selection as herbivore pressure is selective on palatability traits (Salgado-Luarte and Gianoli, 2012). Thus, the impacts of herbivory on plant community structure and function are often mediated through community-level changes in plant functional traits.

In many instances, the uncontrolled rise in ungulate populations has led to habitat destruction and effects that cascade through multiple trophic levels. This could be due to direct damage, competition for resources, altering the habitat quality for other species or even through habitat heterogeneity induced by predator avoidance or 'the ecology of fear' (Brown et al., 1999; Ripple and Beschta, 2004). A classic example is the case of Yellowstone National Park in the United States where extirpation of wolves (*Canis lupus*) caused a proliferation of elk (*Cervus elaphus*), leading to a decrease in browse plants. A significant shift in the size class distribution of browse plants was reported as a result of this intense herbivory (Beschta and Ripple, 2009). Wolf reintroduction resulted in the recovery of these species and of bison (*Bison bison*) and beavers (*Caster canadensis*) due to increased forage availability and competitive release (Ripple and Beschta, 2012). In the temperate forests of Patagonia, introduced red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) caused shifts in community composition through preferences in browsing (Barrios-Garcia et al., 2011). However, no effect of browsing was detected on litter and soil properties after excluding these deer from plots (Relva et al., 2014).

Island systems are particularly interesting in this context, since they are highly vulnerable to establishment of introduced species. Endemic species in islands have often evolved in the absence of stresses like strong competition and herbivory (Courchamp et al., 2003). Introduced species in islands can lead to extinctions of endemic species while also affecting their simplified trophic webs. Because islands represent closed ecosystems with simplified trophic webs, they also allow for strong and conclusive inferences about ecosystem functioning (Courchamp et al., 2003). The introduction of Sitka black-tailed deer (*Odocoileus hemionus*) to the Haida Gwaii archipelago off the coast of British Columbia in Canada, more than 50 years ago, has resulted in lower vegetation cover in the understory, lower plant species richness, loss of biodiversity and a simplification of community composition (Allombert et al., 2005; Martin et al., 2011; Stockton et al., 2005). This has cascaded into a decrease in songbird abundance and diversity, possibly through declines in habitat quality (Allombert et al., 2005). The temperate forests of New Zealand have been subjected to massive introductions across taxa like plants, mammals, amphibians and arthropods. Long-term studies in these systems on goats (*Capra hircus*) and white-tailed deer (*Odocoileus virgianus*) using exclosures have revealed

effects on seedling establishment, seedling survivorship as well as shifts in species composition (Bellingham and Allan, 2003; Bellingham et al., 2010). These species have also been shown to alter existing interactions, like plant-soil feedbacks, causing ecosystem dysfunction (Kardol et al., 2014).

The Andamans islands, an archipelago in the Bay of Bengal, face a similar situation. In the early 1900s, spotted deer or chital (*Axis axis*), along with barking deer (*Muntiacus muntjak*) and hog deer (*Axis porcinus*) were introduced into the islands. Since then, owing to the absence of predators and native competitors (the only other mammalian herbivore in the island are the Andaman wild pig, *Sus scrofa andamanensis*), the populations of chital have grown and are now widespread in almost all the islands of the archipelago. In these habitats, chital extensively browse in the understory, as well as feed on the leaf litter (personal observation), potentially altering multiple community and ecosystem properties.

This system provides a natural microcosm experiment to study the mechanisms that shape and maintain the high richness and diversity that is characteristic of tropical evergreen forests. Chital, being a potential keystone herbivore, can have impacts on multiple trophic levels, causing community or species-level shifts in functional traits, altering community composition and modifying interactions with other species and the abiotic environment. They could also affect the partitioning of carbon stocks in this carbon-rich landscape. Although there are several studies that deal with the effect of introductions in temperate islands pertaining to the structure, composition and function of ecosystems, there are few studies that deal with this question in a tropical scenario where biomass, productivity and turnover are much higher. A comprehensive understanding of the system, its networks and feedbacks is a mandatory foundation for any planned management effort.

This study employs the principles of community ecology to understand the impacts of deer introduction on the vegetation of the evergreen forests of the Andaman islands. It poses the following specific questions:

i. Has chital herbivory impacted the size class distributions of woody tree species?

ii. Does the intensity of habitat use by chital affect species richness and abundance of the understory and adult trees at the island level?

iii. Are the species composition and dominance of understory and adult tree communities altered by herbivory? Is there a mismatch in species compositions of understory and overstory tree communities in response to introduced herbivores?

iv. Is there a community-level shift in leaf functional traits of understory species, namely, SLA and leaf thickness, as a response to intensity of habitat use by chital?

The response of the vegetation community is expected to vary along a gradient of intensity of herbivory rather than being an on-off response. As a proxy for intensity of herbivory by chital, the study uses dung pellet group counts and encounter rates in camera traps to build an index of habitat use by chital across the islands. The study was conducted in six islands where populations of chital are assumed to be closed and independent. The abiotic conditions and biogeography of the islands being similar, the study also assumes similar community properties prior to introduction. Since no data about community structure before introduction is available, Little Andaman, the only island in the archipelago without the presence of chital, sizable enough for community studies, was chosen as the control.

The following predictions were made about the responses of the system:

i. The size class distributions of the adult tree community in the islands with chital are expected to be skewed, with lower frequencies of trees with smaller girths. In case of high intensities of herbivory, missing size classes are expected in the size class distribution of trees because of impaired recruitment.

ii. Herbivory has an immediate effect on understory properties through browsing. The abundance of understory individuals, measured as number of stems in a plot, is expected to decrease with an increasing intensity of habitat use by chital.

iii. All other parameters being similar, the species richness of the understory is expected to decrease along a gradient of increasing habitat use by the introduced herbivore. Given sufficient time, this is expected to reflect in a decrease in species richness in the adult tree community.

iv.   The species composition of the understory is expected to shift towards dominance of less palatable or herbivore-resistant species. Given sufficient time, this composition shift is expected to be reflected in the adult tree community.

v.   Along a gradient of herbivory, leaf thickness is expected to increase at the community level since it directly affects the damage incurred by a plant from herbivory. Plants with higher leaf thickness are expected to be avoided by herbivores, thus increasing their proportion in the community.

vi.   Along a gradient of intensity of habitat use by chital, the specific leaf area (SLA) at the community level is expected to decrease through species composition differences. This is following the assumption that leaves with higher fibre content and toughness, are less palatable to chital, which leads to a higher survival of seedlings with these properties. Leaves with higher fibre content would have lower SLA due to higher structural carbon in a unit area.

There is a lack of literature from the Andamans on the community composition of its adult tree as well as understory vegetation communities and their correlates. This study is the first of its kind in this landscape that integrates effects on community species composition, size structure and functional traits in evergreen forests in both the understory and overstory.

Materials and Methods

<u>The study system</u>

The Andamans is an archipelago of over 250 continental islands in the Bay of Bengal. They are part of the larger archipelago of the Andaman and Nicobar Islands and are separated from the Nicobar group by the 10˚ channel. These islands, covering a total geographical area of 6286 km^2, house diverse ecosystems such as tropical wet evergreen forests, semi-evergreen forests, littoral forests and mangroves surrounded by coral reef systems. These islands also harbour several endemic species of trees, birds, insects and reptiles. In this region, with biogeography similar to the Malayan peninsula, are dense tropical evergreen forests with disproportionately high carbon stocks (Sankaran et al., unpublished data) relative to tropical forests with similar climatic conditions in mainland India. Introduced to the island in the early 1900s, chital (spotted deer, *Axis axis*) have spread to most of the islands in the archipelago, in the absence of predators and native competitors (Ali and Pelkey, 2013). An earlier study conducted across the islands (Ali, 2004) reported low seedling densities in many evergreen forests with introduced deer, loss of vegetation cover in the understory in several areas and resultant soil erosion. The degradation of habitat was also recorded in a study that compared NDVI, an index of vegetation density, from satellite images between sites over time (Ali and Pelkey, 2013). Another study recorded a decrease in litter herpetofaunal densities and richness in highly browsed islands (Mohanty, 2013).

Field sampling for this study was conducted from September 2014 to January 2015, in six islands of the archipelago; Alexandra, Hobday, Redskin, Tarmugli, Rutland and Little Andaman. The first four are part of the Mahatma Gandhi Marine National Park which was created in 1983 and has been protected under the Wildlife Protection Act (1972) since. Rutland lies adjacent to the park, to its southeast and its forests houses two settlements and a large area of reserve forest. Little Andaman is the southernmost island of the Andaman archipelago and the only island that has no records of the presence of deer. It, therefore, serves as the control in this study. In Rutland and Little Andaman comparative areas of evergreen forest, away from human habitation were selected for the study.

The study area was selected following an initial reconnaissance of the islands. The above six islands were chosen because of similar biogeography, climatic conditions and relatively low disturbance from logging. The areas sampled are relatively undisturbed by cattle and other domestic herbivores. Moreover, similar data had been collected in an earlier study (Ali, 2004), making longitudinal comparisons of shifts in community structure and composition possible.

The methodology of the study was designed to cover the following three broad objectives:

1. Estimating an index of habitat use by chital

2. Measuring parameters of community structure and composition

3. Quantifying leaf functional traits

Estimating an index of habitat use by chital

Distance sampling using line transects has been shown to be the most accurate method for density estimation of large mammals. However the habitat in these islands are dense and closed, rendering probability of sightings very low. Since a robust estimation of actual densities was not feasible within the scope of this study, an index of habitat use was arrived upon by two independent methods : camera trapping and dung pellet group counts. An index of habitat use was preferred since densities of chital do not affect vegetation community properties directly, but act through browsing intensity and habitat use intensity making it a reasonable choice for a predictor. For the purposes of the study, we make the assumption that the population of chital in an island is closed. Although there have been records of chital swimming across channels, these are assumed to not contribute significantly to our estimate.

Camera trapping is used regularly in estimating populations of large mammalian herbivores, especially those of an elusive nature. Although line transects have been shown to provide more accurate estimates of densities than camera trapping, the

nature of the habitat and the duration of the study made this method unsuitable in this case. Camera trapping is a non-invasive method that requires minimal labour and provides robust estimates of population densities, especially in terrains where other methods fail (Karanth and Nichols, 1998; Rowcliffe and Carbone, 2008; Silveira et al., 2003). Cameras with infrared sensors have been used extensively in estimating population densities of organisms with morphologically identifiable markers by using a capture-recapture methodology. For organisms that are not visually distinguishable, encounter rates have been shown to correlate with estimates of density from other independent methods (Rovero and Marshall, 2009; Rowcliffe et al., 2008).

In the islands sampled, encounter rates of chital in cameras were measured using Bushnell Trophy Cam Trail Cameras. The points for deploying these cameras were randomly chosen within a grid of 40 hectare cells using QGIS Version 2.4, 'Chugiak'. The camera was then attached to a tree, opportunistically within a radius of 30 m to obtain maximum field of vision and probability of sighting. 10 cameras were deployed for a stretch of 5-7 days in each island during the course of sampling. The cameras were set to click three photographs on a motion-trigger at intervals of 1s each. The photographs captured were then transferred from the SD card and the images analysed visually for presence of deer. An independent observation was counted only if an individual was sighted in one of the three photographs. Encounter rates were then calculated by dividing the total number of independent sightings with the total number of trap nights in an island. Camera trapping was carried out in the islands of Alexandra, Redskin, Tarmugli and Rutland with a total of 228 trap nights, ranging from 49 trap nights in Tarmugli to 65 trap nights in Redskin.

As an independent estimator of deer habitat use intensity, dung pellet group counts were also used. This is yet another method that has been shown to be effective in estimation of densities in areas of poor visibility and low abundances (Camargo-Sanabria and Mandujano, 2011; Eberhardt and Etten, 1956), as is the case of the habitat in question. Dung pellet groups were counted in belt transects of size 100m x 5m. The start points were picked using QGIS from a grid of cell size 20 hectares and an arbitrary, fixed, northern direction was chosen for each transect. In the larger islands of Rutland and Little Andaman where it was infeasible to cover the entire

area, ~25 points were chosen from a similar-sized grid in large patches of reserve forest (Jahazi in Rutland and Krishnanallah in Little Andaman). Since land cover information was not available at the necessary resolution, Google earth images were used to decide the boundaries of the islands. In the field, the points were located using a Garmin e-trex Vista Global Position System and ropes were laid towards an arbitrary bearing of north, using a Suunto hand-held compass. Within the transects, any dung pellet group that fell outside twice the radius of any other group, visually, was counted and the total within a 100m x 5m transect was recorded. Since the region has high temperature, humidity and rainfall, resulting in high rates of decomposition, errors in estimating densities by counting dung accumulated over seasons was ruled out.

It has been repeatedly shown that line transect counts of dung pellet groups provides the most reliable estimate of densities over other count methods such as faecal accumulation rates (FAR) and faecal standing crop (FSC). Although line transects provide a higher accuracy than belt transects (Camargo-Sanabria and Mandujano, 2011), this study uses counts from belt transects due to their relative ease of execution given the habitat and the time frame of the study.

Measuring parameters of community structure and composition

For the adult tree community, belt transects of 100m x 5m, were walked in a fixed direction from a random start point, simultaneous with the dung counts. Within this transect, all individuals of adult, woody, angiosperm tree species, with their roots inside the plot, with girth >10 cm at breast height (1.3 m from the ground) were measured for girth at breast height (gbh) and identified at the species level. All species were identified using the vernacular, while the scientific names were identified for most of the species. A tree on the periphery was included if more than half its basal area was inside the plot. In case there was a hollow or a bulge at 1.3m, the measurement was taken at the first point above it, after the aberration. In case of buttress roots at the point of measurement, diameter of the tree was taken excluding these roots using two scales tangential to the tree trunk and measuring the distance between them.

Google earth images showing positions of transect start points.

For the understory community, three 5m x 5m quadrats were laid one each at the start, middle and end of the adult tree transects. The area of the quadrat was standardised after sampling in quadrats of side 1m, 3m and 5m in various islands during the reconnaissance and subsequently plotting species accumulation curves. Within each of these plots, seedling and saplings of woody tree species with height >10cm and gbh <10cm were counted species-wise. The lower cut-off was made to avoid recording seasonal fluctuations in understory species composition since the sampling period was spread out over the southwest monsoon, the intermediate dry period and the northeast monsoon. The upper cutoff was decided so as to demarcate the understory individuals from the adult trees.

<u>Quantifying leaf functional traits</u>

Plant functional traits are characteristics of a plant that determine its responses to a changing environment (Perez-Harguindeguy et al., 2013). The response of plants to novel stresses in the environment is often mediated through strategic shifts in functional traits to avoid or tolerate these stresses. In the context of this study, herbivory poses a novel stress to a climax community of evergreen forests with no native herbivore browsers. It is assumed that since the system has not been subjected to any major herbivory events in the past, leaf traits have not evolved to avoid herbivory. However, we predict community-level shifts in functional traits, Specific Leaf Area (SLA) and leaf thickness, in response to varying intensities of browsing pressure by chital.

From each of the six islands sampled, a minimum of 5 leaves each, from 5 individuals of the 20 most abundant species among saplings of woody trees counted in the understory quadrats were collected. The leaves were collected from individuals that fall within the browse height of chital, 1.5 m, and only mature leaves were collected. In the field station, measurements were taken on the leaves immediately before drying. Scan of each leaf lamina was taken on an A4 size paper, with 300 dpi resolution using a CanoScan Lide110 scanner. Fresh weight of leaf was measured using Essae FB 600 Precision Weighing Balance. Two measurements of leaf thickness were taken using a Mituyoyo digital calliper, one on either side of the primary vein. Care was taken to avoid the primary and secondary veins while thickness measurements were taken.

The leaves were then air dried in paper bags and further drying was done under a 100W lamp to prevent fungal growth in humid conditions. In the laboratory, the final step of drying was carried out in an oven after which dry weight of the samples were recorded using a weighing balance, Sartorius GP 3202.

<u>Statistical Analysis</u>

Statistical analyses, data management and reorganisation were performed using the statistical software R version 3.1.0, on the RStudio interface (Team, 2009). For community-level analyses, the package *vegan* (Oksanen et al., 2015) was used while *plyr* (Wickham, 2011) was used for restructuring and organising data. The graphical package *ggplot2* (Wickham, 2009) was also used for generating plots.

1. Index of habitat use intensity by chital

For calculating an index of habitat use by chital, the mean dung pellet count per 100m x 5m belt transect in an island was calculated. Encounter rates of chital from camera trap data were calculated as

$$\frac{Number\ of\ independent\ observations\ of\ chital\ in\ an\ island}{Number\ of\ trap\ nights\ in\ the\ island}$$

2. Response of vegetation community structure to intensity of herbivory

To observe the effects of herbivory on community structure of adult trees, histograms of girth classes in intervals of 10cm girth were plotted for each island. A bin size of 10cm was chosen to compare patterns of vegetation structure at a fine scale.

Cumulative density function of basal areas of adult trees in each of the islands was plotted simultaneously to visualise the accumulation of or basal area on adding trees with increasing girth or basal area. A plot of the accumulation of basal area along trees ranked by girths for each of the islands was also plotted. Missing size classes in an island would be characterised by the curve attaining the exponential phase before that of the control, Little Andaman.

3. Response of understory properties to intensity of herbivory

To compare the abundance of understory individuals, mean understory counts in an island were plotted against the mean dung pellet count from transects in that island.

To compare richness of the understory plots, species accumulation curves were plotted for all six islands. Further, the species richness, as the mean number of species observes per quadrat was plotted against the mean dung pellet count in the island. A generalised linear model using a Poisson family of distributions was used to test statistical significance of results.

4. Ordination of species composition across sites

Ordination is a method of multivariate analysis used widely in community ecology that groups sites according to multiple variables, species composition in this case, and gives a simplified graphical output for easy interpretation. A herbivore habitat use-induced variation in species composition can be visualised as a clustering of sites from an island along the principal axes of ordination. Detrended Correspondence Analysis (DCA) was chosen to analyse the variation in species composition in the data since the data had a large number of zeroes. Principal Components Analysis (PCA) showed a high degree of arch effect which is a common problem with data that has a large number of zero values. A DCA assumes an underlying unimodality in the data, which is often the case along gradients in community ecology (Zuur et al., 2007). The standard deviation of the principal axis of DCA was >3.5, warranting the use of DCA to remove the arch effect. The community ecology package *vegan* was used inside R for performing the PCA (Oksanen et al., 2015).

5. Analysis of functional traits

Specific Leaf Area (SLA) and leaf thickness of the 20 most abundant species in the understory of the six different islands were measured, with 5 biological replicates (individuals), each of which had 5 statistical replicates (leaves). Leaf thickness values could only be measured for samples from 4 of the 6 sites due to logistical constraints.

For calculating the area of the leaf, image conversion was done using the software ImageJ. The jpeg images of the scans were run in Black Spot Leaf Area Calculator (Varma and Osuri, 2013) to calculate number of pixels on the lamina . Images with faults were processed manually to remove darkness of margins of light in the lamina,

using the software GIMP before running Black Spot. The dpi value of the scans was then used to calculate the area of the leaf. SLA was then calculated as

$$Specific\ Leaf\ Area = \frac{Leaf\ area\ in\ cm2}{Dry\ weight\ in\ g}$$

Leaf thickness of each leaf was calculated as the mean of the two values measured per leaf.

The community weighted SLA and leaf thickness, calculated for each island as the mean SLA of each species weighted by its proportional abundance in the community, were plotted against the mean dung pellet count for each island. To observe intraspecific trends in SLA and leaf thickness, the means of these traits for species common across all the islands were plotted across an increasing gradient of herbivore habitat use intensity.

Results

Index of habitat use intensity by chital

The islands follow a gradient of herbivory with Little Andaman subjected to no herbivory by chital and Tarmugli having the highest intensity (Fig 1).
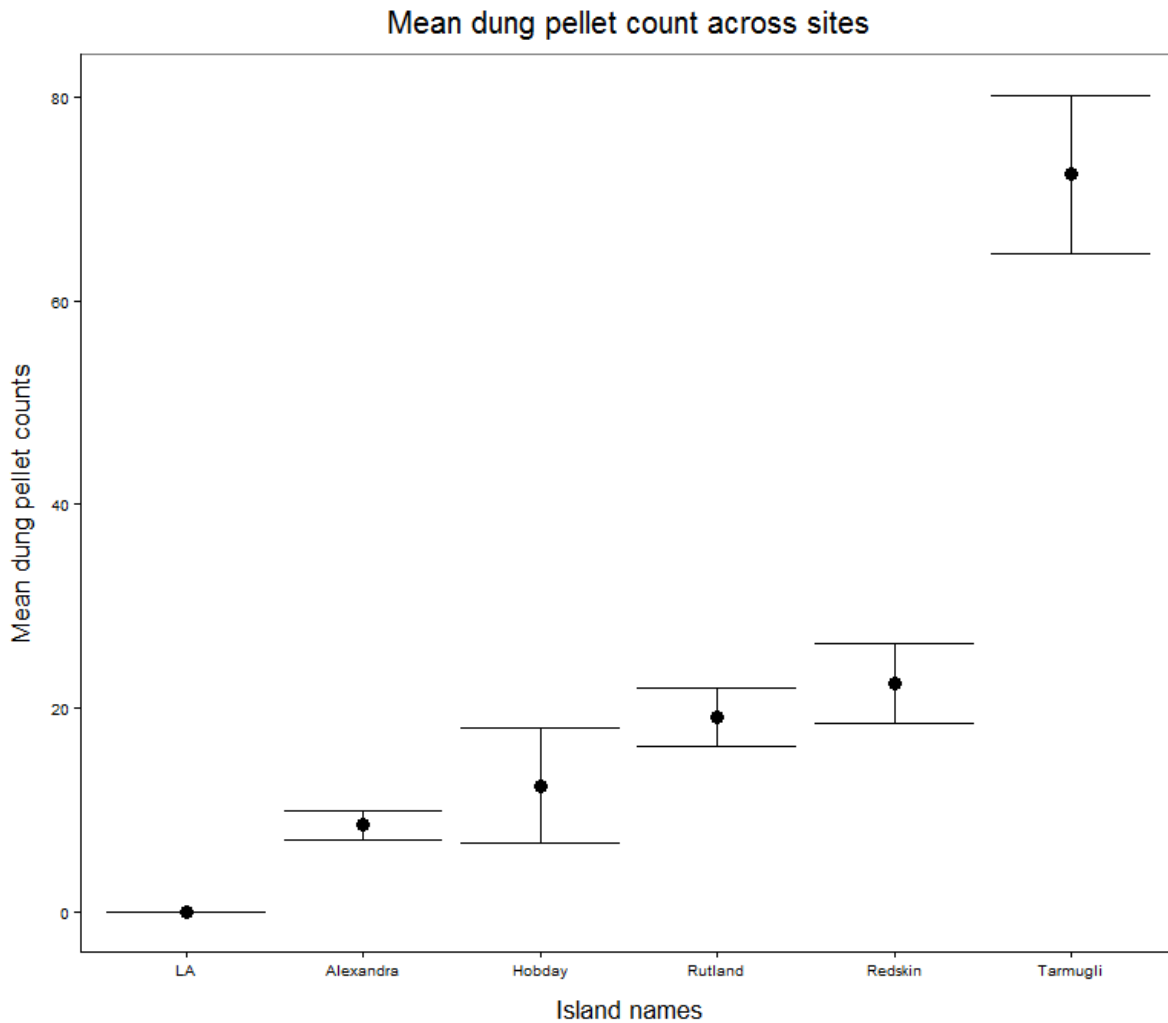

Figure 1. Means and standard errors of dung pellet group counts in 100m x 5m transects across islands. While there was no evidence of chital in Little Andaman, Tarmugli appears to have the highest levels of habitat use by chital amongst the study islands. All the other islands showed low to medium levels of habitat use by chital.

There was a significant correlation between the mean dung pellet counts and the encounter rates from camera trapping (adjusted R squared = 0.7923, p-value = 0.02743, Table 1). Encounter rates by camera trapping were not considered for further analysis since the number of encounters per island was too low for reliable estimation of encounter rates. However, the strong correlation between these two

measures of chital presence suggests that the relative ranking of these islands in terms of chital use as established by this study is robust.

Table 1. Encounter rates from camera trapping pooled across each island (Total number of trap nights=228). Cameras recorded the highest encounter rates with chital in Tarmugli and no encounters in Little Andaman. The remaining islands showed low to medium encounter rates.

Island	No. of encounters	No. of trap nights	Encounter rate
Little Andaman	0	0	0
Alexandra	3	55	0.054545
Rutland	10	59	0.169492
Redskin	15	65	0.230769
Tarmugli	17	49	0.346939

Response of vegetation community structure to intensity of herbivory

The histograms of size class distributions of adult tree communities are shown in Figure 2. Contrary to expectations, these data reveal no obvious missing size classes or shifts in abundances of different size classes of trees across the different islands. The island with the highest intensity of habitat use by chital, Tarmugli, shows a marginally higher proportion of the 10-20 cm girth class which could be an indicator of an early successional stage, a signature of disturbance.
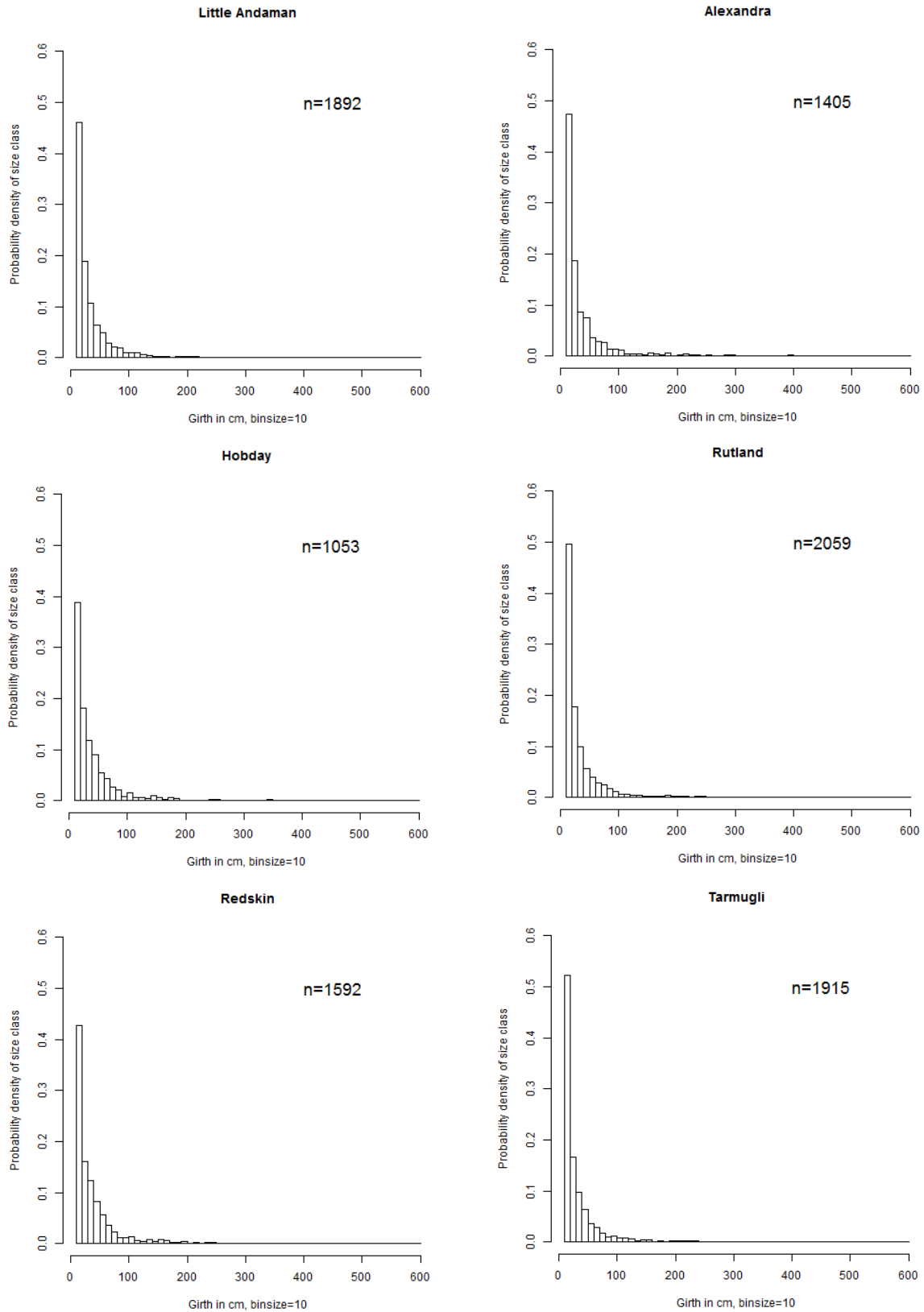
Fig 2. Histogram of adult tree girth classes in each island. Each bar represents the fractional abundance of the corresponding size class in the community. Bin size is 10cm. From top left to bottom right, islands are ordered in increasing order of herbivore habitat use intensity.

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Plots of cumulative basal area as all trees of specific gbh are sequentially added also show no qualitative differences between the islands (Figure 3). All islands are represented by saturating curves, coincident until 30% of the basal area. Again, this is not in accordance with the predictions, which expected a divergence at low basal areas.

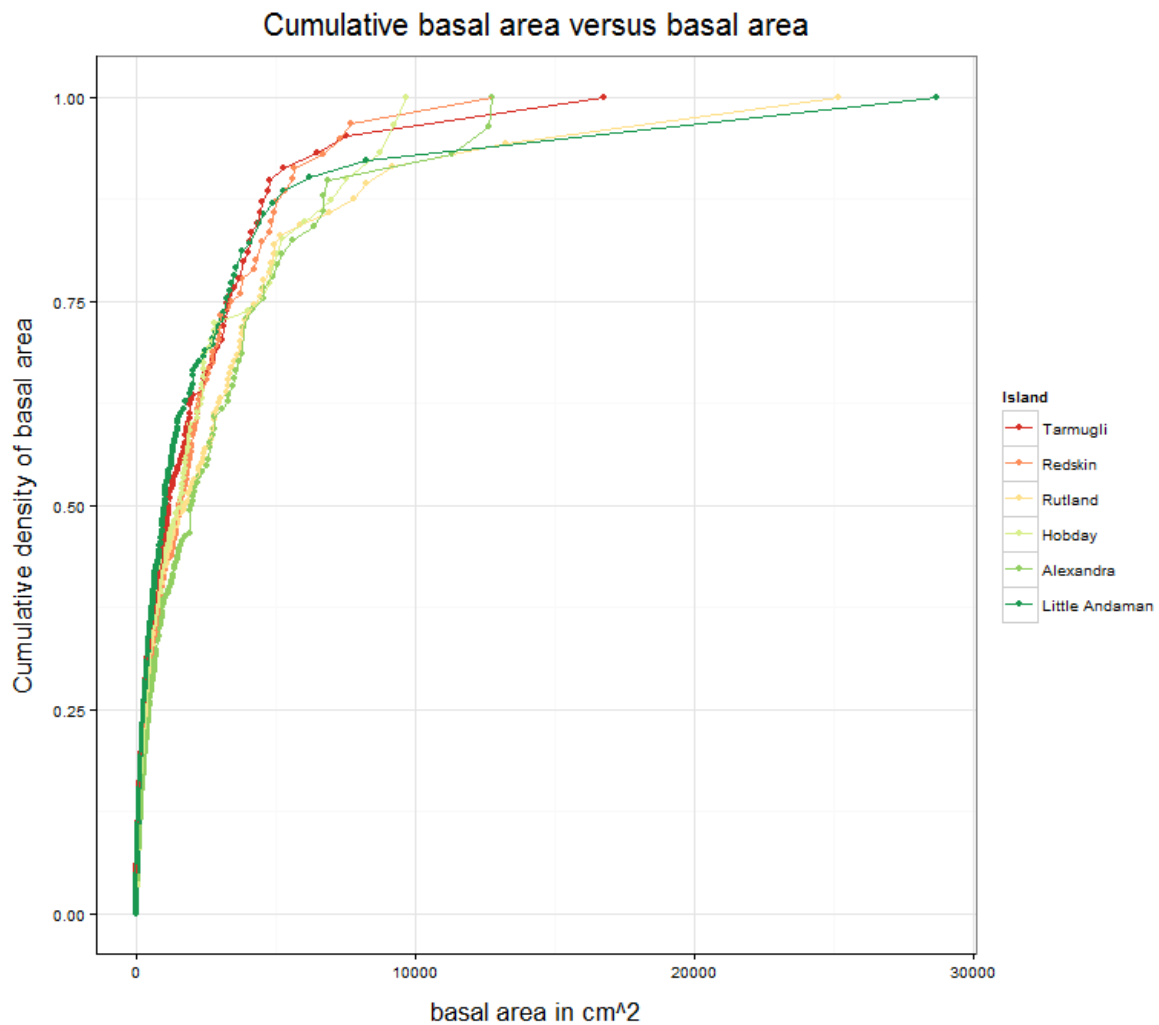

Fig 3. Cumulative density of basal area versus basal area. Y-value is the fraction of total basal area in cm^2 contributed by trees with basal area less than or equal to the value on the x-axis. Each curve represents the cumulative density of basal area pooled across transects from that island. Curves are coloured from dark green to dark red in increasing intensity of herbivore habitat use.

Figure 4 shows the cumulative density function of the basal area, as individual trees are sequentially added in order of increasing gbh. Again, and strikingly, these data show no qualitative differences between the six islands. There is no discernible divergence between the size classes of trees across islands with varying intensities of chital habitat use.

Cumulative basal area versus rank of tree

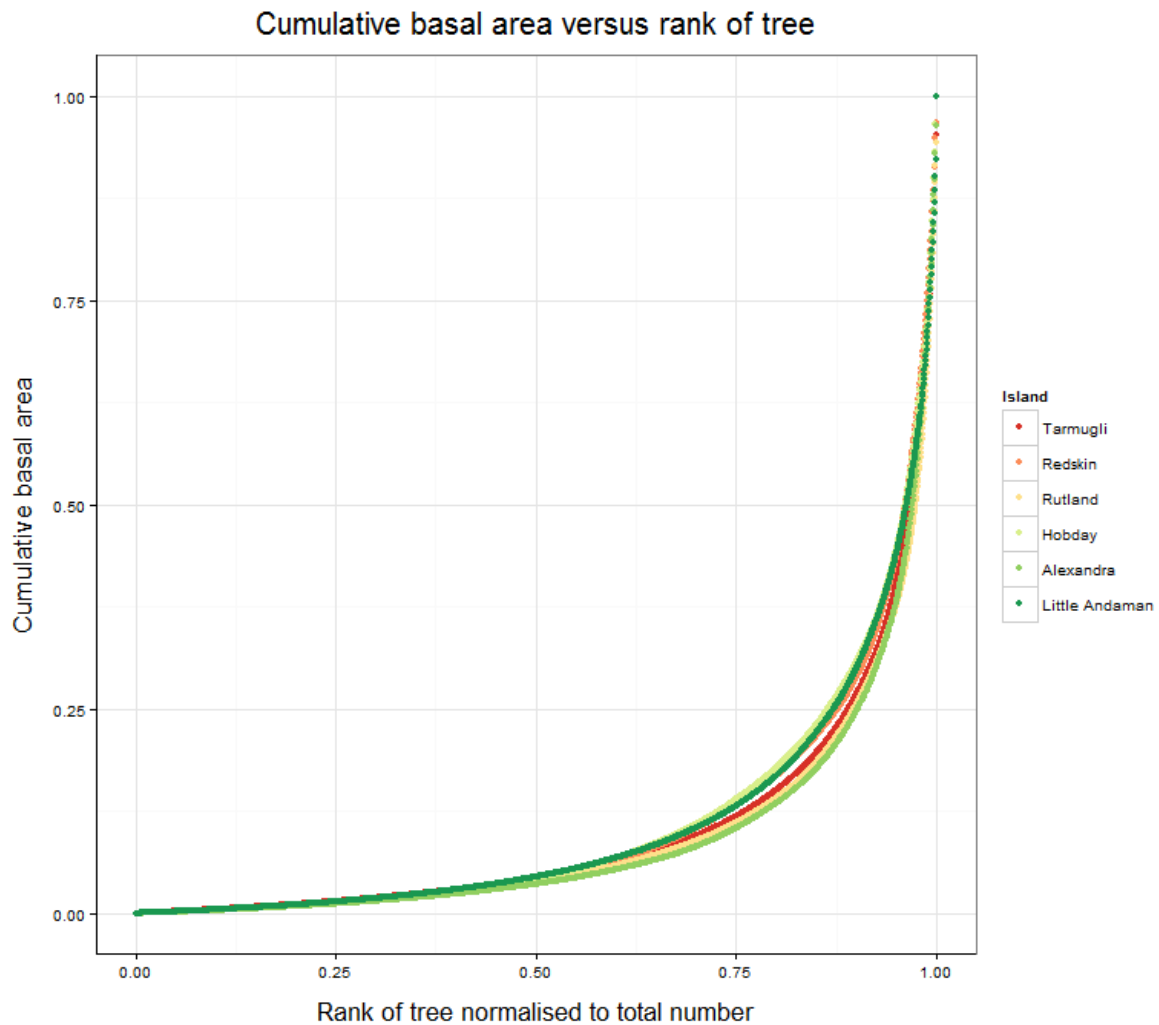Fig 4. Cumulative basal area versus rank of tree. X-value is the rank of the tree, ranked according to gbh, normalised to the number of trees in the island. Y-value is the corresponding cumulative basal area in cm^2. Each curve represents the cumulative density of basal area pooled across transects from that island. Curves are coloured from dark green to dark red in increasing intensity of herbivore habitat use.

Response of understory properties to intensity of herbivory

The mean numbers of understory individuals per plot (averaged across three 5m x 5m quadrats) show no relationship to the intensity of herbivory as indexed by mean pellet group counts (Figure 5). These data are again contrary to the prediction that high herbivory will result in lower densities of individuals in understory plant communities. Although the means appear to follow a roughly hump-shaped curve, the variability in the data makes inferences weak.
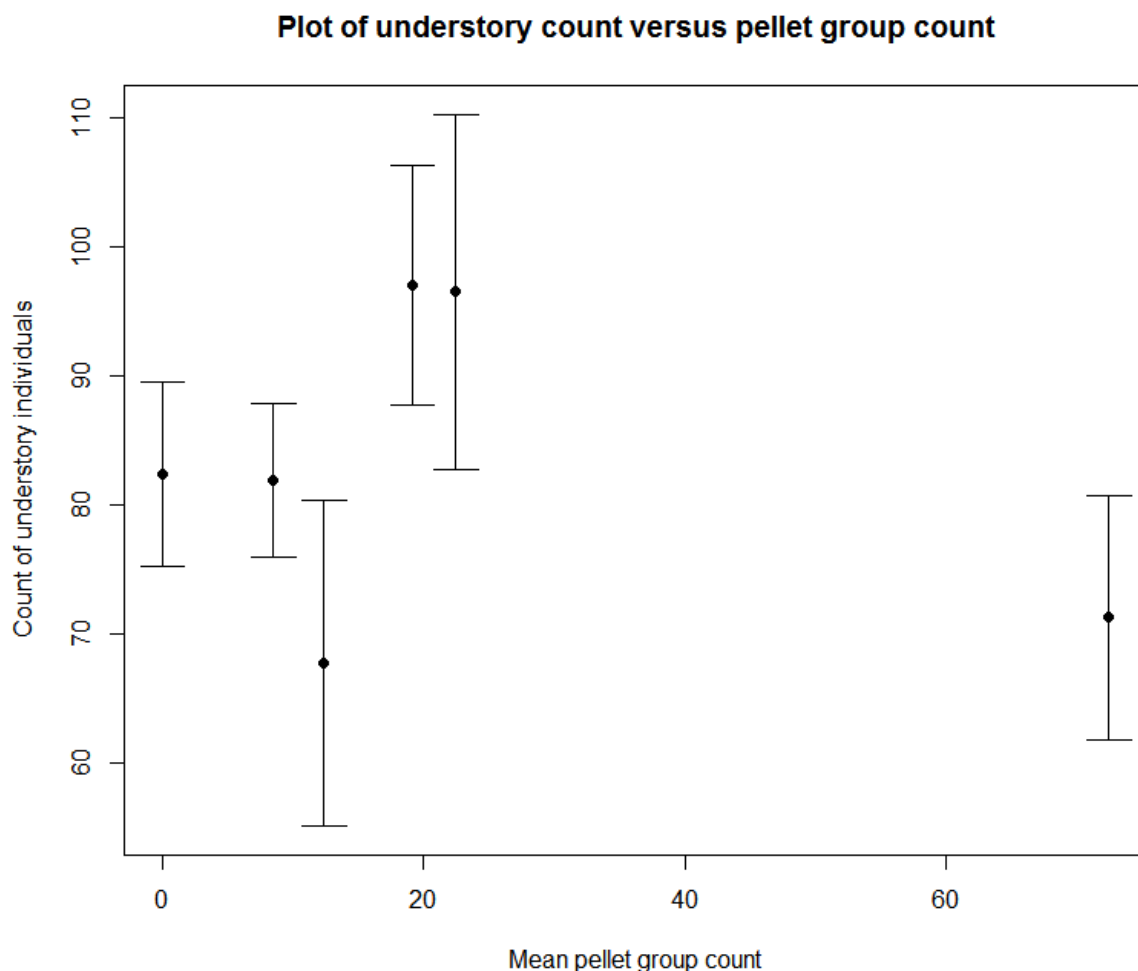

Fig 5. Plot of understory count versus pellet group count. X axis is the mean chital dung pellet group count for an island. The dots represent mean count of understory individuals in 3 5m x 5m plots, summed along transects. The bars represent the standard errors of estimation of the mean.

In contrast to the above, mean understory species richness (in 5m x 5m plots as well as when the data was pooled across 3 plots sampled along a 100m transect) declined sharply with increasing levels of herbivory as indexed by dung pellet counts (Figure 6). There is a marked difference between the control and the rest of the islands. Further, Tarmugli, the island with the highest level of herbivory, shows lowest levels of species richness in the understory. This graph suggests a non-linear or even an on-off response of understory richness with herbivory as opposed to the proposed gradient-driven response. More islands with high herbivory need to be sampled to make strong inferences.
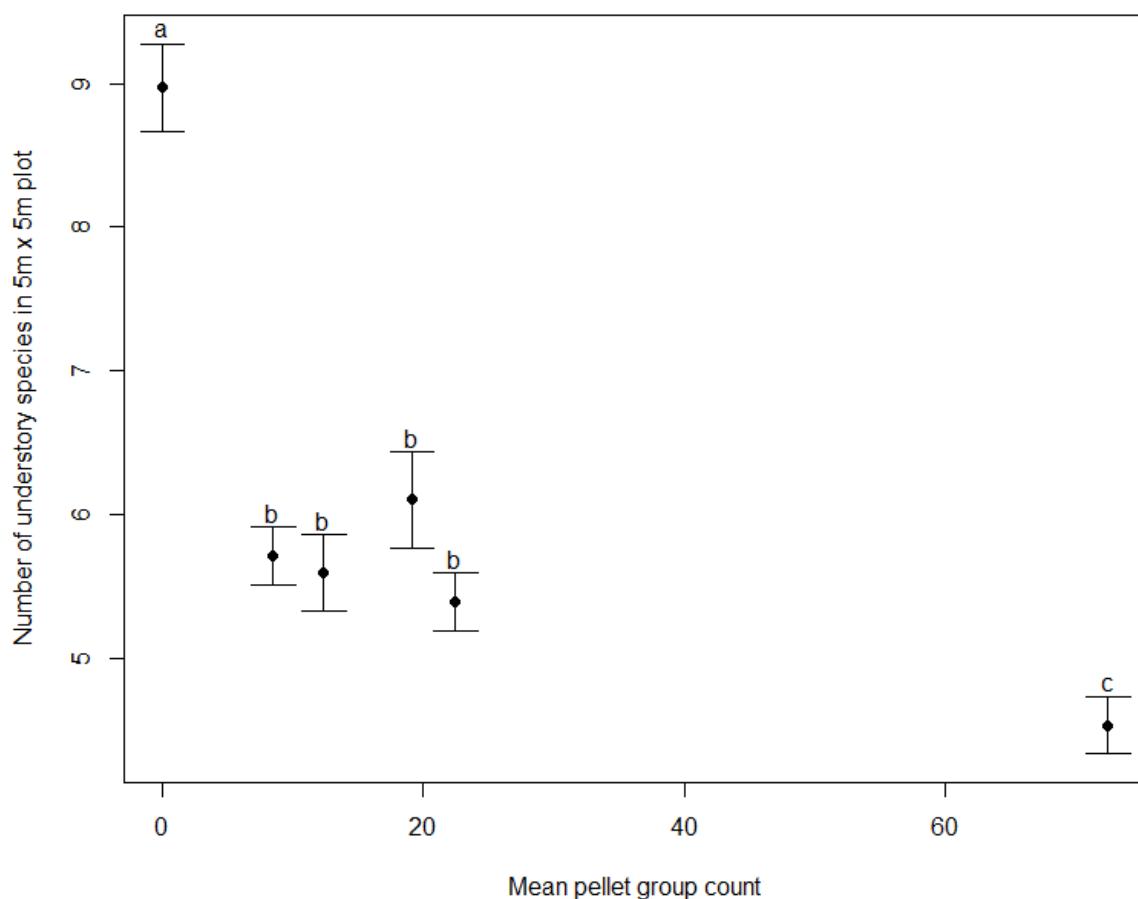

Fig 6. Mean species richness (5m x 5m plots) versus pellet group counts across the islands. The data show that species richness in the understory decreases with herbivory. The bars represent the standard errors of the means. GLM with Poisson family of errors, p<0.001. Distinct alphabets above standard error bars represent distributions statistically distinct (p<0.01) in GLM result.

Response of adult trees to intensity of herbivore habitat use

Since herbivory has persisted in the islands for nearly a century, the effect of reduced richness in the understory is expected to be reflected in species richness in the adult tree community but plot-level abundance is not expected to show a pattern, since trees in plots span a wide range of sizes. In accordance with the predictions, the number of adult tree stems in a plot shows no pattern along a herbivory gradient. There appears to be a hump-shaped pattern in the total basal area of adult trees along a herbivory gradient (Figure 7) showing that carbon stocks are highest at intermediate intensities of herbivore habitat use. The mean species richness of adult trees in a transect decreases along a gradient of habitat use by chital, but the relationship is not linear (Figure 8). More islands with intermediate to high intensities of herbivore habitat use need to be sampled to discern the pattern although there is a clear difference between the control site and the site with maximum habitat use.
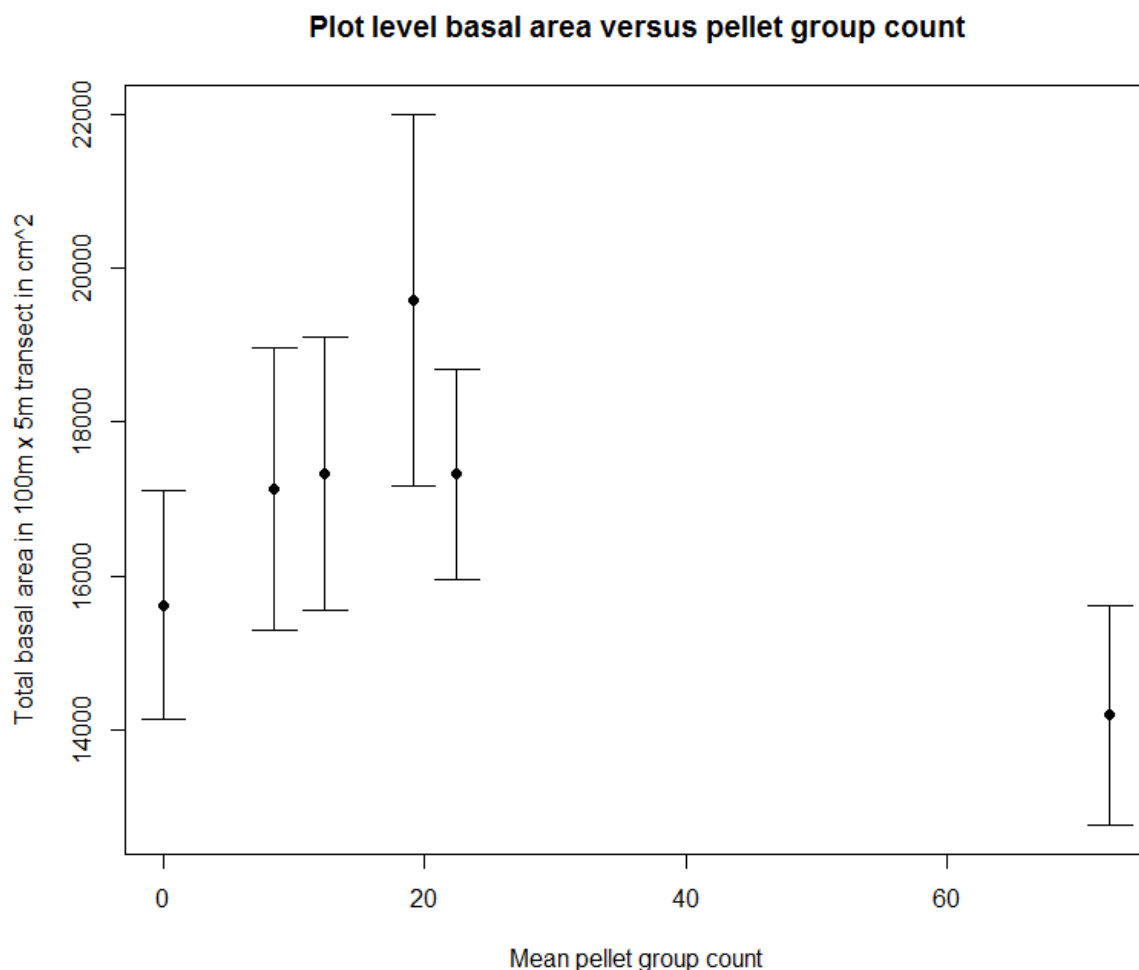

Fig 7. Plot level basal area versus pellet group count. Dots represent mean total basal area of adult tree stems in a 100m x 5m plot, bars represent their associated standard errors. X-axis is the mean chital dung pellet group count in each island.
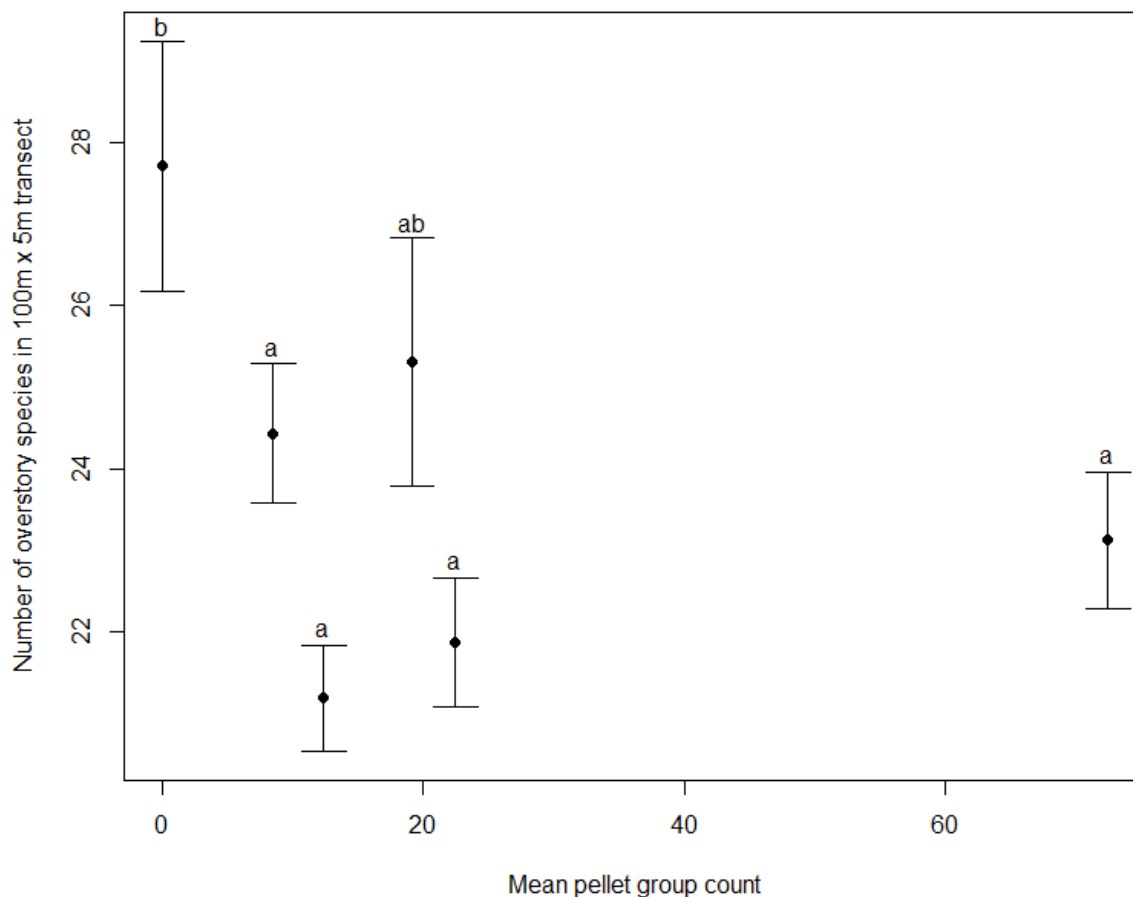
Fig 8. Mean species richness of adult trees in a transect versus pellet group count. Dots represent mean species richness of adult tree stems in a 100m x 5m plot, bars represent their associated standard errors. GLM with quasi-poisson family of errors, p<0.001. Distinct alphabets above standard error bars represent distributions statistically distinct (p<0.01) in GLM result.

Response of community composition to intensity of habitat use by chital

Although there was no evidence of an effect of herbivory on number of species of adult trees per se, the effect could manifest itself as a shift in community composition towards herbivory-resistant species. A list of the 10 most abundant species on the six sites was made for qualitative comparisons (Appendix (i) and (ii)).

Since the effect appears to be pervasive only in the understory plant community, an abundance rank correlation was performed on the understory and overstory species. The ranks of the 20 most abundant species in the overstory were plotted against their corresponding ranks in the understory (Figure 9). The relationship was expected to be linear with a positive slope if herbivory has no effect.

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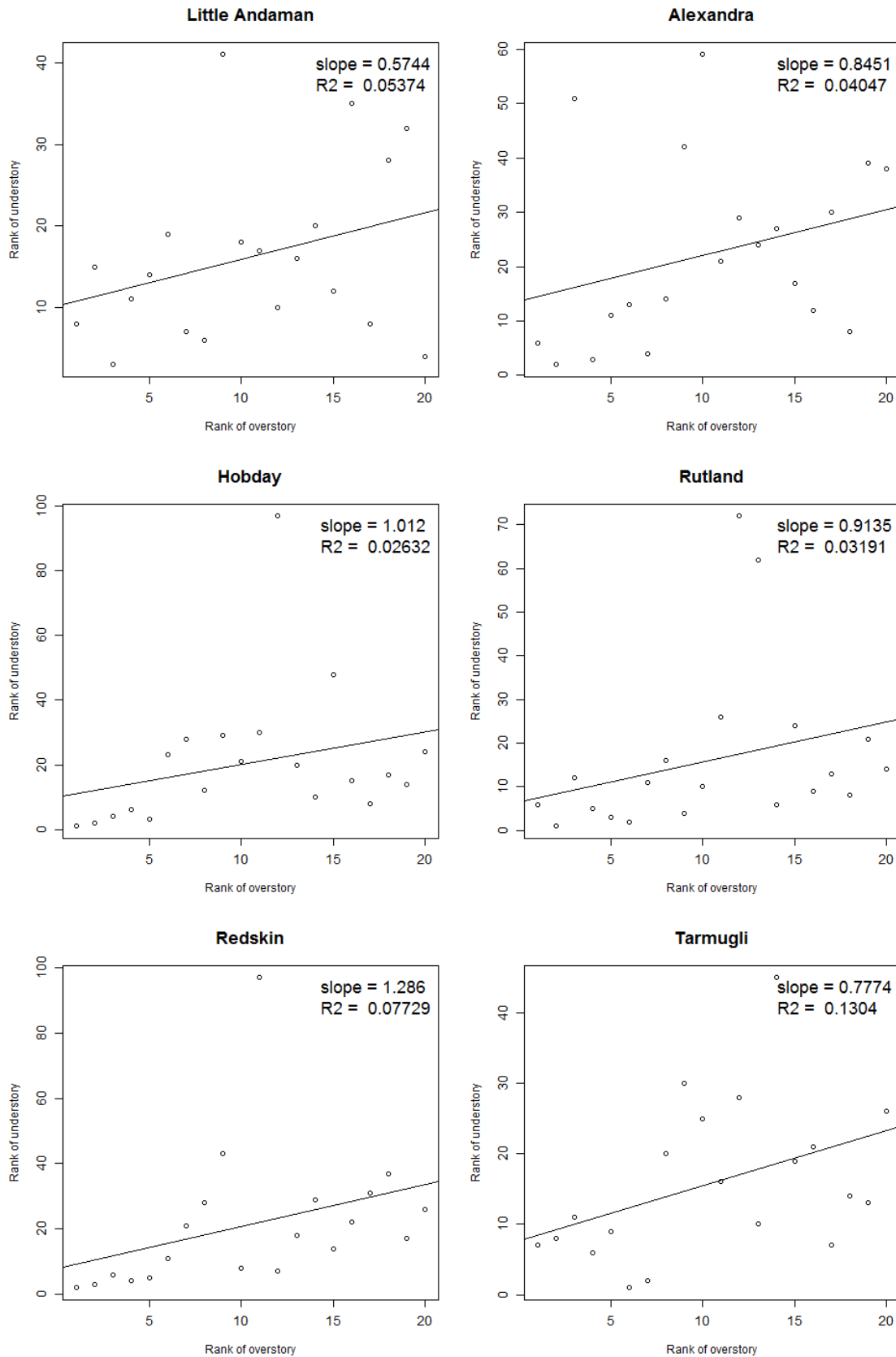Fig 9. Abundance rank plots for all six islands. Top left to bottom right panels are islands ordered in increasing order of chital habitat use. Each dot represents one of the 20 most abundant adult tree species in each island. Linear model fit, slope, adjusted R^2 reported.

There is a weak correlation between the community ranks of the most abundant adult tree species and their corresponding ranks in the understory.

Ordination of species composition across sites

Detrended correspondence analysis was performed on the community composition of the adult tree as well as understory communities. Detrending was chosen since a PCA showed high arch effect. Detrended Correspondence Analysis (DCA) of the species composition of the understory community (Figure 10) resulted in a scatter of points with no strong association between sites in the same island (Length of DCA1 = 5.5308). However, the DCA of the species composition of the adult tree community (Figure 11) shows strong association between the transects in the control site, Little Andaman (Length of DCA1 = 3.6669). There also appears to be an association between the community compositions of Redskin, Hobday and Alexandra islands. The points that represent sites in Rutland are the most scattered in these axes.

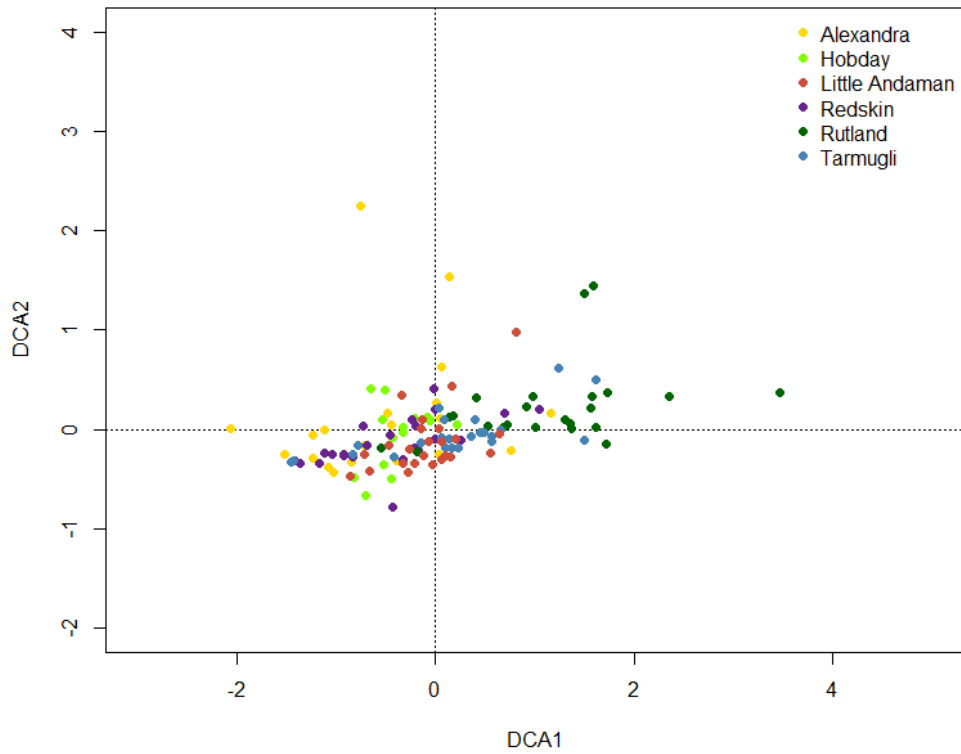## DCA of understory species composition in each transect

Fig 11. Detrended Correspondence Analysis plot of understory community across sites. Length of DCA1 = 5.5308, total inertia = 6.745.

DCA of adult tree species composition of each transect
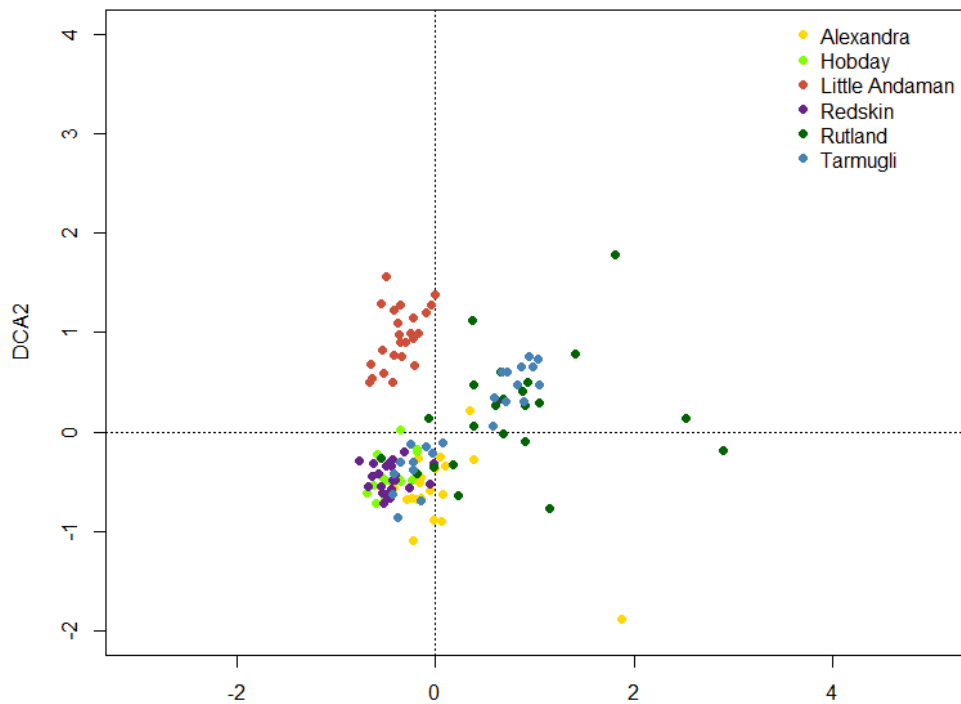
Fig 11. Detrended Correspondence Analysis plot of adult tree community across sites. Length of DCA1 = 3.6669, total inertia = 8.903.

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Analysis of functional traits

The community-weighted SLAs of the understory plots show no consistent variation across islands with increasing habitat use intensity by deer (Figure 12). All the islands with introduced herbivores, except Redskin island, show a decrease in the SLA value from that of the control, which is qualitatively in concurrence with the prediction. Similarly, the community weighted leaf thickness of the understory shows no consistent variation along increasing habitat use intensity by deer (Figure 13). In accordance with the prediction, the leaf thickness in islands with presence of deer is greater as compared to the control. In accordance with the predictions, there is also an increase in leaf thickness between islands with low and high herbivory.

Fig 12. Community weighted SLA of leaves across islands. Each dot represents the mean SLA of the 20 most abundant understory species in one island, weighted by their proportional abundances in a transect, averaged for an island. Total proportional abundance of 20 species is >80%. SLA measured in cm^2/g. ANOVA results : F value = 46.64, p<0.001. Distinct alphabets indicate distributions with pairwise statistically significant variation.

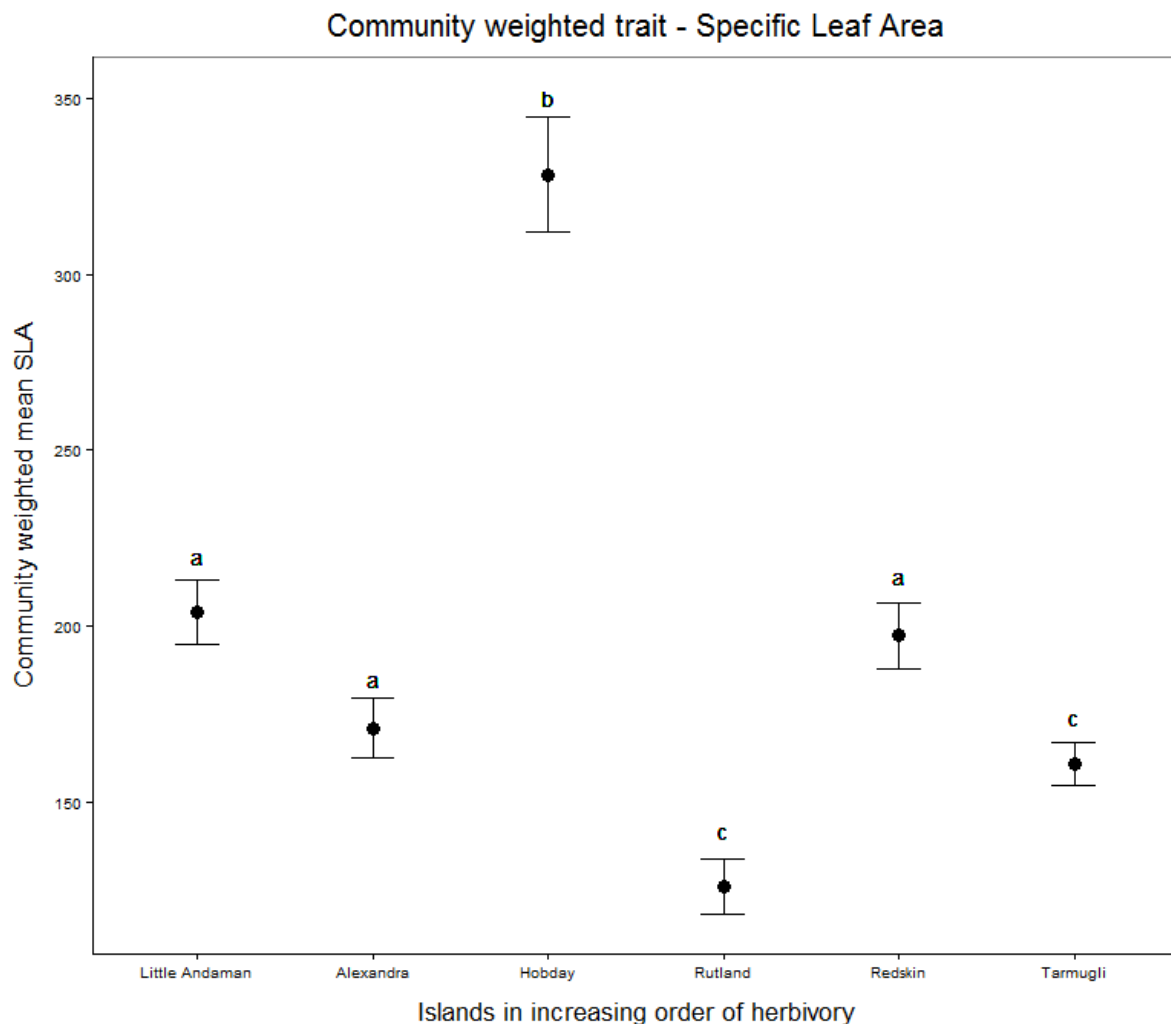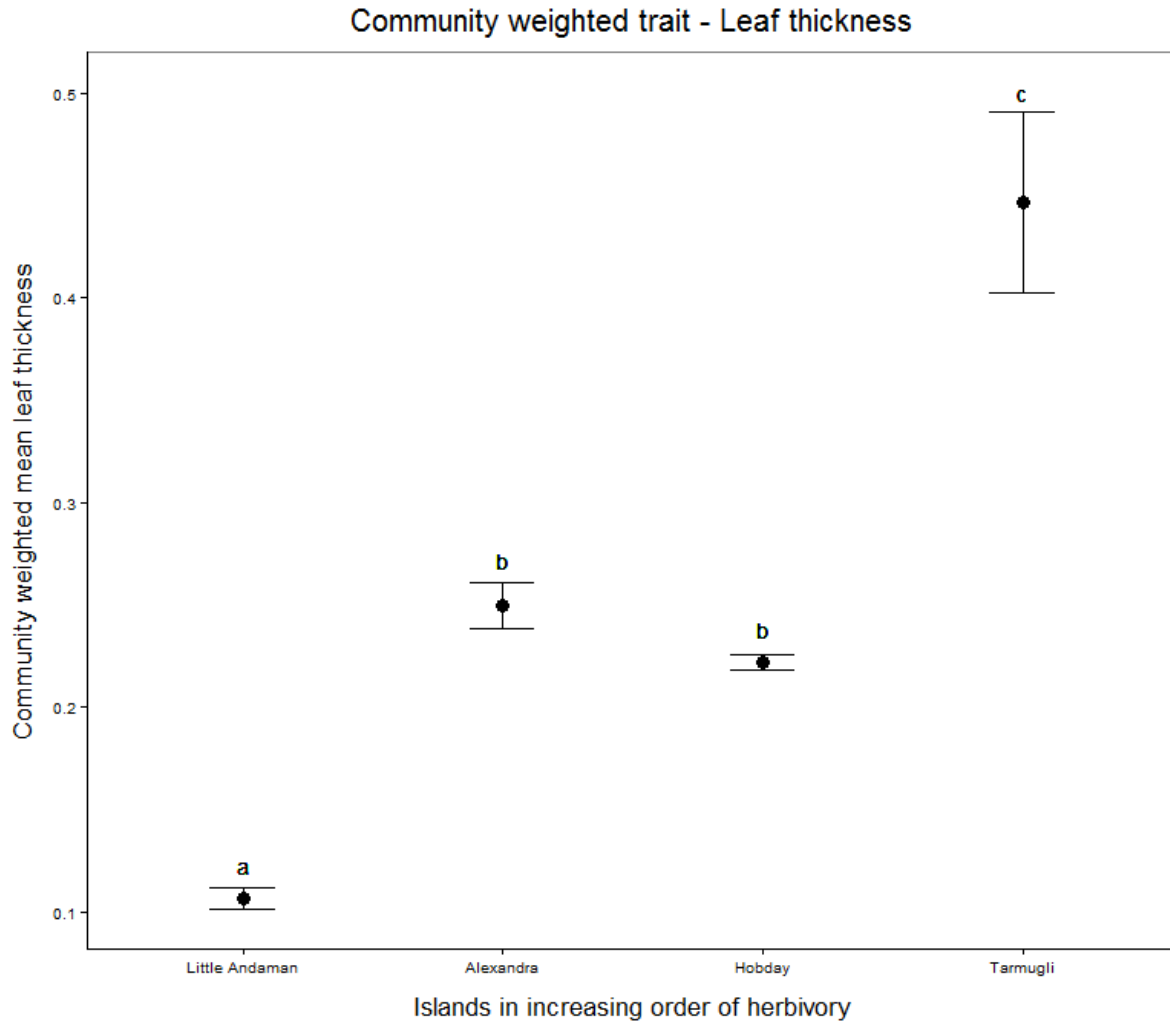Fig 13. Community weighted thickness of leaves across islands. Each dot represents the mean SLA of the 20 most abundant understory species in one island, weighted by their proportional abundances in a transect, averaged for an island. Total proportional abundance of 20 species is >80%. Thickness measured in mm. ANOVA results : F value= 31.99, p<0.001. Distinct alphabets indicate distributions with pairwise statistically significant variation.

Plotting the trends in intraspecific variation in SLA for species common to all the islands revealed a high degree of variation in the traits (Figure 14). The general trend seems to be a higher SLA for the population in Little Andaman while a slightly lower SLA is seen in other islands. There is no other consistent pattern.

There appears to be a high degree of intraspecific variation in leaf thickness as well (Figure 15). The general trend follows that of the community trait, with the control Little Andaman lower than the other islands. As is the case with the community-weighted means, there is a slight decrease in leaf thickness along an increasing gradient of herbivory, contrary to predictions.

Fig 14. Intraspecific variation in SLA across islands with increasing herbivore habitat use of five species commonly abundant in all six islands. X-axis represents islands in increasing order of habitat use. Y-axis represents SLA in cm^2/g. Bold lines are median values, boxes 1st and 3rd quantiles, bars represent 95% confidence intervals.

Fig 15. Intraspecific variation in leaf thickness across islands with increasing herbivore habitat use of five species com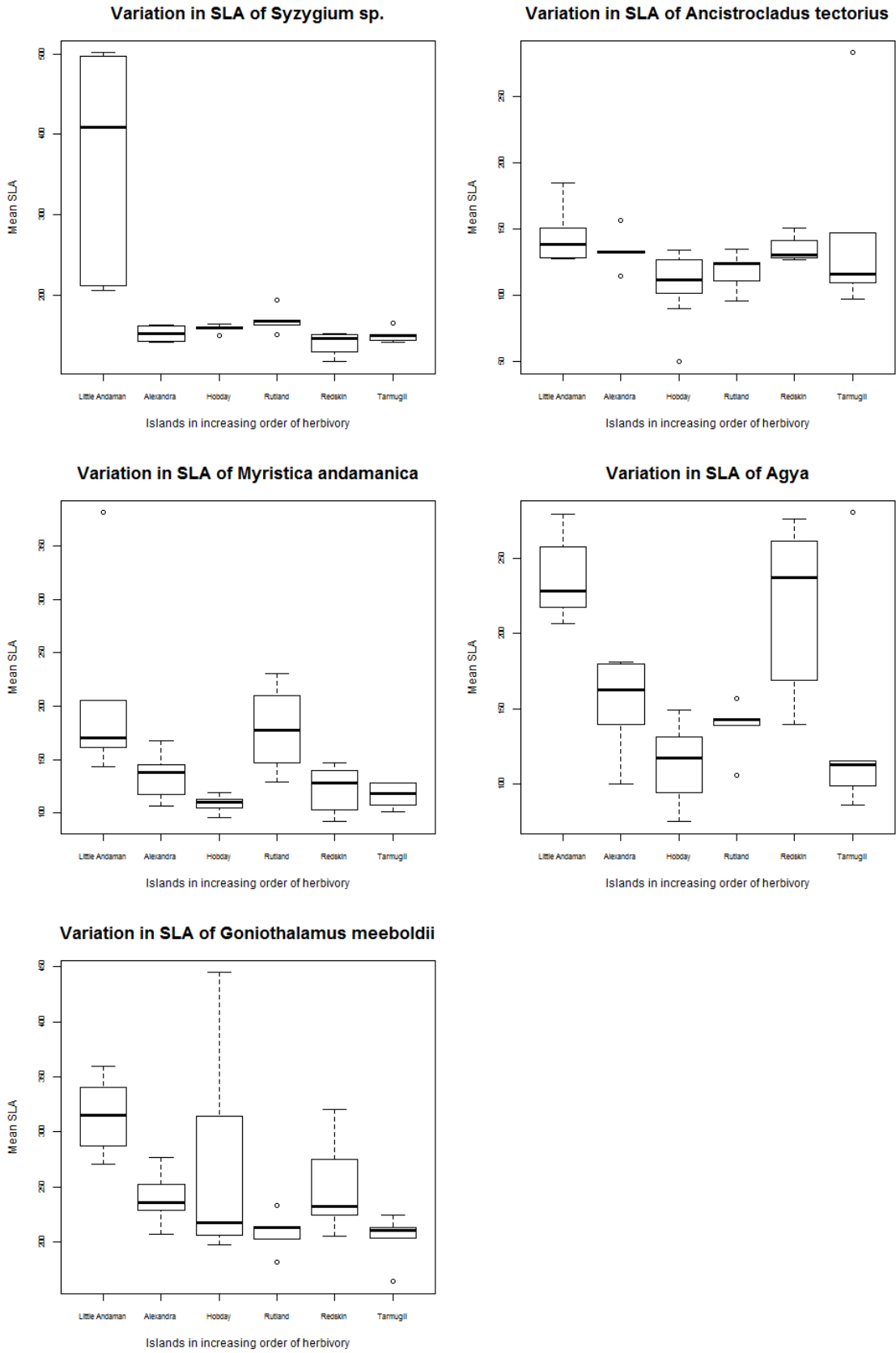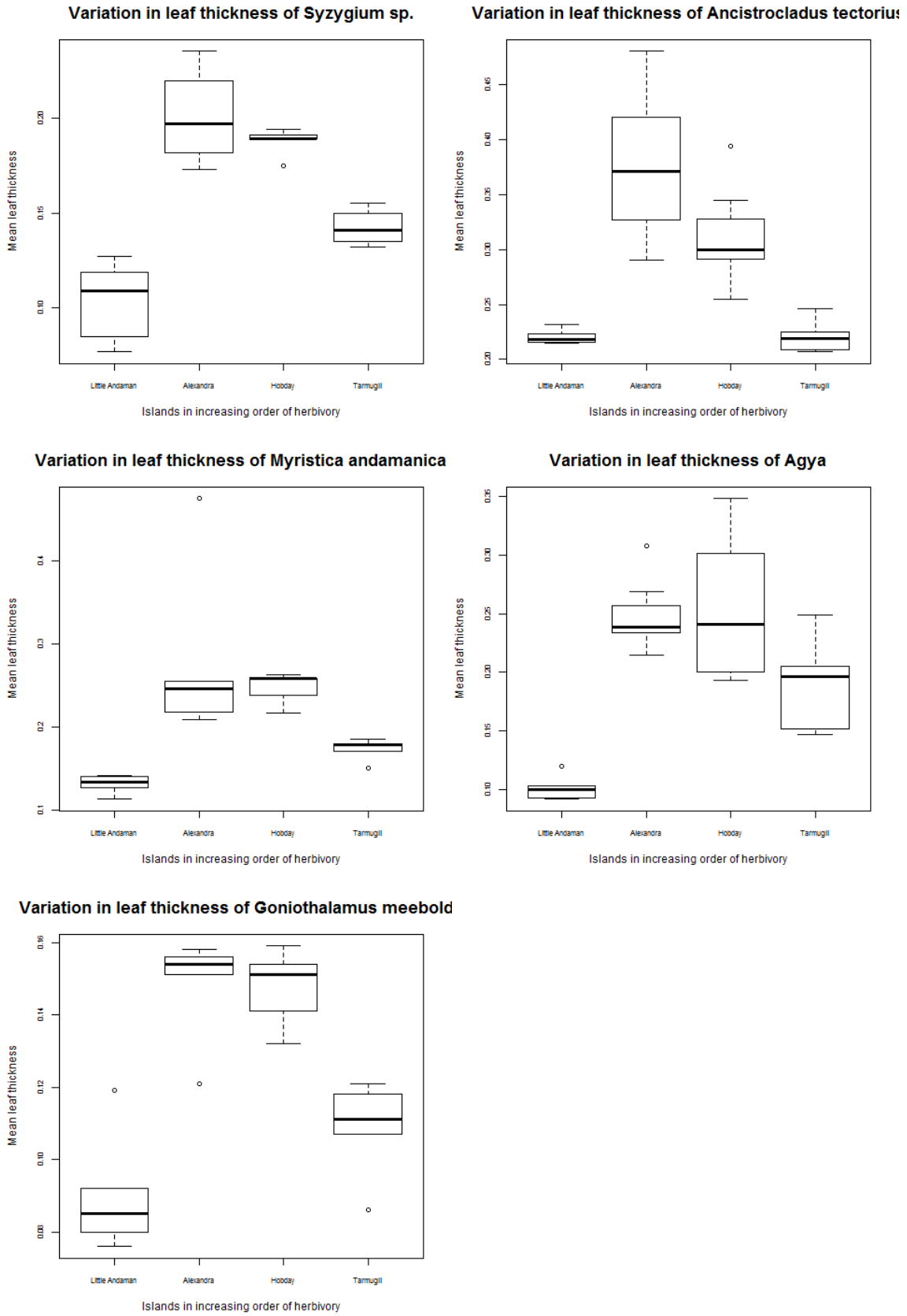monly abundant in all six islands. X-axis represents islands in increasing order of habitat use. Y-axis represents leaf thickness in mm. Bold lines are median values, boxes 1st and 3rd quantiles, bars represent 95% confidence intervals.

Discussion

The study reveals community and species-level responses mediated by functional traits to herbivore intensity although this effect was not manifested in the composition or structure of the community. Results from the analysis of the size class distributions as well as the accumulation of basal area along girth classes suggests no change in overall community structure between the islands with herbivory and the control, Little Andaman. A marginal increase in the proportion of the youngest size class is observed in the island with the highest intensity of herbivore habitat use.

The lack of island-level effects of herbivory on the structure of the plant communities could be due to the relatively short time scale of the disturbance by herbivory. Herbivory has been prevalent in the islands for only less than a century while many of the trees in the upper canopy are much older. The disturbance may not have been prevalent for a long-enough time scale to manifest in an alteration of adult tree community structure. It is also possible that even though a gradient of herbivory is present in the islands studied, the absolute intensities of browsing are too low to produce any effect on the community. It is also likely that the effect of chital browsing operates at local scales, with discontinuous patches, rather than at the scale of an island (Jefferies et al., 1994). Effects of browsing are likely to be disproportionately high in certain patches, for instance, near freshwater streams, which could cause localised effects in community properties.

The results present a case in which understory species richness, in terms of number of species in a given area decreases with increasing intensity of habitat use by deer, but understory abundance, in terms of number of stems per plot, shows no effects of herbivory. Similarly, although overstory species richness was markedly higher in the control island relative to the island with the highest level of herbivory, trends in adult tree basal area were suggestive of a hump-shaped response to the intensity of herbivory. The reduction in species richness is an obvious phenomenon, most likely acting through preferential browsing of some species and avoidance of species with herbivore-resistant strategies. Another explanation for this observation is the large proportion of rare species in a tropical evergreen forest. Upon browsing, rare species become even rarer, often leading to local extinctions and resulting in the observed pattern. The pattern of species richness could just be driven by island size or it could

be the combined effect of island size and deer density. This analysis requires quantification of the total area of contiguous evergreen patches in each island since the extent of mangroves and littoral patches also vary across islands. These patterns are also often confounded by abiotic factors like topology and soil type, and anthropogenic effects such as a history of selective logging. Most islands sampled, including parts of Little Andaman, the control, had been logged until the last 40 years. Therefore, the species composition in the overstory could be influenced by a variety of other factors.

It is interesting, however, that adult tree basal area at the plot level is suggestive of a hump-shaped curve along an increasing herbivore habitat use gradient. The islands with an intermediate intensity of herbivory have maximum total tree basal area per transect. A possible explanation for this pattern is the light limitation in tropical evergreen forests (Wright and van Schaik, 1994). At intermediate levels of disturbance, gaps are created, in which small seedlings are able to escape light limitation due to taller understory plants, thus increasing survivorship and productivity. At even higher levels of herbivory, it is likely that high browsing intensity reduces total basal area by reducing survivorship and recruitment. Similar shifts in positive and negative plant interactions along a herbivory gradient have been demonstrated previously in grazing systems (Graff et al., 2007). Moreover, a number of effects, such as species-specific effects, natural or anthropogenic disturbance, could be interacting to produce these varied patterns (Peltzer et al., 2014).

Chital browsing does not seem to have any major effect on the species composition of different islands with varying levels of herbivore intensity. Species like *Myristica andamanica, Syzygium* sp. and *Endospermum chinense* dominate the understory in most of the islands. The control, Little Andaman, however shows the dominance of a few other species as well. In the case of the adult tree community, *Myristica andamanica* is one of the most dominant species in all the islands except for Little Andaman where it is ranked lower than 10. It is worth mentioning that *Dracaena angustifolia*, a species reported to be highly palatable to the deer is ranked high in the adult tree community of the control site, Little Andaman, while it is ranked one of the least in every other island. Another observation is that although the avoidance of species such as *Lagerstromia hypoleuca* and *Pongamia pinnata* by chital is reported

in literature (Ali and Pelkey, 2013), no community-level patterns of abundances of these species were observed in this study.

Abundance rank plots to capture differences in recruitment from understory to adult tree stages did not show any qualitative differences across the islands. The understory ranks of the most abundant adult tree species were weakly correlated with the corresponding ranks in the adult tree community, with a positive slope. The control, Little Andaman, had the least value for the slope, showing highest degree of divergence between the layers. Ordination of community species composition revealed no marked differences in the understory composition while the adult tree communities in a few islands showed strong association in terms of composition. These data suggest that herbivory is not a major factor in the community composition of the understory. It is likely that other factors such as light intensity in the understory (or inversely, canopy cover) or available nitrogen and phosphorous in the soil are more important in determining understory species composition. The adult tree communities however show marked differences, with the control clustering separately from the rest of the sites. Since similar understory communities result in very different adult trees communities, these data suggest that the recruitment patterns of different species vary between the islands. At this time, we do not have enough information about these processes to speculate on the potential reasons for these divergences in the recruitment trajectories across the islands. Finally, it may be possible that the uniformity of understory compositions may be a sampling artifact, if the protocol used could not effectively control for seasonal effects.

It was hypothesised that the understory could be responding at a finer scale, by altering selection on functional traits that would be directly affected by herbivore browsing. The leaf thickness of the understory communities across islands, represented as a weighted mean of the species means shows a hump-shaped curve with increasing intensity of herbivore habitat use, although it was predicted that leaf thickness should increase with increase intensity of herbivore browsing. There is a two-fold increase in the community-weighted leaf thickness between the control and the other three islands, but across the islands with herbivory, there is a negative trend in community-weighted leaf thickness with herbivory. The increase in leaf thickness from control to the browsed islands could be through a shift in composition, intraspecific variation or an additive effect.

The slight decrease in leaf thickness at the community level in the highest herbivory site could also be due to a release from herbivory by smaller herbivores. Damage to leaves by arthropods and molluscs has been shown to have a strong negative correlation with leaf thickness and toughness parameters in a study conducted in a highly diverse tropical system (Cárdenas et al., 2014). This can be assumed to hold true in the study system as well because of its tropical location and high species diversity. A decrease in the abundance of soil and litter arthropods in the island with the maximum intensity of chital habitat use has been documented (Mohanty, 2013), possibly through habitat alteration. This decrease can potentially produce a slight negative trend in the leaf thickness in the highest herbivory site as compared to the islands with lower herbivory where non-mammalian herbivores are also abundant, and may be a reason for the observed pattern.

Specific Leaf Area (SLA) is a composite trait that differs in the context of habitat and environmental condition (Weiher et al., 1999). In this study, a community weighted mean of SLA across islands showed no pattern with increasing herbivore habitat use intensity. SLA is known to co-vary with several traits like leaf thickness, nitrogen concentration, carbon assimilation rates etc. (Ackerly and Reich, 1999; Perez-Harguindeguy et al., 2013). During this novel disturbance to the community, different traits are likely to be subjected to different selection pressures with the strongest selection being on traits that immediately affect browsing damage to the plant. The strongest effect of browsing is thus likely to be captured on traits such as palatability and leaf tensile strength, rather than on SLA directly. The response of SLA to a gradient of habitat use intensity by deer can thus be non-linear depending on the additive effects of its co-variant traits.

An interesting observation is that the community-wide patterns in SLA and leaf thickness are reflected in the patterns of a few species that exist across all six sites. This suggests that the variation in traits observed could be influenced by phenotypic plasticity operating at the species level. This capacity for plasticity may be present widely due to the high frequency of leaf damage by arthropods and molluscs, taxa that are important primary consumers in the tropics (Huntly, 1991).

Effects of mammalian herbivory, independent of other influences, may be detected in the concentration of tannins and fibre content of leaves across a gradient of

herbivory. Tannins are a class of phenolic compounds that are produced as a chemical defence for herbivore resistance (Perez-Harguindeguy et al., 2013). These compounds have been shown to reduce the available nitrogen even in leaves with a high total nitrogen concentration, reducing reproductive outputs in animals that feed on them in N-limited conditions (Wallis et al., 2012). The fibre content of a leaf is a palatability trait related to forage quality. Deer preference for leaves has been shown to decrease with increasing foliar fibre content (Forsyth et al., 2005). Analysis of both these traits could provide a crucial insight into the effect of chital in this highly diverse landscape.

Strong conclusions about the response of the community or even individual species can only be drawn after sampling more islands spread across the gradient of chital habitat use intensity and island size, to control for the effect of island size. A drawback of this study area is the existence of only one suitable control site, Little Andaman, in the archipelago. Field experiments in each of the islands, using exclosures to keep deer out of plots, could resolve these confounding factors. Multiple replicates across varying soil types, topologies and island sizes can be used to control for these effects. Monitoring the change of understory, soil and litter properties in exclosures, compared to adjacent control plots outside will be indicative of the community level changes in the absence of herbivory, keeping all other factors constant. Finally, the fact that only one of the sampled sites had a high intensity of herbivory also weakens the study. The current data hint that community-level responses to herbivory may well be non-linear, with many effects becoming apparent only after some threshold of herbivory is passed. This could be a critical insight, with important management implications, as it would suggest that low levels of chital herbivory do no impact the ecosystem. Sampling additional islands with high herbivory will be important in making robust conclusions.

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Appendix

Table (i). Table of most abundant understory species, pooled across transects from an island.

Island	1	2	3	4	5	6	7	8	9	10
Tarmugli	*Syzygium* sp.	*Terminalia manii*	*Endospermum chinense*	*Planchonia andamanica*	Chilka, G	Gobrabali	*Myristica andamanica*	*Diospyros oocarpa*	Unknown	Kalachilka
Redskin	*Endospermum chinense*	*Myristica andamanica*	*Ancistrocladus tectorius*	*Dipterocarpus sp.*	*Myristica* sp.	*Goniothalamus meeboldii*	Agya	Chilka, B	*Terminalia manii*	*Tabernaemontana alternifolia*
Rutland	*Syzygium* sp.	Agya	*Diospyros oocarpa*	*Rothmannia pulcherrima*	Unknown	*Myristica andamanica*	Lambaphool	*Tabernaemontana alternifolia*	*Goniothalamus macranthus*	*Myristica* sp.
Hobday	*Myristica andamanica*	*Ancistrocladus tectorius*	*Dipterocarpus* sp.	*Goniothalamus meeboldii*	*Terminalia manii*	*Myristica* sp.	*Endospermum chinense*	*Goniothalamus macranthus*	Chilka, S	*Mangifera sp*
Alexandra	*Endospermum chinense*	*Myristica andamanica*	*Dipterocarpus* sp.	*Leea indica*	Chilka, B	*Ancistrocladus tectorius*	*Terminalia manii*	Agya	Gobrabali	Smooth leaves
Little Andaman	*Endospermum chinense*	Unknown 2	*Mallotus* sp.	*Terminalia manii*	Unknown	*Ancistrocladus tectorius*	*Syzygium* sp.	T27	*Callophyllum inophyllum*	*Pometia pinnata*

Table (ii). Table of most abundant adult tree species, pooled across transects from an island.

Island	1	2	3	4	5	6	7	8	9	10
Tarmugli	*Myristica andamanica*	*Diospyros oocarpa*	*Ancistrocladus tectorius*	Gobrabali	Unknown	*Syzygium* sp.	*Terminalia manii*	*Murrya exotica*	Nimbupatti	Tu
Redskin	*Myristica andamanica*	*Ancistrocladus tectorius*	*Goniothalamus meeboldii*	*Dipterocarpus* sp.	*Myristica* sp.	*Syzygium* sp.	Tu	T27	*Garcinia cowa*	Chilka, B
Rutland	*Myristica andamanica*	*Syzygium* sp.	*Ancistrocladus tectorius*	Unknown	*Diospyros oocarpa*	Agya	Gobrabali	*Goniothalamus meeboldii*	*Rothmannia pulcherrima*	*Myristica* sp.
Hobday	*Myristica andamanica*	*Ancistrocladus tectorius*	*Goniothalamus meeboldii*	*Myristica* sp.	*Dipterocarpus sp.*	*Murrya exotica*	T27	*Syzygium* sp.	*Garcinia cowa*	*Anacardium occidentale*
Alexandra	*Ancistrocladus tectorius*	*Myristica andamanica*	T27	*Dipterocarpus* sp.	*Goniothalamus macranthus*	*Goniothalamus meeboldii*	*Leea indica*	*Syzygium* sp.	*Garcinia cowa*	Tu
Little Andaman	T27	*Dracaena angustifolia*	*Mallotus* sp.	*Murrya exotica*	*Diploknema butyracea*	Gobrabali	*Syzygium* sp.	*Ancistrocladus tectorius*	*Grewia calophylla*	*Dipterocarpus* sp.