



Monitoring the Knysna forest; species, community and forest responses

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Honours dissertation

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Forests are valuable ecosystems to society but are greatly threatened by changing factors from habitat conversion to climate change. South Africa's only extent of indigenous forest is predicted to disappear within the next 30 years. Many challenges are currently faced when trying to detect and interpret directional changes in forests which results in an urgent need to understand any effects that these change factors have on forest ecosystems. We investigate evidence for change in the old growth Lilyvlei Nature Reserve by monitoring growth and dynamics at various levels by examining a 20 year record of tree growth and stand dynamics. Through the inclusion of biodiversity measures and ecologically important plant traits, changes in forest dynamics and growth are investigated. Results show no total change in biomass across the 20 year period, although an intensification of extreme climatic events and dynamics indices were recorded for the second period. Significant correlations were found between community diversity measures and forest growth. Trait variables showed insignificant correlations with forest growth and dynamics. These results suggest that the Knysna forest is controlled by climatic variables and that increased diversity within communities result in increased growth. It is believed that changes in the forest may be masked by compositional shifts of just a few dominant species. These results become important, particularly in the light of changing climatic, atmospheric and environmental changes that threaten global ecosystems in the time to come. However, considering the brief 20 year period observed in a forest where the average individual has a life span of over a century, the importance of long term monitoring becomes an important component in the understanding of forest ecosystems.

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Introduction

There is a need for a proactive focus on creating, maintaining and monitoring resilience to climate change impacts in forest ecosystems (Abbott and Le Maitre, 2010). Forests are rich in biodiversity, providing sought-after products and services such as timber, medicines and ecotourism opportunities (Pretzsch, 2009). With the threat of climatic and atmospheric changes intensifying, responses from forests are expectantly complex due to the integrated effects of these and other changing environmental factors on plants (Clarke, 2007). The resulting impacts on the world's carbon cycle and global biodiversity could have large political and economic ramifications (Clarke, 2007).

There is much evidence to suggest that biodiversity influences the functioning and stability of an ecosystem (Naeem, 2002; Hooper et al., 2005). Increased species diversity influences ecosystem functioning in two ways, as outlined by Loreau et al., (2001). Firstly through dominance, that is brought about by ecological "selection" for species with particular traits that excel within an environment and hence improve ecosystem functioning. Secondly with complementarity among species that combined, enhance ecosystem functioning. It would therefore be expected that diverse communities would be more stable in the face of environmental change and disturbance.

Studying plant traits that reflect important ecological dimensions such as the determination of plant growth rates, longevity, competitive ability, as well as resistance to drought, disturbance and pests, (Wright et al., 2004; Chave et al., 2009; Wright et al., 2010) allow for the prediction of species responses to disturbance and negative change impacts. This may aid in developing species-specific management strategies to conserve indigenous forest ecosystems and allows testing of hypotheses relating biodiversity to ecosystem function.

Monitoring forest dynamics provides a scientific basis for the management of forests by gaining insight into forest growth, mortality and recruitment, and allows for the sustainable utilization of forest resources without sacrificing biodiversity. Particularly in the light of climate change, biodiversity is an important variable to monitor and maintain particularly over a long time frame. The present and anticipated impacts of climate change paint an ominous picture for forest ecosystems with local models predicting the demise of South Africa's only significant extent of indigenous forest by 2050 (Midgley et al., 2001). With less than one percent of South Africa being covered by closed canopy forests (Durrheim, 2010), it is an important commodity to conserve.

However, there has been little evidence of the demise of South African and other forests to date (Lewis et al., 2006; Midgley and Seydack, 2006; Wright and Muller-Landau, 2006; Phillips et al., 2008).

Long-term permanent plots monitoring tree growth and mortality in South African forests only began around 1987 (Geldenhuys and Van Daalen, 1992). Some of these plots have been maintained and are measured roughly every 10 years. There are published studies on forest growth (e.g. Van Daalen, 1991) but only one on the relationship with climate and that only analysed data for the period from 1991 to 2001 (Midgley and Seydack, 2006). This particular study did not investigate species-specific responses due to a limited data set.

The objective of this study is to build on the findings of Midgley and Seydack (2006) and investigate changes in forest dynamics along a larger time frame and across variable climatic conditions. This is done with reference to biodiversity and ecologically important plant traits. Specific questions are asked:

- 1) Have there been major differences in climatic variation between the two inter-survey periods?
- 2) Has total basal area (BA), above ground biomass (AGB) and/or dynamics changed between survey periods and across the entire 20 year period (1991-2001-2012):
 - a. At a stand level: i.e. all sampled individuals across the forest
 - b. At a community level: i.e. individuals within plots across the stand
 - c. At a species level: i.e. individuals within species
- 3) Do plots with greater biodiversity display greater resilience to change in growth and dynamism?
- 4) Is total forest biomass being maintained at a constant level by complementary effects, where declines in some species are being masked by increases in others.
- 5) Can plant functional traits be used to predict species-specific and plot-level growth and dynamism?

Methods

Study site

Knysna forest is the largest complex of natural forests in southern Africa, covering over 60 000ha and is located within the Eastern and Western Cape Provinces of South Africa (Geldenhuys, 1991). They consist of subtropical moist broad leafed forest species characteristic of the Southern Afrotropical forest vegetation type (Mucina and Rutherford, 2006). These forests are intolerant of fire, and the frequent fires of the surrounding fynbos, savannah and grasslands limit the expansion of the forests (Midgley et al., 1997). The Knysna forest is comprised mainly of shade-tolerant species with abundant regeneration and has a mild disturbance regime (most trees die standing, creating small gaps) (Midgley et al., 1990; 1995). The Lilyvlei Nature Reserve (33°55'19.19"S, 23°02'34.83"E), an unutilized section of the indigenous Knysna forest, is where this study takes place.

Climatic variables

Precipitation was measured at Diepwalle (33°56'50.10"S, 23°09'31.90"E) and monitored through monthly averages since 1980. Mean and 95 percentiles were calculated and used to examine the record.

Community sampling

One hundred and eight circular plots of 0.04 ha (radius 11.3 m) each, were laid out on a grid throughout the Lilyvlei old growth forest, sampling 5% of the total area. All trees greater than 10 cm diameter at breast height (dbh) and rooted in the plots were identified to species and individually tagged. These diameters were originally measured when plots were established in 1991 (September to December) and re-measured in 2001/2002 (November to January) and 2012 (February to July). During each survey, tree conditions were recorded to a fixed set of standards (see Appendix: Table 1). For data analysis, two datasets were used, the "Raw" dataset, and "Conditioned" dataset. The conditioned dataset had all trees exhibiting any of the above conditions removed. This was done so as to compare healthy tree growth rates across the community. The raw dataset contained all trees, healthy and unhealthy across the entire forest community.

Data Processing

Both basal area (BA) and above ground biomass (AGB) were calculated for individual stems, plots and species across all three time periods. Basal Area (cm^2) was calculated where D_i is the initial stem diameter in cm (EQ. 1.1):

$$BA = \pi \left(\frac{D_i}{2} \right)^2$$

Basal Area Growth Rate (BAGR) ($\text{cm}^2 \text{ ha}^{-1} \text{ yr}^{-1}$) was calculated following Chao et al. (2008) method where t is the year of survey (EQ. 1.2):

$$BAGR = \frac{(BA_{t_1} - BA_{t_0})}{(t_1 - t_0)}$$

Relative Basal Area Growth Rate (RGR) (%) was determined using Chao et al. (2008). This measure was calculated across plots and species and values obtained were used to compare with trait and biodiversity measures. BA_{t_0} is the basal area at first measurement (EQ. 1.3):

$$RGR = \left(\frac{BAGR}{BA_{t_0}} \right) * 100$$

Above ground biomass (AGB) was calculated using allometric equations from Baker et al. (2004a) and Chave et al. (2005). No allometric equation has been derived for the Knysna forest, hence the use of these two equations. The Chave et al. (2005) allometric equation has been derived for dry tropical forest stands (below $1,500 \text{ mm yr}^{-1}$), with Knysna known to experience only $525 - 1220 \text{ mm yr}^{-1}$ (Geldenhys, 1989). The Baker et al. (2004a) equation was used to allow comparison with Midgley and Seydack (2006). The Chave et al. (2005) equation was used to allow incorporation of wood density measurements in the determination of AGB. Wood density significantly affects AGB measures, hence a constant and a species specific measure of wood density was employed for AGB estimation (Baker et al., 2004a; Chave et al., 2009). T tests were used to test for change in biomass between census periods at the community level. D_i is the initial stem diameter in cm and ρ represents the wood density in g cm^3 .

EQ 2.1) Baker et al. 2004a:

$$AGB = \sum_{i=1}^n \exp [0.33(\ln D_i) + 0.933(\ln D_i)^2 - 0.122(\ln D_i)^3 - 0.37]$$

EQ 2.2) Chave et al. 2005:

Constant Wood density at 0.724 (the average across 26 species in the data set);

$$AGB = \sum_{i=1}^n 0.724 * \exp [1.78(\ln D_i) + 0.207(\ln D_i)^2 - 0.0281(\ln D_i)^3 - 0.677]$$

EQ 2.3) Species-specific wood density;

$$AGB = \sum_{i=1}^n \rho * \exp [1.78(\ln D_i) + 0.207(\ln D_i)^2 - 0.0281(\ln D_i)^3 - 0.677]$$

Net and gross changes in biomass were calculated and compared. Net growth is the difference between final and initial total values, whereas gross growth is the amount of growth of initial stems still alive at second survey plus the new stems in the 10 cm dbh size-class. Growth was analysed with the use of only trees that have survived between initial and final surveys, therefore excluding mortality and recruitment.

Forest dynamics

The measure of dynamics is similar to the basal area/above ground biomass change using the number of stems rather than size of stems. This measure of forest health incorporates mortality and recruitment percentages to determine the effect of successional responses to disturbance events (Midgley and Seydack, 2006). Dynamism was determined using Sheil and May (1996) measures. Mortality and recruitment percentages were calculated for the three time periods across the forest stand as well as for individual species, and compared with relevant RGR values. Where n_0 is the number of original stems at first survey; n_m is the number of stems that died between surveys; n_r is the number of stems recruited at final survey:

$$\text{Recruitment \%} = \left[\left(\frac{n_o + n_r}{n_o} \right)^{1/t} - 1 \right] * 100$$

$$\text{Mortality \%} = \left[1 - \left(\frac{n_o - n_m}{n_o} \right)^{1/t} \right] * 100$$

$$\text{Dynamism} = \frac{[\text{Recruitment \%} + \text{Mortality \%}]}{2}$$

Biodiversity indices

Species diversity and richness was calculated using rarefied samples across the species community matrix. Species richness is a fundamental measurement of community and regional diversity, and underlies many ecological models and conservation strategies (Gotelli and Colwell, 2001). Taxon accumulation curves were used to determine the basic information to validate richness comparisons. Sample-based rarefaction curves depend on the spatial distribution of individuals as well as the size and placement of samples. This allows for meaningful standardization and comparison of datasets and becomes useful in a forest context due to the negative effects of stem density on stem size (e.g. Reineke, 1933).

Rarefied species diversity, species richness, Shannon Weiner's diversity index (H) (which takes into account both the number and relative abundance of species) and Pielou's J (J) Index (an index of pattern diversity or evenness in the relative abundance of species) were calculated and compared to community RGR. Plot biodiversity measures were also compared against plot dynamics. Analysis of co-variance (ANCOVA) was used to statistically test for any differences between time periods for RGR as a function of dynamics and RGR as a function of biodiversity indices.

Species Traits

Plant traits were sampled from twenty-six species that inhabit the Lilyvlei Nature Reserve during the period 14th-21st August 2012 (late winter). I aimed to collect 10 individuals for each of the 26 species and measured various leaf characteristics (average width, maximum width, length, area, specific leaf area, thickness and wet and dry weights) and wood density.

Wood density, defined here as the oven-dry mass divided by green volume (Chave et al., 2009), was calculated from cut branches with an average diameter of 13.06mm (± 0.11 mm, $n=273$). Volume was calculated using immersion. Dry weights were obtained after placing leaf and wood samples in drying ovens at 80°C for two and five days, respectively. Leaf characteristics were measured across three leaves per sample and averaged across the individual.

Trait values were averaged across species and evaluated across species relative growth rate (RGR) values. The natural log of species RGR values were plotted against initial basal area and compared with linear models. The slope and intercept at 10 cm DBH (78.38 cm² basal area) were used to compare with trait data. ANCOVA was used to test for differences between time periods within species. The use of community averaged trait values within functional ecology have more impact on ecosystem functioning than within community trait variation (Garnier, 2004). Therefore, functional diversity was calculated to compare with plot level growth rates, plot level biodiversity indices and dynamism.

Species growth rates were further analysed with the use of Quantile linear regression. Quantile regression is a way to estimate the conditional quantiles of a response variable distribution in a linear model that provides a more complete view of possible causal relationships between variables in ecological processes (Cade and Noon, 2003). Factors that affect ecological processes are not measured and included in statistical models. Therefore there may be stronger, useful predictive relationships with other parts of the response variable distribution. With the use of the median ($\tau=0.5$), upper 50 % ($\tau=0.75$) and upper 10% ($\tau=0.95$) of the species increment distribution plotted against initial DBH, the slope and intercept values of these regressions were used to analyse with trait variables.

All analyses were conducted in either Microsoft Excel (2007) or R 2.15.1 (R Core Team, 2012), with the use of R packages *vegan* (Oksanen et al., 2012) for rarefaction and calculation of biodiversity indices, *FD* (Laliberté and Shipley, 2011) for calculating functional diversity composition and *quantreg* (Koenker, 2012) for obtaining quantile regression values, and other supporting packages.

Results

Climatic variables

Total monthly precipitation had an average of 62.5 mm (0.95 =+110.5; 0.05= -46.4, n=380) from 1980 to 2012 with yearly mean rainfall remaining relatively constant between the first two survey periods (1991-2001) compared to the more variable means experienced between the second two survey periods (2001-2012) (Figure 1). The maximum (112.58mm) and minimum (34.77mm) mean yearly precipitation values for the 32 year record both occurred in the second period.

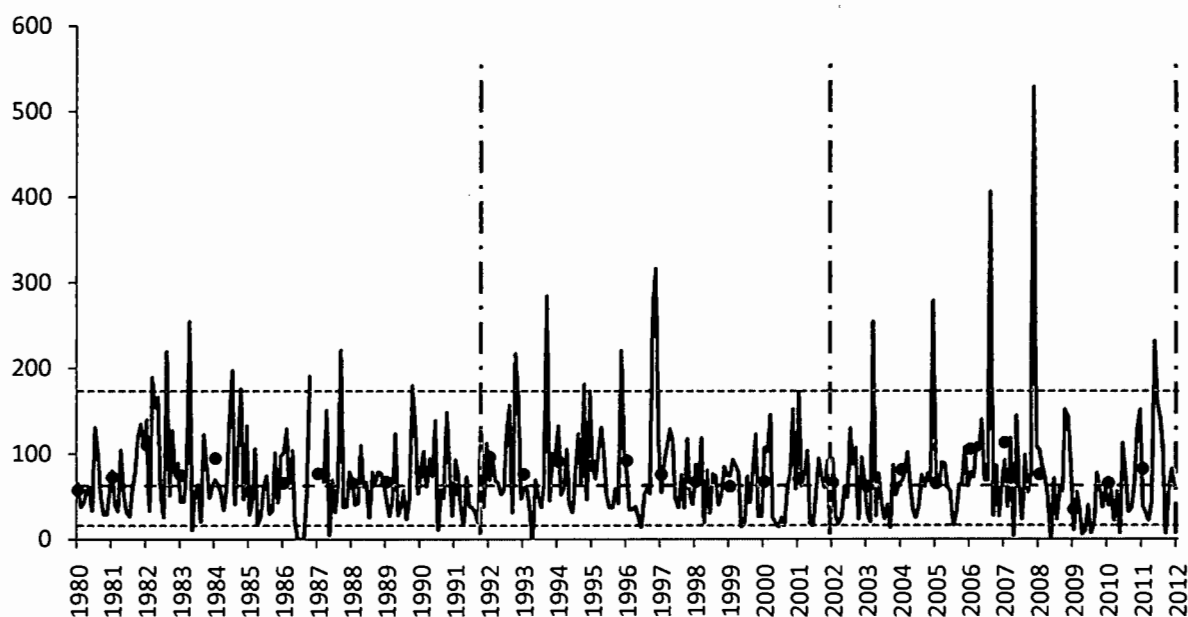


Figure 1: Total monthly precipitation at Diepwalle station. Vertical lines indicate survey times; dashed horizontal lines indicate mean rainfall with 95% percentiles. Solid points indicate mean monthly precipitation per year.

Total stand change

The species-specific abundance weighted average wood density calculated across the stand (i.e. the mean wood density across all stems in the forest) was 0.724 g cm^{-3} , with species means ranging from 0.44 to 0.86 g cm^{-3} (Appendix: Table 2). These values are expectantly high compared to tropical forests (Chao et al., 2008); but comparable to previously sampled values for the same species from the same area (von Breitenbach, 1965). By including wood density values in the Chave et al. (2005) equations, with a constant mean wood density (EQ 2.2) and species-specific wood density (EQ 2.3), AGB was predicted to be less than the AGB predicted by Baker et al. (2004a) equation.

Total stand basal area (BA) and above ground biomass (AGB) (Table 1) increased between 1991 and 2001 by an average of 0.2%, but declined by 0.2% over the second period (2001 and 2012), resulting in a net decline of 0.02% over the total 20 years (Table 2). Change in gross BA and AGB growth between surveys decreased in the second period compared to the first period (Table 2). Dynamism at the stand level increased in mortality and recruitment in the second period (Table 3).

Table 1: Total basal area (BA) and above ground biomass (AGB) for the Lilyvlei Nature Reserve, surveyed in 1991, 2001 and 2012.

		Year		
		1991	2001	2012
BA (m ² ha ⁻¹)		41.3	42.1	41.2
AGB (Mg ha ⁻¹)	EQ 2.1	477.8	487.9	476.9
	EQ 2.2	341.7	348.1	340.1
	EQ 2.3	342.4	349.0	340.8

Table 2: Stand level estimates of biomass change (with percentage change) for the Lilyvlei Nature Reserve for Period 1 (1991-2001), Period 2 (2001-2012) and the Total Period (1991-2012).

		Period 1		Period 2		Total period		
BA (m ² ha ⁻¹ yr ⁻¹) (%)	Net Growth	0.075	(0.18)	-0.089	(-0.22)	-0.007	(-0.02)	
	Gross Growth	0.390	(0.94)	0.320	(0.76)	0.338	(0.82)	
AGB (Mg ha ⁻¹ yr ⁻¹) (%)	EQ 2.1	Net Growth	1.02	(0.21)	-1.10	(-0.23)	-0.04	(-0.01)
		Gross Growth	4.65	(0.97)	3.85	(0.79)	4.03	(0.85)
	EQ 2.2	Net Growth	0.64	(0.19)	-0.80	(-0.23)	-0.08	(-0.02)
		Gross Growth	3.26	(0.95)	2.64	(0.76)	2.80	(0.82)
	EQ 2.3	Net Growth	0.66	(0.19)	-0.81	(-0.23)	-0.08	(-0.02)
		Gross Growth	3.27	(0.95)	2.65	(0.76)	2.81	(0.82)

Table 3: Dynamism experienced in the Lilyvlei Nature Reserve for time periods (Period 1- 1991 to 2001; Period 2 – 2001 to 2012 and the Total Period – 1991 to 2012).

	Period 1	Period 2	Total Period
Mortality (%)	0.71	0.80	0.76
Recruitment (%)	0.79	0.86	0.77
Dynamism (%)	0.75	0.83	0.76

Community level

The Lilyvlei Nature Reserve shows significant changes in community level AGB between time periods when only the growth of stems that were present in all surveys are considered (i.e. stems gained or lost through recruitment or mortality) (Table 4a), but no difference in total AGB between the two survey periods (Appendix: Table 3). The results indicate an increase in AGB across both periods, albeit smaller in the second period (2001-2012). Correlations between community relative growth rate (RGR) and biodiversity indices show significant correlations with community species diversity and Shannon Weiner's H (Table 5). Both diversity measures show stronger correlations over the second period than the first period. Significant differences exist in correlations between both time periods; Species Diversity ($F=27.849$, $Df=1$, $P<0.001$), Shannon Weiner's H ($F=26.173$, $Df=1$, $P<0.001$) (Figure 2). If RGR is plotted as a function of the number of individuals present in the community, a positive correlation is witnessed ($F= 11.68$, $Df=106$, $P=0.001$) (Figure 3).

RGR as a function of community dynamics show variable results (Table 6 and Figure 3). Across all time periods, mortality shows highly significant results ($p<0.001$) with a negative slope, while recruitment indicates positive correlations between periods, but is less significant ($p<0.01$) than mortality. Dynamics (mortality + recruitment/2) indicate that mortality has a greater impact on the regression (slope <0) for the first and the total period.

The relationship between dynamism and community biodiversity indices was varied (Table 7). Recruitment and dynamism were correlated against species richness, species diversity and Shannon Weiner (H) index. Dynamics show significant results with species richness and species diversity. An ANCOVA analysis revealed a significant difference between both time periods across all dynamics measures, recruitment ($F=27.849$, $Df=1$, $P<0.001$), mortality ($F=26.173$, $Df=1$, $P<0.001$), dynamics ($F=26.173$, $Df=1$, $P<0.001$) (Figure 4).

Species level

Species level T tests show significant changes in AGB between time periods when only the growth of stems that were present in all surveys are considered (i.e. stems gained or lost through recruitment or mortality) (Table 4b), but no difference in total AGB between these survey periods (Appendix: Table 3). The results indicate an increase in AGB across both periods, albeit smaller in the second period (2001-2012). Species relative growth rates (RGR) showed no correlation with sampled species traits and no correlation with dynamics (Appendix: Table 6 and Table 7). Species averaged trait values related with species dynamics indicate no correlations (Appendix: Table 8).

RGR correlations with species traits at an intercept of 10 cm show no correlation with species traits. Quantile RGR indicates no correlations with species traits at the median, upper 50% and upper 10% quantiles (Appendix: Table 9).

Table 4a: Change in total AGB over the two time periods, measured across communities when mortality and recruitment is ignored.

PLOTS		Mean change	Mean change			
Periods	AGB Equation	Period 1	Period 2	t_s	DF	p
		(kg ha⁻¹yr⁻¹)	(kg ha⁻¹yr⁻¹)			
1991-2001	EQ 2.1	0.0397	0.028	11.147	107	<0.001
&	EQ 2.2	0.0272	0.0184	8.916	107	<0.001
2001-2012	EQ 2.3	0.0272	0.0184	8.498	107	<0.001

Table 4b: Change in total AGB over the two time periods, across species when mortality and recruitment is ignored.

SPECIES		Mean change	Mean change			
Periods	AGB Equation	Period 1	Period 2	t_s	DF	p
		(kg ha⁻¹yr⁻¹)	(kg ha⁻¹yr⁻¹)			
1991-2001	EQ 2.1	0.159	0.112	2.353	26	0.027
&	EQ 2.2	0.109	0.074	2.434	26	0.022
2001-2012	EQ 2.3	0.109	0.074	2.407	26	0.023

Table 5: Community relative growth rate correlations with community species diversity and Shannon Weiner's species diversity index for periods 1, 2 and the total period.

		r²	P	DF	Slope	Intercept
Species	Period 1	0.097	<0.001	106	0.066	2.16
Diversity	Period 2	0.128	<0.001	106	0.073	1.81
	Total period	0.063	<0.001	106	0.054	2.08
Shannon	Period 1	0.044	0.02	106	0.419	2.01
Weiner's H	Period 2	0.080	0.002	106	0.530	1.51
	Total period	0.032	0.04	106	0.367	1.91

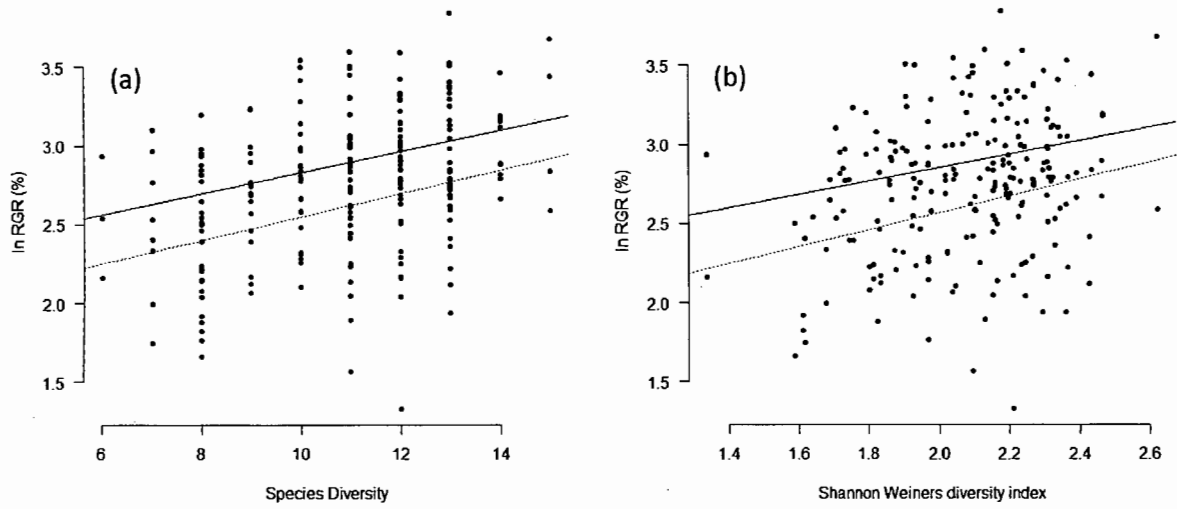


Figure 2: Community RGR for period 1 (black, solid) and period 2 (grey, dashed) plotted as a function of community species diversity (a) and Shannon Weiner's diversity index (b). Periods show a significant difference in correlations between time periods; a($F=27.849$, $DF=1$, $P<0.001$), b($F=26.173$, $DF=1$, $P<0.001$).

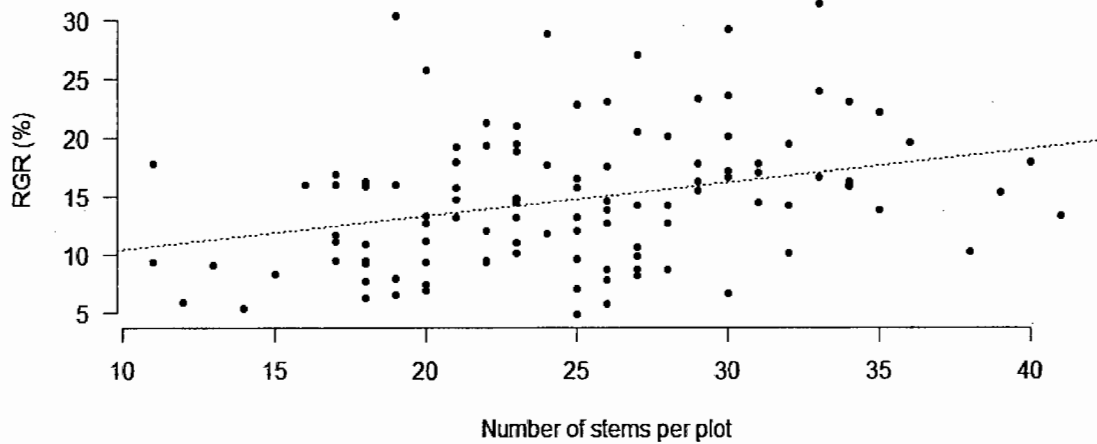


Figure 3: Number of individual stems per plot as a function of community level Relative Growth Rates ($F = 11.68$, $DF = 106$, $p = 0.001$).

Table 6: Community relative growth rate correlations with Dynamics indices for periods 1, 2 and the total period.

		r^2	p	DF	Slope	Intercept
Recruitment	Period 1	0.064	0.008	91	0.239	0.210
	Period 2	0.087	0.004	81	0.274	-0.043
	Total period	0.013	0.138	92	0.256	-0.146
Mortality	Period 1	0.358	<0.001	91	-0.575	0.729
	Period 2	0.097	<0.001	81	-0.391	0.494
	Total period	0.250	<0.001	92	-0.860	0.658
Dynamics	Period 1	0.037	0.034	91	-0.300	0.612
	Period 2	-0.009	0.630	81	0.071	0.179
	Total period	0.051	0.016	92	-0.588	0.510

Table 7: Community biodiversity indices (species richness, species diversity, Shannon Weiner's H, Pielou's J) correlated against Community Dynamism indices (mortality, recruitment, dynamics) for total 20 year period. (* = p<0.05)

	Dynamism indices	r^2	p	DF	Slope	Intercept
Species Richness	Recruitment	0.077	0.002*	106	0.587	7.120
	Mortality	0.005	0.218	106	0.209	7.435
	Dynamics	0.070	0.003*	106	0.739	7.002
Species Diversity	Recruitment	0.022	0.067	106	0.739	10.178
	Mortality	0.001	0.306	106	0.362	10.496
	Dynamics	0.027	0.048*	106	1.042	9.940
Shannon Weiner's H	Recruitment	0.031	0.038*	106	0.093	1.994
	Mortality	-0.007	0.635	106	0.019	2.056
	Dynamics	0.018	0.086	106	0.102	1.989
Pielou's J	Recruitment	0.009	0.162	106	0.012	0.867
	Mortality	-0.001	0.350	106	-0.006	0.883
	Dynamics	-0.009	0.832	106	0.002	0.875

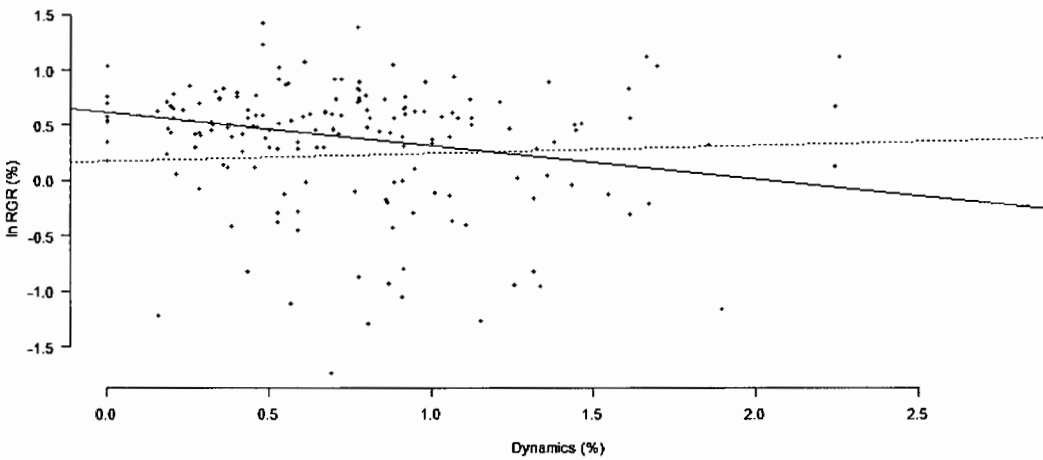
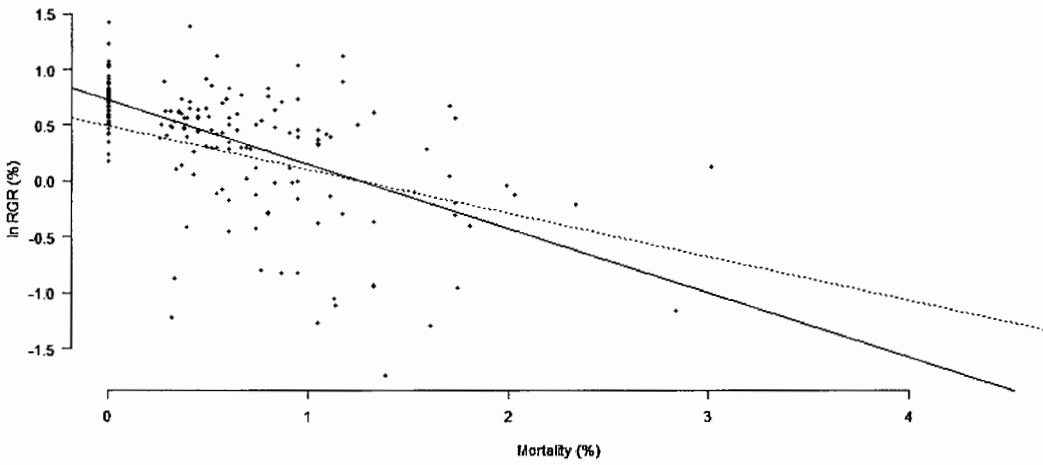
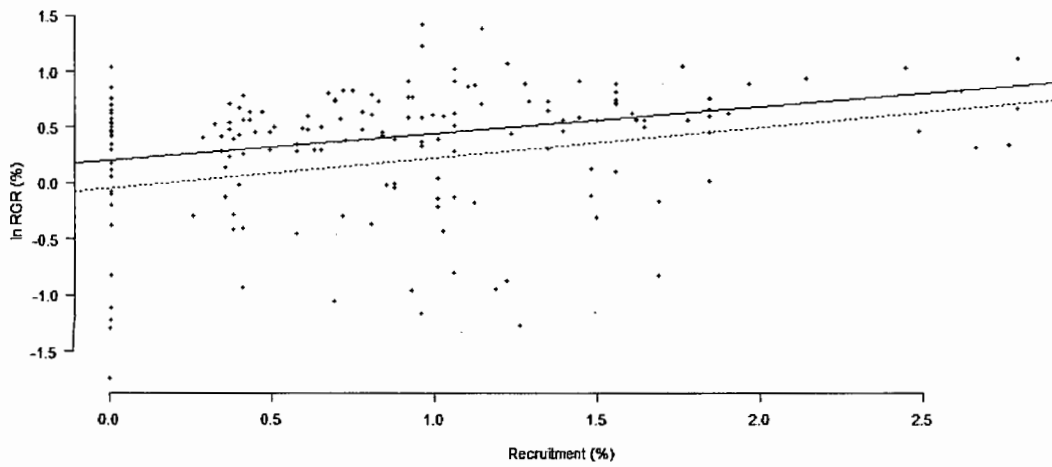


Figure 4: Community RGR for period 1 (black, solid) and period 2 (grey, dashed) plotted as a function of community dynamics (recruitment, mortality and dynamics). Periods show significant difference in correlations between two time periods: recruitment ($F=27.849$, $DF=1$, $P<0.001$), mortality($F=26.173$, $DF=1$, $P<0.001$), dynamics($F=26.173$, $DF=1$, $P<0.001$).

Functional composition

Plot level functional composition shows no correlation with plot level dynamics or RGR results (Appendix: Table 10).

Discussion

By monitoring growth and dynamics at various levels, an understanding of impacts affecting the forest can be quantified. With the inclusion of biodiversity and the ecologically important plant traits, changes in forest dynamism and growth can be monitored. This becomes important, given the anticipated climatic, atmospheric and environmental changes that threaten global ecosystems.

Total change in biomass and dynamics

The Lilyvlei Reserve shows no change in total net basal area (BA) and above ground biomass (AGB). The first period witnessed an increase in biomass of 0.2%, but a net decrease in biomass of 0.2% for the following ten years. The total biomass and change in biomass results support the findings of Midgley and Seydack (2006) that recorded no change in biomass for the same time period. Within Amazonian tropical forests, an increase of 1.22 Mg ha⁻¹ in AGB has been recorded (Lewis et al., 2006; Wright, 2006; Phillips et al., 2008). Our results are comparatively lower (1.02 Mg ha⁻¹) for the same period (1991-2001). Gross growth rates of 0.8% imply a residence time of well over a century for the average individual. This means that over relatively short periods such as the 20 years studied, the AGB of this forest is more sensitive to negative/stressful conditions that would increase mortality, than to factors which may increase growth (Midgley and Seydack, 2006). Temperate forests are more vulnerable to stress during the successional process than are tropical forests as succession is generally a slower process, particularly in terms of plant growth and other developmental features (Murphy and Lugo, 1986). Our results confirm this trend as relative growth rates (RGR) across both time periods is more highly correlated with mortality than any of the other dynamics indices.

The second ten year period of the precipitation record indicated an intensification of extreme rainfall events compared to previous periods. This intensification of extreme events could have also played a role in biomass changes, considering the four year drought prior to the final survey. It is well understood that prolonged periods of drought temporarily increase mortality, with as few as two or three dry months being sufficient to alter significantly the composition and structure of an ecosystem (Murphy, 1986). Other climatic variables (e.g.: temperature) are known to effect tree growth and dynamics (Clark, 2007; Phillips et al., 2008) but were unable to be tested for the time period as data was unavailable. Plot and species level changes in biomass, excluding recruitment and mortality, indicate an increase in biomass for both time periods, with the first period experiencing a greater plot growth rate compared to the second period.

All dynamics measures intensified between the survey periods, with mortality experiencing a greater increase compared to recruitment. Over the same time period as this study, Amazonia has also experienced an intensification of dynamics measures (Phillips et al., 2008; Laurance, 2009). But, these values measured are considerably higher than those observed in Livillei Reserve where dynamics estimates barely exceed 1%, compared to tropical estimates of over 1.5%. Therefore Knysna forest appears to experience low dynamism relative to tropical forests (Phillips et al., 1994). Compared to other temperate forests (Stephenson and van Mantgem, 2005), our stand average of 0.76% is below the mean of 1.19% for mixed temperate forests, potentially due to resource limitation imposed by strong seasonality (Saugier et al., 2001) and infertile soils (Phillips et al., 2004).

One of the most frequent explanations for such findings is that forest productivity is rising, possibly in response to increasing CO₂ fertilization or some other regional or global drivers (Phillips & Gentry, 1994; Lewis et al., 2004a), such as increasing irradiance (Wielicki et al., 2002) or rainfall variability (Gu et al., 2007; Lau and Wu, 2007). This hypothesis (the "Rising Productivity Hypothesis" (Gloor et al., 2006)) is controversial; however, with others advancing alternative explanations (e.g. Nelson, 2005; Wright, 2005; Clark, 2007) and emphasizing that trends observed in Amazonia are not universal elsewhere in the tropics (Clark et al., 2003; Feeley et al., 2007; Chave et al., 2008) let alone temperate areas. It goes beyond the scope of our study to delve into this controversy, other than to note that our findings seem broadly consistent with above data.

The effects of biodiversity

Feeley et al. (2007) noted that one potential limitation of measuring stand level growth rates is that it provides little information about the dynamics of most species, as changes may be driven by compositional shifts and/or the responses of just a few dominant species. Simultaneously collecting information at the ecosystem and species levels allows for the connection of plant level influences to the functioning of ecosystems. The results show that communities with greater biodiversity display increased growth rates. This is demonstrated by a positive correlation between RGR and species diversity indices. What the results also show is that during a time of environmental stress (e.g. intensification of dynamics and extreme rainfall events in the second period), species rich communities show increased relative growth rates.

It is well established that species composition, richness, evenness, and interactions all both respond to as well as influence ecosystem properties (Loreau et al., 2001; Naeem, 2002; Hooper et al., 2005). By this justification, the Knysna forest communities are driven by certain species that are compensating for a decline in others. Some of these species observed include *Nuxia floribunda*, *Psydrax obovata obovata* and *Gonioma kamassi* which are common within surveyed plots and had over all increases in biomass. Common species that declined include *Curtisia dentata* and *Olea capensis macrocarpa*. This compensatory effect has been attributed to communities with more species having a greater probability of containing higher phenotypic trait diversity.

This can also be seen by the more diverse communities having increased growth rates. However, it has long been recognized that the number of species increases with the number of individual's sampled (Fisher et al., 1943; Sanders, 1968). Ecological processes that have been postulated to affect species richness directly can also affect density and, thus, indirectly affect richness through the number of individuals sampled. Our results show this trend as an increase in stem density results in an increase in RGR. Shannon Weiner's index is calculated with this issue in mind, therefore the significance of the Shannon Weiner's index provides evidence for diverse communities having increased growth rates.

Unfortunately the traits measured in this study showed inconclusive results. The expectation was that certain species would have higher growth rates compared to other species within each community. This provides a baseline to look at common ecological strategies amongst species and hopefully see which strategies are able to manage the changing climatic conditions. This inconsistency with global trends could be attributed to within community trait variation having less impact than community averaged trait values (Garnier et al., 2004) however, functional composition showed inconclusive results. There is a potential that the traits measured in this study are not important to the functioning of this ecosystem, but more likely is that trait level interaction with community level functioning is not of a linear nature. This result clearly demonstrates the need for increased research into functional composition and its affects within temperate forest ecosystems.

The Knysna forest is an old growth forest comprised of predominantly shade-tolerant species with abundant regeneration and has a mild disturbance regime (Midgley et al., 1990; 1995). The soils of these forests are generally acidic and nutrient-poor (Van der Merwe, 1998) and findings suggest that water and nutrient stress lead to convergent trait syndromes (e.g.: Diaz et al., 2004).

With low dynamics compared to other tropical and temperate forests and species diversity per area richer than any of its worldly counterparts (Silander, 2000), biodiversity must surely play a role in the functioning of this ecosystem.

In conclusion, the Lilyvlei Nature Reserve has experienced little change in biomass over the last 20 years. Even with the increasing threat of climatic and atmospheric changes intensifying. The decrease in biomass and growth rates during the second period and the relation to climatic intensifications may be indicative of the negative effects of drought on the composition and structure of Lilyvlei. Individualistic species responses are disguising a decline in the forest due to the compensatory effects amongst species. Within this study, there is evidence to suggest that more diverse communities have increased growth rates. However, considering the brief 20 year period observed in a forest where the average individual has a life span of over a century, there is still much to research, particularly the complex interactions of traits and their use in the prediction of species responses to disturbance and negative change impacts.

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Appendix:

Table 1: Standards used to condition trees.

TREE CONDITION CODES: indicate tree condition

Recorded as 2 digit code with 2 conditions per measurement event.

00 Healthy

1 Stem rotting:

- 10 Stem rotting
- 11 Stem rotting: light (2012 measurement)
- 12 Stem rotting: medium (2012 measurement)
- 13 Stem rotting: severe (2012 measurement)

2 Dying:

- 21 Main shoot dead
- 22 < 1/3 crown dead
- 23 1/3 - 2/3 crown dead
- 24 > 2/3 crown dead
- 25 Moribund = at the point of death

3 Damage:

- 31 Bole snapped off
- 32 Main shoot broken off / dead
- 33 Major branch broken off / dead
- 34 Bark removed with fungi / insect attack
- 35 Bark removed without fungi / insect attack
- 36 Stem split
- 37 Stem rotting due to damage
- 38 Fork broken off / dead

4 Leaning:

- 41 Leaning 30° - 60° from vertical axis
- 42 Leaning > 60° from vertical axis
- 43 Down
- 44 Sweep

5 Coppice:

- 50 Has coppice shoots, but none measurable (≥ 10 cm)
- 51, 52, etc. Main stem and measurable coppice shoots, for stump 1, 2, etc.

6 Forked below DBH:

- 61, 62, etc. Measurable forks for tree 1, 2, etc.

7 Agony shoots

- 70 Agony shoots

8 Leader shoots:

- 80 Has leader shoots, but none measurable (≥ 10 cm)
- 81, 82, etc. Main stem and measurable leader shoots, for tree 1, 2, etc.

9 Shelf / bracket fungi

- 90 Has shelf fungi

Table 2: Specific wood density values for species sampled in the Lilyvlei Nature Reserve.

Species Code	Species Name	Density (g cm ³)	n
16	<i>Podocarpus falcatus</i>	0.612	10
18	<i>Podocarpus latifolius</i>	0.646	10
74	<i>Faurea macnaughtonii</i>	0.730	10
118	<i>Ocotea bullata</i>	0.537	12
141	<i>Platylophus trifolius</i>	0.440	9
142	<i>Trichocladus crinitus</i>	0.777	11
397	<i>Ilex mitis</i>	0.498	5
401	<i>Maytenus peduncularis</i>	0.755	10
409	<i>Pterocelastrus tricuspidatus</i>	0.750	11
413	<i>Cassine eucliformis</i>	0.800	11
415	<i>Eleaodendron croceum</i>	0.710	10
422	<i>Apodytes dimidiata</i>	0.675	7
479	<i>Ochna arborea</i>	0.791	10
513	<i>Olinia ventosa</i>	0.732	12
570	<i>Curtisia dentata</i>	0.711	10
578	<i>Rapanea melanophloeos</i>	0.629	10
611	<i>Diospyros whyteana</i>	0.610	10
618	<i>Olea capensis macrocarpa</i>	0.810	10
619	<i>Olea capensis capensis</i>	0.864	10
634	<i>Nuxia floribunda</i>	0.622	10
641	<i>Gonioma kamassi</i>	0.747	10
670	<i>Halleria lucida</i>	0.608	10
688	<i>Burchellia bubalina</i>	0.711	12
693	<i>Rothmannia capensis</i>	0.732	10
710	<i>Canthium mundianum</i>	0.755	10
711	<i>Psyrax obovata obovata</i>	0.794	10

Table 3: T test indicating comparisons of survey periods for both plot level changes and species level changes

EQ	Inter survey Period	Plot					Species				
		ts	df	p	Initial mean Mg ha yr	Final mean Mg ha yr	ts	df	p	Initial mean Mg ha yr	Final mean Mg ha yr
2.1	1991-2001	-1.846	107	0.07	4.42	4.52	-1.631	26	0.12	17.69	18.07
	2001-2012	1.636	107	0.10	4.52	4.42	1.056	26	0.30	18.07	17.66
2.2	1991-2001	-1.440	107	0.15	3.16	3.22	-1.717	26	0.10	12.66	12.89
	2001-2012	1.534	107	0.13	3.22	3.15	1.167	26	0.25	12.89	12.59
2.3	1991-2001	-1.312	107	0.19	3.18	3.24	-1.596	26	0.12	12.72	12.94
	2001-2012	1.584	107	0.12	3.24	3.16	1.125	26	0.27	12.94	12.65

Table 4: Table of Traits with units and codes.

Code	Trait	Unit	Code	Trait	Unit
SWD	Specific wood density	g cm ⁻³	AW	Average width	mm
LWW	Leaf wet weight	g	MW	Maximum width	mm
LDW	Leaf dry weight	g	T	Leaf thickness	mm
A	Leaf area	mm ⁻²	SLA	Specific leaf area	g mm ⁻³
L	Leaf length	mm			

Table 5: Species number (n), basal area, basal area increments and basal area RGR for all species across the three surveys and periods.

Species Codes	(n)	Basal area (m ² ha ⁻¹)			Increment Growth (m ² ha ⁻¹ yr ⁻¹)			Relative Growth Rate (%)		
		Survey 1	Survey 2	Survey 3	Period 1	Period 2	Total Period	Period 1	Period 2	Total Period
16	(38)	4.528	4.391	4.111	-0.01364	-0.02799	-0.04163	-0.3	-0.64	-0.92
18	(370)	9.268	9.365	9.338	0.0097	-0.00272	0.00698	0.1	-0.03	0.08
74	(154)	2.637	2.694	2.682	0.00573	-0.00115	0.00458	0.22	-0.04	0.17
118	(70)	2.258	2.279	2.339	0.00211	0.00601	0.00813	0.09	0.26	0.36
141	(11)	0.126	0.139	0.148	0.00133	0.00088	0.00222	1.06	0.63	1.76
142	(1)	0.002	0.002	0.002	0	0	0	0.2	0	0.2
397	(6)	0.026	0.032	0.038	0.0006	0.00059	0.0012	2.28	1.83	4.53
401	(63)	0.33	0.379	0.406	0.00498	0.00268	0.00766	1.51	0.71	2.33
409	(4)	0.042	0.046	0.052	0.00041	0.00064	0.00105	0.99	1.39	2.52
413	(9)	0.051	0.049	0.064	-0.00014	0.00147	0.00133	-0.28	3	2.63
415	(72)	0.281	0.34	0.433	0.00593	0.00923	0.01515	2.11	2.71	5.39
422	(79)	1.017	1.074	0.904	0.00568	-0.01703	-0.01136	0.56	-1.59	-1.12
479	(38)	0.128	0.144	0.142	0.00157	-0.00018	0.00139	1.22	-0.12	1.09
513	(1)	0.002	0.002	0.003	0.00002	0.00005	0.00007	0.98	2.3	3.5
570	(137)	1.76	1.952	1.723	0.01923	-0.02293	-0.00371	1.09	-1.17	-0.21
578	(2)	0.008	0.004	0.01	-0.00041	0.00062	0.00021	-5.02	15.18	2.55
611	(56)	0.223	0.236	0.23	0.00128	-0.00061	0.00067	0.57	-0.26	0.3
615	(1)	0.005	0.005	0.006	0.00007	0.00006	0.00013	1.56	1.07	2.8
618	(648)	12.816	12.992	12.336	0.01762	-0.06559	-0.04797	0.14	-0.5	-0.37
619	(29)	0.189	0.173	0.157	-0.00161	-0.00156	-0.00317	-0.85	-0.9	-1.68
634	(108)	1.333	1.441	1.634	0.01086	0.01932	0.03017	0.81	1.34	2.26
641	(457)	2.454	2.467	2.482	0.00128	0.00159	0.00286	0.05	0.06	0.12
670	(20)	0.117	0.125	0.131	0.00084	0.00056	0.0014	0.72	0.45	1.2
688	(116)	0.343	0.356	0.365	0.00127	0.00084	0.00211	0.37	0.24	0.61
693	(5)	0.014	0.017	0.022	0.00034	0.00045	0.00078	2.38	2.57	5.57
710	(45)	0.216	0.218	0.226	0.00018	0.00079	0.00097	0.08	0.36	0.45
711	(100)	1.169	1.168	1.215	-0.00003	0.00469	0.00465	0	0.4	0.4

Table 6: Species relative growth rate correlations with species trait estimates for periods 1, 2 and the total period.

		r^2	p	DF	Slope	Intercept
SWD	Period 1	-0.03	0.63	24	1.87	1.67
	Period 2	-0.03	0.56	24	2.26	1.06
	Total period	-0.03	0.56	24	2.27	1.09
LWW	Period 1	0.06	0.12	24	-0.67	3.99
	Period 2	0.03	0.18	24	-0.58	3.51
	Total period	0.04	0.17	24	-0.58	3.56
LDW	Period 1	0.00	0.32	24	-1.13	3.64
	Period 2	-0.02	0.44	24	-0.87	3.15
	Total period	-0.02	0.44	24	-0.89	3.20
A	Period 1	0.05	0.14	24	-0.05	3.97
	Period 2	0.05	0.14	24	-0.05	3.63
	Total period	0.05	0.15	24	-0.05	3.67
L	Period 1	-0.01	0.42	24	-0.13	4.04
	Period 2	-0.02	0.45	24	-0.12	3.64
	Total period	-0.01	0.43	24	-0.13	3.71
AW	Period 1	0.04	0.17	24	-0.62	4.36
	Period 2	0.04	0.16	24	-0.64	4.06
	Total period	0.04	0.17	24	-0.62	4.06
MW	Period 1	0.05	0.14	24	-0.46	4.52
	Period 2	0.05	0.15	24	-0.45	4.18
	Total period	0.04	0.16	24	-0.44	4.17
T	Period 1	-0.04	0.83	24	1.30	2.69
	Period 2	-0.03	0.57	24	3.39	1.90
	Total period	-0.03	0.60	24	3.09	2.01
SLA	Period 1	-0.01	0.43	24	-0.02	3.88
	Period 2	0.01	0.25	24	-0.03	3.95
	Total period	0.01	0.26	24	-0.03	3.96

Table 7: Species relative growth rate correlations with dynamics estimates for periods 1, 2 and the total period

		r^2	p	DF	Slope	Intercept
Recruitment	Period 1	-0.037	0.74	24	<0.001	0.284
	Period 2	-0.040	0.79	23	<0.001	0.434
	Total period	0.049	0.14	25	<0.001	0.174
Mortality	Period 1	-0.039	0.78	24	-0.002	0.377
	Period 2	0.064	0.09	23	0.281	0.116
	Total period	-0.034	0.71	25	0.001	0.313
Dynamics	Period 1	-0.030	0.61	24	0.003	0.353
	Period 2	0.047	0.15	23	0.336	0.080
	Total period	-0.030	0.63	25	0.005	0.305

Table 8: Species averaged trait values plotted as a function of dynamics

	Trait	r^2	p	DF	Slope	Intercept
Recruitment (%)	SWD	-0.014	0.40	18	-0.0622	0.7578
	LWW	-0.055	0.97	18	-0.0306	1.4024
	LDW	-0.042	0.63	18	-0.1407	0.6602
	A	-0.050	0.76	18	-3.0140	21.3080
	L	-0.045	0.67	18	-0.9191	8.7417
	AW	-0.053	0.85	18	-0.1508	2.2721
	MW	-0.046	0.69	18	-0.4422	3.5990
	T	-0.035	0.55	18	0.0349	0.1878
	SLA	-0.037	0.74	18	0.0012	3.5989
Mortality (%)	SWD	-0.037	0.74	18	-0.0947	0.5244
	LWW	-0.013	0.40	18	-0.3345	1.7176
	LDW	0.002	0.32	18	-0.1574	0.7136
	A	-0.055	0.93	18	-0.4583	19.5064
	L	-0.051	0.79	18	-0.3076	8.3619
	AW	-0.056	0.99	18	0.0063	2.1524
	MW	-0.052	0.82	18	0.1380	3.1272
	T	0.061	0.15	18	-0.0450	0.2595
	SLA	-0.003	0.34	18	-0.0033	3.6197
Dynamics (%)	SWD	-0.013	0.42	18	-0.0773	0.5218
	LWW	-0.024	0.47	18	-0.4833	1.8053
	LDW	0.009	0.29	18	-0.2799	0.8012
	A	-0.053	0.83	18	-1.9908	20.7975
	L	-0.045	0.68	18	-0.8202	8.7739
	AW	-0.055	0.93	18	-0.0619	2.2133
	MW	-0.056	1.00	18	-0.0037	3.2700
	T	-0.009	0.37	18	-0.0478	0.2562
	SLA	-0.033	0.66	18	-0.0023	3.6146

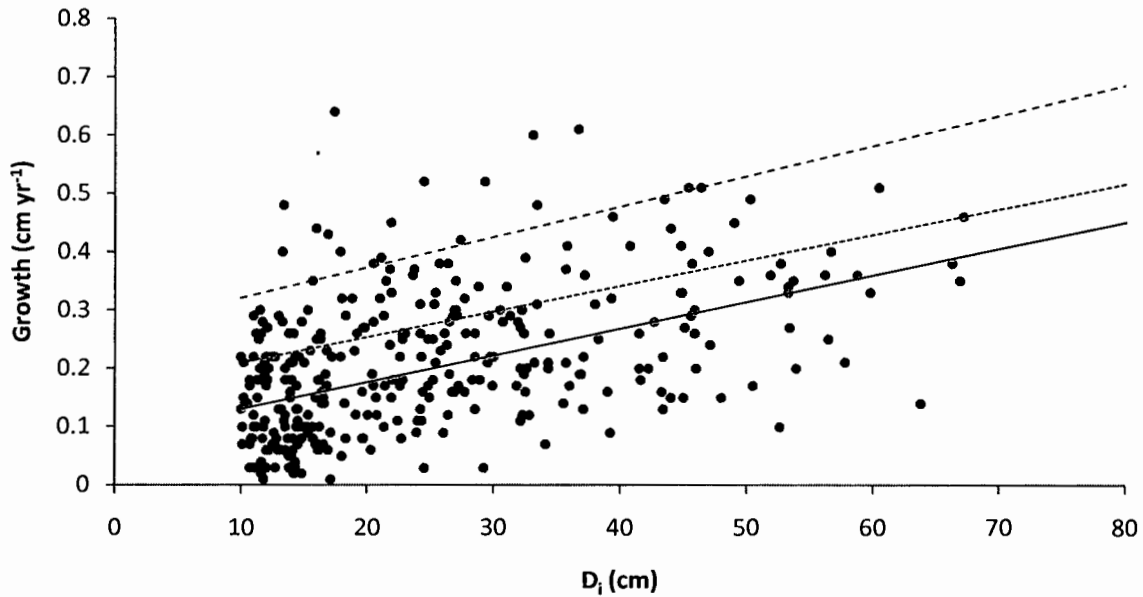


Figure 1: Growth $((D_t - D_i)/t)$ of species plotted as initial basal area, with quantile regressions of median, upper 50 % and upper 10% for *Olea capensis macrocarpa* (618).

Table 9: Growth $((D_t - D_i)/t)$ of species as a function of initial basal area, with quantile regression of median, upper 50 % and upper 10% .

Species Code	Median			Upper 50%			Upper 10%		
	Intercept	Slope	n	Intercept	Slope	n	Intercept	Slope	n
16	0.094	0.003	21	0.235	0.002	21	0.322	0.007	21
18	0.106	0.001	252	0.162	0.001	252	0.280	0.002	252
74	0.117	0.000	86	0.208	-0.001	86	0.256	-0.001	86
118	0.101	0.002	16	0.213	0.000	16	0.630	-0.008	16
401	0.109	0.001	23	0.049	0.007	23	0.192	0.007	23
415	0.143	-0.002	43	0.121	0.003	43	-0.052	0.020	43
422	0.209	-0.005	30	0.342	-0.008	30	0.515	-0.012	30
479	-0.013	0.004	23	-0.059	0.010	23	-0.037	0.012	23
570	0.085	0.005	57	0.152	0.005	57	0.177	0.007	57
611	0.128	-0.004	21	0.234	-0.009	21	0.404	-0.014	21
618	0.084	0.005	332	0.165	0.004	332	0.268	0.005	332
619	-0.048	0.009	8	-0.153	0.018	8	-0.056	0.014	8
634	0.138	0.002	9	-0.042	0.019	9	0.096	0.014	9
641	0.104	-0.001	174	0.136	-0.001	174	0.155	0.003	174
670	0.250	-0.011	6	0.391	-0.018	6	0.286	-0.008	6
688	0.036	0.002	38	0.177	-0.006	38	0.197	-0.003	38
710	0.211	-0.007	20	0.380	-0.013	20	0.937	-0.038	20
711	0.099	0.003	42	0.278	-0.001	42	0.229	0.007	42

Table 10: Community level RGR plotted as a function of community functional composition for the total period.

Trait	r^2	p	DF	Slope	Intercept
SWD	-0.0094	0.96	106	-1.73	-1.07
LWW	-0.0057	0.53	106	-2.06	1.15
LDW	-0.0048	0.48	106	-5.53	1.38
A	0.0037	0.24	106	-0.30	4.23
L	0.0021	0.27	106	-1.66	13.07
AW	-0.0015	0.36	106	-2.64	3.63
MW	0.0007	0.30	106	-2.00	4.52
T	-0.0047	0.48	106	33.92	-9.87
SLA	0.0010	0.29	106	-0.22	5.66