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# **Comparative Demography and Life history Evolution of Plants**

*By*

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A thesis submitted to Plymouth University

in partial fulfillment for the degree of

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**RESEARCH  
DEGREES  
WITH  
PLYMOUTH  
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# *Comparative demography and life history evolution of plants*

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## *Abstract*

Explaining the origin and maintenance of biodiversity is a central goal in ecology and evolutionary biology. Some of the most important, theoretical explanations for this diversity centre on the evolution of life histories. Comparative studies on life history evolution, have received significant attention in the zoological literature, but have lagged in plants. Recent developments, however, have emphasised the value of comparative analysis of data for many species to test existing theories of life history evolution, as well as to provide the basis for developing additional or alternative theories. The primary goal of this study was to explore existing theories of life history evolution using a dataset of demographic information in the form of matrix population models for a large number of plant species. By projecting average matrix population models for 207 plant species, life tables and fecundity schedules were obtained and, in turn, were used to estimate relevant life history parameters. These parameters were then used to explore the i) lability of life history traits in plants ii) their continuum of life history variation, iii) the evolution of senescence and iv) the significance of demographic entropy in population ecology. Elasticities and sensitivities of life history traits showed significant phylogenetic signal compared to other life history traits, although, all the values of phylogenetic signal observed were  $< 1$  indicating that life history traits are generally labile. Eighty one percent of species in the dataset had mortality curves that increased with age compared to one hundred percent of species that showed a reproductive value curve that decreases with age at the end of life. In particular, the parameters that measured pace and duration were inversely related suggesting in general, the presence of senescence in our data set. Finally, the tenets of the directionality theory based on demographic entropy were generally not confirmed. This study provides an important contribution to the life history evolution of iteroparous perennial plants and confirms existing theories on life history evolution.

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## ***Dedication***

This work is dedicated to my wonderful family and, in particular, to my very patient and understanding wife, Michelle, who has put up with these many years of research, and to my precious daughters, Erika and Praise who are the joy to our lives. Finally, I dedicate this work to my dad, Asong Sabas and my mum, Margaret Bellohquia for their unwavering support and encouragement throughout my research at Plymouth University.

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### *List of Publications*

- **Cyril Mbeau-ache** and Franco Miguel (2013). The time distribution of reproductive value measures the pace of life. *Journal of Ecology*, 101, 1273-1280
  
- Annette Baudisch, Roberto Salguero-Gomez, Owen R. Jones, Toamasz Wrycza, **Cyril Mbeau-ache**, Miguel Franco and Fernando Colchero (2013). The pace and shape of senescence in angiosperms. *Journal of Ecology*, 101, 596-606.
  
- Peter B. Adler, Roberto Salguero-Gomez, Aldo Compagnoni, Joanna S. Hsu, Jayanti Ray-Mukherjee, **Cyril Mbeau-Ache** and Miguel Franco (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United State of America*, 111(2): 740-745.
  
- Roberto Salguero-Gomez, Owen R. Jones, Eelke Jongejans, Simon P Blomberg, Miguel Franco, David Hodgson, **Cyril Mbeau-Ache**, Pieter A Zuidema, Hans de Kroon, Yvonne M Buckley. Maintenance and reproduction are independent axes of vascular plant life history. Manuscript submitted to *Science*.

### ***Oral presentations***

- Senescence in iteroparous perennial plants. Marine Biology Ecology and Research Centre (MBERC) seminar series, June 2011, Plymouth University, UK.
- The time distribution of reproductive value measures the pace of life, School of Biomedical and Biological Sciences seminar series, May 2013, Plymouth University, UK.

### ***Workshops and poster presentations***

- Attendance to a workshop on Integral Projection Models imparted by Dr Roberto Salguero Gómez and colleagues. University of Amsterdam, October 2012
- Demonstrator in the workshop Phylogenetic Reconstruction and the use of the Comparative Method imparted by Dr Miguel Franco. The Society for Economic Botany 54<sup>th</sup> Annual Meeting, July 2013, Plymouth University UK.

*Skilled courses attended with dates*

Introduction to R course, 14/01/2011

Excel conditioning formatting, 09/03/2011

End-note user's clinic, 12/05/2011

Presenting to an audience, 09/11/2011

Preparing to transfer, 21/11/2011

Power point presentation: enhancing your presentation, 11/03/2011

Developing professional writing skills, 04/05/2011

SPSS statistical package, 27/05/2011

Overview to searching and accessing information resources, 15/11/2011

Introduction to applying for research funding, 27/03/2012

Careers in academia, 16/05/2012

Making progress, avoiding defeatism and self-sabotage, 18/05/2012

Leadership and management: selection interviewing, 28/03/2012

Social networking for scientists, 06/02/2013

Leading and managing: Exploring leadership, 26/02/2013

Preparing for your viva, 06/03/2013

Career planning for 2<sup>nd</sup>, 3<sup>rd</sup> and final year students, 12/03/2013



*Author's declaration*

At no time during the registration for the degree of Doctor of Philosophy has the author, been registered for any other University award without prior agreement of the Graduate Committee.

This study was self-sponsored.

The work described in this thesis was conducted by the author, under the supervision of Dr. Miguel Franco and Dr. Paul Ramsay.

Relevant scientific seminars and conferences were attended at which work was presented. One paper has been published from this work.

Word count of the thesis: 40,659 (including tables, figures and references)

Signed: \_\_\_\_\_

Date:

## *Thesis outline*

### **Chapter 1:** General introduction.

This chapter introduces the reader to the subject of plant life history and describes the database on which the dissertation is based.

### **Chapter 2:** General methodology

This chapter describes the general methods employed in this study. It explains matrix population models, their analysis and interpretation. The phylogenetic comparative method employed is also explained.

### **Chapter 3:** Phylogenetic signal in the demography of iteroparous perennial plants.

This chapter investigates the life history constraints and opportunities offered to different plant taxa by their phylogenetic history. The degree to which life history traits are evolutionarily hard-wired or ecologically labile is investigated using the comparative method in a phylogenetic framework.

### **Chapter 4:** Evolution of senescence in iteroparous perennial plants.

The evolution of senescence in perennial plants under natural conditions is explored by investigating the mortality and reproductive value patterns of 207 species of iteroparous perennial plants.

### **Chapter 5:** The time distribution of reproductive value measures the pace of life

In this chapter, a generalised time distribution is employed to investigate the best metric for measuring senescence in natural populations of iteroparous perennial plants. The results of this investigation have been published in the *Journal of Ecology*.

### **Chapter 6:** Demographic entropy

This chapter investigates the correlation between demographic entropy and demographic and life history parameters/attributes. These relationships are then used to evaluate the claim that entropy is a better measure of fitness than the Malthusian parameter.

**Chapter 7:** General discussion and conclusion.

These results from the individual investigations are brought together into the role that comparative demography currently plays in the study of the ecology and evolution of plant life histories.

## ***Chapter 1: Introduction***

## ***1.0 General introduction***

Explaining the origin and maintenance of biodiversity is a central goal in evolutionary biology. The ecological theories that seek to explain this diversity are centered on the evolution of life histories. A life history encompasses events with demographic consequences in the life cycle of a species. When reproduction first occurs, the number of reproductive events during life, the number of offspring at each reproductive event, etc., characterise the life history of an organism. Because these events have consequences on fitness, they are subject to selection. Differences in the intensity and timing of selection on these attributes lead to the variety of life histories found in nature, and to understand the origin and maintenance of such variability a powerful study tool is the comparative method (Harvey and Pagel, 1991). The comparative method is founded on the principle that similar environments exert similar selective forces on different sets of species resulting in convergent evolution, while dissimilar environments exert different selective forces on the same species resulting in divergent evolution (Harvey and Pagel, 1991). While comparative studies have received significant attention in the zoological literature they have concentrated on fewer traits in plants and there is a shortage of empirical and comparative data to test existing theories of life history evolution as well as to provide the basis for developing additional or alternative theories (Dunham et al., 1989).

Life history evolution is contingent on the survival and fertility schedules that an organism is likely to experience at each stage of its life cycle and, as such, demography plays a crucial role in accounting for life history evolution.

Demography deals with the quantitative aspects of birth, growth, reproduction and death in a population (Silvertown and Charlesworth, 2001). Although originally developed for the study of human populations, demography now encompasses the study of the causes and consequences of numerical changes in species of living organisms (Andrewartha

1961, Harper and White, 1974). Demographic studies of plants have increased during the last decades (Franco and Silvertown 1990) and the development of a standard analysis framework (projection matrix) allows demographers to conduct meaningful comparisons (Silvertown and Franco, 1993, Franco and Silvertown 2004). These models summarise the vital rate values (survival and transition probabilities between life cycle stages, as well as mean individual fecundity at each stage) and thus allow the quantification of life history traits of interest, such as time (age) at first reproduction (sexual maturity), life expectancy, etc. (Caswell 2001). This analysis thus allows us to quantify the degree of correspondence between attributes of, for example, the particular environment in which different plants live and their life history characteristics. In other words, it allows us to pinpoint the demographic and life history attributes that enable plants to thrive under particular environmental conditions and ecological circumstances. Silvertown et al. (1993) used matrix population models from published studies of 21 species of woody plants and 45 herbaceous perennial plants to explore the continuum of life history variation. They divided each demographic matrix (see Chapter 2 for an explanation of matrix population models) into six regions (Fig. 1) and each region was then allocated into one of three main components: “fecundity” (seed and seedling recruitment), “growth” (progression and clonal recruitment) and “survival” (stasis and retrogression)<sup>1</sup>. The summed up elasticity within each region provides estimates of the relative influence that each of these three demographic processes has on population growth rate ( $\lambda$ ). Silvertown et al. (1993) observed that herbs differed significantly from woody plants in many respects. For example, they noticed that seedling recruitment was more important in herbs than it was in woody plants. Equally, retrogression (assigned to

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<sup>1</sup> In reality, the values in these matrix regions only approximate the three demographic processes, in quotes, that they are meant to represent. In a subsequent paper, Franco and Silvertown (2004) isolated these three demographic processes, or vital rates, from the individual elements of the matrix. For simplicity, however, I describe their original proposition.

“survival”) occurred only in herbs with preference to those having tubers. Silvertown et al. (1993) then used the three major components of elasticity (growth, fecundity and survival) to locate individual species in a triangular space defined by these three demographic attributes. It was observed that plants belonging to four distinct ecological groups tended to occupy different positions in this space. These four groups were semelparous herbs, iteroparous herbs in open habitats, iteroparous forest herbs and woody plants. Silvertown et al. (1993) then suggested that these demographic differences represented alternative demographic solutions to the environmental differences confronted by those life forms in the habitats where they are found. Understanding life history variation, therefore, requires knowledge of the contributions of individual differences and environmental variation on fitness (Benton et al., 2006). The recent expansion of a worldwide database of demographic information for plants presented in matrix format (COMPADRE) offered the opportunity to investigate aspects of life history variation in plants not previously investigated with a larger number of species than previously studied.

	Seed	Seedling	Juvenile	Small adult	Large adult
Seed	Stasis			Seed recruitment	recruitment
Seedling		Stasis		Seedling recruitment	recruitment
Juvenile			Stasis	Clonal recruitment	recruitment
Small adult				Stasis	Retrogression
Large adult					Stasis

Figure 1. The six regions into which individual elements of each population matrix model were classified. Their actual location varied from study to study depending on the categorisation of the life cycle employed by the authors of the original studies, but in general tended to occur in these relative positions in the matrix. The number of cells that they occupied also varied from species to species. Notice that in this example three transitions at the top of the matrix would not occur as seedlings and juveniles do not reproduce and juveniles do not retrogress to the seedling stage.

### 1.1 Database

The original plant demography database was compiled by J. Silvertown, M. Franco and collaborators. In recent years, it has been expanded through its integration with other databases and input of additional studies compiled by R. Salguero-Gómez. The database is currently held at the Max Planck Institute for Demographic Research, Rostock,

Germany. It is expected that the expanded version will go online by the end of 2014 for public use. The released database will contain demographic information in the form of population matrix models for over 500 plant species, from published papers and personally communicated to R. Salguero-Gómez, often with replicates for different years, study areas and treatment conditions. Information for an additional ~400 species is in the process of verification in digitilisation. Life forms vary from annuals, such as *Arabidopsis thaliana* (Metcalf, 2009), to the very long-lived *Sequoia sempervirens* (Namkoong and Roberds, 1974). As described in figure 1 above, these matrix population models contain the essential demographic information from which life history attributes can be calculated. The database is taxonomically diverse and contains species from most World biomes. Sampling effort, however, varies greatly across continents and countries, with most studies conducted in the Holarctic zone (North America and Europe), and Oceania Asia, South America and Africa lagging behind. A full description of the database will be published by Salguero-Gómez and collaborators shortly.

The dataset employed in this dissertation is a subset of the current database that had been curated (i.e., was ready for analysis) when this PhD project was started four years ago, and consists of average matrix models for 207 species of perennial plants (Appendix 1).

The 207 species are distributed in 70 families and four major plant taxonomic classes- Cycadophyta (3 species), Liliopsida (52 species), Magnoliopsida (139 species) and Pinopsida (13 species) [yet only represent of the order of 1/1000 of all iteroparous seed plants. Their life histories also varied considerably. For instance, the age at first reproduction ( $\alpha$ ) varied between 1 year (e.g. *Agropyron repens*, Poaceae) and 211 years (*Dicymbe altsonii*, Fabaceae) and mean life expectancy varied between 4 years (e.g *Plantago coronopus*, Plantaginaceae) and 567 years (*Dicymbe altsonii*, Fabaceae) (see



appendix 1). In addition, the species covered a wide range of life forms (see table 1) and came from all major terrestrial habitats. Thus, despite their relative low numbers, the variety of taxa, life forms and habitats represented results in a variety of life histories that spans a wide range of values, which gives some confidence about the ability to generalise patterns of life history across the seed plants.

Table 1: Table 2: Taxonomic distribution and life forms of species used in the dataset.

		Life form					Subtotal
		Herbs from open habitat	Herbs from forest habitat	Shrubs	Palms	Trees	
Class	Cycadophyta	0	0	0	3		3
	Liliopsida	17	16	0	15	4	52
	Magnoliopsida	63	17	22	1	36	139
	Pinopsida	0	0	0	0	13	13

### 1.2 Limitation of the dataset

The existence of a large number of matrix projection models is essential for conducting robust comparative studies. However, projection matrices have some limitations. The most important limitation is the fact that one does not usually have the original field censuses from which the matrix models were parameterised. There is therefore small scope to check for effects of the categorisation employed, i.e., the number and width of the categories into which the population was divided. Differences in categorisation of the life cycle stages are known to have consequences on the resulting estimates of vital rates (Vandermeer 1978, Moloney 1986) and may in turn produce differences in life history estimates (Enright et al 1995; Salguero-Gomez & Plotkin 2010). However,

despite these effects, differences in categorisation does not tend to bias estimates in a particular direction, but make vital rates and life history estimates sway as category boundary change. The larger effect of categorisation is loss of resolution as the number of categories decreases. Thus, species where vital rates change abruptly through the life cycle require more stages to capture this variability. An illustrative example is an insect with life cycle stages (egg, larvae, pupae and adult) that have very different requirements. Among plants, dormant stages, trunk formation after a “herbaceous” juvenile period, or leaves with different light requirements in different parts of the plant or at different life cycle stages are also good examples. In short, not having the original field data to test the effect of categorisation on matrix parameterisation means that the matrix data used in this dissertation have to be taken at face value. Although interpretation should proceed with caution, this is particularly relevant when drawing conclusions about individual species (e.g., the pattern of mortality towards the end of the life cycle, when individual numbers are low). Multiple-species comparisons of broad life history signatures (e.g., generation time and lifespan) would, however, be expected to provide sufficiently robust qualitative answers to questions such as what the effect of increasing adult mortality would have on the age at sexual maturity. In summary, the aim of the research presented in this thesis is to conduct a comparative study on the demography and life history evolution of iteroparous perennial plants using a dataset of demographic information in the form of matrix population models. The particular objectives of the study are:

- (i) to investigate the constraints and opportunities offered to different taxa by their phylogenetic history. The degree to which life history traits are evolutionary labile is uncertain and the database provides the opportunity to explore which traits are “hard-wired” and which traits are subject to environmental variability.

- (ii) to explore the evolution of senescence in plants. Most studies on evolutionary senescence have been conducted on relatively few and short-lived species. This database provides the opportunity to test existing theories of plant senescence across a large sample of species employing the comparative method.
- (iii) to investigate the ecological correlates of demographic entropy with other life history attributes and evaluation of the claim that entropy is a better measure of fitness than the intrinsic rate of population increase.

## **Chapter 2: *General Methodology***

## 2.0: Matrix Population Models

Matrix population models are the tool of choice in the study of the dynamics of structured populations – and structured populations are groups of individuals of the same species whose demography varies with age/stage. Thus the method is based on recording the fate of individuals in each of the age, size or stage categories so defined. Various methods to define categories have been devised (Vandermeer, 1978, 1978, Moloney, 1986, Enright et al., 1995, Salguero-Gomez and Plotkin, 2010, Picard et al., 2010), but these do not concern us here because matrix sizes were defined by the authors of the original studies and we do not have the information on individual fates that would allow us to categorise them differently. Moreover, recent work confirms that whatever bias is produced by different categorisations, the errors produced are both small and likely to equally underestimate or overestimate the different parameters derived from the matrices, and thus cancel each other out (Picard and Liang 2014).

Plant life cycles can be efficiently represented by a life cycle graph (Hubbell and Werner, 1979) from which a population projection matrix can be derived (Caswell, 1989). Given a decomposition of the life cycle of a plant into classes (by age, size or stage), the transition structure of the life cycle can be represented by a life cycle graph (fig 2a). The nodes in this graph represent the life cycle stages and the arrows represent possible fates or contributions of an average individual over a time interval,  $t$  to  $t+1$ . These transitions can also represent recruitment contributions via sexual or asexual methods of reproduction/propagation. Unlike the more general matrix illustrated in Fig. 1, the one in Fig. 2 only contains one recruitment class, the first one, and retrogression does not occur. This limits the process types to three: stasis ( $S$ ), progression ( $P$ ) and fecundity ( $F$ ). The symbols  $n_1$ ,  $n_2$ , and  $n_3$  represent the number of individuals or density in each of the three classes or stages.  $S$  and  $P$  values are quantified as probabilities while fecundity contributions are expressed as average (sexual or asexual) offspring number

per individual over the time interval  $t$  to  $t+1$ . By ordering the stages of the life cycle in columns (source stages 1, 2 and 3) and rows (fate stages 1, 2 and 3), a population projection matrix can be constructed (fig 2b). Evidently, certain transitions/contributions are not biologically possible (e.g., pre-reproductive stages have zero fecundity) and these have values of zero. A state-of-the-art account of matrix population models is provided by Caswell (2001).

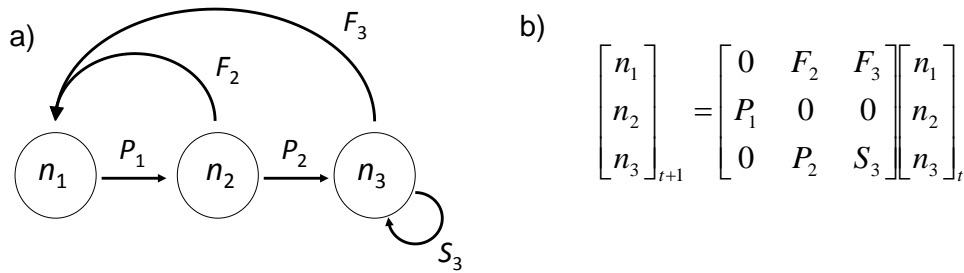


Figure 2: A simple post-breeding census life cycle represented in two forms: a) a life cycle graph, b) a matrix model formulation with population vectors at two successive times and the transition matrix derived from the life cycle graph in (a). There are three stage classes with corresponding densities  $n_1$ ,  $n_2$  and  $n_3$ , and the  $S$ ,  $P$  and  $F$  values represent the progression, stasis and fecundity transitions/contributions, respectively, in the stages indicated by their corresponding subscript. In general, subscripts are used to indicate stage, e.g.,  $n_i$  would stand for the number of individuals in a given stage  $i$ .

The analysis of matrix projection models employing matrix algebra provides a powerful tool for describing and understanding the population dynamics and life history evolution of plants (Caswell 2001). When a matrix of mean vital rates is multiplied by a vector of abundance (describing the population size by stage at time  $t$ ) it results in a vector of abundance expected one unit time later,  $t+1$  (Fig. 2b). Iteration of this product would yield a temporal sequence of population abundance vectors and, consequently, a projection of the population into the future. In shorthand matrix algebra notation the model is written as  $\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t$ , where  $\mathbf{N}$  are the population vectors at two successive times and  $\mathbf{M}$  is the population matrix). For an iterative projection over the time interval 0 to  $t$ ,  $\mathbf{N}_t = \mathbf{M}^t \mathbf{N}_0$ ). Although it is clear that, for a variety of reasons, the matrix is unlikely to remain constant year after year, and that the projection would depart from

reality as the iteration period is increased, the model iteration is conceptually valuable because it allows us to calculate essential analytical properties of the population during the period when the data to construct the matrix were collected. The mathematical derivation of these analytical properties is beyond our objectives here and we will only briefly describe essential properties relevant to this investigation.

The first of these properties is the dominant eigenvalue of the matrix, represented by the Greek letter  $\lambda$ , which is equivalent to the finite rate of population growth. Analytically, this is the largest root or eigenvalue of the characteristic equation, which is equal to the determinant of matrix  $\mathbf{M}$  minus the product of  $\lambda$  and the identity matrix:  $|\mathbf{M} - \lambda\mathbf{I}| = 0$ .

Furthermore,  $\lambda$  is related to matrix  $\mathbf{M}$  by the following relationships:  $\mathbf{M}\mathbf{w} = \lambda\mathbf{w}$  and  $\mathbf{v}\mathbf{M} = \lambda\mathbf{v}$ . These relationships mean that there exist two vectors, called right and left eigenvectors ( $\mathbf{w}$  and  $\mathbf{v}$ , respectively) that when right- and left-multiplied, respectively, by matrix  $\mathbf{M}$  are equal to their product with  $\lambda$ . These vectors correspond to the stable stage distribution (the stable proportion of individuals in each stage) and the reproductive value by stage, respectively. Reproductive value measures the expectancy of future contribution to reproduction of an individual already in stage  $i$ . For a detailed account of these properties see Caswell (2001) or “characteristic equation” and “eigenvalue” in Wolfram MathWorld (<http://mathworld.wolfram.com>).

The right and left eigenvectors are useful in their own right, but can also be used to compute the absolute and relative effects that changes in vital rates would have on population growth (known as sensitivities and elasticities, respectively; Caswell, 1978, de Kroon et al., 1986). If, for generality, we write the matrix element in row  $i$  and column  $j$  as  $a_{ij}$ , its sensitivity ( $s_{ij}$ ) is defined as the term in the left-hand side of the equation below, and is calculated as the product of element  $i$  of the reproductive value vector and element  $j$  of the stable stage distribution vector divided by the product (a scalar) of  $\mathbf{v}$  (a row vector) and  $\mathbf{w}$  (a column vector):

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\mathbf{v} \mathbf{w}}$$

In turn, elasticity ( $e_{ij}$ ) is defined and calculated as:

$$\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = s_{ij} \frac{a_{ij}}{\lambda}$$

A useful property of elasticity is that, because their sum across the whole matrix produces a constant value of one, it can be used to compare the relative effect that a change in different types of matrix elements (Figs. 1 and 2) has on population growth rate. Because a matrix model is essentially a quantitative representation of the life cycle of the average organisms in the sampled population, elasticity measures the relative contribution that each matrix element (and the vital rates contributing to it, Franco & Silvertown 2004) makes to fitness. This provides a powerful method not only to compare the influence that different demographic processes have on fitness of individual populations or species, but crucially on the influence that the physical and biotic environment in which each species lives has had on the evolution of their particular life history (Silvertown et al., 1993, Franco and Silvertown 2004).

In order to link demography to life history, it is also necessary to estimate age-based life history parameters, such as age at sexual maturity and lifespan, from the matrix models. Cochran and Ellner (1992) and Caswell (2001, chapter 5) provide methods to calculate important age-based life history variables, such as survival and reproductive schedules, and attributes such as age at first reproduction and expected life span. These age-based demographic and life history attributes were calculated employing the program STAGECOACH (Cochran and Ellner, 1992) with additional calculations in MATLAB (2012) when required.



## 2.1: *Transition Matrix Analysis*

In this study transition population projection matrices from the COMPADRE Database were used to generate age-based survival and reproductive schedules and to compute life history parameters (described below). At the start of this study only 380 species had demographic information presented in the form of matrix models. However, a few of the 380 stage projection matrices had negative mortalities, which were likely due to error in the data. Other matrices were reducible, reflecting the fact that data was missing for some stage transitions. These matrices were excluded from the analyses. Small dimension, particularly two by two projection matrices of annual plants were also not included because of their low resolution when dealing with age-related parameters and the difficulties of dealing with the variable temporal scale employed in periodic matrix models of annual plants. Finally, non-convergent matrices were also omitted from this study. In a few species, studies were conducted at more than one site or over several annual periods. Where this occurred, the average population projection matrix was used for analysis. In the end, population projection matrices for 207 species were analysed. These species were classified into five life forms: trees (*t*), palms (*p*), shrubs (*s*), forest herbs (*f*), and herbs from open or disturbed habitats (*o*).

The following parameters were calculated: age-dependent survival and fecundity schedules, the dominant eigenvalue of the matrix ( $\lambda$ , equivalent to the finite rate of population increase), the intrinsic rate of population growth ( $r$ , calculated as the natural logarithm of  $\lambda$ ), the net reproductive rate ( $R_0$ , the number of offspring over the individual's life), the age at first reproduction ( $\alpha$ , the average age at which an individual enters a stage class with positive fecundity), the total lifespan ( $L$ , the life expectancy at birth,  $e_0$ ), and two measures of generation time (ABAR, the mean age of parents of offspring produced at stable stage distribution (Cochran and Ellner's, 1992, Eq.26) and MUIR, the mean age at which members of a cohort produce offspring (Cochran and

Ellner's, 1992, Eq.27)). In a previous study, Silvertown et al. (2001) found that the age-based reproductive value ( $v_x$ , where  $x$  is age) calculated from the projected age-based survival and fecundity schedules could remain constant or even be increasing towards the end of life because these schedules are not constrained by a maximum longevity. This is an artifact of the matrix projection model, which necessarily assumes a constant survival probability in the last stage class, thus artificially prolonging lifespan. To prevent this, we assumed that the number of individuals surviving to age  $L$  would be too small and they would be unlikely to live much longer, and thus we set maximum longevity to this value ( $L$ , the life expectancy at birth). This meant that reproductive value ( $v_x$ ) calculated using the discrete version of Fisher's formula assuming  $l_x$  had effectively decreased to zero at age  $L$  would also be zero at this age. The life table parameters were also used to compute entropy ( $S$ ) (Demetrius, 1974), which measures the variability in the age at which individuals reproduce throughout the organism's life cycle. The conditional vital rates (representing the underlying demographic processes that shape the population dynamics) of survival ( $\sigma$ ), growth ( $\gamma$ ) and fecundity ( $\phi$ ) and their corresponding sensitivities and elasticities were calculated using the method described by Franco and Silvertown (2004). Results obtained from this analysis were then used to test for correlations among life history traits employing non phylogenetic and phylogenetic comparative methods in chapters five and six.

## ***2.2: Non Phylogenetic Comparative Method***

Test of associations that are not adjusted for phylogeny, are commonly used in comparative studies to test for relationships between traits among taxa that might explain trait diversity (Harvey and Pagel, 1991, Miles and Dunham, 1993). On its own, this method is generally seen as weak for inferring historical patterns of adaptations (Gould, 1986, Lauder, 1990, McKittrick, 1993) because relationships between life

history traits among existing taxa may simply reflect common ancestry rather than adaptations. This makes it difficult to differentiate between adaptations from natural selection and inheritance from common ancestors. Nonetheless, this approach can provide an indication of possible relationships between life history traits and may be considered in exploratory analysis. Traditional non comparative phylogenetic methods use conventional statistical inference methods under the assumption that individual samples or data points are statistically independent of each other. Comparative studies that use this method can only speculate on the adaptive nature of these traits because they do not incorporate a historical component. For this, it is necessary to adopt a phylogenetic comparative method (Gittleman and Kot, 1990).

### ***2.3: Phylogenetic Comparative Method***

Variations in life history traits are often phylogenetically constrained by associations within ancestries to intrinsic or abiotic factors (Stearns, 1992, Harvey and Pagel, 1991). The phylogenetic comparative approach allows the adaptive significance of life history traits to be tested. The inclusion of phylogenetic information provides a historical context for hypothesis testing and allows identification of unique independently originated adaptive variations versus maintenance of traits through common ancestry (Felsenstein, 1985, Freckleton et al., 2002). Several statistical methods that include phylogenetic information have been developed and are now widely used in comparative analyses (Garland et al., 1992, Clobert et al., 1998, Housworth et al., 2004). These methods usually assume a simple model of trait evolution (e.g. Brownian motion for continuous characters or parsimonious change for discrete characters).

In this study, both the Phylogenetically Independent Contrasts method, PIC (Felsenstein, 1985), and the Phylogenetic Generalised Least Squares method, PGLS (Martins and Hansen, 1997), were tested. However, only the results from PGLS are

presented because the two methods produced similar results, confirming their equivalence (Blomberg et al, 2012). PGLS is preferred in most analysis because of the advantages that it has over PIC, such as more flexibility regarding the model of evolution, the ability of the analysis to also incorporate discrete traits, the fact that the intercept is not forced through zero and the fact that it also allows for polytomies.

The PIC method assumes a Brownian motion model of divergence and uses a phylogeny to define a set of mutually independent pieces of information. Thus a contrast on a phylogeny is defined as a difference between two species, a species and an internode (or ancestor) of the phylogeny, or between two nodes (Felsenstein, 1985). A careful choice of the contrast yields a set of difference scores such that each score is statistically independent of all the others and together they account for the observed variability among species' life history traits. PIC is the most used phylogenetically based statistical methods after PGLS.

The PGLS method, on the other hand, can be viewed as a generalised case of PIC. This method uses a linear model procedure that allows non independent data points to be fitted when expected correlation between data points is known. PGLS uses a matrix containing the expected correlations between trait values of all pairs of species. The expected correlation between any pair is the proportion of evolutionary history from root to tip of a phylogenetic tree that these species share through common ancestry.

#### **2.4: Comparative Analysis of Demography and Life History Dataset**

In order to test for correlation between life history traits, the phylogenetic comparative methods mentioned above were used. First, an exploratory exercise using the non-phylogenetic comparative analysis was conducted to have an idea as to the possible correlations between different life history traits followed by the PIC and PGLS methods.

For phylogenetic analysis using PIC and PGLS, a phylogenetic tree for the dataset was generated using Phylomatic, an online tool for applied phylogenetics (Webb and Donoghue, 2005). Phylomatic takes as input a list of taxa with family and genus information, and then matches the taxa to the most resolved position possible in any of a set of master trees in the database and returns the phylogeny in different formats. The phylogenetic tree produced from Phylomatic contained polytomies. These polytomies were resolved manually at family level in MESQUITE (Midford et al., 2005) using information from the Angiosperm Phylogeny Website (Stevens, 2001) and a combination of classical taxonomy and specific molecular/morphological studies within families and tribes. For example to resolve the polytomies that occurred in *Neobuxbaumia* sp, the phylogeny for tribe *Pachycereeae* (*Cactaceae*) based on chloroplast and nuclear DNA sequences produced by Arias et al (2003) was used. After employing this method to resolve most polytomies, some species in the final tree were still unresolved. However, the PDTREE module of MESQUITE and the R software used in this study can handle unresolved nodes (Midford et al 2005). Phylogenetic distances were interpolated employing the *bladj* function of PHYLOCOM (Webb et al., 2008), using estimated node ages from Wikström *et al* (2001).

The phylogenetic independent contrast method as proposed by Felsenstein (1985) in the PDAP package (Midford et al., 2005, Felsenstein, 1985) of MESQUITE and the PGLS method employing the *caper* package in R (Orme et al., 2012) were used to test for

correlations amongst trait data. However, for reasons explained above, only the results from the PGLS analyses are presented in this thesis.

**Chapter 3: *Phylogenetic Signal in the Demography of Iteroparous  
Perennial Plants***

### ***3.0 Abstract***

The effect that phylogeny has on the evolution of life histories is a central issue in ecology and evolutionary biology. The link between the effects from common ancestry and phenotypic similarity has led to the acknowledgment that degree of phylogenetic relatedness can be a confounding factor in the interpretation of independent evolutionary outcomes in comparative studies. Thus, several methods have been developed to control for this effect. However, few studies have considered the effect of phylogeny on the evolutionary potential of life history traits in plants and the validity of some of these methods is itself under debate. In this study three different measures, Blomberg et al's  $K$ , Pagel's lambda (model based methods) and Moran's  $I$  (statistical method) were used to measure the degree of phylogenetic signal in 15 demographic life history traits for 207 species of iteroparous perennial plants. The results showed that demographic life history traits are generally evolutionarily labile. However, elasticities and sensitivities of vital rates were less variable and had a greater significant phylogenetic component than other life history traits considered in this study. In addition, there exists a strong correlation between the statistical and model based approaches used in this study, thus suggesting that statistical approaches do reflect the results obtained from modelling exercises, and thus could be employed in situations where trait evolution is difficult to investigate by more conventional evolutionary models.



### **3.1: Introduction**

Although adaptation through natural selection is recognised as the primary basis for the diversity of life history traits that we observe in nature, its influence does have limitations. The limitation to evolutionary change or the relative difficulty of modifying the rate of evolutionary change is referred to as phylogenetic constraint (Wilson, 1975). Phylogenetic constraint describes any result or component of the phylogenetic history of a lineage that stops an expected course of evolution in that lineage (Ewads and Naeem, 1993, McKittrick 1993). Phylogenetically constrained species are generally similar and tend to share many features belonging to a variety of traits (Blomberg and Garland, 2002, Hansen and Martins, 1996). Phylogenetic constraint may result from different processes such as the lack of suitable genetic variation for the origin of an adaptive trait, stabilizing selection, pleiotropy or lack of selection (Wiens et al., 2010, Etersson and Shaw, R.G., 2001). Many animals and plants exhibit traits that are less perfectly suited to their individual needs than might be expected and, as a consequence, some researchers have viewed phylogenetic constraint as a weak explanation with regards to why particular types of traits that would seem to make an organism well adapted to its environment are absent. Natural selection results in organisms showing traits that reflect their evolutionary history. However, in some cases, such traits may prohibit or constrain the evolution of new or different responses to a particular environmental condition. Nonetheless, it seems clear that a consideration of the evolutionary history of many traits is crucial to understanding the relationship between organisms and their environment (Freckleton et al., 2002).

Phylogenetic effects, niche conservatism and phylogenetic inertia are some of the terms that are used in the literature to describe this concept of history in character evolution and considerable debates exist in the literature on the use of these terms. For instance, Blomberg et al (2003) has argued that the use of these terms conveys a sense that the

phylogeny itself is responsible for the resemblance amongst closely related species and have suggested the use of the term “phylogenetic signal” to emphasize the fact that the resemblance observed amongst closely related species is a pattern and by itself does not reveal the underlying evolutionary processes involved. Accordingly, there has been a mounting interest in how phylogenetic signal can be used to understand the broad - scale evolutionary and ecological processes (Martins, 2000, Diniz-Filho, 2001, Cooper et al., 2010, Hof et al., 2010). Life history traits can exhibit low or high phylogenetic signal. When phylogenetic signal is high, traits are more similar in close relative as opposed to distant relatives and are considered less labile and conserved (Losos, 2008, Blomberg et al., 2003). On the contrary traits that are more similar in distant relatives than close relative or are randomly distributed across a phylogeny are said to show low phylogenetic signal and thus are said to be more labile (Kamilar and Muldoon, 2010, Blomberg et al., 2003).

The link between the effects from phylogeny and phenotypic similarity has led to the acknowledgment that degree of phylogenetic signal can be a confounding factor in the interpretation of independent evolutionary outcomes in comparative studies (Hansen and Martins, 1996). As a result, several phylogenetic comparative methods have been developed to control for this effect, including both autocorrelation methods and methods that use an explicit model of trait evolution (Cheverud et al., 1985, Gittleman and Kot, 1990, Lynch, 1991, Pagel, 1999, Abouheif, 1999, Blomberg et al., 2003,). However, there is still no consensus on the most effective phylogenetic comparative method. Each method has its advantages and disadvantages and differs in their statistical and theoretical approaches in the way phylogenetic signal is quantified (Pavoine et al., 2008).

Few studies have considered the effect of phylogenetic signal on the evolutionary potential of life history traits in plants. Franco and Silvertown (1996) employed a

hierarchical analysis of variance on the demographic life history traits of 83 species of perennial plants to determine the taxonomic levels at which most variation occurred. They showed that traits that can be described as being dependent on biological age: age at sexual maturity, generation time and life expectancy at age of maturity had their variation concentrated at the phylum level, with the total variance explained at this level being between 40% and 75%, whereas traits that describe time-dependent rates, such as the intrinsic rate of natural increase ( $r$ ), and net reproductive rate ( $R_0$ ) had their variation (44% and 58%) concentrated at the species level. Furthermore, traits that describe the rate of decrease in the intensity of natural selection with age ( $Hp_x$  and  $Hm_x$ ) were shown to have their variation concentrated at intermediate levels (genus and order, respectively). This might be regarded as a rough way of measuring phylogenetic signal but it has the advantage of pinpointing the depth in the tree at which variation of different traits is concentrated. Burns et al (2010) have further explored this issue in plants. They used PGLS models to test for phylogenetic signal in 204 species of terrestrial plants surveyed from the literature and showed that statistical models without phylogeny were preferred to models with phylogeny for vital rates and elasticities. The effect of phylogeny was, however, shown to be greater in the sensitivity of vital rates than their elasticities.

The aim of this investigation was to quantify phylogenetic signal in 15 demographic life history traits and population performance metrics of 207 species of perennial plants studied in their natural environment. This had a double purpose: to understand how labile demographic life history traits are, and to evaluate the performance of three measures of phylogenetic signal currently used in comparative studies. The results of this study should provide justification for the later use of the phylogenetic comparative approach in analysing the datasets of chapters 5 and 6 of this thesis.

### **3.2: Material and Methods**

The demographic and life history variables and phylogeny used in this study were obtained as described in Chapter 2. The dataset analysed in this chapter contained 10 demographic and 5 life history traits: (1) population growth rate ( $\lambda$ ), (2) survival ( $\sigma$ ), (3) growth ( $\gamma$ ), (4) fecundity ( $\phi$ ), (5) sensitivity of survival ( $S_\sigma$ ), (6) sensitivity of growth ( $S_\gamma$ ), (7) sensitivity of fecundity ( $S_\phi$ ), (8) elasticity of survival ( $E_\sigma$ ), (9) elasticity of growth ( $E_\gamma$ ), (10) elasticity of fecundity ( $E_\phi$ ), (11) lifespan ( $L$ ), (12) age at sexual maturity ( $\alpha$ ), (13) reproductive lifespan ( $L_\alpha$ ), (14) generation time ( $\mu$ ) and (15) demographic entropy ( $S$ ).

### 3.2.1: Data Analysis

#### *Metrics for measuring phylogenetic signal in comparative dataset*

Three methods of quantifying phylogenetic signal were used in this study: Pagel's  $\lambda$  (Pagel, 1999)  $\lambda$ , Blomberg's  $K$  (Blomberg *et al.*, 2003) and Abouheif's method (Abouheif 1999) which is a particular case of Moran's  $I$  (Paradis, 2009). The first two measures represent model-based approaches and the latter a statistical approach.

#### *Pagel's $\lambda$*

$\lambda$  is a quantitative measure of phylogenetic dependence introduced by Pagel (1999). Lambda uses Brownian motion as an explicit model of trait evolution. To estimate Pagel's  $\lambda$  a maximum likelihood optimization method is used to find the value of  $\lambda$  that best explains trait variation among species at the tip of the phylogeny.  $\lambda$  is a tree transformation parameter and has a multiplying effect on the off-diagonal elements of the variance/covariance matrix of the tree topology and branch lengths by values between zero and one. This has the effect of gradually eliminating the phylogenetic structure under the Brownian motion model of trait evolution. The off-diagonal/covariance values are equal to the sum of the shared branch lengths of the species. The  $\lambda$  value varies between zero to unity. A  $\lambda$  value of 0 indicates that there is no phylogenetic signal in the trait – equivalent to a star phylogeny. In other words, this suggests traits have evolved independently of phylogeny and close relatives are no more similar on average than distant relatives. When  $\lambda$  is equal to 1 (unity) this indicates that there is a strong phylogenetic signal in the trait and thus, that closely related species are more similar in that trait than distant relatives. Intermediate values of  $\lambda$  indicate that, although there is a degree of phylogenetic signal in the trait, it has evolved following a different process other than pure Brownian motion (Pagel, 1997, Pagel, 1999, Freckleton *et al.*, 2002). It is possible that  $\lambda$  can also be greater than 1, indicating that

close relatives are more similar than expected under a pure Brownian motion model of trait evolution.  $\lambda$  was calculated using the package “Geiger” implemented in the R working environment (Harmon et al., 2008). In order to determine whether  $\lambda$  was significantly different from zero (equivalent to no phylogenetic signal) or 1 (the Brownian motion expectation) a likelihood ratio test was used. A likelihood ratio test is used to compare the fits of two models. This test was used to compare a model with the observed maximum log likelihood value of  $\lambda$  to a model with a fixed  $\lambda$  value of either 0 or 1.

### *Blomberg’s K*

Blomberg’s  $K$  measures phylogenetic signal by quantifying the amount of observed trait variation relative to the trait variation expected under Brownian motion.  $K$  is calculated as a ratio of two other ratios, one observed and the other expected. The observed numerator ratio is the mean square error (MSE) of the tip data, measured from the phylogenetically corrected mean, divided by the MSE of the data calculated using the variance covariance matrix derived from the phylogeny. The expected, denominator ratio is similarly calculated from the tree assuming Brownian motion as the evolutionary process.

$$K = \text{observed} \frac{MSE_0}{MSE} / \text{expected} \frac{MSE_0}{MSE}$$

Thus,  $K$  compares the observed phylogenetic signal in a trait to that under Brownian motion evolution.  $K$  values vary continuously from 0 to 1. A  $K$  value of zero indicates that there is no phylogenetic signal in the trait. This means that traits have evolved independently of phylogeny and, as such, closely related species are not more similar on average than distant relatives. A  $K$  value of 1 indicates that there is a strong phylogenetic signal and thus the trait has evolved according to the Brownian motion of

trait evolution. Intermediate values of  $K$  indicate that close relatives are less similar than expected under the Brownian motion model of trait evolution. It is, however, possible for  $K$  values to be greater than unity. Where this occurs, it indicates that close relatives are more similar than expected under a Brownian motion model of trait evolution; this is known as trait conservatism. The package “*picante*” implemented in the R software working environment was used to calculate values of  $K$  (Kembel et al., 2010). To evaluate the statistical significance of phylogenetic signal in life history traits, observed patterns of the variance of independent contrasts of the trait were compared to a null model involving shuffling species across the tips of the phylogenetic tree using 1000 permutations (Kembel et al., 2010). This was achieved by using the *phylosignal* function of “*picante*”.

#### *Abouheif's (1999) method*

Abouheif's method is derived from a test for serial independence (TFSI). The TFSI identifies dependencies in a sequence of observations by comparing the average square differences between two successive observations to the sum of all successive square differences (Pavoine et al., 2008). Abouheif (1999) adaptation of this test for phylogenetic comparative data is based on the observation that any single-tree topology can be represented in several ways by rotating the nodes within the tree. Each of these rotations yields a specific sequence of species and consequently, a specific sequence of the trait values of interest from which an observed statistic  $C_{mean}$  can be computed. This statistic denotes the critical values of TFSI and therefore allows estimation of the significance of the serial independence (see Abouheif, 1999, for more details). A randomized  $C_{mean}$  is also calculated by randomly shuffling the original data so that species are placed on the tip of the original phylogeny and the TFSI is applied to all possible permutations of the given phylogeny. This new  $C_{mean}$  is then compared to the

observed  $C_{mean}$ , with the null hypothesis of no phylogenetic signal in the data being accepted or rejected.

Pavoine et al (2008) has shown that the  $C_{mean}$  statistic is in fact a Moran  $I$  test, i.e. a measure of autocorrelation across the tips of the tree that uses a specific matrix of proximity (Matrix A). The diagonal elements of the matrix (representing proximity of a species to itself) are equivalent to the inverse product of the number of branches descending from each interior node in the path connecting this species to the root of the tree. Conversely, the off-diagonal elements (representing proximity between two species) are equivalent to the inverse product of the number of branches descending from each interior node in the path joining these two species (Pavoine et al., 2008). However, Abouheif test does not require information on branch lengths and does not follow any evolutionary model and as such it has been criticised by Blomberg et al (2003) because it is unclear how results would be affected by other evolutionary models. Nonetheless, Pavoine et al. (2008) suggested that the tree topology is a critical component of evolutionary history and suggest that the absence of an underlying evolutionary model is rather an advantage than a disadvantage of the approach. Calculations of Abouheif/Moran's  $I$  statistics were carried out in the R software environment employing package “*ade4*” (Dray et al., 2007) and 999 random permutations were used to obtain the p-values.

### **3.3: Results**

Because the results from Pagel  $\lambda$  and Blomberg's  $K$  were similar, and because they both employ the same model of trait evolution, only results using  $K$  and Moran's  $I$  are presented in this section. However, results using  $\lambda$  are presented in the appendix section of this thesis.



Using Blomberg's  $K$ , statistically significant levels of phylogenetic signal were found in all six measures of sensitivity/elasticity (Fig. 3;  $n = 207$  in all cases): sensitivity of survival ( $K = 0.36, p = 0.02$ ), sensitivity of growth ( $K = 0.26, p = 0.02$ ), sensitivity of fecundity ( $K = 0.16, p = 0.03$ ), elasticity of survival ( $K = 0.22, p = 0.01$ ), elasticity of growth ( $K = 0.14, p = 0.03$ ), and elasticity of fecundity ( $n = 207, K = 0.12, p = 0.01$ ). Of the remaining traits, only survival ( $n = 207, K = 0.15, p = 0.04$ ) and generation time ( $n = 207, K = 0.49, p = 0.03$ ) exhibited statistically significant ( $p < 0.05$ ) phylogenetic signal. All traits had  $K$ -values that varied between zero and unity ( $< 1$ ), indicating they were not phylogenetically conserved. Across life history traits, phylogenetic signal was observed to be highest in generation time ( $\mu$ ), followed by entropy ( $S$ ), reproductive life span ( $L_\alpha$ ), age at sexual maturity ( $\alpha$ ) and lifespan ( $L$ ). In demographic traits, phylogenetic signal was highest for any expression of survival (raw, sensitivity or elasticity), followed by those of growth and then those of fecundity. Population growth rate showed a relatively weak phylogenetic signal with  $K = 0.15$

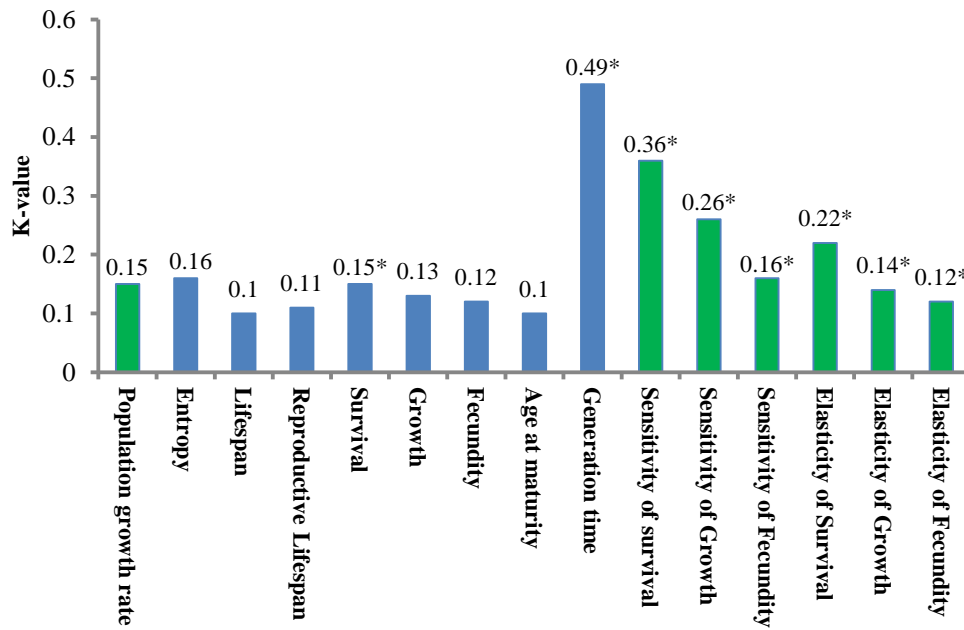


Figure 3: Phylogenetic signal in demographic and life history traits using Blomberg's et al  $K$ . Demographic traits are highlighted in green and other life history traits are highlighted in blue. \* represents life history traits with significant level of phylogenetic signal ( $p < 0.05$ )

Using Abouheif's (1999) method, significant values of Moran's  $I$  were found for precisely the same demographic and life history traits than those which had significant  $K$ : generation time ( $n = 207$  for all traits,  $I = 0.05$ ,  $p = 0.04$ ), sensitivity of survival ( $I = 0.07$ ,  $p = 0.02$ ), sensitivity of fecundity ( $I = 0.04$ ,  $p = 0.04$ ) and sensitivity of growth ( $I = 0.06$ ,  $p = 0.01$ ). These results were generally consistent with the findings employing Pagel's  $\lambda$  and Blomberg's  $K$  except that the strength of phylogenetic signal in these population performance metrics was smaller. As observed in Blomberg's  $K$  and Pagel's  $\lambda$ , the value of Moran's  $I$  had similar variations across the demographic and life history traits (Fig. 4).

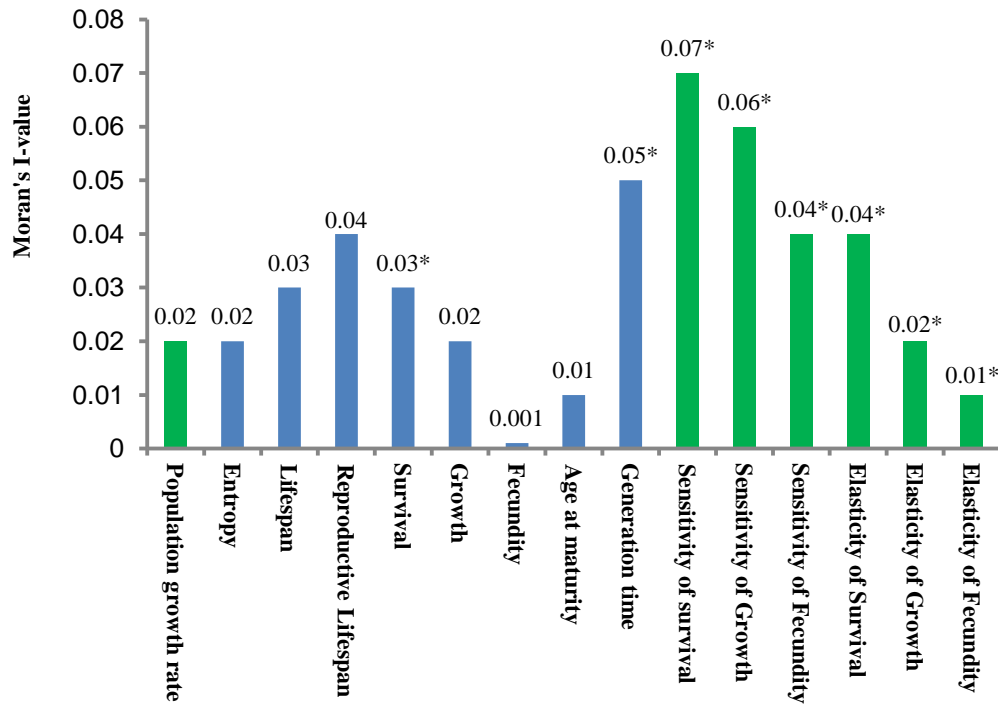


Figure 4: Phylogenetic signal in demographic and life history traits using Moran's I. \* represents life history traits with significant level of phylogenetic signal ( $p < 0.05$ ).

All three metrics (Pagel  $\lambda$ , Blomberg et al's  $K$ , and Moran's  $I$ ) showed positive relationships with each other (Fig. 5), but the only significant one ( $p < 0.05$ ) employing Spearman's correlation was that between  $K$  and  $\lambda$  (Table 1).

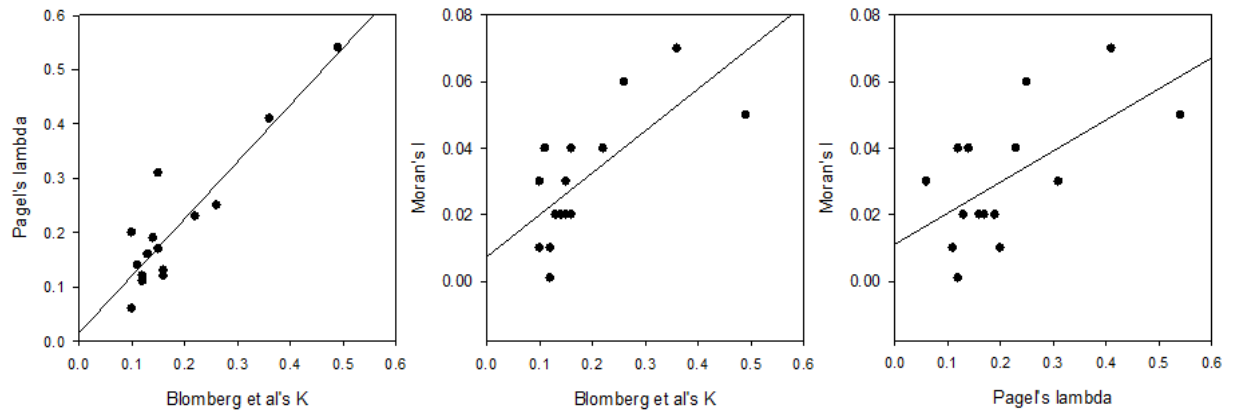


Figure 5: Bivariate relationship between the three phylogenetic signal measures employed in this study (Blomberg's  $K$ , Pagel's  $\lambda$  and Moran's  $I$ ).

Table 3: Spearman correlations between the three phylogenetic signal metrics used in this study.

	<b>Blomberg et al's K</b>	<b>Pagel <math>\lambda</math></b>
Pagel $\lambda$	0.822*	
Moran's I	0.511	0.378

\*  $p < 0.05$

### **3.4: Discussion**

#### **3.4.1: Comparison of Methods**

Despite the fact that Moran's  $I$  method has been criticised for not taking into account a specific evolutionary model and also for ignoring the use of branch length information in estimating phylogenetic signal in comparative data (Blomberg et al., 2003), the results from the current study indicates that the statistical method (Moran's  $I$ ) and model based approaches (Blomberg's  $K$  and Pagel's  $\lambda$ ) are comparable, albeit not equivalent. Interestingly, all three indices revealed significant phylogenetic signal in the same eight traits (sensitivities and elasticities of survival, growth and fecundity, generation time and survival). However, the values of phylogenetic signal in traits employing Moran's  $I$  method were generally lower than those in traits using Blomberg's  $K$  and Pagel's  $\lambda$ . These differences, however, make no difference to their statistical significance which was similar across the three indices. The merit of using the model-based methods is that they provide a reference value for departure from Brownian motion, whereas the statistical method measures the strength of the signal independently of any model of evolution.

### ***3.4.2: Phylogenetic Signal in Demographic Life History Traits.***

The sensitivities and elasticities of the vital rates, raw survival and generation time were the only traits that exhibited significant phylogenetic signal, suggesting that, because closely-related species tend to resemble each other in these traits, they vary in accordance to a model of gradual evolutionary change. Thus, the finding of significant phylogenetic signal in the sensitivities of vital rates means that closely related species share similar effects of their underlying vital rates on fitness and are only expected to diverge slowly from each other. For example, all species in our data set were perennial iteroparous plants with a minimum life span of four years. Thus, it would be expected that species that are closely related would share sensitivities if the absolute changes in survival are likely to increase the population growth rate as in most long live woody perennial plants. These results of significant levels of phylogenetic signal revealed in the sensitivities of vital rates is also consistent with the taxonomic conservation of transient (short term) demographic dynamics in other studies (Stott et al, 2010). In a study conducted by Burns et al. (2010) using phylogenetic generalised least square analysis (PGLS), phylogenetic signal was found in the sensitivities of vital rates but not in their elasticities. However, in the present study, significant levels of phylogenetic signal were observed in both sensitivities and elasticities of vital rates, albeit it was lower in the latter. Two reasons for the observed differences are the different methods used (PGLS vs TIPs fits in Burns et al.'s study vs phylogenetic signal indices in this study) and the resolution of the phylogenetic trees employed (with many polytomies in Burns et al.'s [126 internal nodes out of 203 expected for a fully resolved phylogeny of 204 species, or 62% resolution] and highly resolved in our case [204 internal nodes out of 206 expected, or 99% resolution]). The resolution of tree topology has been shown to affect the estimation of phylogenetic signal (Datson et al., 2008, Tank and Olmsteas, 2008). Although the elasticities of vital rates showed significant levels of phylogenetic

signal, this was smaller than the phylogenetic signal of vital rate sensitivities. This suggests that sensitivities of vital rates, which measure their absolute influence on fitness, are less evolutionarily labile than elasticities, which measure relative effects on fitness.

The finding of a significant level of phylogenetic signal in raw survival, but not in growth and fecundity is intriguing. Several studies have suggested that environmental variation should select for life history traits that exhibit less variability (Pfister, 1998, Morris et al., 2008). Using sensitivity and elasticity analyses Pfister (1998), analysed the stage-specific demography of 30 field populations selected from the literature for pattern between the variance of a demographic component and its contribution to population growth rate. She observed that there was an inverse relationship between the variance in a vital rate and its contribution (sensitivity or elasticity) to population growth rate in many organisms. Specifically, in woody perennial plants she noted that the survival term (vital rate) was less variable than the growth and fecundity terms. This observation is relevant to this study because life history traits that have low phylogenetic signal would be expected to have high variability while those with high phylogenetic signal would be less variable. As mentioned earlier, our dataset was made up of perennial plants with a minimum lifespan of four years, making survival to be the more relevant, vital rate influencing population growth rates and thus it would be expected that survival would be buffered against environmental variability. Therefore the finding of significant phylogenetic signal in survival is consistent with Pfister's (1998) observation. The relatively low phylogenetic signal found in growth and fecundity could be attributed to the relatively low importance they play in the population growth rate of the perennial species employed in this study. Thus, while closely related species may vary in the influence that growth and fecundity have on fitness, survival will tend to show a similar, and high, influence. This suggests that, if

resources fluctuate, their effect would be absorbed by changes in growth and reproduction, and prioritising survival.

Significant phylogenetic signal was also observed in generation time. Generation time has been described as the most suitable single-number metric for describing a species' life history because it incorporates all other demographic rates (Gaillard et al., 2005). Thus, important life history traits are expected to be buffered against environmental variability. In addition, the presence of significant phylogenetic signal in generation time may be in part due to the correlation between this variable and the sensitivity and elasticity of survival which had a significant phylogenetic signal. (Dalglish et al., 2010).

Phylogenetic signal in the remaining demographic and life history traits was relatively low. The weaker phylogenetic signal observed in life span and reproductive life span could be accounted for by the correlation that these variables have with the elasticity of survival (Franco and Silvertown, 2004). Previous research has also demonstrated the variability of these life history traits and, thus, is unsurprising and, indeed, consistent with the weak phylogenetic signal found in these traits (Franco and Silvertown, 1996, Van Dijk, 2009). The correlation between entropy and other life history traits could also account for the small phylogenetic signal present in this trait.

Phylogenetic signal in population growth rate was also relatively low, indicating that the population growth rate is evolutionarily labile. This is perhaps predictable, given that the dataset of 207 species employed in this study came from different eco-regions and habitats of the world where their vital rates are likely to be subjected to varying environmental conditions that might influence temporal variations in population growth rates. This result is consistent with Buckley et al.'s (2010) study on the causes and consequences of variation in population growth rate. Their analysis, employing 50 species of perennial plants drawn from different habitats suggested that population



dynamics can vary greatly from species to species even within the same genus, making population growth rate both ecologically and evolutionarily labile.

However, it is crucial to note that the relatively low phylogenetic signal observed in some of the demographic life history traits in this study may reflect sampling bias. Simulation studies have shown that polytomies and missing branch length information have insignificant effects on estimates of  $K$  and  $\lambda$  (Munkemuller et al., 2012). In contrast to Burn et al.'s study, the phylogeny employed here contained only 0.44% of polytomies. Consequently, polytomies are likely to have only a small effect in our results. On the other hand, species sampling bias and errors in trait estimates can influence Pagel's  $\lambda$  (Boettiger et al., 2012). Since our dataset only contains of the order of 1/1000 of all iteroparous seed plant species and these are distributed over a wide range of plant families, providing few closely related species (present in three polytomies), this is likely to lower the estimated level of phylogenetic signal. This is an issue that requires wider investigation.

$K$  is also known to be sensitive to measurement errors which lower its value (Hardy and Pavoine, 2012). However, despite the ecological variability of some traits (e.g., population growth rate), we are confident that most demographic and life history characteristics estimated by the matrix method are close representations of the species averages under natural conditions (e.g., lifespan, age at sexual maturity, generation time). To ensure that this was the case, only matrices that represented at least four years of field demographic data collection were used. Thus, the possibility of large measurement errors in trait data is small. Nonetheless, this could account for some of the relatively low phylogenetic signal found in some of the traits analysed.

Finally, the relatively low value of phylogenetic signal observed in some traits could be due to variation in the taxonomic scale at which phylogenetic signal occurs. Franco and Silvertown (1996) showed that measures of phylogenetic signal in demographic and life

history traits varied with taxonomic level. For instance a trait may show high phylogenetic signal at family level, but not at higher or lower levels. The three methods employed here are measures of phylogenetic signal at the tips of the tree (i.e., at species level) and, thus, do not directly address the issue of variability among tree branches at different levels of resolution. In summary, because these factors tend to reduce rather than inflate phylogenetic signal, the tendency is for it to be underestimated.

In conclusion, this study showed that there exists a trend for the three indices used to measure phylogenetic signal to covary, confirming the conceptual link between Blomberg's  $K$  and Moran's  $I$  (Pavoine and Ricotta 2012) and empirically confirming the similarity of numerical results between  $\lambda$  and  $K$ , despite these measuring different aspects of the phylogeny, one comparing the correlation of a trait among closely related species with that expected under a model of Brownian evolution, while the other is a scaled ratio of their variances. Moran's  $I$  has the advantage of being independent of any particular evolutionary model (Pavoine and Ricotta 2012). Regardless of their statistical significance, the low values of  $K$  and  $\lambda$  obtained suggest a degree of ecological plasticity in life history traits (Silvertown et al., 2006, Küster et al., 2008, Burns et al., 2010). Somewhat surprisingly, demographic traits that measured the influence of vital rates on fitness were less evolutionarily labile. This suggests that because these traits contribute to fitness, they are buffered against environmental variability and thus are expected to be more conserved than other life history traits examined. Future studies should attempt to unravel the influence of specific selective pressures shaping broad life history types.

***Chapter 4: Evolution of Senescence in Iteroparous Perennial Plants***

#### ***4.0 Abstract***

Classical evolutionary theory of senescence predicts an increase in mortality and a decrease of fertility with age after maturity. Consequently, in order to understand the evolution of senescence in natural populations, the age trajectory of mortality and fertility needs to be considered. However, the difficulties of ageing plants in their natural environment has meant that few studies and in relatively few short lived species have successfully been able to track the fate of aged individuals. The possibility of estimating age-based parameters from stage structured, matrix population models offer the possibility of investigating patterns of death and fecundity with age in a large sample of species which is ecologically and taxonomically diverse species. A comparative study based on examining the survival and reproductive value patterns of 207 species of iteroparous perennial plants studied in their natural habitat was conducted. Life tables and fecundity schedules derived from stage projection matrices were obtained and used to evaluate how mortality and reproductive value varied with age. Eighty one per cent of species showed an increase in mortality rate with age that reached a maximum at the end of life while one hundred per cent of species showed a decline in reproductive value with age after peaking in midlife. These results confirm the general existence of senescence in the iteroparous perennial plants used in this study.

#### **4.1: Introduction**

Senescence is defined as a decline in physiological functioning with age that results in a decrease in reproductive rate, increase in mortality rate or both. (Rose, 1991a, Finch, 1990, Abrams, 1991). From the life history viewpoint, senescence means a restriction of the life history options open to an organism over time (Partridge and Barton, 1996). Because senescence seems to be a non-adaptive trait, the understanding of its evolution and persistence in natural populations is a considerable challenge to evolutionary ecologists. The commonly accepted explanation to account for its persistence is that, species senesce because natural selection tends to act less strongly on traits expressed late in life than on traits that are expressed early on in life (Hamilton, 1966). Accordingly, two major corollaries are derived from this hypothesis (Charlesworth, 1994): (i) there is the non-adaptive explanation, according to which late acting mutations accumulate in populations over many years; and (ii) the adaptive explanation in which senescence results from the optimisation of the life history. Here, late-life performance is sacrificed for early survival or reproduction. The first assumption is considered in the mutation accumulation theory (Medawar, 1952) and the second in the antagonistic pleiotropy theory (Williams, 1957).

Rapid senescence is generally known to occur among annual plants having a single reproductive event, but the extent to which it occurs in plants with multiple reproductive events is uncertain (Watkinson, 1992). It has been suggested that in plants with more than one reproductive event, senescence might be gradual or even negligible (Tatar et al., 1993). Other evolutionary ecologists have argued that certain animals and plants with multiple reproductive events fail to show signs of senescence (Comfort, 1956). For instance, Vaupel et al (2003) argued the case of negative senescence, whereby, mortality rates are observed to decrease with age in organisms with multiple reproductive events. That is, certain species of plants and animals display no observable

increase in age-specific mortality rate or any decrease in age-related physiological functioning defining senescence. Notably, the case of senescence in clonal plants has been widely cited in the literature where it is argued that, plants that exhibit clonal growth can effectively escape senescence. This, however, is not necessarily true. Clonal reproduction does not automatically exempt genets from the evolution of senescence (Silvertown et al., 2001). Although genets of clonal plants seem to be immortal, ramets, i.e., those parts of a genet that constitute an integrated physiological unit (sensu Watson and Casper, 1984, and Watson, 1986) have limited lifespans and thus presumably senesce. The issue of whether the genet senesces remains, however, an open question. This assertion is congruent with Gardner and Mangel (1997), who argued that senescence is present in clonal plants, even if adult mortality is small, except in the case where sexual reproduction rises dramatically with age. In fact, among clonal plants, rapid senescence has been observed in some long-living plants such as the semelparous bamboos (Watkinson, 1992).

Understanding the evolution of senescence in natural populations has thus become an important area of research in the last decade and, in order to investigate senescence in natural populations, several measures have been proposed to measure it. These measures typically include separate estimations of the decrease in survival and reproduction with age (Moller and De Lope, 1999, Silvertown et al., 2001). Alternatively, the measurement of longitudinal aging patterns in as many life history traits as possible has also been suggested to empirically explore this deterioration of state with age (Nussey et al., 2008). Different traits, however, often have conflicting effects on the components of fitness (Michod and Hesson, 1990). For instance, evolution may favour life history traits that can increase survival by decreasing fecundity, or vice versa. For example, in long-lived species, where survival is emphasized over immediate fecundity, evolution selects for life history traits that

increase lifespan. This is reflected in life history models that are based on reproductive effort (Gadgil and Bossert, 1970, Schaffer, 1974, Michod, 1978). Thus, a decrease in survival probability with age may result in a tradeoff of increased reproductive investment in late life. It is argued accordingly that empirical studies that indicate a simultaneous decline in both reproduction and survival in wild populations should provide a better case for the effect being due to senescence (Bonduriansky and Brassil, 2002). Consequently, a better definition of senescence should account for the deterioration of the state of the individual determined jointly by age specific survival probability and reproduction in late life. This view of senescence is captured in Fisher's (1930) reproductive value. Reproductive value is the expected reproductive contribution of each age group to the next generation and, hence, is a compound of the probability of surviving to a given age and the expected reproductive contribution if the organism does survive. It generally increases as the organism approaches the age at first reproduction and, depending on the pattern of change in the survival and reproductive schedules, it peaks at an age during the reproductive stage before declining towards zero as a result of continued mortality and a decline in the rate of reproduction. Thus, age specific changes in reproductive value can be used as an index for comparing the patterns of senescence among populations because it is a measure of how an individual's contribution to fitness is expected to change with age (Partridge and Barton, 1996).

The aim of this study was to test for the signs of senescence in age-specific trajectories of mortality rate and reproductive value using matrix population models for 207 species of perennial plants studied in their natural environment. Evolutionary theory of senescence predicts an increasing mortality and a decreasing fertility with age. Thus, one would expect to find these patterns exhibited in the reproductive value and mortality schedules of the species investigated.

#### **4.2: Material and Methods**

All the survival and reproductive schedules employed in this study were derived as described in Chapter 2. However, in order to investigate how mortality rate varied with age, the force of mortality ( $\mu_x$ ), corresponding to the instantaneous rate of mortality at a given age ( $x$ ) was calculated as  $\mu_x = -\ln (l_{x+1}/l_x)$  where  $l_x$  is the age specific survival (Tatar et al., 1993). The reproductive value, ( $v_x$ ) was also calculated employing Fisher's formula on the life table survivorship and fecundity schedules estimated from matrix projection (method described in Chapter 2). Graphs of mortality ( $\mu_x$ ) and reproductive value ( $v_x$ ) against age were produced employing SigmaPlot v12.5 (Systat Software 2011) and unique patterns of their change with age were identified. These patterns, easily distinguishable by eye, were classified into three types (see results). The reason for a simple classification by curve shape (and not attempting to conduct a statistical fit of, for example, mortality to specific models such as Gompertz or Weibull) is due to the fact that, by assuming a constant survival value in the last matrix category, projection of matrix models produces a constant mortality rate at advanced ages. This defeats the purpose of investigating the changing pattern of mortality at advanced ages. Provided a maximum lifespan is established, the constant mortality rate in the last category, and consequently in the oldest ages, does not represent a problem for reproductive value because this decreases to zero when the individual eventually dies (a matrix model is a quantitative representation of the life cycle of the average individual). Not having the raw data to investigate in detail the pattern of change in the force of mortality at advanced ages, we restrict ourselves to providing a classification that pinpoints species or patterns that may deserve more investigation in the form of detailed longitudinal studies. In the next chapter, however, we present a novel analysis to investigate the variation in the time distribution of reproductive value across the sample of 207 species of perennial plants as a means to quantify the trade-off between the speed and duration



of life, irrespective of the pattern of change of either mortality or reproductive value itself.

### **4.3: Results**

#### **4.3.1: Age Specific Mortality**

The relationship between mortality rate ( $\mu_x$ ) and age ( $x$ ) showed three different patterns. In Type 1 (Fig. 6a) mortality rate initially decreases and then increases with age. Type 2 (Fig. 6b) showed an (often only slight) increase in mortality rate with age in the early years, followed by an asymptotic decrease in later years. Type 3 (Fig. 6c) showed an asymptotic increase of  $\mu_x$  value with age. Type 1 trend was predominant (133 species), followed by type 2 (38 species) and type 3 (36 species) (Table 4). Sixty seven species that showed type 1 trend were herbaceous perennial plants, constituting 59% (67/113) of herbs in the dataset; 81% trees, 63% shrubs, and 47% palms also showed the type 1 trend. Of the 38 species that displayed type 2 curves 23% were herbs, 4% trees, 23% shrubs, and 21% palms. Similarly, of the 36 species in the dataset displaying a type 3 trend 17% were herbs, 15% trees, 14% shrubs and 32% palms. Appendix (2) lists the pattern displayed by each species in the dataset.

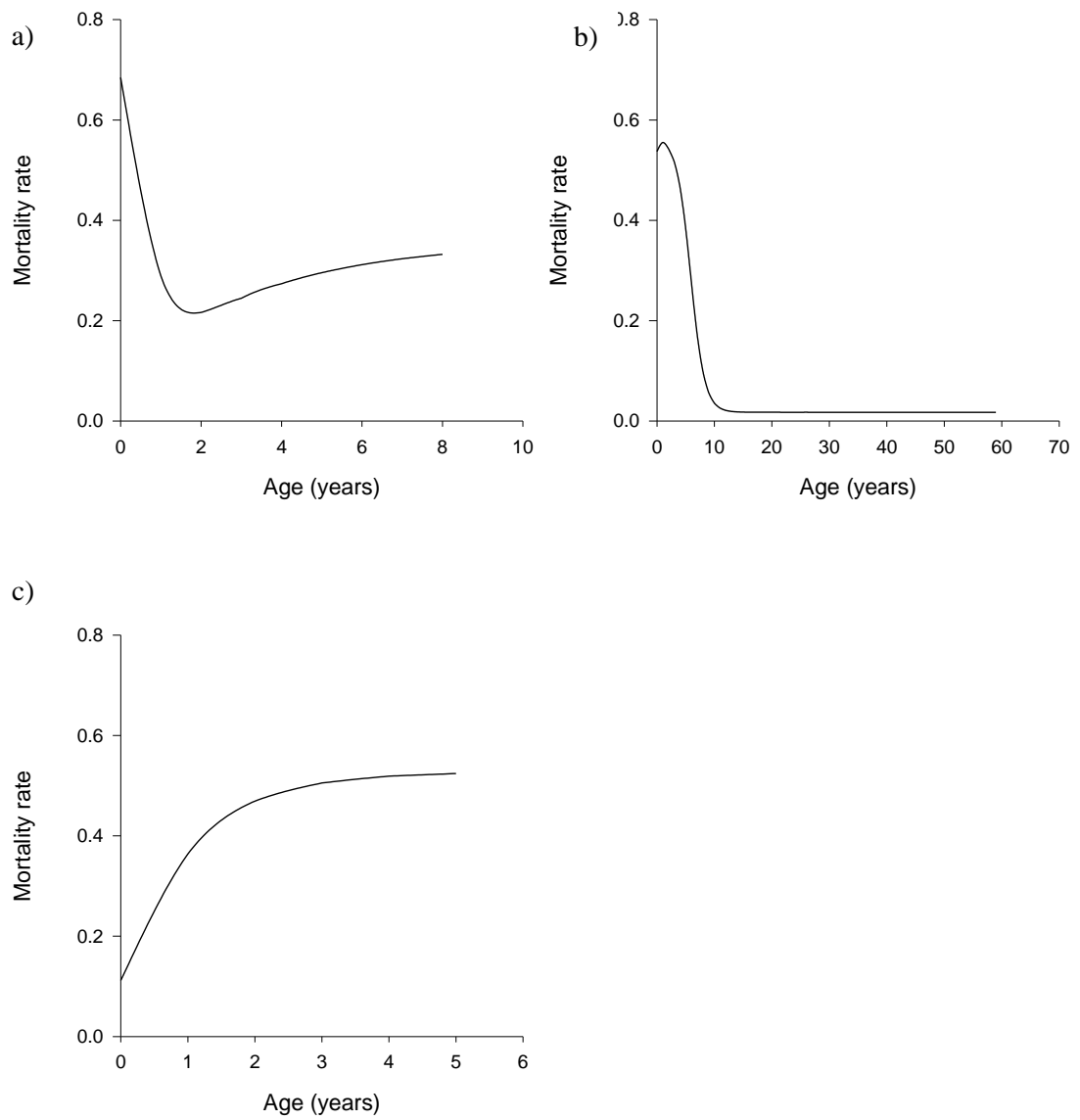


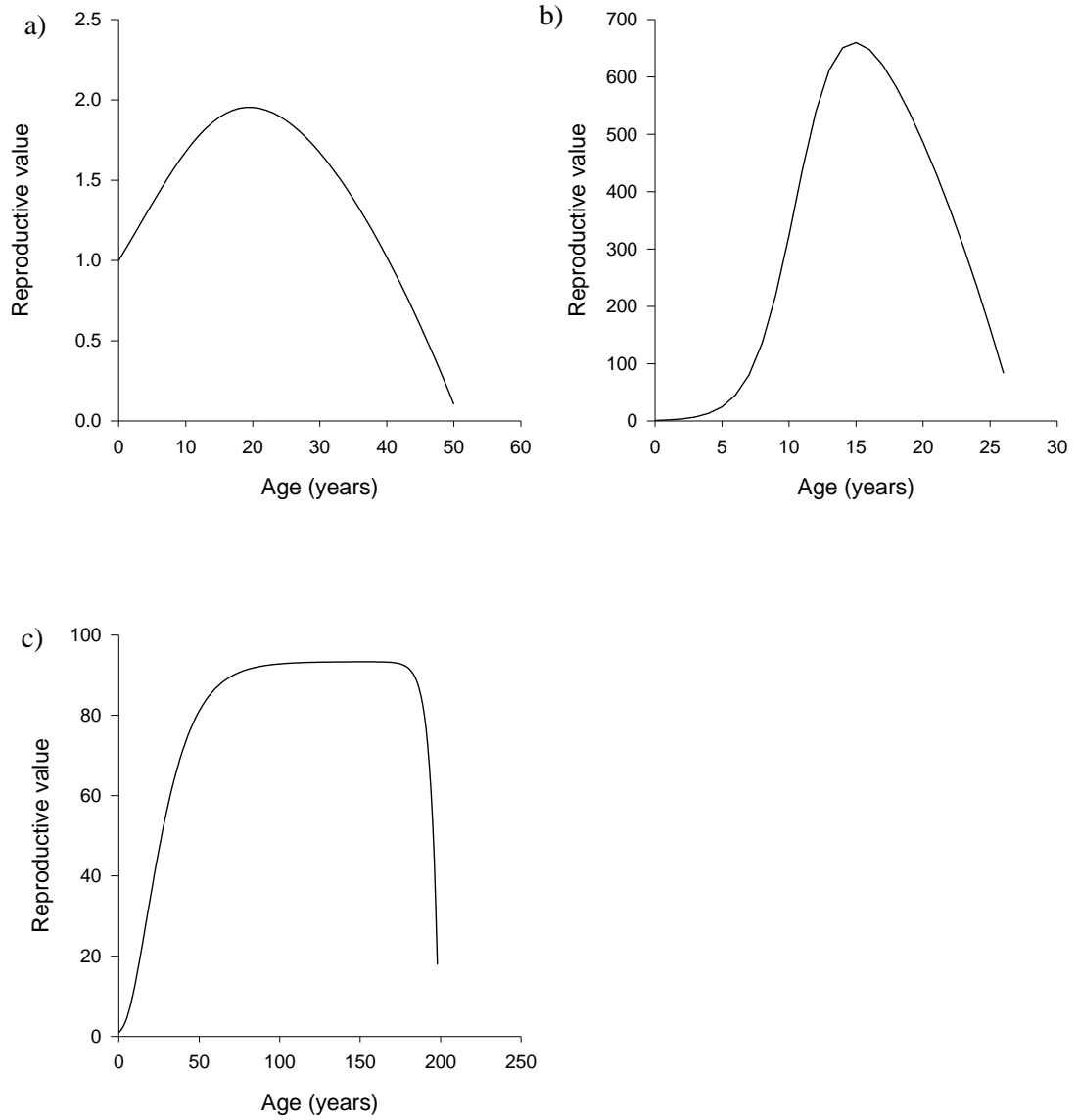
Figure 6: Relationship between age-specific mortality ( $\mu_x$ ) and age. (a) Type 1 mortality shown by *Andropogon semiberberis*, (b) Type 2 shown by *Lindera benzoin*, (c) Type 3 shown by *Aechmea nudicaulis*.

Table 4. The number of species with each type of mortality and reproductive value curves described in the text for each of the four life forms in which the 207 study species were classified.

Life form	Type 1		Type 2		Type 3	
	$\mu_x$ (n=133)	$v_x$ (n=129)	$\mu_x$ (n=38)	$v_x$ (n=30)	$\mu_x$ (n=36)	$v_x$ (n=48)
Herbs (n=113)	67	70	27	15	19	25
Shrubs (n=22)	14	15	5	6	3	6
Palms (n=19)	9	9	4	3	6	7
Trees (n=53)	43	35	2	6	8	10

#### 4.3.2: Age Specific Reproductive Value

As with mortality rate, reproductive value against age revealed three distinct patterns, which were again categorised into three types. Type 1 (Fig. 7a) showed a close to linear initial increase in reproductive value for the first few years of the plant's life, reached a maximum value and then decreased continuously towards the end of life. This type of curve was displayed by 62% species of herbs, 68% species of shrubs, 47% species of palms, and 66% species of trees. Type 2 (Fig. 7b) increased in an exponential fashion during the first few years of the plant life, reached a brief maximum value, followed by a sharp fall, and was shown by 13% herbs, 27% shrubs, 11% trees, and 16% palms. Type 3 (Fig.7c) increased linearly, remained constant over a substantial proportion of the plant's life, and declined sharply towards the end of life. This type of curve was displayed in, 23% of herbs, 22% of shrubs, 20% of trees and 37% of palms.



**Figure 7:** The relationship between age-specific reproductive value ( $v_x$ ) and age ( $x$ ). (a) Type 1 shown by *Abies concolor* (b) Type 2 shown by *Hudsonia montana*, (c) Type 3 shown by *Acacia bilimekii*.

#### **4.4: Discussion**

It is usually assumed that age-specific mortality is the most suitable demographic metric for evaluating evolutionary theories of senescence (Tatar et al., 1993). Accordingly, senescence involves a progressive increase in the age-specific mortality rate with age (Kirkwood and Rose, 1991). In the present study more than 80% of species (169/207) in our dataset showed an increase in mortality rate with age that reached a maximum at the end of life. This is reflected in Type 1, and Type 3 mortality ( $\mu_x$ ) trends (fig. 6a and 6c). Eighteen percent (38/207) of species in our dataset showed a decrease in mortality rate with age, followed by a levelling-off of mortality towards the end of life (Fig. 6b). A decline in mortality with age has been reported in several studies, including nematodes, insects and even humans (Vaupel et al., 2003). For instance, studies on the mortality pattern of mayflies have revealed a deceleration with age (Drapeau et al., 2000, Carey et al., 1992. Mueller and Rose (1996) have suggested that such trends occur when the force of selection becomes infinitesimally small at old age and becomes weaker than the forces of mutation. This may be due to alleles that are selected because of early beneficial effects that have pleiotropic deleterious effects at old age. The decline in the beneficial effect is expected to result in an exponential increase in mortality rate. But this does not proceed indefinitely because the force of natural selection becomes effectively zero relative to the effect of mutation and remain so thereafter. This results in a mortality plateau. In addition, it has also been suggested that as a population size reduces with age, population density decreases. If population density in turn influences mortality, the observed levelling off and deceleration of mortality with age might be an artefact of such changes in density (Graves and Mueller, 1993). However, this explanation has been dispelled following experiment with medflies in which density was varied (Carey et al., 1995). For their part, Vaupel et al.(2003) have argued the case of negative senescence, where the force of mortality decreases with age or remains

negligible for a substantial period and is not accompanied by a decrease in reproductive value with age. However, in all the species displaying this mortality trend in our dataset (27/207), we did not observe any increase in reproductive value late in life. All species showed a decline in reproductive value at old age (Fig.7). If one considers fitness to be the lifetime joint result of survival ( $l_x$ ) and fecundity ( $m_x$ ) then there should be no reason why a plant should continue to live when its fitness is zero (i.e. when the reproductive value is zero). This point of view was held by Watkinson (1992) and Charlesworth (1994) who argued that there is no reason for life to be prolonged past the reproductive period. Although evolutionary theory predicts post-reproductive life span in humans and other animals (Reznick et al., 2005), this occurs only when they can provide parental care. Some plants such as *Plantago lanceolata* have been shown to partially thermoregulate reproduction and the embryonic development of their seeds. This thermoregulation, produces an adaptive parental effect and has been likened to a mechanism by which this species provides parental care (Lacey and Herr, 2005). Thus, this type of parental care may be more widespread in plants. However, there is no evidence of post reproductive life span in plants and the evolution of prolonged parental care. Therefore, our result of a decreasing mortality rate or a levelling off with age is not a necessary indication of negative or negligible senescence. It is likely that this is an artefact of the imprecision in the estimation of mortality rate in the last category of stage-classified matrix population models, which in turn is influenced by the inevitably small sample size at old ages.

Hamilton (1966) argued that Fisher's (1930) reproductive value was not an effective index to measure senescence and that mortality trends provided a better index. Studies in mammals and birds have, however, provided substantial evidence for a decline in reproductive value with age (Newton and Rothery, 1997). And indeed, in this study, we found that 100% (207/207) of the species in our data set showed a decline in

reproductive value with age at the end of life falling in line with other empirical studies cited above. Of particular interest was the pattern of reproductive value classified as Type 3 here (Fig.7c), which remains relatively constant over a number of years before declining sharply towards the end of life. This pattern suggests that it would be possible for a species to delay the onset of senescence for relatively long periods of time if the influence of fecundity on reproductive value balances that of mortality. This has been demonstrated to be likely only in cases where fecundity increases continuously with age (Gardner and Mangel 1997), which obviously has physical limits. Although this pattern was shown by a minority of species (25 herbs, 6 shrubs, 7 palms and 10 trees constituting 23% of species in our dataset) its presence is suggestive of a capacity for the prolongation of adult life.

All the three types of mortality patterns observed in this study were similar to those observed in Silvertown et al (2001). However, the reproductive value patterns were not similar. In Silvertown et al (2001), only 6 out of 65 (9%) species of plants in their data set showed a reproductive value pattern that decrease with age. 50 out of 65 species, constituting 77% of species in their data set showed a reproductive value pattern that increased with age. However, in the current study all species (100%) showed a reproductive value trend that decreased with age at the end of life. The difference in this observation is due to the fact that, as mentioned in Chapter 2, Silvertown et al used age-based reproductive value schedules calculated directly from matrix projection assuming a constant mortality rate in the last stage category, while in this study the reproductive value ( $v_x$ ) was calculated employing the discrete version of Fisher's formula, assuming  $l_x$  was effectively zero at the longevity estimated by life expectancy at birth ( $L$ ). We believe the evidence for absence of immortality in all species argues in favour of the latter assumption. The contrast between these two studies, however, calls for detailed longitudinal studies of a large number of individuals under both natural and

experimental conditions. Most field studies will monitor the fate of hundreds, and rarely thousands of individuals, but the studies of, for example, medflies (Carey et al 1992) indicate the need for much larger sample sizes. This would represent a huge increase in sampling effort (and the consequent costs) in field studies.

The mortality and reproductive value pattern for the species analysed in this study showed a great deal of variation. All the different life forms were represented in all the three patterns of mortality and reproductive value described above. This showed that mortality and reproductive patterns are not confined to particular life forms. Although several theories have been put forward to explain the mechanism of ageing, theories to explain the evolutionary causes of the variety of mortality and reproductive patterns as observed here, are limited. Differences in life history trade-offs among species and the resulting differences in optimal resource allocation among vital processes, as pointed out in the disposable soma theory may partly provide an explanation for this variation in mortality and reproductive patterns (Baudisch, 2008). In the next chapter we explore how survival and fecundity combine via reproductive value to produce the variety of lifespans observed.

#### **4.5: Conclusion**

The results presented here support the existence of senescence in the majority of the perennial plants studied, and that these findings fall in line with theoretical expectations. Some species, however, leave the possibility of delayed senescence open, although these results could be due to data quality deteriorating as sample size on which the estimations in the last(s) stage(s) of the life cycle are based decreases. Longitudinal monitoring of individual species under a variety of conditions is required to provide a more definitive explanation of the mortality and reproductive value trends observed. Because the reproductive value of these species also decreases with age, it is difficult to



determine whether or not the declining portion of the  $v_x$  curve is likely to be compatible with negligible or even negative senescence, as suggested by Vaupel et al. (2003).

***Chapter 5: The Time Distribution of Reproductive Value Measures the Pace of Life***

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- The results of this chapter were presented by Miguel Franco at the BIOVEL, Population Modelling Workshop, Amsterdam, March 2013 and in the School of Biological and Biomedical Science seminar series by Cyril Mbeau ache, May 2013, Plymouth University, UK

## ***5.0 Abstract***

It is agreed that, for senescence to occur, the intensity of natural selection must decline with age. Measures of the change in the intensity of natural selection with age include reproductive value and sensitivity of fitness to changes in survival and fecundity. In order to investigate the performance of these indices in predicting the pace and duration of life, which must be inversely related for senescence to occur, the temporal distribution of these measures were quantified employing a generalised logistic distribution tailored for this purpose. This distribution has three parameters two of which measure pace (units:  $\text{time}^{-1}$ ) and one which measures duration (units: time). We hypothesised that, given their influence on the shape of the distribution, the time-distribution parameters would also be correlated with specific life history attributes. These hypotheses were tested by employing demographic projections for a sample of 207 perennial plant species of varied life form and ecology.

The results confirmed the expected relationships for the time distribution parameters of reproductive value, but not in general for other indices. In particular, a tight inverse relationship between one of the parameters of pace and the duration parameter of the time distribution of reproductive value ordered species along a fast-slow continuum where these two attributes compensate each other. That is, reproductive value was spread over a temporal scale that was in inverse proportion to its accrument.

## 5.1: Introduction

The definition of senescence as the deterioration of state with age (reviewed by Finch 1990 and Rose, 1991) and the realisation that for senescence to occur the intensity of natural selection must decrease with age (Medawar, 1952) led to the proposition of specific measures of this decline (Hamilton, 1966). These theoretical measures consist of separate estimators of the sensitivity of fitness (measured as population growth rate) to changes in survival and fecundity as the organism ages. Because deterioration of state is likely to be reflected in an increase in the probability of death, a decrease in the ability to reproduce, or both, it has also been suggested that the joint pattern of age specific survival and reproduction expressed by reproductive value must provide an appropriate measure of the changing value of selection with age (Medawar, 1952, Partridge and Barton, 1996). It was Fisher himself, who when developing the concept of reproductive value, suggested that “the direct action of natural selection must be proportional to this contribution” (Fisher 1930, p. 27). Despite the clarity of this statement, the fact that Fisher could *easily see* (our emphasis) the mathematical form that such a measure ought to take may account for his lack of emphasis on the relevance of reproductive value in the context of senescence. Fisher had derived a formula that only later would be found to be equivalent to the left eigenvector of a population model expressed in matrix form (Leslie, 1948) and thought this formula was too obvious to be worried about it. Fisher died six years before the publication of Hamilton’s paper and we can only speculate about what opinion he would have had about Hamilton’s work. What must be acknowledged, however, is the fact that Fisher suggested reproductive value specifically as a measure proportional to the changing value of natural selection with age.

Twenty-two years after the publication of Fisher’s book, Medawar (1952) established the demographic dimension of the problem of senescence. Although Medawar was clear

about the relevance of the changing reproductive value of the individual with age, his emphasis on the demographic signature of the decline of physiological state with age in the shape of the mortality curve may account for the weight placed by subsequent authors on it (see Finch 1990 and Ricklefs 1998). For reasons that should become clearer later, we believe reproductive value may better capture the selection conditions determining the duration of life.

Baudisch (2005) generalised Hamilton's indices of selection and found that alternative measures of the sensitivity of fitness to changes in either survival or fecundity with age predicted increased selection before it eventually declined. Our proposition here is that because these measures are still separate estimators of the intensity of natural selection with age, reproductive value may be a better measure of it.

The aim of this study was to evaluate the performance of the available measures of senescence as proposed by Fisher, Hamilton and Baudisch by using a generalised time distribution whose parameters are related to familiar life history traits. The criteria to evaluate the performance of each of the indices suggested by Fisher and Hamilton and Baudisch would be their ability to conform to this distribution. Applied to the different measures of selection, the parameters of this distribution represent (see Materials and Methods section): (a) the rate at which the intensity of selection initially increases, (b) a measure of how this initial rate decreases with age; this rate also measures the concentration of the temporal spread of selection, and (c) an overall measure of duration or temporal delay in the distribution of selection. These three parameters were estimated on a sample of 207 perennial plant species for which detailed demographic information allowed estimation of the different selection indices.

The general hypothesis in this investigation is that, the reproductive value would produce the more consistent estimation of the parameters and thus the best measure of senescence. The specific hypotheses tested in this investigation are:

- The initial rate of increase of an efficient estimator of selection would correlate directly with age at sexual maturity
- Its temporal concentration would correlate inversely with demographic entropy (a measure of the spread of reproduction)
- Its temporal delay would correlate directly with life expectancy
- Furthermore, because the parameters of the time distribution constitute measures of either pace (the first two parameters have units  $\text{time}^{-1}$ ) or duration (the third parameter has units time), we hypothesised a positive relationship across species between the first two parameters and negative relationships between each of these first two parameters and the third. These negative correlations would be the clearest measures of a fast-slow continuum of selection, and thus of life history variation across species (e.g., Franco & Silvertown 1996). The trade-off implied by these negative relationships would then bear on the issue of senescence

## ***5.2: Material and Methods***

### ***5.2.1: A Biological Meaningful Time Distribution***

If the time course of reproductive value or of any of the measures of selection proposed by Hamilton (1966) and Baudisch (2005) were to occur at a constant rate, it would follow an exponential distribution:

$$y = 1 - (1 - g)^x \quad (1)$$

where  $g$  is the rate of change of the measure of selection  $y$ , the latter expressed as a fraction of its total cumulative distribution, and  $x$  is age. More generally, however, this rate is likely to change as the organism ages. The simplest situation where the rate of change  $g$  varies monotonically with time (with probability  $b$ ) is described by the logit, the logarithm of the odds in a binomial process. The inverse logit converts the logarithm

of the odds into a probability (e.g., Liao 1994). In addition to this, biological processes are generally subject to time delays (e.g., sexual maturity takes time to be reached). This is taken into account by the lagged form of the inverse logit function,  $\frac{1}{1+e^{-b(x-t)}}$ , where  $t$  is the time lag.

Thus, the rate of change of  $g$  becomes  $\frac{g}{1+e^{-b(x-t)}}$  and its substitution into (1) yields

$$y = 1 - \left( 1 - \frac{g}{1+e^{-b(x-t)}} \right)^x \quad (2)$$

This cumulative distribution function (*cdf*) allows quantification of three different aspects of the cumulative temporal distribution of the measure of selection under investigation. Parameter  $g$  determines the rate at which the *cdf* rises, producing “diverging” trajectories when  $b$  and  $t$  are held constant (Fig. 8a). Parameter  $b$ , on the other hand, shortens the timespan over which the majority of the process occurs: increasing values of  $b$  reducing the temporal spread of the process (Fig. 8b). Finally, parameter  $t$  delays the process producing “parallel” *cdfs* (Fig. 8c). In the case of reproductive value ( $v_x$ ), a steep rise of its *cdf* would indicate sexual precocity and, thus,  $g$  would be expected to be negatively correlated with age at sexual maturity ( $\alpha$ ). On the other hand, by being a measure of concentration of the time distribution of  $v_x$ ,  $b$  should be inversely related to the unstandardized form of demographic entropy ( $S$ ), a measure of the temporal spread of reproduction (Demetrius 1974; Demetrius later differentiated between what he then termed standardised entropy,  $H$  (eqn. 4.87 in Caswell 2001), and the numerator of this measure, which he called unstandardized entropy,  $S$ ; eqn. 4.96 in Caswell 2001). Finally, because  $t$  is an overall measure of the duration or delay of the distribution, we expect it to be positively correlated with life expectancy ( $L$ ).

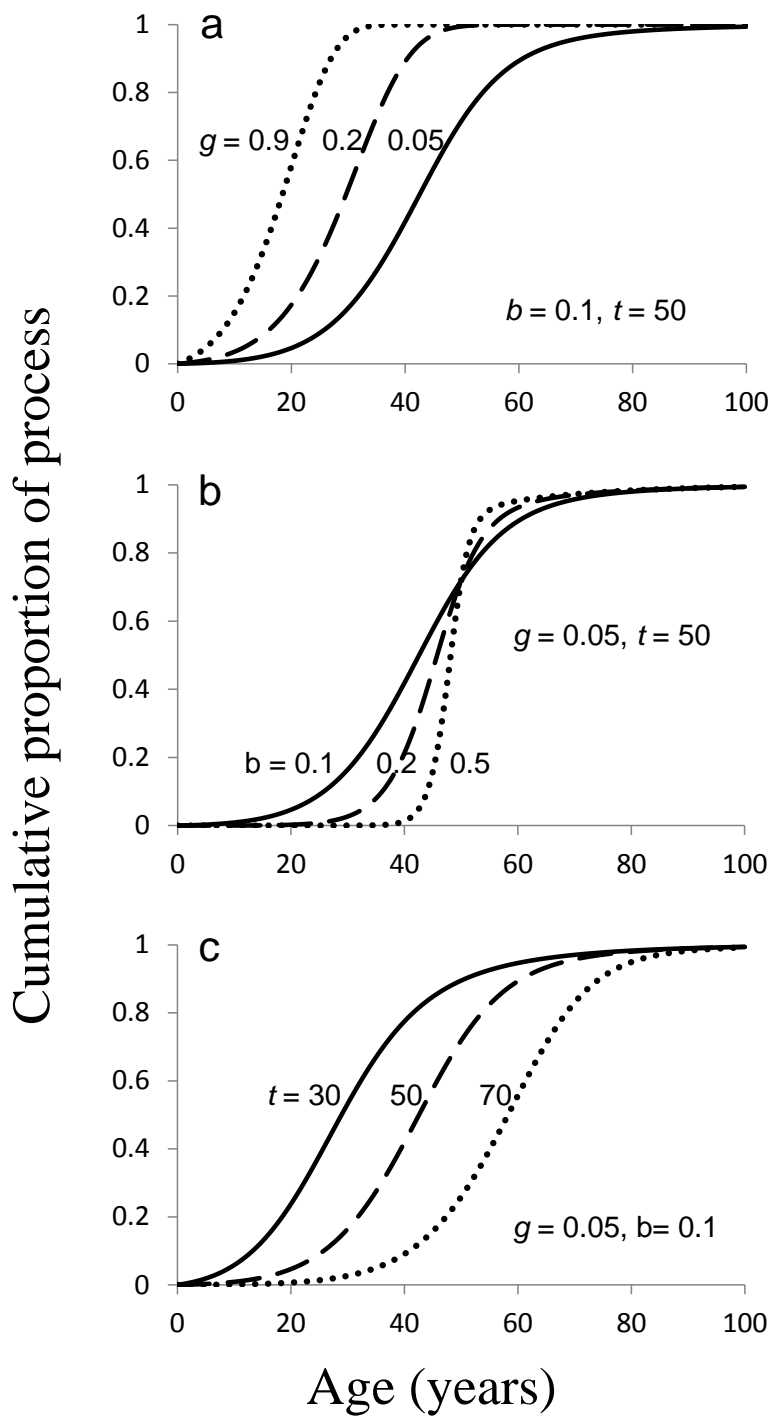


Figure 8: The effect of parameter values of a generalised logistic proposed to quantify the time distribution of measures of selection on the shape of the distribution. In each of the three graphs one parameter is changed (from a to c:  $g$ ,  $b$  and  $t$ ), in the order continuous, dashed and dotted curves, while the other two are fixed at the values shown.



### ***5.2.2: Plant Demography Data and Population Projection***

The variables and phylogeny used in this study were obtained as described in Chapter 2 of the thesis. The life table parameters obtained as described in Chapter 2 were used to calculate the several measures of change in the force of selection as outlined in Table 1 of Baudisch (2005). These are all measures of the sensitivity of  $r$  to changes in either linear or logarithmic measures of survival/mortality and fecundity. All correlation of life history traits were carried out employing PGLS as described in Chapter 2.

### ***5.2.3: Data Analyses***

In order to quantify the parameters of the time distribution of the different measures of selection, their cumulative distribution were obtained by successively adding up their respective terms from  $x=0$  to  $x=L$ . Each cumulative distribution was then standardised by dividing the series by their total sum (the last term of the cumulative distribution). The distribution function was fitted to the cumulative distributions of the individual selection measures for each individual species with the generalized non-linear regression option of SPSS version 19, using the Levenberg-Marquart algorithm and least square loss function. Starting values of 0.1, 0.2 and 0.4 for  $t_0$ ,  $b$  and  $g$  were used respectively. These starting values allowed rapid convergence of the parameters of the model fit employing the algorithm. For *cdfs* that proved difficult to fit, alternative fitting methods were employed, but for some indices of selection these did not produce better results: the algorithm would either fail to converge or produce evidently absurd parameter values (e.g., values of  $g \gg 1$  or negative  $b$  values that produced declining or even oscillating *cdfs*, usually with large standard errors).

The expected relationships between the distribution and life history parameters mentioned above were investigated by phylogenetic generalised least squares (PGLS) models employing the *caper* package in R (Orme et al., 2012) as described in chapter

two. In order to conduct these analyses, a phylogeny of the species in our dataset was first constructed as explained in chapter two.

### **5.3: Results**

#### **5.3.1: Model Fit**

The model produced highly significant fits to the time distribution of the cumulative reproductive value for all 207 species of perennial plants used in this study with  $R^2$  values ranging from 0.981 to  $>0.999$  (see figure 9). However, with the exception of the sensitivity of population growth rate ( $r$ ) to the logarithm of fecundity ( $dr/d\ln m_x$ ; last equation in Table 1 of Baudisch 2005), it performed poorly for all the other measures of the force of selection acting separately on survival and fecundity, often failing to converge (as explained in the Methods section). For this reason, parameter estimation could only be achieved for a handful of species in most measures of the sensitivity of  $r$  to survival/mortality and fecundity. This is understandable because many of these functions tend to decline monotonically, yielding *cdfs* that are convex, rather than sigmoidal, in shape. For  $dr/d\ln m_x$ , the fits were also highly significant but slightly lower and more variable than those for  $v_x$  (mean  $R^2 \pm SD$  for the time distribution fits of  $v_x$  and  $dr/d\ln m_x$ :  $0.997 \pm 0.006$  and  $0.996 \pm 0.011$ , respectively). Interestingly there was no correspondence (correlation) between the values of each of the three parameters for the distributions of  $v_x$  and  $dr/d\ln m_x$  ( $R^2=0.0051$ ,  $P>0.20$ ;  $R^2=0.0135$ ;  $P>0.08$ ;  $R^2=0.0076$ ,  $P>0.15$ ; one = tailed tests for the correlations between  $g$ ,  $b$  and  $t$  of  $v_x$  vs.  $dr/d\ln m_x$ , respectively).

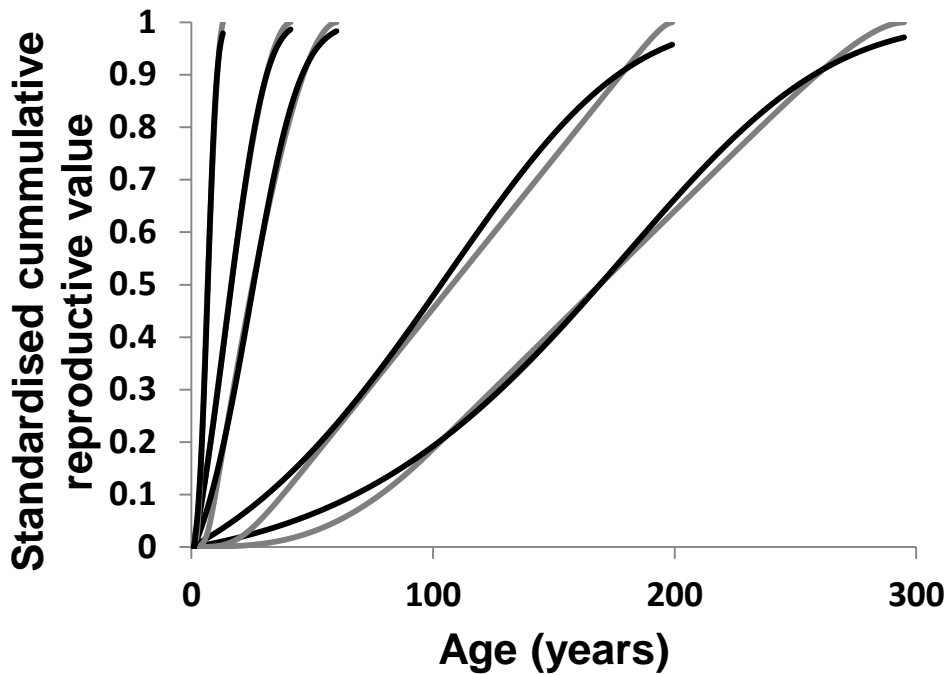


Figure 9: Illustration of the fit of the time distribution to the  $v_x$  data of five species, one from each of the life forms defined in the text. From left to right, and in the approximate order of life expectancy that one might expect the life forms to occur: *Aquilegia* sp. (O), *Guarianthe aurantica* (F), *Lindera benzoin* (S), *Euterpe edulis* (P) and *Garcinia lucida* (T). Grey line:  $v_x$  projected from the matrix model; black line: model fit.

### 5.3.2: Expected Relationships Between Life History Attributes and the Parameters of the Time Distributions of $v_x$ and $dr/d\ln m_x$ .

Before describing these relationships, it is important to note that, although with plenty of overlap, there were significant differences in age at sexual maturity ( $\alpha$ ), entropy ( $S$ ) and life expectancy ( $L$ ) among the five life forms (Table 3). The degree of difference among these life forms in the parameters of the distribution function for reproductive value, however, was lower than that for life history attributes. Parameters  $g$  and  $t$  showed significant differences between life forms, but  $b$  did not (Table 3).

As hypothesised for the time distribution of  $v_x$ ,  $g$  was inversely related to  $\alpha$ ,  $b$  was inversely related to  $S$  and  $t$  was directly related to  $L$ , but the proportion of variance accounted for by each of these three relationships was small (Fig. 10, Table 4). The equivalent relationships for  $dr/d\ln m_x$ , had lower proportion of variance accounted for (Table 3; figures not shown). Life form had no influence in any of these relationships

( $P > 0.10$  in all cases). In the case of  $t$  of  $v_x$  vs.  $L$ , regression through the origin produced a slope equal to 0.96, indicating a close one to one match despite substantial variation from species to species (the identical scale on both axes of Fig. 10c should allow the reader to mentally draw a line of equality). In these three PGLS models, phylogenetic signal (Pagel's  $\lambda$ ) was equal to zero and thus the results are essentially undistinguishable from ordinary least squares.

Notice that the relationships depicted in Fig. 10a and b are in reality “wedges” in which any value is allowed within their confines. Thus, a wide range of values of  $g$  and  $b$  are possible at low values of  $\alpha$  and  $S$ , respectively, but both  $g$  and  $b$  become restricted to smaller values as, respectively,  $\alpha$  and  $S$  increase. We will come back to interpret the wedge shape of these relationships in the discussion.

Among the three parameters of the time distribution of reproductive value (log transformed),  $t$  was negatively correlated with  $g$  (Pearson  $r = -0.308$ ) and  $b$  ( $r = -0.891$ ), and the latter two were consequently positively correlated with each other ( $r = 0.310$ ). As it would be expected from the positive correlation between  $t$  and  $L$  described above, the relationship between  $g$  and  $t$  was negative and also formed a wedge (figure not shown). The most consistent relationship was that between  $b$  and  $t$ , as this did not form a wedge, but was characterised by a tight power relationship ( $R^2 = 0.80$ ) with a PGLS slope equal to -0.96 and whose 95% confidence interval includes -1, suggesting almost perfect compensation (Fig. 11; Table 4). The equivalent relationship for  $b$  and  $t$  of  $dr/d\ln m_x$  accounted for a smaller proportion of variance ( $R^2 = 0.312$ ) and was shallower (slope = -0.51) (Table 4). Interestingly, the relationships between  $b$  and  $t$  showed evidence of phylogenetic signal for both  $v_x$  and  $dr/d\ln m_x$  (Pagel's  $\lambda = 0.365$  and 0.389, respectively).

Table 5: Descriptive statistics for the parameters of the time distribution of reproductive value ( $g$ ,  $b$  and  $t$ ) and the life history attributes expected to be correlated with them [age at sexual maturity ( $\alpha$ ), entropy, ( $S$ ) and life expectancy ( $L$ )] for a sample of 207 perennial plants classified by life form (O: herbs from open habitats, F: herbs from forest understory, S: shrubs, P: palms, T: trees). The last column summarises the results of univariate analyses of variance of the difference between life forms in each of the six parameters/attributes. Homogeneous subsets of life forms at  $P < 0.05$  (Tukey's HSD) are indicated by superscripts. Because some species did not yield some life history attributes (N = sample sizes in each group), the denominator degrees of freedom varied between 198 and 202. \*:  $P < 0.001$ ; ns:  $P = 0.67$

Parameter or Attribute	Life form						$F_{4,198-202}$
	O	F	S	P	T		
	N	80/81	34/35	20/21	18	51/52	
$\alpha$	Mean	6.4 <sup>a</sup>	7.6 <sup>a</sup>	7.9 <sup>a</sup>	34.4 <sup>b</sup>	42.3 <sup>b</sup>	21.702*
	SD	9.6	6.1	7.2	25.4	44.0	
	Mean	1.944 <sup>ab</sup>	1.830 <sup>a</sup>	2.594 <sup>bc</sup>	3.250 <sup>c</sup>	3.100 <sup>c</sup>	14.091*
$S$	SD	1.011	0.814	1.005	1.353	1.213	
	Mean	37.6 <sup>a</sup>	23.6 <sup>a</sup>	68.2 <sup>ab</sup>	119.8 <sup>b</sup>	133.0 <sup>c</sup>	13.518*
$L$	SD	74.1	14.2	105.3	104.4	116.3	
	Mean	0.512 <sup>b</sup>	0.413 <sup>ab</sup>	0.390 <sup>ab</sup>	0.242 <sup>a</sup>	0.272 <sup>a</sup>	7.567*
$g$	SD	0.285	0.271	0.297	0.216	0.278	
	Mean	0.120	0.117	0.135	0.045	0.109	0.590 <sup>ns</sup>
$b$	SD	0.159	0.139	0.147	0.029	0.320	
	Mean	62.29 <sup>a</sup>	59.18 <sup>a</sup>	95.99 <sup>ab</sup>	143.53 <sup>b</sup>	133.91 <sup>b</sup>	8.786*
$t$	SD	63.69	58.63	106.27	114.44	102.57	

Table 6: Phylogenetic generalised least squares models of the relationships between the parameters of the time distribution of reproductive value and life history attributes, and those between the parameters of the time distribution of Baudisch's  $dr/d\ln m_x$  and the same life history attributes in a sample of 207 species of perennial plants.  $\alpha$ : age at sexual maturity,  $S$ : demographic entropy,  $L$ : life expectancy. Life form was not significant in any of these relationships and is therefore not included in the models

Dependent variable	Effect	Slope (SE)	$F_{2,201-205}$	P	$R^2$
$g$ of $v_x$	$\alpha$	-0.0035 (0.0007)	27.88	<0.001	0.117
$b$ of $v_x$	$S$	-0.0608 (0.0110)	30.39	<0.001	0.125
$t$ of $v_x$	$L$	0.568 (0.0513)	122.5	<0.001	0.372
$g$ of $dr/d\ln m_x$	$\alpha$	-0.0014 (0.0007)	4.42	0.01	0.017
$b$ of $dr/d\ln m_x$	$S$	-0.440 (0.1729)	6.47	0.002	0.026
$t$ of $dr/d\ln m_x$	$L$	0.585 (0.0674)	75.38	<0.001	0.266

Table 7: Phylogenetic generalised least squares models of the relationships between parameters  $t$  and  $b$  (log transformed) of the distributions of reproductive value and the distribution of Baudisch's  $dr/d\ln m_x$  for 207 species of perennial plants.

Dependent variable	Effect	Intercept (SE)	Slope (SE)	$F_{2,205}$	P	$R^2$
$t$ of $v_x$	$\log(b)$	0.583 (0.082)	-0.955 (0.034)	802.5	<0.001	0.796
$t$ of $dr/d\ln m_x$	$\log(b)$	1.002 (0.212)	-0.510 (0.053)	94.3	<0.001	0.315

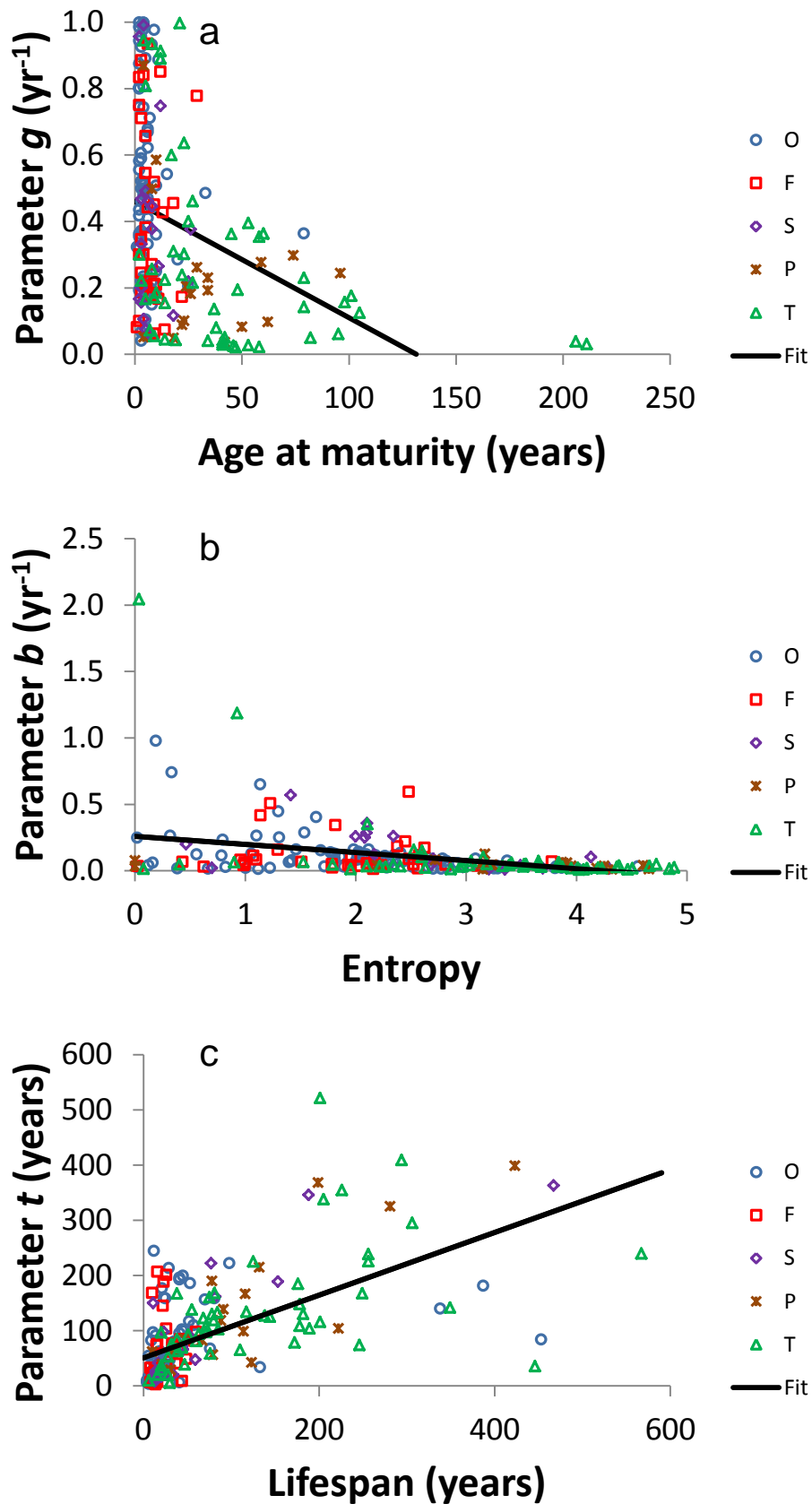


Figure 10: The relationships between model parameters and life history attributes: (a)  $g$  vs.  $\alpha$ , (b)  $b$  vs.  $S$ , and (c)  $t$  vs.  $L$  in a sample of 207 species of perennial plants classified by life form: O: herbs from open habitats, F: herbs from forest understory, S: shrubs, P: palms, T: trees.

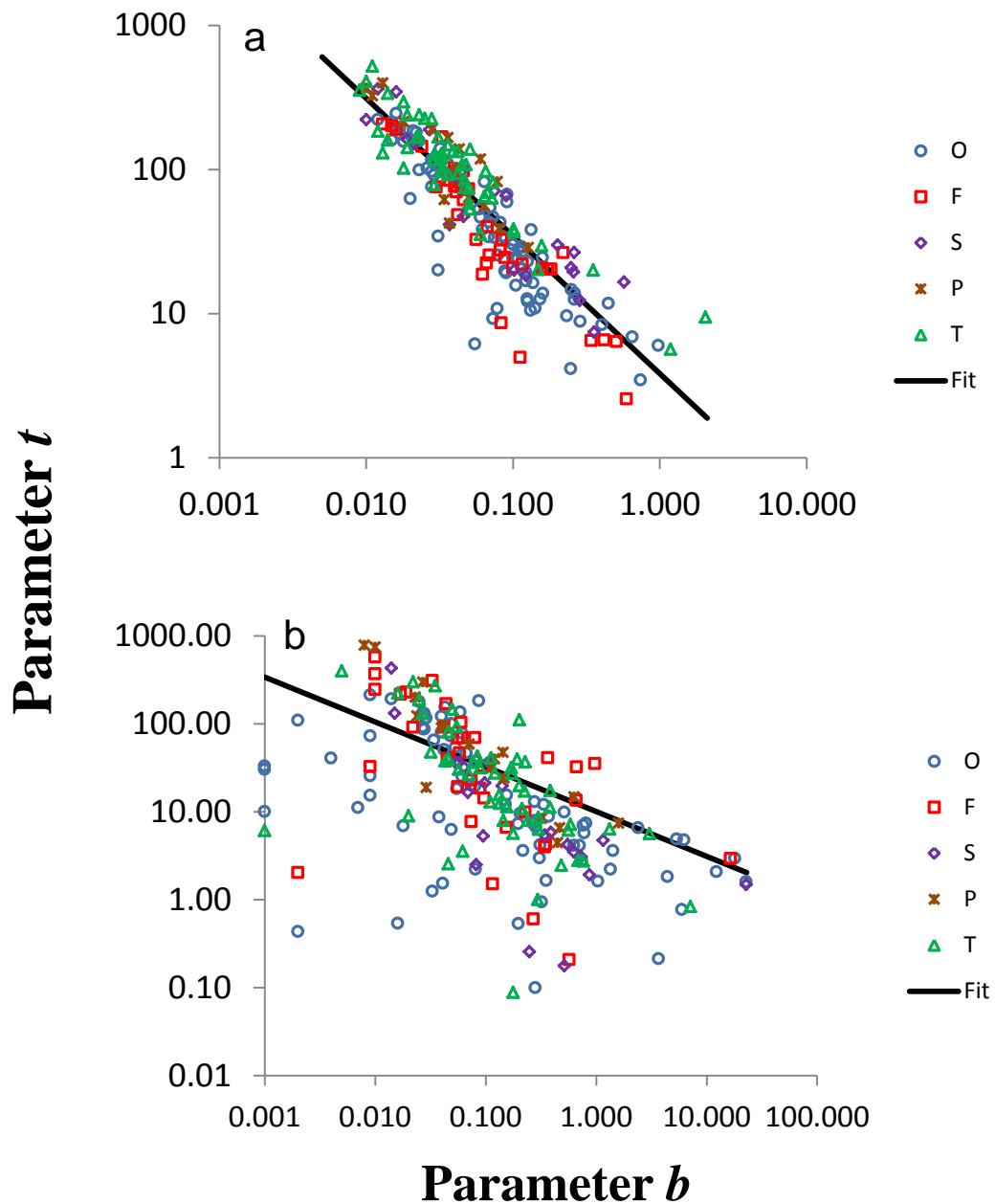


Figure 11: Power relationship between parameters  $b$  and  $t$  of the distribution of (a) reproductive value and of (b) the distribution of  $dr/d\ln m_x$  in a sample of 207 species of perennial plants. Symbols as in Fig. 10.

#### 5.4: Discussion

Although many studies have investigated the possible relevance of reproductive value to the process of senescence (e.g., Vahl 1981, Thompson 1984, Moller and De Lope 1999, Newton and Rothery 1997, Brown and Roth 2009, Bouwhuis et al. 2012), this study is the first to quantify three different aspects of its temporal distribution across a number of species of varied ecology. This distribution allowed us to quantify two measures of



pace ( $g$ , related to how rapidly sexual maturity is reached, and  $b$ , related to the temporal concentration of reproduction throughout the life cycle) and one measure of duration ( $t$ , correlated with life expectancy) similar in spirit to the characterisation of pace and shape suggested by Baudisch (2011). All three parameters measured on  $v_x$  correlated with the hypothesised life history attributes better than the parameters estimated on the only measure of selection that fitted the time distribution model,  $dr/d\ln m_x$ . Life history theory predicts that the rate with which individual species mature must be negatively correlated with lifespan (Williams, 1966, Tinkle et al., 1970, Stearns and Crandall, 1981, Charnov, 1990) and, among other studies, earlier age at first reproduction has been associated with an earlier onset of reproductive senescence in red deer (*Cervus elaphus*) (Nussey et al., 2006), male blue-footed boobies (*Sula nebouxii*) (Kim et al 2011) and twenty other mammal and bird species (Jones *et al.* 2008). Similarly, an increase in reproductive effort early in life has been associated with accelerated senescence in fertility of collared flycatchers (*Ficedula albicollis*) (Gustafsson and Part, 1990). The literature in this respect is large and consistent with the idea of trade-offs between survival and reproduction, and our comparative results agree with these observations.

While parameters  $b$  and  $t$  may be more clearly related to the ageing process, parameter  $g$  is also relevant to this issue because it determines the speed with which the peak of the reproductive value is reached and thus, if a trade-off between reproduction and survival exists, the ensuing decline in the intensity of natural selection. The negative influence of the spread of reproductive value ( $b$ , conceptually related to demographic entropy) on its duration ( $t$ , conceptually linked to  $L$ ), however, does not seem to have received attention previously. On a broad scale, the relationships between the parameters quantifying the distribution of reproductive value and life history attributes related to the ageing process go in the directions hypothesised and reinforce our confidence in reproductive value as a measure of the changing value of selection. We were initially enthusiastic about the

idea of using the parameters of the time distribution of reproductive value to quantify the aspects of pace and shape of senescence suggested by Baudisch (2011). However, the units in which each of these parameters is measured made us reconsider these terms because they specifically quantify two aspect of pace ( $g$  and  $b$  units are  $\text{time}^{-1}$ ) and one of duration ( $t$  units are time). If anything, the literature on sigmoid functions would refer to parameter  $b$  as a measure of shape, not  $t$  or its life history proxy,  $L$  (see Baudisch *et al.* 2013). Significantly, our method identifies the pace and duration of life by reference to a single measure of expected future contribution to fitness, the reproductive value.

Specifically, despite confirmation of the direction of the relationships hypothesised, it was interesting to observe that only  $b$  and  $t$  showed a tight (presumably “functional”) relationship, and that this relationship was characterised by almost perfect compensation. This suggests that the attributes of pace and duration of life are antagonistic, and that the former constrains the latter. This relationship also suggests a compensatory symmetry resulting in a life history invariant, i.e., a power relationship with slope close to unity (Charnov, 1993). This was not the case for all the other parameters whose relationships suggested limiting maximum combinations of their values, not theoretically bijective functional relationships. The fact that life history traits only approximate expected general bivariate trends implies that they are not selected independently of each other. By incorporating all relevant demographic traits (mortality and reproductive schedules, but also age at sexual maturity, degree of iteroparity, and life expectancy), the time distribution of reproductive value more accurately quantifies the variation in an individual’s expected future contribution to fitness. If the relationship between  $b$  and  $t$  describes a general rule, the answer to the question of whether all plants senesce would have to be affirmative: different species senesce at different rates and this determines their maximum life expectancy. Although with varying degrees of overlap in the attributes investigated across the five life forms here defined (Table 3),

there is a continuum of species along the pace-duration relationship (Fig. 11). Incorporating life form into the model produces a slightly better fit ( $R^2 = 0.83$ ), with larger intercept for woody plants than herbaceous ones for  $v_x$ . A similar, but weaker signal was obtained for  $dr/d\ln m_x$ .

Given the varied relationships that life history attributes have (Charlesworth, 1980, Roff, 1992, McNamara and Houston, 1996), it is perhaps remarkable that the pace and duration of life can be summarised by reference to the time distribution of a single parameter combining the age-specific schedules of survival and reproduction (Williams 1957, Partridge and Barton 1996). The opposition to the use of reproductive value as a measure of the intensity of selection seems to have arisen because of a misunderstanding of the significance of early mortality and the belief that the intensity of natural selection must necessarily decline with age (Hamilton 1966). The wasteful production of gametes and offspring, particularly in organisms with limited parental care, is a consequence of endless selection for the acquisition of more and more “lottery tickets” with little chance of success. Under these conditions, selection favours the profligate spending on more and more offspring. This situation severely limits the value of the individual in early life (and consequently, their selection must be weak), but increases it as the individual develops and its chances of reproduction increase. Thus, for life to ever evolve beyond bacterial form, the intensity of natural selection for attributes that confer higher chances of survival and reproduction must necessarily increase with age and size (see Caswell & Salguero-Gómez 2013). As Baudisch (2011) and Caswell & Salguero-Gómez (2013) have shown, this depends on the measure of selection adopted. Our results advocate a re-evaluation of the significance of reproductive value as a measure of selection.

***Chapter 6: Demographic Entropy in Iteroparous Perennial Plants.***

## ***6.0 Abstract***

A central issue in evolutionary ecology is to understand the relationship between ecological constraints, the agents of selection, and the kind of life history traits that these agents select for. Directionality theory, an analytical model of the evolutionary process based on demographic entropy as a measure of Darwinian fitness has been invoked as a solution to this problem. The theory predicts that equilibrium species, that is, populations that spend the greater part of their evolutionary history in the stationary growth phase, will be characterised by a large degree of iteroparity, strong demographic stability and long lifespan. On the other hand, opportunistic species, that is, populations which spend the greater part of their evolutionary history in the exponential growth phase, will be characterised by a large population size, weak iteroparity, weak demographic stability, and short lifespan and, when population size is small, by random variation in these demographic attributes. This study examines the validity of these predictions, using 207 species of iteroparous perennial plants studied in their natural environment. The results of this empirical study were generally inconsistent with these predictions. Nonetheless, as a measure of iteroparity, entropy offers insight into a poorly unexplored aspect of life history evolution.

## **6.1: Introduction**

The principal aim of the study of life history evolution is to explain the remarkable diversity of life histories that are observed in the plant and animal kingdoms. It is generally agreed among evolutionary biologists that the diversity of life histories that we observe in nature is the result of evolution by natural selection (Flatt and Heyland, 2011). Natural selection acts on the variation in the ability to survive and reproduce – the two major demographic components of fitness (Falconer, 1960, Stearns, 2000) – among individuals in a particular environment favouring the survival and reproductive schedules that result in highest fitness. The probability of survival and reproduction varies greatly among individuals in a population (Albon et al., 1992, Schaffer, 2010) and natural selection acts on this variation to produce, or more accurately track, the optimal life history in a given (physical and biotic) environment.

Darwin's concept of evolution by natural selection is a notion of differences in the ability of organisms to propagate, and over the years the researchers responsible for the development of what became known as Neo-Darwinism or the Modern Synthesis developed quantitative measures of Darwinian fitness that would predict the evolutionary advantage of some organisms (with particular traits or genes) over others. Specifically, Fisher (1930) proposed the Malthusian parameter ( $r$ ) as a quantitative measure of Darwinian fitness. The Malthusian parameter, a function of the age specific schedules of fecundity and survival, describes the increase in population numbers (Brommer, 2000) and it takes a small step to consider the growth of two genotypes which differ in their survival and reproductive schedules under a particular set of environmental conditions. Implicit in Fisher's model is the assumption of a constant environment, density independent population growth, stable age distribution, and an infinite population. In populations where these assumptions are taken into account, the Malthusian parameter determines the directional changes in the evolutionary process

(Charlesworth and Williamson, 1975, Pollack, 1976, Roff, 1992a, Stearns, 1992). Since Fisher's (1930) proposition, several classical life history evolutionary models have incorporated the Malthusian parameter as a measure of Darwinian fitness to predict the outcome of competition between a mutant and a resident population (Pianka, 1970, Kirkwood, 1977, Finch and Kirkwood, 2000).

However, Demetrius and Gundlach (1999, 2000) have argued that although the Malthusian parameter continues to influence most theoretical and empirical studies of invasion dynamics in evolutionary biology and ecology today, its generalisation as a fitness measure does not hold for populations with a finite size or in populations that lack a demographic structure. They claim that this argument is supported by empirical observations of invasion studies that suggest that the amplitude of population changes, but not the Malthusian parameter, is the chief determinant of selection outcome (Lawton and Brown, 1986) and by their own analytical studies of invasion in genetic models (Demetrius and Gundlach, 1999). In view of these presumed limitations, Demetrius and Gundlach (1999, 2000) have suggested that in populations that lack a demographic structure or that have a finite size, the ability of a variant or a mutant to invade and succeed a resident population is described by a stochastic process that is dependent on two properties: (i) the rate at which the population returns to its steady state after perturbation, which is a population parameter, and (ii) the variability and abundance of resources which the mutant and resident populations compete for, which is an environmental factor. Accordingly, invasion success is said to be characterised by a demographic parameter called evolutionary entropy, a measure of the uncertainty in the age of the mother of a randomly chosen newborn (Demetrius, 1974). Thus, in populations of finite size, entropy ought to predict the outcome of competition between a variant type and a resident population (Demetrius and Gundlach, 2000, Demetrius, 2001). In a population of infinite size, entropy reduces to the Malthusian parameter

(Ziehe and Demetrius, 2005). Hence, entropy can be viewed as a natural generalisation of the Malthusian parameter. In view of these assertions, Demetrius (1977, 2000a) has suggested what he terms directionality theory, an analytical model of the evolutionary process that invokes entropy as the appropriate measure of Darwinian fitness (Demetrius, 1992, Demetrius, 1997, Demetrius and Gundlach, 2000). Directionality theory is said to *predict the directional changes of entropy* as one population type replaces another under the joint processes of mutation and selection. Directionality theory has three major principles that link ecological constraints to directional changes in entropy. These principles are:

(1a) In equilibrium species or in populations which spend the greatest part of their evolutionary history in the stationary phase (bounded growth), evolution will result in a unidirectional increase in entropy

(1b) In opportunistic species with large population sizes (unbounded growth), evolution will result in a unidirectional decrease in entropy.

(1c) In opportunistic species with smaller population size, evolution will result in a random non-directional change in entropy.

Specific issues addressed with directionality theory include: the incidence of mortality plateaus in humans and other animal populations (Demetrius, 2001), the evolutionary trajectory of body size (Demetrius, 2000b) and body size, metabolic rate and maximum lifespan (Demetrius 2009).

## **6.2: Demographic entropy**

Darwin's mechanism of evolution is a gradual process involving mutation and selection that results in the myriad life history traits that we observe in nature. Mutation brings about genetic variation within the population and selection orders this variability through competition between the new variant and the resident type for the available



resources. This combination naturally leads to the replacement over time of one population type by another. Demetrius directionality theory is a mathematical model meant to represent this evolutionary process in structured populations. It appeals to the fundamental elements of demographic entropy as a quantitative measure of Darwinian fitness and is said to account for the observed variation in morphological, physiological and behavioural traits that are produced from the mutation-selection process.

Standardised entropy, the property that Demetrius proposes is a more appropriate measure of Darwinian fitness is defined as:

$$H = - \frac{\int_0^{\infty} p(x) \log p(x) dx}{\int_0^{\infty} x \cdot p(x) dx} \equiv \frac{S}{T} \quad (1)$$

Where  $p(x)$  represents the probability distribution of the age of reproducing individuals in the population and is given by  $p(x) = \exp(-rx) V(x)$ . Here,  $V(x)$  is a fecundity function obtained from the product of  $l(x)$ , describing the probability of an individual in the population surviving to age  $x$ , and  $m(x)$ , the average number of offspring produced at age  $x$ . The parameter  $r$ , the intrinsic rate of population growth or Malthusian parameter, is derived from Lotka's (1925) model of the population dynamics of age-structured populations. Lotka (1925) showed that a population in which survival and fecundity variables are a continuous function of age, would eventually reach a constant growth rate,  $r$ , which is the real root of the equation:

$$1 = \int_0^{\infty} e^{-rx} V(x) dx \quad (2)$$

The numerator  $S$  in equation 1 above is a probability density function that describes the age of the mother of a randomly chosen newborn. Because of its mathematical equivalence with Shannon's entropy/diversity index, in turn based on Gibbs entropy, Demetrius calls  $S$  unstandardised entropy.  $S$  measures the degree of variability in the

age of reproducing individuals in the population.  $S$  is positive in iteroparous populations and zero in strictly semelparous populations. Thus, large values of  $S$  characterise life histories with small brood size, broad reproductive lifespan and late age at sexual maturity, while smaller values of  $S$  characterise species with larger clutch sizes, shorter reproductive lifespans and earlier onset of reproduction. These patterns of life history are distributed along what is known as a fast-slow continuum (Promislow and Harvey, 1990, Franco & Silvertown, 1996). Unstandardised entropy ( $S$ ) is therefore a measure of the position of a population along this continuum. It would be expected, for example, that herbs in disturbed environments (low entropy species, low  $S$  value) occupy the fast end of the continuum while trees and palms (high entropy species, high  $S$  value) occupy the slow end (Ziehe and Demetrius, 2005). The denominator  $T$  in equation 1 is a measure of generation time, the average age of the parents of a cohort when at stable age distribution. Thus,  $H$  is standardised entropy, i.e.,  $S$  standardised by generation time,  $T$ .

$S$  is also directly related to the demographic stability of a population, that is, the rate at which a randomly perturbed population will return to its steady state conditions (Demetrius, 1978, Tuljapurkar, 1982, Tuljapurkar, 1993, Kim and Schoen, 1993, Demetrius, 2003, Demetrius et al., 2004). Populations with high entropy will be more resilient to fluctuations in the demographic variables than populations with low entropy. The use of entropy as a measure of the demographic stability of a population makes it relevant in conservation studies where it can be used to evaluate the vulnerability of a population to extinction due to demographic or environmental stochasticity (Caswell 2001 and references therein).

Directionality theory involves the study of directional changes in entropy in populations subject to different classes of ecological constraint. The model is said to distinguish between different types of constraints that can be classified in terms of the availability

of resources, that is, resources that are constant, but limited, and resources which are abundant but sporadic. Populations that are subject to constant, but limited resource condition (equilibrium species), will have a growth rate that is constant or stationary ( $r = 0$ ). Populations which are subject to abundant but variable resource condition (opportunistic species) will be characterised by exponential increase in growth rate followed by decline towards extinction, i.e., their dynamics are explosive but sporadic. The reproductive potential ( $\Phi$ ), an additional demographic parameter, can be used to describe these extremes of ecological conditions.  $\Phi$  is given by:

$$\Phi = \frac{\int_0^{\infty} p(x) \log V(x)}{\int_0^{\infty} xp(x)dx} \equiv \frac{E}{T} \quad (3)$$

Where  $E$  describes the logarithm of net-offspring production,  $\log V(x)$ , averaged over the different age classes. The quantity  $\Phi$  is related to the Malthusian parameter ( $r$ ) and standardised entropy ( $H$ ) by the following equality:

$$\Phi = r - H \quad (4)$$

Thus, from equation 4, it follows that, when  $\Phi < 0 \Rightarrow 0 \leq r < H$  and when  $\Phi > 0 \Rightarrow r > H$

Equilibrium species, that is populations that are subject to constant but limited resources, are described by the condition  $\Phi < 0$  (bounded growth) and opportunistic species, that is populations subject to abundant but sporadic resources, by the relation  $\Phi > 0$  (unbounded growth, Demetrius and Ziehe, 2007).

Following the above, directionality theory can be expressed in terms of the reproductive potential ( $\Phi$ ) as follows:

(IIa). In bounded growth ( $\Phi < 0$ ), evolution results in a unidirectional increase in entropy.

(IIb). Under unbounded growth conditions ( $\Phi > 0$ ) and large population size, evolution results in a unidirectional decrease in entropy.

(IIc). Under unbounded growth conditions ( $\Phi > 0$ ) and small population size, evolution results in random non-directional change in entropy.

These principles predict a series of evolutionary correlations between ecological norms and parameter  $H$ .

Demetrius asserts that analytical studies of the properties of  $H$  and  $S$  have shown that evolutionary changes in the two parameters are positively correlated (Demetrius, 2000).

Thus, if  $H$  and  $S$  are positively correlated to each other, Demetrius proposes that:

$$\Delta H \cdot \Delta S > 0 \tag{5}$$

Thus, from equation (3) above,  $E = \Phi T$  and one could use (IIa)-(IIc) together with equation 5 to infer the following relationships between  $E$  and changes in  $S$ :

(IIIa).  $E < 0$ : a unidirectional increase in  $S$ .

(IIIb).  $E > 0$ , large population size: a unidirectional decrease in  $S$ .

(IIIc).  $E > 0$ , small population size: random, non-directional change in  $S$ .

Thus, in terms of the correlation expected for a diverse phylogenetic tree, principles (IIIa)-(IIIc) can also be expressed as follows:

(IVa).  $E < 0$ : the smaller the value of  $E$ , the larger the value of  $S$ , i.e., large values of  $S$  will be correlated with small, negative values of  $E$ .

(IVb).  $E > 0$ :

(i) for populations with large size, the larger the value of  $E$ , the smaller the value of  $S$ , i.e., small values of  $S$  will be correlated with large, positive values of  $E$ .

(ii) for populations with small size, the values of  $E$  and  $S$  will be uncorrelated.

It is important to notice that here Demetrius argument has changed from one of stable vs unstable dynamics to one of large vs small population size. However, size is only meaningful in terms of the amount of the limiting resource: small population size

leading to strong competition (i.e., density-dependent regulation and stable population dynamics) if the limiting resource is scarce.

Demetrius also states that the entropy-stability principle can also be evaluated by using a generally held ecological principle that the fluctuation intensity in population size is inversely related to generation time (Emlen, 1984, Bonner, 1988). This fluctuation intensity-generation time theory can then be combined with the entropy-stability principle following equation (4) above to predict that entropy and generation time will be positively correlated. Thus:

$$\Delta S \cdot \Delta T > 0 \tag{6}$$

Demetrius maintains that directionality theory, a model that invokes demographic entropy as the fundamental measure of Darwinian fitness, is a misunderstood concept in ecology. The aim of this study was to investigate the validity of directionality theory and the relevance of demographic entropy as a better measure of Darwinian fitness as opposed to the Malthusian parameter employing matrix population models for 207 species of perennial plants studied in their natural environment.

### **6.3: *Material and Methods***

The life history variables and phylogeny used to test this model were obtained as described in Chapter two. Only iteroparous perennial plants were considered because strictly semelparous plants yield  $S=H=0$ . The life tables produced as described in chapter two were used to calculate all the relevant parameters of the model.

### **6.4: *Results***

In opposition to the prediction of directionality theory, the correlations between standardized entropy ( $H$ ) and either maximum lifespan ( $L$ ) and generation time ( $T$ ) were negative (Fig. 12;  $r^2 = 0.427$ ,  $n = 207$ ,  $p < 0.01$ , and  $r^2 = 0.707$ ,  $p < 0.01$ ). In these

PGLS models, the effect of phylogenetic signal was not evident (Pagel  $\lambda = 0$ ) and life form had no effect on any of these relationships ( $P > 0.01$  in all cases). Evidently, generation time, the average age of parents of offspring produced at stable age distribution, increases with lifespan ( $r^2 = 0.56$ ,  $df = 207$ ,  $P < 0.01$ ; figure not shown). On the other hand, unstandardised entropy ( $S$ ) was positively correlated with both  $L$  and  $T$  (Fig. 13;  $r^2 = 0.238$ ,  $df = 207$ ,  $P < 0.01$  and  $r^2 = 0.502$ ,  $df = 207$ ,  $P < 0.01$  respectively).

As expected from the relationship  $\Phi = r - H$ , the reproductive potential ( $\Phi$ ) showed a negative relationship with standardised entropy ( $H$ ), but had a funnel shape when regressed against unstandardized entropy ( $S$ ) (Fig. 14;  $r^2 = 0.438$ ,  $df = 207$ ,  $p < 0.01$ , and  $r^2 = 0.234$ ,  $P < 0.01$  respectively). Funnel relationships were also found between reproductive potential and both lifespan and generation time (Fig. 15;  $r^2 = 0.121$ ,  $df = 207$ ,  $P < 0.01$  and  $r^2 = 0.155$ ,  $P < 0.01$ , respectively). Finally, offspring production rate ( $E$ ) was negatively correlated with both generation time and unstandardized entropy, contradicting the expected positive relationship for  $T$  in  $E = rT - S$  and matching the negative expectation for  $S$  (Fig. 16;  $r^2 = 0.261$ ,  $df = 207$ ,  $P < 0.01$  and  $r^2 = 0.294$ ,  $df = 207$ ,  $P < 0.01$ ). The percentage of variance accounted for by these relationships was 26% and 29%, respectively.

## **6.5: Discussion**

Populations that are defined by age specific fecundity and age specific survival will, under constant environmental conditions, reach a steady state in which the relative number of individuals within each stage class or age classes remains constant and the population number changes at a fixed rate. In natural populations, however, this scenario does not persist for long. In addition to eventual resource limitation, changes in the birth and death rates due to environmental and demographic stochasticity result in variations in age distribution and population growth rate. These changes may have

relevant ecological and demographic implications. In populations of small size and of conservation concern, these fluctuations in population numbers may result in the extinction of the population and the rate of decay of fluctuations towards the population steady state which characterises demographic stability is a crucial aspect in the dynamics and evolution of populations (Real and Ellner, 1992). In order to provide a measurable property that will predict demographic stability in a population, Demetrius (1977) suggested that demographic entropy should positively correlate with demographic stability. That is, high entropy species are expected to be more stable and consequently have a longer lifespan than low entropy species. This is confirmed by the results presented here, but only if unstandardized entropy ( $S$ ) is used. Demetrius original stand, however, was that given the equality  $H = S/T$ , both  $H$  and  $S$  should be positively correlated with measures of the duration of life. His position was changed when, as confirmed here, unpublished results by Franco showed  $S$ , but not  $H$ , to be positively correlated with generation time (Fig. 2 in Ziehe and Demetrius, 2004).

The relationships here investigated suggest that the predicted relationships are either trivial mathematical consequences of the definition of the parameters involved or, when they go in opposite direction to the predictions, are a consequence of not taking into account the inevitable biological trade-offs that occur in all organisms because of resource and time limitations and how these trade-offs impact on selection for optimal life histories under different ecological scenarios including, for example, stable vs unstable environments. Thus,  $H$  is not positively correlated with measures of the duration of life simply because both  $S$  and  $T$  are selected to increase in highly competitive, stable environments, but  $T$  increases faster than  $S$  and thus  $H$  decreases with lifespan and generation time.

An important issue in evolutionary studies is to understand how ecological constraints determine life history patterns (Garth, 1968, Winemiller and Kenneth, 1991) and

directionality theory is said to predict the relationship between ecological norms, as described by either reproductive potential ( $\Phi$ ) or offspring production rate ( $E$ ), and entropy ( $S$ ). Being a parameter derived from the life table, similar to  $S$ ,  $T$ , and  $H$ , is not clear why  $\Phi$  and  $E$  are taken to represent the ecological conditions acting as selective agents. Accepting that this is the case, one can also see that the nature of the relationships between either  $\Phi$  or  $E$  and entropy varies with the measure of entropy chosen. In particular, directionality theory predicts a negative relationship between  $E$  and  $S$  for populations under bounded growth conditions ( $E < 0$ ). Although the result of the present study showed a negative relationship between  $E$  and  $S$ , this may not reflect the action of evolutionary processes. Demetrius (2000) showed that  $E = rT - S$ . Consequently, the relationship between  $E$  and  $S$  is dependent on the values of  $r$  and  $T$ . Since  $r$  varies around zero in a similar funnel fashion to reproductive potential against lifespan and generation time (Fig. 15; recall also that  $\Phi = r - H$ ), the variability in the mathematically expected negative relationship between  $E$  and  $S$  is due to variation in generation time (see Fig. 16). There is no evidence that populations with  $E > 0$  are under unbounded growth and with a small population size while those with  $E < 0$  are under bounded growth conditions and have large population sizes. It is therefore artificial to separate these two sets of data. There is a continuum of variation in all measured parameters and the relationships, if they have any meaning, are accountable by existing theory based on  $r$  as a measure of fitness. This parameter, the intrinsic rate of population increase, is more variable in populations with low generation time and lifespan than at the opposite duration of life. Extended life is only possible in more stable environments, and this is accounted for by standard life history theory. Whatever entropy one chooses to observe, it varies in accordance to the particular life history (Bulmer 2006), thus the relationships in Figs. 12 and 13. It seems clear that the parameters of directionality theory are variously employed as either determinants or



consequences of each other to suit a mathematical argument that lacks biological reality. The response offered to Bulmer's critique evades the relevant issues (Demetrius et al., 2006).

Table 8: Phylogenetic generalised least squares models of the relationships between the parameters used. Life form was not significant in any of the relationships and is therefore not included in the model.

Dependent variable	Effect	Slope (SE)	F <sub>statistics</sub>	P	R <sup>2</sup>
<i>H</i>	<i>L</i>	-0.1308 (0.0106)	1.86	<0.001	0.427
<i>H</i>	<i>T</i>	-0.1198 (0.00054)	5.25	<0.01	0.707
<i>S</i>	<i>L</i>	0.0062 (0.0008)	36.41	<0.01	0.238
<i>S</i>	<i>T</i>	0.0363 (0.0025)	42.05	<0.01	0.502
$\phi$	<i>H</i>	-0.7889 (0.0623)	10.62	<0.01	0.438
$\phi$	<i>S</i>	0.1153 (0.0146)	7.38	<0.01	0.234
$\phi$	<i>L</i>	0.0011 (0.0002)	3.06	<0.05	0.121
$\phi$	<i>T</i>	0.0048 (0.0008)	4.45	<0.05	0.155
<i>E</i>	<i>T</i>	-0.0280	4.82	<0.05	0.261
<i>E</i>	<i>S</i>	-0.5809 (0.0628)	9.32	<0.05	0.294

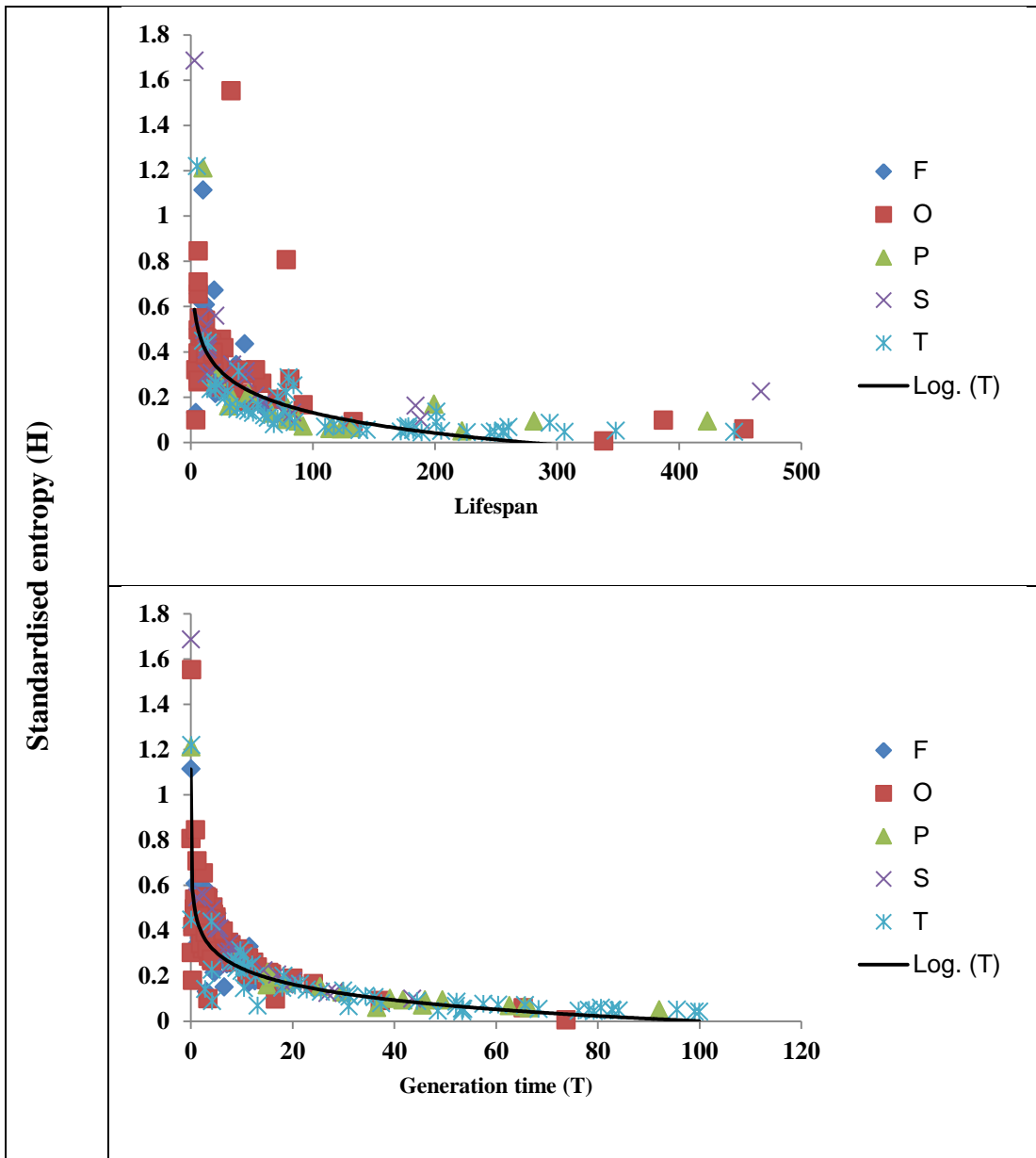


Figure 12: Scatter plot of the relationships between (a) standardised entropy ( $H$ ) and maximum lifespan ( $L$ ) and (b) standardised entropy and generation time ( $T$ ). The logarithmic function describing this relationship is  $H = -0.054 \ln x + 0.4411$  ( $r^2 = 0.022$ ;  $P < 0.01$ ),  $H = -0.101 \ln x + 0.4658$  ( $r^2 = 0.706$ ,  $P < 0.01$ ) respectively. In this and the following figures,  $F$  represents understorey forest herbs;  $O$ , herbs from open, frequently disturbed habitat;  $P$ , palms;  $S$ , shrubs from open, frequently disturbed habitats;  $T$ , trees).

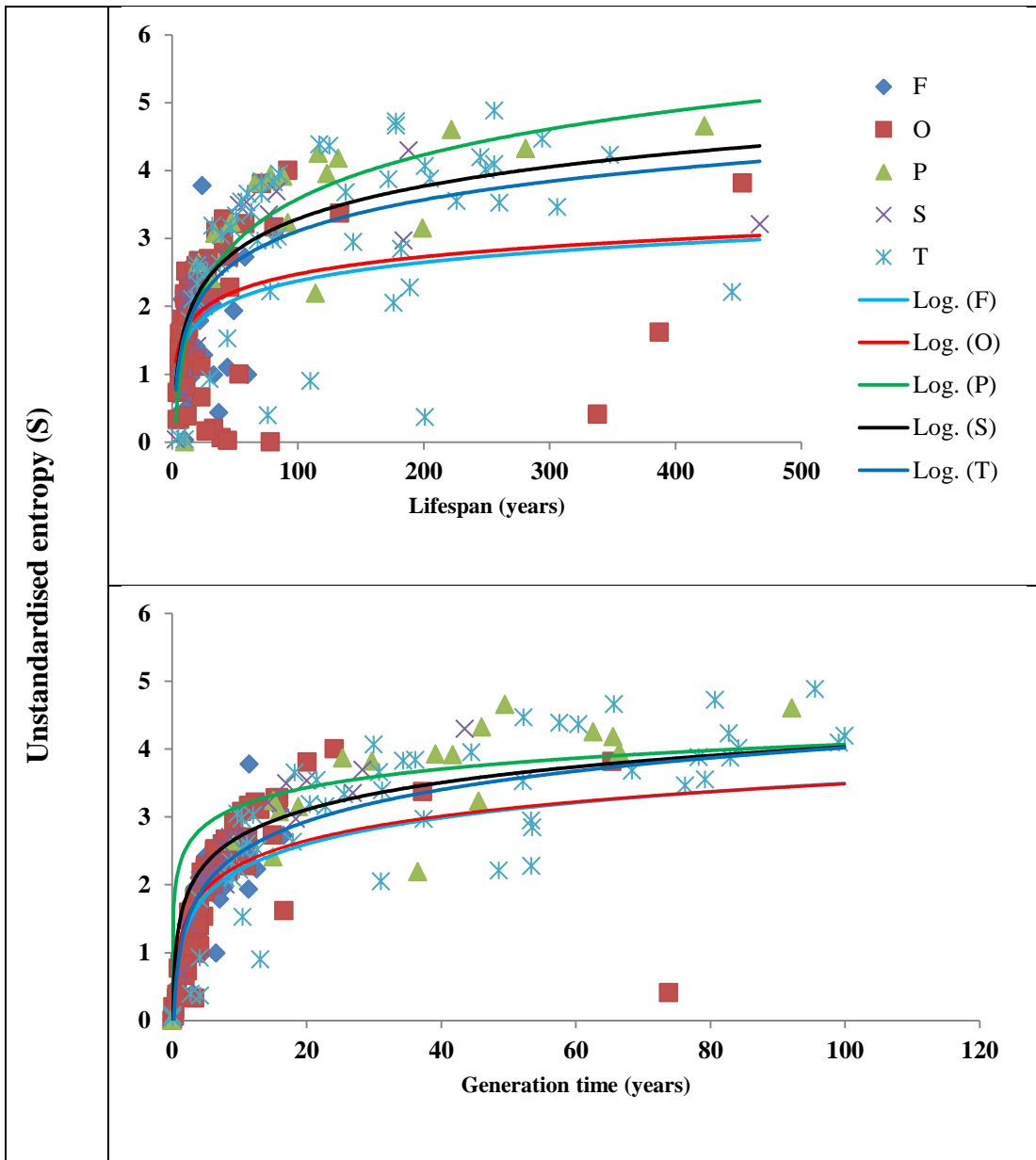


Figure 13: The relationships between (a) unstandardised entropy ( $S$ ) and lifespan and (b) unstandardized entropy and generation time. In both graphs, the logarithm function describing this relationship are: light blue fit for forest herbs, red fit for herbs from frequently disturbed habitat, green fit for palms, black fit for shrubs, and dark blue fit for trees,

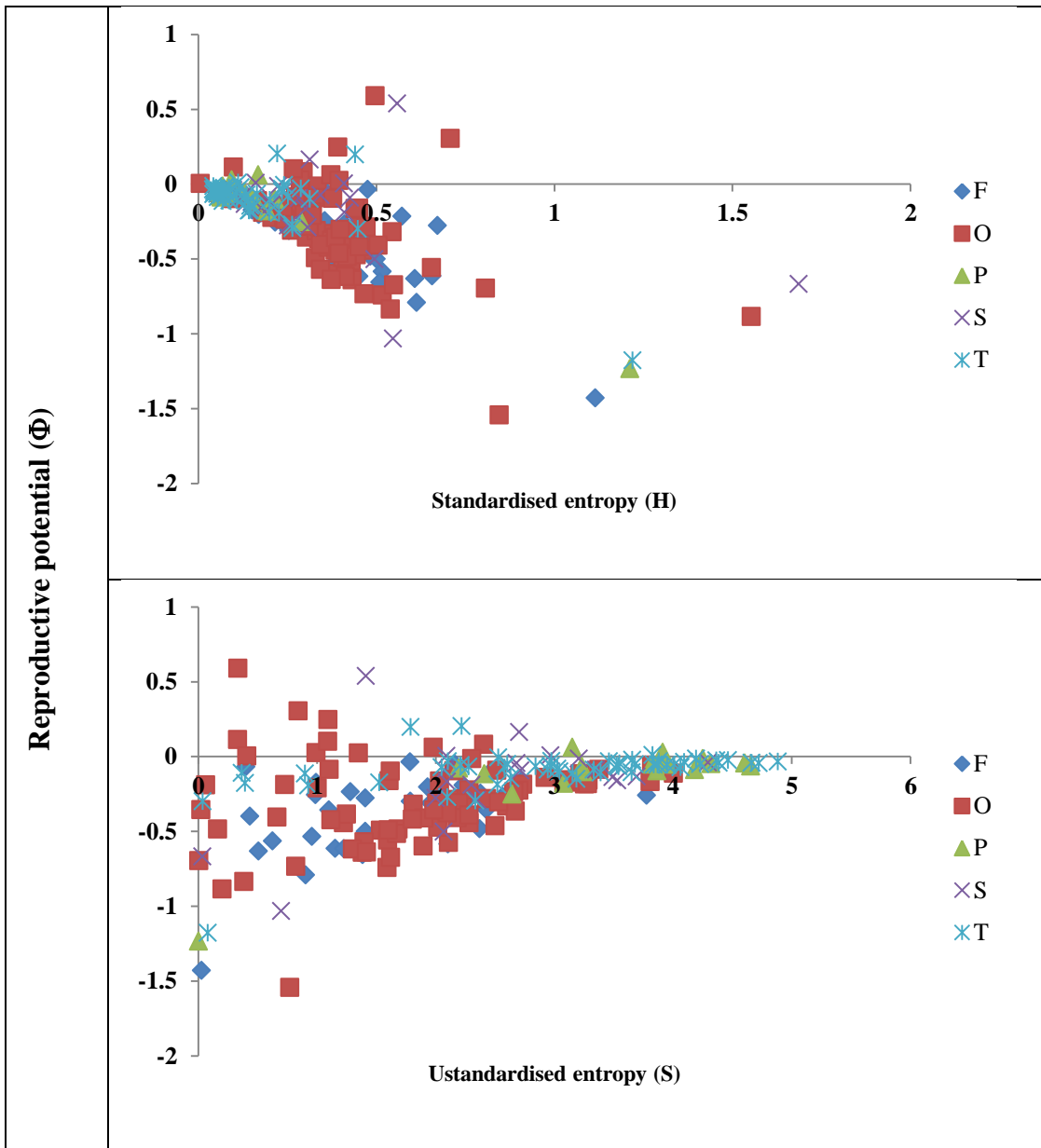


Figure 14: Relationships between (a) reproductive potential ( $\Phi$ ) and standardised entropy ( $H$ ), and (b) reproductive potential and unstandardized entropy ( $S$ )

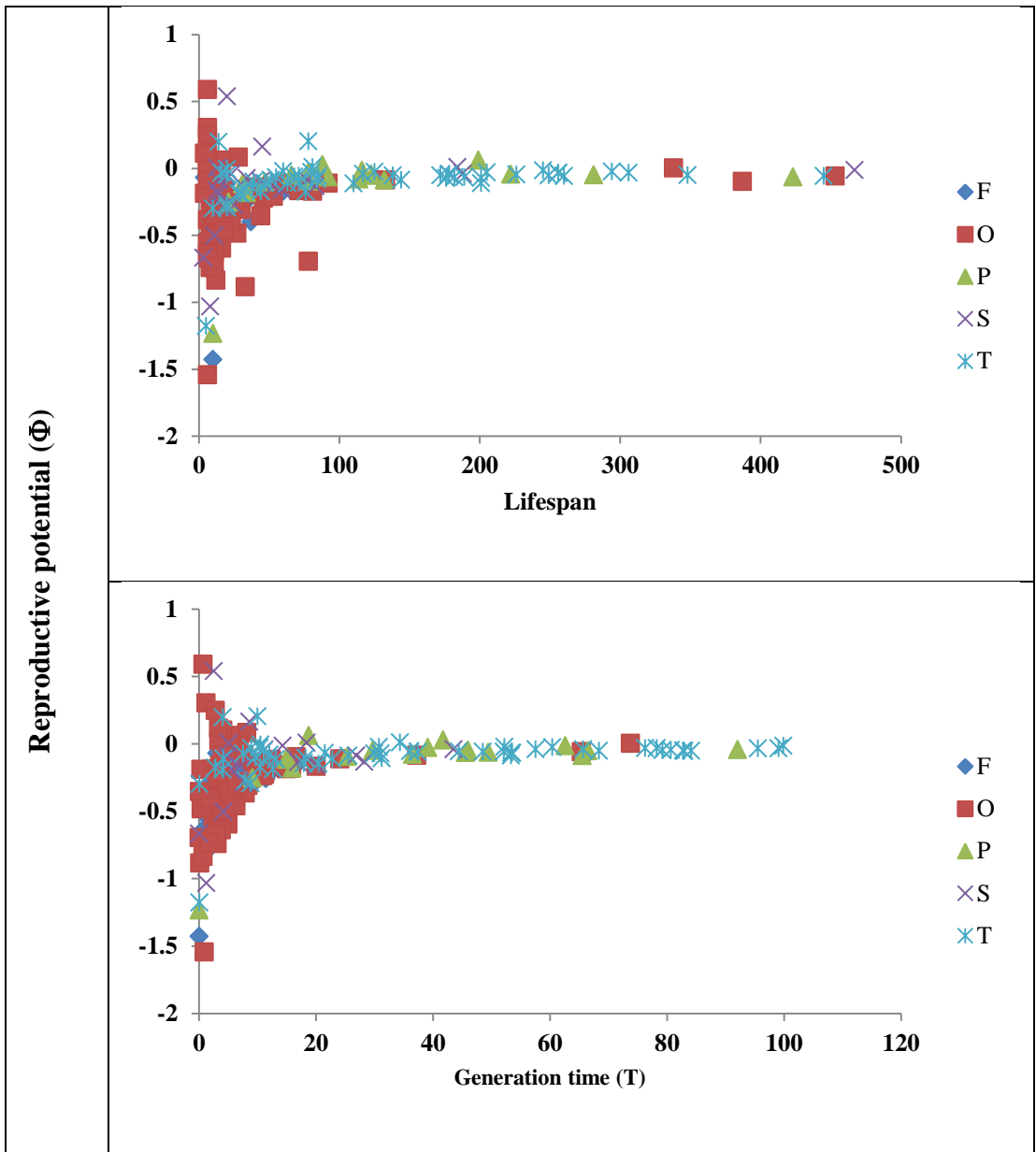


Figure 15: Relationships between (a) reproductive potential and lifespan, and (b) reproductive potential and generation time

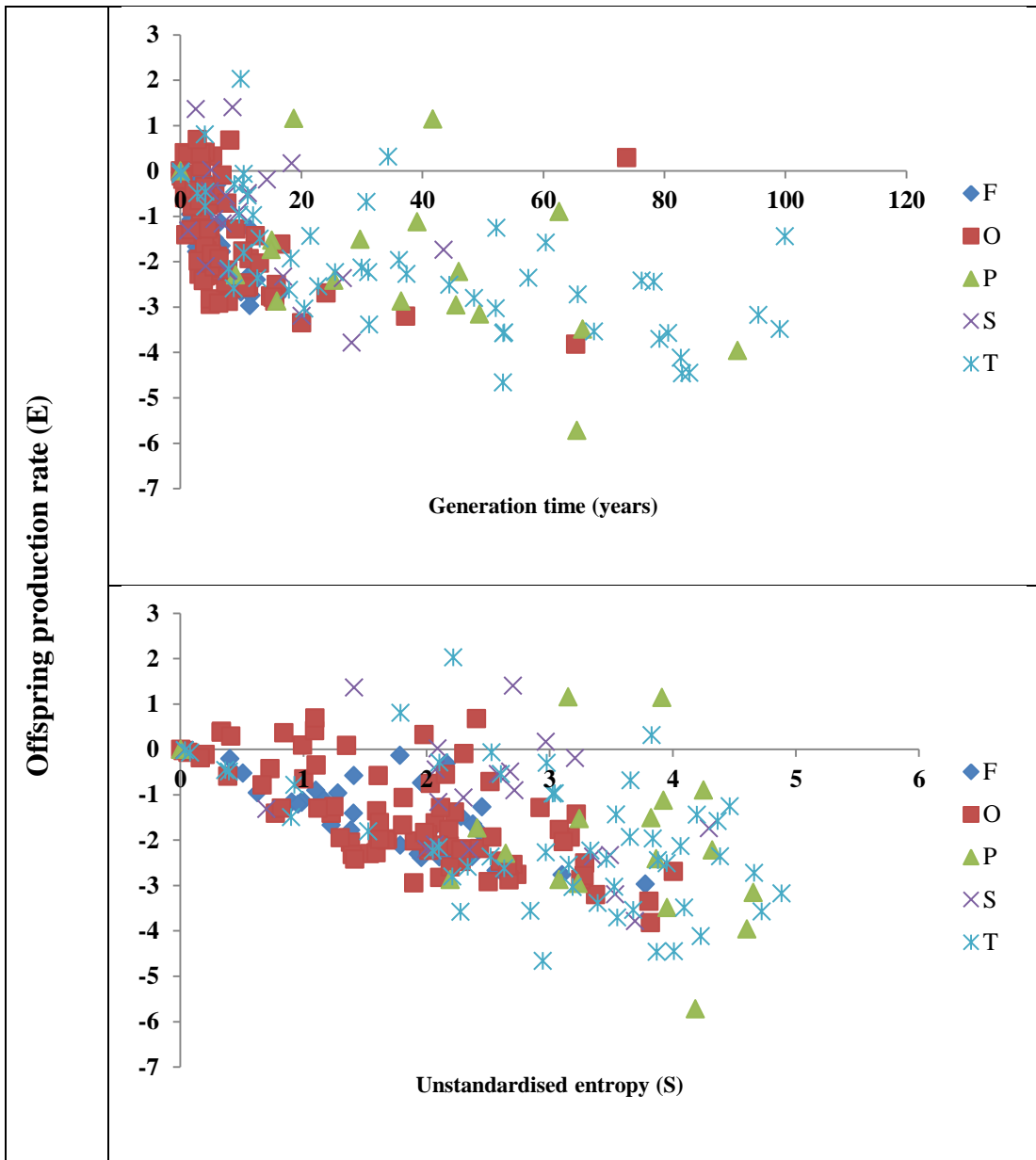


Figure 16: The relationships between (a) offspring production rate ( $E$ ) and generation time and (b) offspring production rate and unstandardized entropy ( $S$ )

## ***Chapter 7: General Discussion***



## **7.0: *General Discussion and Conclusion***

A crucial question in the comparative study of life histories is whether observed variation is the result of local adaptation or of phenotypic plasticity to local environmental conditions (Caswell, 1983, Sultan, 2000). Clearly, the demography of organisms changes with environmental conditions, resource abundance and interactions with other species, but life history attributes which are consequences of selection on demography over evolutionary time, are less variable: elephants live longer and have larger body size than mice.

In this thesis, matrix population models were employed to conduct a comparative analysis on the demography and life history evolution of 207 species of iteroparous perennial plants studied in their natural environment in order to examine: i) the evolutionary lability of plant life history traits ii) senescence in plants and iii) the use of demographic entropy in ecology.

Previous studies have suggested that phylogenetic signal is important in plants (Hodgson and Mackey, 1986, Kochmer and Handel, 1986, Herrera, 1981, Baldwin and Schultz, 1988, Willson and Whelan, 1990, Chazdon, 1991, Lee et al., 1991) but few have attempted to consider their effect explicitly and quantitatively (Partridge and Harvey, 1988, Franco and Silvertown, 1996, Burns et al., 2010). Accordingly, in Chapter three, the evolutionary lability of fifteen life history traits was investigated by quantifying the amount of phylogenetic signal in each trait using three different approaches, Pagel's lambda, Blombergs et al's K and Abouheif's test of serial independence. Although the three methods were correlated, these correlations varied between 0.38 and 0.82 (Spearman rank correlation) indicating that the methods measure slightly different properties all broadly characterised as phylogenetic signal. The results also showed that demographic life history traits are generally evolutionarily labile, although the degree of lability varies from trait to trait. Generation time, survival and all

six measures of sensitivity/elasticity of survival, growth and fecundity showed statistically significant phylogenetic signal, revealing that these traits are less evolutionarily labile than the other life history traits investigated. While life history traits are generally found to be evolutionarily labile across many taxa (Reznick and Endler, 1982), the high phylogenetic signal of sensitivity and elasticity of vital rates indicates that the “life history strategy”, characterised by the position of species in elasticity space (see Franco & Silvertown, 2004) is highly conserved: closely related species have similar life histories. This is somehow surprising because it means that sensitivities and elasticities are more conserved than other life history attributes, such as generation time, longevity and age at sexual maturity. Traits with low phylogenetic signal are more variable and, consequently, are expected to have a higher rate of evolution (they are more evolutionarily labile) than traits with significantly high phylogenetic signal. This also suggests that the latter are more tightly linked to fitness (Falconer, 1990).

Despite their numerical differences, the three approaches used to quantify phylogenetic signal produced similar results across the demographic and life history variables. It has been suggested that Abouheif’s method is less reliable because it does not take a specific evolutionary model into account. However, our results showed the contrary. Although the autocorrelation indices employed in Abouheif’s method were not originally designed to offer a quantitative interpretation (Li et al., 2007) the correlation among all three approaches indicated they could be employed in cases with poor phylogenetic resolution.

Unfortunately, interpreting phylogenetic signal is not as straightforward as it appears. Revell et al (2008) explored a variety of evolutionary processes using individual based models of drift, mutation and selection in populations evolving along a phylogeny, to examine the relationship between the rate of evolution and the resulting phylogenetic

signal in a continuous trait. They noted that different evolutionary processes can produce similar  $K$  values, especially when  $K$  is low. They also found no direct relationship between  $K$  and evolutionary rate under constant rate of genetic drift. Furthermore, although it is common for people to refer to high or low phylogenetic signal in comparative studies, the exact meaning of these words varies among studies in the literature. For instance, low phylogenetic signal can refer to  $K$  and  $I$  values from zero to any value less than unity, whereas high phylogenetic signal could imply  $K$  and  $I$  values from significantly greater than zero to infinity (Kamila and Cooper, 2013). Thus this, and several other practical issues highlighted in the discussion section of chapter two may question the significant values of phylogenetic signal or weak signals observed in some of the life history traits examined. Part of the problem is that one is trying to simplify complex patterns of evolutionary diversification into simple scalar measures, and it may be necessary to develop multidimensional measures (perhaps similar at least in spirit to principal component analysis) that are congruent with this complexity.

In Chapter four, the trends in the age trajectory of mortality and reproductive value of 207 species of iteroparous perennial plants were investigated. Recognising these patterns is a first step in identifying possible sources of variation and selection in natural populations. More than 80 % of the species studied in this chapter, showed a mortality trajectory that increases with age. This result is generally consistent with the predictions of the evolutionary theory of senescence. However, a few species (13%) showed a mortality pattern that decreases with age, thus deviating from the predictions of the evolutionary theory of senescence. There is a large body of literature that has argued the case for negative senescence where species show mortality trajectories that decrease with age or show no observable increase with age (Curtsinger et al., 1992, Carey et al., 1992, Tatar et al., 1993). However, for reasons explained in the discussion section of that chapter, this pattern may not represent a case of negative senescence. Other

plausible reasons that could account for this anomaly might be trade-offs that are brought about by the direct connection between survival and fecundity at different ages under optimal conditions or related to genetic or environmental heterogeneity between individuals in the population whereby older plants are a particularly robust sub-set of their cohort (Vaupel, 1985, Vaupel, 1990, Brooks et al., 1994). One issue that the proponents of negative senescence do not address is the physical impossibility for biological organisms to quite literally disintegrate if senescence rates were to continue increasing at an exponential rate at advanced ages.

Because the intensity of natural selection acting on age-specific fecundity is contingent upon survival to that age, and selection on age-specific survival, in turn, being contingent upon the ability to reproduce, the pattern of reproductive value may represent a better way to inspect senescence in natural populations than mortality patterns alone. Indeed, in the same chapter, 100 % of the 207 species of perennial plants examined showed a reproductive value pattern that decreased with age, consistent with other empirical studies cited therein (see discussion section of Chapter four).

The above result naturally led us to investigate further the reproductive value as a more efficient parameter for measuring the rate of living and, thus, the duration of life, and to compare its performance in this respect to that of other measures of senescence proposed in the literature. Thus, in Chapter five, the performance of the reproductive value, as proposed by Fisher and other measures of senescence as put forward by Hamilton and Baudisch were investigated, using a generalised time distribution model whose parameters can be interpreted in terms of familiar life history traits measuring the duration and speed of life. The results of this chapter showed that all three parameters of the time distribution of reproductive value performed better in terms of correlation with the hypothesised related life history traits (lifespan, age at sexual maturity and entropy) than indexes that are separate estimators of the sensitivity of fitness to changes in age-

specific survival and fecundity taken independently as the individual species ages (Hamilton, 1966, and Baudisch, 2005). This is consistent with other published work cited in the discussion section of Chapter five. The most striking result from this chapter was the strong negative power correlation between the pace and duration of reproductive value as measured by two of the three distribution parameters which orders species along a fast/slow continuum of life histories: the duration of life is proportional to the rate at which life, as measured by reproductive value, runs. These findings suggest that the reproductive value is a more accurate measure of the rate of living and, as a consequence, senescence in natural populations than the mortality and fecundity patterns examined separately.

In the course of writing this dissertation the article “Diversity of ageing across the tree of life” (Jones et al., 2014) was published. This article examined the different patterns of mortality and fertility curves for 48 populations in 41 species that included vertebrates, invertebrates and plants. The authors found variations in the patterns of mortality and fertility curves covering all three possibilities (increasing, constant and decreasing) and attributed these variations to a deviation for many species from accepted senescence theory. However, their findings were consistent with the mortality patterns observed in chapter four of this thesis, but because the authors concentrated on how mortality and fertility varied independently of each other with age, it is difficult to ascertain whether or not the patterns observed would be at odds with the evolutionary theory of senescence had they observed the joint pattern of mortality and fertility as expressed in reproductive value. In order to test this alternative, their data were analysed to investigate whether they would fit the pattern between parameters  $t$  and  $b$  of the time distribution of reproductive value, as was done in Chapter five.

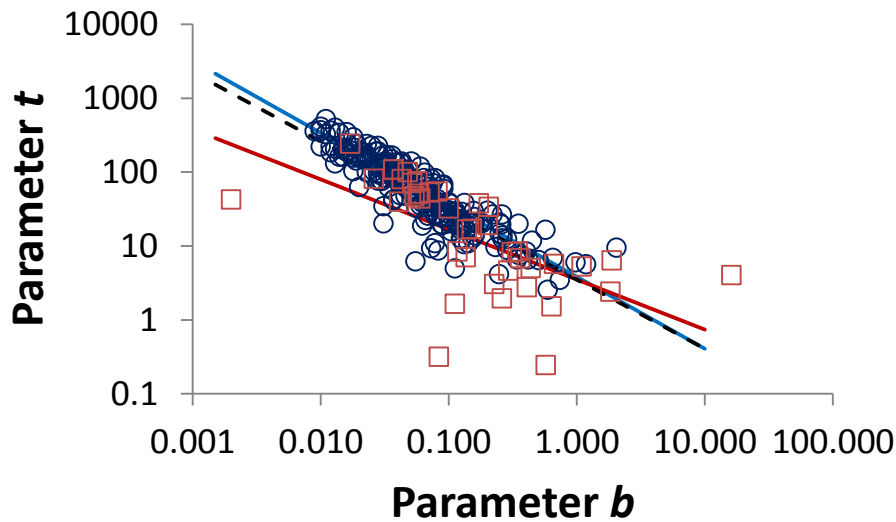


Figure 17: The relationship between parameters  $b$  and  $t$  of the time distribution of reproductive value for the 207 species of seed plants investigated in this thesis (207 blue circles) and the 40 populations in Jones et al. (2014) (40 red squares). The continuous colour lines correspond to the respective power regressions and the black dashed line to that for all 247 populations in 240 species.

Because we needed to standardise the time interval (units) employed to one year, as in our 207 species (Chapter 5), and we could not easily do this from their matrix data, eight of their 48 populations whose lifespans were measured in days or months had to be excluded. This left 40 populations in 33 species. Analysing Jones et al. (2014) data separately did produce a slope (on a log-log scale) that differed significantly ( $P = 0.035$ ) from the one obtained in our dataset (Fig. 17; Table 7). However, the difference between the overall slope ( $n=247$ ) and the slope for the species studied in this thesis only ( $n=207$ ) was minimal and not significant ( $P = 0.46$ ; Table 7). Furthermore, the shallower slope produced by Jones et al.'s data is heavily influenced by the two most extreme points in the value of the  $b$  parameter (leftmost and rightmost points in Fig. 17). These two points correspond to two species present in our dataset too: *Geonoma orbignyana* and *Hypericum cumulicola*. In fact, the original matrix data for these two species are exactly the same in the two datasets. The difference in the values of the parameters  $b$  and  $t$  obtained is due to the fact that, while our lifetable data were cut at the life expectancy at birth (taken as a measure of lifespan after which no individuals

were deemed likely to survive), Jones et al set the maximum age for their lifetables “at the terminal age to which only 5% of adults survive” (the number of adults meaning the number of survivors of a cohort that reached the age of sexual maturity). This more arbitrarily set limit influences the resulting life tables more in some species than in others, thus accounting for the very different values of the parameters obtained (Table 8).

Table 9: Comparison of the slopes obtained from simple regression analyses for the data presented in this thesis (207 species), Jones et al data (40 populations in 33 species)

<b>Dataset</b>	<b>Slope (SE)</b>	<b>Adj. R<sup>2</sup></b>	<b>t-value (df)</b>	
40 populations	-0.678 (0.135)	0.383	2.12 (243)	
207 species	-0.973 (0.035)	0.793		0.734 (450)
All 247 populations	-0.934 (0.040)	0.692		
		P < 0.001 in all three cases	P = 0.035	P = 0.463

Table 10: Comparison of the parameters of the time distribution of reproductive value obtained from the lifetables derived from the analyses presented in this thesis and those from Jones et al (2014) for two plant species whose original matrix data were the same.

	<i>Geonoma orbignyana</i>		<i>Hypericum cumulicola</i>	
<b>Study</b>	<i>b</i>	<i>t</i>	<i>b</i>	<i>t</i>
This thesis	0.028	190.1	0.073	46.8
Jones et al.	0.002	42.5	16.181	4.03

Two other (animal) species, *Marmota flaviventris* and *Ovis aries* also departed from the overall trend. These two species would reduce the intercept of the overall relationship, but would contribute to increase its slope. Thus, although also suspect, these points would not significantly influence the overall relationship. The excess variation observed in Jones et al’s dataset is likely an artifact of data handling. Despite the variation introduced by the 40 additional populations, the fact that the overall dataset (n=247) confirmed our original results (n=207) suggests that this method of quantifying the pace and duration of life could be applied across the tree of life and that “unusual” patterns of mortality and fertility on their own cannot be taken as evidence of departure from the evolutionary theory of senescence

Finally, in Chapter 6, the validity of the use of the demographic entropy as a measure of Darwinian fitness was examined. After an appraisal of its tenets and the empirical evidence provided by our dataset, it was concluded that directionality theory is a statement of the algebraic relationships among several demographic parameters (intrinsic rate of population growth, entropy, generation time, and two others whose precise meaning is not immediately obvious, identified by Demetrius by the names reproductive potential and offspring production rate). It lacks the essential biological constraints and trade-offs necessary to place these equations in an ecologically realistic



setting. Despite this, demographic entropy is an informative life history trait which covaries (i.e. coevolves) with other life history traits, such as longevity, age at sexual maturity and generation time. What selective factors are responsible for this covariation (e.g., temporal variation in resource abundance, as in Verhulst et al., 2008) is an important question in the elucidation of the determinants of life history evolution.

The research presented in this thesis addressed some essential issues in life history evolution of iteroparous perennial plants employing the comparative method. It is inevitably limiting, however, to employ mathematical, statistical and phylogenetic approaches exclusively in the context of the comparative method to explain the evolution of life history traits in plants. Other approaches ought to consider the mechanistic workings of life history constraints and trade-offs. For instance, it would be interesting to investigate what genetic and physiological mechanisms regulate the trade off between the pace ( $v_b$ ) and the duration ( $v_t$ ) of life as measured on reproductive value (chapter five). Thus, the integration of mechanistic and comparative approaches might help address in more detail the proximate causes that modulate the evolution of life histories. This integration would also help us to understand the significance of phylogenetic signal and the role of environmental variation in life history evolution in plants and other organisms

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## *Appendices*

## Appendix 1

Table 11: Life history data used in chapter three.

Species	LF	$\lambda$	(year <sup>l</sup> )	$L$	$\alpha$	$\mu$	$L_\alpha$	$S_\sigma$	$S_\gamma$	$S_\phi$	$E_\sigma$	$E_\gamma$	$E_\phi$	$\sigma$	$\gamma$	$\phi$	$S$
<i>Abies concolor</i>	T	1.044		51	27	50.4	24	0.40	0.56	0.03	0.92	0.05	0.03	0.73	0.21	1.28	3.33
<i>Abies magnifica</i>	T	0.974		44	23	42.8	21	0.49	0.48	0.04	0.96	0.03	0.01	0.53	0.21	0.32	1.53
<i>Acacia bilimekii</i>	S	1.235		467	18	446.4	449	0.43	0.57	0.00	0.83	0.13	0.05	0.82	0.41	48.80	4.21
<i>Acer saccharum</i>	T	1.892		38	5	12.7	33	0.78	0.22	0.00	0.19	0.81	0.00	0.69	0.58	15.31	1.79
<i>Aconitum noveboracense</i>	O	0.990		39	15	106.6	24	0.55	0.32	0.13	0.81	0.11	0.08	0.88	0.23	0.36	0.12
<i>Aechmea nudicaulis</i>	F	1.044		12	4	2.5	8	0.54	0.45	0.01	0.84	0.15	0.01	0.61	0.46	0.43	1.15
<i>Agrimonia eupatoria</i>	O	0.998		45	7	41.1	38	0.73	0.27	0.00	0.94	0.06	0.00	0.81	0.33	0.22	2.77
<i>Agropyron repens</i>	O	2.963		6	1	1.5	5	0.15	0.82	0.03	0.56	0.44	0.00	0.58	0.29	28.40	0.33
<i>Alnus incana</i>	T	0.971		32	4	14.2	28	0.65	0.16	0.19	0.90	0.1	0.00	0.88	0.09	0.18	2.54
<i>Ambrosia deltoidea</i>	S	0.615		11	3	5.3	8	0.76	0.22	0.02	0.86	0.09	0.05	0.88	0.11	0.18	0.70
<i>Andropogon semiberberis</i>	O	1.252		8	2	18.9	6	0.69	0.28	0.03	0.68	0.18	0.14	0.57	0.22	4.91	1.81
<i>Anemone patens</i>	O	1.019		13	2	5.0	11	0.74	0.10	0.17	0.96	0.03	0.00	0.89	0.28	0.12	2.28
<i>Annamocarya sinensis</i>	T	0.976		189	47	109.3	142	0.76	0.24	0.00	0.68	0.32	8E-05	0.94	0.02	0.17	2.38
<i>Aquilaria malaccensis</i>	T	1.224		16	8	10.8	8	0.58	0.42	0.00	0.64	0.29	0.07	0.50	0.07	12522.26	2.10
<i>Aquilegia chrysantha</i>	F	0.849		8	5	6.3	3	0.77	0.23	0.00	0.85	0.14	0.02	0.48	0.29	30.45	1.23
<i>Aquilegia sp</i>	O	0.849		12	6	8.1	6	0.57	0.43	0.00	0.73	0.26	0.01	0.56	0.33	29.45	1.53
<i>Araucaria cunninghamii</i>	T	1.018		256	95	174.7	161	0.33	0.67	0.00	0.95	0.04	0.01	0.19	0.00	1624.33	4.88
<i>Araucaria hunsteinii</i>	T	0.987		182	41	99.6	141	0.89	0.07	0.03	0.99	0.01	0.00	0.90	0.05	0.15	2.84
<i>Ardisia elliptica</i>	S	1.060		188	25	172.1	163	0.677	0.32	0.00	0.80	0.19	0.01	0.85	0.13	13.79	4.29
<i>Arisaema serratum</i>	F	0.990		23	8	14.2	15	0.743	0.26	0.00	0.44	0.08	0.48	0.68	0.07	1.07	2.62
<i>Arisaema triphyllum</i>	F	1.073		24	8	30.9	16	0.72	0.28	0.00	0.92	0.06	0.02	0.64	0.26	1.99	3.78
<i>Aristida bipartita</i>	O	1.188		25	2	14.7	23	0.38	0.42	0.20	0.72	0.08	0.21	0.94	0.23	1.05	2.23
<i>Armeria maritima</i>	O	1.458		28	5	19.9	23	0.77	0.23	0.00	0.67	0.25	0.08	0.79	0.10	139.93	2.40
<i>Aster amellus</i>	O	0.943		19	7	15.1	12	0.93	0.07	0.00	0.98	0.02	0.00	0.78	0.43	0.15	1.22
<i>Astragalus scaphoides</i>	O	1.378		15	3.0	10.5	12	0.29	0.66	0.04	0.63	0.22	0.15	0.89	0.48	0.06	2.30
<i>Astragalus tyghensis</i>	O	1.009		13	4	8.1	9	0.38	0.62	0.00	0.76	0.2	0.04	0.72	0.25	1.38	2.19
<i>Astrocaryum mexicanum</i>	P	1.007		123	42	94.0	81	0.66	0.34	0.00	0.95	0.04	0.01	0.91	0.08	10.37	3.95
<i>Avicenia marina</i>	T	1.237		39	3	33.5	36	0.55	0.43	0.02	0.81	0.18	0.02	0.51	0.12	156.59	3.04
<i>Banksia ericifolia</i>	S	1.609		45	12	28.2	33	0.55	0.43	0.02	0.70	0.2	0.11	0.90	0.07	24.59	2.70
<i>Betula nana</i>	S	0.992		11	2	6.7	9	0.97	0.03	0.00	0.84	0.16	0.00	0.76	0.33	0.11	2.07
<i>Borderea chouardii</i>	O	1.002		133	10	109.7	123	0.71	0.28	0.01	0.96	0.04	0.00	0.88	0.23	0.07	3.37
<i>Bothriochloa insculpta</i>	O	1.094		14	2	12.7	12	0.46	0.27	0.27	0.85	0.06	0.10	0.84	0.26	0.30	2.07
<i>Bothriochloa ischaemum</i>	O	0.808		16	4	6.1	12	0.29	0.70	0.01	0.72	0.23	0.05	0.78	0.24	1.78	1.89
<i>Bouteloua rigidiseta</i>	O	0.932		13	3	9.4	10	0.68	0.31	0.02	0.83	0.15	0.02	0.57	0.23	0.69	1.68



<i>Brosimum alicastrum</i>	T	1.067	201	17	127.4	184	0.4	0.56	1E-05	0.85	0.1	0.03	0.779	0.10	4238.78	4.06
<i>Bursera glabrifolia</i>	T	1.099	71	18	58.4	53	0.09	0.91	0.00	0.86	0.09	0.05	0.84	0.20	27.13	3.65
<i>Calathea ovandensis</i>	F	1.551	15	2	19.1	13	0.23	0.77	0.00	0.81	0.15	0.04	0.75	0.08	18.10	1.78
<i>Callitris intratropica</i>	T	1.264	20	12	18.7	8	0.53	0.47	3E-06	5E-01	5E-01	1E-03	0.01	0.20	6E+01	2.53
<i>Calluna vulgaris</i>	S	2.995	20	5	14.2	15	0.04	0.96	0.00	0.58	0.26	0.17	0.77	0.25	74444.07	1.41
<i>Calocedrus macrolepis</i>	T	0.968	144	41	71.1	103	0.65	0.35	0.00	0.97	0.02	0.01	0.92	0.08	3.95	2.94
<i>Calochortus albus</i>	O	1.542	16	3	10.7	13	0.35	0.63	0.02	0.66	0.22	0.12	0.81	0.13	48.47	1.98
<i>Calochortus lyallii</i>	F	0.989	23	8	15.0	15	0.38	0.57	0.05	0.83	0.13	0.05	0.85	0.13	0.61	2.56
<i>Calochortus macrocarpus</i>	F	0.946	26	10	16.5	16	0.70	0.21	0.09	0.93	0.05	0.02	0.86	0.13	1.26	1.96
<i>Calochortus obispoensis</i>	O	1.023	70	20	50.7	50	0.49	0.51	0.00	0.88	0.08	0.04	0.63	0.34	4.57	3.81
<i>Calochortus pulchellus</i>	F	1.115	30	3	25.5	27	0.40	0.60	0.01	0.80	0.13	0.07	0.74	0.10	8.03	2.38
<i>Calochortus tiburonensis</i>	O	1.156	57	5	52.0	52	0.46	0.45	0.10	0.85	0.08	0.07	0.96	0.09	0.61	3.22
<i>Camellia japonica</i>	T	1.014	178	25	155.5	153	0.46	0.53	0.01	0.96	0.03	0.01	0.90	0.14	1.12	4.72
<i>Carex humilis</i>	O	1.102	16	9	4.5	7	0.78	0.22	0.00	0.87	0.13	0.00	0.50	0.40	0.76	1.59
<i>Cassia nemophila</i>	S	1.207	44	3	27.1	41	0.64	0.36	0.01	0.76	0.18	0.07	0.75	0.04	567.11	2.71
<i>Catopsis sessiliflora</i>	F	0.822	16	9	11.7	7	0.18	0.81	0.00	0.80	0.19	0.01	0.70	0.23	4.43	0.62
<i>Cecropia obtusifolia</i>	T	1.012	28	5	26	23	1.00	0.00	0.00	0.83	0.14	0.04	0.53	0.16	53605.06	2.52
<i>Centaurea corymbosa</i>	O	0.996	6	4	4.8	2	0.85	0.15	0.00	0.80	0.2	0.00	0.41	0.50	77.70	1.25
<i>Chamaecrista keyensis</i>	O	0.963	15	6	10.1	9	0.31	0.69	0.00	0.76	0.23	0.01	0.70	0.17	2.06	2.02
<i>Chamaedorea radicalis</i>	P	1.120	47	8	44.7	39	0.55	0.43	0.02	0.82	0.12	0.05	0.80	0.15	2.40	3.24
<i>Chamaelirium luteum</i>	F	1.004	58	13	50	45	0.94	0.01	0.06	0.87	0.12	0.01	0.85	0.52	32.21	2.73
<i>Chlorocardium rodiei</i>	T	0.998	446	206	301.6	240	0.62	0.38	0.00	0.98	0.02	0.00	0.69	0.08	126.36	0.00
<i>Cimicifuga elata</i>	F	1.154	33	6	11.1	27	0.38	0.60	0.02	0.81	0.19	0.00	0.89	0.25	3.11	2.28
<i>Cirsium acaule</i>	O	0.983	46	3	31.9	43	0.97	0.03	0.00	0.99	0.01	0.00	0.76	0.55	0.05	2.28
<i>Cirsium pannonicum</i>	O	0.944	98	3	16.1	95	0.93	0.03	0.04	0.99	0.01	0.00	0.84	0.43	0.05	1.12
<i>Cirsium vulgare</i>	O	2.750	6	4	4.5	2	0.70	0.30	0.00	0.70	0.3	0.00	0.41	0.36	47.84	0.84
<i>Cleome droserifolia</i>	O	1.118	76	8	34	68	0.13	0.87	0.00	0.79	0.15	0.05	0.78	0.03	18255.78	0.00
<i>Clidemia hirta</i>	S	1.511	13	3	11.2	10	0.46	0.53	0.01	0.71	0.17	0.13	0.83	0.17	4.32	2.09
<i>Clintonia borealis</i>	F	1.128	13	4	8.0	9	0.54	0.23	0.23	0.81	0.05	0.14	0.88	0.26	0.32	2.43
<i>Coccothrinax readii</i>	P	1.055	116	96	114.8	20	0.57	0.43	0.00	0.93	0.06	0.01	0.34	0.02	58.74	4.25
<i>Coryphantha robbisorum</i>	O	1.050	41	8	40.2	33	0.97	0.03	0.00	0.91	0.09	0.00	0.67	0.25	33.13	3.28
<i>Cryptantha flava</i>	O	0.864	13	2	5.4	11	0.78	0.18	0.04	0.88	0.07	0.05	0.72	0.17	0.70	2.11
<i>Cynoglossum virginianum</i>	F	1.103	11	2	7.1	9	0.45	0.50	0.05	0.67	0.2	0.12	0.65	0.30	3.37	0.40
<i>Cypripedium acaule</i>	F	1.081	25	4	10	21	0.02	0.96	0.02	0.00	0.45	0.55	0.41	0.52	0.03	1.28
<i>Cytissus scoparius</i>	S	1.217	23	6	20.3	17	0.02	0.98	0.00	0.76	0.17	0.06	0.80	0.16	843.91	2.68
<i>Dacrydium elatum</i>	T	0.993	172	46	116.9	126	0.20	0.02	0.78	0.72	0.24	0.05	0.95	0.07	0.86	3.87
<i>Danthonia sericea</i>	O	1.196	41	2	32.7	39	0.35	0.64	0.01	0.73	0.19	0.08	0.81	0.13	4.57	2.92
<i>Daucus carota</i>	O	1.367	6	4.0	4.2	2	0.43	0.56	0.00	0.60	0.23	0.17	0.77	0.29	12.15	0.99

Species	LF	$\lambda$ (year <sup>-1</sup> )	$L$ (years)	$\alpha$ (years)	$\mu$ (years)	$L\alpha$	$S\sigma$	$S\gamma$	$S\phi$	$E\sigma$	$E\gamma$	$E\phi$	$\sigma$	$\gamma$	$\phi$	$S$
<i>Dicerandra frutescens</i>	O	0.813	8	4	5.9	4	0.58	0.42	0.00	0.80	0.14	0.06	0.53	0.27	12.84	1.38
<i>Dicorynia guianensis</i>	T	1.001	349	60	188.8	289	0.98	0.00	0.02	1.00	0	0.00	0.99	0.11	0.01	4.23
<i>Dicymbe altsonii</i>	T	1.028	567	211	467.1	356	0.33	0.67	0.00	0.95	0.04	0.01	0.92	0.11	195.65	4.19
<i>Digitaria eriantha</i>	O	1.203	10	4	11.2	6	0.70	0.22	0.08	0.73	0.27	0.00	0.57	0.65	2.35	2.11
<i>Dipsacus sylvestris</i>	O	2.3219	6	4	4.5	2	0.12	0.88	0.01	0.54	0.27	0.19	3.68	0.20	322.38	1.09
<i>Disporum smilacinum</i>	F	1.427	12	3	5.9	9	0.59	0.39	0.01	0.73	0.27	0.01	0.84	0.36	0.68	1.96
<i>Duguetia neglecta</i>	T	1.006	256	101	199.6	155	0.62	0.38	0.01	0.97	0.02	0.01	0.97	0.02	0.64	4.09
<i>Echeveria longissima</i>	O	0.954	30	4	16.1	26	0.49	0.44	0.07	0.89	0.1	0.02	0.92	0.12	0.09	2.19
<i>Echinacea angustifolia</i>	O	1.025	41	5	32.3	36	0.57	0.31	0.12	0.91	0.05	0.04	0.87	0.24	0.09	3.25
<i>Encephalartos cycadifolius</i>	P	1.031	423	34	7.1	389	0.551	0.45	0.00	0.72	0.28	0.00	0.90	0.12	2.00	4.65
<i>Encephalartos villosus</i>	P	1.047	281	22	279.8	259	0.515	0.48	0.00	0.72	0.28	0.00	0.95	0.12	0.13	4.32
<i>Epilobium latifolium</i>	O	1.949	33	6	19.5	27	0.91	0.08	0.01	0.92	0.08	0.00	0.76	0.24	0.00	0.20
<i>Eremospatha macrocarpus</i>	F	0.979	60	18	55.7	42	0.80	0.01	0.19	0.99	0.01	0.00	0.71	0.02	0.10	0.99
<i>Eryngium cuneifolium</i>	O	0.797	9	5	6.9	4	0.00	1.00	0.00	0.70	0.23	0.07	0.53	0.19	260.19	1.40
<i>Erythronium japonicum</i>	F	1.001	14	2	23.1	12	0.33	0.66	0.00	0.77	0.2	0.03	0.86	0.07	2.34	2.37
<i>Escontria chiotilla</i>	T	1.019	68	53	65.4	15	0.73	0.27	0	0.80	0.20	0.00	0.87	0.09	0.67	2.97
<i>Eupatorium perfoliatum</i>	F	0.837	10	2.0	6.3	8	0.50	0.19	0.31	0.67	0.31	0.02	0.45	0.35	0.24	0.90
<i>Eupatorium resinolum</i>	F	0.865	10	5.0	6.5	5	0.42	0.22	0.36	0.76	0.19	0.05	0.54	0.27	0.42	1.38
<i>Euterpe edulis</i>	P	1.258	199	23	239.6	176	0.52	0.48	0.00	0.80	0.16	0.04	0.51	0.07	98.99	3.15
<i>Euterpe precatorea</i>	P	0.982	114	50	94.5	64	0.66	0.34	0.00	0.96	0.03	0.01	0.93	0.04	3.37	2.19
<i>Fagus grandifolia</i>	T	0.939	28	27	23.4	1	0.75	0.14	0.11	0.91	0.05	0.04	0.86	0.11	0.41	3.19
<i>Festuca gracillima</i>	O	0.799	8	3	3.9	5	0.80	0.20	0.00	0.92	0.08	0.00	0.62	0.33	0.63	1.59
<i>Fritillaria meleagris</i>	O	1.018	19	3	11.0	16	0.39	0.40	0.21	0.81	0.18	0.02	0.66	0.15	0.33	2.60
<i>Fumana procumbens</i>	S	1.018	17	5	12.8	12	0.47	0.29	0.24	0.84	0.09	0.07	0.82	0.22	0.06	2.35
<i>Garcinia lucida</i>	T	1.063	294	82	195.7	212	0.35	0.65	0.00	0.93	0.05	0.02	0.98	0.13	25.46	4.46
<i>Gardenia actinocarpa</i>	S	1.143	13	6	11.1	7	0.76	0.24	0.00	0.73	0.18	0.09	0.71	0.10	112.95	2.10
<i>Gaura neomexicana</i>	O	1.521	6	5	4.5	1	0.92	0.08	0.00	0.64	0.25	0.11	0.66	0.24	207.29	1.35
<i>Gentiana pneumonanthe</i>	O	1.335	11	2	8.9	9	0.17	0.83	0.00	0.75	0.18	0.07	0.63	0.38	581.83	1.61
<i>Geonoma brevispatha</i>	P	1.039	21	4.0	16.8	17	0.80	0.20	0.00	0.95	0.05	0.00	0.88	0.07	0.70	2.64
<i>Geonoma macrostachys</i>	P	0.977	132	26	53.9	106	0.72	0.27	0.01	0.95	0.04	0.01	0.87	0.05	1.32	4.18
<i>Geonoma orbignyana</i>	P	1.074	78	34	70.4	44	0.77	0.21	0.02	0.92	0.06	0.02	0.97	0.06	4.88	3.92
<i>Geranium sylvaticum</i>	F	1.082	44	14	192.3	30	0.16	0.82	0.02	0.68	0.32	0.00	0.82	0.14	0.79	1.10
<i>Geum reptans</i>	O	1.056	21	4	122.9	17	0.41	0.58	0.01	0.92	0.08	0.01	0.99	0.24	0.13	4.00
<i>Geum rivale</i>	O	1.014	29	8	25.3	21	0.61	0.37	0.02	0.85	0.11	0.04	0.79	0.24	0.37	2.70
<i>Grias peruviana</i>	T	1.035	30	19	32.4	11	0.67	0.33	0.00	0.92	0.06	0.02	7.07	0.13	210.20	0.93
<i>Guarianthe aurantiaca</i>	F	0.987	40	9	35.8	31	0.59	0.20	0.21	0.93	0.05	0.02	0.92	0.22	0.06	2.23
<i>Haplopappus radiatus</i>	O	0.918	10	4	7.3	6	0.84	0.16	0.00	0.89	0.11	0.00	0.65	0.27	2.41	1.67

Species	LF	$\lambda$ (year <sup>-1</sup> )	$L$ (years)	$\alpha$ (years)	$\mu$ (years)	$L\alpha$	$S\sigma$	$S\gamma$	$S\phi$	$E\sigma$	$E\gamma$	$E\phi$	$\sigma$	$\gamma$	$\phi$	$S$
<i>Harrisia fragrans</i>	F	0.945	37	3	16.5	34	0.85	0.11	0.04	0.97	0.02	0.00	0.84	0.10	0.02	0.43
<i>Helenium virginicum</i>	O	1.115	81	79	79.6	2	0.11	0.89	0.00	0.90	0.1	0.00	0.45	0.17	3751.83	3.17
<i>Helianthemum juliae</i>	S	1.246	14	3	14.3	11	0.67	0.33	0.00	0.88	0.12	0.00	0.87	0.22	1.04	2.30
<i>Helianthus divaricata</i>	O	1.100	11	2.0	6.4	9	0.61	0.39	0.00	0.80	0.2	0.00	0.72	0.88	0.04	2.18
<i>Heteropogon contortus</i>	O	0.974	21	2	6.6	19	0.33	0.52	0.15	0.74	0.19	0.07	0.82	0.30	0.59	2.67
<i>Hieracium floribundum</i>	O	1.012	19	2	14.4	17	0.94	0.06	0.01	0.98	0.02	0.00	0.61	0.26	0.29	2.28
<i>Hilaria mutica</i>	O	0.972	11	2	6.5	9	0.42	0.58	0.00	0.80	0.2	0.00	0.68	0.19	1.58	2.02
<i>Himantoglossum hircinum</i>	O	1.319	17	8	10.3	9	0.94	0.06	0.00	0.81	0.19	0.00	0.74	0.24	285.65	2.03
<i>Hudsonia montana</i>	S	0.975	25	3	17.8	22	0.16	0.83	0.02	0.81	0.15	0.04	0.73	0.08	0.00	2.00
<i>Hypericum cumulicola</i>	O	1.325	26	6	3.2	20	0.04	0.96	0.00	0.81	0.12	0.07	0.60	0.15	438.07	2.15
<i>Hypochaeris radicata</i>	O	0.811	11	6	7.2	5	0.59	0.41	0.00	0.84	0.16	0.00	0.49	0.09	1.38	1.30
<i>Ipomoea leptophylla</i>	O	1.136	35	11	27.2	24	0.16	0.84	0.00	0.97	0.03	0.00	0.94	0.55	9.99	3.08
<i>Iriartea deltoidea</i>	P	1.081	67	29	9.1	38	0.49	0.49	0.02	0.95	0.03	0.02	0.92	0.23	1.67	3.82
<i>Iris germanica</i>	O	0.950	44	33	42.5	11	0.53	0.47	0.00	1.00	0	0.00	0.36	0.43	62.00	0.02
<i>Isatis tinctoria</i>	O	1.237	4	3.0	3.1	1	0.94	0.06	0.00	0.58	0.23	0.19	0.36	0.43	62.00	0.33
<i>Laccosperma secundiflorum</i>	F	0.961	33	29	32.4	4	0.86	0.14	0.00	0.98	0.02	0.00	0.88	0.42	2.85	0.99
<i>Lathyrus vernus</i>	F	1.021	42	9	34.5	33	0.42	0.51	0.07	0.85	0.12	0.04	0.84	0.18	0.24	3.10
<i>Limonium carolinianum</i>	O	1.008	25	5	18.1	20	0.01	0.99	0.00	0.75	0.21	0.04	0.59	0.07	3711.56	2.66
<i>Limonium delicatulum</i>	O	1.264	19	6	15	13	0.61	0.39	0.00	0.75	0.16	0.09	0.59	0.02	3711.56	2.51
<i>Lindera benzoin</i>	S	1.017	59	4	65.6	55	0.50	0.50	0.00	0.91	0.07	0.03	0.60	0.01	29.83	3.53
<i>Lindera umbellata</i>	S	1.037	77	26	47.9	51	0.64	0.32	0.04	0.96	0.03	0.01	0.84	0.10	0.23	3.35
<i>Lomatium bradshawii</i>	O	0.976	11	3	8.2	8	0.58	0.35	0.06	0.76	0.16	0.09	0.71	0.22	1.13	1.90
<i>Lomatium cookii</i>	O	1.021	12	6	9.5	6	0.76	0.22	0.02	0.81	0.1	0.09	0.76	0.14	3.03	2.01
<i>Lonicera maakii</i>	S	2.771			2.0	0	0.23	0.77	0.00	0.77	0.23	0.00	0.76	0.05	178.65	0.03
<i>Lupinus arboreus</i>	S	1.398	14	4	8.5	10	0.02	0.98	0.00	0.74	0.17	0.09	0.56	0.13	3.26	2.07
<i>Lupinus tidestromii</i>	O	0.919	9	4	7.2	5	0.64	0.36	0.00	0.84	0.16	0.00	0.71	0.40	0.56	1.60
<i>Mammillaria crucigera</i>	O	0.936	27	2	20.8	25	1.00	0.00	0.00	1.00	0	0.00	0.79	0.12	1.06	0.16
<i>Mammillaria pectinifera</i>	O	0.744	12	5	8.6	7	0.37	0.63	0.00	0.89	0.1	0.00	0.51	0.10	2.23	0.38
<i>Manglietia fordiana</i>	T	0.956	110	34	78.4	76	0.58	0.42	0.00	0.96	0.03	0.01	0.91	0.07	0.56	0.90
<i>Manilkara zapota</i>	T	1.030	178	53	176.9	125	0.39	0.61	0.00	0.92	0.07	0.01	0.87	0.12	1041.18	4.66
<i>Mauritia flexuosa</i>	P	1.046	31	24	34.7	7	0.96	0.04	0.00	0.85	0.01	0.13	0.00	0.09	0.18	2.41
<i>Miconia albicans</i>	S	1.185	153	8	175.1	145	0.37	0.63	0.00	0.80	0.16	0.04	0.84	0.09	1086.82	2.97
<i>Miconia prasina</i>	S	0.997	82	11	45.4	71	0.64	0.36	0.00	0.95	0.05	0.00	0.87	0.15	0.39	3.69
<i>Minuartia obtusiloba</i>	O	1.000	453	3	169.2	450	0.05	0.95	0.00	0.99	0.01	0.01	0.96	0.06	0.38	3.82
<i>Myrsine guianensis</i>	T	1.101	60		11.4	60	0.86	0.13	0.01	0.88	0.10	0.03	11.90	0.26	13.50	3.66
<i>Narcissus pseudonarcissus</i>	F	0.976	12	1	18.3	11	0.73	0.27	0.00	0.97	0.03	0.00	0.88	0.45	0.07	0.51

Species	LF	$\lambda(\text{year}^{-1})$	$L$ (years)	$\alpha$ (years)	$\mu$ (years)	$L\alpha$	$S\sigma$	$S\gamma$	$S\phi$	$E\sigma$	$E\gamma$	$E\phi$	$\sigma$	$\gamma$	$\phi$	$S$
<i>Neobuxbaumia macrocephala</i>	T	1.033	85	37	72.8	48	0.55	0.45	0.00	0.90	0.08	0.02	0.85	0.04	234.13	3.95
<i>Neobuxbaumia mezcalaensis</i>	T	1.128	81	45	72.7	36	0.42	0.58	0.00	0.80	0.18	0.02	0.89	0.05	1367.94	3.83
<i>Neobuxbaumia tetetzo</i>	T	1.036	117	48	101.1	69	0.61	0.39	0.00	0.92	0.06	0.02	0.86	0.03	157.98	4.39
<i>Nothofagus fusca</i>	T	1.006	246	42	222.8	204	0.24	0.76	0.00	0.79	0.01	0.20	0.96	0.01	2.08	3.52
<i>Panax quinquefolium</i>	F	1.045	26	5	26.6	21	0.47	0.05	0.48	0.05	0.80	0.15	14.50	0.00	3.01	2.04
<i>Parashorea chinensis</i>	T	0.995	249	41	124.8	208	0.75	0.25	0.00	0.69	0.31	0.00	0.94	0.11	1.41	4.01
<i>Paronychia pulvinata</i>	O	1.000	387	3	183.6	384	0.38	0.62	0.00	0.64	0.36	0.00	0.94	0.12	0.07	1.62
<i>Pedicularis furbishiae</i>	O	1.035	12	3	6.3	9	0.73	0.27	0.00	0.60	0.40	0.00	0.82	0.20	7.26	1.80
<i>Pentaclethra macroloba</i>	T	1.002	138	79	113.7	59	0.49	0.51	0.00	0.85	0.04	0.11	0.85	0.20	216.08	3.68
<i>Periandra mediterranea</i>	S	1.071	53	8.0	34.2	45	0.62	0.31	0.06	0.71	0.11	0.18	0.87	0.23	0.58	3.49
<i>Phaseolus lunatus</i>	O	0.768	6	2	3.8	4	0.14	0.86	0.00	0.57	0.30	0.12	0.21	0.28	169.33	1.42
<i>Phyllanthus emblica</i>	T	0.992	20	7	18.2	13	0.60	0.40	0.00	0.71	0.09	0.19	0.62	0.20	549.35	2.10
<i>Phytelephas seemanii</i>	P	1.059	79	18	50.9	61	0.33	0.67	0.00	0.88	0.08	0.03	5.35	0.03	46.23	3.86
<i>Pinguicula alpina</i>	O	1.033	41	10	22.6	31	0.38	0.62	0.00	0.66	0.16	0.17	0.83	0.10	1.54	3.28
<i>Pinguicula villosa</i>	O	0.997	13	5	6.6	8	0.43	0.57	0.00	0.66	0.00	0.34	0.72	0.17	3.99	2.10
<i>Pinguicula vulgaris</i>	O	1.086	35	10	25.4	25	0.31	0.69	0.00	0.67	0.19	0.14	0.87	0.09	4.72	3.11
<i>Pinus kwangtungensis</i>	T	0.978	201	58	119.9	143	0.38	0.61	0.00	0.92	0.07	0.00	0.94	0.06	0.37	0.37
<i>Pinus lambertiana</i>	T	1.027	47	21	45.9	26	0.37	0.61	0.02	0.67	0.33	0.00	0.91	0.21	0.66	3.15
<i>Pinus nigra</i>	T	1.530	78	8	74.8	70	0.59	0.41	0.00	0.66	0.27	0.07	0.72	0.14	140.43	2.22
<i>Pinus palustris</i>	T	0.998	226	38	158	188	0.50	0.49	0.00	0.97	0.03	0.00	0.87	0.94	0.03	3.55
<i>Pinus sylvestris</i>	T	1.204	20	12	17.9	8	0.31	0.69	0.00	0.58	0.42	0.00	0.85	0.18	15.47	2.60
<i>Plantago coronopus</i>	O	1.142	4	2	3	2	0.85	0.15	0.00	0.55	0.25	0.20	0.32	0.25	91.43	0.73
<i>Plantago media</i>	O	0.940	23	8	19.9	15	0.76	0.23	0.01	0.81	0.06	0.13	0.62	0.24	0.33	0.66
<i>Podococcus barteri</i>	P	1.013	34	10	25.4	24	0.63	0.16	0.21	0.92	0.04	0.04	5.81	0.17	0.81	3.08
<i>Podophyllum peltatum</i>	F	1.158	13	3	5.2	10	1.00	0.00	0.00	0.48	0.00	0.52	0.38	0.44	1.22	1.41
<i>Potentilla anserina</i>	O	0.883	7		3	7	0.26	0.35	0.39	0.80	0.15	0.05	0.87	0.19	0.32	1.62
<i>Primula farinosa</i>	O	1.032	19	6	16.2	13	0.82	0.18	0.00	0.80	0.07	0.13	0.87	0.31	0.22	2.43
<i>Primula veris</i>	O	1.117	53	10	48.9	43	0.44	0.56	0.00	0.70	0.15	0.15	0.72	0.22	2.84	1.00
<i>Prioria copaifera</i>	T	1.019	205	98	184.4	107	0.70	0.23	0.07	0.97	0.02	0.01	0.99	0.14	0.07	3.88
<i>Prosopis glandulosa</i>	T	1.2949	80	9	72.8	71	0.10	0.89	0.00	0.75	0.18	0.07	0.98	0.12	3.19	2.98
<i>Prunus serotina</i>	T	1.216	6	2	0.5	4	0.90	0.10	0.00	0.59	0.24	0.17	0.62	0.12	94.43	0.04
<i>Psidium guajava</i>	T	0.994	176	9	121	167	0.96	0.04	0.00	0.85	0.11	0.04	0.66	0.19	39.77	2.05
<i>Pterocarya rhoifolia</i>	T	1.103	55	23	53.5	32	0.20	0.80	0.00	0.68	0.10	0.22	0.82	0.17	382.34	3.54
<i>Pterocereus gaumeri</i>	T	1.000	38	14	32.8	24	0.83	0.17	0.01	0.58	0.09	0.33	0.81	0.07	5.35	2.63
<i>Ranunculus acris</i>	O	1.206	6	3	3	3	0.71	0.26	0.03	0.98	0.02	0.00	0.85	0.18	0.05	0.70

Species	LF	$\lambda(\text{year}^{-1})$	$L$ (years)	$\alpha$ (years)	$\mu$ (years)	$L\alpha$	$S\sigma$	$S\gamma$	$S\phi$	$E\sigma$	$E\gamma$	$E\phi$	$\sigma$	$\gamma$	$\phi$	$S$
<i>Ranunculus bulbosus</i>	O	1.8953	6	2	5	4	0.41	0.57	0.02	0.75	0.17	0.09	0.25	0.16	3.70	1.09
<i>Ranunculus repens</i>	O	0.498	6	4	2	2	0.59	0.40	0.00	0.86	0.12	0.02	0.73	0.73	37.15	0.77
<i>Rhizophora mangle</i>	T	1.078	75	14	15.1	61	0.43	0.57	0.00	0.91	0.08	0.01	0.74	0.19	15.47	0.08
<i>Rhopalostylis sapida</i>	P	1.007	222	62	166.2	160	0.87	0.13	0.00	0.85	0.03	0.12	0.88	0.04	300.76	4.60
<i>Sabal yapa</i>	P	1.006	91	59	84.2	32	0.63	0.37	0.00	0.94	0.04	0.02	0.84	0.05	42.12	3.23
<i>Sanicula europaea</i>	F	0.893	15	6	11.1	9	0.73	0.21	0.06	0.45	0.09	0.46	0.72	0.24	0.80	0.96
<i>Scabiosa columbaria</i>	O	1.03	12	7	7	5	0.35	0.65	0.00	0.85	0.15	0.00	0.33	0.43	8.41	1.98
<i>Scaphium borneense</i>	T	1.014	306	105	232.6	201	0.55	0.44	0.01	0.98	0.00	0.02	0.90	0.21	3.26	3.46
<i>Setaria incrassata</i>	O	0.936	18	4	5.8	14	0.50	0.50	0.00	0.72	0.28	0.00	0.76	0.18	2.16	2.50
<i>Silene acaulis</i>	O	1.010	338	25	274.4	313	0.69	0.29	0.02	0.76	0.00	0.24	0.81	0.09	17.19	5.41
<i>Stryhnodendron excelsum</i>	T	1.047	125	79	104.7	46	0.76	0.24	0.00	0.90	0.08	0.02	0.85	0.32	1835.05	4.36
<i>Syzygium jambos</i>	T	1.185	84	10	55.8	74	0.11	0.89	0.00	0.73	0.07	0.20	0.85	0.08	458.76	3.03
<i>Tachigali vasquezii</i>	T	1.053	71	58	59.0	13	0.55	0.14	0.01	0.68	0.00	0.32	0.93	0.00	2.10	3.84
<i>Taxus floridana</i>	T	0.965	76	14	51.4	62	0.60	0.40	0.00	0.90	0.10	0.00	0.89	0.36	9.73	0.39
<i>Themeda triandra</i>	O	0.997	52	2	9.9	50	0.51	0.45	0.04	0.79	0.12	0.09	0.84	0.12	0.81	2.53
<i>Thrinax radiata</i>	P	1.129	88	74	87.3	14	0.51	0.49	0.00	0.88	0.11	0.02	8.40	0.05	553.33	3.91
<i>Tillandsia multicaulis</i>	F	0.955	22	11	18.0	11	0.27	0.73	0.00	0.61	0.11	0.28	0.72	0.15	18.72	1.79
<i>Tillandsia punctulata</i>	F	0.731	10	5	6.4	5	0.21	0.78	0.00	0.63	0.17	0.20	0.69	0.11	0.58	0.03
<i>Tolumnia variegata</i>	F	1.359	16	9	10.7	7	0.41	0.59	0.00	0.18	0.21	0.61	0.79	0.15	140.77	2.16
<i>Trillium grandiflorum</i>	F	0.968	49	22	30.3	27	0.97	0.01	0.02	0.03	0.97	0.00	0.76	0.20	117.16	1.93
<i>Ulex gallii</i>	S	1.310	34	2	20.6	32	0.43	0.57	0.00	0.99	0.01	0.01	0.21	0.15	622.08	2.58
<i>Vatica hainanensis</i>	T	1.000	63	22	46.9	41	0.71	0.29	0.00	0.43	0.10	0.47	0.71	0.08	394.84	3.39
<i>Viola fimbriatula</i>	F	1.484	16			16	1.00	0.00	0.00	1.00	0.00	0	0.85	0.09	0.12	1.17
<i>Werauhia sanguinolenta</i>	F	1.109	20	12	18.7	8	0.70	0.30	0.01	0.72	0.14	0.14	0.80	0.08	22.05	2.45
<i>Zamia amblyphyllidia</i>	P	0.979	10	4	41.4	6	0.16	0.84	0.00	0.55	0.45	0.00	0.80	0.18	0.47	0.00
<i>Zea diploperennis</i>	O	0.765	11	5	7.4	6	0.08	0.92	0.00	0.91	0.09	0.00	0.70	0.16	55.84	0.82

Note: All demographic parameters are defined in the thesis. Missing values in the table indicate that values for these parameters could not be computed employing the method used. LF = life form.

## Appendix 2.

Phylogenetic tree in newick format, employed to conduct PGLS of life history parameters. The tree contains all 207 species used in this dissertation.

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\_variegata:8.666667,Guarianthe\_aurantiaca:8.666667):8.666667)Orchidaceae:81.0)Asparagale  
s:10.800003):10.800003,((Erythronium\_japonicum:24.0,Fritillaria\_meleagris:24.0):24.0,((Clintonia\_bor  
ealis:20.571428,Disporum\_smilacinum:20.571428):20.571428,(Calochortus\_lyallii:34.285713,(Calochort  
us\_macrocarpus:27.428572,(Calochortus\_obispoensis:20.571428,(Calochortus\_albus:13.714286,(Caloch  
ortus\_tiburoniensis:6.857143,Calochortus\_pulchellus:6.857143):6.857143):6.857142):6.857143):6.85714  
1)Calochortus:6.857143):6.857143)Liliaceae:48.0,(Chamaelirium\_luteum:48.0,Trillium\_grandiflorum:48  
.0):48.0)Liliales:32.600006):10.799988,Borderea\_chouardii:139.399994):10.800003)Monocots:10.8)mon  
ocotneudicot:18.0,((Chlorocardium\_rodiei:34.0,(Lindera\_benzoin:17.0,Lindera\_umbellata:17.0)Lindera:1  
7.0)Lauraceae:108.666672,(Duguetia\_neglecta:106.333336,(Magnolia\_salicifolia:70.0,Manglietia\_fordia  
na:70.0)Magnoliaceae:36.333336):36.333336):36.333332)angiosperms:146.0,((((((Pinus\_palustris:106.33  
3336,(Pinus\_nigra:53.166668,Pinus\_sylvestris:53.166668):53.166668):53.166664,(Pinus\_kwangtungensi  
s:79.75,Pinus\_lambertiana:79.75):79.75)Pinus:53.166672,(Abies\_concolor:106.333336,Abies\_magnifica:  
106.333336):106.333336)Pinaceae:53.166672,((Dacrydium\_elatum:132.916672,(Araucaria\_cunninghami  
i:66.458336,Araucaria\_hunsteinii:66.458336)Araucariaceae:66.458336):66.458328,(Taxus\_floridana:132  
.916672,(Calocedrus\_macrolepis:66.458336,Callitris\_intratropica:66.458336):66.458336):66.458328):66.  
458344):53.166668,(Zamia\_amblyphyllidia:212.666672,(Encephalartos\_cycadifolius:106.333336,Enceph  
alartos\_villosus:106.333336):106.333336):106.333336)gymnosperms:6.0)seedplants:1.0;

### Appendix 3

Table 12: Trends in mortality and reproductive value curves for species used in chapter four.

Species	Lifeform	$\nu x$ trend	$\mu x$ trend	$L$
<i>Abies concolor</i>	T	1	1	51
<i>Abies magnifica</i>	T	1	1	44
<i>Acacia bilimekii</i>	S	3	2	467
<i>Acer saccharum</i>	T	1	1	38
<i>Aconitum noveboracense</i>	O	3	2	39
<i>Aechmea nudicaulis</i>	F	2	1	12
<i>Agrimonia eupatoria</i>	O	1	1	45
<i>Agropyron repens</i>	O	2	1	6
<i>Alnus incana</i>	T	1	1	32
<i>Ambrosia deltoidea</i>	S	1	3	11
<i>Andropogon semiberberis</i>	O	1	1	8
<i>Anemone patens</i>	O	1	3	13
<i>Annamocarya sinensis</i>	T	2	1	189
<i>Aquilaria malaccensis</i>	T	1	2	16
<i>Aquilegia chrysantha</i>	F	2	2	8
<i>Aquilegia sp</i>	O	2	2	12
<i>Araucaria cunninghamii</i>	T	2	3	256
<i>Araucaria hunsteinii</i>	T	1	1	182
<i>Ardisia elliptica</i>	S	2	3	188
<i>Arisaema serratum</i>	F	2	2	23
<i>Arisaema triphyllum</i>	F	3	1	24
<i>Aristida bipartita</i>	O	1	1	25
<i>Armeria maritima</i>	O	1	1	28
<i>Aster amellus</i>	O	1	1	19
<i>Astragalus scaphoides</i>	O	1	1	15
<i>Astragalus tyghensis</i>	O	1	1	13
<i>Astrocaryum mexicanum</i>	P	1	1	123
<i>Avicenia marina</i>	T	1	1	39
<i>Banksia ericifolia</i>	S	1	1	45
<i>Betula nana</i>	S	1	1	11
<i>Borderea chouardii</i>	O	1	1	133
<i>Bothriochloa insculpta</i>	O	1	3	14
<i>Bothriochloa ischaemum</i>	O	1	1	16
<i>Bouteloua rigidiseta</i>	O	1	3	13
<i>Brosimum alicastrum</i>	T	3	1	201
<i>Bursera glabrifolia</i>	T	1	1	71
<i>Calathea ovandensis</i>	F	3	1	15
<i>Callitris intratropica</i>	T	2	1	20
<i>Calluna vulgaris</i>	S	2	1	20
<i>Calocedrus macrolepis</i>	T	2	1	144
<i>Calochortus albus</i>	O	1	1	16
<i>Calochortus macrocarpus</i>	F	1	1	26
<i>Calochortus obispoensis</i>	O	1	3	70



Species	Lifeform	$\nu x$ trend	$\mu x$ trend	$L$
<i>Calochortus pulchellus</i>	F	3	1	30
<i>Calochortus tiburonensis</i>	O	1	2	57
<i>Camellia japonica</i>	T	1	1	178
<i>Carex humilis</i>	O	1	1	16
<i>Cassia nemophila</i>	S	1	2	44
<i>Catopsis sessiliflora</i>	F	3	1	16
<i>Cecropia obtusifolia</i>	T	2	1	28
<i>Centaurea corymbosa</i>	O	1	1	6
<i>Chamaecrista keyensis</i>	O	1	1	15
<i>Chamaedorea radicalis</i>	P	1	1	47
<i>Chamaelirium luteum</i>	F	3	1	58
<i>Chlorocardium rodiei</i>	T	1	1	446
<i>Cimicifuga elata</i>	F	3	1	33
<i>Cirsium acaule</i>	O	1	1	46
<i>Cirsium pannonicum</i>	O	1	3	98
<i>Cirsium vulgare</i>	O	2	2	6
<i>Cleome droserifolia</i>	O	2	1	76
<i>Clidemia hirta</i>	S	1	1	13
<i>Clintonia borealis</i>	F	3	3	13
<i>Coccothrinax readii</i>	P	2	1	116
<i>Coryphantha robbisorum</i>	O	1	1	41
<i>Cryptantha flava</i>	O	1	1	13
<i>Cynoglossum virginianum</i>	F	1	3	11
<i>Cypripedium acaule</i>	F	3	1	25
<i>Cytissus scoparius</i>	S	2	1	23
<i>Dacrydium elatum</i>	T	2	1	172
<i>Danthonia sericea</i>	O	1	1	41
<i>Daucus carota</i>	O	1	1	6
<i>Dicerandra frutescens</i>	O	1	3	8
<i>Dicorynia guianensis</i>	T	1	1	349
<i>Dicymbe altsonii</i>	T	1	1	567
<i>Digitaria eriantha</i>	O	1	1	10
<i>Dipsacus sylvestris</i>	O	1	2	6
<i>Disporum sessile</i>	F	3	1	8
<i>Disporum smilacinum</i>	F	3	1	12
<i>Duguetia neglecta</i>	T	1	1	256
<i>Echeveria longissima</i>	O	1	1	30
<i>Echinacea angustifolia</i>	O	1	3	41
<i>Encephalartos cycadifolius</i>	P	1	2	423
<i>Encephalartos villosus</i>	P	3	1	281
<i>Epilobium latifolium</i>	O	1	2	33
<i>Eremospatha macrocarpus</i>	F	1	1	60
<i>Eryngium cuneifolium</i>	O	1	1	9
<i>Erythronium japonicum</i>	F	3	2	14
<i>Escontria chiotilla</i>	T	3	1	68
<i>Eupatorium perfoliatum</i>	F	1	1	10

Species	Lifeform	vx trend	$\mu$ x trend	L
<i>Eupatorium resinosum</i>	F	3	3	10
<i>Euterpe edulis</i>	P	3	2	199
<i>Euterpe precatoria</i>	P	1	1	114
<i>Fagus grandifolia</i>	T	1	2	28
<i>Festuca gracillima</i>	O	1	3	8
<i>Fritillaria meleagris</i>	O	1	2	19
<i>Fumana procumbens</i>	S	1	1	17
<i>Garcinia lucida</i>	T	1	3	294
<i>Gardenia actinocarpa</i>	S	1	1	13
<i>Gaura neomexicana</i>	O	1	1	6
<i>Gentiana pneumonanthe</i>	O	2	2	11
<i>Geonoma brevispatha</i>	P	1	1	21
<i>Geonoma macrostachys</i>	P	3	3	132
<i>Geonoma orbignyana</i>	P	3	1	78
<i>Geranium sylvaticum</i>	F	1	2	44
<i>Geum reptans</i>	O	3	2	21
<i>Geum rivale</i>	O	1	3	29
<i>Grias peruviana</i>	T	2	1	30
<i>Guarianthe aurantiaca</i>	F	3	2	40
<i>Haplopappus radiatus</i>	O	1	1	10
<i>Harrisia fragrans</i>	F	1	3	37
<i>Helenium virginicum</i>	O	1	1	81
<i>Helianthemum juliae</i>	S	1	1	14
<i>Helianthus divaricata</i>	O	3	1	11
<i>Heteropogon contortus</i>	O	1	1	21
<i>Hieracium floribundum</i>	O	1	2	19
<i>Hilaria mutica</i>	O	1	3	11
<i>Himantoglossum hircinum</i>	O	1	1	17
<i>Hudsonia montana</i>	S	2	2	25
<i>Hypericum cumulicola</i>	O	2	2	26
<i>Hypochaeris radicata</i>	O	1	1	11
<i>Ipomoea leptophylla</i>	O	1	3	35
<i>Iriartea deltoidea</i>	P	1	2	67
<i>Iris germanica</i>	O	1	1	44
<i>Isatis tinctoria</i>	O	1	3	4
<i>Laccosperma secundiflorum</i>	F	1	1	33
<i>Lathyrus vernus</i>	F	1	1	42
<i>Limonium carolinianum</i>	O	2	1	25
<i>Limonium delicatulum</i>	O	3	1	19
<i>Lindera benzoin</i>	S	1	2	59
<i>Lindera umbellata</i>	S	1	1	77
<i>Lomatium bradshawii</i>	O	1	1	11
<i>Lomatium cookii</i>	O	1	1	12
<i>Lonicera maakii</i>	S	1	1	
<i>Lupinus arboreus</i>	S	2	3	14
<i>Lupinus tidestromii</i>	O	2	2	9

Species	Lifeform	vx trend	$\mu x$ trend	<i>L</i>
<i>Mammillaria crucigera</i>	O	3	2	27
<i>Mammillaria pectinifera</i>	O	2	2	12
<i>Manglietia fordiana</i>	T	2	1	110
<i>Manilkara zapota</i>	T	2	1	178
<i>Mauritia flexuosa</i>	P	2	1	31
<i>Miconia albicans</i>	S	1	2	153
<i>Miconia prasina</i>	S	1	1	82
<i>Minuartia obtusiloba</i>	O	1	2	453
<i>Myrsine guianensis</i>	T	2	1	60
<i>Narcissus pseudonarcissus</i>	F	3	1	12
<i>Neobuxbaumia macrocephala</i>	T	1	1	85
<i>Neobuxbaumia mezcalaensis</i>	T	3	1	81
<i>Neobuxbaumia tetetzo</i>	T	1	3	117
<i>Nothofagus fusca</i>	T	1	3	246
<i>Panax quinquefolium</i>	F	3	3	26
<i>Parashorea chinensis</i>	T	2	1	249
<i>Paronychia pulvinata</i>	O	1	2	387
<i>Pedicularis furbishiae</i>	O	1	2	12
<i>Pentaclethra macroloba</i>	T	1	1	138
<i>Periandra mediterranea</i>	S	1	1	53
<i>Phaseolus lunatus</i>	O	2	2	6
<i>Phyllanthus emblica</i>	T	2	3	20
<i>Phytelephas seemanii</i>	P	2	3	79
<i>Pinguicula alpina</i>	O	1	1	41
<i>Pinguicula villosa</i>	O	1	1	13
<i>Pinguicula vulgaris</i>	O	1	1	35
<i>Pinus kwangtungensis</i>	T	1	3	201
<i>Pinus lambertiana</i>	T	1	1	47
<i>Pinus nigra</i>	T	1	1	78
<i>Pinus palustris</i>	T	1	1	226
<i>Pinus sylvestris</i>	T	1	1	20
<i>Plantago coronopus</i>	O	1	3	4
<i>Plantago media</i>	O	1	3	23
<i>Podococcus barteri</i>	P	2	3	34
<i>Podophyllum peltatum</i>	F	3	1	13
<i>Potentilla anserina</i>	O	1	1	7
<i>Primula farinosa</i>	O	1	1	19
<i>Primula veris</i>	O	1	1	53
<i>Prioria copaifera</i>	T	1	1	205
<i>Prosopis glandulosa</i>	T	1	1	80
<i>Prunus serotina</i>	T	1	3	6
<i>Psidium guajava</i>	T	1	1	176
<i>Pterocarya rhoifolia</i>	T	1	1	55
<i>Pterocereus gaumeri</i>	T	1	3	38
<i>Ranunculus acris</i>	O	2	2	6
<i>Ranunculus bulbosus</i>	O	1	2	6

Species	Lifeform	$v_x$ trend	$\mu_x$ trend	$L$
<i>Ranunculus repens</i>	O	2	2	6
<i>Rhizophora mangle</i>	T	1	1	75
<i>Rhopalostylis sapida</i>	P	1	1	222
<i>Sabal yapa</i>	P	1	1	91
<i>Sanicula europaea</i>	F	1	1	15
<i>Scabiosa columbaria</i>	O	1	1	12
<i>Scaphium borneense</i>	T	1	1	306
<i>Setaria incrassata</i>	O	1	1	18
<i>Silene acaulis</i>	O	3	1	338
<i>Strychnodendron excelsum</i>	T	1	1	125
<i>Syzygium jambos</i>	T	1	1	84
<i>Tachigali vasquezii</i>	T	2	1	71
<i>Taxus floridana</i>	T	1	3	76
<i>Themeda triandra</i>	O	1	2	52
<i>Thrinax radiata</i>	P	2	3	88
<i>Tillandsia multicaulis</i>	F	3	1	22
<i>Tillandsia punctulata</i>	F	3	1	10
<i>Tolumnia variegata</i>	F	1	1	16
<i>Trillium grandiflorum</i>	F	1	2	49
<i>Ulex gallii</i>	S	2	1	34
<i>Vatica hainanensis</i>	T	1	1	63
<i>Viola fimbriatula</i>	F	3	1	16
<i>Werauhia sanguinolenta</i>	F	1	1	20
<i>Zamia amblyphyllidia</i>	P	2	3	10
<i>Zea diploperennis</i>	O	2	1	11

## Appendix 4

Table 13: Life history data used in chapter six

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Abies concolor</i>	T	0.043059	51	3.331448566	25.56179627	0.130329204	-2.035636044	-0.079635876
<i>Abies magnifica</i>	T	0.026755	44	1.525352296	10.47014972	0.145685815	-1.805478402	-0.172440552
<i>Acacia bilimekii</i>	S	0.210909	467	4.205529501	34.27969498	0.224481651	-0.193813118	-0.013572637
<i>Acer saccharum</i>	T	0.637582	14	1.788113548	4.060809271	0.440334285	0.800983786	0.19724733
<i>Aconitum noveboracense</i>	O	-0.01005	195	0.124471056	1.311229503	0.094926979	-0.083094657	-0.063371558
<i>Aechmea nudicaulis</i>	F	0.043155	6	1.152575171	1.754807549	0.656810014	-1.076845977	-0.613654744
<i>Agrimonia eupatoria</i>	O	-0.00166	45	2.774848043	15.33230455	0.180980493	-2.800320817	-0.182641873
<i>Agropyron repens</i>	O	1.086236	6	0.333618198	0.672180201	0.49632256	0.396528146	0.589913457
<i>Alnus incana</i>	T	-0.02943	20	2.536304665	10.03957606	0.252630654	-2.831757448	-0.282059465
<i>Ambrosia deltoidea</i>	S	0.486084	8	0.697808042	1.276842391	0.546510711	-1.318460995	-1.032594943
<i>Andropogon semiberberis</i>	O	0.224742	8	1.810331646	3.32803425	0.543964247	-1.062381665	-0.319221975
<i>Anemone patens</i>	O	0.018429	13	2.28182538	4.955339513	0.460478111	-2.190502757	-0.442048976
<i>Annamocarya sinensis</i>	T	0.024518	189	2.376944026	56.94540704	0.04174075	-1.201147622	-0.021092968
<i>Aquilaria malaccensis</i>	T	0.202369	16	2.103185747	8.942814948	0.235181625	-0.293434974	-0.032812372
<i>Aquilegia chrysantha</i>	F	-0.16379	8	1.225455105	2.714708582	0.451413133	-1.670098107	-0.615203458
<i>Aquilegia sp</i>	O	-0.1632	12	1.534626433	4.670907929	0.328549921	-2.296925685	-0.491751437
<i>Araucaria cunninghamii</i>	T	0.01784	256	4.88312548	95.54405234	0.051108629	-2.460084123	-0.025748166
<i>Araucaria hunsteinii</i>	T	-0.01341	182	2.842582163	53.52234239	0.053110197	-2.087936205	-0.039010554
<i>Ardisia elliptica</i>	S	0.058646	188	4.293397571	43.50323252	0.098691461	-1.738182225	-0.039955243
<i>Arisaema serratum</i>	F	0.010414	23	2.624614204	11.67417078	0.224822324	-2.746189466	-0.235236362
<i>Arisaema triphyllum</i>	F	0.070458	24	3.777390442	11.44644161	0.330005653	-2.970891752	-0.25954719
<i>Aristida bipartita</i>	O	0.172271	25	2.225681208	4.896056071	0.454586544	-1.382231651	-0.282315323
<i>Armeria maritima</i>	O	0.377066	28	2.404834276	8.163189952	0.294594918	0.673224115	0.082470715
<i>Aster amellus</i>	O	0.058774	19	1.223785054	3.185893036	0.384126221	-1.411032207	-0.442900057
<i>Astragalus scaphoides</i>	O	0.320851	15	2.302516673	6.888021817	0.334278365	-0.092488979	-0.01342751

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Astragalus tyghensis</i>	O	0.008861	13	2.185453497	5.705020576	0.38307548	-2.134903429	-0.374214852
<i>Astrocaryum mexicanum</i>	P	0.006976	123	3.952415476	66.48123226	0.059451598	-3.488668079	-0.052475984
<i>Avicenia marina</i>	T	0.213012	39	3.042458569	9.710700309	0.313309903	-0.973958951	-0.100297499
<i>Banksia ericifolia</i>	S	0.475613	45	2.702556892	8.633218568	0.313041639	1.403512952	0.162571229
<i>Betula nana</i>	S	-0.00803	11	2.066375235	4.176525946	0.494759344	-2.099921809	-0.502791515
<i>Borderea chouardii</i>	O	0.00449	133	3.373146268	37.22239213	0.090621426	-3.098938128	-0.083254674
<i>Bothriochloa insculpta</i>	O	0.089841	14	2.068893621	5.002797616	0.413547335	-1.619438761	-0.323706631
<i>Bothriochloa ischaemum</i>	O	-0.21281	16	1.89457363	4.930521606	0.384254199	-2.943836112	-0.59706383
<i>Bouteloua rigidiseta</i>	O	-0.07087	13	1.683297648	4.062391417	0.414361265	-1.971212367	-0.485234475
<i>Brosimum alicastrum</i>	T	0.064476	201	4.062564067	29.95796073	0.135608832	-2.129649811	-0.071087943
<i>Bursera glabrifolia</i>	T	0.09431	71	3.650984903	18.22854986	0.200289377	-1.931856208	-0.105979698
<i>Calathea ovandensis</i>	F	0.4389	15	1.784186362	3.754599863	0.475200135	-0.136292916	-0.036300251
<i>Callitris intratropica</i>	T	0.234519	20	2.526407175	10.4894507	0.24085219	-0.066435783	-0.006333581
<i>Calluna vulgaris</i>	S	1.096944	20	1.411428981	2.52704492	0.558529439	1.360598367	0.538414793
<i>Calocedrus macrolepis</i>	T	0.032244	144	2.943995026	53.32338634	0.055210204	-3.589505976	-0.067315792
<i>Calochortus albus</i>	O	0.43308	16	1.979870348	5.319256658	0.372208088	0.323794789	0.060872187
<i>Calochortus lyallii</i>	F	-0.01081	23	2.563296131	10.03294084	0.255488014	-2.67173415	-0.266296213
<i>Calochortus macrocarpus</i>	F	-0.05558	26	1.956896585	7.693486318	0.254357583	-2.384470833	-0.30993372
<i>Calochortus obispoensis</i>	O	0.022739	71	3.806474777	20.03781581	0.189964556	-3.350825126	-0.167225069
<i>Calochortus pulchellus</i>	F	0.108854	16	2.376551704	6.703839877	0.354506036	-1.646809204	-0.245651632
<i>Calochortus tiburonensis</i>	O	0.144966	58	3.215054768	12.33994539	0.260540437	-1.42618508	-0.115574667
<i>Camellia japonica</i>	T	0.014199	178	4.720910303	80.63733936	0.058544966	-3.010926153	-0.037339106
<i>Carex humilis</i>	O	0.097036	6	1.594523539	2.436105259	0.654538031	-1.358133721	-0.557502068
<i>Cassia nemophila</i>	S	0.188138	44	2.714057727	9.601007448	0.282684681	-0.907743944	-0.094546739
<i>Catopsis sessiliflora</i>	F	-0.19588	16	0.624426646	1.698862172	0.367555801	-0.957201592	-0.563436874
<i>Cecropia obtusifolia</i>	T	0.011929	28	2.51956037	12.68384089	0.198643328	-2.368260275	-0.186714757
<i>Centaurea corymbosa</i>	O	-0.0039	6	1.247895846	3.28082059	0.380360892	-1.260683125	-0.384258478
<i>Chamaecrista keyensis</i>	O	-0.03761	15	2.017314566	5.630177833	0.358303881	-2.229056622	-0.395912294
<i>Chamaedorea radicalis</i>	P	0.113329	47	3.239841678	15.07914542	0.214855788	-1.530941952	-0.101527103
<i>Chamaelirium luteum</i>	F	0.003992	58	2.725350932	16.57700955	0.164405463	-2.659175158	-0.160413442

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Chlorocardium rodiei</i>	T	-0.01228	445	1.21011E-08	4.85445E-09	2.492793759	-1.21607E-08	-2.50506879
<i>Cimicifuga elata</i>	F	0.143321	14	2.280380843	5.558565996	0.410246248	-1.483722609	-0.266925428
<i>Cirsium acaule</i>	O	-0.01729	46	2.28024117	11.05022356	0.206352492	-2.471283956	-0.223641082
<i>Cirsium pannonicum</i>	O	-0.05776	23	1.117100717	3.064321775	0.364550722	-1.294084419	-0.422306962
<i>Cirsium vulgare</i>	O	1.01171	6	0.840066752	1.187263259	0.707565694	0.361099356	0.304144303
<i>Cleome droserifolia</i>	O	0.111541	78	0.002902112	0.003597663	0.806665887	-0.00250082	-0.695123624
<i>Clidemia hirta</i>	S	0.412573	13	2.088746799	5.107024902	0.408994833	0.018274396	0.003578286
<i>Clintonia borealis</i>	F	0.120446	13	2.426846479	5.103016088	0.475571003	-1.812207822	-0.35512485
<i>Coccothrinax readii</i>	P	0.053541	116	4.249110858	62.5783508	0.067900653	-0.898617963	-0.014359886
<i>Coryphantha robbisorum</i>	O	0.049076	41	3.284694183	15.83314787	0.207456799	-2.507669188	-0.158380962
<i>Cryptantha flava</i>	O	-0.14611	13	2.107330148	4.922818245	0.428073929	-2.826618225	-0.574186997
<i>Cynoglossum virginianum</i>	F	0.062411	4	0.401242162	3.05997276	0.131126057	-0.210265406	-0.068714797
<i>Cypripedium acaule</i>	F	0.077887	25	1.279367838	4.080125119	0.313560933	-0.961581015	-0.235674394
<i>Cytissus scoparius</i>	S	0.196142	23	2.680433163	11.16589614	0.240055355	-0.490328883	-0.043913079
<i>Dacrydium elatum</i>	T	0.007166	172	3.870372133	82.94253253	0.046663298	-2.694359425	-0.032484653
<i>Danthonia sericea</i>	O	0.178983	41	2.92216596	9.170029249	0.318664846	-1.280889774	-0.139682191
<i>Daucus carota</i>	O	0.312911	6	0.992509694	3.466942077	0.28627813	0.092335057	0.026632997
<i>Dicerandra frutescens</i>	O	-0.20742	8	1.381112696	3.199334728	0.431687464	-2.04471183	-0.639105315
<i>Dicorynia guianensis</i>	T	0.001299	348	4.2285422	82.72980178	0.051112684	-2.480532438	-0.029983541
<i>Dicymbe altsonii</i>	T	0.027518	245	4.194539369	99.90776728	0.041984117	-1.068578151	-0.010695646
<i>Digitaria eriantha</i>	O	0.184818	10	2.113134468	4.480431312	0.471636394	-1.285068156	-0.286817957
<i>Dipsacus sylvestris</i>	O	0.367832	6	1.090593892	4.088861865	0.266723095	0.413422253	0.101109372
<i>Disporum sessile</i>	F	-0.06614	8	2.103027085	4.06921915	0.516813425	-2.372164436	-0.582953227
<i>Disporum smilacinum</i>	F	0.355574	12	1.959356801	3.427979968	0.571577669	-0.740455091	-0.216003331
<i>Duguetia neglecta</i>	T	0.006081	256	4.092581	99.04987	0.041318	-1.7286	-0.01745
<i>Echeveria longissima</i>	O	-0.0472	30	2.193290341	8.380520791	0.261712893	-2.588821044	-0.308909328
<i>Echinacea angustifolia</i>	O	0.024497	41	3.252657536	15.59059739	0.208629436	-2.870727319	-0.184131964
<i>Encephalartos cycadifolius</i>	P	0.030335	423	4.654055753	49.43841078	0.094138458	-3.049303849	-0.06167884
<i>Encephalartos villosus</i>	P	0.045738	281	4.320272255	45.97953387	0.093960767	-2.199669458	-0.047840186
<i>Epilobium latifolium</i>	O	0.667298	33	0.201073845	0.129473406	1.553012708	-0.114676504	-0.885714733

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Eremospatha macrocarpus</i>	F	-0.02102	60	0.992060719	6.550091651	0.151457532	-1.129739501	-0.1724769
<i>Eryngium cuneifolium</i>	O	-0.22698	9	1.396101053	4.064881823	0.343454278	-2.318731204	-0.570430164
<i>Erythronium japonicum</i>	F	0.001	14	2.367953909	4.900634296	0.483193351	-2.363055724	-0.482193851
<i>Escontria chiotilla</i>	T	0.018527	68	2.968940642	37.39848118	0.079386664	-2.276047589	-0.060859359
<i>Eupatorium perfoliatum</i>	F	-0.17781	10	0.903987493	1.47584399	0.612522393	-1.166409883	-0.790334135
<i>Eupatorium resinsum</i>	F	-0.14526	10	1.383999889	2.713657128	0.510012807	-1.778177617	-0.65526982
<i>Euterpe edulis</i>	P	0.229682	199	3.149687401	18.74781831	0.168002876	1.156351407	0.061679252
<i>Euterpe precatoria</i>	P	0.018602	114	2.192389162	36.49987851	0.060065656	-2.871358018	-0.078667605
<i>Fagus grandifolia</i>	T	0.007273	32	3.186761844	20.45721954	0.155776881	-3.037966586	-0.148503397
<i>Festuca gracillima</i>	O	-0.22437	8	1.590770642	3.080665259	0.516372442	-2.281977356	-0.740741744
<i>Fritillaria meleagris</i>	O	0.01784	19	2.598360993	7.451360282	0.348709617	-2.465429336	-0.330869699
<i>Fumana procumbens</i>	S	0.01784	17	2.349080966	7.651694386	0.30700141	-2.212575365	-0.289161492
<i>Garcinia lucida</i>	T	0.061377	294	4.463494716	52.20445539	0.085500264	-1.25976193	-0.024131311
<i>Gardenia actinocarpa</i>	S	0.133569	13	2.09579453	6.959547387	0.301139487	-1.166215497	-0.167570595
<i>Gaura neomexicana</i>	O	0.419302	6	1.349363095	3.418925324	0.394674632	0.084200037	0.024627633
<i>Gentiana pneumonanthe</i>	O	0.288931	11	1.607434296	3.568135783	0.450496952	-0.576488214	-0.16156566
<i>Geonoma brevispatha</i>	P	0.038162	21	2.641615445	9.121648296	0.289598476	-2.293510897	-0.251436015
<i>Geonoma macrostachys</i>	P	-0.02352	132	4.182130101	65.52981978	0.063820259	-5.085466193	-0.077605374
<i>Geonoma orbignyana</i>	P	0.071576	78	3.923191864	39.1290162	0.100262982	-1.122485634	-0.028686784
<i>Geranium sylvaticum</i>	F	0.078626	44	1.100285674	2.529194597	0.435034012	-0.901424409	-0.356407692
<i>Geum reptans</i>	O	0.054393	92	4.003629295	24.09345519	0.166170824	-2.693102329	-0.11177734
<i>Geum rivale</i>	O	0.014297	29	2.700855011	11.24249409	0.240236285	-2.540117648	-0.22593898
<i>Grias peruviana</i>	T	0.034015	30	0.926232869	4.089988167	0.226463459	-0.787112418	-0.192448581
<i>Guarianthe aurantiaca</i>	F	-0.01322	40	2.23094431	12.56478901	0.177555254	-2.39701263	-0.190772215
<i>Haplopappus radiatus</i>	O	-0.08508	10	1.669931737	3.890979984	0.429180244	-2.000971257	-0.514258944
<i>Harrisia fragrans</i>	F	-0.05655	37	0.433472422	1.264482195	0.342806268	-0.504977863	-0.399355455
<i>Helenium virginicum</i>	O	0.108406	81	3.167489576	11.35164406	0.279033553	-1.936904683	-0.170627679
<i>Helianthemum juliae</i>	S	0.220259	14	2.300157749	5.609460502	0.410049727	-1.064621367	-0.189790331
<i>Helianthus divaricata</i>	O	0.095128	10	2.179669862	4.320652974	0.504476956	-1.768653295	-0.409348611
<i>Heteropogon contortus</i>	O	-0.02634	21	2.670239322	7.900537791	0.337981969	-2.878370895	-0.364325945



Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Hieracium floribundum</i>	O	0.011929	19	2.281355146	5.678964524	0.401720267	-2.213613215	-0.389791696
<i>Hilaria mutica</i>	O	-0.02797	11	2.016349817	4.54623251	0.44352105	-2.143496434	-0.471488519
<i>Himantoglossum hircinum</i>	O	0.277177	17	2.03087826	4.615888932	0.439975547	-0.751459608	-0.16279846
<i>Hudsonia montana</i>	S	-0.02511	25	1.999056908	7.94284833	0.251680106	-2.198523282	-0.276792807
<i>Hypericum cumulicola</i>	O	0.281111	10	2.153233622	5.705367979	0.377404863	-0.549394623	-0.096294336
<i>Hypochaeris radicata</i>	O	0.205525	11	1.29803978	3.146440126	0.412542343	-1.944710878	-0.618067022
<i>Ipomoea leptophylla</i>	O	0.127161	35	3.079823296	10.33000015	0.298143587	-1.766248643	-0.170982441
<i>Iriartea deltoidea</i>	P	0.077887	66	3.822547849	29.67851437	0.12879849	-1.510991092	-0.050911952
<i>Iris germanica</i>	O	-0.05108	44	0.021947945	0.072361786	0.3033085	-0.025644387	-0.354391291
<i>Isatis tinctoria</i>	O	0.212285	4	0.330288334	3.348194029	0.098646712	0.380482393	0.113638096
<i>Laccosperma secundiflorum</i>	F	-0.0397	33	0.985845279	4.574342408	0.215516284	-1.167435817	-0.255213911
<i>Lathyrus vernus</i>	F	0.02088	42	3.101238327	16.01376842	0.193660745	-2.766863195	-0.172780268
<i>Limonium carolinianum</i>	O	0.00777	25	2.657673352	10.90316693	0.243752422	-2.57295861	-0.235982685
<i>Limonium delicatulum</i>	O	0.23436	11	2.514869013	7.694039758	0.326859373	-0.711690727	-0.092498967
<i>Lindera benzoin</i>	S	0.016857	59	3.531161571	20.02367185	0.176349353	-3.193620191	-0.159492236
<i>Lindera umbellata</i>	S	0.036621	77	3.35184829	26.88379782	0.124679121	-2.367331797	-0.088057938
<i>Lomatium bradshawii</i>	O	0.024149	11	1.900436408	4.912695336	0.386841902	-2.019074366	-0.410991162
<i>Lomatium cookii</i>	O	0.020978	12	2.008548155	6.059521594	0.331469758	-1.881429048	-0.310491351
<i>Lonicera maakii</i>	S	1.019208	3	0.034982572	0.020747251	1.686130508	-0.013836803	-0.666922242
<i>Lupinus arboreus</i>	S	0.335114	14	2.074311122	4.865272993	0.426350407	-0.443889191	-0.091236235
<i>Lupinus tidestromii</i>	O	-0.08434	8	1.600827404	3.942717332	0.406021347	-1.933350618	-0.490359936
<i>Mammillaria crucigera</i>	O	-0.066	27	0.161441005	0.38633115	0.417882444	-0.186939218	-0.483883367
<i>Mammillaria pectinifera</i>	O	-0.29608	12	0.383656424	0.711773357	0.539014871	-0.594396296	-0.835092085
<i>Manglietia fordiana</i>	T	0.045301	110	0.899292189	13.12394121	0.068523028	-1.49381669	-0.113823787
<i>Manilkara zapota</i>	T	0.029462	178	4.659799926	65.66217669	0.070966273	-2.597146609	-0.03955316
<i>Mauritia flexuosa</i>	P	0.045165	31	2.409978143	14.98981492	0.160774376	-1.732969869	-0.115609824
<i>Miconia albicans</i>	S	0.17008	184	2.967705159	18.41176602	0.161185253	0.163772979	0.008895017
<i>Miconia prasina</i>	S	-0.0033	83	3.692719432	28.28386325	0.130559231	-3.785926753	-0.133854655
<i>Minuartia obtusiloba</i>	O	-1E-05	453	3.817767742	65.33985936	0.058429384	-2.45325001	-0.037545995

Species	LF	<i>r</i>	<i>L</i>	<i>S</i>	<i>T</i>	<i>H</i>	<i>E</i>	$\phi$
<i>Myrsine guianensis</i>	T	0.096582	60	3.655674285	30.75064576	0.11888122	-0.685712408	-0.022299122
<i>Narcissus pseudonarcissus</i>	F	0.024293	12	0.506880763	0.833661411	0.608017544	-0.527132644	-0.632310237
<i>Neobuxbaumia macrocephala</i>	T	0.03237	85	3.950393516	44.45495181	0.088862846	-2.511369832	-0.056492466
<i>Neobuxbaumia mezcalaensis</i>	T	0.120535	81	3.827058727	34.33322738	0.111468074	0.311290025	0.009066728
<i>Neobuxbaumia tetetzo</i>	T	0.035174	117	4.385176601	57.52893524	0.076225583	-2.361649518	-0.041051508
<i>Nothofagus fusca</i>	T	0.009455	260	3.524528679	52.13160657	0.067608288	-2.414620688	-0.046317788
<i>Panax quinquefolium</i>	F	0.038162	32	2.036192765	6.757659501	0.301316272	-1.778303848	-0.26315381
<i>Parashorea chinensis</i>	T	0.005214	249	4.009936002	84.13799145	0.047659041	-2.503923493	-0.029759725
<i>Paronychia pulvinata</i>	O	0	387	1.617067318	16.61960383	0.097298788	-1.617067318	-0.097298788
<i>Pedicularis furbishiae</i>	O	0.034401	12	1.803924305	3.989704269	0.452144867	-1.666672786	-0.41774344
<i>Pentaclethra macroloba</i>	T	0.001998	138	3.677780892	68.35809607	0.053801687	-3.114673074	-0.04556407
<i>Periandra mediterranea</i>	S	0.068219	53	3.491007023	16.97216546	0.205690136	-2.333178812	-0.137470897
<i>Phaseolus lunatus</i>	O	-0.2645	6	1.415581254	3.789872908	0.373516814	-2.418000904	-0.638016356
<i>Phyllanthus emblica</i>	T	-0.00755	20	2.098151932	7.968780759	0.263296481	-2.158303618	-0.270844899
<i>Phytelephas seemanii</i>	P	0.057231	79	3.864287359	25.35781682	0.152390381	-2.413043439	-0.095159747
<i>Pinguicula alpina</i>	O	0.032467	41	3.278785591	15.29225058	0.214408309	-2.782289184	-0.181941119
<i>Pinguicula villosa</i>	O	0.003005	13	2.096717981	5.602472974	0.374248656	-2.113550662	-0.377253165
<i>Pinguicula vulgaris</i>	O	0.082501	35	3.110109527	13.05144231	0.238296232	-2.033349594	-0.155795011
<i>Pinus kwangtungensis</i>	T	0.022685	201	0.365513527	4.15697905	0.087927681	-0.45981617	-0.110613059
<i>Pinus lambertiana</i>	T	0.026642	47	3.154074532	22.77437079	0.13849228	-2.547321318	-0.111850349
<i>Pinus nigra</i>	T	0.425137	78	2.216828463	9.984545164	0.222025984	2.027971194	0.203111024
<i>Pinus palustris</i>	T	0.002002	226	3.547829755	79.20194186	0.044794732	-1.794248667	-0.022654099
<i>Pinus sylvestris</i>	T	0.185649	20	2.603587292	11.09260677	0.234713746	-0.544252089	-0.049064399
<i>Plantago coronopus</i>	O	0.132781	4	0.728545879	2.274540012	0.32030471	-0.426529929	-0.187523599
<i>Plantago media</i>	O	-0.06223	23	0.66273027	1.931884594	0.343048581	-0.782944743	-0.405275111
<i>Podococcus barteri</i>	P	0.012916	34	3.076499054	15.94141343	0.192987847	-2.870596167	-0.180071622
<i>Podophyllum peltatum</i>	F	0	6	1.406255725	2.813687832	0.499790954	-1.406255725	-0.499790954
<i>Potentilla anserina</i>	O	-0.12443	7	1.619436701	2.951245421	0.548729933	-1.9866604	-0.673160011

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Primula farinosa</i>	O	0.031014	19	2.430070154	7.80316022	0.311421281	-2.188062525	-0.280407228
<i>Primula veris</i>	O	0.110647	53	1.002184168	3.134489146	0.319728071	-0.655363852	-0.209081551
<i>Prioria copaifera</i>	T	0.018331	205	3.880042127	78.24783265	0.049586576	-1.68548787	-0.021540378
<i>Prosopis glandulosa</i>	T	0.258433	80	2.975644184	10.35163982	0.28745631	-0.300433964	-0.029022838
<i>Prunus serotina</i>	T	0.149712	10	0.035670679	0.079614766	0.448040997	-0.023751372	-0.298328724
<i>Psidium guajava</i>	T	0.006028	176	2.04905254	31.02891249	0.066036879	-1.251688629	-0.04033943
<i>Pterocarya rhoifolia</i>	T	0.098034	55	3.53952918	21.48950408	0.164709673	-1.432832718	-0.066675932
<i>Pterocereus gaumeri</i>	T	0.0004	38	2.62956612	17.94395538	0.146543282	-2.622389973	-0.146143362
<i>Ranunculus acris</i>	O	0.187641	6	1.102999744	4.036397146	0.273263434	-0.346945835	-0.085954336
<i>Ranunculus bulbosus</i>	O	0.639377	6	1.093030162	2.788765079	0.391940566	-0.690042471	-0.247436572
<i>Ranunculus repens</i>	O	0.697959	6	0.770999759	0.912167197	0.845239515	-1.407654824	-1.543198253
<i>Rhizophora mangle</i>	T	0.042197	5	0.078544702	0.064393085	1.219769207	-0.075827504	-1.177572158
<i>Rhopalostylis sapida</i>	P	0.006976	222	4.602862852	92.07757098	0.049988969	-2.658816793	-0.028875836
<i>Sabal yapa</i>	P	0.005982	92	3.230304761	45.53639928	0.070938959	-2.957902756	-0.064956887
<i>Sanicula europaea</i>	F	-0.11296	15	0.955581766	2.272936186	0.420417332	-1.212323443	-0.533373286
<i>Scabiosa columbaria</i>	O	0.029559	12	1.984092436	5.138618183	0.386114003	-1.832201037	-0.356555201
<i>Scaphium borneense</i>	T	0.013607	306	3.459683509	76.2287014	0.045385576	-1.328030778	-0.017421663
<i>Setaria incrassata</i>	O	-0.06614	18	2.500305834	6.323802379	0.395380134	-2.918560875	-0.461519937
<i>Silene acaulis</i>	O	0.009455	338	0.408414025	73.74721449	0.073337197	-2.093161218	-0.028382919
<i>Stryhnodendron excelsum</i>	T	0.046024	125	4.363346769	60.3878966	0.07225532	-1.582925389	-0.026212627
<i>Syzygium jambos</i>	T	0.169996	84	3.025633483	12.02969927	0.251513643	-0.980633844	-0.081517736
<i>Tachigali vasquezii</i>	T	0.051738	71	3.83749381	36.11556511	0.106255954	-1.968939645	-0.054517758
<i>Taxus floridana</i>	T	-0.03513	76	0.394442685	2.783941424	0.14168498	-0.492242246	-0.176814872
<i>Themeda triandra</i>	O	0.094128	18	2.530338016	6.357161481	0.398029533	-1.931953265	-0.30390187
<i>Thrinax radiata</i>	P	0.121244	88	3.912377973	41.69952586	0.093823081	1.143427135	0.027420627
<i>Tillandsia multicaulis</i>	F	-0.04626	22	1.786502836	7.076599059	0.252452177	-2.113893609	-0.298716035
<i>Tillandsia punctulata</i>	F	-0.31337	10	0.027243595	0.024439033	1.114757471	-0.034902034	-1.428126651
<i>Tolumnia variegata</i>	F	0.306896	16	2.16045818	6.049310859	0.357141207	-0.303947112	-0.050244915
<i>Trillium grandiflorum</i>	F	-0.03273	49	1.931661325	11.35787414	0.170072436	-2.303402554	-0.202802261
<i>Ulex gallii</i>	S	0.27018	34	2.580165905	7.521819689	0.343024163	-0.547922186	-0.072844366

Species	LF	$r$	$L$	$S$	$T$	$H$	$E$	$\phi$
<i>Vatica hainanensis</i>	T	0	63	3.390426704	31.2111626	0.108628658	-3.390426704	-0.108628658
<i>Viola fimbriatula</i>	F	0.394741	19	1.169686479	45.58333979	0.025660394	0.000268798	0.226610555
<i>Werauhia sanguinolenta</i>	F	0.103549	20	2.449949188	11.3975853	0.214953354	-1.269742045	-0.111404478
<i>Zamia amblyphyllidia</i>	P	0.021019	10	0.001970905	0.001626796	1.211525822	-0.002005099	-1.232545189
<i>Zea diploperennis</i>	O	-0.26747	11	0.821283597	1.7656862	0.465135649	-1.293559275	-0.732609948

Note: All demographic parameters are defined in the thesis. Missing values in the table indicate that values for these parameters could not be computed employing the method used. L.F = life form

## Appendix 5

Table 14: Species used in chapter five, their life history data.  $g$ ,  $b$ ,  $t$  are parameters of the time distribution of reproductive value (subscript  $v$ ) and of Baudisch's sensitivity of population growth rate to the logarithm of fecundity (subscript  $B$ ).  $R^2$  (subscripted for the corresponding time distribution parameters) corresponds to the proportion of variance accounted for by each model fit.

Species	Life form	$\lambda$ (year <sup>-1</sup> )	$L$ (years)	$\alpha$ (years)	$S$	$g_v$	$b_v$	$t_v$	$R^2_v$	$g_B$	$b_B$	$t_B$	$R^2_B$
<i>Abies concolor</i>	T	1.044	51	27	3.331	0.461	0.036	92.51	1.000	0.035	0.067	46.498	0.998
<i>Abies magnifica</i>	T	0.974	44	23	1.525	0.636	0.067	69.43	0.998	0.037	0.081	37.489	0.998
<i>Acacia bilimekii</i>	S	1.235	467	18	3.206	0.116	0.012	362.9	0.998	0.023	0.516	9.882	0.999
<i>Acer saccharum</i>	T	1.892	38	5	1.790	0.808	0.047	84.52	0.997	0.652	5.983	0.770	0.999
<i>Aconitum noveboracense</i>	O	0.990	39	15	0.124	0.542	0.041	75.62	0.997	0.149	0.014	191.838	0.998
<i>Aechmea nudicaulis</i>	F	1.044	12	4	1.074	0.3	0.112	4.964	0.997	0.788	0.016	0.535	1.000
<i>Agrimonia eupatoria</i>	O	0.998	45	7	2.775	0.199	0.015	199	0.999	0.037	0.038	8.668	0.999
<i>Agropyron repens</i>	O	2.963	6	1	0.334	0.323	0.74	3.473	0.943	0.131	1.422	3.597	0.956
<i>Alnus incana</i>	T	0.971	32	4	2.341	0.945	0.047	75.26	0.998	0.126	0.151	12.088	0.999
<i>Ambrosia deltoidea</i>	S	0.615	11	3	0.698	0.331	0.021	150.2	0.998	0.303	0.740	2.775	0.999
<i>Andropogon semiberberis</i>	O	1.252	8	2	1.810	0.985	0.088	19.77	0.996	0.621	0.001	10.037	0.964
<i>Anemone patens</i>	O	1.019	13	2	2.282	0.799	0.079	25.47	0.986	0.279	0.308	2.979	0.998
<i>Annamocarya sinensis</i>	T	0.976	189	47	2.402	0.021	0.033	104	0.999	0.018	0.029	116.115	0.998
<i>Aquilaria malaccensis</i>	T	1.224	16	8	2.103	0.935	0.352	20.02	0.999	0.026	5.365	4.872	0.945
<i>Aquilegia chrysantha</i>	F	0.849	8	5	1.225	0.545	0.506	6.393	0.999	0.399	0.781	5.731	0.997
<i>Araucaria cunninghamii</i>	T	1.018	256	95	4.883	0.061	0.025	225.9	0.999	0.025	0.061	78.526	1.000
<i>Araucaria hunsteinii</i>	T	0.987	182	41	2.860	0.035	0.013	130.2	1.000	0.018	0.028	86.922	0.998
<i>Ardisia elliptica</i>	S	1.060	188	25	4.293	0.218	0.016	345.8	0.998	0.020	0.109	36.213	1.000
<i>Arisaema serratum</i>	F	0.990	23	8	2.625	0.249	0.173	20.3	0.998	1.103	0.336	12.079	0.998
<i>Arisaema triphyllum</i>	F	1.073	24	8	3.777	0.271	0.069	25.45	0.994	0.317	0.004	40.718	0.998
<i>Aristida bipartita</i>	O	1.188	25	2	2.226	0.192	0.031	34.4	0.994	0.815	0.002	109.534	0.999
<i>Armeria maritima</i>	O	1.458	28	5	2.405	0.651	0.133	38.22	0.999	0.876	17.998	2.949	0.998
<i>Aster amellus</i>	O	0.943	19	7	1.224	0.054	0.020	62.79	0.997	0.073	0.322	0.943	0.999
<i>Astragalus scaphoides</i>	O	1.378	15	3.0	2.311	0.956	0.062	38.33	0.986	0.852	0.081	2.213	0.998
<i>Astragalus tyghensis</i>	O	1.009	13	4	2.270	0.998	0.108	24.04	0.998	0.249	0.311	4.208	0.997
<i>Astrocaryum mexicanum</i>	P	1.007	123	42	3.952	0.036	0.037	42.46	0.999	0.041	0.040	121.394	0.999
<i>Avicenia marina</i>	T	1.237	39	3	3.044	0.222	0.072	63.3	0.987	0.162	0.205	9.576	0.999
<i>Banksia ericifolia</i>	S	1.609	45	12	2.703	0.747	0.090	66	0.998	0.320	0.629	4.125	0.999
<i>Betula nana</i>	S	0.992	11	2	2.166	0.956	0.122	18.43	0.995	0.910	0.061	25.038	0.991
<i>Borderea chouardii</i>	O	1.002	133	10	3.373	0.184	0.075	33.61	0.999	0.057	0.027	91.912	0.928
<i>Bothriochloa insculpta</i>	O	1.094	14	2	1.895	0.321	0.029	91.23	0.997	0.581	0.009	25.622	0.994
<i>Bothriochloa ischaemum</i>	O	0.808	16	4	2.262	0.99	0.109	28.12	0.998	0.248	0.353	1.641	0.999
<i>Bouteloua rigidiseta</i>	O	0.932	13	3	1.683	0.606	0.153	12.62	0.999	0.958	0.009	15.272	0.995
<i>Brosimum alicastrum</i>	T	1.067	201	17	4.063	0.600	0.011	521.5	0.997	0.341	2.391	6.563	0.998
<i>Bursera glabrifolia</i>	T	1.099	71	18	3.651	0.310	0.045	107.4	0.999	0.054	0.074	19.998	0.999
<i>Calathea ovandensis</i>	F	1.551	15	2	1.785	0.75	0.05	73.4	0.997	0.245	0.027	87.579	0.994
<i>Callitris intratropica</i>	T	1.264	20	12	2.526	0.913	0.157	29.57	0.999	0.088	0.278	12.908	0.919

<i>Calluna vulgaris</i>	S	2.995	20	5	1.411	0.075	0.57	16.57	0.987	0.079	0.049	6.27	0.993
<i>Calocedrus macrolepis</i>	T	0.968	144	41	2.944	0.043	0.032	125.1	1.000	0.025	0.048	72.756	0.998
<i>Calochortus albus</i>	O	1.542	16	3	1.982	0.925	0.159	24.54	0.999	0.249	1.350	2.219	0.999
<i>Calochortus lyallii</i>	F	0.989	23	8	2.563	0.172	0.016	188.6	0.998	0.086	0.275	7.854	0.999
<i>Calochortus macrocarpus</i>	F	0.946	26	10	1.957	0.209	0.015	200.8	0.998	0.074	0.269	7.336	0.999
<i>Calochortus obispoensis</i>	O	1.023	70	20	3.806	0.285	0.018	156.5	0.998	0.169	0.009	212.159	0.998
<i>Calochortus pulchellus</i>	F	1.115	30	3	2.377	0.710	0.182	20.35	0.999	0.380	0.155	15.389	0.998
<i>Calochortus tiburonensis</i>	O	1.156	57	5	3.215	0.437	0.036	109.4	0.998	0.094	0.042	50.735	0.998
<i>Camellia japonica</i>	T	1.014	178	25	4.721	0.400	0.048	108.5	0.999	0.368	0.043	154.456	0.999
<i>Carex humilis</i>	O	1.102	16	9	0.786	0.976	0.114	29.14	0.997	0.375	3.677	0.213	0.999
<i>Cassia nemophila</i>	S	1.207	44	3	2.714	0.468	0.075	71.07	0.999	0.351	0.707	4.129	1.000
<i>Catopsis sessiliflora</i>	F	0.822	16	9	0.624	0.062	0.030	75.64	0.998	0.130	0.373	8.832	0.999
<i>Cecropia obtusifolia</i>	T	1.012	28	5	2.599	0.166	0.148	20.3	0.997	0.998	12.250	2.074	0.999
<i>Centaurea corymbosa</i>	O	0.996	6	4	1.423	0.743	0.078	10.83	0.994	0.862	0.281	0.099	0.995
<i>Chamaecrista keyensis</i>	O	0.963	15	6	2.017	0.331	0.125	12.65	0.999	0.218	0.285	6.709	0.997
<i>Chamaedorea radicalis</i>	P	1.120	47	8	3.240	0.498	0.045	84.61	0.999	0.035	0.055	18.262	0.998
<i>Chamaelirium luteum</i>	F	1.004	58	13	2.812	0.427	0.044	81.09	1.000	0.155	0.053	53.764	0.998
<i>Chlorocardium rodiei</i>	T	0.998	446	206	3.412	0.039	0.060	35.46	0.997	0.103	0.027	132.897	0.998
<i>Cimicifuga elata</i>	F	1.154	33	6	2.526	0.442	0.046	61.71	0.996	0.119	0.198	0.532	0.999
<i>Cirsium acaule</i>	O	0.983	46	3	2.280	0.371	0.023	99.15	0.998	0.065	0.007	11.151	0.998
<i>Cirsium pannonicum</i>	O	0.944	98	3	1.117	0.220	0.012	222.3	0.998	0.068	0.218	3.607	0.999
<i>Cirsium vulgare</i>	O	2.750	6	4	0.020	0.998	0.248	4.148	0.984	0.997	0.002	0.432	0.999
<i>Cleome droserifolia</i>	O	1.118	76	8	2.787	0.441	0.091	67.37	0.999	0.267	0.040	79.875	0.996
<i>Clidemia hirta</i>	S	1.511	13	3	2.102	0.2	0.357	7.452	0.998	0.257	1.036	1.617	0.999
<i>Clintonia borealis</i>	F	1.128	13	4	2.480	0.84	0.088	24.53	0.989	0.687	0.070	23.215	0.994
<i>Coccothrinax readii</i>	P	1.055	116	96	4.249	0.244	0.036	166.6	0.999	0.024	0.049	100.421	0.999
<i>Coryphantha robbisorum</i>	O	1.050	41	8	3.285	0.217	0.017	195.6	0.999	0.046	0.018	6.881	0.998
<i>Cryptantha flava</i>	O	0.864	13	2	2.203	0.999	0.1	24.27	0.994	0.472	0.041	1.536	0.997
<i>Cynoglossum virginianum</i>	F	1.103	11	2	1.817	0.300	0.342	6.516	0.997	0.430	0.196	7.276	0.999
<i>Cypripedium acaule</i>	F	1.081	25	4	1.295	0.207	0.158	20.64	0.998	0.796	6.249	4.762	1.000
<i>Cytissus scoparius</i>	S	1.217	23	6	2.680	0.063	0.045	97.78	0.999	0.373	0.809	7.421	0.998
<i>Dacrydium elatum</i>	T	0.993	172	46	3.870	0.026	0.029	78.69	0.997	0.019	0.028	130.542	0.998
<i>Danthonia sericea</i>	O	1.196	41	2	2.922	0.417	0.055	6.158	0.998	0.720	0.009	72.777	0.994
<i>Daucus carota</i>	O	1.367	6	4.0	1.055	0.989	0.126	12.22	0.998	0.405	4.421	1.822	0.995
<i>Dicerandra frutescens</i>	O	0.813	8	4	1.300	0.479	0.447	11.79	0.995	0.962	0.001	33.071	0.994
<i>Dicorynia guianensis</i>	T	1.001	349	60	4.229	0.363	0.019	142	0.999	0.235	0.025	177.992	0.999
<i>Dicymbe altsonii</i>	T	1.028	567	211	4.195	0.031	0.023	239.6	1.000	0.688	0.087	182.886	0.998
<i>Digitaria eriantha</i>	O	1.203	10	4	2.181	0.234	0.116	26.88	0.998	0.774	0.033	1.240	0.999
<i>Dipsacus sylvestris</i>	O	2.3219	6	4	1.135	0.98	0.65	6.89	0.995	0.888	22.740	1.590	0.999
<i>Disporum sessile</i>	F	0.936	8	3	2.103	0.185	0.056	32.61	0.998	0.772	0.001	30.210	0.995
<i>Disporum smilacinum</i>	F	1.427	12	3	1.959	0.885	0.1	20.85	0.987	0.824	0.080	19.506	0.997
<i>Duguetia neglecta</i>	T	1.006	256	101	4.093	0.176	0.019	238.6	0.998	0.267	0.059	136.060	0.999
<i>Echeveria longissima</i>	O	0.954	30	4	2.193	0.509	0.060	46.58	1.000	0.515	0.034	65.039	0.999
<i>Echinacea angustifolia</i>	O	1.025	41	5	3.253	0.192	0.016	192.3	0.998	0.040	0.074	7.673	0.998
<i>Encephalartos cycadifolius</i>	P	1.031	423	34	4.654	0.230	0.013	398.9	0.998	0.086	0.010	369.772	0.998
<i>Encephalartos villosus</i>	P	1.047	281	22	4.320	0.089	0.011	325.2	1.000	0.048	0.042	91.189	0.996

<i>Epilobium latifolium</i>	O	1.949	33	6	2.832	0.469	0.028	76.1	0.998	0.597	0.974	35.081	0.998
<i>Eremospatha macrocarpus</i>	F	0.979	60	18	0.992	0.455	0.046	97.87	0.998	0.035	0.045	40.353	0.999
<i>Eryngium cuneifolium</i>	O	0.797	9	5	1.396	0.172	0.064	82.16	0.999	0.083	0.364	40.997	0.998
<i>Erythronium japonicum</i>	F	1.001	14	2	2.481	0.1	0.592	2.557	0.964	0.252	0.666	32.097	0.994
<i>Escontria chiotilla</i>	T	1.019	68	53	2.969	0.395	0.033	122.5	0.998	0.036	0.080	69.542	0.998
<i>Eupatorium perfoliatum</i>	F	0.837	10	2.0	0.994	0.834	0.062	18.69	0.994	0.454	0.009	32.372	0.998
<i>Eupatorium resinosum</i>	F	0.865	10	5.0	1.509	0.657	0.066	22.42	0.996	0.300	0.271	0.600	0.999
<i>Euterpe edulis</i>	P	1.258	199	23	3.150	0.101	0.010	367.9	0.999	0.221	0.662	13.499	0.999
<i>Euterpe precatoria</i>	P	0.982	114	50	2.192	0.083	0.041	99.01	1.000	0.071	0.060	103.230	0.999
<i>Fagus grandifolia</i>	T	0.939	28	27	3.187	0.216	0.051	53.06	0.998	0.249	0.056	68.938	0.998
<i>Festuca gracillima</i>	O	0.799	8	3	1.717	0.46	0.031	20.08	0.995	0.659	0.116	1.511	1.000
<i>Fritillaria meleagris</i>	O	1.018	19	3	2.656	0.589	0.096	27.82	0.998	0.297	0.097	14.278	0.999
<i>Fumana procumbens</i>	S	1.018	17	5	2.349	0.492	0.037	41.47	0.994	0.210	0.227	9.827	0.998
<i>Garcinia lucida</i>	T	1.063	294	82	4.463	0.050	0.010	409.1	1.000	0.683	0.044	167.990	0.999
<i>Gardenia actinocarpa</i>	S	1.143	13	6	2.096	0.462	0.285	12.4	0.998	0.778	16.478	2.936	1.000
<i>Gaura neomexicana</i>	O	1.521	6	5	1.307	0.104	0.25	14.69	0.989	0.654	0.570	0.208	0.996
<i>Gentiana pneumonanthe</i>	O	1.335	11	2	1.641	0.362	0.404	8.39	0.996	0.100	0.343	3.979	0.994
<i>Geonoma brevispatha</i>	P	1.039	21	4.0	2.717	0.869	0.081	39.18	0.999	0.614	0.095	33.055	0.999
<i>Geonoma macrostachys</i>	P	0.977	132	26	4.182	0.182	0.018	215	0.999	0.035	0.058	46.585	0.999
<i>Geonoma orbignyana</i>	P	1.074	78	34	3.923	0.192	0.028	190.1	0.999	0.037	0.062	68.885	0.998
<i>Geranium sylvaticum</i>	F	1.082	44	14	1.100	0.074	0.083	8.61	0.999	0.210	0.017	215.416	0.998
<i>Geum reptans</i>	O	1.056	21	4	4.004	0.209	0.017	176.5	0.998	0.332	0.019	228.489	0.998
<i>Geum rivale</i>	O	1.014	29	8	2.701	0.241	0.015	213.2	0.997	0.046	0.154	6.590	0.999
<i>Grias peruviana</i>	T	1.035	30	19	0.926	0.043	1.186	5.66	1.000	0.656	0.033	308.384	0.998
<i>Guarianthe aurantiaca</i>	F	0.987	40	9	2.231	0.450	0.041	69.9	1.000	0.038	0.089	18.409	0.998
<i>Haplopappus radiatus</i>	O	0.918	10	4	1.811	0.495	0.126	22.99	0.994	0.329	0.349	4.221	0.998
<i>Harrisia fragrans</i>	F	0.945	37	3	0.433	0.245	0.067	40.18	0.997	0.471	0.010	572.791	0.999
<i>Helenium virginicum</i>	O	1.115	81	79	3.167	0.363	0.021	158.6	0.998	0.162	0.010	244.624	0.998
<i>Helianthemum juliae</i>	S	1.246	14	3	2.342	0.2	0.261	26.55	0.999	0.275	0.002	2.017	0.997
<i>Helianthus divaricata</i>	O	1.100	11	2.0	2.239	0.354	0.073	9.228	0.996	0.977	0.074	22.771	0.999
<i>Heteropogon contortus</i>	O	0.974	21	2	2.725	0.943	0.069	43.16	0.998	0.350	0.056	19.225	1.000
<i>Hieracium floribundum</i>	O	1.012	19	2	2.349	0.435	0.115	20.42	0.998	0.831	0.022	91.128	0.968
<i>Hieracium floribundum</i>	O	1.012	19	2	2.349	0.435	0.115	20.42	0.998	0.831	0.022	91.128	0.968
<i>Hilaria mutica</i>	O	0.972	11	2	2.118	0.802	0.16	20.82	0.998	0.529	0.082	2.501	0.999
<i>Himantoglossum hircinum</i>	O	1.319	17	8	2.036	0.932	0.085	34.27	0.997	0.127	0.249	0.255	0.996
<i>Hudsonia montana</i>	S	0.975	25	3	1.999	0.156	0.258	19.51	0.997	0.075	0.141	19.623	0.999
<i>Hypericum cumulicola</i>	O	1.325	26	6	2.821	0.621	0.073	46.84	0.997	0.237	0.515	0.176	1.000
<i>Hypochaeris radicata</i>	O	0.811	11	6	1.459	0.669	0.16	13.84	0.999	0.25	0.553	4.241	0.997
<i>Ipomoea leptophylla</i>	O	1.136	35	11	3.087	0.886	0.091	59.5	0.998	0.177	0.064	31.883	1.000
<i>Iriartea deltoidea</i>	P	1.081	67	29	0.000	0.261	0.078	82.3	0.998	0.047	0.107	35.420	0.999
<i>Iris germanica</i>	O	0.950	44	33	0.022	0.485	0.026	102	0.997	0.039	0.057	36.333	0.998
<i>Isatis tinctoria</i>	O	1.237	4	3.0	0.191	0.521	0.978	6.004	0.999	0.998	22.733	1.487	1.000
<i>Laccosperma secundiflorum</i>	F	0.961	33	29	0.986	0.778	0.040	76.56	0.998	0.043	0.098	21.194	0.999
<i>Lathyrus vernus</i>	F	1.021	42	9	3.101	0.519	0.037	84.24	0.999	0.049	0.069	16.564	0.999
<i>Limonium carolinianum</i>	O	1.008	25	5	2.658	0.176	0.023	158.1	0.997	0.501	1.155	4.727	0.998
<i>Limonium delicatulum</i>	O	1.264	19	6	2.157	0.5	0.1	30.28	0.974	0.202	0.627	3.474	0.999

<i>Lindera benzoin</i>	S	1.017	59	4	3.531	0.106	0.046	47.26	0.997	0.775	0.014	429.095	0.999
<i>Lindera umbellata</i>	S	1.037	77	26	3.352	0.376	0.010	221.9	0.997	0.036	0.053	36.272	0.999
<i>Lomatium bradshawii</i>	O	0.976	11	3	2.028	0.499	0.142	10.9	0.998	0.304	0.343	5.395	0.999
<i>Lomatium cookii</i>	O	1.021	12	6	2.009	0.410	0.082	43.02	0.999	0.156	0.388	5.821	0.998
<i>Lonicera maakii</i>	S	2.771			0.464	0.978	0.201	29.92	0.999	0.128	0.015	131.735	0.998
<i>Lupinus arboreus</i>	S	1.398	14	4	2.082	0.991	0.249	20.82	0.999	0.560	0.871	1.913	1.000
<i>Lupinus tidestromii</i>	O	0.919	9	4	1.789	0.518	0.132	10.51	0.997	0.294	0.732	3.072	0.999
<i>Mammillaria crucigera</i>	O	0.936	27	2	0.161	0.874	0.059	53.24	1.000	0.059	0.095	5.293	0.999
<i>Mammillaria pectinifera</i>	O	0.744	12	5	0.384	0.500	0.016	244.4	0.999	0.180	0.468	6.558	0.999
<i>Manglietia fordiana</i>	T	0.956	110	34	0.899	0.040	0.064	65.25	0.998	0.027	0.040	89.642	0.999
<i>Manilkara zapota</i>	T	1.030	178	53	4.660	0.027	0.036	148.2	1.000	0.102	0.144	47.169	1.000
<i>Mauritia flexuosa</i>	P	1.046	31	24	3.170	0.204	0.127	28.79	0.998	0.050	0.112	31.138	0.999
<i>Miconia albicans</i>	S	1.185	153	8	2.968	0.445	0.027	188.9	0.998	0.469	1.593	7.372	1.000
<i>Miconia prasina</i>	S	0.997	82	11	3.693	0.265	0.019	161.5	0.999	0.040	0.029	18.805	0.998
<i>Minuartia obtusiloba</i>	O	1.000	453	3	3.818	0.067	0.032	83.56	0.998	0.048	0.010	745.401	0.998
<i>Myrsine guianensis</i>	T	1.101	60		3.656	0.392	0.073	81.24	1.000	0.053	0.043	97.151	0.998
<i>Narcissus pseudonarcissus</i>	F	0.976	12	1	2.573	0.081	0.116	22	0.998	0.559	0.147	24.144	0.996
<i>Neobuxbaumia macrocephala</i>	T	1.033	85	37	3.950	0.136	0.018	102.3	0.999	0.051	0.120	39.952	0.999
<i>Neobuxbaumia mezcalaensis</i>	T	1.128	81	45	3.827	0.362	0.031	168.2	0.998	0.278	0.630	14.654	1.000
<i>Neobuxbaumia tetetzo</i>	T	1.036	117	48	4.385	0.194	0.039	134.1	0.999	0.036	0.071	58.875	0.998
<i>Nothofagus fusca</i>	T	1.006	246	42	3.525	0.051	0.050	74.11	0.999	0.889	0.027	298.587	0.998
<i>Panax quinquefolium</i>	F	1.045	26	5	2.036	0.545	0.034	103.3	0.998	0.107	0.321	8.431	0.999
<i>Parashorea chinensis</i>	T	0.995	249	41	4.010	0.029	0.022	167.7	0.998	0.018	0.024	122.609	0.998
<i>Paronychia pulvinata</i>	O	1.000	387	3	3.865	0.299	0.022	181.2	0.998	0.289	0.023	200.696	0.998
<i>Pedicularis furbishiae</i>	O	1.035	12	3	1.862	0.22	0.105	15.68	0.998	0.274	0.448	4.433	0.995
<i>Pentaclethra macroloba</i>	T	1.002	138	79	3.678	0.142	0.029	127.2	1.000	0.518	0.008	781.806	0.997
<i>Periandra mediterranea</i>	S	1.071	53	8.0	3.491	0.377	0.041	89.27	0.999	0.069	0.071	26.396	0.996
<i>Phaseolus lunatus</i>	O	0.768	6	2	1.416	0.745	0.070	54.49	0.999	0.306	1.323	6.347	0.999
<i>Phyllanthus emblica</i>	T	0.992	20	7	2.098	0.072	0.033	96.98	0.997	0.054	0.173	27.130	0.999
<i>Phyttelephas seemanii</i>	P	1.059	79	18	3.864	0.049	0.064	56.2	0.999	0.034	0.057	30.353	0.998
<i>Pinguicula alpina</i>	O	1.033	41	10	3.279	0.507	0.036	95.03	0.999	0.069	0.134	12.452	0.999
<i>Pinguicula villosa</i>	O	0.997	13	5	2.097	0.891	0.123	19.24	0.998	0.247	0.686	2.794	0.996
<i>Pinguicula vulgaris</i>	O	1.086	35	10	3.110	0.360	0.042	80.3	0.999	0.068	0.110	12.932	0.999
<i>Pinus kwangtungensis</i>	T	0.978	201	58	2.271	0.022	0.029	115.9	0.999	0.019	0.027	130.020	0.998
<i>Pinus lambertiana</i>	T	1.027	47	21	3.154	0.997	0.101	38.68	1.000	0.035	0.077	36.266	0.998
<i>Pinus nigra</i>	T	1.530	78	8	2.217	0.256	0.033	129.8	0.999	0.117	0.559	6.153	0.998
<i>Pinus palustris</i>	T	0.998	226	38	4.023	0.08	0.009	354.9	0.999	0.028	0.016	223.644	0.998
<i>Pinus sylvestris</i>	T	1.204	20	12	2.597	0.890	0.102	37.1	0.999	0.100	0.225	17.059	0.999
<i>Plantago coronopus</i>	O	1.142	4	2	0.796	0.555	0.232	9.655	0.984	0.260	0.046	2.554	0.998
<i>Plantago media</i>	O	0.940	23	8	0.663	0.149	0.015	159.9	0.997	0.059	0.241	7.972	0.998
<i>Podococcus barteri</i>	P	1.013	34	10	3.138	0.585	0.05	64.11	0.999	0.166	0.089	31.422	0.998
<i>Podophyllum peltatum</i>	F	1.158	13	3	2.171	0.346	0.084	32.7	0.998	0.308	0.295	1.002	0.999
<i>Potentilla anserina</i>	O	0.883	7		1.772	0.775	0.137	16.34	0.984	0.939	0.145	7.967	0.998
<i>Primula farinosa</i>	O	1.032	19	6	2.430	0.678	0.068	34.1	0.997	0.205	0.155	11.394	0.996
<i>Primula veris</i>	O	1.117	53	10	1.002	0.249	0.021	185.7	1.000	0.043	0.020	8.991	0.999



<i>Prioria copaifera</i>	T	1.019	205	98	4.840	0.157	0.014	338.1	1.000	0.026	0.025	186.407	0.998
<i>Prosopis glandulosa</i>	T	1.2949	80	9	3.518	0.171	0.032	119.1	0.998	0.053	0.032	47.547	0.997
<i>Prunus serotina</i>	T	1.216	6	2	0.036	0.300	2.044	9.47	0.999	0.309	0.201	111.119	0.998
<i>Psidium guajava</i>	T	0.994	176	9	1.955	0.055	0.012	184.6	0.999	0.080	0.005	400.793	0.999
<i>Pterocarya rhoifolia</i>	T	1.103	55	23	3.540	0.302	0.051	138.2	0.999	0.109	0.202	19.818	1.000
<i>Pterocereus gaumeri</i>	T	1.000	38	14	2.630	0.224	0.023	167.1	0.998	0.046	0.121	27.406	0.999
<i>Ranunculus acris</i>	O	1.206	6	3	1.103	0.04	0.263	13.85	0.998	0.130	0.001	6.102	0.998
<i>Ranunculus bulbosus</i>	O	1.8953	6	2	0.321	0.803	0.262	12.56	0.997	0.186	7.120	0.832	0.999
<i>Ranunculus repens</i>	O	0.498	6	4	0.559	0.223	0.123	16.92	0.994	0.773	0.178	0.088	1.000
<i>Rhizophora mangle</i>	T	1.078	75	14	0.079	0.154	0.014	160.4	0.999	0.252	0.050	146.008	0.998
<i>Rhopalostylis sapida</i>	P	1.007	222	62	4.603	0.097	0.041	104.2	1.000	0.044	0.046	81.064	0.999
<i>Sabal yapa</i>	P	1.006	91	59	3.230	0.277	0.043	138.8	0.999	0.054	0.055	92.705	1.000
<i>Sanicula europaea</i>	F	0.893	15	6	0.956	0.935	0.082	27.53	0.999	0.204	0.301	6.325	0.995
<i>Scabiosa columbaria</i>	O	1.03	12	7	2.062	0.711	0.09	19.23	0.998	0.238	0.482	2.447	0.993
<i>Scaphium borneense</i>	T	1.014	306	105	4.504	0.125	0.018	295.2	0.999	0.146	0.022	299.320	0.998
<i>Setaria incrassata</i>	O	0.936	18	4	2.500	0.806	0.089	33.33	0.996	0.300	3.024	5.632	0.994
<i>Silene acaulis</i>	O	1.010	338	25	4.557	0.205	0.032	139.5	0.999	0.956	0.035	270.494	0.998
<i>Strychnodendron excelsum</i>	T	1.047	125	79	4.363	0.230	0.028	224.9	0.998	0.084	0.193	39.715	1.000
<i>Syzygium jambos</i>	T	1.185	84	10	3.026	0.185	0.042	132.7	1.000	0.307	0.584	7.172	0.999
<i>Tachigali vasquezii</i>	T	1.053	71	58	3.837	0.354	0.065	97.29	0.999	0.047	0.112	40.889	0.999
<i>Taxus floridana</i>	T	0.965	76	14	0.403	0.045	0.050	58.33	0.998	0.035	0.046	40.006	0.997
<i>Themeda triandra</i>	O	0.997	52	2	2.520	0.582	0.028	116.7	0.998	0.085	0.062	3.537	0.994
<i>Thrinax radiata</i>	P	1.129	88	74	3.912	0.298	0.060	118.3	0.999	0.094	0.227	36.897	1.000
<i>Tillandsia multicaulis</i>	F	0.955	22	11	1.787	0.166	0.024	144.8	0.998	0.072	0.213	10.895	0.999
<i>Tillandsia punctulata</i>	F	0.731	10	5	0.027	0.381	0.033	168.1	0.998	0.220	0.767	2.744	0.917
<i>Tolumnia variegata</i>	F	1.359	16	9	2.160	0.212	0.013	206.6	0.999	0.119	0.300	8.625	0.999
<i>Trillium grandiflorum</i>	F	0.968	49	22	1.932	0.172	0.042	48.4	0.999	0.040	0.133	15.654	0.998
<i>Ulex gallii</i>	S	1.310	34	2	4.130	0.166	0.102	20.06	0.999	0.080	0.171	31.737	1.000
<i>Vatica hainanensis</i>	T	1.000	63	22	3.390	0.239	0.042	94.28	0.998	0.051	0.084	43.061	0.998
<i>Viola fimbriatula</i>	F	1.484	16		1.139	0.1	0.417	6.557	0.995	0.450	0.177	5.699	0.998
<i>Werauhia sanguinolenta</i>	F	1.109	20	12	2.450	0.850	0.220	26.52	0.997	0.100	0.382	11.203	0.999
<i>Zamia amblyphyllidia</i>	P	0.979	10	4	0.002	0.052	0.034	61.84	0.998	0.035	0.043	37.797	0.948
<i>Zea diploperennis</i>	O	0.765	11	5	0.821	0.078	0.028	96.87	0.998	0.136	0.385	17.371	1.000

Note: All demographic parameters are defined in the thesis. Missing values in the table indicate that values for these parameters could not be computed employing the method used. L.F = life form

## Appendix 6

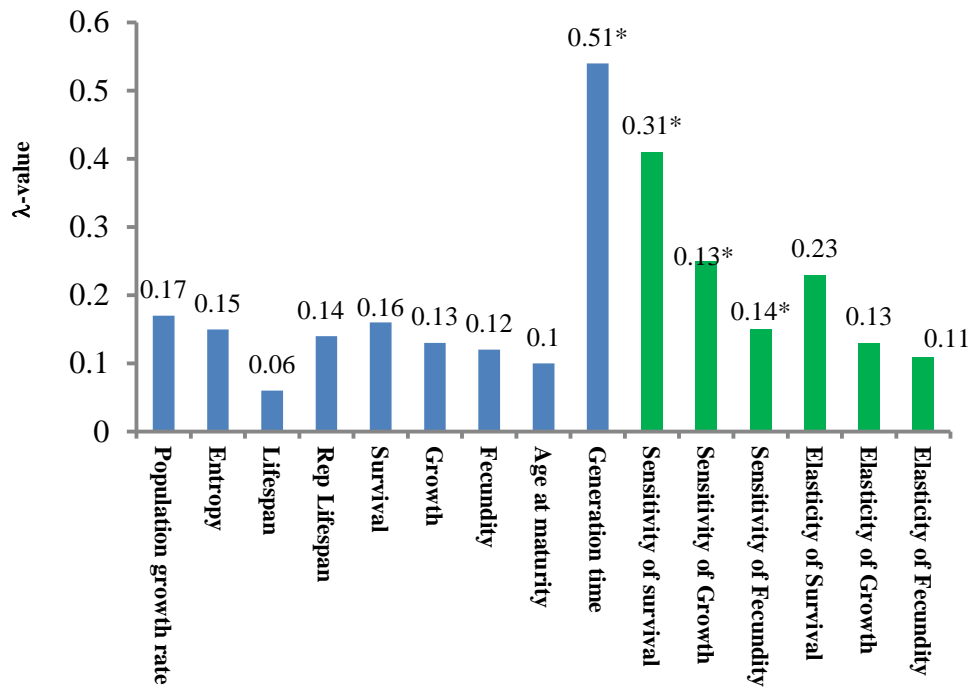


Figure 18: Phylogenetic signal in demographic life history traits using Pagel  $\lambda$ . Traits that measure population performance are highlighted in green and other life history traits are highlighted in blue. \* represents life history traits with significant level of phylogenetic signal ( $p < 0.05$ )