Effects of environmental variability on forest tree growth and demography

A Thesis

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Indian Institute of Science Education and Research Pune in partial fulfilment of the requirements for the BS-MS Dual Degree Programme
by

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Certificate

This is to certify that this dissertation entitled “Effects of environmental variability on forest tree growth and demography” towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents work carried out by Anisha Ajay Karnail at National Centre for Biological Sciences - Tata Institute of Fundamental Research, Bengaluru under the supervision of Dr Mahesh Sankaran, Associate Professor, Dept. of Ecology & Evolution during the academic year 2021-2022.

Anisha Ajay Karnail

Dr Mahesh Sankaran

Declaration

I hereby declare that the matter embodied in the report entitled “Effects of environmental variability on forest tree growth and demography” 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.

Anisha Ajay Karnail

Dr Mahesh Sankaran

This thesis is dedicated to Sugat Kokiloo
30th April 1998 - 9th August 2022

Remember when you were young
You shone like the Sun
Shine on, you crazy diamond

- Shine On You Crazy Diamond, Pink Floyd

Table of Contents

Abstract

Understanding forest ecosystems is an enormous task, and long term monitoring of individuals traits and processes give us critical insights into this subject. Studies on tree growth are rare in the Indian subcontinent, however, data from permanent plots as well as tree ring records have been studied across the Americas, Africa, and South-East Asia. Amongst climatic factors, precipitation and the subsequent soil water content, solar radiation, and temperature influence tree growth patterns on a pan-tropical scale. Other site-specific studies show that growth rate positively correlates with rainfall, although the strength varies, and sunlight.

In this thesis, I analysed the tree growth rates in permanent forest plots in South India. I show that species averages of growth rates vary significantly within plots. Absolute growth rates increase slightly with size, while relative growth rates decline with the same. Species identity and size are better indicators of growth rates than rainfall; however, developing a simple model that captures these effects better, and the effects of other abiotic factors, with limited data, is challenging.

Acknowledgement

This thesis has been a long time in the making, and it would not have been possible without the following people.

Firstly I would like to thank my supervisor, Dr Mahesh Sankaran, for his constant guidance and insight into the subjects of his expertise. I also thank all the lab members for their support and encouragement and for making my time in the lab so cherished. I thank, in particular, Dayani for her direct supervision, and Manaswi and Ron for helping me out when I was stuck with problems. Dr Deepak Barua, my supervisor at IISER Pune, has also supported me and given valuable advice. All of these people have been incredibly kind and patient, and collectively kept the flame of curiosity and scientific endeavour alive in me, and for that, I am truly grateful.

I would also like to thank IISER Pune and NCBS Bangalore for providing me with the avenues and resources to pursue the field of my passion.

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List of Figures

List of Tables:

Introduction:

Globally, forests cover about 30.7% of land area across various climatic zones. Out of this, almost half of forested land is present in the tropical zone. These tropical forests are home to over 90% of the world's living organisms; the trees themselves contain 70% of the planet's biomass (Pan et al. 2013). On account of their sheer size, land area cover, and biodiversity, tropical forests play a critical role in maintaining local climatic processes as well as the global biogeochemical cycle. They strongly affect, as well as respond to, global climate change in a continuous feedback loop. It is crucial to study these important communities over a period of multiple years to understand their role in mitigating climate change through these responses.

The process of tree growth is of particular interest as it is a part of various ecological processes. Trees are a significant carbon sink for carbon dioxide absorbed from the atmosphere during photosynthesis. Much of this carbon is stored as woody biomass in the aboveground tree trunks. Studies estimate that forests sequester almost 80% of aboveground terrestrial carbon. The amount of carbon stock in forests and the rates of sequestration vary across latitudes, with the tropical and arctic zones containing more than 85% of forest C stock and the mid-latitude forests containing up to 15% (Dixon et al. 1994).

As trees photosynthesise atmospheric carbon into biomass, analysis of individual tree growth during their lifetime - rather than tree ring analysis of past growth - allows us to study their mitigating role in the current context and develop plans for forest conservation and management (Köhl et al. 2017). The growth and survival of individuals depend on intrinsic factors like species identity and life stage, as well as abiotic conditions, resources, community interactions, etc. Because trees have a long lifespan - between a few decades and thousands of years - their interaction with the local environment varies in complex ways over time; these changes can be periodic or brought by sporadic events (Sheil et al. 2017).

Biotic and Abiotic Factors:

Environmental temperature is a major factor driving metabolic reactions and thus growth rate in most living organisms. In aerobic conditions, the rate of metabolism of increases, then rapidly decreases with increasing temperature. As global warming is a major component of present-day climate change, understanding and mitigating the effects of rising temperatures on the planet's ecosystems is an urgent need (Sinclair et al. 2016). Tree growth has been reported to be negatively correlated with temperature, whether tested with maximum or minimum averages; in the same studies, rainfall and growth rates were found to be positively correlated (Clark et al. 2003, Clark et al. 2010, Feeley et al. 2007, Schippers et al. 2015). The relationship between rainfall and growth however is observed to be weak, and stronger between growth and variation and in rainfall, and sometimes no effect is observed (Rahman et al. 2017). Solar irradiance and cloud cover also weakly affect growth, although this effect is variable with canopy cover and height variability in a stand (Dong et al. 2012).

Measuring Tree Growth:

Many studies looked at the past growth of wood assembly in cut-down tree stands and examined their tree ring profile. Researchers developed a less intrusive method by way of extracting wedges or "wood cores" from tree trunks (Swenson & Enquist 2008). These methods were particularly useful in seeing the effects of major disruptions like fires and droughts. However, the key limitation of these methods evidently is their retrospective nature. Growth could only be understood in the context of past events (Bowman et al. 2013). Hence attempts were made to study forest ecosystems in real-time.

The first such effort for establishing permanent plots came about in 1980 with the Long Term Ecological Research (LTER) sites in North America. While they started out with vegetation plots in the North American tundra and prairie grassland, the Pacific Northwest conifer forest, and the Great Lakes ecosystem, the project has expanded to plots in the Pacific coral reef, Antarctic regions, and most recently, urban ecosystems as well (Chen et al. 2022, Gray et al. 2012). The Forest Global Earth Observatory (ForestGEO) project followed suit to look at global forest diversity and function (Anderson-Teixeira et al. 2015). The Amazon Forest Inventory Network (RAINFOR) and Global Ecosystem Monitoring Network (GEM) established permanent plots across the Amazon rainforest in 2000. They continue to monitor plant traits, soil content, and water availability for the overall health of the Amazons (Malhi et al. 2002).

Such long-term monitoring plots could be extremely beneficial to a country such as India, owing to our diversity of climate and vegetation types, soil profiles, and land use needs. Keeping these factors in mind, the Long Term Ecosystem Monitoring Project (LEMoN) set up forest plots in the Indian subcontinent and islands.In the 1980s, ForestGEO, then known as the Centre for Tropical Forest Research (CTFS), established one such plot in Mudumalai, Tamil Nadu, India. A growth rate study was carried out between 1988 and 2000 to understand the effects of species, canopy cover, tree size, and environmental factors (Nath et al. 2006). They found that species identity strongly influenced growth rates, followed by size, and slightly by environmental factors. Researchers have similarly studied the effects of environmental factors on tree mortality in the same period (Suresh et al. 2010).

The LEMoN plots are established following standard protocols developed by the RAINFOR-GEM and CTFS, and aim to study forest communities’ dependence on environmental facots and response climate change in the Indian context.

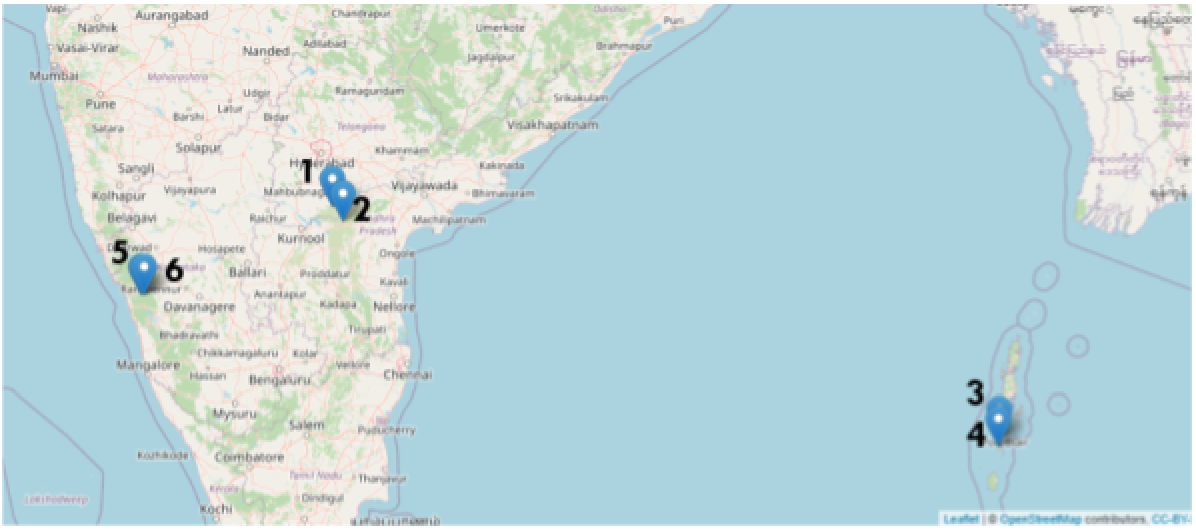

Figure 1: Sites from the Long-term Ecosystem Monitoring Network (LEMoN). Figure generated using the `leaflet` package in RStudio.

Motivations and Questions:

The sites have been selected for this project, and further long-term studies are of key national and global importance. The Sirsi plots - Hosagadde and Mulagunda - are located in the Western Ghats of India. The Western Ghats are a biodiversity hotspot for species across domains, including plants, mammals, birds, reptiles, and insects. It is a listed UNESCO World Heritage Site and an important location for the conservation of biodiversity and habitat (Myers et al. 2000, Reddy et al. 2016). There are three tiger reserves, 26 sanctuaries, and 17 national parks across the Western Ghats. Additional spots such as Kaas Plateau and the Nilgiris are included in the World Heritage Site status.

Andaman and Nicobar Islands consist of 572 islands, of which only 38 are permanently inhabited. They are also biodiversity hotspots (Davidar and Ganesh 2001) and face a particular threat from climate change resulting in sea level change and extreme weather events (Porwal et al. 2011).

While not in the conservation spotlight, the Eastern Ghats of India are also home to a large variety of flora and fauna (Nayaka et al. 2013, Kadavul & Parthasarathy 1999, Venkata Ramana 2010) and face the same natural and anthropogenic risks to the landscape (Naidu & Kumar 2016, Ramachandran et al. 2018). The plots at Mannanur and Tummalabylu themselves are contained in Amrabad Tiger Reserve and Nallamala Forest, respectively; they are part of the larger Nagarjunasagar Srisailam Tiger Reserve - the largest of its kind in India. In addition to NSTR, there are three more tiger reserves, 24 wildlife sanctuaries, and three national parks.

Management and conservation of these ecosystems are of utmost importance to many stakeholders, including the government and Indian Forest Services, forest-dwelling communities, researchers and conservationists. Since tropical forests reserve a significant part of the land C sink, their growth processes are key to determining their role in mitigating CO_2-induced climate change. While the increase of CO_2 itself affects the sensitivity of tree growth to climatic factors, mean climate determines how these changes manifest (Zuidema et al. 2020). The long-term study of these ecosystems will provide a comprehensive understanding of their function and services and ultimately form effective and sustainable strategies for their management and conservation.

In this thesis, I attempted to answer the following questions:

- Do species within a site have a significant variation in growth rates?
- Does rainfall have a significant effect on growth rates, leading to higher variability between sites than among the two plots in a site?

I used a simple generalised linear mixed model to explain the effects of size, species, and rainfall and compare the role of each factor.

Methods and Materials:

Study Sites:

The data was collected from six locations as part of the Long-term Ecosystem Monitoring Network (LEMoN) - in India. Mannanur and Tummalabylu are part of the protected forest area in Nagarjuna Sagar Tiger Reserve (NSTR) across Andhra Pradesh and Telangana; Alexandria and Rutland are small islands, part of the Andaman archipelago. Hosagadde and Mulagunda are part of the upper Western Ghats in Uttara Kannada district (near Sirsi) (Fig 2). Each location consists of a one-hectare forest plot established between 2011 and 2013. The plots were set up following protocols standardized by RAINFOR and CTFS projects. We collect data periodically on tree count, life stage, traits, species diversity, leaf litter and nutrient content. Table 1 below contains the specific location of each plot and the time periods of data collection. Two other LEMoN sites, Sigur and Valparai (Tamil Nadu), were excluded from this analysis as data was unavailable for a sufficient time interval.

NSTR: Mannanur and Tummalabylu are savanna-type ecosystems in the Eastern Ghats. Mannanur is part of the Amrabad Tiger Reserve to the north of the Krishna river in Telangana; Tummalabylu is part of NSTR Forest to the south, in Andhra Pradesh. The larger area is hilly terrain with plateaus, streams, and lakes. The trees are mixed deciduous interspersed within a dense undergrowth of grass, shrubs and bamboo. Being in the rain shadow area of the Eastern Ghats, they receive 700 mm of rainfall annually. The region receives rainfall from June to October, with a dry season of 7 months.

Andamans: Alexandria and Rutland are small islands at the southern tip of South Andaman Island. The plots consist of tropical forests with evergreen trees, palms, and some grasses. The plots are established and maintained in partnership with Andaman and Nicobar Environmental Trust (ANET). They receive rainfall from two branches of the

Indian monsoon - firstly, the southwest branch, from May to September and then from the northeast branch, from November to January.

Sirsi: Hosagadde and Mulagunda are located in the middle Western Ghats, at the northernmost end of the Karnataka coast. They face the windward side of the Ghats, and hence receive extremely heavy rainfall in the months of June through November from the easterly jet as well as the receding monsoon. The vegetation consists of dense tropical evergreen forests.

Figure 2: LEMoN sites Clockwise from top-left: Sirsi, Andamans, and NSTR. Sirsi and Andaman images by Dayani Chakravarthy

Data Collection:

LEMoN teams conducted annual censuses starting earliest in Andamans from 2012 to 2020. Mature trees were tagged with numbered aluminium markers in the first census. New saplings were added to the set of tagged individuals upon reaching 10 cm in girth each census henceforth.

To measure individual girth, an appropriate location on the stem was chosen- approximately 1.3 meters from ground level, i.e at "breast height" (Fig. 3). Two measurements were taken at the position with a tape measure. The point of measurement was marked with red paint for future reference. Steel dendrobands were attached 10 cm higher than the measurement mark. The calliper segment gives us the change in circumference since installation at each census. Only individuals with a minimum of 10 cm GBH are included in growth rate calculations and analysis.

Figure 3: A typical measurement setup with an identification tag and a dendroband at Mannanur, NSTR

Table 1: Details of the six plots located in South India, listed in order of increasing annual rainfall

No.	Site	Plot	Coordinates	MAP (mm)	No. of individuals	Initial Census	Final Census	Time difference (yrs)
1	Nagarjunasagar Srisailam Tiger Reserve	Mannanur	16.25 °N; 78.68 °E	713	1054	2014	2020	6
2	Nagarjunasagar Srisailam Tiger Reserve	Tummalabailu	15.96 °N; 78.91 °E	713	977	2013	2020	7
3	Andaman Islands	Rutland	11.39 °N; 92.60 °E	2449	1500	2012	2018	6
4	Andaman Islands	Alexandria	11.58 °N; 92.60 °E	2465	886	2013	2018	5
5	Sirsi	Hosagadde	14.48 °N; 74.76 °E	3730	2214	2013	2020	7
6	Sirsi	Mulagunda	14.47 °N; 74.69 °E	4228	1895	2014	2020	6

We estimated the heights of trees via a tape measure if they were lesser than 2 meters in height. We used a clinometer to measure the height of taller trees.

Trees with multiple stems were combined to give a single GBH value for each individual with the equation, such that the combined cross-sectional area of the stems is equal to the cross-section of a single stem with the equivalent GBH:

$$gbh \ = \ \sqrt{\sum_{i=1}^{n} (gbh_i)^2} \qquad \ldots(1)$$

Where n is the number of stems in a given individual, and gbh_i is the GBH value of the i[th] stem.

We obtained the mean annual precipitation (MAP) values for each plot from the WorldClim database. This value is the average rainfall received annually at each plot.

Growth Rate Calculations:

I calculated absolute growth rate (AGR) as the rate of change of girth/biomass per year from the initial year to the final year of recording (Hunt 1982). I calculated the relative growth rate (RGR) as the rate of change of the natural logarithm of the girth per year. This formula is derived based on the observation that the increase in plant size is proportional to the initial size of the plant (Blackman 1919, Pommerening & Mustza 2016). GBH-specific growth rate (GBHGR) in the same time period using the following formulae:

$$AGR \ = \ \frac{g2 - g1}{\Delta\, t} \qquad \ldots(2)$$

where AGR is Absolute Growth Rate, g1 is initial girth, g2 is final girth, and $\Delta\, t$ is the difference between the years of the final census and the initial census.

$$RGR \ = \ \frac{ln(g2) - ln(g1)}{\Delta\, t} \qquad \ldots(3)$$

where ln() is the natural logarithm function, and,

$$GBHGR = \frac{1}{g1} * \frac{g2 - g1}{\Delta t} \qquad \text{...(4)}$$

where GBHGR is initial GBH-specific Growth Rate

Modelling:

Individuals that had died, been damaged, had missing/incorrect measurements, or were unidentified at the species level were excluded from further analysis. We defined dominant species as those with 20 or more tagged individuals within a given plot.

I used a generalised linear mixed model (i.e. including both fixed and random effects) to model the growth rates based on their initial size and the MAP value at each plot. The interaction of initial girth and rainfall is represented in the first bracket in equations 5 and 6. The interaction term is included for the assumption that the effect of rainfall influences the effect of initial girth on growth rates. Species and plots are random effects with species nested within the plot. Species and plots vary across trees; they have been taken as random effects. The dominant species in a one-hectare plot are a subset sample of the larger forest population.

$$AGR \sim (Initial\ Girth\ *\ MAP) + (1 \mid Plot\ /\ Species) \qquad \text{...(5)}$$

$$RGR \sim (Initial\ Girth\ *\ MAP) + (1 \mid Plot\ /\ Species) \qquad \text{...(6)}$$

The intercepts are varied among plots and among species within each plot; slopes are varied between plots and remain constant for species within a plot. Girth and MAP values were standardized plot-wise by centring around the average value and dividing by standard deviation before running the models, as the measured values were of different orders of magnitude.

I conducted the statistical tests and analysis in RStudio version 4.1.3 (R Core Team 2022, RStudio Team 2020) with `stats`, `dplyr` (Wickham et al. 2022), `psych`

(Revelle 2022), and `smart` (Warton 2012). Plots and maps were generated using `ggplot` (Wickham 2016) and `leaflet` (Graul 2016) . The models were run using the `glmmTMB` and `DHARMa` packages (Brooks et al. 2017, Hartig 2022) in RStudio as well.

Results:

Growth Rate Patterns:

Between 10 and 20 dominant species account for around 50% of individuals and between 80% to 85% of basal area in the plots at Sirsi and NSTR. In Andamans however, they occupy about 20% basal area at Alexandria and Rutland.

The species' average growth rates vary among species in a plot as well as with some common species between two plots close to each other (Fig 4 and 5). *Chloroxylon swietenia* and *Bridelia retusa* trees grow at 1.23 cm yr^{-1} and 0.91 cm yr^{-1} at Mannanur, while in Tummalabylu they grow at 0.74 cm yr^{-1} and 0.78 cm yr^{-1} respectively, even though both plots receive the same amount of rainfall.

Regression Analysis:

Here initial GBH is the predictor and growth rates are the response variables. Since the standard error of AGR and RGR was lower than the standard error in GBH, an ordinary least-squares linear regression was not suitable. Using Mardia's test (Mardia 1970), GBH and AGR at respective plots were determined to be bivariate normally distributed (p-values >= 8, alpha = 0.05), as were GBH and RGR (p-values >= 8, alpha = 0.05). The correlation between AGR and GBH and RGR and GBH were also significant and correlated positively except at Tummalabylu (Pearson's coefficient -0.069, p=0.045).

Standard Major Axis (SMA) regression shows that growth rates of only a handful of species are well explained by initial girth alone (Appendix 2). Overall 2 out of 64 species show a statistically significant negative correlation, while 32 show a positive correlation of AGR with initial girth, and 53 species show a negative correlation between RGR and initial girth ($p<0.05$). AGR shows a strong positive correlation with initial girth for eight species, with R^2 values greater than 25%, maximum for *Hopea wightiana* with R^2 of 47.1% ($p<0.05$). Similarly, RGR correlation with initial girth is negative and smaller in magnitude than AGR correlation, with R^2 values greater than 25%, maximum for *Bridelia retusa* at 68.36% ($p<0.05$).

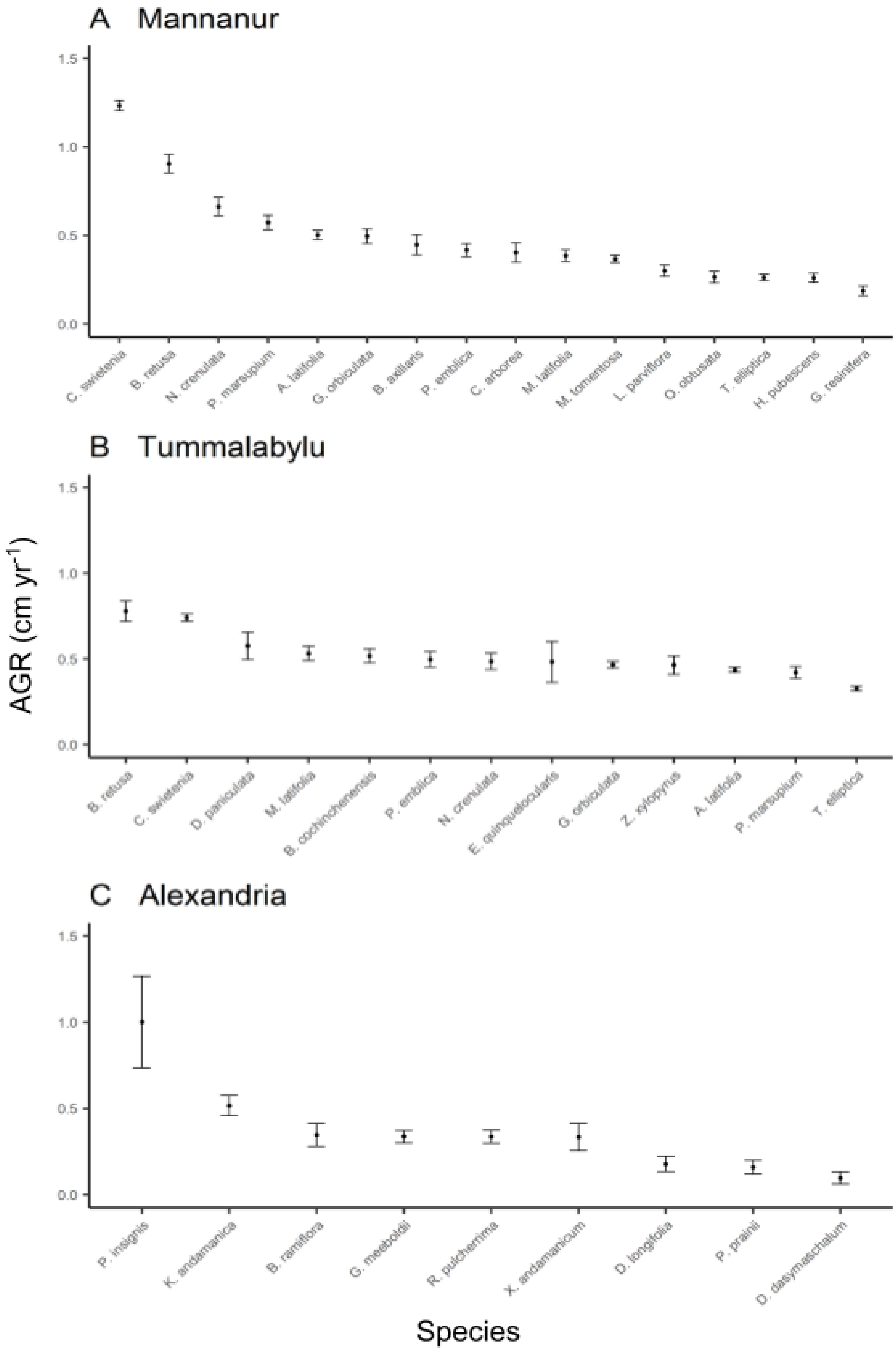

Fig 4: Species average AGR at A: Mannanur, B: Tummalabylu, C: Alexandria. Error bars represent standard error

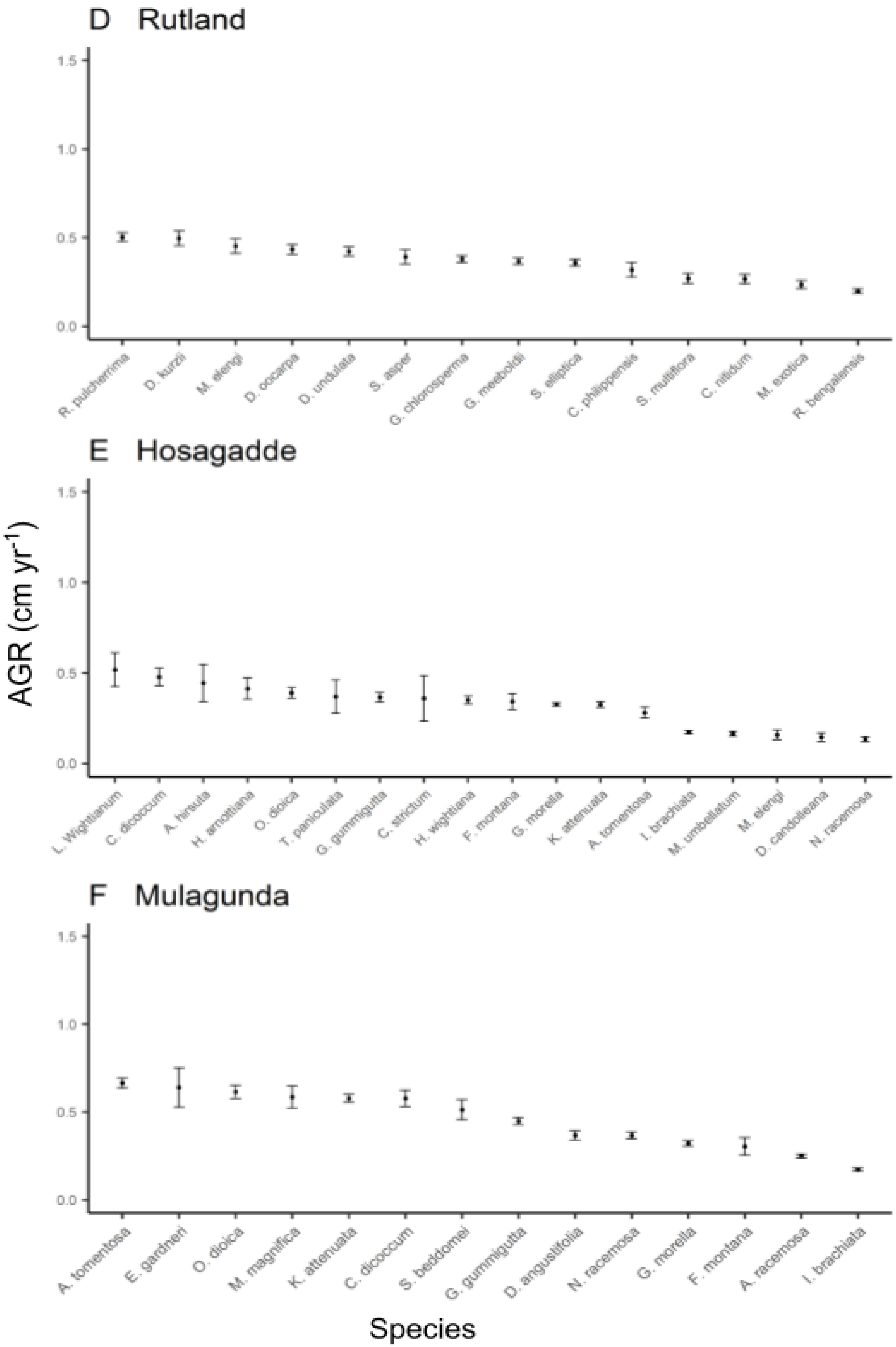

Fig 4 (cont) : Species average AGR at D: Rutland, B: Hosagadde, C: Mulagunda. Error bars represent standard error

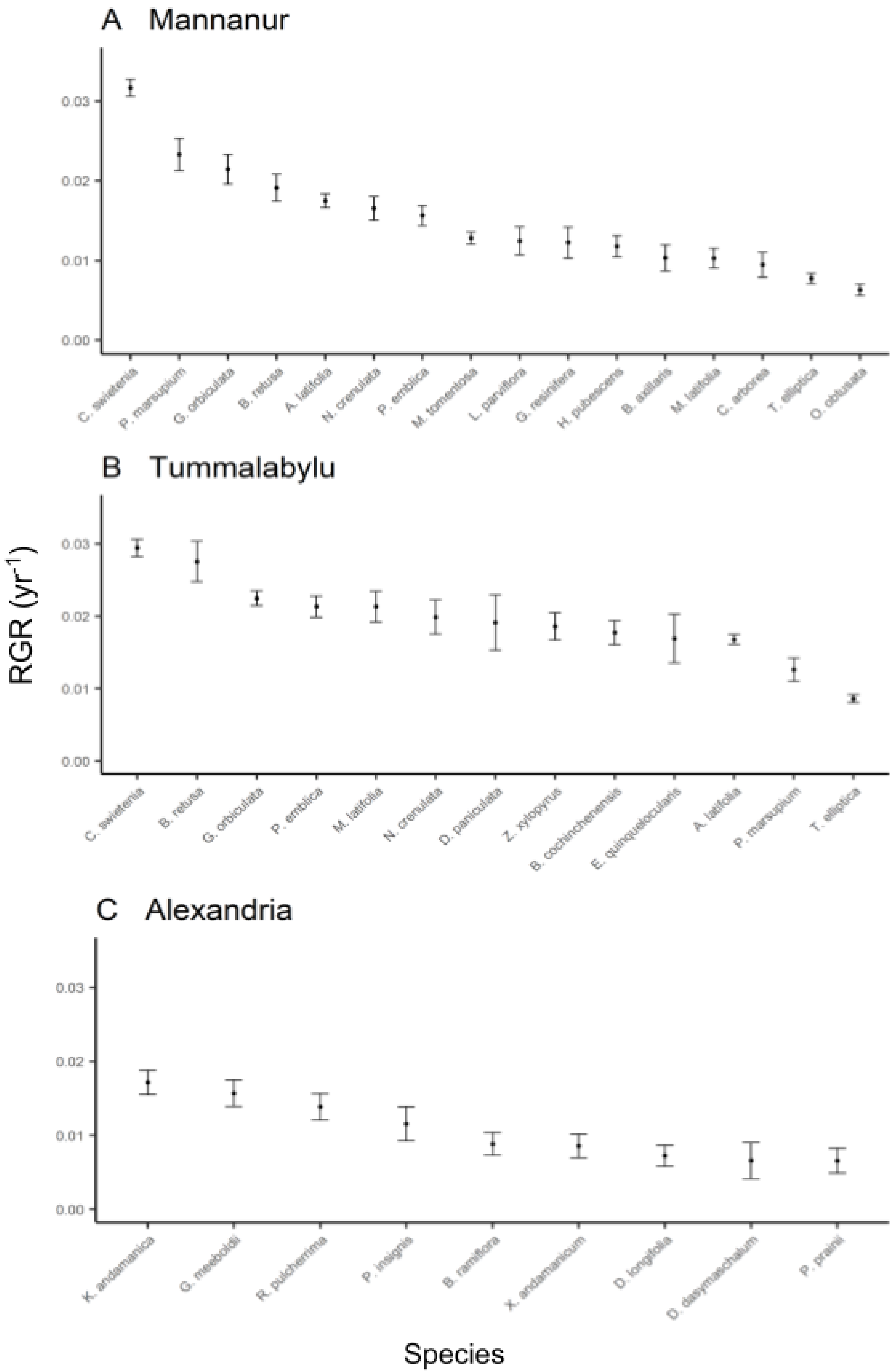

Fig 5: Species average RGR at A: Mannanur, B: Tummalabylu, C: Alexandria. Error bars represent standard error

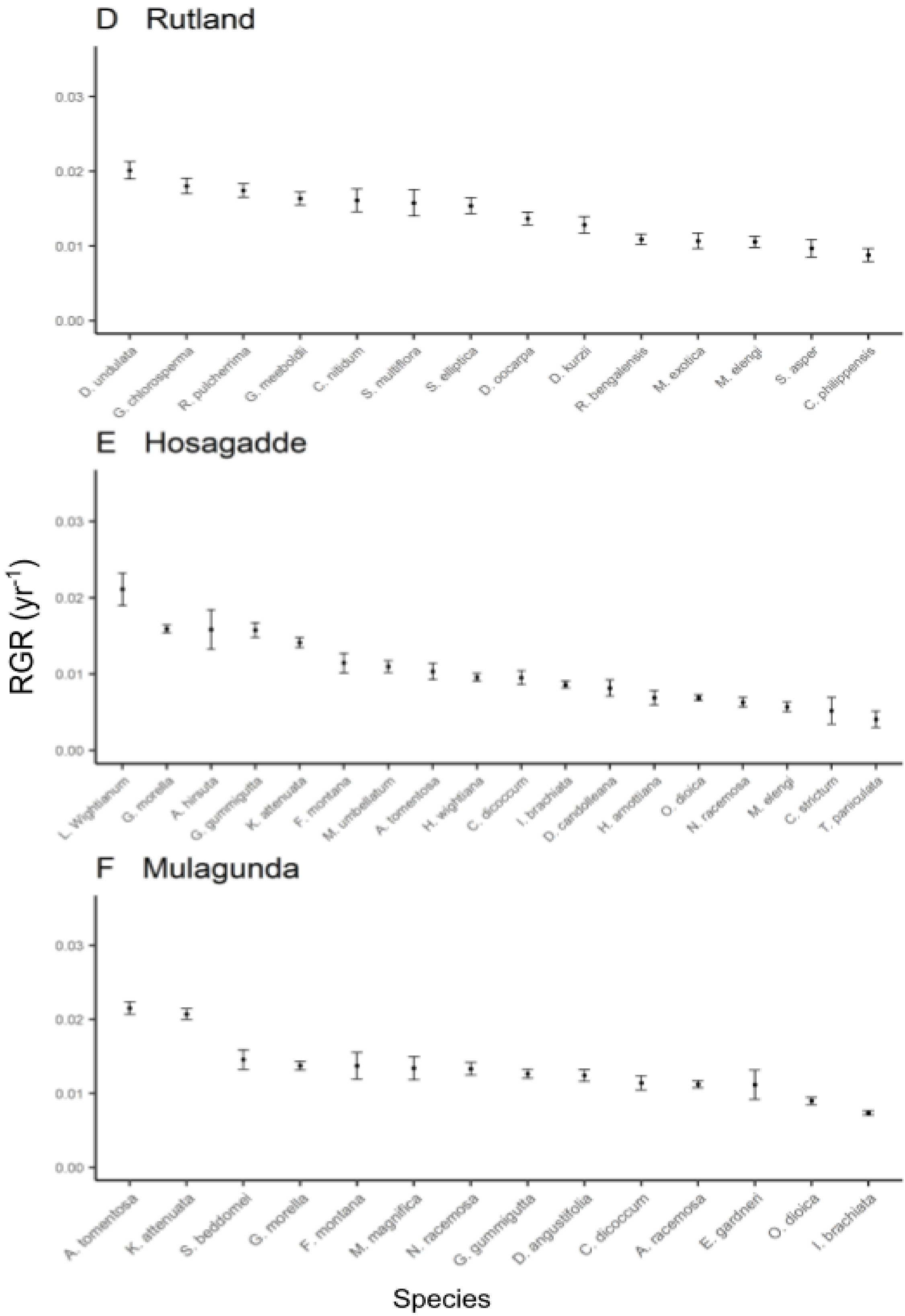

Fig 5 (cont) : Species average RGR at D: Rutland, B: Hosagadde, C: Mulagunda. Error bars represent standard error

GLMM Analysis:

Dispersion tests indicate that the models fit well with the data, with dispersion ratios close to 1 - 0.9997 for the AGR response model, and 1.014 for the RGR response model (Fig 6 and 7). The estimates indicate that a 1 unit increase in girth increases AGR by 4.278×10^{-3} cm yr^{-1} ($p<0.001$), and a 1 unit increase in MAP decreases AGR by 4.145×10^{-5} cm yr^{-1} ($p<0.01$). The interaction effect is positive and comparable to that of initial girth (0.056; $p<0.001$). For RGR, a unit increase in initial girth and MAP, respectively lead to a decrease of 1.603×10^{-4} yr^{-1} ($p<0.001$) and 1.615×10^{-6} yr^{-1} ($p<0.01$).

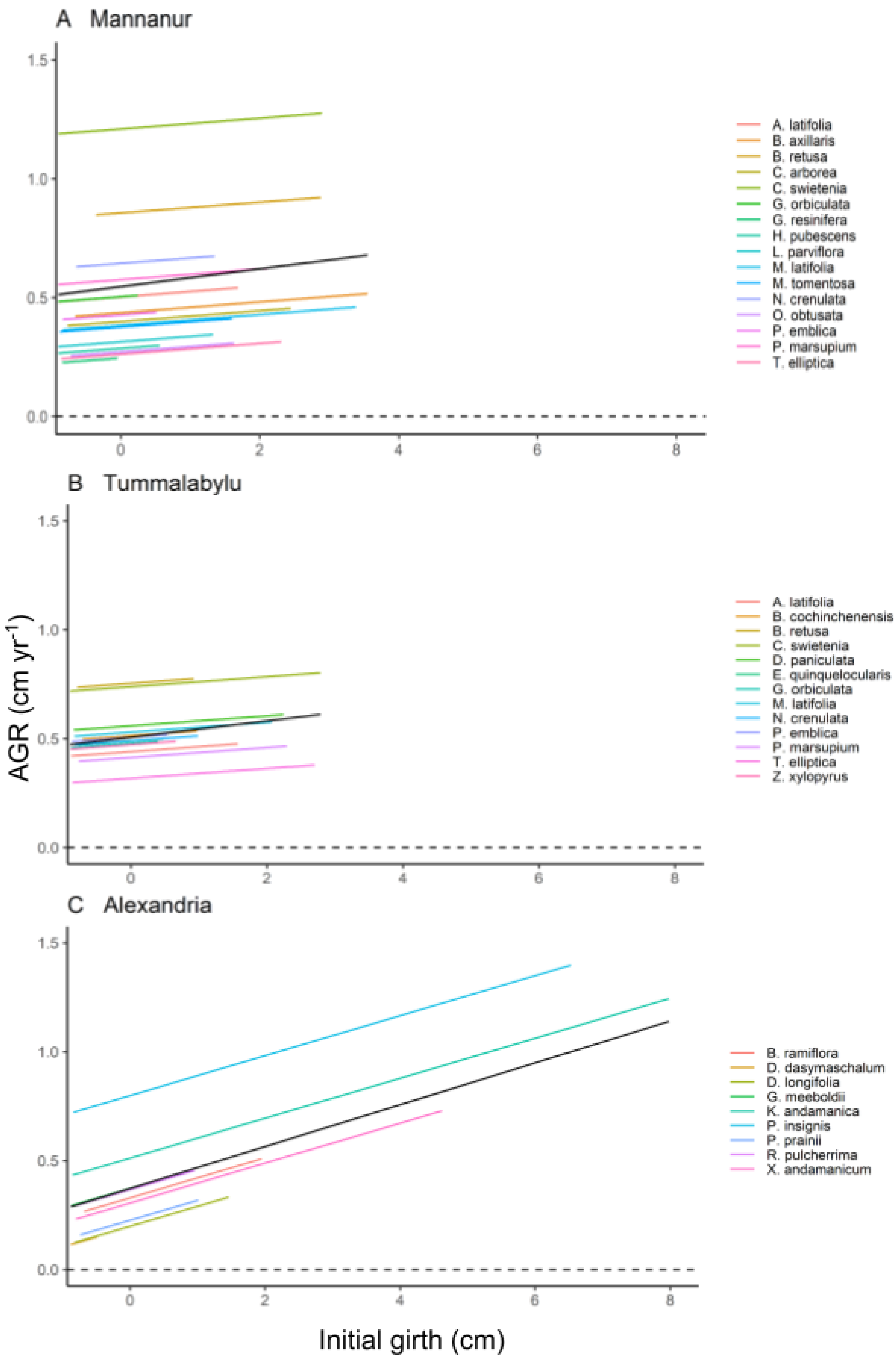

Fig 6: AGR v Initial girth curves predicted by model AGR ~ Initial Girth * MAP + (1|Plot/Species). Black line represent values by model AGR ~ Initial Girth * MAP + (1|Plot)

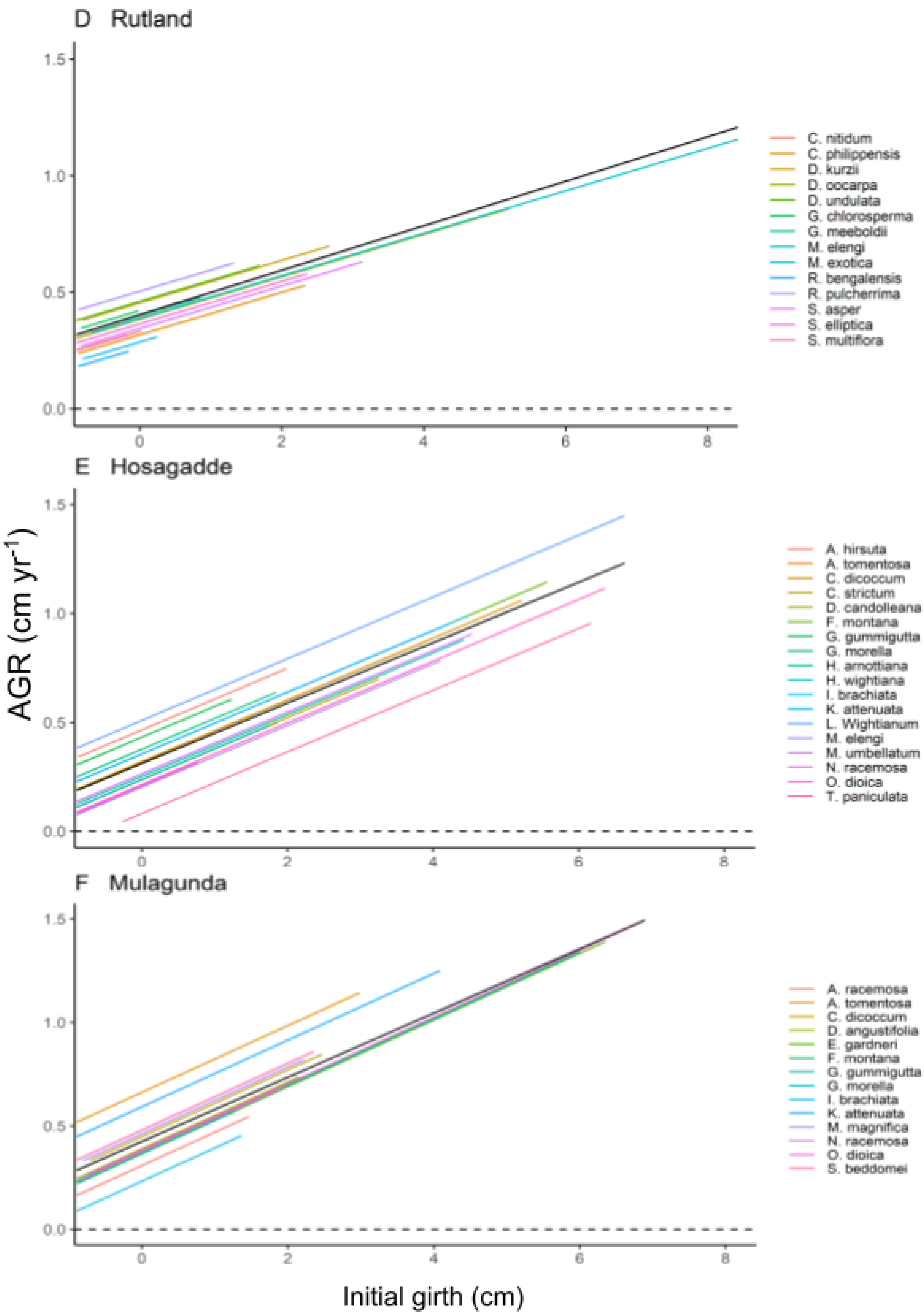

Fig 6 (cont): AGR v Initial girth curves predicted by model AGR ~ Initial Girth * MAP + (1|Plot/Species). Black line represent values by model AGR ~ Initial Girth * MAP + (1|Plot)

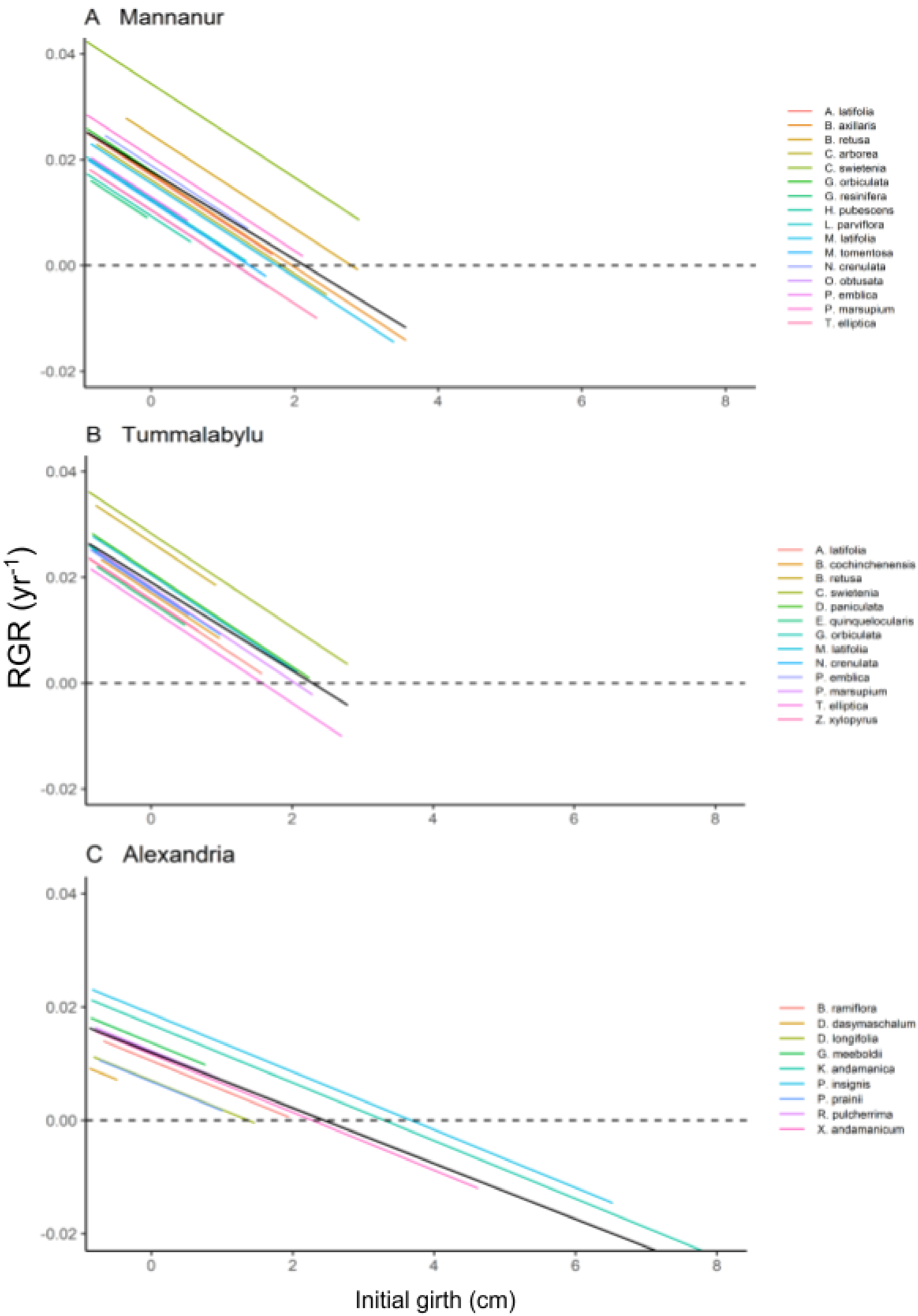

Fig 7: RGR v Initial girth curves predicted by model RGR ~ Initial Girth * MAP + (1|Plot/Species). Black line represent values by model RGR ~ Initial Girth * MAP + (1|Plot)

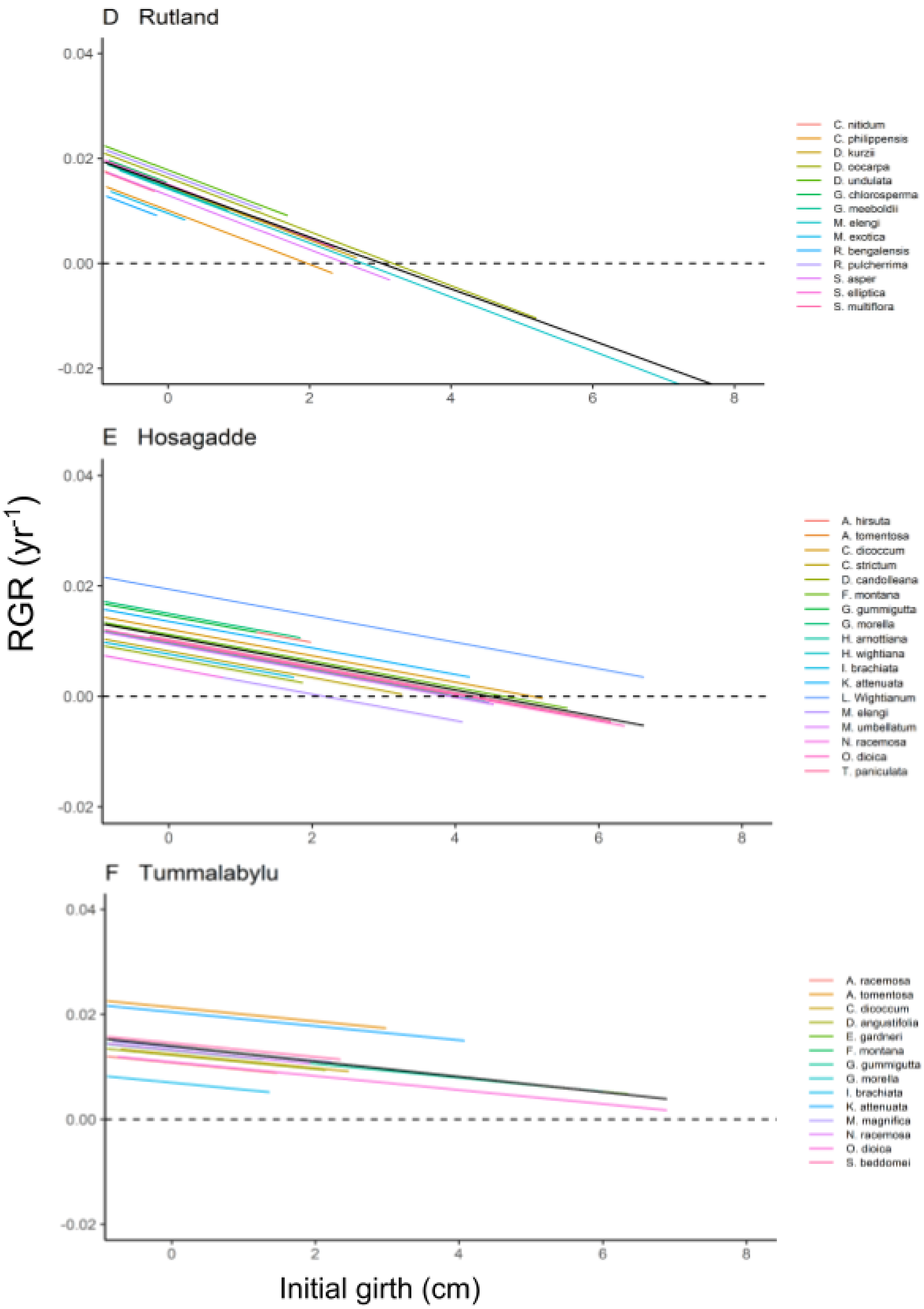

Fig 7 (cont): RGR v Initial girth curves predicted by model RGR ~ Initial Girth * MAP + (1|Plot/Species). Black line represent values by model RGR ~ Initial Girth * MAP + (1|Plot)

The small basal area proportion of dominant species in Andamans is due to many individuals (~160) being unidentified/identified up to the genus level and a larger proportion of smaller individuals in the dominant species in Alexandria and Rutland.

Typically vascular plants grow continuously for a part of their lifetime and reach a maximum size after maturation. They may also shrink with the natural process of ageing, even while not accounting for injury or pathogen attacks which disrupt life processes in many different ways. Juveniles may go through a “growth spurt”, or multiple spurts periodically, wherein the girth increases exponentially with time. Since we have selected individuals to exclude juveniles, such a pattern is not seen in any species in any plot. The absolute growth rate of a plant at a given time may then be positive or negative and may hold a constant value for a particular time period. I observed that for most species in our plots, the AGR remains constant or increases slightly with an increase in the size of the tree at the beginning of the census. This is probably a consequence of the tree maturation stage. The absolute growth rate is expected to decrease as a tree gets closer to its maximum size.

Temperature is an important factor to investigate next. As seasonal temperature fluctuations and extremes become more common with climate change, growth rates and carbon sequestration in tropical forests will be affected. The relation between growth and phenological and functional traits such as leaf flush and fall, leaf and stem hydraulic safety margins can tell us how trees will grow in longer/shorter dry seasons without leading to loss of physiological function. Long-term ecosystem monitoring is a promising area of research. Studies in previously established long-term plots go on to look at growth rates in multiple intervals of 2 or more years. Such studies will help us get a clearer picture of how growth rates change within a changing forest community.

Appendix 1: List of Dominant Species

Plot	Code	Full name	Genus
Mannanur	ANOLAT	Anogeissus latifolia	Anogeissus
Mannanur	BRERET	Bridelia retusa	Bridelia
Mannanur	BUCAXI	Buchanania axillaris	Buchanania
Mannanur	CARARB	Careya arborea	Careya
Mannanur	CHLSWI	Chloroxylon swietenia	Chloroxylon
Mannanur	EMBOFF	Phyllanthus emblica	Phyllanthus
Mannanur	GARRES	Gardenia resinifera	Gardenia
Mannanur	GREORB	Grewia orbiculata	Grewia
Mannanur	HOLPUB	Holarrhena pubescens	Holarrhena
Mannanur	LAGPAR	Lagerstroemia parviflora	Lagerstroemia
Mannanur	MADLAT	Madhuca latifolia	Madhuca
Mannanur	MILTOM	Miliusa tomentosa	Miliusa
Mannanur	NARCRE	Naringi crenulata	Naringi
Mannanur	OCNOBT	Ochna obtusata	Ochna
Mannanur	PTEMAR	Pterocarpus marsupium	Pterocarpus
Mannanur	TERELL	Terminalia elliptica	Terminalia
Hosagadde	AGLTOM	Aglaia tomentosa	Aglaia
Hosagadde	ARTHIR	Artocarpus hirsuta	Artocarpus
Hosagadde	CANDIC	Canthium dicoccum	Canthium
Hosagadde	CANSTR	Canarium strictum	Canarium
Hosagadde	DIOCAN	Diospyros candolleana	Diospyros
Hosagadde	FLAMON	Flacourtia montana	Flacourtia
Hosagadde	GARGUM	Garcinia gummigutta	Garcinia
Hosagadde	GARMOR	Garcinia morella	Garcinia
Hosagadde	HOLARN	Holigarna arnottiana	Holigarna
Hosagadde	HOPWIG	Hopea wightiana	Hopea

Hosagadde	IXOBRA	Ixora brachiata	Ixora
Hosagadde	KNEATT	Knema attenuata	Knema
Hosagadde	LOPWIG	Lophopetalum Wightianum	Lophopetalum
Hosagadde	MEMUMB	Memecylon umbellatum	Memecylon
Hosagadde	MIMELE	Mimusops elengi	Mimusops
Hosagadde	NOTRAC	Nothopegia racemosa	Nothopegia
Hosagadde	OLEDIO	Olea dioica	Olea
Hosagadde	TERPAN	Terminalia paniculata	Terminalia
Mulagunda	AGLTOM	Aglaia tomentosa	Aglaia
Mulagunda	ATARAC	Atalantia racemosa	Atalantia
Mulagunda	CANDIC	Canthium dicoccum	Canthium
Mulagunda	DIOANG	Diospyros angustifolia	Diospyros
Mulagunda	EUGGAR	Eugenia gardneri	Eugenia
Mulagunda	FLAMON	Flacourtia montana	Flacourtia
Mulagunda	GARGUM	Garcinia gummigutta	Garcinia
Mulagunda	GARMOR	Garcinia morella	Garcinia
Mulagunda	IXOBRA	Ixora brachiata	Ixora
Mulagunda	KNEATT	Knema attenuata	Knema
Mulagunda	MYRMAG	Myristica magnifica	Myristica
Mulagunda	NOTRAC	Nothopegia racemosa	Nothopegia
Mulagunda	OLEDIO	Olea dioica	Olea
Mulagunda	SYMBED	Symplocos beddomei	Symplocos
Tummalabylu	ANOLAT	Anogeissus latifolia	Anogeissus
Tummalabylu	BUCCOC	Buchanania cochinchenensis	Buchanania
Tummalabylu	BRERET	Bridelia retusa	Bridelia
Tummalabylu	CHLSWI	Chloroxylon swietenia	Chloroxylon
Tummalabylu	DALPAN	Dalbergia paniculata	Dalbergia
Tummalabylu	EMBOFF	Phyllanthus emblica	Phyllanthus
Tummalabylu	ERIQUI	Eriolaena quinquelocularis	Eriolaena
Tummalabylu	GREORB	Grewia orbiculata	Grewia

Tummalabylu	MADLAT	Madhuca latifolia	Madhuca
Tummalabylu	NARCRE	Naringi crenulata	Naringi
Tummalabylu	PTEMAR	Pterocarpus marsupium	Pterocarpus
Tummalabylu	TERELL	Terminalia elliptica	Terminalia
Tummalabylu	ZIZXYL	Ziziphus xylopyrus	Ziziphus
Rutland	AGLAND	Aglaia andamanica	Aglaia
Rutland	CELPHI	Celtis philippensis	Celtis
Rutland	CLENIT	Cleidion nitidum	Cleidion
Rutland	DIOKUR	Diospyros kurzii	Diospyros
Rutland	DIOUND	Diospyros undulata	Diospyros
Rutland	DIOOOC	Diospyros oocarpa	Diospyros
Rutland	DIOUND	Diospyros undulata	Diospyros
Rutland	GLYCHL	Glycosmis chlorosperma	Glycosmis
Rutland	GONMEE	Goniothalamus meeboldii	Goniothalamus
Rutland	MIMELE	Mimusops elengi	Mimusops
Rutland	MUREXO	Murraya exotica	Murraya
Rutland	RINBEN	Rinorea bengalensis	Rinorea
Rutland	ROTPUL	Rothmannia pulcherrima	Rothmannia
Rutland	SAGELL	Sageraea elliptica	Sageraea
Rutland	STRASP	Streblus asper	Streblus
Rutland	SURMUL	Suregada multiflora	Suregada
Alexandria	BACRAM	Baccaurea ramiflora	Baccaurea
Alexandria	DESDAS	Dasymaschalon dasymaschalum	Dasymaschalon
Alexandria	DRYLON	Drypetes longifolia	Drypetes
Alexandria	GONMEE	Goniothalamus meeboldii	Goniothalamus
Alexandria	KNEAND	Knema andamanica	Knema
Alexandria	PARINS	Parishia insignis	Parishia
Alexandria	PSEPRA	Pseuduvaria prainii	Pseuduvaria
Alexandria	ROTPUL	Rothmannia pulcherrima	Rothmannia

Alexandria	XANAND	Xanthophyllum andamanicum	Xanthophyllum

Appendix 2: SMA Regression for Growth Rate vs Initial Girth

		AGR				RGR			
Plot	Species	Intercept	Slope	R sq	p-value	Intercept	Slope	R sq	p-value
ALXA	BACRAM	-0.7419	0.0276	0.0001	0.9424	0.03421	-0.00064	0.02835	0.02835
ALXA	DESDAS	1.2026	-0.0742	0.1012	0.0990	0.08527	-0.00528	0.14287	0.04735
ALXA	DRYLON	1.1300	-0.0320	0.0299	0.0954	0.03746	-0.00101	0.10937	0.00113
ALXA	GONMEE	1.0199	-0.0297	0.0051	0.6716	0.04957	-0.00147	0.11926	0.03371
ALXA	KNEAND	-0.0867	0.0186	0.0396	0.0680	0.03424	-0.00052	0.04537	0.05032
ALXA	PARINS	-0.8940	0.0258	0.2951	0.0009	-0.00468	0.00022	0.00669	0.64558
ALXA	PSEPRA	-0.2210	0.0150	0.0065	0.7364	0.02309	-0.00065	0.02910	0.47212
ALXA	ROTPUL	-0.3635	0.0285	0.0085	0.5506	0.04673	-0.00134	0.03216	0.24407
ALXA	XANAND	-0.1110	0.0096	0.0516	0.3095	0.01752	-0.00019	0.07846	0.20674
HSGD	AGLTOM	-0.1253	0.0157	0.4118	0.0000	0.02485	-0.00056	0.00041	0.86480
HSGD	ARTHIR	-0.3925	0.0330	0.0773	0.1298	0.03694	-0.00083	0.00028	0.92912
HSGD	CANDIC	-0.2123	0.0113	0.1536	0.0031	0.02244	-0.00021	0.09439	0.02251
HSGD	CANSTR	-0.7637	0.0196	0.0660	0.2051	-0.01046	0.00027	0.01825	0.51053
HSGD	DIOCAN	-0.1256	0.0158	0.0958	0.0027	0.02054	-0.00072	0.00118	0.74511
HSGD	FLAMON	-0.0212	0.0121	0.1485	0.0244	0.02217	-0.00036	0.00596	0.66431
HSGD	GARGUM	-0.4519	0.0399	0.2288	0.0000	-0.01326	0.00141	0.00082	0.74177
HSGD	GARMOR	-0.0358	0.0154	0.0037	0.3175	0.03424	-0.00078	0.19608	0.00000
HSGD	HOLARN	-0.4359	0.0135	0.1630	0.0018	0.02034	-0.00021	0.02667	0.22482
HSGD	HOPWIG	-0.1848	0.0168	0.4714	0.0000	-0.00258	0.00038	0.01115	0.03840
HSGD	IXOBRA	-0.0964	0.0126	0.0871	0.0006	0.02181	-0.00062	0.04327	0.01712
HSGD	KNEATT	0.0261	0.0110	0.1912	0.0000	0.02625	-0.00044	0.06695	0.00095
HSGD	LOPWIG	0.1601	0.0120	0.3605	0.0003	0.02931	-0.00028	0.09007	0.09513
HSGD	MEMUMB	0.0202	0.0094	0.2108	0.0000	0.01979	-0.00058	0.01348	0.23147
HSGD	MIMELE	-0.2043	0.0143	0.2365	0.0000	-0.00292	0.00034	0.00033	0.86598
HSGD	NOTRAC	-0.2809	0.0212	0.0809	0.0034	-0.01291	0.00098	0.00125	0.72197
HSGD	OLEDIO	-0.4298	0.0127	0.0716	0.0006	0.01787	-0.00017	0.06614	0.00095

HSGD	TERPAN	-0.7396	0.0117	0.0332	0.4293	0.01701	-0.00014	0.02514	0.49244
MANR	ANOLAT	1.2792	-0.0246	0.0009	0.7683	0.04331	-0.00082	0.24422	0.00000
MANR	BRERET	1.9241	-0.0199	0.0025	0.8061	0.05160	-0.00063	0.38224	0.00059
MANR	BUCAXI	1.0632	-0.0115	0.0382	0.3098	0.02797	-0.00033	0.32523	0.00124
MANR	CARARB	-0.2561	0.0128	0.0338	0.3304	0.02819	-0.00036	0.28012	0.00263
MANR	CHLSWI	0.3893	0.0202	0.0075	0.3767	0.06320	-0.00075	0.51403	0.00000
MANR	EMBOFF	-0.8061	0.0496	0.0675	0.0629	0.05734	-0.00169	0.00236	0.73211
MANR	GARRES	0.5879	-0.0239	0.1927	0.0319	0.04045	-0.00167	0.39225	0.00106
MANR	GREORB	-0.4639	0.0419	0.0014	0.8247	0.06485	-0.00189	0.12293	0.03338
MANR	HOLPUB	0.8202	-0.0237	0.0317	0.1980	0.04123	-0.00125	0.18672	0.00110
MANR	LAGPAR	0.8683	-0.0177	0.1539	0.0012	0.04379	-0.00098	0.38177	0.00000
MANR	MADLAT	0.0095	0.0080	0.0197	0.5128	0.02425	-0.00029	0.24708	0.01347
MANR	MILTOM	-0.0323	0.0133	0.0833	0.0042	0.02728	-0.00048	0.11255	0.00078
MANR	NARCRE	-0.4375	0.0274	0.0773	0.1369	0.04789	-0.00078	0.09409	0.09921
MANR	OCNOBT	-0.5706	0.0194	0.0195	0.2633	0.02423	-0.00042	0.04526	0.08635
MANR	PTEMAR	-0.0360	0.0240	0.0914	0.0411	0.05294	-0.00117	0.06810	0.07983
MANR	TERELL	-0.2770	0.0134	0.0006	0.8130	0.02735	-0.00049	0.16697	0.00007
MLGD	AGLTOM	-0.1053	0.0237	0.1824	0.0000	0.04442	-0.00071	0.09365	0.00007
MLGD	ATARAC	-0.1870	0.0186	0.0396	0.0001	0.03113	-0.00085	0.08212	0.00000
MLGD	CANDIC	-0.5272	0.0211	0.0217	0.3645	0.03388	-0.00043	0.09517	0.05278
MLGD	DIOANG	-0.2523	0.0213	0.1739	0.0000	0.03188	-0.00067	0.01335	0.13586
MLGD	EUGGAR	-0.1654	0.0107	0.0975	0.0637	0.02529	-0.00019	0.11167	0.04638
MLGD	FLAMON	-0.2836	0.0257	0.0314	0.3492	0.03501	-0.00093	0.03580	0.31661
MLGD	GARGUM	0.0292	0.0094	0.1232	0.0001	0.02490	-0.00027	0.17606	0.00000
MLGD	GARMOR	-0.0972	0.0177	0.1144	0.0010	0.03062	-0.00071	0.06324	0.01561
MLGD	IXOBRA	-0.1088	0.0119	0.1999	0.0000	0.01711	-0.00041	0.01418	0.18778
MLGD	KNEATT	0.0242	0.0185	0.3132	0.0000	0.03831	-0.00059	0.09822	0.00004
MLGD	MYRMAG	0.0073	0.0119	0.2123	0.0309	0.02794	-0.00030	0.30003	0.00832
MLGD	NOTRAC	-0.1141	0.0154	0.0519	0.0542	0.03374	-0.00065	0.20671	0.00006
MLGD	OLEDIO	-0.6396	0.0181	0.1133	0.0001	0.02493	-0.00023	0.02517	0.06923

MLGD	SYMBED	-0.2777	0.0217	0.2807	0.0000	0.03273	-0.00050	0.06014	0.05471
RTLD	AGLAND	0.0194	0.0169	0.0000	0.9921	0.03450	-0.00057	0.23838	0.00000
RTLD	CELPHI	-0.0794	0.0110	0.3870	0.0001	0.01711	-0.00023	0.01254	0.52194
RTLD	CLENIT	0.7996	-0.0317	0.0087	0.5570	0.04798	-0.00190	0.21032	0.00225
RTLD	DIOKUR	-0.0917	0.0137	0.0703	0.0657	0.02829	-0.00036	0.24161	0.00034
RTLD	DIOOOC	0.0541	0.0081	0.0764	0.0017	0.02489	-0.00024	0.36611	0.00000
RTLD	DIOUND	-0.1230	0.0249	0.0273	0.1352	0.04534	-0.00115	0.09223	0.00525
RTLD	GLYCHL	-0.2505	0.0309	0.0161	0.3792	0.04976	-0.00156	0.18777	0.00167
RTLD	GONMEE	-0.1273	0.0211	0.0005	0.8797	0.03962	-0.00099	0.26073	0.00011
RTLD	MIMELE	0.1152	0.0066	0.2706	0.0027	0.01670	-0.00012	0.13574	0.04141
RTLD	MUREXO	0.6258	-0.0168	0.0021	0.8061	0.02870	-0.00078	0.32095	0.00089
RTLD	RINBEN	-0.1739	0.0209	0.1155	0.0049	0.03063	-0.00111	0.03331	0.13936
RTLD	ROTPUL	1.3140	-0.0257	0.0095	0.3633	0.04759	-0.00095	0.34577	0.00000
RTLD	SAGELL	0.1080	0.0079	0.0109	0.3438	0.02901	-0.00043	0.46706	0.00000
RTLD	STRASP	-0.0379	0.0089	0.0000	0.9724	0.02189	-0.00025	0.28895	0.00126
RTLD	SURMUL	0.9587	-0.0400	0.0089	0.5434	0.05783	-0.00244	0.16256	0.00665
TBLU	ANOLAT	0.9649	-0.0179	0.0012	0.6648	0.04262	-0.00088	0.28386	0.00000
TBLU	BRERET	1.7707	-0.0302	0.1228	0.0859	0.07439	-0.00143	0.68359	0.00000
TBLU	BUCCOC	0.0858	0.0143	0.0754	0.2414	0.03549	-0.00059	0.33450	0.00755
TBLU	CHLSWI	1.2838	-0.0181	0.0002	0.8576	0.06020	-0.00102	0.36388	0.00000
TBLU	DALPAN	1.4403	-0.0219	0.1173	0.0690	0.05991	-0.00103	0.36897	0.00047
TBLU	EMBOFF	-0.8371	0.0609	0.0354	0.1572	0.06416	-0.00195	0.04528	0.10879
TBLU	ERIQUI	-1.2886	0.0667	0.0359	0.3157	0.06641	-0.00186	0.02524	0.40171
TBLU	GREORB	-0.2372	0.0346	0.0147	0.2346	0.06052	-0.00187	0.11999	0.00048
TBLU	MADLAT	0.9843	-0.0146	0.0042	0.7583	0.04445	-0.00075	0.36258	0.00145
TBLU	NARCRE	-0.2350	0.0266	0.0000	0.9788	0.05585	-0.00133	0.22355	0.01472
TBLU	PTEMAR	0.8944	-0.0097	0.0430	0.3093	0.03441	-0.00045	0.55664	0.00001
TBLU	TERELL	0.7976	-0.0098	0.0003	0.8595	0.02985	-0.00044	0.33313	0.00000
TBLU	ZIZXYL	-0.5437	0.0414	0.0710	0.0414	0.05352	-0.00144	0.05436	0.07554

Appendix 3: GLMM Parameters for AGR ~ (Initial Girth * MAP) + (1 | Plot / Species)

AIC	**BIC**	**logLikelihood**	**deviance**	**df.resid**
5017.7	5065.5	-2501.9	5003.7	6749
Fixed Effects	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.389919	0.021037	18.535	< 2e-16 ***
Initial girth	0.108665	0.005035	21.581	< 2e-16 ***
MAP	-0.002203	0.0007107	-3.1	0.00194 **
Initial girth * MAP	0.0028098	0.0001789	15.71	< 2e-16 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				
Number of obs: 6756 Groups: Species:Plot, 85; Plot 6				
Dispersion estimate for gaussian family (sigma^2): 0.119				
Random effects	**Name**	**Variance**	**Std.Dev.**	
Species : Plot	Intercept	0.0242568	0.15575	
Plot	Intercept	0.0005594	0.02365	
DHARMa nonparametric dispersion test via sd of residuals fitted vs. simulated				
dispersion	0.99966	p-value	0.896	
alternative hypothesis: two.sided				

Appendix 4: GLMM Parameters for RGR ~ (Initial Girth * MAP) + (1 | Plot / Species)

AIC	**BIC**	**logLikelihood**	**deviance**	**df.resid**
-41768.9	-41721.2	20891.5	-41782.9	6749
Fixed Effects	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.0135204	0.0007412	18.24	< 2e-16 ***
Initial girth	-0.0040719	0.0001578	-25.81	< 2e-16 ***
MAP	-0.056522	0.020138	-2.807	0.00501 **
Initial girth * MAP	-0.002203	0.0007107	-3.1	0.00194 **
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1				
Number of obs: 6756 Groups: Species:Plot, 85; Plot 6				
Dispersion estimate for gaussian family (sigma^2): 0.000117				
Random effects	**Name**	**Variance**	**Std.Dev.**	
Species : Plot	Intercept	0.0242568	0.15575	
Plot	Intercept	0.0005594	0.02365	
DHARMa nonparametric dispersion test via sd of residuals fitted vs. simulated				
dispersion	1.014	p-value	0.624	
alternative hypothesis: two.sided				

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