

Demographic and functional determinants of large-scale population
dynamics and ecological niches of 26 serotinous Proteaceae

by

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March 2018

DECLARATION

I, Martina Treurnicht, submit this dissertation electronically and declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

This dissertation includes one (1) original paper published in a peer-reviewed journal and two (2) unpublished publications (prepared for submission to peer-reviewed journals). The development and writing of the papers (published and unpublished) were my principal responsibility. Declaration(s) is/are included in the dissertation indicating the nature and extent of the contributions of co-authors, where relevant.

I am now presenting the thesis for examination for the degree of Doctorate of Philosophy.

Sincerely,

Martina Treurnicht

March 2018

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DEDICATION

To my friends and family – who encouraged, supported and cheered all the way.

Brummer, this thesis is also dedicated to you – a modest attempt to celebrate your life and your contribution to my research. I know you are cheering too!



Protea laurifolia in the Riviersonderend Mountains, Cape Floristic Region (South Africa).

ACKNOWLEDGEMENTS

A huge thank you to my excellent supervisors – Frank, Jörn, Karen and Jasper. Thank you for leading by example; for sophisticated guidance, continued encouragement, friendship and confidence to complete the task at hand. I am also very grateful for equipment, office space, lab facilities and financial support from your different departments and organisations. Frank and Jörn – to you I also say thank you for showing me the ropes in R and for making me see the light when it seemed rather dark.

A big thank you to many helpers and friends - during ca. 16 months of field work I was assisted by loyal, spontaneous, dedicated and motivated individuals whom spent many months (and kilometres!) in the field with me: Francois Nkosi Burger, Barbara Zoar Seele, Justine Ystervrou Rudman, Magali le tigre Justice, Sune Ocean-breeze Janse van Vuuren, Laura Hill-billy Hill. Most of you have since been very dear friends. Barbara and Justine, thank you for ploughing through some of my chapters, for your comments, for caring and keeping me sane.

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I am very grateful to various working groups, organisations and their members for supporting my PhD journey: Department of Conservation Ecology (Stellenbosch University, South Africa), the Institute of Landscape and Plant Ecology (University of Hohenheim, Germany), ISEM Metapopulation group (University of Montpellier II, France) and the Institute of Plant Ecology & Nature Conservation (University of Potsdam, Germany). Then also, two conservation organisations (CapeNature and SANParks) have been important partners in this work. A special thanks to AnneLise Schutte-Vlok (CapeNature) and Tineke Kraaij (SANParks, now with Nelson Mandela Metropolitan University). Many reserve managers, landowners and farmers (unfortunately too many to list individually) were open, kind-hearted and receptive of my research. Thank you to each of you - the custodians of fynbos for granting access to hills and mountains full of pristine fynbos.

Indeed, this doctoral journey would not have been possible without the support of my family. I would like to express gratitude to them for endless encouragement, mindful discussions and weekend distractions. Thank you to my parents for being supportive of my diverse interests (be it horses, rare plants, pretty Proteas and/or sports) and for cultivating a deep appreciation of the

natural world. My three siblings for being fearless role models and the “go-getter” types – because cowboys don’t cry!

Finally, a very special thank you to friends and colleagues in the northern hemisphere: Henning Nottebrock, Elena (Lena) Bryanskaya, Christine Sheppard, Alexander Kubisch, Julia Walter and Carsten Buchmann. In the southern hemisphere; Suzaan Kritzing-Klopper, Mirijam Gaertner (now in the northern hemisphere), Odette Curtis, Ismail Ebrahim, Rupert Koopman and friends of the lively Fynbos Forum community. Thanks also to my office friends at the Department of Conservation Ecology for humour, conversations, brainstorming and postgraduate sanity.

All of you contributed to this journey – an intercontinental fynbos networking flame.

Thank you.

The financial assistance of the National Research Foundation (NRF, South Africa) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

PROLOGUE - Author Bio

I am intrigued by questions in ‘real-world ecology’ and applied conservation. In particular, understanding and documenting the plant diversity of the Cape Floristic Region (CFR, South Africa), a global biodiversity hotspot of conservation priority, is my key interest. I am (something between) an amateur botanist, researcher and applied conservationist. I strive to engage people in research and interact with a diverse network of stakeholders in academia and beyond (researchers, conservation staff, private landholders, members of the public, school groups, conservation and research institutes and non-profit organisations).

So far, my early-career journey provided opportunities to work in research both locally and internationally. After completing my MSc (2010), I worked at the interface between research and applied conservation by documenting historical plant discovery rates in the CFR. This research represented a time-series analysis of plant species accumulation over 250 years of botanical exploration and discovery in the CFR. Results revealed distinct temporal patterns in taxonomic activity, botanical exploration and cumulative species descriptions in the CFR hotspot. Additionally, this study provided insights on finding the ‘missing species’ of the region (an exciting quest, even after decades of botanical discovery!). This research was recently published in an international peer-review journal (see CV for details). Another internship opportunity landed me at the South African National Biodiversity Institute (SANBI; Kirstenbosch branch in Cape Town) working for the Custodians of Rare and Endangered Wildflowers (CREW). This further provoked my interest to explore the exceptionally diverse and endemic flora of the CFR. In particular, I had the opportunity to develop a deep understanding of the many rare and threatened species, and the immense challenge of conserving a highly endemic flora in a rapidly changing world.

Following these internships, I was approached by an international research project to collect large-scale (range-wide) demographic and functional trait data on serotinous Proteaceae in the

CFR. It is this international collaboration, transpiring almost by chance (thank you, Henning!), that paved the way for my doctoral studies. It would be a challenge of what was initially perceived as a “Chuck Norris project”, but since I’ve always seen myself as a “Chuck Nora”, I of course accepted the challenge. During 2012-2014, I collected demographic and trait data across the geographical ranges of several Proteaceae species. I particularly enjoyed the field work which required careful logistical planning and allowed me to dash-off to the mountains on a weekly basis. With the completion of field work, I was recruited as a scientific researcher (2013-2015) to analyse and write-up the research from various institutions in Germany and France.

In 2015, I returned to South Africa and the CFR, and I am now a self-proclaimed ‘Fynbosser’, principally (but not exclusively) intrigued by the charismatic Cape Proteaceae – the ‘flagship’ plant family of the Cape Floristic Region. By focusing on the demographic and functional trait variation of the Proteaceae family, the over-arching goal of my research is to look for efficient and informative approaches to understand the large-scale dynamics of plants. This PhD dissertation (and, hopefully, my ongoing work as an ecologist) is meant to be a stepping stone in this direction. It thus contains ‘macro- and micro-tactics’ to boost this type of research in biodiverse regions that face ongoing and rapid environmental change.

ABSTRACT

Understanding how organisms respond to the environment at large spatial scales is central to ecology, biodiversity research and conservation. Environmental variation affects the fitness (or performance), population dynamics and geographical distributions of species via morphological traits. Quantifying how demographic rates and functional traits vary across environmental gradients may thus yield insights into the underlying determinants of ecological performance and geographical distribution. However, studies of demographic and trait variation widely rely on observations from a few species, at small spatial scales and seldom include multiple abiotic and biotic drivers. A basic understanding of the drivers of large-scale demographic variation and how functional traits relate to population dynamics and species' niches remains limited.

Using the Hutchinsonian niche concept (i.e. the set of environmental conditions in which populations can grow), I investigated how environmental conditions and functional traits affect the demography, population dynamics and ecological niches of 26 serotinous Proteaceae species with fire-dependent life cycles from the Cape Floristic Region (South Africa). My objectives were to: (i) identify the environmental drivers of large-scale demographic variation, (ii) investigate whether plant functional traits explain demographic performance and Hutchinsonian niches, and (iii) study geographical variation in population sensitivity to wildflower harvesting. I addressed these objectives using data on key demographic rates and plant functional traits sampled across species' entire geographical ranges.

Environmental drivers (climate, fire disturbance, soil nutrient status and population density) explained variation in key demographic rates of reproduction and survival across species' geographical distributions. The relative importance of these drivers varied throughout the life cycle of the study species: fecundity was mostly driven by fire interval whereas recruitment depended more on climate. A trade-off between survival and reproduction was also found where

species with fire-protected buds (resprouters) had substantially higher fire survival compared to species without fire-protected buds (nonsprouters). Overall, intraspecific variation in fecundity and recruitment was greater than that of fire survival.

I also investigated whether variation in functional traits (leaf, plant-architectural and seed traits) explains the Hutchinsonian niches of species. Results showed that interspecific trait variation explained considerable variation in global maximum population growth rates (r_{max}), as well as niche optima and widths along different environmental gradients. Intraspecific trait variation had positive effects on niche widths. Overall, relatively few individual traits stood out as predictors of species' demographic niches.

Finally, I integrated range-wide demographic data and dynamic population models to assess spatial variation in sensitivity to harvesting across species' geographical distributions. I detected considerable variation in sensitivity to harvesting across species and populations. Range-wide intraspecific variation in sensitivity to harvesting showed distinct geographical and environmental relationships. Notably, sensitivity to harvesting was highest at the environmental limits of species' ranges.

Combined, these range-wide demographic and functional approaches on species niches provide fundamental and applied perspectives in ecology and conservation biogeography. These are necessary steps to understand how range dynamics emerge from variation in demography and functional traits, and how species may be affected by ongoing global change.

OPSOMMING

'n Begrip van hoe organismes op 'n groot ruimtelike skaal op die omgewing reageer, is van belang vir ekologie, biodiversiteitsnavorsing en bewaring. Omgewingsvariasie beïnvloed die geskiktheid (of prestasie), populasiedinamiek en geografiese verspreiding van spesies deur middel van morfologiese kenmerke. 'n Kwantifisering van hoe demografiese koerse en funksionele kenmerke oor omgewingsgradiënte wissel, kan dus waardevolle insig bied in die onderliggende bepalers van ekologiese prestasie en geografiese verspreiding. Bestaande studies van demografiese en kenmerkvariasie maak egter meestal staat op waarnemings van slegs 'n paar spesies op 'n klein ruimtelike skaal, en neem selde 'n verskeidenheid abiotiese en biotiese dryfvere in ag. 'n Basiese begrip van die dryfvere van grootskaalse demografiese variasie, en die verband tussen funksionele kenmerke, populasiedinamiek en spesie-nisse, is nog beperk.

Met behulp van Hutchinson se niskonsep (d.w.s. die stel omgewingsfaktore waarin populasies kan groei) het ek ondersoek watter invloed omgewingsomstandighede en funksionele kenmerke het op die demografie, populasiedinamiek en ekologiese nisse van 26 laatbloeiende *Proteaceae*-spesies met brandafhanklike lewensiklusse in die Kaapse planteryk (Suid-Afrika). My oogmerke was (i) om te bepaal watter omgewingsdryfvere grootskaalse demografiese variasie veroorsaak, (ii) om te ondersoek watter funksionele plantkenmerke demografiese prestasie en Hutchinson se nisse verklaar, en (iii) om geografiese variasie in populasiesensitiwiteit vir veldblomoesting te bestudeer. Om hierdie oogmerke te verwesenlik, het ek gebruik gemaak van data oor die vernaamste demografiese koerse en funksionele plantkenmerke wat ingesamel is oor geografiese verspreidingsgebiede van spesies.

Omgewingsdryfvere (klimaat, brandontwrigting, grondvoedingstatus en populasiedigtheid) het 'n verklaring gebied vir variasie in die vernaamste demografiese voortplantings- en oorlewingskoerse oor geografiese spesieverspreidings heen. Die relatiewe belang van hierdie dryfvere wissel deur die lewensiklus van die studiespesies: Vrugbaarheid word meestal deur

brandgereeldheid bepaal, terwyl aanwas meer op klimaat berus. 'n Kompromis tussen oorlewing en voortplanting blyk ook uit die beduidend hoër brandoorlewingskoerse onder spesies met brandbeskernde knoppe (heruitlopers) vergeleke met spesies daarsónder (nie-uitlopers). Intraspesifieke variasie in vrugbaarheid en aanwas was oor die algemeen hoër as variasie in brandoorlewing.

Daarbenewens het ek ondersoek of variasie in funksionele kenmerke (blaar-, plantargitektuur- en saadkenmerke) Hutchinson se spesie-nisse verklaar. Resultate toon dat interspesifieke kenmerkvariasie beduidende variasie in globale maksimum populasiegroeiempo's (r_{maks}) sowel as nis-optima en -breedtes oor verskillende omgewingsgradiënte verklaar. Intraspesifieke kenmerkvariasie het 'n positiewe uitwerking op nisbreedtes. Oor die algemeen staan betreklik min individuele kenmerke uit as voorspellers van demografiese spesie-nisse.

Laastens het ek grootskaalse demografiese data en dinamiese populasie Modelle geïntegreer om ruimtelike variasie in oestingsensitiwiteit oor die geografiese verspreidings van spesies heen te beoordeel. Ek het bevind dat daar beduidende variasie in oestingsensitiwiteit is tussen spesies en populasies. Intraspesifieke variasie in oestingsensitiwiteit oor spesies se verspreidingsgebiede heen bring duidelike geografiese en omgewingsverwantskappe aan die lig. Oestingsensitiwiteit is veral die hoogste op die omgewingsperke van spesies se verspreidingsgebiede.

Tesame bied hierdie grootskaalse demografiese en funksionele benaderings tot spesie-nisse fundamentele en toegepaste perspektiewe vir ekologie en bewaringsbiogeografie. Dit voorsien nodige inligting om te verstaan hoe verspreidingsgebieddinamiek uit variasie in demografie en funksionele kenmerke ontstaan, en hoe voortdurende globale verandering spesies kan raak.

TABLE OF CONTENTS

Declaration	i
Dedication	ii
Acknowledgements	iii
Prologue – Author bio	v
Abstract	vii
Opsomming	ix
Table of Contents	xi
List of Figures	xiii
List of Tables	xix
List of Supporting Information	xx

CHAPTER 1 1-26

GENERAL INTRODUCTION

1.1. Problem statement	2
1.2. Research context and rationale	3
1.2.1. <i>The Hutchinsonian niche, demography and the environment</i>	3
1.2.2. <i>Functional traits, demographic performance and the niche</i>	6
1.2.3. <i>Demographic variation and applied conservation</i>	8
1.3. Research aims and questions	10
1.4. References	17

CHAPTER 2 **27-54**

ENVIRONMENTAL DRIVERS OF DEMOGRAPHIC VARIATION ACROSS
THE GLOBAL GEOGRAPHICAL RANGE OF 26 PLANT SPECIES

*Published as a Standard Research Paper in Journal of Ecology, **104**, 331-241.

CHAPTER 3 **55-113**

FUNCTIONAL TRAITS EXPLAIN THE HUTHINSONIAN NICHE OF
PLANT SPECIES

CHAPTER 4 **114-162**

GEOGRAPHICAL VARIATION IN SENSITIVITY TO WILDFLOWER
HARVESTING INFERRED FROM RANGE-WIDE DEMOGRAPHIC DATA

CHAPTER 5 **163-174**

CONCLUSION AND SYNTHESIS

APPENDIX A **175-197**

DESCRIPTION OF DEMOGRAPHIC NICHE MODELS

LIST OF FIGURES

CHAPTER 1

Fig. 1.1. Conceptual diagram of research chapters (Chapters 2-4) of the dissertation. Chapter 2 and 3 are fundamental research investigations while Chapter 4 follows an applied conservation approach. Chapter 2 forms the basis for all subsequent investigations, i.e. Chapter 3 and 4 (indicated by the yellow arrows). The three chapters focus on the same 26 serotinous Proteaceae species in the Cape Floristic Region (South Africa).

CHAPTER 2 *Refers to Figs 1-5 in the published version of this chapter*

Fig. 2.1. (a) The fire-dependent life cycle of serotinous Proteaceae showing key demographic rates measured in this study (fecundity, post-fire recruitment and adult fire survival), (b) Map of study sites for recruitment (squares) and fecundity (triangles) surveys in the Cape Floristic Region, South Africa. White dots depict the known geographical distribution of the entire Proteaceae family (presence records from the Protea Atlas Project; Rebelo, 2001) which largely covers the fynbos biome, a major constituent of the CFR.

Fig. 2.2. Range-wide demographic variation in 26 serotinous Proteaceae species of two life history types (resprouters and nonsprouters, respectively). (a) Probability of adult fire survival (only 18 species with > 10 records plotted); (b) individual fecundity (F); (c) per-capita recruitment rate (R).

List of Figures (continued)

Fig. 2.3. Range wide variation in (a) fecundity and (b) recruitment of *Protea punctata* in response to fire interval (time since fire), adult population density and soil moisture stress (% days with soil moisture stress). Response variables are plotted on the $\log(x+1)$ scale; lines indicate mean predictions of the best model and grey areas show 95% confidence intervals. Partial R^2 values are given for variables retained in the best models.

Fig. 2.4. Variance in (a) fecundity and (b) recruitment of 26 serotinous Proteaceae species that is explained by density (adult population density), fire (fire interval), climate (soil moisture stress, heat units, frost days, altitude anomaly) and soil (soil nutrient status). Variance explained is the partial R^2 of the respective variable(s) in the best model for each species.

Fig. 2.5. Shape of environmental effects on (a) fecundity and (b) recruitment of 26 serotinous Proteaceae species. The barplots show the number of species for which the best model predicts a given environmental response (u-shaped (\cup); negative (-); unimodal (\cap) or positive (+)). See Table 1 for descriptions on environmental variables. We classified the shape of environmental responses based on the sign of coefficients, and whether the best model contained a quadratic effect.

CHAPTER 3

Fig. 3.1. Conceptual diagram of Hutchinsonian niche characteristics (following Hutchinson's (1978) definition of the realised niche): maximum population growth rate (r_{max}), niche optima and widths, as functions of intrinsic growth rates (r_0) along environmental axes (e.g. E1, E2). Niche optima (indicated by the cross) are defined as the combination of environmental conditions where r_0 is maximal along environmental axes (E1, E2). Maximum population growth rate (the global r_{max}) is the highest value of r_0 in the niche optimal environment (i.e. the global optimum of r_0). Niche widths are then defined as the environmental range where

List of Figures (continued)

population growth is positive ($r_0 > 0$) along environmental axes (E1, E2). Table S3.3 gives estimated values for r_{max} , niche optima and widths along environmental gradients of climate (aridity, T_{min} , T_{max}), an edaphic variable (soil fertility) and fire disturbance (fire return interval) for the 26 Proteaceae study species. See Methods for details on niche characteristics and Table S3.2 for details on environmental variables.

Fig. 3.2. (a) Map of study sites for functional trait data (red points) and demographic data (black stars; as per Treurnicht *et al.* (2016)) for 26 Proteaceae species in the Cape Floristic Region (CFR, South Africa) with the geographical distribution of CFR Proteaceae (white area; Protea Atlas Database from Rebelo 2001); (b) variance partitioning of large-scale interspecific and intraspecific trait variation for eleven functional traits compiled for the study species. Proportion variance (%) are from trait-specific linear mixed effect models (see Methods, Table S3.5). Functional traits were measured for a total of 305 populations (8-22 populations per species) and 1220 individual plants (Table S3.1).

Fig. 3.3. Proportion variance explained (R^2 from phylogenetic generalised least square average models ($\Delta AICc < 10$)) by species-mean trait values (light blue bars) for (a) r_{max} , (b) niche optima and (c) niche widths, and by intraspecific trait variation (grey bars) for niche widths for 26 Proteaceae species. Niche optima and widths were defined along environmental axes of climate (aridity, T_{min} , T_{max}), soil nutrient status (soil fertility) and fire interval (see Table S3.2).

Fig. 3.4. Effects of species-mean trait values on the global maximum population growth rate (r_{max}) for 26 Proteaceae species. Bars are standardised regression coefficients with associated errors (whiskers) of eleven functional traits from phylogenetic generalised least squares averaged models ($\Delta AICc < 10$). ‘Sprouting’ is a dichotomous variable (0: nonsprouter; 1: resprouter).

Fig. 3.5. Effects of eleven functional traits [leaf traits = green bars; plant-architectural traits = maroon-brown bars; seed traits = light blue bars] on niche characteristics for 26 Proteaceae

List of Figures (continued)

species: (a,b) species-mean trait values on niche optima and widths, respectively, and (c) intraspecific trait variation on niche widths. Bars are standardised regression coefficients with associated errors (whiskers) from phylogenetic generalised least squares averaged models ($\Delta\text{AICc} < 10$). Asterisks denote levels of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Niche optima is the value for which population growth is maximal whereas niche widths are the environmental range for which population growth is positive along environmental axes of climate (aridity, T_{\min} , T_{\max}), soil fertility and fire interval (see Fig. 3.1 and Methods). ‘Sprouting’ is a dichotomous variable (0: nonsprouter; 1: resprouter).

CHAPTER 4

Fig. 4.1. Example of the stochastic extinction analyses showing simulated population dynamics over time for the persistence of one population (*P. repens*) in response to 0% (blue lines) and 50% (red lines) wildflower harvesting, respectively. Multiple extirpation events (X; years) are recorded per simulation. The intrinsic mean time to extinction (T_m ; following Grimm & Wissel 2004) and the probability of extirpation over 100 years (P_{100}) are recorded as measures of population viability per harvesting scenario. Note that only a subset ($n=10$) of the total replicated simulations are depicted. Full simulations specified a maximum time horizon of 100 000 years, ran 10 000 time step replications and included 26 serotinous Proteaceae species (see Methods for details).

Fig. 4.2. Intraspecific variation in sensitivity to wildflower harvesting across the geographical distributions of three *Leucadendron* species, (a) *L. rubrum*, (b) *L. xanthoconus*, (c) *L. coniferum*. P_{100} 0% (x-axis) and P_{100} 50% (y-axis) are estimated probabilities of extirpation (or extinction) over 100 years in response to two harvesting scenarios, respectively, derived from stochastic extinction analyses. Horizontal and vertical dashed [blue] lines indicate ‘extinction risk

List of Figures (continued)

categories' of 'LOW', 'INT' and 'HIGH' that correspond to the extinction probability thresholds of the IUCN (method E. Quantitative Analysis; IUCN 2001). Species arranged (left to right) according to increasing proportion (%) of populations sensitive to harvesting. For example, the bottom-left quadrat (no label) indicates the percentage of populations per species at 'very low risk' in response to harvesting whereas the upper-right quadrat ('HIGH') indicates the percentage of populations at 'high' risk of extinction. See Fig. S4.1 for all 26 serotinous Proteaceae study species.

Fig. 4.3. Interspecific variation in sensitivity to wildflower harvesting across the geographical distributions of 26 serotinous Proteaceae species. Individual bars [blue: nonsprouter (n=19); grey: resprouters (n=7)] show the mean proportion of populations per species that increase in sensitivity, i.e. shift from a no/low risk category to a higher risk category (LOW, INT or HIGH), due to harvesting. Across all species, the mean proportion of populations that increased in response to harvesting was 12% (n=26). See also Figs 4.2 and S4.1. Square brackets [] after species names indicate the National Red List Status (Raimondo *et al.* 2009; Red List of South African Plants 2017) per species.

Fig. 4.4. Range-wide variation and geographical patterns in sensitivity (P_{abs}) to wildflower harvesting for four serotinous Proteaceae species in the study region (Cape Floristic Region, South Africa). Pink dots indicate grid cells ($1' \times 1'$) within the range of a species (white area; presence records from Rebelo 2001) where the absolute change in extirpation probability (P_{abs} ; i.e. the difference between 0% and 50% harvesting) is > 0.1 (10%). Black area depicts the geographical distribution of CFR Proteaceae (Rebelo 2001). The four species include: (a) *L. rubrum*, (b) *L. xanthoconus*, (c) *P. punctate* and (d) *P. repens*. See Fig. S4.2 for all 26 study species.

Fig. 4.5. Shape of relationships between sensitivity to wildflower harvesting across species' geographical ranges and environmental variation of the study region (CFR, South Africa) for

List of Figures (continued)

26 serotinous Proteaceae species (see also Table S4.1). Barplot shows the number of species for which an environmental effect was detected. The shape of environmental responses was specified as either: positive (“+”), negative (“-”), unimodal [negative quadratic; “∩”], u-shaped [positive quadratic; “U”] or no effect (“ns”). Responses were quantified from the best model per species that describe the response of P_{abs} (sensitivity to harvesting; log-transformed) to these multiple environmental variables in linear regressions and a model selection approach. Environmental variables include: climate variables (summer aridity index (aridity), winter minimum temperature in the month of July (T_{min} ; °C), summer maximum temperature in the month of January (T_{max} ; °C)), soil nutrient status (index; soil fert) and fire return interval (years).

LIST OF TABLES

CHAPTER 2 *Refers to Table 1 in the published version of this chapter*

Table 2.1. Environmental variables (population density, fire interval, climate and soil) used to analyse range-wide demographic data of 26 serotinous Proteaceae species (Cape Floristic Region, South Africa) with explanations and data sources

LIST OF SUPPORTING INFORMATION

CHAPTER 2 Refers to Figs S1-3 and Table S1 in the published version of this chapter

Fig. S2.1. Variance in fecundity (a, b) and recruitment (c, d) of 26 serotinous resprouting and nonsprouting Proteaceae species that is explained by environmental drivers and population density.

Fig. S2.2. Response of fecundity (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae species.

Fig. S2.3. Response of recruitment (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae study species.

Table S2.1. List of 26 serotinous Proteaceae study species (Cape Floristic Region, South Africa) with abbreviations (used in 1 Fig. S2 and Fig. S3), range size and 2 fire persistence type, i.e. resprouter or nonsprouter (Rebelo, 2001); and number of populations sampled (n) to estimate demographic variation in fecundity, 3 recruitment and adult fire survival. Range size was calculated based on occurrence records from the Protea Atlas Project (Rebelo 2001) aggregated to a spatial 4 resolution of $1' \times 1'$.

CHAPTER 3

Appendix S3.1 (TEXT). Detailed description of field methods for the measurement of eleven functional traits (*leaf traits*: SLA, leaf width, leaf longevity, leaf nitrogen content (leaf N); *plant-architectural traits*: plant height, wood density, ramification index (ramification); *seed traits*: seed mass, seed N content (seed N) and seed N:P ratio (seed N:P)) compiled for 26 Proteaceae study species, measured from a total of 305 populations (8-22 populations per

List of Supporting Information (continued)

species) and 1220 individual plants (Table S3.1) in the Cape Floristic Region (South Africa; see also Fig. 3.2a).

Fig. S3.1. Maximum likelihood phylogeny of the 26 Proteaceae study species, reconstructed from a recent supermatrix (J. Tonnabel, unpublished data).

Fig. S3.2. Position of the 26 Proteaceae study species' functional traits (scaled and log-transformed) on the first two axes of a principal component analysis; (a) species-mean trait values explained 52% (PC1 = principal component 1; PC2 = principal component 2; explained 28% and 24%, respectively) of the variance; (b) intraspecific trait variation (calculated as the standard deviations of population-level variation per trait) explained 43% (PC1 = principal component 1; PC2 = principal component 2; explained 25% and 18%, respectively) of the variance. See Methods (main text) for details and Appendix S1 for trait measurement protocols.

Fig. S3.3. Trait variation across the global geographical distributions of the 26 Proteaceae study species in the study region, Cape Floristic Region (South Africa). (A) leaf traits (SLA, leaf width, leaf longevity, leaf N), (B) plant-architectural traits (plant height, wood density, ramification) and (C) seed traits (seed mass, seed N, seed N:P ratio). 'Sprouting' not shown since resprouting ability does not vary intraspecifically for our study species (Rebelo 2001).

Table S3.1. List of 26 Proteaceae study species with sample size (populations sampled [N], plants sampled per population [n]) and (a) species-mean trait values and (b) intraspecific trait variation (SD: standard deviations of population-level variation per trait) for eleven functional traits (see also Appendix S3.1 TEXT for detailed methods). Trait categories for the measured traits follow major axes of plant specialisation as defined by the LHS-scheme (Westoby 1998); L = leaf traits (green), H = plant-architectural traits (reddish brown) and S = seed traits (light blue)), colour-coded according to Figs 3.4 and 3.5.

List of Supporting Information (continued)

Table S3.2. Environmental variables (with abbreviations, explanations, data sources and variation in the study biome) used to define niche characteristics of 26 serotinous Proteaceae species.

Table S3.3. Estimated values of niche characteristics for 26 Proteaceae species, Cape Floristic Region (South Africa). Niches are defined for the global maximum population growth rate (r_{max} ; log-transformed), as well as niche optima and widths along environmental gradients of climate (aridity: aridity index ($\text{mm}/^{\circ}\text{C}$), calculated as the ratio between monthly precipitation (P) and average daily maximum temperature (T) in the summer month of January [(aridity = $P/(T + 10)$]; T_{min} : July mean of minimum temperature ($^{\circ}\text{C}$); T_{max} : January mean of maximum temperature ($^{\circ}\text{C}$); soil fertility (soil nutrient status index, ranging from 0 (low fertility) to 10 (high fertility)) and fire interval (time since last fire; $\log(\text{years})$). See Fig. 3.1 for conceptual diagram of Hutchinsonian niche characteristics, APPENDIX A for methodological details, Table S3.2 and Methods (main text) for details on environmental variables. Note that for aridity (expressed as an index), low values represent more arid conditions. However, when reporting parameter estimates for trait effects (see Results), this variable was inverted to describe effects on niche optimum along increasing aridity.

Table S3.4. Spearman rank correlation coefficients for eleven functional traits measured from 26 serotinous Proteaceae species: (a) species-mean trait values, (b) intraspecific trait variation (calculated as the standard deviations of population-level variation per trait). See Appendix S3.1 for trait measurement protocols; “Sprouting” (binary variable [0: nonsprouter; 1: resprouter]) was omitted since this trait does not vary intraspecifically for the study species (Rebelo 2001).

Table S3.5. Eleven functional traits measured for 26 Proteaceae species with interspecific and intraspecific trait variation (expressed as proportion variation [%]; estimated from linear mixed

List of Supporting Information (continued)

effect models (see also Fig. 3.2b). Details on trait measurements are provided in Appendix S3.1; note that ‘Sprouting’ does not vary within species (Rebello 2001).

CHAPTER 4

Fig. S4.1. Intraspecific variation in sensitivity to wildflower harvesting across the global geographical distributions of 26 serotinous Proteaceae species. $P_{100} 0\%$ (x-axis) and $P_{100} 50\%$ (y-axis) are estimated probability of extirpation over 100 years in response to two harvesting scenarios, respectively, derived from stochastic extinction analyses (described in main text). Horizontal and vertical dashed [blue] lines indicate ‘extinction risk categories’ of ‘LOW’, ‘INT’ and ‘HIGH’ that correspond to the extinction probability thresholds of the IUCN (method E. Quantitative Analysis; IUCN 2001). Per species, the bottom-left quadrat (no label) indicates the percentage (%) of populations per species at ‘very low risk’ in response to harvesting whereas the upper-right quadrat (‘HIGH’) indicates the percentage of populations at ‘high’ risk of extinction. The diagonal [solid grey] line indicates the 1:1 association that would be expected if 50% harvesting had no impact on population viability and sensitivity. See also Fig. 4.2 in main text.

Fig. S4.2. Range-wide variation and geographical patterns in sensitivity (P_{abs}) to wildflower harvesting for 26 serotinous Proteaceae species in the Cape Floristic Region (South Africa). Pink dots indicate grid cells ($1' \times 1'$) within the range of a species (white area; presence records from Protea Atlas Project; Rebello 2001) where the absolute change in extirpation probability (P_{abs} ; i.e. the difference between 0% and 50% harvesting) is > 0.1 (10%). Species name abbreviations follow Rebello (2001), see Table S4.1 for full names.

Table S4.1. Relationships of range-wide sensitivity to wildflower harvesting and large-scale environmental variation for 26 serotinous Proteaceae species (with abbreviations, range size;

List of Supporting Information (continued)

Rebello 2001 and National Red List status (Red List of South African Plants 2017)). Environmental variables include: climate variables of drought, cold and heat stress [i.e. an aridity index (Aridity), winter minimum temperature in the month of July (Tmin; °C), summer maximum temperature in the month of January (Tmax; °C)], soil nutrient status (index; soil fert) and fire return interval (years; fire interval). The shape of environmental responses was specified as either positive (“+”), negative (“-”), unimodal [negative quadratic; “∩”] or u-shaped [positive quadratic; “U”]. Responses were quantified from the best model per species from linear regressions that describe the response of P_{abs} (sensitivity to harvesting; log-transformed) to multiple environmental variables in a model selection approach. Bottom panel of the table summarises the number of species for which a particular environmental effect (or shape) was detected. See also Fig. 4.5.

CHAPTER 1

GENERAL INTRODUCTION

PROBLEM STATEMENT

Understanding how species respond to large-scale environmental variation across their geographical ranges is central to ecology, biodiversity research and conservation. Developing a more refined understanding of species' responses to environmental variation is particularly urgent in biodiversity research. This is important given the uncertainty on how populations, species, communities and entire ecosystems will respond to ongoing global change (Thuiller 2004; Midgley & Bond 2015; Urban 2015). Recent evidence suggests that environmental change will progress too rapidly to allow evolutionary adaptations in many species, leading to extinctions through changes in species' abundance and geographical ranges (Sala *et al.* 2000; Urban 2015; Ducatez & Shine 2017). Without understanding the drivers of demographic variation, population dynamics and the ecological niches of species it seems nearly impossible to assess the impacts of global change on biodiversity. This is especially relevant for biodiversity hotspots (i.e. exceptionally species-rich regions vulnerable to recent environmental change; Myers *et al.* 2000) where the sheer number of species often prevents species-specific assessments. Although there have been a variety of approaches and major advances to address this challenging research agenda (Ehrlén & Morris 2015; Estrada *et al.* 2016 for reviews), studies of demographic and trait variation that span the geographical ranges of several species are still sparse (Schurr *et al.* 2012a; Violle *et al.* 2014). Many studies in plant ecology have widely relied on observations from single (or few) species, collected at few locations and seldom include abiotic and biotic drivers of population and niche dynamics. An important step to address this paucity of knowledge is to study demographic and functional trait variation across populations, species and environmental gradients at large spatial extents (McGill *et al.* 2006; Gaston 2009; Schurr *et al.* 2012a; Ehrlén & Morris 2015). Focusing demographic research on multiple species and populations across entire geographical distributions may also provide invaluable insights to understand the potential responses of species to global change

and range dynamics (Schurr *et al.* 2012a; Thuiller *et al.* 2014; Ehrlén & Morris 2015; Griffith *et al.* 2016). In addition, identifying the trait-determinants of species' niches is useful for improving predictions of climate-driven range shifts (Estrada *et al.* 2016; Evans *et al.* 2016). In summary, without understanding the range-wide demographic and functional determinants of population dynamics and species' niches, ecologists are unable to provide comprehensive forecasts of how global change will affect populations, species, communities and ecosystems (McGill *et al.* 2006; Thuiller *et al.* 2014; Ehrlén & Morris 2015; Díaz *et al.* 2016; Griffith *et al.* 2016).

RESEARCH CONTEXT AND RATIONALE

THE HUTCHINSONIAN NICHE, DEMOGRAPHY AND ENVIRONMENT

The concept of the ecological niche, notably the Hutchinsonian niche (Hutchinson 1957; 1978), is central to ecology and biodiversity research (Pulliam 2000; Chase & Leibold 2003; Holt 2009; Schurr *et al.* 2012a). G. E. Hutchinson suggested that the niche of a species is quantifiable from an 'n-dimensional hypervolume' space. This, according to Chase & Leibold (2003), was the "revolutionary step" of Hutchinson's niche definition compared to earlier niche definitions (e.g. Grinnell 1917; Elton 1927). Hutchinson also distinguished (and coined) the terms 'realised' and 'fundamental' niches based on interspecific interactions, with a particular emphasis on competition (Hutchinson 1957; 1978). The fundamental niche is defined as the entire set of conditions under which an organism can *occur*, or 'exist indefinitely' (Hutchinson 1957). In particular, the realised Hutchinsonian niche (Hutchinson 1978) of a species is defined as the set of environmental conditions in which population growth rates are positive in the presence of competitors (Maguire 1973, Holt 2009). The Hutchinsonian niche describes how population growth and demographic processes vary across environmental gradients through geographical space and with interspecific interactions (Pulliam 2000; Chase & Leibold 2003;

Holt 2009). These gradients and interactions ultimately determine the local dynamics of populations (Pulliam 2000). Despite the central importance of the Hutchinsonian niche in ecology, it is rarely used to characterise requirements of species and to study species' responses to environmental variation (Holt 2009; Schurr *et al.* 2012a; but see Merow *et al.* 2014).

The more widespread approach in ecology when studying the large-scale dynamics of species is to study patterns of abundance (or occurrence) in geographical space. For example, species responses to environmental variation are often inferred from species distributions models (SDMs; or climate envelope models) which relate the occurrence probability of species to the environment, in particular to climate. These models are commonly interpreted as describing variation in species performance across large spatial extents and thus widely used to predict species' responses to climate change and forecast range shifts under different climate scenarios (Guisan & Thuiller 2005; Dormann *et al.* 2012). However, the currency of occurrence integrates across several biological processes and cannot resolve how responses of performance, notably demographic rates, relate to environmental variation (Lavergne *et al.* 2010; Thuiller *et al.* 2014). SDMs also do not account for intraspecific variation in demographic rates and assume that species' responses to the environment are uniform across geographical space (Pearson & Dawson 2003; Lavergne *et al.* 2010). Furthermore, these bioclimatic approaches rarely include disturbance factors like fire and variation in soil conditions, which are also important drivers of species' population dynamics (Evans, Holsinger & Menges 2010; Thuiller 2013). While SDMs are useful for understanding the biotic impacts of climate change (Pearson & Dawson 2003; Guisan & Thuiller 2005; Franklin *et al.* 2017), it is now widely recognised that alternative approaches should be developed to better unravel and understand the drivers of population dynamics and species' relationships with the environment (Schurr *et al.* 2012a; Ehrlén & Morris 2015; Ehrlén *et al.* 2016; Griffith *et al.* 2016; Franklin *et al.* 2017). This is an increasingly

important research agenda in the face of ongoing global change currently causing unprecedented biodiversity loss (Sala *et al.* 2000; Urban 2015).

The Hutchinsonian niche links demography and the environment since the concept can be expressed in terms of how reproduction and mortality vary in response to environmental variation (Maguire 1973; Hutchinson 1978). Thus, a prerequisite for studying species' niches would be to study variation in key demographic rates across considerable spatial and environmental gradients (Hutchinson 1978; Holt 2009; Schurr *et al.* 2012a). A demographic research agenda for biogeography (*sensu* Schurr *et al.* 2012a), i.e. studying demographic rates across geographical gradients, has been proposed as a promising means to better unravel the drivers of population dynamics and species' niches, with important implications for range dynamics (Pagel & Schurr 2012; Schurr *et al.* 2012a). Accounting for intraspecific density dependence within the demographic research agenda is also important since, for example, intraspecific competition may decrease observed rates of reproduction and survival (Schurr *et al.* 2012a; Ehrlén & Morris 2015). Hence, there has been a recent upsurge to invoke the niche concept, in particular the Hutchinsonian niche, in biodiversity research and in predicting the future range dynamics of species (Schurr *et al.* 2012a; Ehrlén & Morris 2015; Ehrlén *et al.* 2016). This interest in the drivers of demography is also essential for developing mechanistic estimates of species responses to environmental variation and to better forecast the impacts of global change (Schurr *et al.* 2012a; Ehrlén & Morris 2015).

FUNCTIONAL TRAITS, DEMOGRAPHIC PERFORMANCE AND THE NICHE

Trait-based approaches have a long history in ecology (Violle *et al.* 2007; Shipley *et al.* 2016 and references therein). Functional traits are measurable morphological, physiological, phenological, or behavioural features that affect fundamental processes of growth, reproduction and survival (Violle *et al.* 2007). Trait-based approaches generally aim to quantify the relationships between functional traits and environmental variation with a number of functional response traits that are predictors (or proxies) of organisms' performance along environmental axes (McGill *et al.* 2006; Violle *et al.* 2007; Violle *et al.* 2014). For example, interspecific differences in leaf traits generally respond to variation in climate, such as drought and heat stress (e.g. Lamont, Groom & Cowling 2002; Wright *et al.* 2004; Yates *et al.* 2010a; Carlson, Holsinger & Prunier 2011) and soil conditions (e.g. Maire *et al.* 2015; Reich *et al.* 2003), whereas leaf, architectural and reproductive traits may respond to climate, soil and fire disturbance gradients (e.g. Ackerly 2004; Chave *et al.* 2009; Lamont & Groom 2013; see also Appendix S3.1 (Chapter 3) for a review). Establishing trait-environment relationships allows ecologists to quantify and predict how plants optimise fundamental processes of growth, reproduction and survival at geographical scales (Violle & Jiang 2009; Violle *et al.* 2014). Several studies highlight the potential of traits to explain interspecific variation in plant performance (Wright *et al.* 2010; Poorter & Bongers 2006; Poorter *et al.* 2008). More recently, Paine *et al.* (2015), however, found that functional traits were poor predictors of tree growth. These authors suggested that an approach relying on key demographic rates of reproduction and survival may reveal more defined relationships but direct measurements of these demographic rates are challenging to obtain, especially across a broad range of species (Schurr *et al.* 2012a).

A key aim for the emerging fields of functional population ecology (e.g. Adler *et al.* 2014; Salguero-Gómez *et al.* 2016) and functional biogeography (i.e. studying the distribution of trait diversity across organisational and ecological scales; *sensu* Violle *et al.* 2014) is to test if traits explain demographic performance and species niches. This would help to better understand range-wide variation in population dynamics, life history variation and species-environment relationships (McGill *et al.* 2006; Salguero-Gómez *et al.* 2016; Díaz *et al.* 2016). To unravel these drivers and determinants of population- and community ecology, McGill *et al.* (2006) suggested to link traits, environmental gradients and species performance. One promising means of doing so is to rely on the ecological niche concept (Violle *et al.* 2007; Violle & Jiang 2009) which provides a means to directly relate demographic performance with trait variation whilst resolving the environmental context. Indeed, the use of functional traits to understand demographic performance and population dynamics is increasingly recognised in functional population ecology and functional biogeography (Adler *et al.* 2014; Violle *et al.* 2014). Despite the fact that this is a promising research agenda in functional ecology, few studies have been able to resolve relationships between traits, environmental variation and large-scale demographic performance. This is largely due to a limited availability of trait data for multiple species across geographical scales (McGill *et al.* 2006). Previous studies that aimed to link traits with proxies of demographic performance, such as vital rate elasticities and individual growth rates, could also not resolve underlying environmental variation (e.g. Adler *et al.* 2014; Paine *et al.* 2015). A key question that remains in trait-based studies is thus to quantify the extent to which functional traits explain intra- and interspecific variation in large-scale population dynamics and species niches.

DEMOGRAPHIC VARIATION AND APPLIED CONSERVATION

Large-scale demographic data spanning multiple species and their entire geographical distributions is also relevant for applied conservation questions (Frederiksen *et al.* 2014 for a review). Human exploitation of natural resources, such as harvesting of non-timber forest products, from wild populations directly affects species' abundance, persistence and population growth rates (e.g. Lamont *et al.* 2001; Peres *et al.* 2003) and overharvesting may increase extinction risk (e.g. Nantel, Gagnon & Nault 1996; Raimondo & Donaldson 2003). Understanding the impacts of harvesting on population dynamics and how populations in different environments may respond to harvesting are seen as important prerequisites for the sustainable management of species (Ticktin 2004). For example, the vulnerability of species and/or populations to anthropogenic threats is usually not homogeneous throughout their geographical ranges. Instead, vulnerability may vary due to intraspecific differences in demographic rates and responses of vital rates to environmental variation, and/or differences in life history traits (Ticktin *et al.* 2002; Ticktin 2004). Studying range-wide inter- and intraspecific variation in response to harvesting is necessary for understanding how population viability depends or responds to environmental gradients. Also, understanding the vulnerability of species and populations in response to harvesting may identify which species are likely to be more affected by ongoing global change, particularly in the case of already threatened species (Bomhard *et al.* 2005; Pearson *et al.* 2014). Since long-term monitoring data for species are generally scarce, ecologists and conservation practitioners often rely on available demographic data to perform population viability analyses (PVAs) and model simulations to assess the future status of species (Beissinger & Westphal 1998; Menges 2000; Crone *et al.* 2013). These approaches are useful to understand the impacts of anthropogenic harvesting on plant species (e.g. Peres *et al.* 2003; Raimondo & Donaldson 2003; Ticktin 2004; Frederiksen *et al.* 2014). However, limited data across spatial scales prevent a predictive understanding of the fate of

populations across different landscapes and species' ranges in response to harvesting (Frederiksen *et al.* 2014). Moreover, modelling approaches widely ignore the influence of the underlying environment which may play a particularly important role in determining species responses to harvesting (e.g. Akçakaya *et al.* 2004; Crone *et al.* 2013).

Proteaceae are a characteristic family of shrubs in the Cape Floristic Region (South Africa) global biodiversity hotspot (Myers *et al.* 2000). Harvesting the inflorescences of the Proteaceae family from natural populations is an economically important activity in the region (Turpie, Heydenrych & Lamberth 2003; Van Wilgen *et al.* 2016). Many Proteaceae are serotinous (=bradysporous) and follow a fire-dependent life cycle (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991; Bond & Van Wilgen 1996). They rely on canopy-stored seed reserves to regenerate after fire, making species potentially vulnerable to flower harvesting (Mustart & Cowling 1992; Maze & Bond 1996). This removal of flowers, or potential seed-cones, is known to affect the population dynamics of these species by notably reducing the size of their canopy-stored seedbanks (Mustart & Cowling 1992; Maze & Bond 1996; Witkowski & Lamont 1996; Lamont *et al.* 2001; Cabral *et al.* 2011). Harvesting practices should thus ensure that sufficient seed reserves remain on parent plants to allow the accumulation of seeds needed for post-fire recruitment (Maze & Bond 1996). This would reduce the risk of local population crashes following large-scale disturbances such as fire. In order to safeguard populations and species against overexploitation, current conservation guidelines recommend that no more than 50% of the current year's flowers or stems be removed during a single harvesting event (e.g. Van Wilgen & Lamb 1986; D'Alton *et al.* 2015). Indeed, a few studies found that harvesting above this level severely compromised lifetime fecundity, post-fire seed dispersal and recruitment of species (Mustart & Cowling 1992; Maze & Bond 1996). However, these studies were generally limited in spatial and taxonomic extent. The development of species-specific and locally

adapted management guidelines thus remains severely limited due to insufficient data for multiple species across the CFR. Further spatial and taxonomic generalisation on the impacts of harvesting is needed since a substantial number of serotinous shrub species are economically-important to the local wildflower industry and are harvested across the region (Rebelo 2001). From an applied conservation perspective, an incomplete understanding on the ecological effects of harvesting limits the spatial prioritization of harvesting levels and the possibility to derive both locally and regionally adapted sustainable management and monitoring guidelines in the CFR (Pressey *et al.* 2007).

RESEARCH AIMS AND QUESTIONS

Finding informative and efficient approaches to build a better understanding of the large-scale (i.e. covering complete geographical ranges) dynamics of species is an important task in ecology. Using the Hutchinsonian niche (Hutchinson 1957; 1978) as a theoretical framework, I investigate how environmental conditions and plant functional traits affect demography, population dynamics and ecological niches of 26 plant species with fire-dependent life cycles in the South African Cape Floristic Region (CFR). The research presented here addresses three major aims, i.e. to: (1) investigate how key demographic rates respond to environmental variation and population density across species' entire geographical ranges, (2) relate large-scale variation in functional traits to the demographic niches of species, and (3) demonstrate how range-wide demographic data can be used to answer pressing conservation questions. This dissertation thus involves two fundamental research studies and an applied conservation study. Below, I provide a brief overview of the study region and species, followed by a break-down of the specific questions that I addressed in each research chapter.

I focus on 26 Proteaceae species in the genera *Leucadendron* and *Protea* which are serotinous (=bradysporous) and endemic to the Cape Floristic Region (CFR). Of the total 333 Proteaceae species in the CFR, 321 are endemic with a high number of endemics in both of these genera (*Leucadendron*: 84 spp., *Protea*: 80 spp.; Rebelo 2001) and contain a high number of threatened species (Raimondo *et al.* 2009).

The CFR is an ideal study region for various reasons. The CFR is a global biodiversity hotspot of conservation priority (Myers *et al.* 2000) and characterised by a largely Mediterranean-type climate, yet covers steep variation in climate, topography as well as small-scale variation in soil conditions (Allsopp, Colville & Verboom 2014). This region is expected to be highly affected by future climate change, posing a serious threat to the region's biodiversity (Yates *et al.* 2010b; Wilson *et al.* 2015). From a plant diversity perspective, the CFR is dominated by overstorey Proteaceae shrubs which are considered 'the flagship species' of the CFR (Rebelo 2001; Schurr *et al.* 2012b). Proteaceae are "model organisms for biodiversity research" (*sensu* Schurr *et al.* 2012b), notably due to extensive data collection efforts (Protea Atlas Project; Rebelo 2001) and long-term post-fire monitoring data (Bond, Vlok & Viviers 1984). These efforts yielded a comprehensive taxonomic understanding of Proteaceae and detailed spatial information on their occurrence (CFR and southern Africa). The Proteaceae also harbours a diversity of life history types, including resprouters (species with fire-protected buds) and nonsprouters (species vulnerable to fire; Clarke *et al.* 2013), as well as remarkable demographic and plant-trait features (Rebelo 2001). For example from a demographic perspective, for serotinous Proteaceae the size of the canopy seed bank is a measure of the total fecundity between two fires given that the plant would burn at the time of sampling (Nottebrock, Esler & Schurr 2013). The size of the canopy seed bank measures potential lifetime fecundity if the plant is killed by fire since fire usually destroys large amounts of above ground biomass (Bond, Vlok & Viviers 1984;

Bond & Van Wilgen 1996). From a functional or trait-based perspective, variation in plant traits (e.g. leaf size and shape, wood density) are associated with climatic variation such as drought and heat stress (Yates *et al.* 2010a; Carlson, Holsinger & Prunier 2011; see also Appendix S3.1 in Chapter 3 of this dissertation for a review). Together, these factors make the CFR an ideal study region, and serotinous Proteaceae suitable study species for the large-scale demographic and trait-based investigations across species' geographical ranges that I present in this dissertation.

This dissertation consists of five chapters. Chapters 2-4 (see Fig. 1.1) constitute three self-contained research articles written in scientific paper format and follow the layout of a chosen journal. These chapters are a result of multi-authored manuscripts on which I was the primary author and contributor. The publication status and co-authors are indicated on a title page provided per chapter, while authors' contributions are acknowledged below.

Chapter 1, this chapter, provides a general introduction to the context and the rationale behind the research, followed by the aims and key questions of each research chapter. Broadly, this introduction provides general context to the research in a condensed manner by referring to key literature and also outlines the major themes of this dissertation.

Chapter 2 addresses fundamental research questions within the 'demographic research agenda for biogeography' (*sensu* Schurr *et al.* 2012a). Specifically, I investigate the environmental determinants of range-wide variation in total fecundity, post-fire seedling recruitment and adult fire survival. The key questions that I address are: (1) do demographic rates differ inter- and intraspecifically, and between life history types? (2) how do species' demographic rates

(fecundity, recruitment and fire survival) respond to environmental drivers (climate, fire, soil fertility) and population density? (3) What is the relative importance of different environmental drivers for range-wide variation in key demographic rates? (4) Do species show consistency or differentiation in demographic responses to different environmental gradients and population density? This work was published as a standard research article entitled “*Environmental drivers of demographic variation across the global geographical range of 26 plant species*” in *Journal of Ecology* (Vol. 104; 331-342), as part of the cross-journal special feature titled “Demography beyond the Population”, and was awarded the [Harper Prize 2016](#) of the British Ecological Society. All work in this chapter was primarily conducted by myself (M. Treurnicht). I collected and analysed data, interpreted results, prepared figures and wrote the manuscript. F.M. Schurr and J. Pagel contributed towards the conceptual development of the study and assisted with the demographic analyses; A. Schutte-Vlok, H. Nottebrock, T. Kraaij contributed portions of demographic data; T. Rebelo contributed presence records and occurrence data for the study species (from Rebelo 2001); all co-authors made contributions to improve the manuscript.

In Chapter 3, I relate functional traits to demographically-derived Hutchinsonian niches of 26 plant species to assess the extent to which demographic niches are governed by traits. Specifically, I tested if range-wide variation in functional traits (including inter- and intraspecific variation) are determinants of species’ niche characteristics. The key questions that I address include: (1) Does interspecific variation in traits (major leaf, plant-architectural and seed traits) explain different niche characteristics? More specifically, can functional traits explain maximum population growth rates, niche optima and widths? (2) Does intraspecific trait variation explain niche widths in addition to interspecific trait variation? All work in this chapter is principally by me (M. Treurnicht). I collected and analysed data, interpreted results, prepared figures and wrote the manuscript. F.M. Schurr and J. Pagel assisted with statistical

analyses and interpreting results. J. Pagel performed the statistical estimation of niche characteristics from range-wide demographic data (collected in Chapter 2); Jeanne Tonnabel developed the supermatrix phylogeny for the phylogenetically controlled trait analyses. All co-authors contributed to revisions of the manuscript.

Chapter 4 explores how demographic data, spanning multiple species and their geographical ranges, can be useful to applied conservation biology. I investigate spatial variation in sensitivity to wildflower harvesting inferred from range-wide demographic data for 26 serotinous Proteaceae species. The key questions I address include: (1) how does wildflower harvesting affect inter- and intraspecific variation in sensitivity across species' geographical ranges? (2) Are certain areas within the range of a species more sensitive to harvesting? And lastly, (3) is sensitivity to harvesting associated with environmental variation of the study region? All work in this chapter was my (M. Treurnicht's) primary responsibility. I developed the research concept, analysed data, interpreted results, prepared figures and wrote the manuscript. J. Pagel developed the extinction simulations and stochastic population dynamic models used in the analyses (see below for details); F.M. Schurr and J. Pagel assisted with the analyses. F.M. Schurr, J. Pagel, J. A. Slingsby & K.J. Esler also contributed to the conceptual development of the study and made comments to improve the manuscript.

Chapter 5 is a conclusion and synthesis of the research: I briefly highlight the significance of my research, as well as perspectives for future research.

Finally, this dissertation was initiated as part of a collaborative project (funded by the German Research Foundation (DFG) grants: SCHU 2259/5-1 and SCHU 2259/3-1) that aims to

understand how demographic rates, functional traits and phylogenetic determinants shape the ecological niches and large-scale dynamics of serotinous Proteaceae. I (M. Treurnicht) collected and compiled the demographic and functional trait data that forms the basis of this project while J. Pagel integrated this demographic data into a process-based modelling approach to estimate species' niches. These statistical estimates of species' niches are used in chapters 3 and 4 of this dissertation. Notably, Chapter 3 relied on the demographic niche models to derive Hutchinsonian niche characteristics, whereas Chapter 4 used these models to simulate population viability of species in response to harvesting. Although the manuscript that addresses the estimation of niches is currently in preparation (i.e. Pagel *et al. in prep.*), Appendix A is provided for clarity which describes the process-based modelling of species' demographic niches. Analyses in Chapter 3 relied on a recently developed supermatrix phylogeny (J. Tonnabel, unpublished data) that combined the most recent molecular markers for major Proteaceae genera (see Chapter 3 of the dissertation).

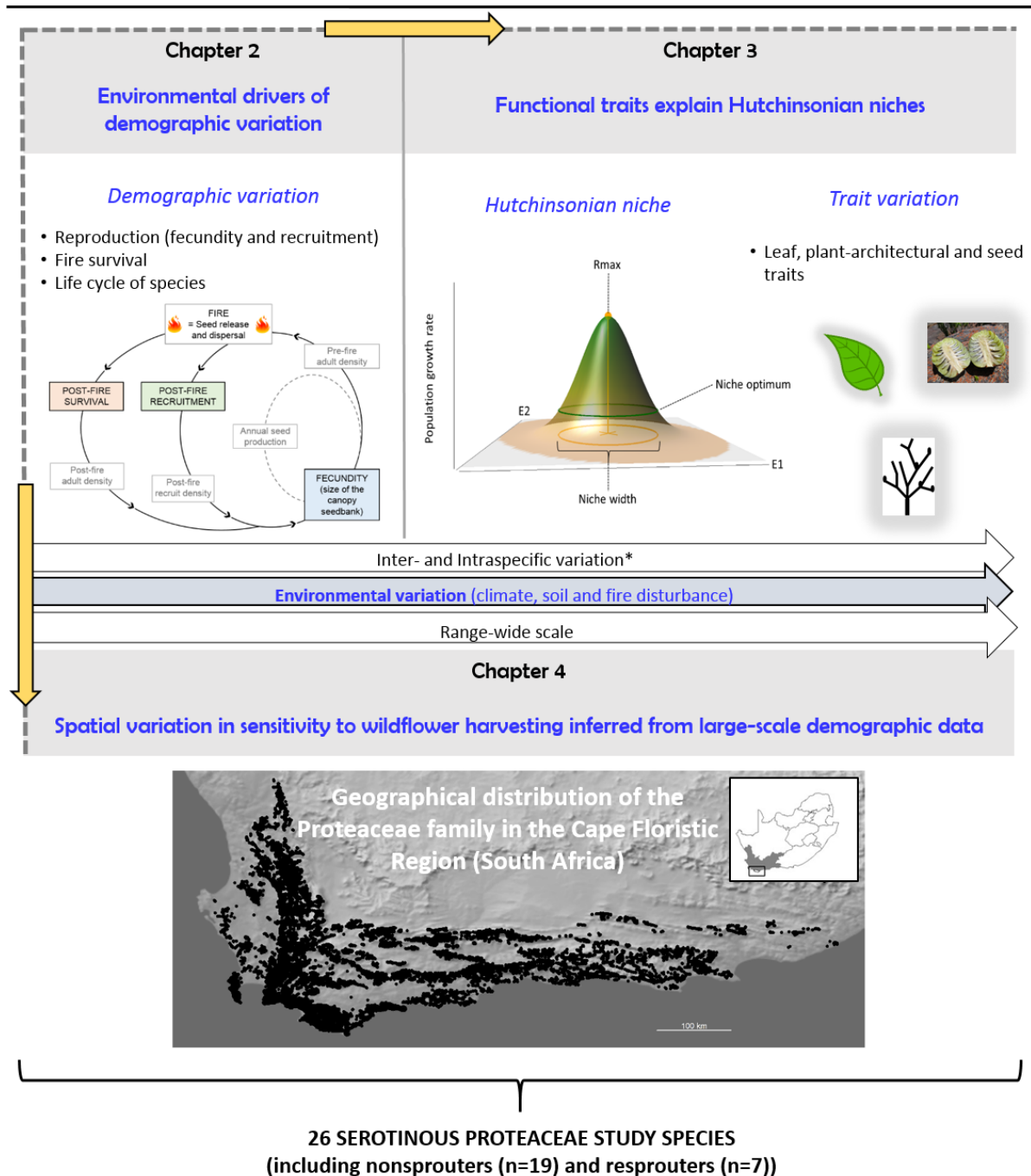


Fig. 1.1. Conceptual diagram of research chapters (Chapters 2-4) of the dissertation. Chapters 2 and 3 are fundamental research investigations while Chapter 4 follows an applied conservation approach. Chapter 2 forms the basis for all subsequent investigations, i.e. Chapter 3 and 4 (indicated by the yellow arrows). The three chapters focus on the same 26 serotinous Proteaceae species in the Cape Floristic Region (South Africa).

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CHAPTER 2

ENVIRONMENTAL DRIVERS OF DEMOGRAPHIC VARIATION ACROSS THE GLOBAL GEOGRAPHICAL RANGE OF 26 PLANT SPECIES

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DEMOGRAPHY BEYOND THE POPULATION

Environmental drivers of demographic variation across the global geographical range of 26 plant species**Martina Treurnicht^{1,2*}, Jörn Pagel¹, Karen J. Esler², AnneLise Schutte-Vlok^{3,4}, Henning Nottebrock^{1,5}, Tineke Kraaij^{6,7}, Anthony G. Rebelo⁸ and Frank M. Schurr^{1,5}**

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Summary

1. Understanding how rates of reproduction and survival respond to environmental variation across species' geographical ranges is a key task for both basic and applied ecology. So far, however, environmental drivers of range-wide demographic variation have only been studied in a few plant species without considering the potentially confounding effects of population density on demographic rates.

2. We present a large-scale demographic study of 26 shrub species (Proteaceae) from the Cape Floristic Region. All study species have a fire-dependent life cycle and are serotinous: they exclusively form a canopy seed bank which contains the seeds produced since the last fire. Fire triggers seed release from the canopy so that recruitment is largely limited to a short period after fire.

3. Across the global geographical ranges of the study species, we collected 3454 population-level records of total fecundity since the last fire (size of individual canopy seed banks), per-capita recruitment (ratio between post-fire recruits and pre-fire adults) and adult fire survival. We used linear regressions to quantify how climate, population density, fire interval and soil nutrients affect demographic variation.

4. A trade-off between survival and reproduction is evident throughout the geographical ranges of our study species: resprouting species with fire-protected buds had much higher fire survival than nonsprouters without fire-protected buds (97% vs. 2%) but they also had substantially lower fecundity and recruitment rates. We found little intraspecific variation in fire survival rates but considerable intraspecific variation in fecundity and recruitment.

5. Range-wide variation in fecundity was dominated by fire interval whereas recruitment was mostly climate-driven. Population density and soil nutrients generally had smaller effects but were important for the fecundity and recruitment of several species. Effects of fire interval on fecundity were consistent across species, but other demography–environment relationships showed substantial interspecific differentiation.

6. *Synthesis.* This study extends demographic research beyond the population to cover the geographical ranges of multiple species. Such large-scale studies are a necessary first step of a research agenda that aims to understand how range dynamics emerge from first principles of demography, how they are shaped by functional traits and macroevolution and how they will be impacted by global change.

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Introduction

The fundamental demographic processes of reproduction and survival are central to evolutionary biology, biogeography and ecology (Pulliam 2000; Metcalf & Pavard 2007; Gaston 2009; Schurr *et al.* 2012a). In population ecology, reproduction and survival play a key role since they jointly determine the local dynamics of populations in the absence of dispersal. Notably, the realized niche of a species *sensu* Hutchinson (1978) can be defined as the set of environments in which intrinsic population growth rate (the sum of reproduction and survival rates) is positive in the presence of competing species (Maguire 1973; Holt 2009). To quantify a species' Hutchinsonian niche, one thus has to identify the environmental drivers of variation in reproduction and survival (Holt 2009; Schurr *et al.* 2012a). The growing interest in large-scale niches furthermore requires us to quantify how environmental heterogeneity drives reproduction and survival across the geographical ranges of species (Schurr *et al.* 2012a). From a fundamental perspective, large-scale variation in reproduction and survival impacts the geographical distribution and range dynamics of species (Schurr *et al.* 2012a). From an applied perspective, identifying the environmental drivers of range-wide variation in reproduction and survival is essential for understanding and forecasting how global change will impact population performance and the dynamics of species' ranges (Schurr *et al.* 2012a; Ehrlén & Morris 2015; Ehrlén *et al.* 2016).

While large-scale variation in reproduction and survival is central to both fundamental and applied ecology, the drivers of this variation are still poorly understood. This is due to a dearth of data on large-scale demographic variation across multiple populations and species (Ehrlén & Morris 2015; Salguero-Gómez *et al.* 2015; Ehrlén *et al.* 2016; Griffith *et al.* 2016). Given this lack of demographic data, it is not surprising that many studies resorted to other ways of inferring large-scale variation in species' performance. Notably, species distribution models (SDMs) which relate the occurrence probability of species to environmental variation (Guisan & Thuiller 2005) are commonly interpreted as describing large-scale variation in species performance. This interpretation of SDMs is, however, problematic since spatial population dynamics (Pagel & Schurr 2012; Schurr *et al.* 2012a) and interspecific interactions (Svenning *et al.* 2014) can cause mismatches between the niche and the geographical distribution of species. Moreover, SDMs cannot unravel how variation in occurrence arises from the response of individual vital rates to environmental variation (Lavergne *et al.* 2010). It is thus not surprising that recent studies found unclear relationships between occurrence probability predicted by SDMs and estimates of intrinsic population growth (Thuiller *et al.* 2014). Hence, recent reviews have called for a demographic research agenda that identifies the environmental drivers of demographic variation across the geographical ranges

of species (Schurr *et al.* 2012a; Ehrlén & Morris 2015; Ehrlén *et al.* 2016).

Plant ecology has long identified climate, soil conditions, disturbances and biotic interactions as the main drivers of small-scale variation in plant reproduction and survival. Key climatic drivers of plant reproduction and survival are heat, frost and drought (McDowell *et al.* 2011; Bykova *et al.* 2012). Soil conditions, notably nutrient availability, are also important drivers of population dynamics (Thuiller 2013). Major disturbances caused by floods, storms or fire alter demographic rates periodically and characteristics of the disturbance regime, for example fire return intervals, strongly affect population viability (e.g. Evans, Holsinger & Menges 2010). In response to fire disturbance, plants have evolved distinct life histories: resprouters have fire-protected buds, whereas buds of nonsprouters are vulnerable to fire (Clarke *et al.* 2013). Resource allocation to bud protection increases the fire survival of adult plants, but may reduce fecundity and per-capita recruitment of resprouters (Bond & Van Wilgen 1996). Yet, there are still few comparative analyses of whether increased investment in fire survival causes reduced reproduction (Bond & Midgley 2003; Clarke *et al.* 2013). In addition to disturbance, biotic interactions with competitors, mutualists and antagonists can shape plant demography in multiple ways (e.g. Svenning *et al.* 2014). In particular, plant demography has long established that reproduction and survival of plants depend strongly on intraspecific density and that this density dependence can be negative (Stoll & Weiner 2000; Teller *et al.* 2016) or positive (causing Allee effects; Lamont, Klinkhamer & Witkowski 1993; Courchamp, Berec & Gascoigne 2008).

While determinants of small-scale demographic variation are thus reasonably well understood, only a few studies have identified environmental drivers of range-wide variation in key plant demographic rates (Angert 2009; Doak & Morris 2010; Merow *et al.* 2014). Angert (2009) showed increased demographic performance at high-elevation sites for two plant species. Doak & Morris (2010) emphasized that compensation in individual demographic rates along a latitudinal gradient may buffer species against the adverse effects of climate warming. Merow *et al.* (2014) presented a multiple regression approach and showed that the interaction of climate variables (e.g. summer soil moisture stress) and large-scale fire disturbance may limit population growth and the geographical distribution of their study species. Ehrlén & Morris (2015), however, pointed out that previous studies of large-scale demographic variation did not control for population density (but see Thuiller *et al.* 2014). This is important because density is likely to be correlated with environmental drivers of demographic variation. For instance, in environments that enable high intrinsic population growth rates, population density is likely to be high and intense intraspecific competition

is likely to decrease observed rates of reproduction and survival. Analyses of demographic responses to environmental variation thus need to account for such potentially confounding effects of intraspecific density dependence (Ehrlén & Morris 2015; Ehrlén *et al.* 2016). Additionally, analysing the range-wide effects of intraspecific density is important since the strength and shape of density dependence can profoundly affect range dynamics (Cabral & Schurr 2010).

The scarcity of data on range-wide demographic variation currently limits our ability to test assumptions that are frequently made in biogeographical theory and analyses. For instance, it is commonly assumed that the geographical ranges of plant species are more strongly limited by climate than by soil conditions, disturbance or population density (Pearson & Dawson 2003; but see Thuiller 2013; Merow *et al.* 2014; Ehrlén & Morris 2015). Moreover, niche theory commonly assumes that demographic rates respond to range-wide environmental variation in a monotonic or unimodal fashion (e.g. Maguire 1973; Pulliam 2000). However, for the realized niches of species, biotic interactions can cause seemingly counter-intuitive demographic responses to abiotic gradients. For example, stress-tolerant species may benefit from increasing environmental stress that releases them from superior competitors that are less tolerant to abiotic stress (Grime 2006). Interspecific competition can even cause u-shaped responses to abiotic gradients: a classic example is the pedunculate oak (*Quercus robur*), which in the absence of interspecific competition performs best at intermediate soil moisture. Under these intermediate conditions, the pedunculate oak is, however, out-competed by beech (*Fagus sylvatica*), so that its realized response to soil moisture is u-shaped (Ellenberg 1988). In general, one may expect that the demography of different woody plant species shows differentiated responses to climate and soil conditions, whereas responses to disturbance and density are more constrained and hence more consistent across species. Yet, a lack of data for multiple populations and species prevents comparative analyses examining whether the shape of demographic responses is consistent or differentiated across species. In summary, there is a need for large-scale demographic studies that (1) comprise multiple species, (2) span their entire geographical range, (3) cover their full life cycle and (4) account for population density (Gaston 2009; Schurr *et al.* 2012a; Ehrlén & Morris 2015).

We aim to close this gap by studying large-scale variation in reproduction and survival of 26 shrub species in the Cape Floristic Region (CFR; Manning & Goldblatt 2012), South Africa. The CFR is a global biodiversity hotspot (Myers *et al.* 2000) expected to be particularly threatened by global climate change (Yates *et al.* 2010a). However, current climate change biodiversity assessments in the CFR are largely based on SDMs and thus involve substantial uncertainty (Yates *et al.* 2010a). The notable exception is the study of Merow *et al.* (2014), who analysed range-wide demographic variation in one Proteaceae species. Many CFR Proteaceae have a fire-dependent life cycle that simplifies demographic data collection (Schurr *et al.* 2012b). In light of this, we assembled in total 3454 population-level records of fecundity, post-fire

recruitment and adult fire survival across the global geographical ranges of 26 Proteaceae species. We analyse this data set to test (i) whether life-history strategies (resprouters and non-sprouters) differ in rates of adult fire survival, fecundity and recruitment, (ii) whether range-wide variation in these key demographic rates depends more strongly on climate than on population density, disturbance and soil conditions and (iii) whether the study species show interspecific differentiation in demographic responses to climate and soil conditions, but greater consistency in demographic responses to density and disturbance.

Materials and methods

STUDY AREA AND STUDY SPECIES

The CFR is a geographically confined region (~91 000 km²; Manning & Goldblatt 2012) that covers much variation in climatic and topographic conditions. The region generally experiences a Mediterranean-type climate with cool, wet winters and hot, dry summers and is characterized by largely nutrient-poor soils (Allsopp, Colville & Verboom 2014). The vegetation of the CFR is dominated by fire-prone shrublands (Bond & Van Wilgen 1996). Fires are typically large in spatial extent, burn most above-ground biomass and occur on average every 10–21 years (Kraaij & Van Wilgen 2014). The overstorey of CFR shrublands is frequently dominated by serotinous (=bradysporous) species of the genera *Leucadendron* and *Protea* (Proteaceae). We studied 26 species of these genera which are endemic to the CFR (Rebello 2001). Study species were selected to include contrasting life-history strategies (nonsprouters and resprouters) and to cover different geographical distribution patterns (species differing in range size and position along major environmental gradients, Table S1 in Supporting Information).

Fire plays an important role in the life cycle of serotinous Proteaceae (Fig. 1a). In global comparison, the study species are strongly serotinous as they accumulate seeds in fire-protected woody cones and form long-lived canopy seed banks, but not soil seed banks (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991). The size of the canopy seed bank is a measure of the total fecundity between two fires given that the plant would burn at the time of sampling (Bond, Maze & Desmet 1995; Nottebrock, Esler & Schurr 2013). Seed release from cones and dispersal are triggered by fire (Bond & Van Wilgen 1996; Rebello 2001), and the establishment of new seedlings (or recruits) is confined to the immediate post-fire environment (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991). Germination follows after a cool, wet winter and once the established recruits are about three years old, plants have a low mortality risk until the next fire (Lamont *et al.* 1991; Manders & Smith 1992; Bond & Van Wilgen 1996). Fire usually destroys large amounts of the above-ground biomass and can kill plants. However, some Proteaceae species have the ability to resprout from meristems that are protected underground or by thick bark ('resprouters'). Adult resprouters are therefore more likely to survive a fire than adult nonsprouters that lack fire-protected meristems (Bond & Van Wilgen 1996; Rebello 2001). Overall, the fire-dependent life cycle and synchronous post-fire recruitment events in our study species enable direct measurements and quantification of primary demographic rates (fecundity, recruitment and adult fire survival). Since Proteaceae populations typically establish as single post-fire cohorts (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991), it is possible to directly relate rates of fecundity and recruitment to plant age without having to account for heterogeneity in the age or size-structure.

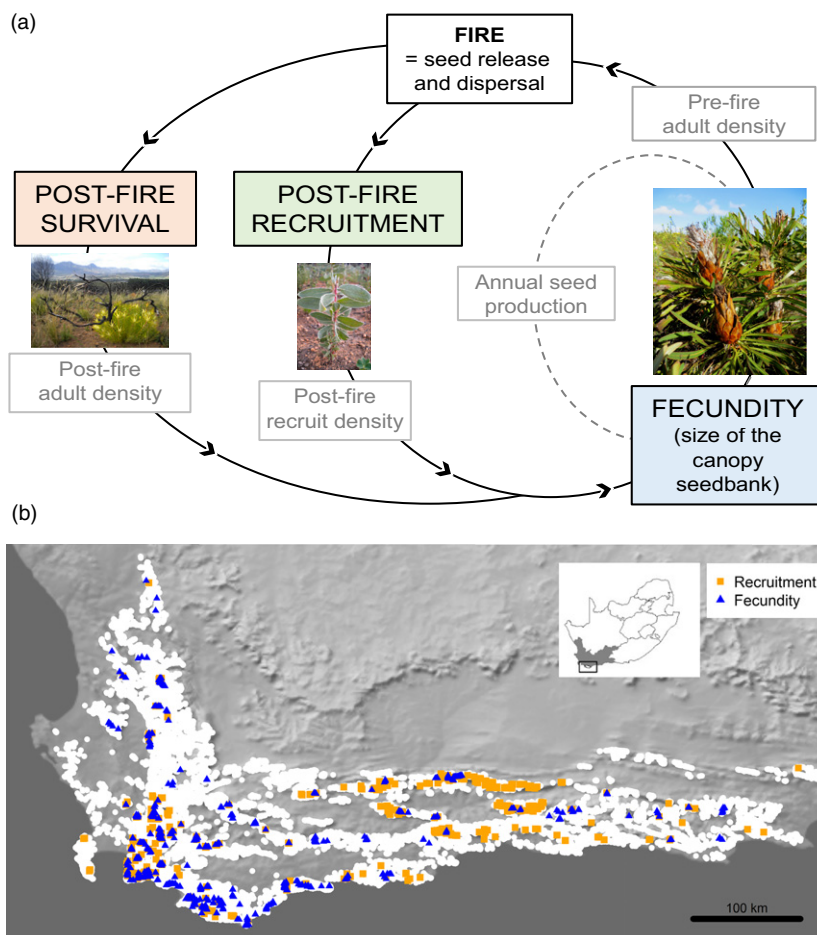


Fig. 1. (a) The fire-dependent life cycle of serotinous Proteaceae showing key demographic rates measured in this study (fecundity, post-fire recruitment and adult fire survival), (b) Map of study sites for recruitment (squares) and fecundity (triangles) surveys in the Cape Floristic Region (CFR), South Africa. White dots depict the known geographical distribution of the entire Proteaceae family (presence records from the Protea Atlas Project; Rebelo 2001) which largely covers the fynbos biome, a major constituent of the CFR.

ture of stands (as done in other studies in this special feature, see Crone 2016; McDonald *et al.* 2016).

DEMOGRAPHIC SAMPLING

We collected data on the total fecundity of adult plants since the last fire (size of individual canopy seed banks), per-capita post-fire seedling recruitment (ratio between post-fire recruits and pre-fire adults, assuming a closed-population) and adult fire survival. These three demographic rates span the entire life cycle of our study species (Fig. 1a). Study sites for demographic sampling were selected to cover major environmental gradients in the geographical distribution of each study species and constituted 3454 population-level records overall (Fig. 1b; Table S1).

Fecundity was measured as the number of fertile seeds in a plant's canopy seed bank. We determined the number of intact, closed cones for five individuals per population (restricted to female individuals for dioecious *Leucadendron* species). From each individual, we randomly selected and harvested (up to) five cones. The harvested cones were either cut open with secateurs (cutting across seeds, for *Protea* species) or dried until seeds were released (for *Leucadendron* species) to determine the number of viable seeds per cone (e.g. Nottebrock, Esler & Schurr 2013). The product of total cone number (counted on each focal plant) and seed set per cone (from counting number of viable seeds per cone) yields an estimate of an individual's total fecundity since the last fire (Nottebrock, Esler & Schurr 2013). Since the random sample of cones comprised young and old cones, our measure of fecundity incorporates potential losses of seed viability in older cones. These individual fecundity values were then averaged at the popula-

tion level and comprised 1575 populations. At every site, we also estimated the density of conspecific plants by counting the number of adults in a defined area (at least 100 m²).

Recruitment was measured as the number of seedlings per adult (recruit: parent ratio) in at least five transects of 20 × 2 m on a recently burnt site. On each transect, we counted the number of living post-fire recruits (seedlings) and the number of pre-fire adults [comprising both fire survivors and fire-killed plants, which are identifiable as skeletons carrying burnt leaves or cones that opened after fire (Bond, Vlok & Viviers 1984; Bond, Maze & Desmet 1995)]. Adult population density was estimated as the density of conspecific (parent) plants counted per transect. Recruitment was measured at least one year post-fire, after the phase of highest seedling mortality (Lamont *et al.* 1991; Mustart & Cowling 1993). Comparable data on post-fire recruitment measurements have long been collected through both local (CapeNature) and national (SANParks) conservation organizations' fire monitoring protocols (for description see Bond, Vlok & Viviers 1984). In our analysis, we integrated these existing data sets collected by CapeNature from 1979–2011 (CapeNature unpublished data) and SANParks from 2007 to 2012 (Kraaij *et al.* 2013a). Additionally, we also included post-fire recruitment data from Heelemann *et al.* (2008, 2011) and other unpublished data sources (W.J. Bond; R.M. Cowling; F.M. Schurr respectively). Combining all these data sources, our recruitment data consisted of 1308 populations.

Finally, on a subset of the recently burnt sites sampled for the recruitment data, we recorded fire survival by counting the number of living (fire survivors) and dead (fire-killed) pre-fire adult plants in the sampling transects. Fire survival rates for a total of 571 populations on these sites were then calculated as the proportion of adult fire survivors.

ENVIRONMENTAL DRIVERS

We assembled an initial subset of ecologically meaningful environmental variables expected to be main determinants of the performance and survival of serotinous Proteaceae in the hot, seasonally dry, nutrient-poor and topographically diverse CFR (Latimer *et al.* 2006; Yates *et al.* 2010a; Merow *et al.* 2014). This subset of major environmental factors represented effects of precipitation, drought, heat, temperature, frost and soil conditions. We, however, avoided combinations of highly correlated variables (Spearman correlation coefficient > 0.5) and retained soil moisture stress (% days with soil moisture stress in the month of January), summer heat units (sum of mean temperatures exceeding a threshold value of 10 °C from October – March; Schulze 2007) and frost days (average number of days with frost per annum). As an edaphic variable, we used a ‘soil fertility index’ [ranging from 0 (no fertility) to 5 (highest fertility)] which we refer to as soil nutrient status. The soil nutrient variable and all climate variables (averaged from 1950–2000) were extracted from the South African Atlas of Climatology and Agrohydrology (Schulze 2007) and have a resolu-

Table 1. Environmental variables (population density, fire return interval, climate and soil) used to analyse range-wide demographic data of 26 serotinous Proteaceae species (Cape Floristic Region, South Africa) with explanations and data sources

Environmental variables	Description	Source
<i>Density</i>		
Population density	Adult density; number of adult individuals per m ²	Field measurements
<i>Fire</i>		
Fire return interval	<i>Fecundity:</i> Time since fire (years) <i>Recruitment:</i> Length of the previous fire interval (years)	Field observations (node counts on adult plants) and/or personal communication with landowners or conservation staff; and/or historical fire data base (De Klerk 2008; Kraaij <i>et al.</i> 2013b) or satellite observations (MODIS; Roy <i>et al.</i> 2008)
<i>Climate</i>		
Summer soil moisture stress	Summer days with soil moisture stress (% days with soil moisture stress in the month of January)	Schulze (2007)
Summer heat units	Sum of daily temperatures exceeding 10 °C (October–March)	Schulze (2007)
Frost days	Average number of days per year with frost	Schulze (2007)
Altitude anomaly	Difference between altitude of field sites and mean altitude of the grid cell (Schulze 2007)	Field observations and Schulze (2007)
<i>Soil</i>		
Soil nutrient status	Soil fertility index, ranging from 0 (no fertility) to 5 (highest fertility)	Schulze (2007)

tion of 1' × 1' (1.55 × 1.85 km). Additionally, we calculated an ‘altitude anomaly’ as the difference between our site-recorded altitude measurement (by GPS) and the average grid cell altitude (Schulze 2007) to account for the effect of small-scale altitudinal variation (see Table 1).

To investigate the effects of fire return intervals, we recorded the time since last fire on each study site based on two types of information. First, we always recorded the age of the vegetation at the time of demographic sampling: serotinous Proteaceae shrubs can be aged by counting the number of branches and internodes on the tallest stem; an established proxy for plant age (Bond, Maze & Desmet 1995; Carlson, Holsinger & Prunier 2011). Secondly, for most study sites we also had direct information on the fire history either from landowners and conservation managers, from a historical fire data base (De Klerk 2008; Kraaij *et al.* 2013b) or from satellite observations (MODIS, Roy *et al.* 2008). We used these data sources to cross-check the vegetation age that we estimated from node counts. This was done to validate the use of node counts as a proxy for time since the last fire on sites that lacked direct information on the fire history. For sites where we collected recruitment and fire survival data, these various data sources on fire history were used to determine the length of the previous fire interval, i.e. vegetation age of the parent generation at the time of the most recent fire. The median time since last fire was 11 years on sites with fecundity data (range 1–48 years) and 2 years on sites with recruitment and survival data (range 1–6 years). The median length of the previous fire interval for the latter was 14 years (range 2–66 years).

STATISTICAL ANALYSES

All analyses were carried out with R.3.1.2. (R Development Core Team 2014). First, we tested if resprouters and nonsprouters differ in rates of fecundity, recruitment and adult fire survival. For individual fecundity and per-capita recruitment, we used linear mixed effect models (lme4 package; Bates *et al.* 2015) applying a log($x + 1$) transformation (since these response variables are always non-negative), and for adult fire survival, we used a generalized linear mixed effect model with binomial errors. All models included a fixed effect of life-history strategy (resprouting vs. nonsprouting) and a random effect of species.

We then estimated environmental responses of demographic rates separately for each species. Since intraspecific variation in fire survival was very low (Fig. 2a), we did not analyse environmental effects on adult fire survival. For log($x + 1$)-transformed fecundity and recruitment, we formulated linear regression models that describe their response to variation in population density, fire interval, climate and soil nutrients (see Table 1). All continuous, numerical explanatory variables were scaled and centred to ensure comparability among variables. We included all linear and quadratic terms in the maximal models to allow for the possibility of monotonic or unimodal response curves. In the fecundity models, population density and fire interval were represented by the adult density at time of sampling and the time since the last fire, respectively. In the recruitment models, however, population density was represented as the density of pre-fire adults (parent generation) and fire interval was represented as the length of the previous fire interval (see Table 1, Fig. 1a). These measures determine the size of the canopy seed bank at the time of the last burn, that is the maximum potential number of recruits.

The recruitment models used time since the most recent fire to account for seedling mortality, which generally occurs within three years after fire in CFR Proteaceae (Manders & Smith 1992). An exploratory data analysis indeed showed a negative loglinear relation-

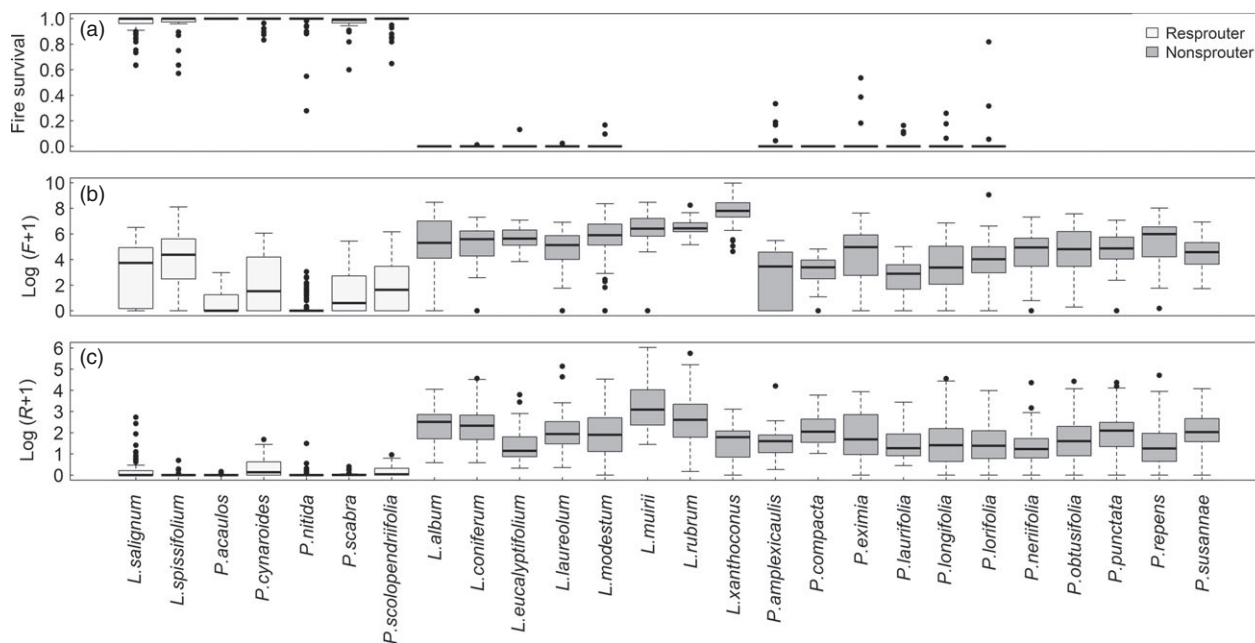


Fig. 2. Range-wide demographic variation in 26 serotinous Proteaceae species of two life-history types (resprouters and nonsprouters, respectively). (a) Probability of adult fire survival (only 18 species with > 10 records plotted); (b) individual fecundity (F); and (c) per-capita recruitment rate (R).

ship between seedling number and time since fire in the first three years. We thus included a log-transformed variable of time since last fire t as $\max[\log(t/3), 0]$ in the recruitment models. This transformation ensures that the other explanatory variables in the model describe the per-capita number of recruits after the self-thinning phase, which is a good proxy of the per-capita reproductive rate (Bond, Maze & Desmet 1995). Finally, to account for the fact that recruitment rates were quantified for different numbers of parents in different populations, we used the number of parents per population as model weights.

We used automated model selection (R package MuMin; Barton 2015) among all combinations of explanatory variables, but excluded models that contained quadratic terms without the respective linear terms. The best model for each demographic rate per species was determined according to the lowest sample size corrected Akaike's information criterion (AICc; Burnham & Anderson 2002). The best models were then evaluated to show the relevant environmental determinants for each demographic rate across all 26 study species. For the best model of each species, we quantified the proportion of variance explained by each group of environmental determinants (population density, fire interval, climate and soil nutrients) by calculating partial R^2 values, that is the difference between the coefficient of determination (R^2) of the best model and the R^2 of a reduced model without the respective explanatory variables. Finally, based on whether the best model contained a quadratic effect of an environmental variable and on the sign of the coefficients, we classified the shape of effects (positive, negative, unimodal or u-shaped) for each retained variable.

Results

Adult fire survival shows a clear dichotomy with almost complete fire mortality in nonsprouting species (mean fire survival rate 2%) compared to high fire survival in resprouters (mean

fire survival rate 97%) and no species with intermediate fire survival (Fig. 2a; likelihood ratio test for resprouting effect on fire survival: $\chi^2_{1df} = 73.1$, $P < 0.001$). For non-sprouters, our measure of fecundity thus represents a close proxy of lifetime fecundity and per-capita recruitment approximates fitness (the number of offspring contributed to the next generation). While resprouters had much higher fire survival than nonsprouters, they had lower fecundity (Fig. 2b, $\chi^2_{1df} = 12.4$, $P < 0.001$) and strongly reduced per-capita recruitment (Fig. 2c, $\chi^2_{1df} = 38.9$, $P < 0.001$). In addition to these differences between life-history types, our study species showed considerable intraspecific variation in fecundity and recruitment (Fig. 2b,c).

Environmental variables explained on average 52% of the range-wide variation in fecundity and 49% of the range-wide variation in recruitment of our study species (multiple R^2 of the best models). Examples of the estimated demographic responses are shown in Fig. 3 for one species (*Protea punctata*), whereas Figs. S2 and S3 provide a complete depiction of the demographic response functions for all 26 species and environmental drivers. Across our 26 study species, the relative contribution of environmental drivers, notably climate and fire interval, differed between fecundity and recruitment (Fig. 4). We also investigated the relative importance of environmental drivers separately for resprouters and nonsprouters, but this showed very similar patterns in both life-history types (Fig. S1).

Environmental drivers of range-wide variation in fecundity showed a clear hierarchy (Fig. 4a). Fecundity was predominantly driven by fire interval (median partial $R^2 = 0.328$) and to a lesser extent by climate (median partial $R^2 = 0.067$). The variance explained (partial R^2) by fire interval was significantly higher than for climate (paired Wilcoxon signed-rank

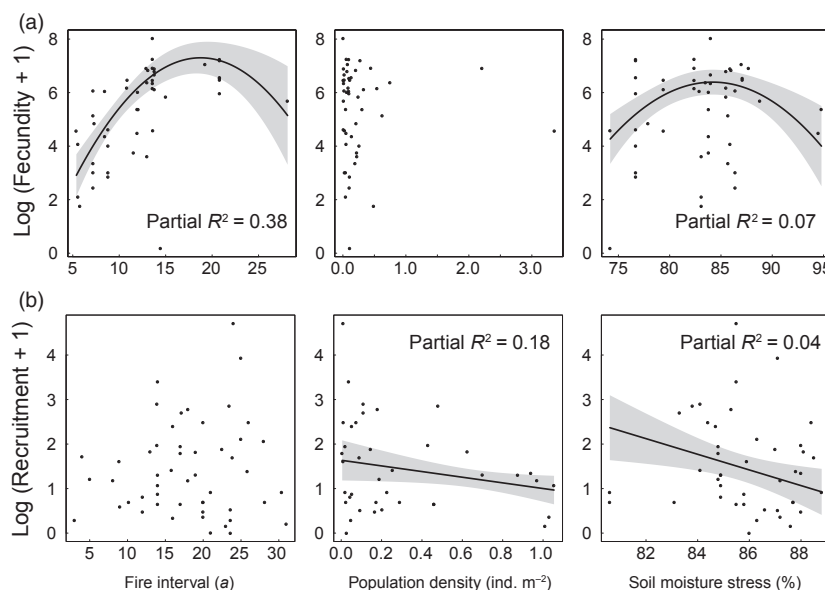


Fig. 3. Range-wide variation in (a) fecundity and (b) recruitment of *Protea punctata* in response to fire interval (time since fire), adult population density and soil moisture stress (% days with soil moisture stress). Response variables are plotted on the log ($x + 1$) scale; lines indicate mean predictions of the best model, and grey areas show 95% confidence intervals. Partial R^2 values are given for variables retained in the best models.

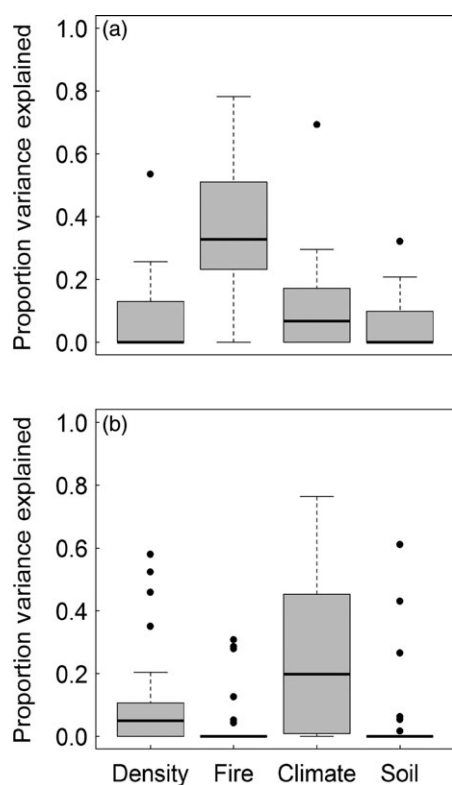


Fig. 4. Variance in (a) fecundity and (b) recruitment of 26 serotinous Proteaceae species that is explained by density (adult population density), fire (fire interval), climate (soil moisture stress, heat units, frost days and altitude anomaly) and soil (soil nutrient status). Variance explained is the partial R^2 of the respective variable(s) in the best model for each species.

test, $n = 26$, $V = 13$, $P < 0.001$) or any other driver (Fig. 4a). Fire interval remained in the best models of 96% of our study species ($n = 25$) and had either unimodal ($n = 20$) or positive ($n = 5$) effects (Figs 5a and S2). Soil moisture stress, heat units and frost days affected 38% of our study species, respec-

tively, with soil moisture stress and heat units having mostly negative and unimodal effects on fecundity (Figs 5a and S2). Overall, fecundity-climate responses are more differentiated compared to the consistent unimodal and positive effects of fire interval (Fig. 5a). Population density had smaller, mostly negative effects on fecundity (Figs 4a and 5a). The soil nutrient variable remained in the best models for several species, but the overall variance explained was small (Figs 4a and 5a).

Recruitment was driven foremost by climate (median partial $R^2 = 0.199$) and to a lesser extent by population density (median partial $R^2 = 0.050$). The variance explained (partial R^2) by climate was significantly higher than that explained by population density (paired Wilcoxon signed-rank test, $n = 26$, $V = 220$, $P < 0.01$) or any other driver (Fig. 4b). Soil moisture stress and heat units affected more study species than frost days and the altitude anomaly, and the shape of these climate effects varied between species (Figs 5b and S3). Population density had largely negative density effects on the recruitment of individual species (Figs 5b and S3). Fire interval generally did not explain much variation in recruitment (Fig. 4b), however, in species for which it played a role the effects were mostly unimodal (Fig. 5b). The overall effect of soil nutrients on recruitment was low, but this variable had a strong effect for a few species (Fig. 4b).

Discussion

This study quantified variation in key demographic rates across the global geographical distribution of 26 plant species. As hypothesized, we found a trade-off between survival and reproduction throughout the geographical ranges of our study species: resprouting species showed much higher fire survival than nonsprouters, but resprouters also had lower fecundity and substantially reduced per-capita recruitment (Fig. 2). In contrast, we found only partial support for the hypothesis that

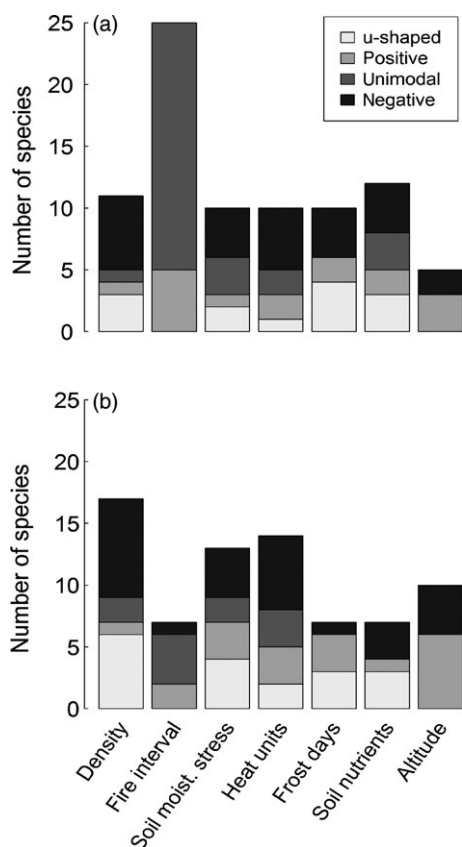


Fig. 5. Shape of environmental effects on (a) fecundity and (b) recruitment of 26 serotinous Proteaceae species. The bar plots show the number of species for which the best model predicts a given environmental response [u-shaped (◡); negative (−); unimodal (∩) or positive (+)]. See Table 1 for descriptions on environmental variables. We classified the shape of environmental responses based on the sign of coefficients and whether the best model contained a quadratic effect.

climate dominates demographic variation within species ranges: while recruitment was indeed dominated by climate, fecundity was mostly driven by fire interval (Fig. 4). Finally, there was mixed support for the hypothesis that demographic responses to climate and soil conditions should show greater interspecific differentiation than responses to density and disturbance: the consistency of responses to fire interval confirmed this hypothesis, but the more variable density responses contradicted it (Fig. 5).

MECHANISMS UNDERLYING ENVIRONMENTAL EFFECTS ON DEMOGRAPHIC RATES

Fecundity is strongly driven by the length of the fire interval and relationships are largely unimodal across our study species (Figs 4a and 5a). Serotinous Proteaceae require several years to reach reproductive maturity and build a fertile canopy seed bank. In fact, if fires occur before the onset of reproduction, populations of nonsprouters risk local extinction (Lamont *et al.* 1991; Kraaij *et al.* 2013a). The decrease in fecundity at longer fire intervals that we found for the majority ($n = 20$) of our study species (see Fig. S2) highlights that reproductive senes-

cence is a common phenomenon in serotinous Proteaceae. Reproductive senescence results if the annual rate of cone opening and seed decay exceeds the annual rate of cone and seed production (Bond & Van Wilgen 1996). This may come about because older plants have older cones which contain fewer viable seeds or because maintaining mechanical support and water supply to cones is costly (Midgley 2000).

Effects of both extremely short and long fire return intervals on fecundity can translate into low post-fire recruitment success (Bond 1980), if populations are seed limited (Maze & Bond 1996). Bond (1980) suggested that low seed production in the aged parent generation (40 year old) was responsible for post-fire recruitment failure. However, in our notably larger taxonomic sample of study species, recruitment was largely independent of the fire interval (Fig. 5b). Potentially, the inclusion of more sites with short previous fire intervals (on which the parent generation had produced few seeds) could have yielded stronger effects of the fire return interval on recruitment (Kraaij *et al.* 2013a). Moreover, it is well known that fire season, fire intensity and the spatial extent of fires also affect recruitment rates (Bond, Vlok & Viviers 1984; Heelemann *et al.* 2008). Since our analyses only considered one element of the fire regime (fire interval), we are likely to have underestimated the overall importance of fire for range-wide variation in recruitment.

The strong climate effects on recruitment (Fig. 4b) must primarily arise from effects on per-seed recruitment probability, since fecundity was more independent of climate (Fig. 4a). Our study species germinate and recruit in post-fire environments with intense solar radiation and soil surface heating, and their seedlings are sensitive to drought (Lamont *et al.* 1991; Mustart *et al.* 2012) and heat (Yates *et al.* 2010b). Hence, it is not surprising that we found negative or unimodal effects of soil moisture stress and heat units for several species (Fig. 5b). In contrast, frost had more positive effects on recruitment, notably in two high-elevation species (*L. album* and *P. cynaroides*) for which frost may act as a germination cue. Additionally, positive frost-responses may arise from the suppression of competing species that are frost-sensitive. In fact, a trade-off between competitive ability and stress tolerance might also explain positive effects of other climatic stressors (Grime 2006). Similarly, the u-shaped climate responses that we found for a number of species might result from interspecific competition in the centre of a species' fundamental niche (Ellenberg 1988; but note that u-shaped responses might also result from model misspecifications, see below). Indeed, evidence for competitive exclusion by sister species, where closely related species are likely to out-compete each other along an environmental gradient (due to overlap of their fundamental niches), has previously been found in CFR Proteaceae (Gelfand *et al.* 2006).

Climate is a less important driver for adult fecundity than for recruitment of our study species (Fig. 4). Hot, dry summers are defining features of the Mediterranean-type climate of the CFR (Allsopp, Colville & Verboom 2014), and specific plant traits may allow adult plants to be more tolerant to climatic variation. For example, adult Proteaceae shrubs have

deep root systems which ensure access to underground water during dry summer months (Manders & Smith 1992), and their often small, narrow leaves may allow cooling under excess heat (especially in *Leucadendron*; Yates *et al.* 2010b). This resilience of adult plants to climatic stress was also observed by West *et al.* (2012) who did not detect adverse effects of a 6-month experimental summer drought on adult plant growth, mortality or cone production in *Leucadendron lauratum*.

Intraspecific density affected fecundity and recruitment rates of many study species (Figs 5, S2 and S3). Density dependence was frequently negative, sometimes positive or unimodal, and we found a number of counter-intuitive u-shaped density responses (Fig. 5). Note, however, that these u-shaped density responses often described negative density dependence over most of the density range and that their upward-facing branch seemed mostly driven by a few outliers (Figs S2 and S3). Negative density dependence of fecundity in CFR Proteaceae has been shown to result from a reduction of cone production due to competition among adults for space, water and soil nutrients (Bond, Maze & Desmet 1995; Nottebrock, Esler & Schurr 2013). In contrast, seed set per cone can show positive density dependence because both pollen availability and densities of animal pollinators are higher in dense stands (Nottebrock, Esler & Schurr 2013). These potentially counteracting effects of density on the two components of fecundity may explain why a number of our study species showed no or weak density dependence of fecundity. However, except in the case of over-compensatory density dependence, denser adult stands will produce higher seedling densities (Bond, Maze & Desmet 1995) that are subject to more intensive density-dependent thinning of seedlings (Lamont, Witkowski & Enright 1993). This additional density dependence of per-seed recruitment probability may explain why recruitment (as the product of fecundity and recruitment probability) shows more pronounced density responses than fecundity.

INTERSPECIFIC CONSISTENCY AND DIFFERENTIATION OF DEMOGRAPHIC RESPONSES

A striking result is that fecundity responses to the fire interval are remarkably similar across species, whereas demographic climate responses show greater interspecific variation (Fig. 5). A likely explanation for the consistency of fecundity–fire relationships is that the size of the serotinous canopy seed bank is strongly constrained by slow plant growth under the nutrient-poor and seasonally dry conditions of the CFR (Allsopp, Colville & Verboom 2014) and by the architectural requirements of serotiny (Harris & Pannell 2010). The more differentiated interspecific responses to climate is likely due to differences in functional traits among CFR Proteaceae which seem to enable more differentiated responses to climatic variation (Yates *et al.* 2010b). This is particularly true for recruitment which integrates over a larger part of the life cycle than fecundity and is thus more equally influenced by several environmental factors, offering opportu-

nities for trait-based differentiation among species. The clear demographic differences between resprouters and nonsprouters and recent comparative studies (see Adler *et al.* 2014; Uriarte *et al.* 2016; Visser *et al.* 2016), highlight the potential of trait-based studies of interspecific variation in demography. In fact, a key task for the emerging field of functional biogeography (Violle *et al.* 2014) is to quantify the extent to which functional traits explain interspecific variation in range-wide demographic responses. The decomposition of species' niches into environmental responses of individual demographic rates and the link of these responses to functional traits may also provide new opportunities for the study of niche macroevolution. In particular, it may help to explain why species' niches are evolutionarily conserved along certain environmental axes and more labile along others (Wiens *et al.* 2010).

COMBINED ENVIRONMENTAL EFFECTS UNDER GLOBAL CHANGE

There is sufficient evidence that climate change alters fire regimes (Westerling *et al.* 2006), and there is an urgent need to understand how changes in climate and fire interact in their effects on biodiversity (Midgley & Bond 2015). In the last decades, the CFR has become hotter and drier (MacKellar, New & Jack 2014) which has led to a shortening of fire intervals by approximately 4 years throughout the region (Wilson *et al.* 2010). A predicted further decrease of fire return intervals (Wilson, Latimer & Silander 2015) will almost certainly reduce fecundity of our study species. Enright *et al.* (2014) showed that resprouters are less sensitive to shortening fire intervals than nonsprouter populations (which produce few seeds during their juvenile periods of 4–9 years; Kraaij *et al.* 2013a). Negative effects of shortening fire intervals can be exacerbated by negative direct effects of climate change (in many of our study species, fecundity and recruitment decrease with soil moisture stress and heat, Figs S2 and S3). This might cause the extinction of populations and a shrinking of species' ranges. Our study, along with that of Merow *et al.* (2014), thus provides first insights into how future changes in climate and fire may jointly impact the large-scale dynamics of plant species.

POTENTIAL AND CHALLENGES OF LARGE-SCALE DEMOGRAPHIC STUDIES

By identifying environmental drivers of range-wide variation in plant demography, this study directly contributes to a demographic research agenda for biogeography (Schurr *et al.* 2012a). It shows that the large-scale collection of demographic data is feasible and demonstrates the value of long-standing data collection by conservation organizations (Kraaij *et al.* 2013a). Simultaneously, our investigation also highlights the challenges of large-scale demographic studies. These studies are almost inevitably observational, implying that inferred demography–environment relationships are not necessarily causal. Moreover, observational studies can only

measure demographic rates in the environmental conditions where a species occurs, which limits the potential to infer environmental determinants of range limits (Schurr *et al.* 2012a). For instance, several Proteaceae species occur on a restricted range of soil conditions (Rebello 2001) which limits our ability to observe effects of soil conditions on demography. In a few cases, our analyses also show that it is particularly difficult to detect environmental limits in species with small geographical ranges that cover little environmental variation (e.g. *Leucadendron muirii* in our study; but see also Ehrlén *et al.* 2016). Furthermore, we expect that certain counter-intuitive responses (e.g. in cases where we find u-shaped climate responses) are linked to more complex interspecific biotic interactions. Given our explicit focus on the realized niches of species (Hutchinson 1978), we did not explicitly resolve these interspecific density effects. Importantly, however, our observational study makes predictions that can be tested experimentally. For instance, in cases where recruitment shows u-shaped responses to a climatic variable whereas fecundity does not, we predict that interspecific competition suppresses per-seed recruitment rates in intermediate climate conditions. This prediction can be tested with a transplant experiment that manipulates interspecific competition. However, the potential of range-wide demographic studies goes beyond the mere formulation of hypotheses for transplant experiments. To fully understand how range dynamics arise from first principles of demography, we need to quantitatively integrate range-wide demographic observations, data from large-scale experiments and records of species distributions with demographic models of range dynamics (Pagel & Schurr 2012; Schurr *et al.* 2012a; Ehrlén *et al.* 2016).

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Data accessibility

All demographic data used in this study are present in the supporting information. In addition to data collected by the authors, demographic data were obtained from provincial and national conservation organizations: CapeNature (Scientific Services, CapeNature, Private Bag X658, Oudtshoorn, 6620, South Africa) and SANParks (Scientific Services, Garden Route, South African National Parks, P.O. Box 176, Sedgefield, 6573, South Africa); and scientific researchers: Prof. William Bond (Chief Research Scientist, South African Environmental Observation Network, P.O. Box 2600, Pretoria, 0001, South Africa) and Prof. Richard Cowling (Research Professor, Nelson Mandela Metropolitan University, Department of Botany, P.O. Box 77000, Port Elizabeth, 6031, South Africa).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

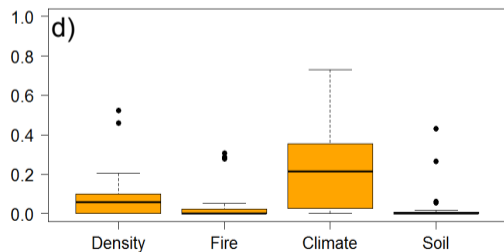
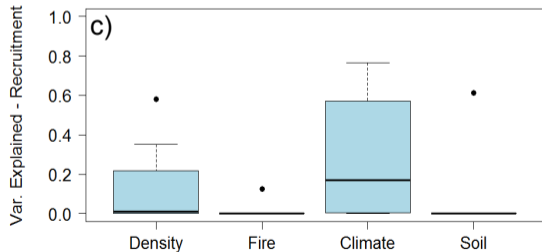
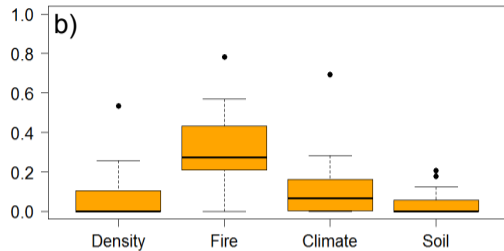
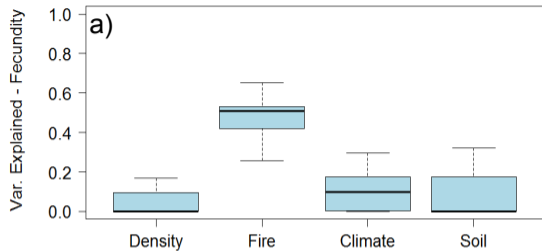
Figure S1. Variance in fecundity (a, b) and recruitment (c, d) of 26 serotinous resprouting and nonsprouting Proteaceae species that is explained by environmental drivers and population density.

Figure S2. Response of fecundity (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae species.

Figure S3. Response of recruitment (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae study species.

Table S1. List of 26 serotinous Proteaceae study species (Cape Floristic Region, South Africa) with number of populations sampled (n) to estimate demographic variation in fecundity, recruitment and adult fire survival.

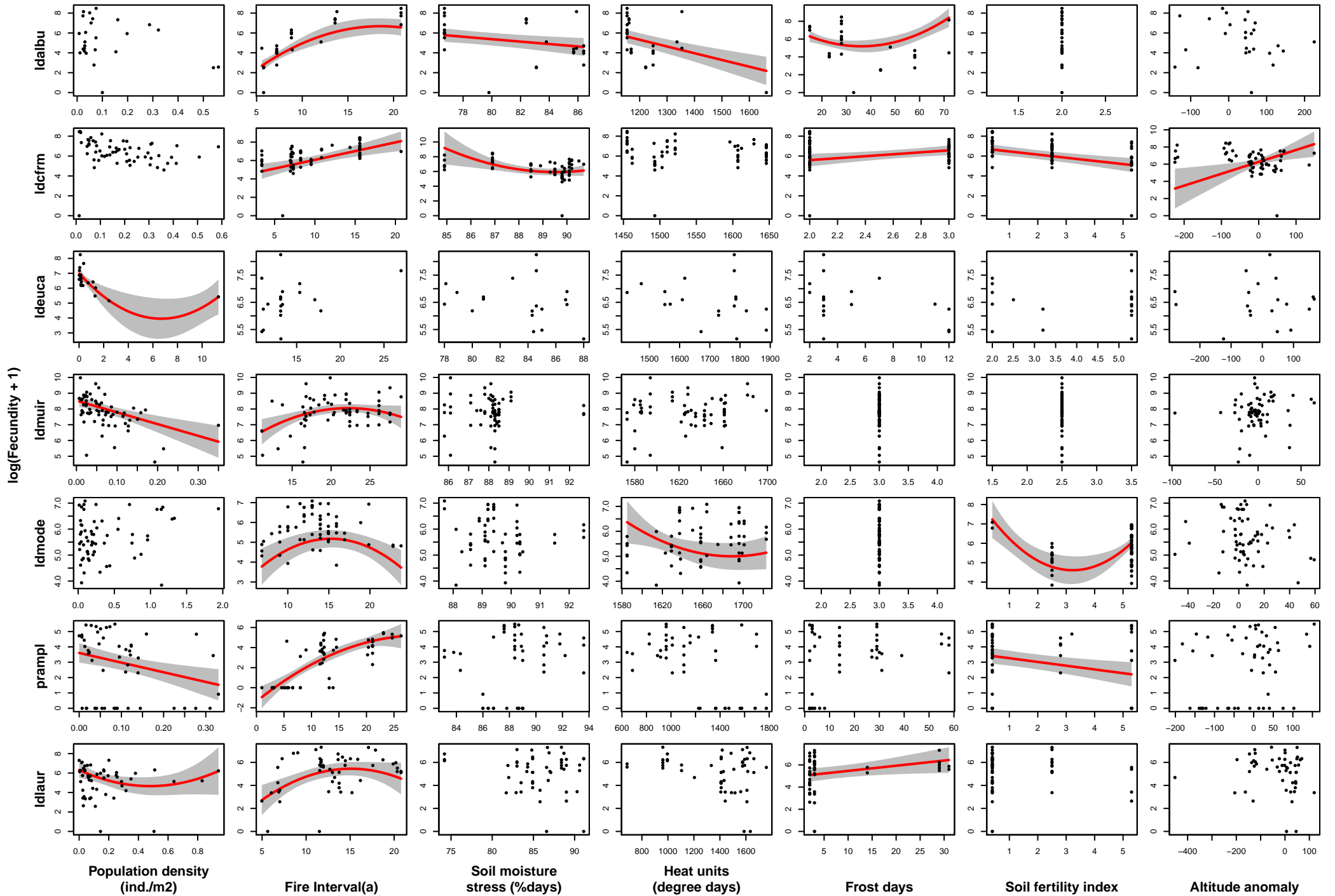
Fig. S2.1. Variance in fecundity (a, b) and recruitment (c, d) of 26 serotinous resprouting and nonsprouting Proteaceae species that is explained by environmental drivers and population density.

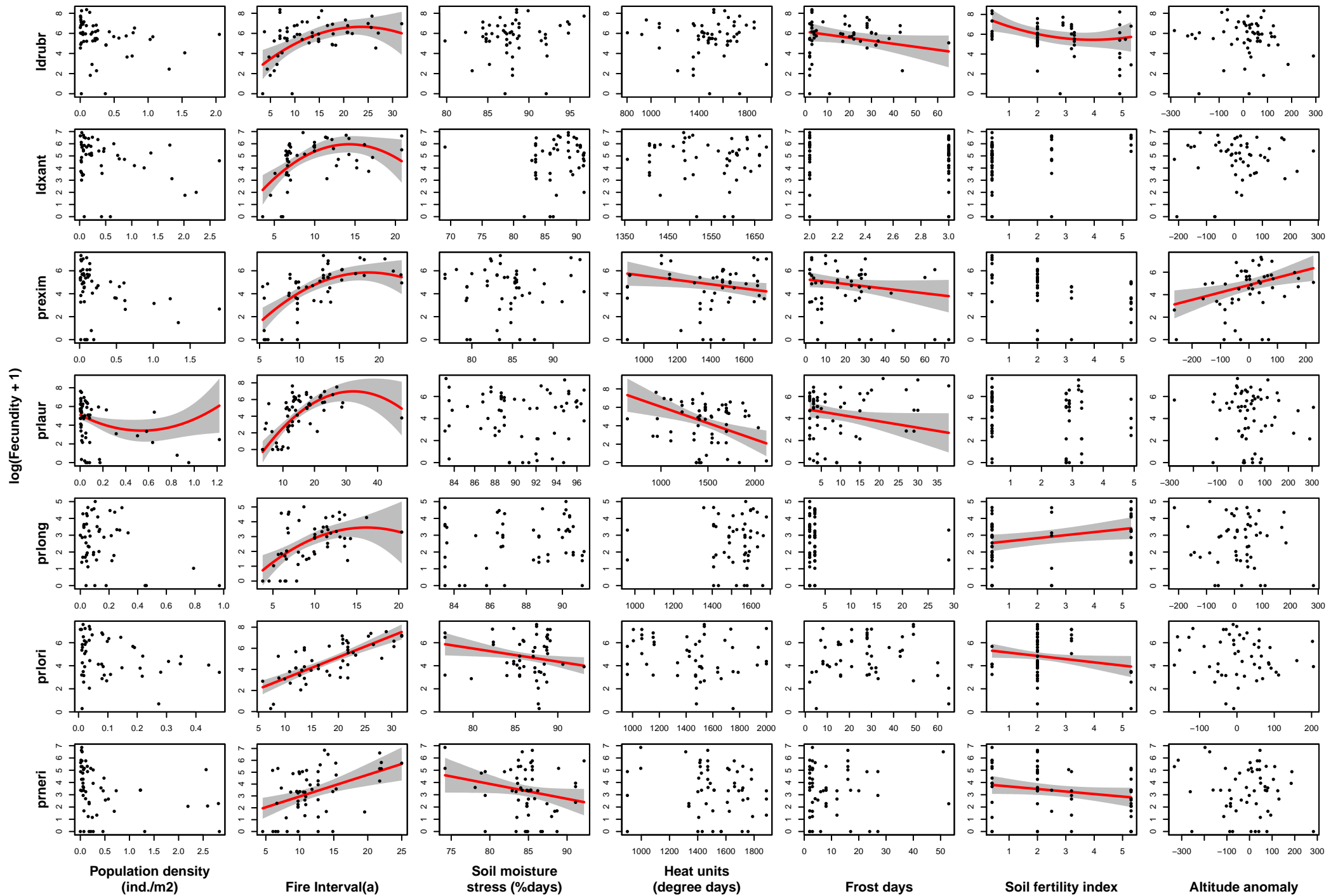


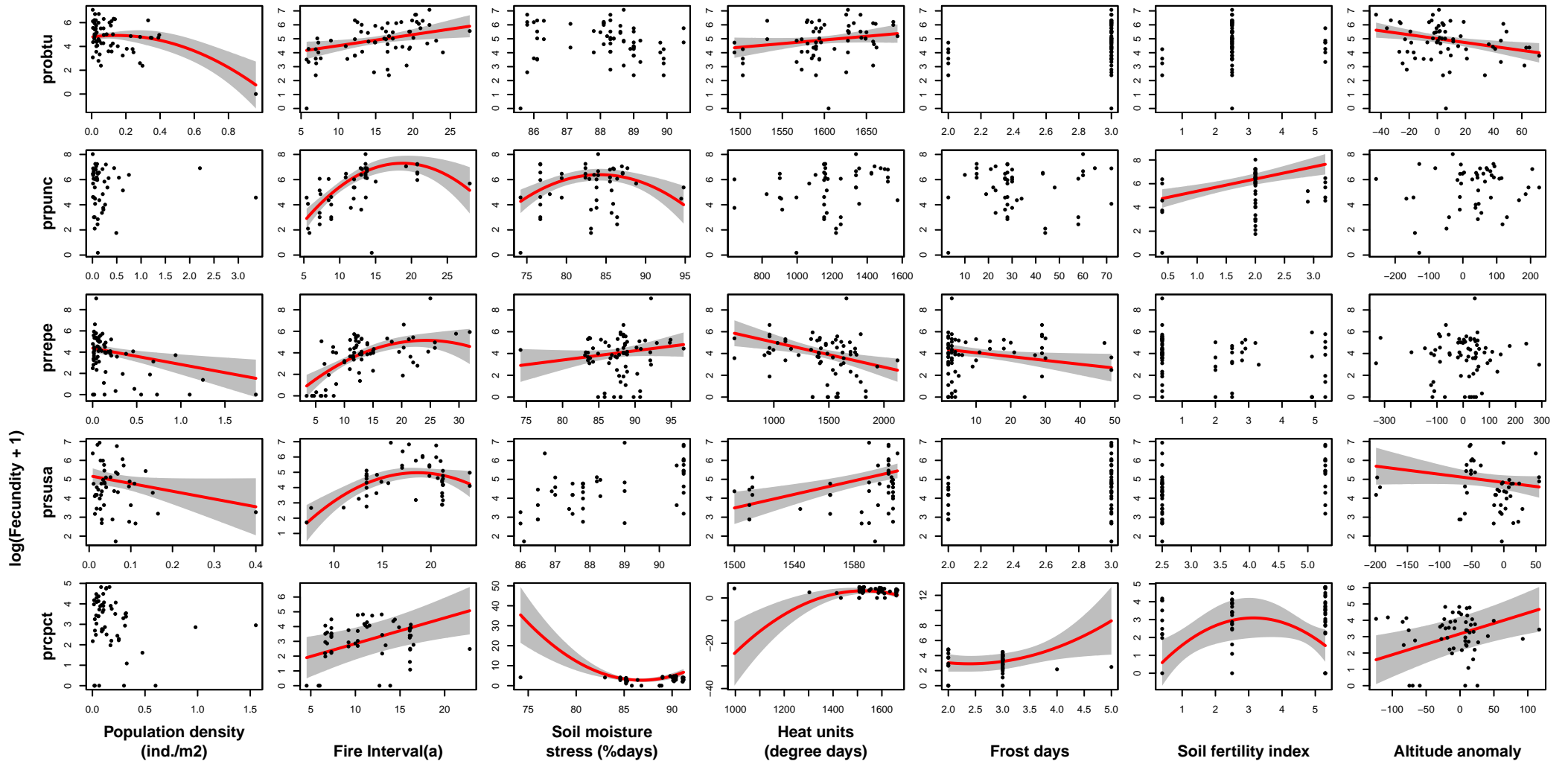
Resprouters (n = 7)

Nonsprouters (n = 19)

Fig. S2.2. Response of fecundity (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae species.







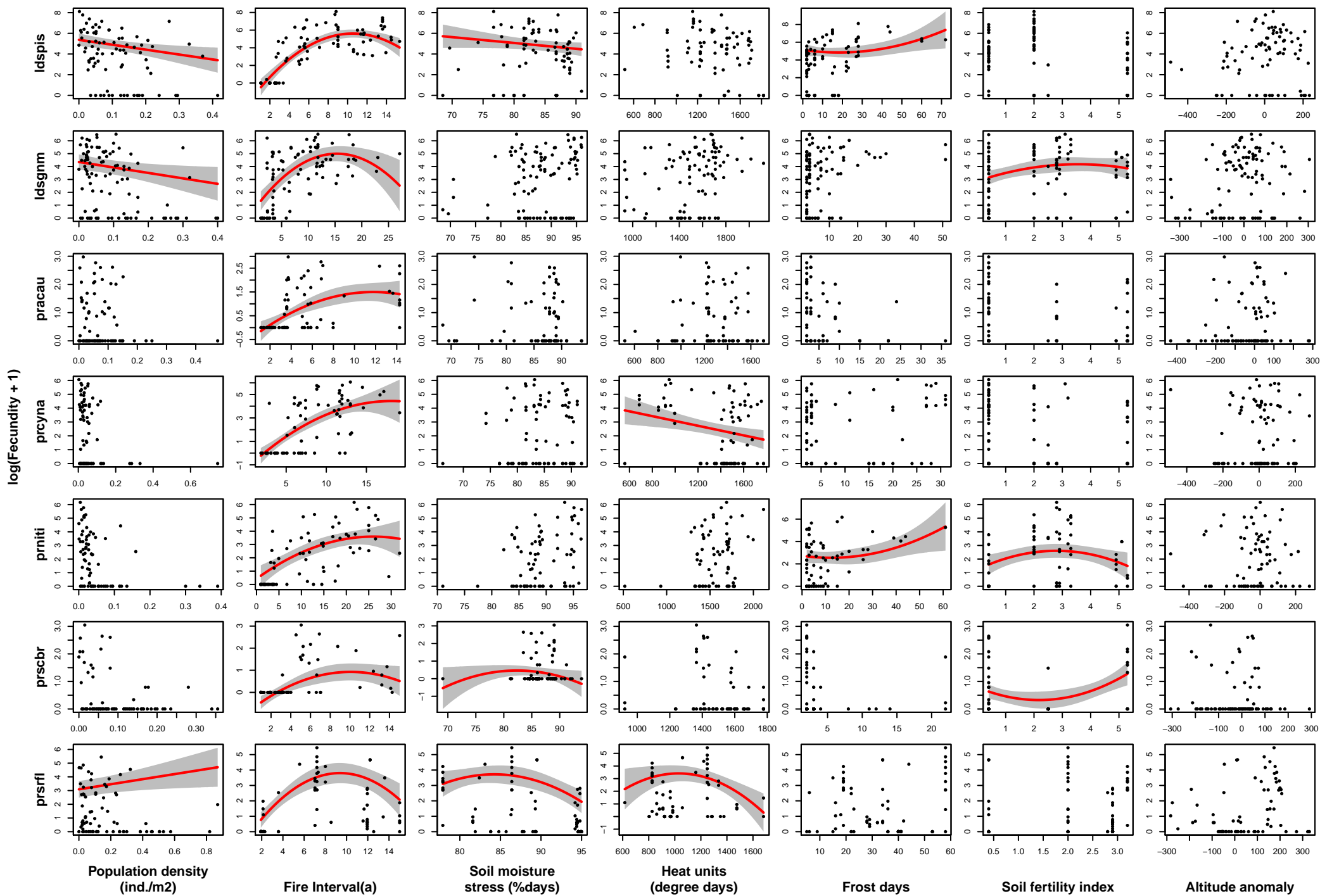
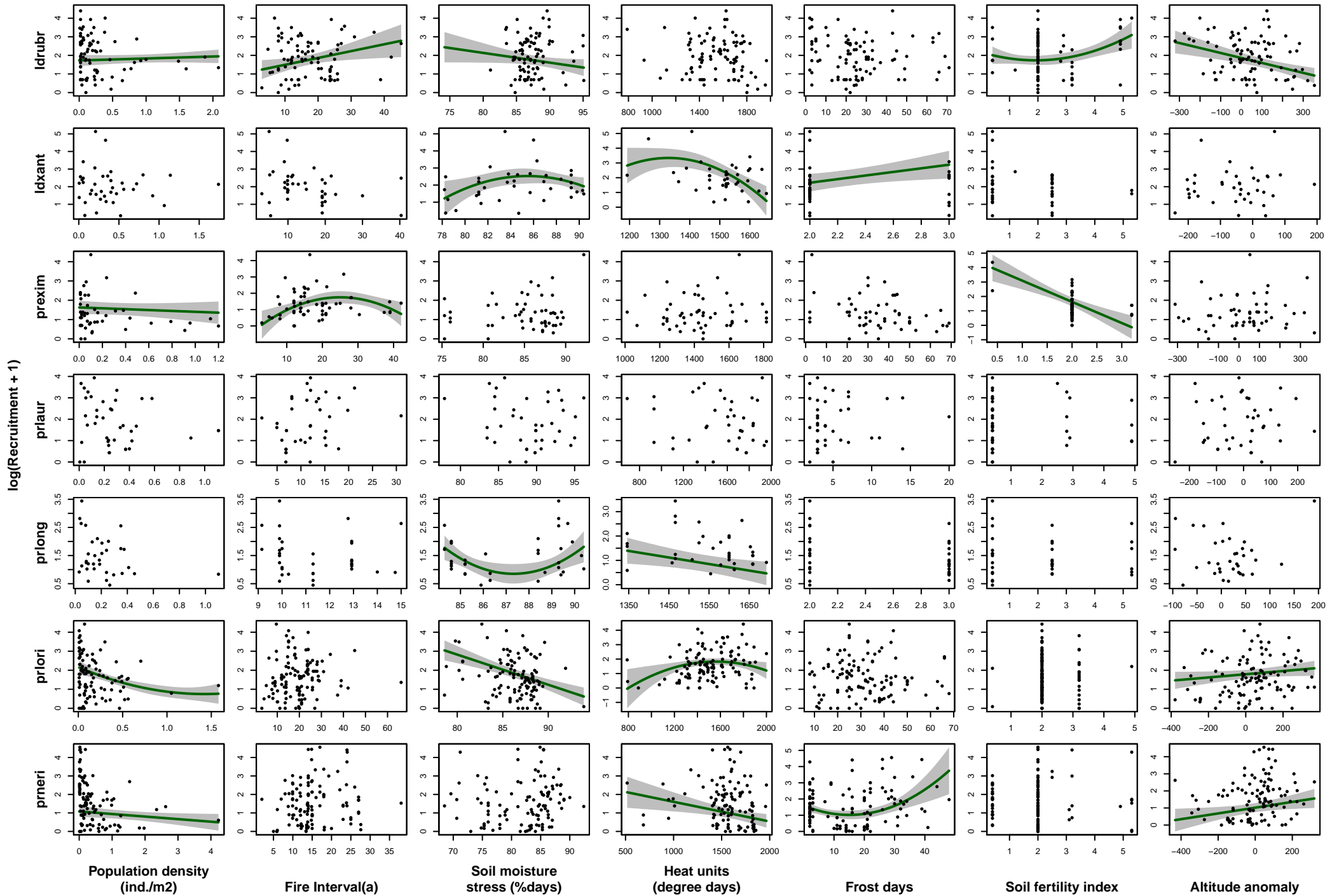
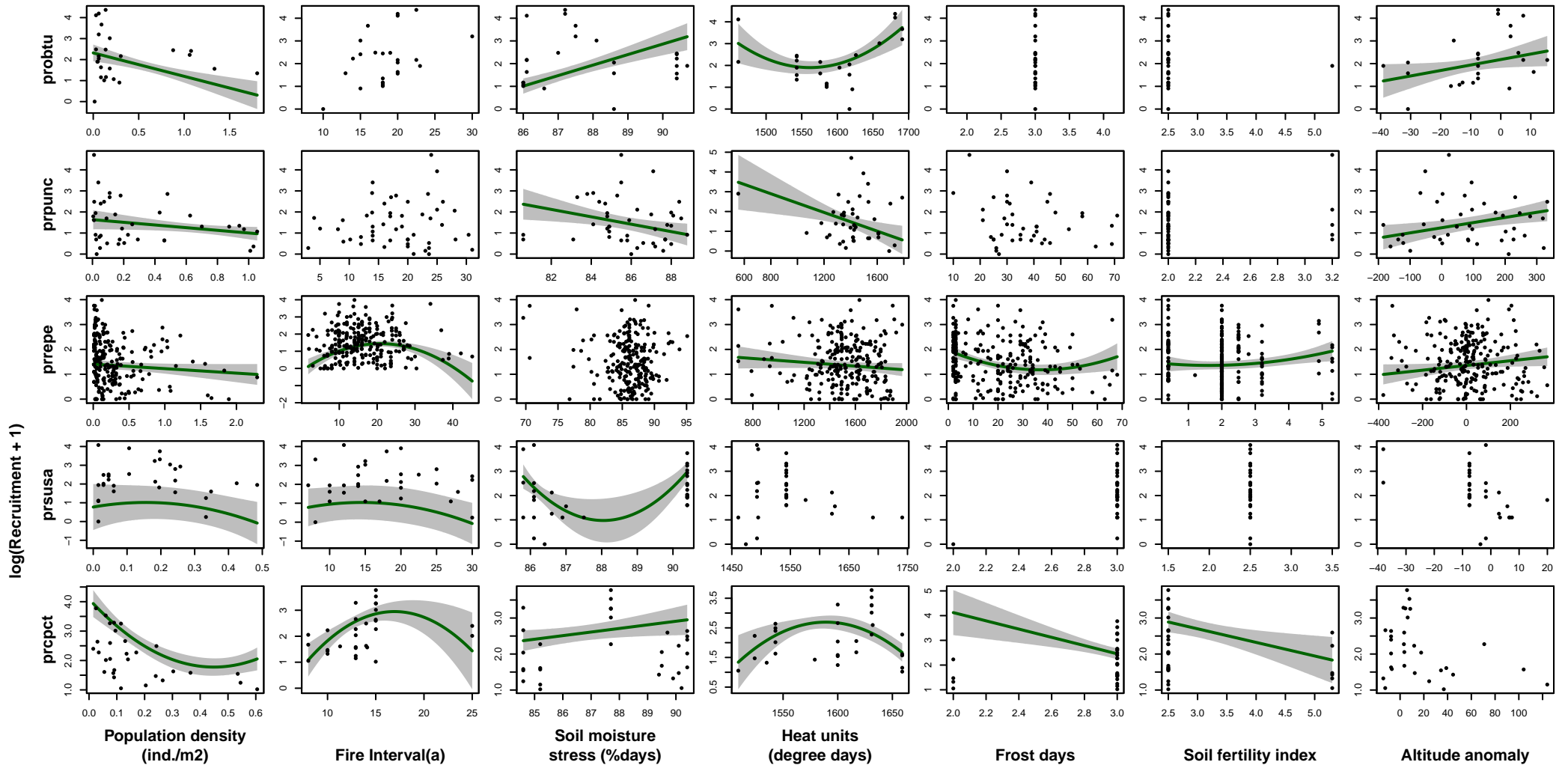


Fig. S2.3. Response of recruitment (plotted on the $\log(x + 1)$ scale) to population density, fire interval, climate variables and soil nutrient status from 26 serotinous Proteaceae study species.





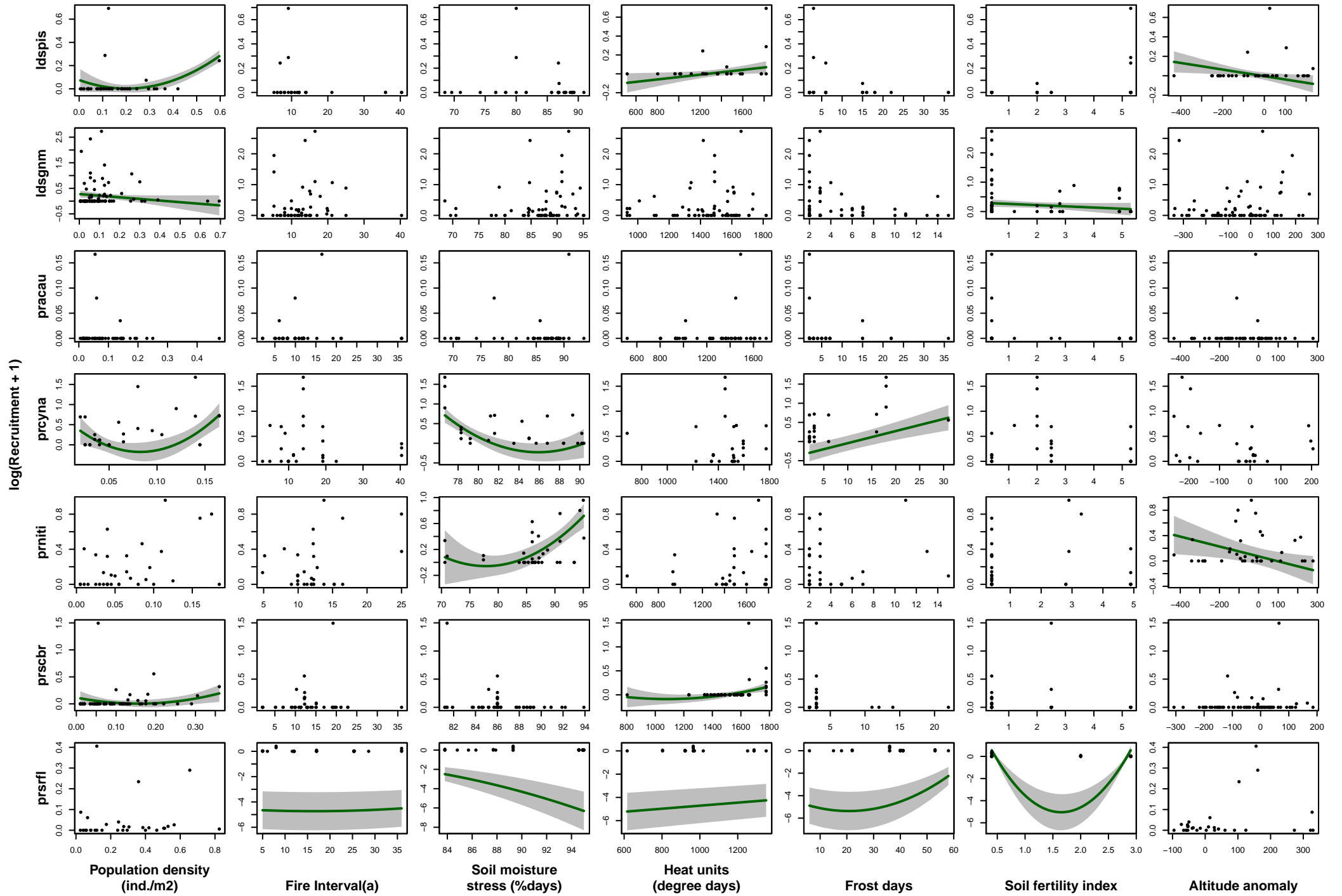


Table S2.1. List of 26 serotinous Proteaceae study species (Cape Floristic Region, South Africa) with abbreviations (used in Fig. S2.2 and Fig. S2.3), range size and fire persistence type, i.e. resprouter or nonsprouter (Rebello, 2001); and number of populations sampled (n) to estimate demographic variation in fecundity, recruitment and adult fire survival. Range size was calculated based on occurrence records from the Protea Atlas Project (Rebello 2001) aggregated to a spatial resolution of $1' \times 1'$.

Table S2.1

Species name	Abbreviation	Range size (1' × 1' grid cells)	Fire persistence type	Fecundity (n)	Recruitment (n)	Fire Survival (n)
<i>Leucadendron album</i>	ldalbu	213	Nonsprouter	26	24	15
<i>Leucadendron coniferum</i>	ldcfrm	287	Nonsprouter	59	22	0
<i>Leucadendron eucalyptifolium</i>	ldeuca	1407	Nonsprouter	19	55	0
<i>Leucadendron laureolum</i>	ldlaur	458	Nonsprouter	51	29	22
<i>Leucadendron modestum</i>	ldmode	223	Nonsprouter	62	18	14
<i>Leucadendron muirii</i>	ldmuir	203	Nonsprouter	64	15	6
<i>Leucadendron rubrum</i>	ldrubr	1538	Nonsprouter	55	80	14
<i>Leucadendron salignum</i>	ldsngm	6007	Resprouter	100	75	85
<i>Leucadendron spissifolium</i>	ldspis	1338	Resprouter	80	33	38
<i>Leucadendron xanthoconus</i>	ldxant	891	Nonsprouter	50	39	16
<i>Protea acaulos</i>	pracau	891	Resprouter	80	51	48
<i>Protea amplexicaulis</i>	prampl	377	Nonsprouter	54	24	24
<i>Protea compacta</i>	prcpct	391	Nonsprouter	55	30	22
<i>Protea cynaroides</i>	prcyna	1719	Resprouter	83	27	24
<i>Protea eximia</i>	prexim	840	Nonsprouter	51	50	2

Table S2.1

Species name	Abbreviation	Range size (1' × 1' grid cells)	Fire persistence type	Fecundity (n)	Recruitment (n)	Fire Survival (n)
<i>Protea laurifolia</i>	prlaur	2752	Nonsprouter	60	38	18
<i>Protea longifolia</i>	prlong	453	Nonsprouter	51	34	28
<i>Protea lorifolia</i>	prlori	1469	Nonsprouter	51	103	4
<i>Protea neriifolia</i>	prneri	1811	Nonsprouter	56	106	15
<i>Protea nitida</i>	prniti	2727	Resprouter	78	31	35
<i>Protea obtusifolia</i>	probtu	470	Nonsprouter	64	24	7
<i>Protea punctata</i>	prpunc	707	Nonsprouter	48	41	2
<i>Protea repens</i>	prrepe	4070	Nonsprouter	69	231	35
<i>Protea scabra</i>	prscbr	476	Resprouter	85	66	66
<i>Protea scolopendriifolia</i>	prsrfl	484	Resprouter	76	30	30
<i>Protea susannae</i>	prsus	359	Nonsprouter	48	32	1

CHAPTER 3

FUNCTIONAL TRAITS EXPLAIN THE HUTCHINSONIAN NICHE OF PLANT SPECIES

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ABSTRACT

The Hutchinsonian niche is a foundational concept in ecology and evolutionary biology. It denotes the set of environments in which populations can grow. However, it is unknown how traits affect demographic performance along environmental gradients and thus the Hutchinsonian niche. We quantified effects of inter- and intraspecific trait variation on demographically-derived Hutchinsonian niche characteristics across the global geographical ranges of 26 plant species. Species-mean trait values explained variation in global maximum population growth rate ($R^2 = 0.27$), as well as niche optima ($R^2 = 0.56$) and widths ($R^2 = 0.66$) along different environmental gradients. Intraspecific trait variation explained ($R^2 = 0.59$) and increased niche widths. Our study provides a novel, theoretically-founded framework relating traits, demographic performance, population dynamics and species' niches. This should advance the fields of functional population ecology and functional biogeography.

INTRODUCTION

The concept of the Hutchinsonian niche is a cornerstone of ecology, evolution and biodiversity research (Pulliam 2000; Holt 2009; Chase & Leibold 2003; Schurr *et al.* 2012a). Hutchinson (1957) distinguished fundamental and realised niches, where the realised niche of a species is the set of environmental conditions at which intrinsic population growth rates are positive in the presence of competitors (Maguire 1973; Hutchinson 1978). As such, the Hutchinsonian niche is a useful concept for linking the formation of species' geographical ranges to environmental effects on local demography (Holt 2009; Schurr *et al.* 2012a). The niche concept is frequently invoked as the basis for species distribution modelling (SDMs; e.g. Guisan & Thuiller 2005) to study how species' geographical ranges may respond to environmental change (Pearson & Dawson 2003; Ehrlén & Morris 2015). Despite the central role of Hutchinson's niche framework for theoretical and applied ecology, there is still limited understanding of the

determinants and drivers of variation in Hutchinsonian niches across species (Holt 2009; Evans *et al.* 2016). In particular, how the realised Hutchinsonian niches of species depend on functional traits is not known, hence the role of traits as underlying determinants of ecological performance and population dynamics remains largely unknown.

Functional traits, i.e. measurable morphological, physiological, phenological or behavioural features that affect fundamental processes of growth, reproduction and survival (*sensu* Violle *et al.* 2007), have taken a central role in ecology (McGill *et al.* 2006; Violle *et al.* 2014; Díaz *et al.* 2016). Focusing on traits is seen as a promising approach for reducing the dimensionality of biological organisation since traits provide generalizable properties, for example, across taxonomic and ecological scales (McGill *et al.* 2006; Violle *et al.* 2014). An important goal of population ecology is to link functional traits and demographic performance (growth, fecundity and survival) along environmental gradients (Violle *et al.* 2007; Adler *et al.* 2014). Doing so may provide a means to simplify biological complexity across taxa, geographical scales and environmental gradients (McGill *et al.* 2006; Kearney *et al.* 2010; Violle *et al.* 2014).

The development of functional population ecology and functional biogeography is currently hampered by a lack of trait and demographic data across the global geographical distributions of multiple species (McGill *et al.* 2006; Violle *et al.* 2007; 2014; but see Treurnicht *et al.* 2016, Chapter 2 of this dissertation). Most existing studies examined relationships between traits and organismal performance by relying on single, life stage-specific proxies of performance from single or few localities. For example, pioneering studies on tropical forest trees have identified relationships between traits and performance parameters such as individual growth (Wright *et al.* 2010; Poorter & Bongers 2006; Poorter *et al.* 2008, 2010). However, more recent studies show that relationships between traits and individual growth (Paine *et al.* 2015) and vital rate

elasticities (Adler *et al.* 2014) are generally rather weak. Notably, these proxies may not fully reflect demographic performance across an organism's life cycle or ecological performance (*sensu* Violle *et al.* 2007), and are not necessarily under strong selection (Silvertown, Franco & Conway 1992; Reich 2014). An alternative approach, relying on key demographic rates of survival and reproduction across the life cycle of species (e.g. Visser *et al.* 2016), is a potential way to better unravel trait-performance relationships.

Trait-performance relationships may be further obscured by assuming that trait variation is greatest between species while neglecting intraspecific trait variation across species' geographical distributions (Albert *et al.* 2010; Bolnick *et al.* 2011; Violle *et al.* 2012; Siefert *et al.* 2015). Notably, intraspecific trait variation has been found to be important for determining species' ranges (Estrada *et al.* 2016). It has been postulated that trait means at species level (from hereon "species-mean trait values") should explain niche optima along environmental gradients (or niche position), but cannot be expected to fully resolve niche widths (or breadth; Violle *et al.* 2007; Violle & Jiang 2009). Greater intraspecific trait variation should allow populations to grow in a wider range of environments (Violle & Jiang 2009; Violle *et al.* 2012; Sides *et al.* 2014). Positive relationships between intraspecific trait variation and niche width may result from phenotypic plasticity or genetically-determined trait divergence between populations (see Bolnick *et al.* 2011; Violle *et al.* 2012 and references therein). Hence, both species-mean trait values and intraspecific trait variation should explain niche widths. Although conceptual expectations exist on the role of trait variation in shaping niche optima and widths (e.g. Violle & Jiang 2009; Violle *et al.* 2012), there are no real-world examples that quantify the effects of such trait variation on the Hutchinsonian niches of multiple species.

A trait-based understanding of species niches requires the identification of functional traits that explain variation in demographic processes across environmental gradients. Plant ecological strategy theory provides a preliminary shortlist of trait spectra that describe plant-responses in relation to competition, environmental stress and large-scale disturbance (Grime 1977; Westoby 1998; Westoby *et al.* 2002; Westoby & Wright 2006). Westoby (1998) initially proposed a leaf-height-seed (LHS) plant ecology strategy scheme that describes the strategy of any species along three trait axes (specific leaf area (SLA), plant height and seed mass) forming a geometric space. However, it is now widely recognised that other traits also explain plant responses to environmental variation (reviewed in Westoby *et al.* 2002; Westoby & Wright 2006). For example, plant responses to variation in climate and soil depend on leaf (leaf economics spectrum; Wright *et al.* 2004), wood (wood spectrum; Chave *et al.* 2009; Reich 2014) and seed traits (Lamont & Groom 2013), while responses to large-scale disturbance, such as fire, depend on plant architectural traits (Corner 1949), resprouting ability (Westoby 1998; Clarke *et al.* 2013) and seed traits (Westoby 1998). In fact, recent studies show that these individual traits interact to define plant form and function (Díaz *et al.* 2016; Messier *et al.* 2017). They have also been linked, to some degree, with performance parameters and position plant species along the slow-fast continuum of plant life histories (Adler *et al.* 2014; Salguero-Gómez *et al.* 2016). Notably, for long-lived, perennial plants, slow growth and delayed reproduction should be promoted by “slow” traits (e.g. low SLA; long leaf longevity, high wood density, large seeds; Reich 2014; Salguero-Gómez *et al.* 2016; Díaz *et al.* 2016). Furthermore, population persistence should increase with the ability to store reproductive potential during periods of adverse environmental conditions (e.g. by longevity of stress-tolerant adults or seed banks (Higgins, Pickett & Bond 2000) or resprouting from storage organs after disturbance (Bond & Midgley 2001)). In a recent confirmation of this idea, Tonnabel *et al.* (in press; Am.

Nat.) showed that traits conferring tolerance to disturbance lead to niche evolution towards increased climatic stress (e.g. frost exposure).

We set out to quantify how trait variation determines the demographically-derived Hutchinsonian niches of plant species (Fig. 3.1). To do this, we measured eleven functional traits (major leaf, plant-architectural and seed traits) across the global geographical range of 26 woody plant species in the Cape Floristic Region (South Africa; Fig. 3.2a). For the study species, we first quantified the magnitude and extent of inter- and intraspecific variation among traits (Fig. 3.2b). Secondly, we used estimates of the realised niche of each species in five environmental dimensions (three climate variables, fire disturbance and soil fertility; Appendix A of this dissertation) to derive the global maximum population growth rate (r_{max}), niche optima (the environmental conditions corresponding to r_{max}) and niche widths (the environmental range for which intrinsic population growth rate is positive (see Fig. 3.1). These realised niches were estimated from extensive data on how reproduction and survival respond to environmental variation across species' global geographical ranges (Treurnicht *et al.* 2016, Chapter 2; Fig. 3.2a). We then quantified the effects of large-scale inter- and intraspecific trait variation (Fig. 3.2) on characteristics of the Hutchinsonian niche. Specifically, we asked to what extent species-mean trait values determine (1) global maximum population growth rates (r_{max}) and (2) niche optima in each environmental dimension. Finally, we asked (3) to what extent niche widths in each dimension are explained by species-mean trait values and intraspecific trait variation.

MATERIALS AND METHODS

STUDY REGION AND STUDY SPECIES

The Cape Floristic Region (CFR, Manning & Goldblatt 2012) is characterised by a Mediterranean-type climate with cool, wet winters and hot, dry summers, and is recognised as an ancient landscape with highly leached, nutrient-deficient soils (Allsopp, Colville & Verboom 2014). The dominant vegetation type of the CFR consists of sclerophyllous, fire-prone shrublands (Bond & Van Wilgen 1996), which are often dominated by members of the Proteaceae family (Rebello 2001). Proteaceae of the CFR harbour high functional diversity and are model organisms for ecological research (e.g. Schurr *et al.* 2012b). We studied 26 serotinous Proteaceae species of the genera *Protea* and *Leucadendron* that have a life cycle closely linked to fire (see Treurnicht *et al.* 2016, Chapter 2). They form long-lived canopy-stored seedbanks, retaining seeds in woody cones for several years until fire (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991). Since recruitment from seed is generally confined to the first few years after fire (Bond & Van Wilgen 1996), they form stands of fairly uniform age (ca. 5-50 years; Bond, Vlok & Viviers 1984; Lamont *et al.* 1991; Treurnicht *et al.* 2016, Chapter 2). Within the global spectrum of plant functional traits, the study species exhibit conservative nutrient-use and reproduce from large, nutrient-rich seeds (Lamont & Groom 2013; Díaz *et al.* 2016).

LARGE-SCALE MEASUREMENT OF LEAF, PLANT-ARCHITECTURAL AND SEED TRAITS

We measured eleven functional traits that follow the Leaf-Height-Seed scheme (Westoby 1998), but also include other leaf, plant-architectural and seed traits (Westoby *et al.* 2002; Westoby & Wright 2006). We measured these traits for 8-22 populations per species (Table S3.1), totalling 305 populations and 1220 individual plants across the 26 study species. Trait study sites corresponded to a set of the demographic study sites described in Treurnicht *et al.* (2016) and cover the major environmental gradients across the global geographical distribution of the study species (Fig. 3.2a). For each population, we randomly selected three adult plants

(for dioecious *Leucadendron* species three plants per sex). For these plants, we measured leaf traits (SLA, leaf width, leaf longevity, leaf nitrogen (N) content), plant-architectural traits (plant height, wood density, ramification index) and seed traits (seed mass, seed N content, seed N:P ratio). All trait measurements followed standard protocols (see Appendix S3.1 in Supporting Information). Nutrient contents were measured for leaf and seed samples pooled at the population level, whereas all other traits were measured at individual level. We also recorded resprouting ability after fire as either nonsprouter (non-persistent semelparous) or resprouter (persistent iteroparous; Bond & Midgley 2001). ‘Resprouting’ comprises a binary variable (0: nonsprouter; 1: resprouter) since resprouting ability does not vary intra-specifically for our study species (Rebelo 2001).

NICHE CHARACTERISTICS

We studied demographic responses to five major environmental gradients: three climate variables (as proxies of drought, cold and heat stress), soil nutrient status and fire disturbance (Table S3.2). These gradients are major drivers of large-scale demographic variation for the 26 study species (Treurnicht *et al.* 2016, Chapter 2). Climate variables included: (i) a summer month aridity index (from hereon “aridity”; mm/°C) calculated as the ratio between monthly precipitation (P) and average daily maximum temperature (T) in the month of January [aridity = $P/(T + 10)$; De Martonne 1926], (ii) minimum temperature (T_{\min} ; °C) defined as the mean of daily minimum temperatures in the winter month of July, and (iii) maximum temperature (T_{\max} ; °C) defined as the mean of daily maximum temperatures in the summer month of January. Note that for aridity (expressed as an index), low values represent more arid conditions. However, when reporting parameter estimates for trait effects (see Results), we inverted this variable to describe effects on niche optimum along increasing aridity. Furthermore, we considered an edaphic variable as an index of soil nutrient status (from hereon “soil fertility”; 0: low fertility;

10: high fertility). These four variables were extracted from the South African Atlas of Climatology and Agrohydrology (Schulze 2007; averaged from 1950–2000) with a resolution of $1' \times 1'$ ($1.55 \text{ km} \times 1.85 \text{ km}$). Finally, fire interval was measured as the time since last fire at the time of sampling demographic data (see Treurnicht *et al.* 2016, Chapter 2).

Following Maguire (1973), we quantify the niche of a species from the response of intrinsic growth rates (r_0) to environmental conditions, extracting the maximum population growth rate (r_{max}), and characterising the niche in terms of niche optimum and niche width along individual environmental gradients (Fig. 3.1). Intrinsic annual growth rates (r_0) were estimated from species-specific demographic niche models fitted to data from 3454 population-level records of per-capita fecundity, recruitment and fire survival (as well as their response to environmental covariates and population density) for the 26 study species (see Appendix A). These demographic rates were measured in natural communities and thus incorporate effects of interspecific biotic interactions. The derived niche models thus represent the realised, or ‘post-interactive’, niche (*sensu* Hutchinson 1978). Note that the responses of fire survival to environmental gradients were not estimated for nonsprouters because they have extremely low fire survival rates with little intraspecific variation (Treurnicht *et al.* 2016, Chapter 2). Niche optimum was then defined as the combination of environmental conditions where r_0 is maximal, derived by optimising the function $r_0(X)$ over all environmental covariates $[X]$. We identified this optimum using numeric global optimization by the box-constraint quasi-Newton method (function *optim*, R version 3.1.0). Maximum population growth rate (from hereon “ r_{max} ”) is then the value of r_0 in the optimal environment, i.e. the global optimum of r_0 . As such, r_{max} represents the global fitness maximum of a species, independent of the local environment. Niche width in the five niche dimensions of the three climate variables, soil fertility and fire interval was defined as the range of each environmental gradient for which r_0 is positive ($r_0 > 0$;

Fig. 3.1) when all other environmental variables are at their niche optimum. Table S3.3 provides a complete overview of the estimated niche characteristics and niche dimensions.

STATISTICAL ANALYSES

We quantified inter- and intraspecific variation in traits, and then investigated the effects of these two trait components on species' niche characteristics. Analyses were performed in R version 3.3.3 (R Core Team 2017). Niche characteristics were scaled, and explanatory trait-variables were log-transformed (Westoby *et al.* 2002; Lamont & Groom 2013) and scaled to ensure comparability across analyses.

First, to quantify the hierarchical partitioning (or variance partitioning) of variation in each trait between species (interspecific) and between populations within species (intraspecific), we fitted linear mixed effect models (R package *lme4*; Bates *et al.* 2016) that contained nested random effects of populations within species (except for nutrient traits which only contained a random effect of species, since samples were pooled at population level; Appendix S3.1). Secondly, we quantified the effects of species-mean trait values on r_{max} , niche optima and widths. To account for phylogenetic non-independence, we used phylogenetic generalised least squares (PGLS), assuming a Brownian Motion correlation structure (R packages: *nmle* (Pinheiro *et al.* 2015), *ape* 3.5 (Paradis, Claude & Strimmer 2004)). A phylogeny (Fig. S3.1) was reconstructed from a supermatrix (J. Tonnabel, unpublished data) that combined the most recent molecular markers for major Proteaceae genera (Sauquet *et al.* 2009; Valente *et al.* 2010; Tonnabel *et al.* 2014). For each niche characteristic, we applied automated model selection (R package *MuMIn*; Barton 2016) among all combinations of explanatory trait-variables and determined a set of plausible models using the sample size corrected Akaike Information Criterion (AICc; Burnham & Anderson 2002). We calculated an AICc-weighted average of all models with

$\Delta AIC_c < 10$ (Burnham & Anderson 2002). This provides a robust basis for evaluating the effect sizes of multiple variables (Grueber *et al.* 2011). For these averaged models, we then evaluated overall model fit as the proportion of variance explained by all traits (R^2 , following Ives (2017)), and consider the effect size of each trait as the corresponding standardised regression coefficient. Finally, we quantified the dependence of niche widths on intraspecific trait variation calculated as the between-population standard deviation (SD) per trait. As above, we used automated model selection and model averaging to evaluate overall model fit and effect sizes.

RESULTS

QUANTIFYING LARGE-SCALE TRAIT VARIATION

Interspecific trait variation generally exceeded intraspecific trait variation, even though the sampled populations covered the global geographical ranges of our 26 study species (Fig. 3.2a; see also Fig. S3.3). Ten of the eleven functional traits varied more between species than between populations (Fig. 3.2b; Table S3.5). Intraspecific variation was highest for leaf N (57%), followed by the two seed nutrient traits and leaf longevity (ranging from 46% to 49%) whereas all other traits varied more substantially (>77%) between species. Note that resprouting ability varies only between species due to the inherent fire survival strategies of our study species (Rebello 2001; Treurnicht *et al.* 2016). Correlations among the eleven inter- and intraspecific trait values, respectively, were generally weak and never exceeded 0.64 (see Table S3.4; Fig. S3.2 for Spearman correlation coefficients).

EFFECTS OF INTERSPECIFIC TRAIT VARIATION ON r_{max}

The estimated maximum population growth rate across the global geographical ranges of our study species (r_{max}) ranged from 0.28 to 1.53 (mean: 0.74; Table S3.3). Functional traits explained a reasonable amount ($R^2 = 0.27$) of the overall variation in the global r_{max} (R^2 of the

averaged model; Fig. 3.3a). Absolute trait-effects on r_{max} were dominated by plant-architectural traits with a notable negative effect of wood density (Fig. 3.4). Although the effect of wood density was not significant in the averaged model, a model containing only this trait explained 14% (R^2) of the overall variance in r_{max} ($P = 0.059$).

EFFECTS OF INTERSPECIFIC TRAIT VARIATION ON NICHE OPTIMA

Demographic niche optima varied substantially between species and niche dimensions (Table S3.3). For example, niche optimum in the T_{min} -dimension ranged from $-1.73 - 9.65$ °C, which corresponds to 95% of the total variation in T_{min} across the study region. For the other environmental variables, niche optima covered between 65% and 100% of the variation in the study region (Tables S3.2, S3.3). Species-mean trait values explained substantial variance in niche optima across environmental gradients (mean $R^2 = 0.57$, range: $0.45 - 0.68$; Fig. 3.3b). Species-mean trait values generally explained niche optima better than they explained the global r_{max} , notably along gradients of aridity ($R^2 = 0.65$), T_{min} ($R^2 = 0.68$) and fire interval ($R^2 = 0.56$; Fig. 3.3a-b). Optima in the aridity and T_{min} -dimensions were explained by significant effects of a single leaf trait (SLA), as well as two seed traits (seed mass and seed N:P), with T_{min} additionally determined by an architectural trait (plant height; Fig. 3.5a). Niche optimum of the fire interval depended exclusively on resprouting ability: the optimal fire interval was much shorter for resprouters than for nonsprouters. In contrast, no individual trait had a strong effect on the niche optima of T_{max} and soil fertility ($R^2 = 0.49$ and 0.45 , respectively; Fig. 3.5a).

EFFECTS OF INTER- AND INTRASPECIFIC TRAIT VARIATION ON NICHE WIDTHS

Demographic niche widths varied strongly between species and niche dimensions: the range of environments for which individual species show positive population growth covered between 21.5% (aridity) and 100% (aridity and soil fertility) of the total environmental range in the study

biome (Table S3.2, S3.3). Species-mean trait values generally explained niche widths better (mean $R^2 = 0.66$, range: 0.55 – 0.78) than they explained the global r_{max} and niche optima ($R^2 = 0.27$ and 0.56, respectively; Fig. 3.3a-c). Niche width in the T_{min} -dimension ($R^2 = 0.71$) was notably explained by a single leaf trait (leaf longevity) and resprouting ability, whereas T_{max} ($R^2 = 0.64$) was largely explained by a plant-architectural trait (wood density; Fig. 3.5b). The niche width of soil fertility ($R^2 = 0.55$) was largely determined by leaf N, while for the aridity width ($R^2 = 0.61$) no trait effect was significant. The width of fire niches ($R^2 = 0.78$) was notably explained by resprouting ability (i.e. fire niche widths were broader for resprouters than nonsprouters), followed by leaf N (Fig. 3.5b).

Niche widths were also well-explained by intraspecific trait variation (mean $R^2 = 0.59$, range: 0.47 – 0.83; Fig. 3.3c). The niche widths of aridity ($R^2 = 0.47$) and T_{min} ($R^2 = 0.51$) were notably explained by intraspecific variation in wood density and leaf N, respectively (Fig. 3.5c). The niche width of soil fertility ($R^2 = 0.56$) was determined by seed N:P. Fire niche width ($R^2 = 0.83$) was determined by resprouting ability and two leaf traits (SLA and leaf longevity). For the niche width of T_{max} ($R^2 = 0.58$), we detected no significant effect of any trait. Importantly, all significant effects of intraspecific trait variation were positive, so that species with greater intraspecific trait variation had wider demographic niches (Fig. 3.5c).

DISCUSSION

In this study, we related demographically-derived Hutchinsonian niches to inter- and intraspecific trait variation across the global geographical ranges of 26 plant species. We detected that trait values generally varied more between than within species, although four traits (leaf longevity, leaf N, seed N and seed N:P) varied substantially within species, across their geographical range (Fig. 3.2b). Interspecific trait variation explained substantial variation in

maximum population growth rate (r_{max}), niche optima and widths (Fig. 3.3). Notably, niche widths were well-explained by intraspecific trait variation, with all significant effects being positive (Fig. 3.5). Our findings validate the theoretical expectations of how large-scale trait variation determine demographic performance and ecological niches (reviewed in Violle *et al.* 2012; see also Sides *et al.* 2014).

The relatively low explanatory power of traits on the global r_{max} (Fig. 3.3) may arise from the fact that demographic performance and fitness are influenced by multiple traits and their interactions (e.g. Adler *et al.* 2014). Plant phenotypes consist of an intricate ensemble of traits, so that multiple alternative phenotypes may perform well in a given environment (Marks & Lechowicz 2005; Messier *et al.* 2017). Even so, we find a negative effect of wood density on the global r_{max} of our study species (Fig. 3.4). This corresponds with the slow-fast scheme (Reich 2014; Salguero-Gómez *et al.* 2016; Díaz *et al.* 2016) and provides large-scale demographic evidence for the wood economics spectrum (Chave *et al.* 2009). Species with high wood density have reduced hydraulic conductance, low embolism resistance and osmotic potential which limits transpiration and promotes plant survival in response to climatic stress (Chave *et al.* 2009; Poorter *et al.* 2010). However, carbon investment in biomechanical structures that govern whole-plant water economics (“hydraulic safety mechanism”) is costly (Chave *et al.* 2009; Reich 2014). Despite such costly investment, high wood density may promote tolerance to seasonal climatic stress (Chave *et al.* 2009; Reich 2014), a defining feature of our Mediterranean-type climate study region (Allsopp, Colville & Verboom 2014). In fact, our results show that high wood density allows species to persist under a wider range of maximum summer temperatures (T_{max} ; Fig. 3.5b). Indeed, the measurement of wood density and its relationship with other architectural traits is increasingly recognised and may provide a

promising means to link mechanical support and hydraulic function (Reich 2014; Messier *et al.* 2017).

In trait-based approaches, the inclusion of multiple functional traits is seen as a promising means to explain trait-performance relationships (e.g. Westoby & Wright 2006). Our study that included eleven leaf, plant-architectural and seed traits showed that relatively few individual traits predict niche characteristics (Fig. 3.5). Notably, the three constituents of Westoby's (1998) LHS-scheme (SLA, plant height and seed mass) predicted optimum aridity and T_{\min} (Fig. 3.5a). The consistent effect of seed mass is likely explained by the strong climatic controls exerted on post-fire seedling recruitment of our study species (Treurnicht *et al.* 2016, Chapter 2). The seemingly counter-intuitive positive effect of SLA on the aridity optimum must be interpreted in the light of recent evidence showing that SLA is a highly context-dependent trait (see Adler *et al.* 2014 and references therein) and that climate-leaf size relationships are not necessarily universal (Wright *et al.* 2017). In contrast, climatic-niche widths were determined by traits beyond the LHS-scheme (Fig. 3.5b,c). For example, interspecific variation in leaf longevity (a resource conservation strategy; Westoby 1998, Wright & Westoby 2002), wood density and resprouting ability (allowing tolerance to stressful environments (Chave *et al.* 2009; Clarke *et al.* 2013)) allow wider T_{\min} and T_{\max} niches. Furthermore, greater intraspecific variation in wood density determines aridity niche widths, whereas leaf N variation allows broader T_{\min} -niches. Overall, this supposes that relatively few traits are truly 'functional' (i.e. link directly to demographic performance; *sensu* Violle *et al.* 2007), that this 'functionality' is niche-parameter specific and that each niche characteristic is determined by a small set of traits.

Our study took a novel approach by utilising the concept of the realised Hutchinsonian niche to estimate the relationships between traits, environmental variation and plant performance (Figs

3.1 and 3.2). For the global r_{max} , species-mean trait values explained substantial variation but these trait values explained even more variation in niche optima and widths along individual environmental axes (Fig. 3.3). Our study thus generally found stronger trait effects on demographic performance than previous studies relating traits to performance measures (e.g. R^2 : 0.08 – 0.29, Adler *et al.* 2014; R^2 : 0.007 – 0.022, Paine *et al.* 2015). The niche characteristics that we derived cover species' full life cycles based on range-wide demographic data. As such, niche responses cover the entire set of environments that a species would experience. Our findings thus greatly extend the known predictive ability of traits in plant population ecology, showing that traits can be used to predict large-scale variation in demographic performance. Hence, we generate first insights on the functional determinants of population dynamics which should reinforce the role of traits in the emerging fields of functional biogeography (Violle *et al.* 2014) and functional population ecology (e.g. Adler *et al.* 2014). Nevertheless, we have notably explored abiotic dimensions of the realised Hutchinsonian niche and resolving the effects of interspecific interactions on population growth (Pulliam 2000) thus remains an important future research agenda. It is conceivable that certain trait effects detected here represent responses of population growth to the abiotic environment (the fundamental niche), whereas others may represent interspecific interactions (the difference between the realised and fundamental niche). Finally, our focus on niche characteristics that integrated individual demographic rates across the life cycle of the study species (Treurnicht *et al.* 2016, Chapter 2; cf. Appendix A) does not resolve trait relationships confined to individual vital rates. Resolving such patterns is also important as recognised by other recent studies (e.g. Larson & Funk 2016; Visser *et al.* 2016).

Global climate change is progressing rapidly with disproportionate impacts on biodiversity (e.g. Urban 2015). In particular, the CFR biodiversity hotspot (Myers *et al.* 2000) is experiencing

shorter fire intervals and hotter, drier weather conditions (Wilson, Latimer & Silander 2015) known to cause species loss (Slingsby *et al.* 2017). Our findings suggest that resprouters are better equipped to withstand these changing environmental conditions. For example, the strong effects of resprouting ability on fire niches (resprouters have shorter optima and broader niches than nonsprouters; Fig. 3.5) can be explained by the distinct fitness advantages of resprouters in both extreme and variable fire return intervals. This is likely due to their exceptionally high fire survival rates (Treurnicht *et al.* 2016, Chapter 2) and ability to rapidly recover after fire (Clarke *et al.* 2013). In contrast, nonsprouters have extended juvenile periods and may face ‘immaturity risk’ (*sensu* Zedler 1995) at short fire intervals and senescence at long fire intervals (Treurnicht *et al.* 2016, Chapter 2). In-line with the ability of resprouters to persist under climatic stress (Lamont & Markey 1995; Clarke *et al.* 2013), we additionally find that resprouters have wider climatic niches (in particular T_{\min} ; Fig. 3.5b). However, our results further suggest that nonsprouters may have some capacity to adapt since investment in leaf N (high leaf N promotes fast growth; Wright *et al.* 2004), along with greater intraspecific variation in SLA and leaf longevity also promote wider fire niches (Fig. 3.5b,c). This supposes that fast-growing nonsprouters may, to some degree, be able to buffer against frequent fires if populations are able to respond to short fire intervals via leaf trait plasticity (e.g. Ackerly 2004). Furthermore, nonsprouters have higher per-capita fecundity (Treurnicht *et al.* 2016, Chapter 2) and their colonization ability is higher (Schurr *et al.* 2007). Even so, there are still slow-growing (serotinous) nonsprouters that may face a more uncertain future under the currently changing fire and climatic conditions of our study region. This may lead to population extirpations, shifts in the proportions of life history types, competitive hierarchies (e.g. Thuiller *et al.* 2007) and overall functional diversity in the CFR (especially since nonsprouters contribute disproportionately to regional diversity, Cowling & Lamont 1998). The range-wide trait-environment relationships that we have documented here thus provide insights on the different

potential responses of the functionally-diverse Proteaceae to ongoing environmental change in the CFR.

Identifying the functional-determinants of species' niches is essential for improving predictions of climate-driven range shifts (Estrada *et al.* 2016; Evans *et al.* 2016). Studying relationships between traits, environmental variation and species' niches across geographical ranges should help to better understand how traits determine range limits. Notably, we can formulate hypotheses to experimentally test the environmental limits of species: for example, intraspecific trait variation that defines climatic niches may reflect the ability of species to cope with climate change (Estrada *et al.* 2016). Since intraspecific trait variation (in wood density, leaf longevity and seed N:P) notably extends niche widths (Fig. 3.5c), an important next step is to unravel whether variation in these traits across the geographical ranges of species arises from genetic differentiation or phenotypically plastic responses to environmental gradients (Bolnick *et al.* 2011). This is also essential for predicting biotic responses to environmental change, since species with wide niches due to genetic differentiation may be susceptible to environmental change, whereas species with wide niches due to phenotypic plasticity may better tolerate environmental change *in situ* (Davis & Shaw 2001; Davis, Shaw & Etterson 2005; Moran, Hartig & Bell 2016). This is a pressing research agenda, given the evidence that the climatic niches of species cannot track the current rate of climate change, which may cause local population extirpations (e.g. Quintero & Wiens 2013; Cang, Wilson & Wiens 2016).

Finally, since few traits determined multiple niche characteristics (Fig. 3.5a-c) and these traits were not strongly correlated, our findings posit that species may be able to independently shift their niches and trait values along different environmental axes (Holt 2009). Hence, if a single environmental variable changes, diversity in the relevant traits should decrease but this will

have little knock-on effects on diversity in other traits. Collectively, an understanding of the sensitivity and capacity of species to respond to environmental change, the spectrum of conditions in relation to tolerance limits and the magnitude of trait plasticity are urgent priors to improve global change biodiversity assessments (e.g. Williams *et al.* 2008; Moran, Hartig & Bell 2016). Our approach linking traits and niche-performance is complementary to the recent development of physiological niche models that predict range dynamics (e.g. Kearney & Porter 2009; Higgins *et al.* 2012). Once these niche models are refined and sufficiently developed, it will be exciting to see whether such mechanistic alternatives can replace relatively simple trait-demography correlations.

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FIGURES

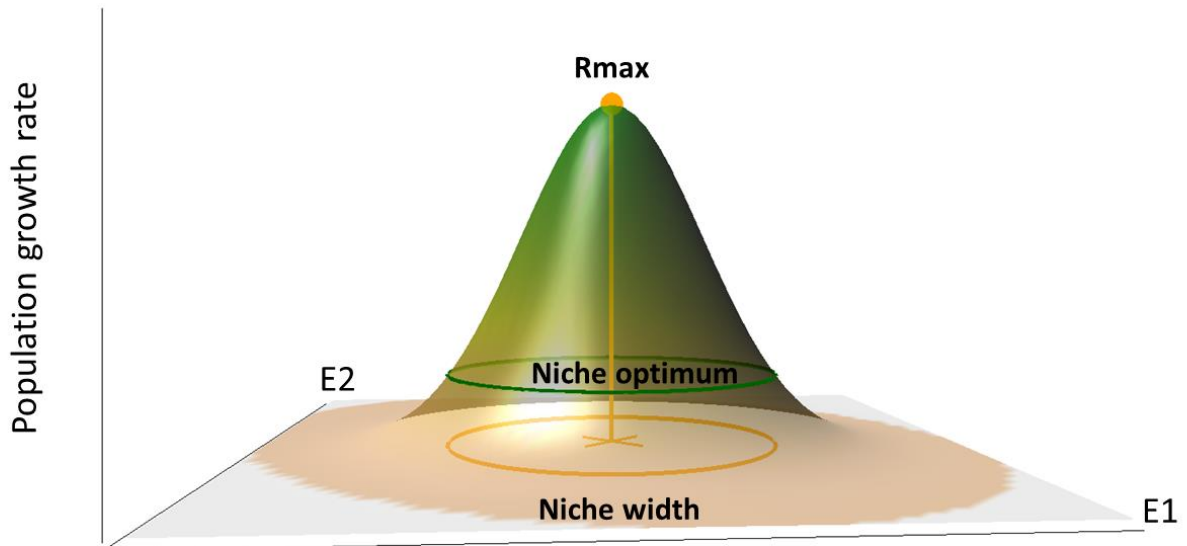


Fig. 3.1. Conceptual diagram of Hutchinsonian niche characteristics (following Hutchinson's (1978) definition of the realised niche): maximum population growth rate (r_{max}), niche optima and widths, as functions of intrinsic growth rates (r_0) along environmental axes (e.g. E1, E2). Niche optima (indicated by the cross) are defined as the combination of environmental conditions where r_0 is maximal along environmental axes (E1, E2). Maximum population growth rate (the global r_{max}) is the highest value of r_0 in the niche optimal environment (i.e. the global optimum of r_0). Niche widths are then defined as the environmental range where population growth is positive ($r_0 > 0$) along environmental axes (E1, E2). Table S3.3 gives estimated values for r_{max} , niche optima and widths along environmental gradients of climate (aridity, T_{min} , T_{max}), an edaphic variable (soil fertility) and fire disturbance (fire return interval) for the 26 Proteaceae study species. See Methods for details on niche characteristics and Table S3.2 for details on environmental variables.

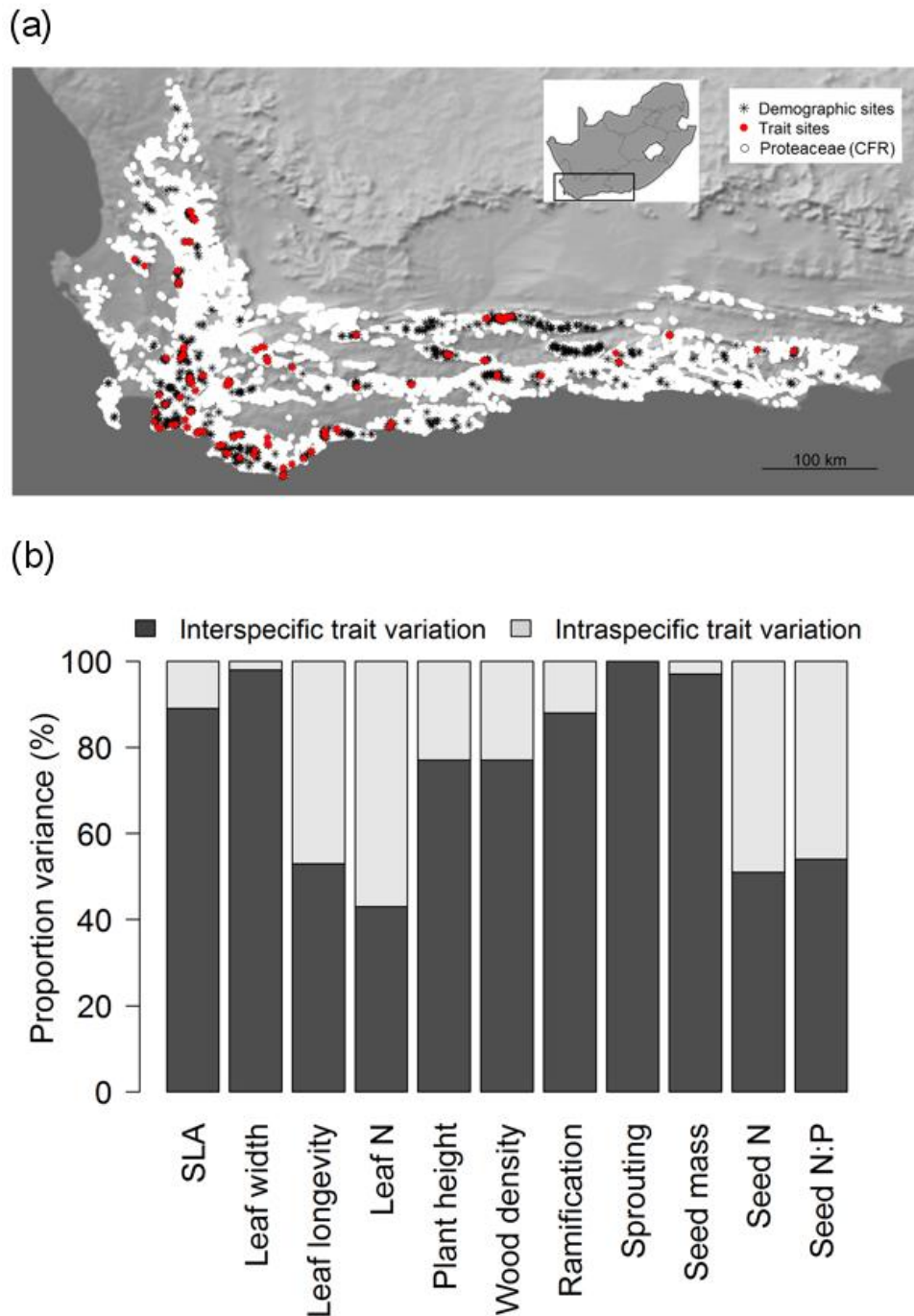


Fig. 3.2. (a) Map of study sites for functional trait data (red points) and demographic data (black stars; as per Treurnicht *et al.* (2016)) for 26 Proteaceae species in the Cape Floristic Region (CFR, South Africa) with the geographical distribution of CFR Proteaceae (white area; Protea Atlas Database from Rebelo 2001); (b) variance partitioning of large-scale interspecific and intraspecific trait variation for eleven functional traits compiled for the study species. Proportion variance (%) are from trait-specific linear mixed effect models (see Methods, Table S3.5). Functional traits were measured for a total of 305 populations (8-22 populations per species) and 1220 individual plants (Table S3.1).

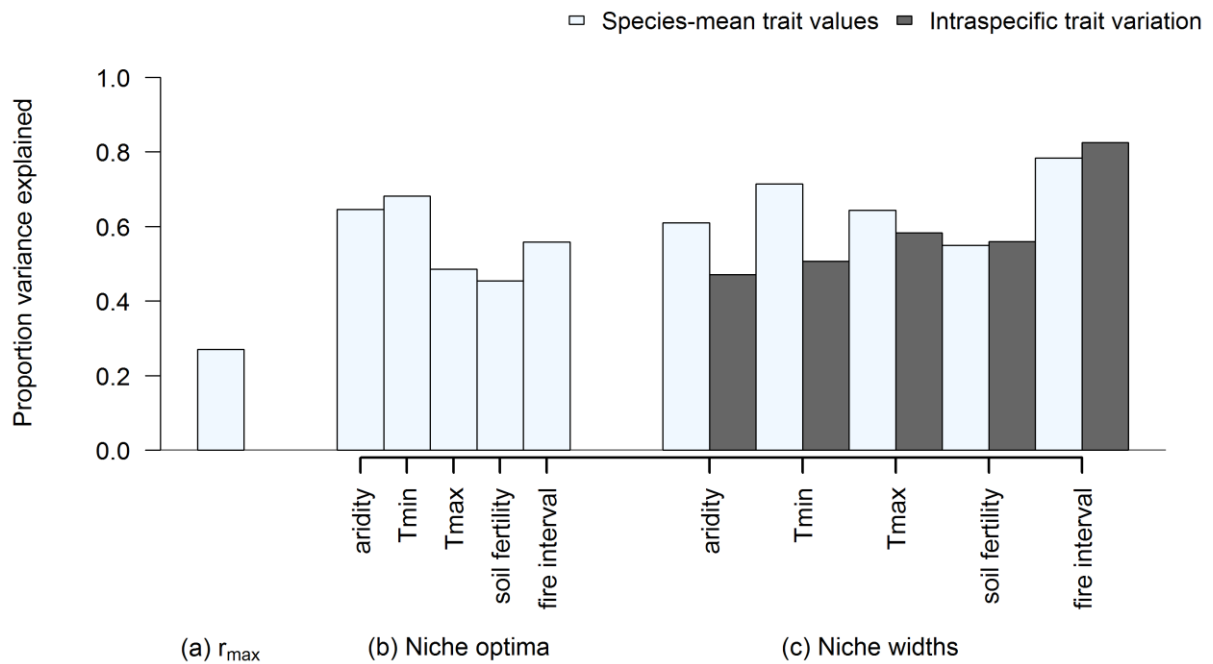


Fig. 3.3. Proportion variance explained (R^2 from phylogenetic generalised least square average models ($\Delta AICc < 10$)) by species-mean trait values (light blue bars) for (a) r_{max} , (b) niche optima and (c) niche widths, and by intraspecific trait variation (grey bars) for niche widths for 26 Proteaceae species. Niche optima and widths were defined along environmental axes of climate (aridity, T_{min} , T_{max}), soil nutrient status (soil fertility) and fire interval (see Table S3.2).

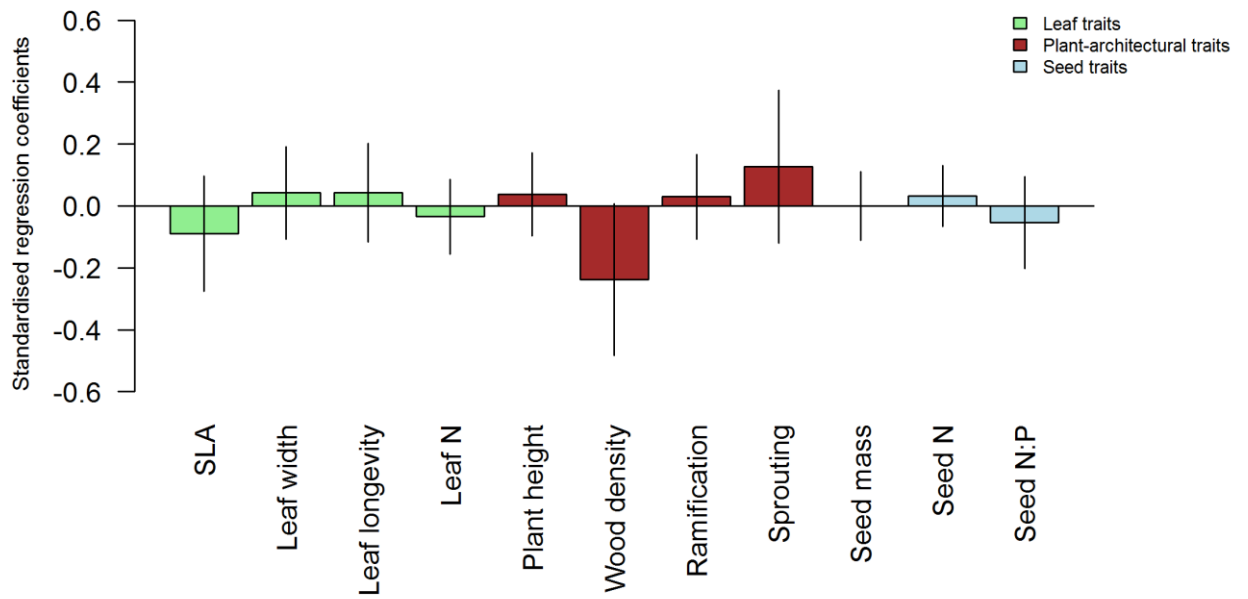


Fig. 3.4. Effects of species-mean trait values on the global maximum population growth rate (r_{max}) for 26 Proteaceae species. Bars are standardised regression coefficients with associated errors (whiskers) of eleven functional traits from phylogenetic generalised least squares averaged models ($\Delta AIC_c < 10$). ‘Sprouting’ is a dichotomous variable (0: nonsprouter; 1: resprouter).

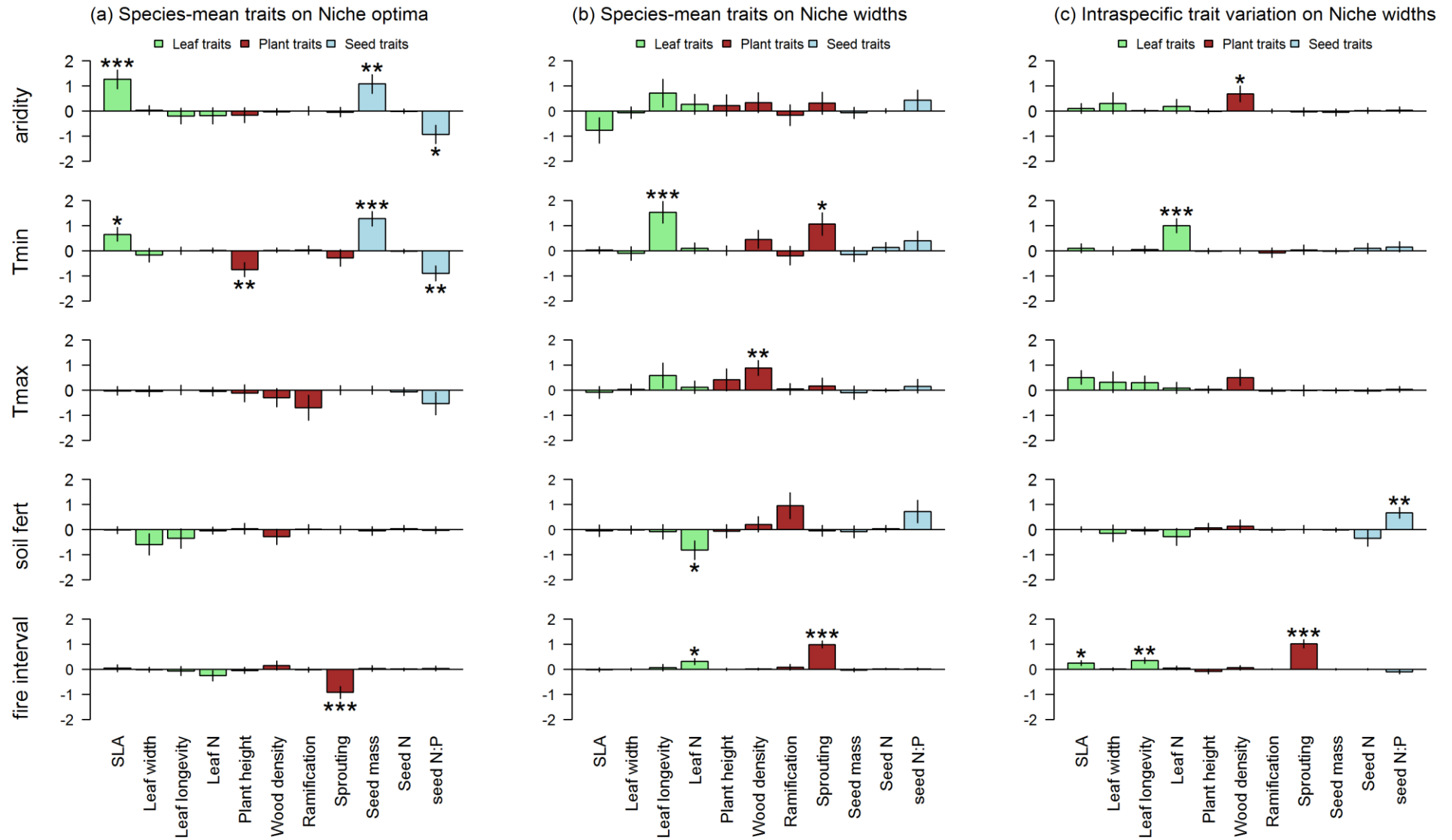


Fig. 3.5 (continued on next page)

Fig. 3.5 (continued). Effects of eleven functional traits [leaf traits = green bars; plant-architectural traits = maroon-brown bars; seed traits = light blue bars] on niche characteristics for 26 Proteaceae species: (a,b) species-mean trait values on niche optima and widths, respectively, and (c) intraspecific trait variation on niche widths. Bars are standardised regression coefficients with associated errors (whiskers) from phylogenetic generalised least squares averaged models ($\Delta\text{AICc} < 10$). Asterisks denote levels of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Niche optima is the value for which population growth is maximal whereas niche widths are the environmental range for which population growth is positive along environmental axes of climate (aridity, T_{min} , T_{max}), soil fertility and fire interval (see Fig. 3.1 and Methods). ‘Sprouting’ is a dichotomous variable (0: nonsprouter; 1: resprouter).

CHAPTER 3

Supporting Information:

FUNCTIONAL TRAITS EXPLAIN THE HUTCHINSONIAN NICHE OF PLANT SPECIES

Appendix S3.1 (TEXT). Detailed description of field methods for the measurement of eleven functional traits (*leaf traits*: SLA, leaf width, leaf longevity, leaf nitrogen content (leaf N); *plant-architectural traits*: plant height, wood density, ramification index (ramification); *seed traits*: seed mass, seed N content (seed N) and seed N:P ratio (seed N:P)) compiled for 26 Proteaceae study species, measured from a total of 305 populations (8-22 populations per species) and 1220 individual plants (Table S3.1) in the Cape Floristic Region (South Africa; see also Fig. 3.2a).

Below, we provide a brief review of the major leaf-, plant-architectural and seed traits used in this study which follow the LHS-scheme (Westoby 1998; Westoby & Wright 2006), reflecting major axes of plant biological function and specialisation (Westoby 1998; Reich *et al.* 2003). We also provide a detailed description of individual trait measurements on leaf-, plant-architectural and seed traits (SLA, leaf width, leaf longevity, leaf nitrogen (N) content, plant height, wood density, ramification index, seed mass, seed N content and seed N:P ratio). All trait measurements followed guidelines from Pérez-Harguindeguy *et al.* (2013); dry-weight measurements were processed with a high precision balance (0,001g; KERN PKP 420-3).

LEAF TRAITS

Leaf traits express plant responses to opportunities for rapid growth (Westoby 1998; Reich *et al.* 1999) and the ‘leaf economics spectrum’ describes how leaves regulate plant function and ecological strategy (Wright *et al.* 2004). For example, SLA is a fundamental measure of allocation strategy; reflecting an expected rate of return on investment and relates to relative growth rate (Westoby 1998; Wright *et al.* 2004; Westoby & Wright 2006). Low SLA leaves consist of thicker, denser tissue making leaves physically robust, increases leaf longevity yet leaves may contain fewer nutrients which, in turn, decrease plant photosynthetic capacity, leaf respiration rates and plant growth (reviewed in Westoby 1998; Reich 2014). Leaf width, leaf

longevity (or leaf life span) and leaf nitrogen (leaf N) also reflect axes of differentiation in leaf functional strategies (Wright *et al.* 2004). For example, leaf size and shape relate to the heat- and gas exchange capacity of the leaf surface in response to (e.g.) temperature fluctuations (Fonseca *et al.* 2000; Yates *et al.* 2010): thinner, narrower leaves facilitate cooling by increasing transpiration rates via a thinner boundary layer (Yates *et al.* 2010; Mitchell *et al.* 2015). On the other hand, increased leaf longevity reflects a resource conservation strategy at the plant level: slowing plant growth rate but increasing plant longevity (Reich *et al.* 1992, 1997, 1998; Wright & Westoby 2002; Ackerly 2004; Wright *et al.* 2004). Finally, leaf nitrogen (N) content reflects aspects of leaf function, resource capture and conservation within the leaf, notably maximum photosynthetic capacity (Lambers *et al.* 1998), net CO₂ assimilation and respiration rates (Reich *et al.* 1998; Garnier *et al.* 1999).

MEASUREMENT OF LEAF TRAITS: To estimate leaf dimensions (specific leaf area (SLA), leaf width, leaf longevity and leaf nitrogen content (leaf N)), we collected three fully expanded, mature and intact (unpredated) leaves (including petioles) from either three [genus *Protea*] or six [genus *Leucadendron*] focal plants per study site. For *Leucadendron album* (a species with relatively narrow leaves; Rebelo 2001), we sampled ten leaves per focal plant. All leaf measurements were then obtained by averaging measurements from the total number of leaves sampled per focal plant. Firstly, to measure one-sided leaf area (m²) and leaf width (leaf functional width; mm²), fresh leaves were scanned digitally and images were processed with Image J software (version 1.47; Rasband 2013). Leaf width was measured from calculating the diameter of the widest possible circle that can be drawn within the boundary of the fresh leaf surface (Reich *et al.* 1997; Yates *et al.* 2010). Secondly, to estimate specific leaf area (SLA), fresh leaves were oven dried (72 hours at 70°C) and weighed to determine dry leaf mass (g). SLA is then the fresh leaf area divided by oven dry leaf mass (m²/kg; Reich *et al.* 1998). Thirdly, we estimated average leaf longevity (in years; Reich *et al.* 1998) per plant from averaging across

the number of branching events or internode segments (along main branches) that contain green, photosynthetic leaves. In our study system, the branching habit of the serotinous study species allows one to directly measure the total number of branching events on a plant which is a good proxy of plant age (e.g. Bond *et al.* 1995; see also Treurnicht *et al.* 2016) and from this one can derive a plant-level estimate of leaf longevity. Finally, leaf nitrogen content (Reich *et al.* 1998) was measured at the population level only, since insufficient leaf material (dry mass (g)) was available for individual plants. Total nitrogen content (mass %) were analysed following standardised procedures (dry combustion by Dumas, VDLUFA Book of Methods Vol. II, 1 and 3.5.2.7 (1995)) using a multi-elemental analyser (Vario EL Cube) at the Analytical Chemistry Unit, University of Hohenheim (Stuttgart, Germany).

PLANT-ARCHITECTURAL TRAITS

Whole-plant-architectural traits widely represent responses to environmental variation (e.g. climate) and large-scale disturbance such as fire (Westoby 1998; Westoby *et al.* 2002). (Westoby 1998; Westoby *et al.* 2002; Westoby & Wright 2006). For example, plant height (a proxy of plant size) informs on plant performance (Violle *et al.* 2007) and resource acquisition (Schenk 2006) associated with responses to climatic variation and disturbance (Westoby 1998; Westoby *et al.* 2002). Plant height also reflects plant competitive ability, primarily limited by water availability (Westoby 1998; Weiher *et al.* 1999). The wood spectrum (*sensu* Chave *et al.* 2009) is primarily defined by the xylem of branches that relate to key physiological functions, growth and mechanical support. Wood density (i.e. the biomass invested per unit wood volume) is a measure of structural support and decay resistance which relates to whole-plant hydraulic function and the growth-mortality trade-off (reviewed in Chave *et al.* 2009; Reich 2014). High wood density confers slow growth, higher construction costs (producing small, compact cells with limited intercellular space making stems resistant to physical damage). Such low hydraulic conductance is associated with low mortality (Chave *et al.* 2009; Poorter *et al.* 2010). Branching

ramification (ramification) also relates to plant hydraulic conductivity since thicker branches (reduced ramification) have thicker xylem vessels and greater hydraulic resistance conducting water more efficiently than thinner (more ramified) branches (Harris & Pannell 2010). Resprouting ability, i.e. the ability of plants to resprout from buds or protected meristems after large-scale disturbance (e.g. fire), relates to the persistence niches of species (Weiher *et al.* 1999; Clarke *et al.* 2013).

MEASUREMENT OF PLANT-ARCHITECTURAL TRAITS: We estimated different dimensions of plant-architectural traits: plant canopy height, wood density and plant-branching ramification (Ramification). We also recorded resprouting ability (life history strategy or regeneration mode) as either nonsprouter (non-persistent semelparous) or resprouter (persistent iteroparous; Bond & Midgley 2001)).

To calculate a mean prediction of plant height per species across study sites, both plant height and fire interval (time since fire; a proxy for plant age) information were used (data from Treurnicht *et al.* 2016). Firstly, plant height was recorded as the aboveground maximum canopy height (cm) along a terminal branch. In addition, plant age was measured by counting the number of branches and internodes along terminal branches (as described in Treurnicht *et al.* 2016). To augment these field measurements of plant height, additional data were also available from a total of 9981 plants (F.M. Schurr unpublished data) for the 26 study species. Westoby (1998) proposed to quantify plant height as “the canopy height a species is designed to achieve by natural selection”. In fire-driven Proteaceae shrublands, one can expect plants to reach this height at ca. 20 years post-fire, i.e. a typical mean fire return interval in this study system (Wilson *et al.* 2010). For each study species, we thus regressed plant height measurements against the current fire interval (both log-transformed) including a random effect of site (linear mixed-effects model; R package lme4 by Bates *et al.* (2015)). Plant height was then calculated

as the mean prediction for 20 years since the last fire. The calculation of the coefficient of variation additionally used the standard deviation of the site random effect and estimates of plant height were then derived from the 95% quantile of all cone-bearing plants.

Wood density was estimated from collecting standardised wood samples (5-10 cm in length) from 3-year-old sapwood (e.g. Carlson *et al.* 2011). We removed bark and placed wood samples in distilled water until complete saturation to determine the fresh volume (cm³) of samples (using the water displacement method; Pérez-Harguindeguy *et al.* (2013)). Hereafter, every wood sample was oven dried (at 105°C for a minimum of 72 hours) and weighed to determine dry mass (g). Wood density (g/cm³) was then calculated as the ratio between oven dry mass (g) and saturated wet volume (cm³; Chave *et al.* 2009).

Cape Proteaceae are generally sympodial: branches or new growth are initiated near the apex of the previous year's branches below a terminal inflorescence (Midgley & Kruger 2000). Small-leaved shrubs are generally finely branched compared to large-leaved shrubs having fewer and thicker branches (Bond & Midgley 1988). Branching ramification was measured along a randomly selected terminal, leaf bearing branch. Moving from the crown to the base of the plant, branches tend to become thicker and highly branched plants have a higher rate of ramification (Harris & Pannell 2010). From the crown inward, we measured branching length and the respective width for (up to) ten sub-branches along a terminal branch using a digital calliper (Perez-Harguindeguy *et al.* 2013). To quantify a plant's branching ramification, we calculated a "ramification index" according to Harris & Pannell (2010). Specifically, we regressed the cross-sectional area (log-transformed) of a branch segment against the relative branch length from the branch tip. This regression was implemented as a linear mixed-effects model (R package lme4, Bates *et al.* (2015)) with nested random effects of population and plant

individual on the intercept and the slope. This model was used to predict the ramification index of each plant as the individual-level slope prediction.

Finally, resprouting ability was recorded from Rebelo (2001) and defined as the ability of plants to resprout from fire-protected buds, bark or meristems after fire disturbance (Clarke *et al.* 2013). Our study species do not vary intraspecifically in resprouting ability (Rebelo, 2001) hence this trait represents a dichotomous, categorical variable (0: nonsprouter; 1: resprouter).

SEED TRAITS

Seeds are packed with essential proteins and nutrients required for seedling growth and survival (reviewed in Lamont & Groom 2013). For example, seed mass (a proxy of seed size) contain the resources available for early seedling establishment and growth (Westoby 1998; Westoby *et al.* 2002). Seed mass is positively correlated to seedling size and increased rooting depth which implies competitive advantages for larger seedlings and predicts the potential of larger seedlings to survive under stressful environmental conditions (e.g. drought; Lamont & Groom 2013). Furthermore, in nutrient-poor environments the spectrum of seed nutrients, notably nitrogen (N) and phosphorous (P), are critical for growth and development of seedlings (Stock *et al.* 1990; Lamont & Groom 2013). Investing in larger, nutrient-rich seeds promote seedling survival through early root establishment which increases photosynthesis and respiration rates (Milberg & Lamont 1997; Lamont & Groom 2013).

MEASUREMENT OF SEED TRAITS: The 26 study species are serotinous and exclusively form long-lived canopy seed banks (rather than soil-stored seed banks; Treurnicht *et al.* 2016 and references therein). We collected three, intact woody cones (or seed heads) from focal plants to determine the following reproductive traits: seed mass (g), seed nitrogen (N) content and seed N:P ratio. Cones were oven dried (for at least 48 hours at 60°C) and (up to) 20 fertile, plump

and intact seeds were removed from harvested cones. Seeds (including seed coats) were weighed and seed mass (g) was calculated as the total dry seed mass weight divided by the total number of seeds. Seeds were then analysed for total nitrogen (N) and phosphorous (P) content using standardised procedures. Seed N content was measured in a similar manner than leaf N content (see ‘LEAF TRAITS’ section above) whereas seed P content was analysed by means of optical emission spectrometry (ICP-OES; Varian VistaPro) following the VDLUFA Book of Methods Vol.II, 2.2.2.6. (2011)) at the Analytical Chemistry Unit, University of Hohenheim (Stuttgart, Germany). Although P content was measured for samples, we excluded this variable from the analyses since it was highly correlated with both seed mass (-0.65; Spearman correlation coefficient) and seed N (0.74).

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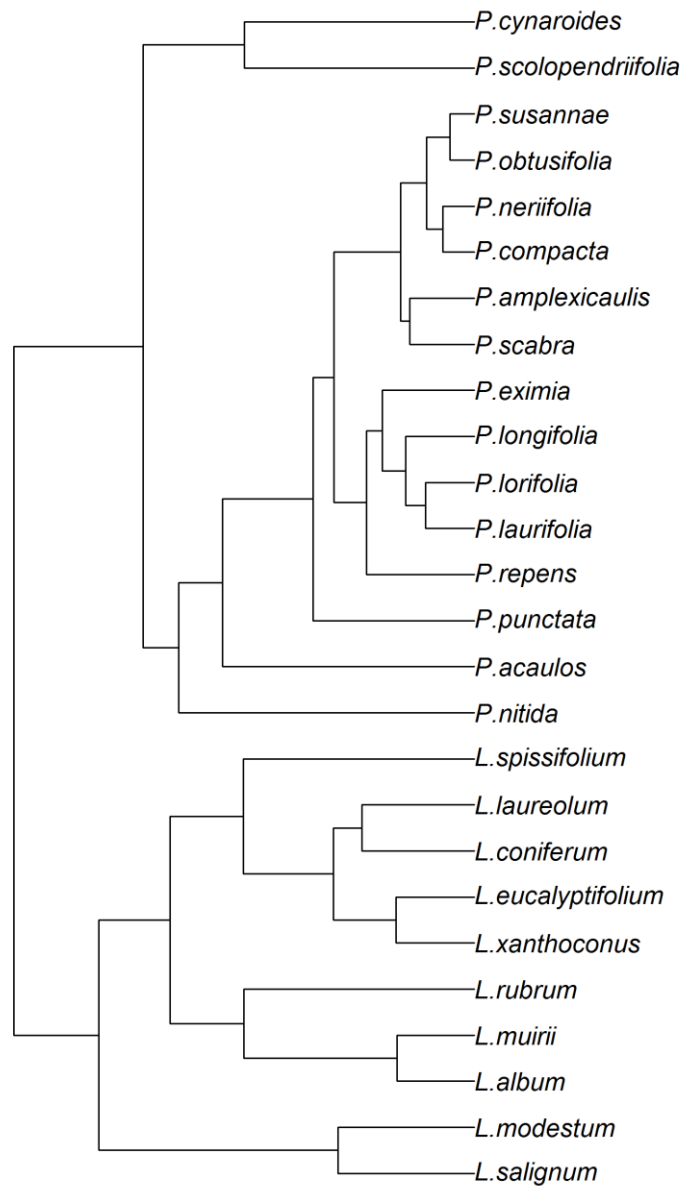


Fig. S3.1. Maximum likelihood phylogeny of the 26 Proteaceae study species, reconstructed from a recent supermatrix (J. Tonnabel, unpublished data).

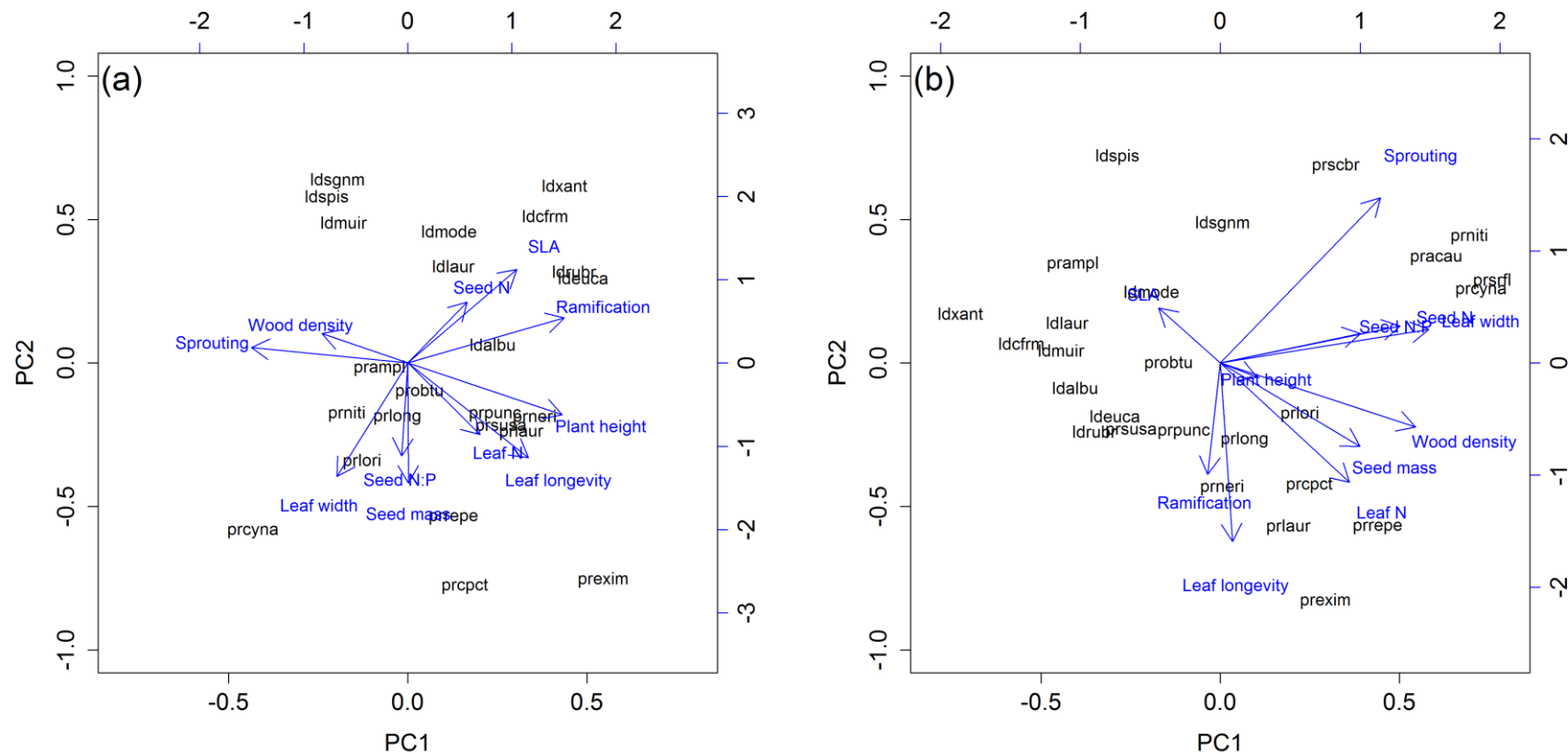


Fig. S3.2. Position of the 26 Proteaceae study species' functional traits (scaled and log-transformed) on the first two axes of a principal component analysis; (a) species-mean trait values explained 52% (PC1 = principal component 1; PC2 = principal component 2; explained 28% and 24%, respectively) of the variance; (b) intraspecific trait variation (calculated as the standard deviations of population-level variation per trait) explained 43% (PC1 = principal component 1; PC2 = principal component 2; explained 25% and 18%, respectively) of the variance. See Methods (main text) for details and Appendix S1 for trait measurement protocols

Fig. S3.3 (continued on next page). Trait variation across the global geographical distributions of the 26 Proteaceae study species in the study region, Cape Floristic Region (South Africa). (A) leaf traits (SLA, leaf width, leaf longevity, leaf N), (B) plant-architectural traits (plant height, wood density, ramification) and (C) seed traits (seed mass, seed N, seed N:P ratio). ‘Sprouting’ not shown since resprouting ability does not vary intraspecifically for our study species (Rebello 2001).

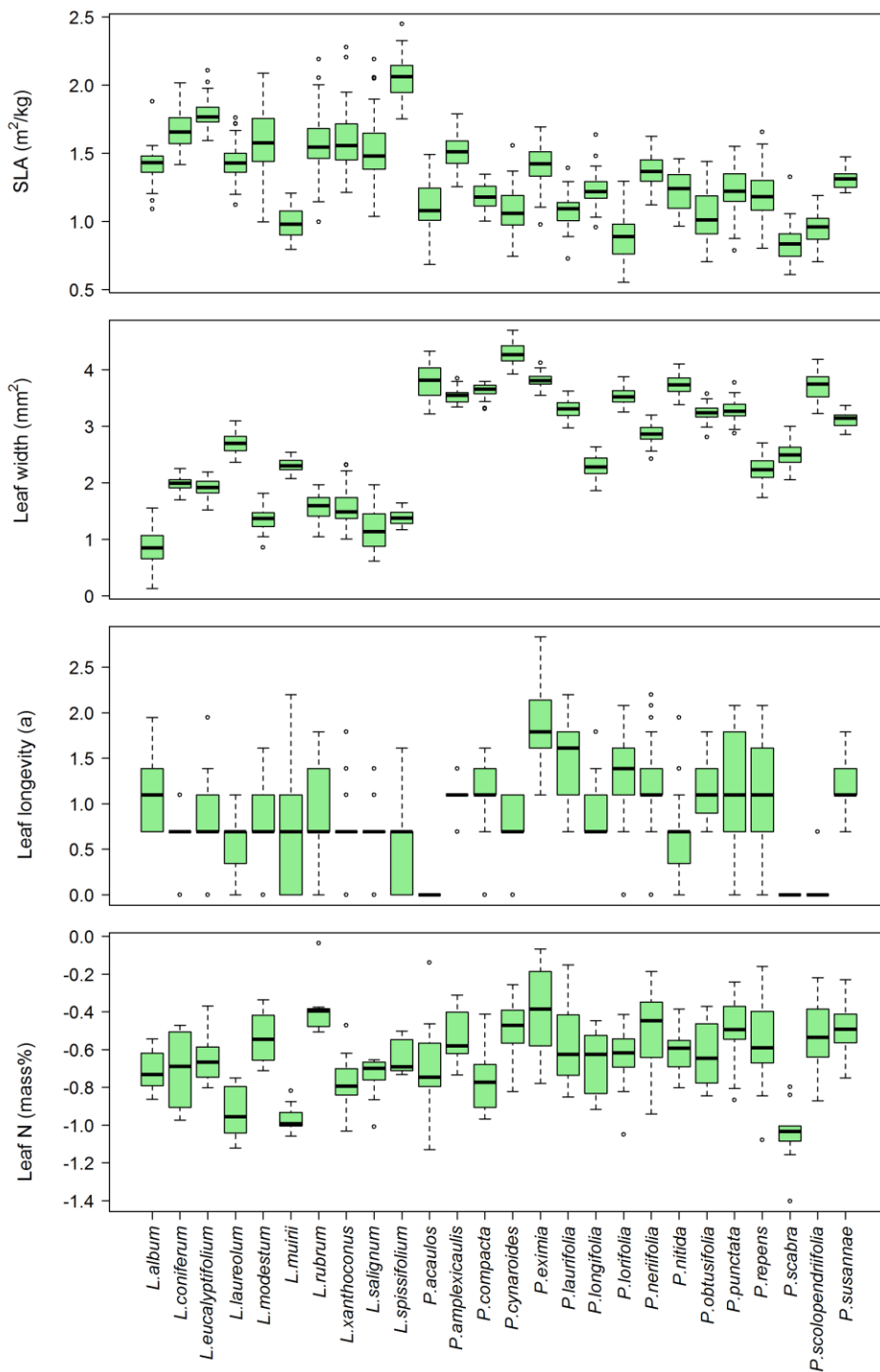


Fig. S3.3 (A)

Fig. S3.3 (continued)

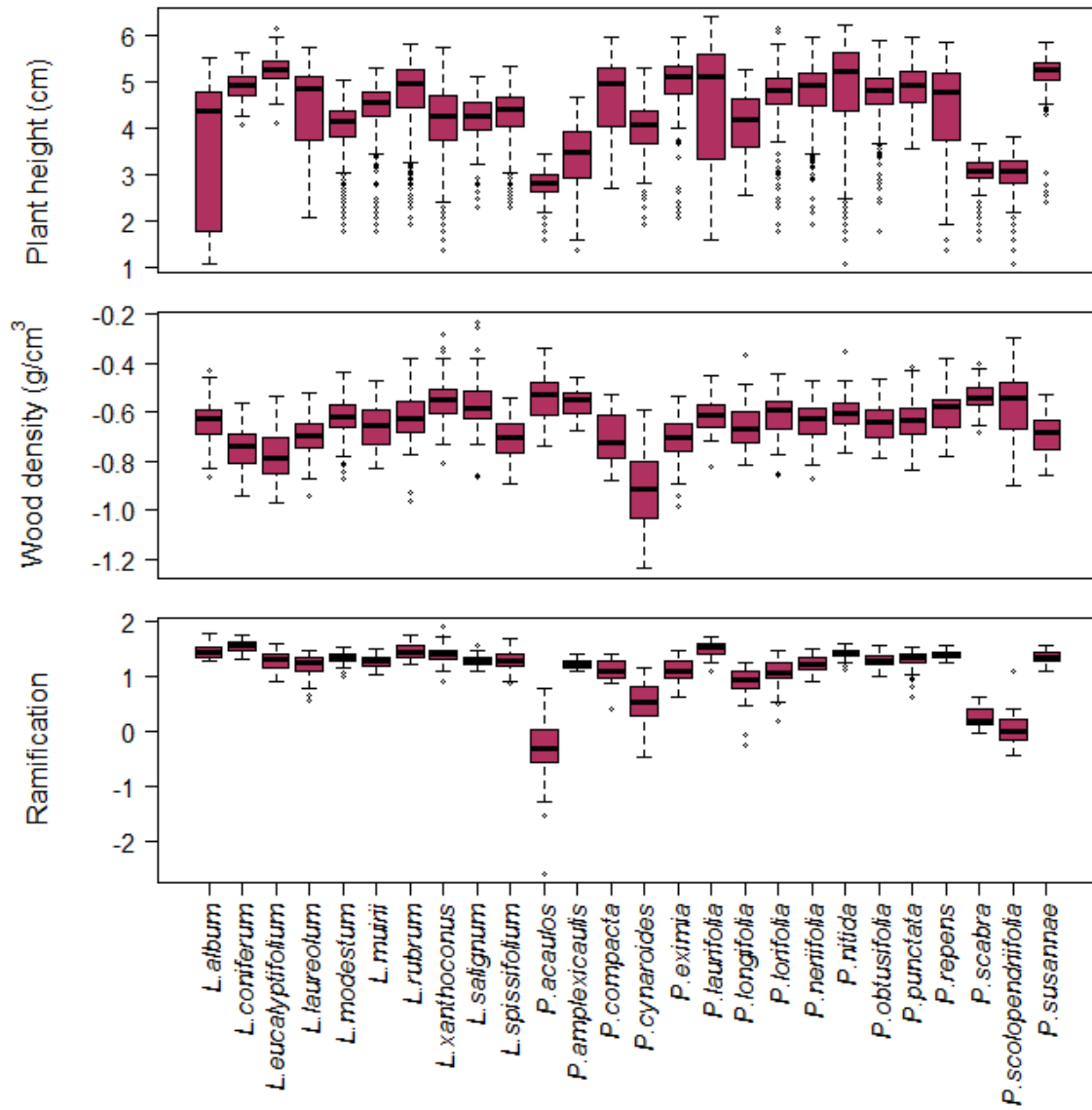


Fig. S3.3 (B)

Fig. S3.3 (continued)

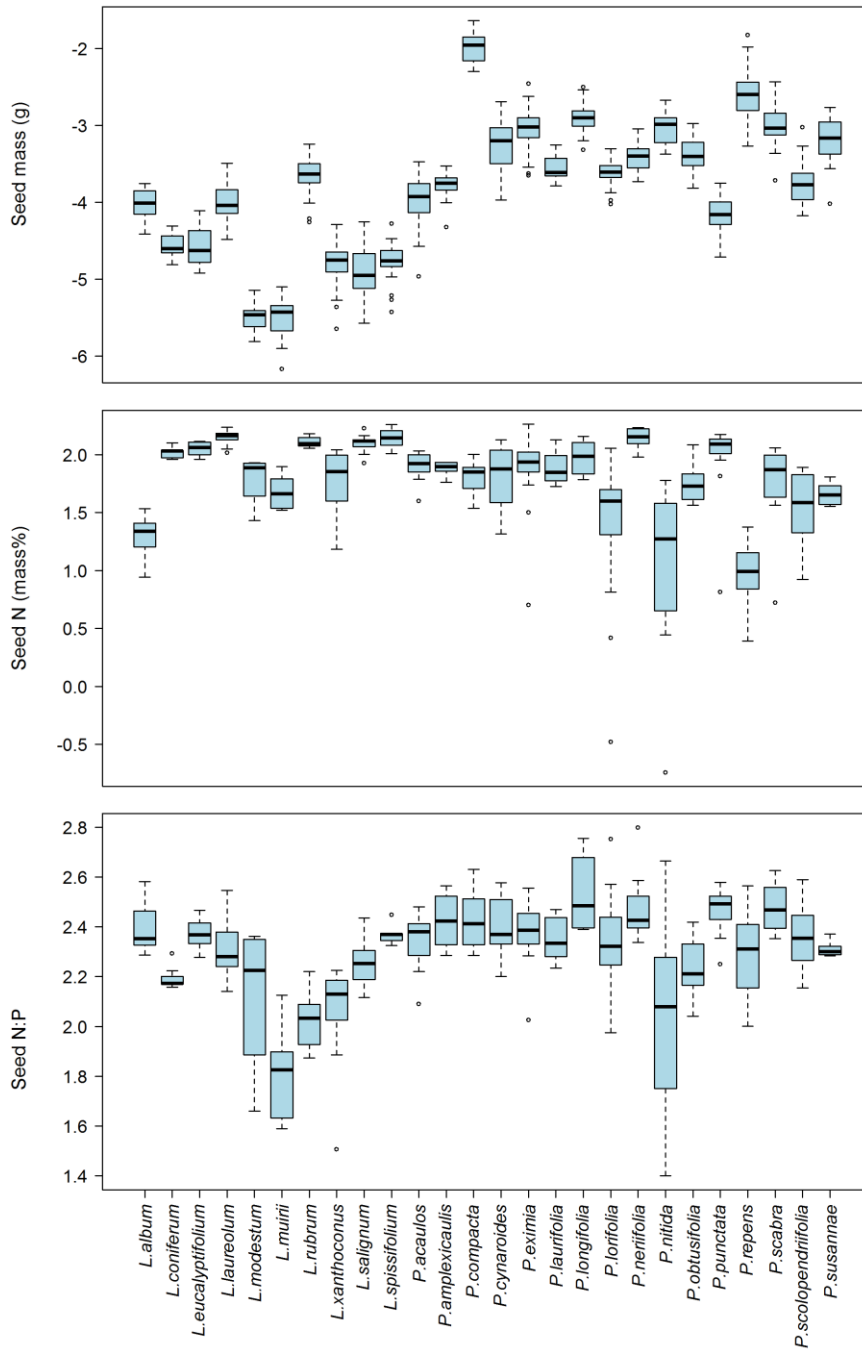


Fig. S3.3(C)

Table S3.1. List of 26 Proteaceae study species with sample size (populations sampled [N], plants sampled per population [n]) and (a) species-mean trait values and (b) intraspecific trait variation (SD: standard deviations of population-level variation per trait) for eleven functional traits (see also Appendix S3.1 TEXT for detailed methods). Trait categories for the measured traits follow major axes of plant specialisation as defined by the LHS-scheme (Westoby 1998); L = leaf traits (green), H = plant-architectural traits (reddish brown) and S = seed traits (light blue)), colour-coded according to Figs 3.4 and 3.5.

Species [¶]	N	n	(a) Species-mean trait values											(b) Intraspecific trait variability										
			L				H				S			L				H				S		
			SLA (m ² /kg ⁻¹)	Leaf width (mm ²)	Leaf longevity (years)	Leaf N (mass %)	Plant height [†] (cm)	Wood density (cm ³)	Ramifi- cation	Sprout- ing	Seed mass (g)	Seed N (mass %)	Seed N:P	SLA (m ² /kg ⁻¹)	Leaf width (mm ²)	Leaf longevity (years)	Leaf N (mass %)	Plant height [†] (cm)	Wood density (cm ³)	Ramifi- cation	Sprout- ing	Seed mass (g)	Seed N (mass %)	Seed N:P
<i>L. album</i>	9	54	4.16	2.45	3.13	0.49	5.17	0.53	4.27	0	0.02	3.64	11.01	0.34	0.47	1.34	0.06	0.34	0.03	0.54	0	0	0.68	1.11
<i>L. coniferum</i>	8	48	5.43	7.33	2.02	0.5	4.89	0.48	4.68	0	0.01	7.52	8.99	0.5	0.31	0.33	0.1	0.23	0.02	0.49	0	0	0.39	0.44
<i>L. eucalyptifolium</i>	8	48	5.98	6.75	2.62	0.53	5.3	0.47	3.61	0	0.01	7.79	10.73	0.18	0.74	0.69	0.08	0.19	0.04	0.59	0	0	0.48	0.65
<i>L. lauroleum</i>	10	60	4.23	15.35	1.88	0.4	5.13	0.5	3.33	0	0.02	8.57	10.14	0.35	2.08	0.37	0.05	0.27	0.02	0.6	0	0	0.56	1.28
<i>L. modestum</i>	9	54	5.09	3.99	2.28	0.59	4.3	0.54	3.78	0	0	6.07	8.62	0.69	0.41	0.82	0.09	0.26	0.02	0.41	0	0	1.28	2.47
<i>L. muirii</i>	9	54	2.68	10.11	2.59	0.38	4.17	0.52	3.54	0	0	5.4	6.25	0.17	0.41	1.47	0.03	0.36	0.02	0.43	0	0	0.8	1.25
<i>L. rubrum</i>	12	72	4.88	4.91	2.72	0.69	5.16	0.54	4.28	0	0.03	8.25	7.6	0.71	0.32	1.09	0.11	0.34	0.04	0.58	0	0	0.36	0.83
<i>L. salignum</i>	13	78	4.94	5.03	2.02	0.47	4.68	0.58	4.13	1	0.01	6.06	7.97	0.82	1.26	0.37	0.08	0.34	0.03	0.65	1	0	1.49	1.4
<i>L. spissifolium</i>	14	81	4.59	3.38	1.99	0.48	4.58	0.57	3.6	1	0.01	8.13	9.71	0.62	1.18	0.54	0.05	0.2	0.02	0.28	1	0	0.71	1.05
<i>L. xanthoconus</i>	10	60	7.85	4.01	1.95	0.53	4.87	0.49	3.7	0	0.01	8.55	10.69	0.7	0.32	0.64	0.05	0.28	0.01	0.62	0	0	0.71	0.41
<i>P. acaulos</i>	11	33	3.08	46.21	1	0.52	2.93	0.58	0.82	1	0.02	6.73	10.46	0.29	13.43	0	0.15	0.16	0.03	0.46	1	0	0.88	1.23
<i>P. amplexicaulis</i>	9	27	4.54	35	3.11	0.59	3.84	0.57	3.41	0	0.02	6.59	11.36	0.56	2.81	0.29	0.09	0.25	0.02	0.26	0	0	0.38	1.21
<i>P. compacta</i>	8	24	3.27	37.61	3.33	0.47	5.42	0.49	3.06	0	0.14	6.11	11.44	0.19	4.51	1.04	0.09	0.29	0.03	0.63	0	0.02	0.96	1.49
<i>P. cynaroides</i>	12	37	3.02	73.92	2.25	0.63	4.47	0.41	1.78	1	0.04	6.28	11.17	0.45	11.5	0.51	0.09	0.22	0.04	0.64	1	0.01	1.6	1.37
<i>P. eximia</i>	17	51	4.15	46.3	7.2	0.68	5.32	0.49	3.07	0	0.05	6.88	10.92	0.47	4.05	2.89	0.16	0.23	0.03	0.64	0	0.01	1.74	1.2
<i>P. laurifolia</i>	9	27	2.98	27.91	4.63	0.58	5.22	0.55	4.46	0	0.03	6.65	10.53	0.41	3.13	1.59	0.14	0.38	0.05	0.6	0	0	0.96	0.95
<i>P. longifolia</i>	10	30	3.47	10.04	2.6	0.52	4.91	0.52	2.32	0	0.06	7.3	12.72	0.32	1.49	0.52	0.08	0.21	0.04	0.83	0	0.01	1.02	1.93
<i>P. lorifolia</i>	17	51	2.44	34.7	4.24	0.53	4.68	0.54	2.93	0	0.03	4.47	10.54	0.37	4.19	1.5	0.08	0.26	0.04	0.67	0	0	1.87	2.02
<i>P. nerifolia</i>	15	45	3.94	17.98	3.91	0.62	5.24	0.53	3.41	0	0.03	8.59	11.98	0.38	2.38	1.77	0.13	0.26	0.04	0.54	0	0	0.7	1.71
<i>P. nitida</i>	10	31	3.44	42.8	2.2	0.55	5.37	0.55	4.12	1	0.05	3.44	8.15	0.44	5.7	1.04	0.07	0.53	0.04	0.4	1	0.01	1.83	3.03
<i>P. obtusifolia</i>	13	39	2.92	25.72	3.26	0.54	4.84	0.53	3.6	0	0.03	5.85	9.42	0.52	2.62	0.89	0.09	0.36	0.03	0.47	0	0	1.03	1.1
<i>P. punctata</i>	21	63	3.45	26.87	3.73	0.62	5.06	0.53	3.68	0	0.02	7.67	11.83	0.42	3.78	1.81	0.09	0.23	0.03	0.57	0	0	1.44	0.9
<i>P. repens</i>	22	66	3.32	9.65	3.82	0.6	5.06	0.56	3.98	0	0.08	2.77	13.04	0.57	2	1.67	0.13	0.36	0.06	0.31	0	0.02	0.68	1.59
<i>P. scabra</i>	9	27	2.35	12.11	1	0.36	3.24	0.58	1.26	1	0.05	5.99	11.96	0.35	2.04	0	0.06	0.19	0.04	0.23	1	0.01	1.89	1.21
<i>P. scolopendriifolia</i>	12	36	2.61	42.53	1.14	0.6	3.23	0.57	1.08	1	0.02	4.82	10.62	0.25	7.8	0.33	0.11	0.32	0.06	0.39	1	0.01	1.43	1.4
<i>P. susannae</i>	8	24	3.73	22.6	3.38	0.62	5.1	0.5	3.85	0	0.04	5.28	10.07	0.21	1.93	0.86	0.1	0.19	0.03	0.47	0	0.01	0.53	0.31

Trait values were obtained from sampling six plants per population for dioecious *Leucadendron* species whereas three plants per population were sampled for *Protea* (see also Appendix S3.1); for one population of *L. spissifolium* only female plants were present. Note that for intraspecific trait variability, we calculated the between-population standard deviation (SD) of each trait.

[¶]L = *Leucadendron*; P = *Protea*; nomenclature follows Rebelo (2001); [†]Plant height on log-scale

Table S3.2. Environmental variables (with abbreviations, explanations, data sources and variation in the study biome) used to define niche characteristics of 26 serotinous Proteaceae species.

Category	Environmental variable	Abbreviations, unit and description	Source	Variation (min-max) per environmental variable [‡]
<i>Climate</i>	Aridity Index	aridity ; aridity index (mm/°C) calculated as the ratio between monthly precipitation (P; mm) and average daily maximum temperature (T; °C) in the month of January: aridity = P/(T + 10)	Schulze (2007) [#] ; De Martonne (1926) [¶]	0.02 - 2.72 (mm/°C)
	Minimum temperature	T_{min} ; mean of daily minimum temperatures in the winter month of July; °C	Schulze (2007)	-3.00 - 9.00 (°C)
	Maximum temperature	T_{max} ; mean of daily maximum temperatures in the summer month of January; °C	Schulze (2007)	18.00 - 33.00 (°C)
<i>Edaphic</i>	Soil fertility (soil nutrient status)	soil fertility ; index ranging from 0 (low fertility) to 10 (high fertility)	Schulze (2007); see also Treurnicht et al. (2016) [†]	0.40 - 5.40 (index)
<i>Fire disturbance</i>	Fire return interval	fire interval ; time since fire (years)	Treurnicht et al. (2016) [†] and references therein.	13.49 - 22.04 (years)

[‡] For the respective environmental variable, the range (min-max) is provided across the study region. See also Table S3.3.

[#] Schulze, R.E. (2007) South African Atlas of Climatology and Agrohydrology, Technical Report 1489/1/06. Water Research Commission, Pretoria, South Africa.

[¶] De Martonne, E. (1926) A new climatological function: the aridity index. *La Météorologie* 2, 449-458 (in French).

[†] Treurnicht, M., Pagel, J., Esler, K.J., Schutte-Vlok, A., Nottebrock, H., Kraaij, T., Rebelo, A.G. & Schurr, F.M. (2016) Environmental drivers of demographic variation across the global geographical range of 26 plant species. *Journal of Ecology*, 104, 331-342.

Table S3.3 (continued on next page). Estimated values of niche characteristics for 26 Proteaceae species, Cape Floristic Region (South Africa). Niches are defined for the global maximum population growth rate (r_{max} ; log-transformed), as well as niche optima and widths along environmental gradients of climate (aridity: aridity index ($\text{mm}/^{\circ}\text{C}$), calculated as the ratio between monthly precipitation (P) and average daily maximum temperature (T) in the summer month of January [(aridity = $P/(T + 10)$]); T_{min} : July mean of minimum temperature ($^{\circ}\text{C}$); T_{max} : January mean of maximum temperature ($^{\circ}\text{C}$); soil fertility (soil nutrient status index, ranging from 0 (low fertility) to 10 (high fertility)) and fire interval (time since last fire; $\log(\text{years})$). See Fig. 3.1 for conceptual diagram of Hutchinsonian niche characteristics, Table S3.2 and Methods (main text) for details on environmental variables. Note that for aridity (expressed as an index), low values represent more arid conditions. However, when reporting parameter estimates for trait effects (see Results), this variable was inverted to describe effects on niche optimum along increasing aridity.

Table S3.3 (continued).

Species ¹	r_{max}	Niche optima					Niche widths				
		aridity (mm/°C)	T _{min} (°C)	T _{max} (°C)	soil fertility (index:0-10)	fire interval (log(years))	aridity (mm/°C)	T _{min} (°C)	T _{max} (°C)	soil fertility (index:0-10)	fire interval (log(years))
<i>L. album</i>	0.77	2.11	-1.73	27.68	2.87	1.69	7.96	7.39	16.83	8.53	2.46
<i>L. coniferum</i>	1.53	0.38	7.08	25.55	5.17	1.17	0.87	7.21	3.34	9.47	2.78
<i>L. eucalyptifolium</i>	0.81	1.52	1.85	26.96	6.46	1.60	8.69	27.87	20.97	9.08	2.51
<i>L. laureolum</i>	1.05	1.05	4.79	20.31	2.82	1.47	7.69	11.26	22.95	9.97	2.71
<i>L. modestum</i>	0.77	0.45	7.20	26.64	4.66	1.71	0.76	3.03	4.27	8.93	2.00
<i>L. muirii</i>	0.79	0.64	6.37	25.98	3.55	2.05	3.48	8.96	5.61	9.33	2.10
<i>L. rubrum</i>	0.65	1.17	7.80	21.94	1.83	1.51	8.26	30.36	22.85	9.97	2.68
<i>L. salignum</i>	0.55	0.13	9.46	26.39	0.49	1.12	5.64	19.01	24.35	9.72	3.47
<i>L. spissifolium</i>	0.84	2.08	1.84	21.59	9.15	1.11	4.84	13.46	21.78	8.00	3.74
<i>L. xanthoconus</i>	0.87	0.65	6.25	22.92	0.64	1.48	2.37	9.27	12.30	9.59	2.74
<i>P. acaulos</i>	0.28	1.32	8.00	24.40	0.54	1.38	6.69	13.64	17.56	6.15	2.85
<i>P. amplexicaulis</i>	0.44	0.51	6.53	22.53	1.89	1.98	1.82	15.17	18.17	9.91	2.50
<i>P. compacta</i>	0.74	0.39	6.92	22.96	1.61	1.86	3.75	4.36	9.00	9.83	1.95
<i>P. cynaroides</i>	0.98	1.49	-0.85	24.14	1.77	1.01	7.52	16.43	24.73	8.64	4.46
<i>P. eximia</i>	0.87	0.59	6.77	25.12	0.36	1.47	7.43	41.20	19.56	4.69	2.76
<i>P. laurifolia</i>	0.80	1.77	3.70	18.70	1.28	1.53	9.73	22.65	29.99	9.94	2.75
<i>P. longifolia</i>	0.54	1.08	5.81	24.82	6.26	1.83	4.34	6.66	10.30	9.96	2.44
<i>P. lorifolia</i>	0.67	3.04	1.06	26.29	1.01	1.71	9.36	16.10	26.60	9.65	2.57
<i>P. neriifolia</i>	0.65	2.33	1.03	20.30	1.40	1.84	9.13	34.11	33.30	9.98	2.54
<i>P. nitida</i>	0.56	0.12	4.90	25.11	2.37	1.47	5.56	20.29	38.10	9.05	3.46
<i>P. obtusifolia</i>	0.62	1.09	6.84	26.20	3.34	1.79	3.86	6.49	15.34	7.67	2.37
<i>P. punctata</i>	0.72	1.07	0.69	22.00	3.80	1.56	4.89	26.75	25.01	8.27	2.44
<i>P. repens</i>	0.42	1.01	9.65	17.92	0.60	1.89	9.56	31.78	41.11	9.99	2.50
<i>P. scabra</i>	0.80	1.51	5.40	27.64	4.40	1.52	4.53	11.94	5.61	9.87	3.10
<i>P. scolopendriifolia</i>	0.79	1.24	2.81	24.83	0.76	1.14	5.04	14.83	11.74	6.61	4.04
<i>P. susannae</i>	0.68	0.56	7.12	23.85	3.49	1.57	3.26	4.26	8.82	5.75	2.42

Table S3.3 (continued)

[¶]L = *Leucadendron*; P = *Protea*; nomenclature follows Rebelo (2001).

[†]Note that for the optimum aridity, low values represent more arid conditions. However, when reporting parameter estimates for trait effects (Results), we inverted this variable; so that trait effects are described along increasing aridity.

Table S3.4. Spearman rank correlation coefficients for eleven functional traits measured from 26 serotinous Proteaceae species: (a) species-mean trait values, (b) intraspecific trait variation (calculated as the standard deviations of population-level variation per trait). See Appendix S3.1 for trait measurement protocols; “Sprouting” (binary variable [0: nonsprouter; 1: resprouter]) was omitted since this trait does not vary intraspecifically for the study species (Rebello 2001).

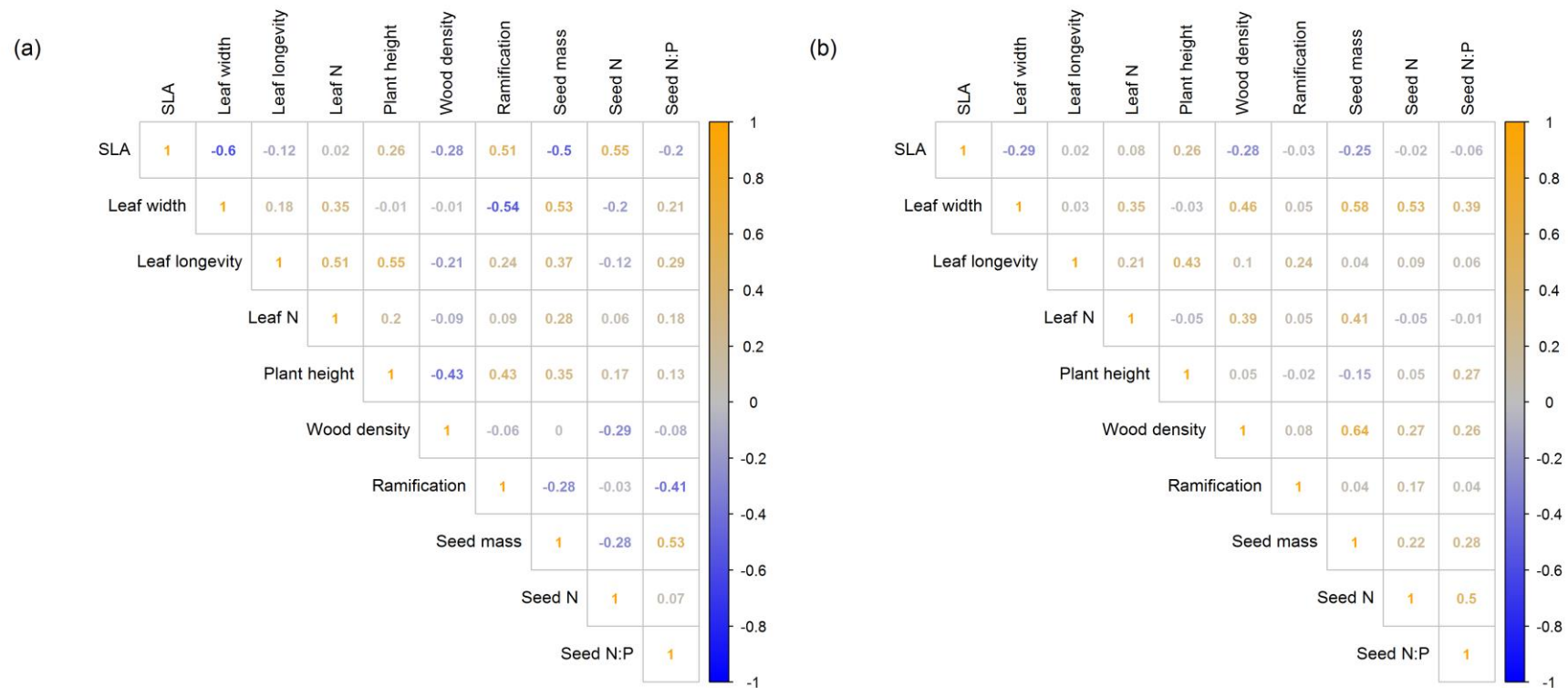


Table S3.5. Eleven functional traits measured for 26 Proteaceae species with interspecific and intraspecific trait variation (expressed as proportion variation [%]; estimated from linear mixed effect models (see also Fig. 3.2b). Details on trait measurements are provided in Appendix S3.1; note that ‘Sprouting’ does not vary within species (Rebello 2001)

Functional trait	Trait name	Unit	Interspecific trait variation	Intraspecific trait variation
Specific leaf area	SLA	m ² /kg	89	11
Leaf width	Leaf width	mm ²	98	2
Leaf longevity	Leaf longevity	years	53	47
Leaf nitrogen (N) content	Leaf N	Mass %	43	57
Plant canopy height	Plant height	cm	77	23
Wood density	Wood density	g/cm ³	77	23
Ramification index	Ramification	--	88	12
Resprouting ability	Sprouting	--	100	0
Seed mass	Seed mass	g	97	3
Seed nitrogen (N) content	Seed N	Mass %	51	49
Seed N:P ratio	Seed N:P	--	54	46

*Inter (between species) and intraspecific (within species) trait variation expressed as proportion trait variation (%), as per Fig. 3.2b (see also Methods)

**Trait names are used in Figs 3.2,3.3 and 3.5, and Table S3.4.

CHAPTER 4

GEOGRAPHICAL VARIATION IN SENSITIVITY TO WILDFLOWER HARVESTING INFERRED FROM RANGE-WIDE DEMOGRAPHIC DATA FOR 26 PROTEACEAE SPECIES

Running title: Geographical variation in sensitivity to wildflower harvesting

Key-words: biogeography, climate, Cape Floristic Region, extinction, fire disturbance, environmental variation, plant conservation, population dynamics, population viability.

Article type: Research Article

This article is in preparation:

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ABSTRACT

1. The ecological effects of harvesting on natural populations are not well understood. Notably, it is largely unknown how populations respond to harvesting across species' geographical distributions. In the Cape Floristic Region (CFR, South Africa) biodiversity hotspot, Proteaceae wildflower harvesting is a widespread and economically important activity. However, there is little information on which to base sustainable harvesting guidelines, with very few species studied and without considering how populations may vary in response to harvesting across species' geographical distributions.

2. We study geographical variation in sensitivity to wildflower harvesting for 26 serotinous Proteaceae in the CFR. Specifically, we use large-scale demographic data (spanning 3454 population-level records of fecundity, seedling recruitment and fire survival) to parameterize dynamic population models and simulate the effects of harvesting across species' ranges and environmental gradients (climate, soil nutrient status and fire disturbance).

3. We perform extinction risk simulations to predict the population-level intrinsic mean time to extinction and then derive probability of extinction over a 100-year (P_{100}) timeframe to evaluate persistence and viability in response to 0% and 50% harvesting. We then examine how these responses of P_{100} to harvesting vary within and between species to quantify intra- and interspecific variation in sensitivity to harvesting. We further identify geographical areas most sensitive to harvesting and, finally, assess whether such sensitivity is driven by environmental variation.

4. Harvesting generally reduced the future population persistence across species' geographical ranges. We detected considerable intra- and interspecific variation in sensitivity to harvesting across the 26 study species. Range-wide intraspecific variation in sensitivity to harvesting showed distinct geographical patterns with high sensitivity at range edges. Sensitivity to

harvesting was also driven by large-scale environmental variation with high sensitivity towards the climatic extremes of species' ranges.

5. Synthesis and applications: Few studies have been able to assess intra- and interspecific variation in sensitivity to harvesting across the geographical distributions of a broad range of species. This work shows the importance of considering range-wide demographic variation, density-dependent population dynamics and environmental variation when assessing sensitivity to harvesting at region-wide scales. Our findings caution against the application of general management guidelines irrespective of species, location or environmental conditions. Our study is useful to refine species-specific, locally and regionally adapted harvesting guidelines, and to identify areas for monitoring to prevent the overexploitation of populations and species.

INTRODUCTION

Understanding the impacts of harvesting on wild populations is central to population biology and conservation management (Beissinger & Westphal 1998; Ticktin 2004; Allendorf *et al.* 2008). This is an increasingly important research agenda in the face of progressing climate change threatening the future persistence of many species (Brook, Sodhi & Bradshaw 2008; Butchart *et al.* 2010; Pimm *et al.* 2014). Harvesting directly affects species' abundance, population dynamics and persistence (Lamont *et al.* 2001; Peres *et al.* 2003; Ticktin 2004; Ghimire *et al.* 2008), causing local population extinctions in extreme cases (e.g. Nantel, Gagnon & Nault 1996; Brook, Sodhi & Bradshaw 2008). However, the effects of harvesting on the population persistence and viability of multiple species and their geographical distributions are currently not well studied (but see Peres *et al.* 2003). From a population ecology perspective, demographic rates of survival and reproduction are known to vary considerably among populations and species in response to large-scale environmental variation (Merow *et al.* 2014; Treurnicht *et al.* 2016, Chapter 2 of this dissertation). Given such inter- and intraspecific variation in demography across the geographical distributions of species, it can reasonably be postulated that species and populations will also respond differentially to harvesting across their ranges. Developing a more refined understanding of the impacts of harvesting on the persistence of populations across multiple species and their geographical ranges is globally recognised as a prerequisite for the sustainable management of species and entire ecosystems (Ticktin *et al.* 2002; Ticktin 2004; Frederiksen *et al.* 2014).

Large-scale monitoring or experimental data that assess the effects of harvesting (e.g. extensive repeated, multigenerational experiments) on population persistence and viability of species are sparse and rarely feasible to obtain across species' geographical distributions. Hence, conservation biologists widely rely on existing data and population viability analysis (PVA) to

extrapolate and evaluate the future status of species (Beissinger & Westphal 1998; Morris & Doak 2002). For example, combining range-wide abundance data and demographic measurements with simulations of population viability have provided valuable insights on the future of plant populations in response to harvesting (e.g. Peres *et al.* 2003; Cabral *et al.* 2011). From a population ecology perspective, population viability depends on demographic rates of reproduction and survival but vary across populations, different environments and are influenced by density dependence (e.g. Beissinger & Westphal 1998; Freckleton *et al.* 2003; Treurnicht *et al.* 2016, Chapter 2). Such a joint consideration of species' ecology, demographic processes and the environmental context is a prerequisite for effective conservation management (Crone *et al.* 2011; Mandle & Ticktin 2012). However, few studies have been able to integrate these aspects across species' geographical distributions when studying the large-scale impacts of harvesting. We address these shortcomings by using comprehensive demographic data, spanning the global geographical ranges of species (Treurnicht *et al.* 2016, Chapter 2), and population models that integrate environmental variation and intraspecific density dependence to investigate spatial variation in sensitivity to harvesting for 26 serotinous Proteaceae species in the Cape Floristic Region (CFR, South Africa).

Proteaceae are a characteristic family of mostly overstorey woody shrubs that contribute significantly to the CFR's plant diversity (Manning & Goldblatt 2012). Harvesting flowering material and stems of Proteaceae from natural populations (wildflower harvesting) is an important economic activity in the Cape Floristic Region (Turpie, Heydenrych & Lamberth 2003; Van Wilgen *et al.* 2016). Many of these Proteaceae are serotinous (=bradysporous) and follow a fire-driven life cycle. These species accumulate long-lived canopy seed banks until fire occurs (Bond, Vlok & Viviers 1984; Lamont *et al.* 1991). Fire kills adult plants, triggers seed release and dispersal from fire-protected cones and populations regenerate and establish

depending on the availability of seeds (Lamont *et al.* 1991; Bond & Van Wilgen 1996). Consequently, these species may be vulnerable to harvesting since a single harvesting event can significantly reduce lifetime fecundity (Mustart & Cowling 1992; Maze & Bond 1996; Lamont *et al.* 2001; Cabral *et al.* 2011). To safeguard species against overexploitation a regional conservation guideline, initially formulated by Van Wilgen & Lamb (1986), recommended that at least 50% of flowers should remain on plants after harvesting (reviewed in Van Wilgen *et al.* 2016). Local-scale experimental studies have shown that this harvesting rate can compromise canopy seedbank dynamics and post-fire seedling recruitment (Mustart & Cowling 1992; Maze & Bond 1996). However, the challenge of performing such experiments across the geographical distributions of multiple species limits generalisation on the impacts of harvesting across species' and geographical locations. Resolving this is important, since an insufficient understanding of the effects of harvesting could limit the possibility to derive locally and regionally adapted management guidelines in the CFR, thereby jeopardising a sustainable resource base for the wildflower industry (Turpie, Heydenrych & Lamberth 2003; Pressey *et al.* 2007; Van Wilgen *et al.* 2016).

In this study, we investigate the ecological impacts of wildflower harvesting on species population dynamics. Specifically, we examine spatial variation in sensitivity to wildflower harvesting for 26 serotinous Proteaceae species across their geographical distributions. We conduct extinction risk analyses using range-wide demographic data (Treurnicht *et al.* 2016, Chapter 2) to parameterise dynamic population models. The extinction analyses then simulate the effects of 0% and 50% harvesting, respectively, on future population persistence as a function of multiple environmental variables. To evaluate persistence and viability of populations (i.e. sensitivity), we compare the population-level probability of extinction over a 100-year timeframe (P_{100}) in response to harvesting. The general aim of our study was to

investigate inter- and intraspecific variation in sensitivity to harvesting across the geographical ranges of the 26 study species. From an applied perspective, this should guide current harvesting practices to prevent the overexploitation of species. Additionally, this may provide an understanding of how demographic variation affects sensitivity to harvesting across species' ranges. Our specific objectives were to assess: (1) interspecific variation in sensitivity to harvesting across our study species, (2) intraspecific variation in sensitivity to harvesting and identify areas across the geographical distribution of each species where populations are more sensitive to harvesting, and (3) whether sensitivity to harvesting is associated with large-scale environmental variation of the study region.

MATERIALS AND METHODS

Study region and study species

The Cape Floristic Region (CFR), a global biodiversity hotspot of conservation priority (Myers *et al.* 2000), is characterised by a Mediterranean-type climate, high topographic and environmental variation with predominantly nutrient-poor soils (Allsopp, Colville, Verboom 2014). The CFR is a fire-prone region where many species depend on periodic fires that occur on average every 10 – 21 years (Kraaij & Van Wilgen 2014) and burn most aboveground biomass (Bond & Van Wilgen 1996). Our study focuses on 26 serotinous (=bradysporous) Proteaceae species from two genera, *Leucadendron* and *Protea* (Rebelo 2001), with varying geographical distributions but endemic to the CFR (Rebelo 2001). The study species included opposing life history types of nonsprouters (n=19) and resprouters (n=7). Resprouters are able to recover from fire due to having fire-protected buds or underground meristems, whereas nonsprouters lack such traits and are fire-killed (Clarke *et al.* 2013).

A stochastic model of population dynamics

In order to investigate effects of harvesting on population viability, we developed a stochastic simulation model that describes how local population dynamics of serotinous Proteaceae are driven by abiotic environmental variation, fire return interval, density-dependent demographic rates and harvesting impacts. The simulation model was parameterised from demographic data that describe range-wide variation in adult fecundity, per capita seedling recruitment and adult fire survival for all study species (Treurnicht *et al.* 2016, Chapter 2). The model simulates density-dependent dynamics of a single population (in an area of size A). According to the fire-dependent life cycle of the study species, it describes the change in population size N in time steps of one fire return interval. Hence, the new population size after one time step (fire return interval of length T) consists of the surviving pre-fire adults (*Survivors*) and newly established post-fire recruits (*Recruits*):

$$N_{t+T} = \text{Survivors}_t + \text{Recruits}_t$$

The changes in population size are driven by three key demographic rates: (i) the fire survival rate ($\pi.\text{surv}$) that gives the probability for each individual to survive a fire, (ii) the total fecundity ($\mu.\text{fec}$) as the average number of fertile seeds in an individual's canopy seed bank at the time of fire, and (iii) a per-seed establishment rate ($\pi.\text{recr}$). These demographic rates vary as functions of a combination of environmental conditions (\mathbf{X}), the stand age at the time of fire (i.e. fire return interval T) and population density ($D_t = N_t/A$). Furthermore, the simulation model accounts for stochasticity in each demographic process.

For each time step, the number of fire surviving adults is drawn from a binomial distribution with a probability parameter $\pi.\text{surv}(\mathbf{X}, T, D_t)$:

$$\text{Survivors}_t \sim \text{Binomial}(N_t, \pi.\text{surv}(\mathbf{X}, T, D_t))$$

The generation of new recruits depends on total seed production and seed establishment. The total number of seeds in the population's canopy seed bank is drawn from a Poisson distribution, where the mean λ_t is a product of the per-individual fecundity $\mu.fec(\mathbf{X}, T, D_t)$ and the number of pre-fire parents (adjusted by the sex ratio $p.fem$ in the case of dioecious *Leucadendron* species):

$$Seeds_t \sim Poisson(\lambda_t)$$

$$\lambda_t = N_t \cdot p.fem \cdot \mu.fec(\mathbf{X}, T, D_t)$$

Flower harvesting is implemented as a proportional reduction of the canopy seed bank by a harvesting rate f_H :

$$Seeds.act_t = Seeds_t \cdot (1 - f_H)$$

Remaining seeds can then establish as new recruits with a probability described by the establishment rate $\pi.recr(\mathbf{X}, SD_t, AD_t)$:

$$Recruits_t \sim Binomial(Seeds.act_t, \pi.recr(\mathbf{X}, SD_t, AD_t))$$

In contrast to survival and fecundity, seed establishment rates are not affected by the density of pre-fire adults, but by the density of available seeds ($SD_t = Seeds.act_t/A$) and the density of surviving adults ($AD_t = Survivors_t/A$).

To parameterise the model for the 26 study species, we use species-specific estimates for the functional responses of the demographic rates ($\pi.surv$, $\mu.fec$, $\pi.recr$) to population density, fire return interval and environmental covariates. For the latter, we specifically considered demographic responses to three climate variables and soil nutrient status (Schulze 2007). Climate variables included: (i) summer aridity index (mm/°C; the ratio between monthly

Chapter 4 – Geographical variation in sensitivity to wildflower harvesting

precipitation and average daily maximum temperature in the month of January), (ii) winter minimum temperature (°C; the mean of daily minimum temperatures in the month of July), and (iii) summer maximum temperature (°C; the mean of daily maximum temperatures in the month of January). A complete description of these variables can be found in Table S3.2 (cf. Chapter 3 of this dissertation). Parameters of these response functions were estimated by integrating demographic data on variation in fecundity, recruitment and adult fire survival across each species' geographical distribution (Treurnicht *et al.* 2016, see Chapter 2) in an hierarchical statistical modelling approach (see Appendix A for details on parameter estimation and the functional form of demographic responses).

Simulation experiments to quantify variation in sensitivity to harvesting

We investigated inter- and intraspecific variation in sensitivity to harvesting in simulation experiments that cover the geographical distributions of the 26 study species. For each species, we identified all grid cells (1'×1') across the CFR in which the species is known to occur (Protea Atlas Project, Rebelo 2001). We simulated the dynamics of one representative population per grid cell, parameterizing the simulation model with the local values of the environmental covariates. For each of these populations, we estimated extinction risks from 10 000 replicated simulations for scenarios of no harvesting ($f_H = 0$) and 50% harvesting ($f_H = 0.5$), respectively. Each simulation was initialised with a population size of $N_0 = 1000$ individuals in an area of $A = 10\,000\text{ m}^2$. For every consecutive time step, the length of the fire return interval (T) was drawn from a Weibull distribution that describes the local distribution of fire return intervals (from a data-driven model of geographical variation in fire return intervals; Wilson, Latimer & Silander 2015) and the population size was updated as described above. The model ran over a maximum time horizon (T_{\max}) of 100 000 years or until an extinction ($N_t = 0$) occurred.

From the recorded extinction times in the 10 000 replicates (per species, population and harvesting scenario) we calculated the intrinsic mean time to extinction T_m (following Grimm & Wissel 2004). T_m is a fundamental measure, complementary to extinction risks, for the viability of an established population and is independent of initial population size N_0 (Grimm & Wissel 2004). T_m can then be used to derive an extinction probability (P_t) over any given time horizon (t). In particular, we derive probability of extinction over a 100-year timeframe, calculated as: $P_{100} = 1 - \exp(-100/T_m)$. This follows the general timeframe threshold of the International Union for Conservation of Nature and Natural Resources (method E. Quantitative Analysis; IUCN 2001). Figure 4.1 provides exemplary results of the simulation model (for 10 replications) showing T_m and P_{100} for one population of *Protea repens* subjected to 0% and 50% harvesting, respectively.

Quantifying inter- and intraspecific variation in sensitivity to harvesting

To assess interspecific variation in sensitivity to harvesting across our study species (objective 1), we summarised the percentage of populations that correspond to different ‘extinction risk categories’ under the two harvesting scenarios for each species. We categorised population-level extinction risk as LOW ($P_{100} > 0.1$), INTERMEDIATE ($P_{100} > 0.2$) or HIGH ($P_{100} > 0.5$), which corresponds to the extinction risk categories (“VU”, “EN”, “CR”) of the IUCN (method E. Quantitative Analysis; IUCN 2001). Per species, sensitivity to harvesting is then summarised as the proportion of populations that shift to a higher extinction risk category when harvested.

To assess intraspecific variation in sensitivity to harvesting and to identify areas across the geographical distribution of each study species where populations are more sensitive to harvesting (objective 2), we compared P_{100} (0%) and P_{100} (50%) across the different populations per species. Specifically, we calculated the absolute change in extinction probability (P_{abs}) as

the difference between the two harvesting scenarios: $P_{\text{abs}} = P_{100}(50\%) - P_{100}(0\%)$. This follows the definition of Morris & Doak (2002) to evaluate sensitivity across multiple populations from population viability and extinction risk analyses. To identify areas that are likely more sensitive to harvesting across the range of a species, we then highlight the $1' \times 1'$ grid cells where $P_{\text{abs}} > 0.1$.

Finally, to investigate the relationship between sensitivity to harvesting (P_{abs}) and environmental variation (objective 3), we fitted linear regressions that describe the response of P_{abs} (log-transformed) to climate variables (summer aridity index, winter minimum temperature, summer maximum temperature), soil nutrient status and fire return interval. All environmental variables were scaled and centred to ensure comparability across variables and species. We included both linear and quadratic terms in the maximal models to allow for the possibility of monotonic or unimodal response curves to environmental variation. We used automated model selection (R package MuMIn; Barton 2015) among all combinations of explanatory variables. The best model for each species, was determined by the lowest sample size corrected Akaike's information criterion (AICc; Burnham & Anderson 2002). We evaluated these best models to show the response of P_{abs} to environmental variation across the study region and summarised these relationships across all study species. The shape of an environmental response (positive, negative, unimodal [negative quadratic] or u-shaped [positive quadratic] effects) was determined from whether the coefficient matrix of each best model contained a quadratic effect of an environmental variable and from the sign of the coefficients. All analyses were performed in R version 3.3.3 (R Core Team 2017).

RESULTS

Harvesting generally reduced population viability and increased the number of populations at risk of extinction across our 26 study species (Figs 4.2 and S4.1). Responses of P_{100} to harvesting varied greatly within and between species (Figs 4.2 and 4.3). We detected varying degrees of intraspecific variation in sensitivity to wildflower harvesting across species' geographical ranges. For example, *Leucadendron rubrum* showed generally low extinction risks irrespective of harvesting (99% of populations in bottom-left quadrat) whereas *L. xanthoconus* and *L. coniferum* showed more intraspecific variation (Fig. 4.2). In addition, *L. coniferum* had a high proportion of populations (27%) at high risk of extinction even without harvesting (top-right quadrat; Fig. 4.2). Overall, we found substantial intraspecific variation and a high proportion of populations at high risk of extinction for many species (e.g. INT and HIGH risk categories in Fig. S4.1). For nonsprouters (n=19), we detected both low and high intraspecific variation in sensitivity to harvesting. Notably, some species had a substantial proportion of populations at very high risk of extinction under 0% harvesting (*L. album*, *L. coniferum*, *L. modestum*, *P. amplexicaulos*, *P. compacta*, *P. lorifolia*, *P. punctata*; i.e. >10% in top-right quadrats of Fig. S4.1). Other nonsprouters generally showed less intraspecific variation with most populations at low risk of extinction (*L. eucalyptifolium*, *L. rubrum*, *P. laurifolia*, *P. neriifolia*, *P. repens*; i.e. >99% of populations in bottom-left quadrat of Fig. S4.1). Although some resprouters (n=7) showed a moderate degree of intraspecific variation (e.g. *L. salignum* and *L. spissifolium*), they generally had a lower (<10%) proportion of populations at high risk of extinction compared to nonsprouters (Fig. S4.1). There was substantial interspecific variation in sensitivity to harvesting among the 26 study species (Fig. 4.3). The mean proportion of populations that shifted to a higher extinction risk category was low (12%), but some species had a high proportion of populations for which extinction risk increased substantially under harvesting (>35% for *L. xanthoconus*, *P. amplexicaulis*, *P. compacta* and *P. eximia*; Fig 4.3).

Sensitivity to harvesting showed distinct geographical patterns across the ranges of our study species and the study biome (Figs 4.4 and S4.2). Sensitivity to harvesting was often high along geographical range edges and areas of high sensitivity tended to cluster in the north-western part of the study biome, notably for species with large geographical distributions (e.g. *L. rubrum*, *P. repens* in Fig 4.4; see Table S4.1 for range size). In contrast, other species were more sensitive to harvesting in the central and eastern parts of their geographical range (e.g. *L. xanthoconus*, Fig. 4.4; *P. eximia*, Fig. S4.2) while some species showed no distinct geographical pattern (e.g. *L. album*; Fig S4.2). Sensitivity to harvesting was often driven by environmental variation across the study region and responses were largely u-shaped with sensitivity increasing towards the environmental extremes of species' geographical ranges. These responses were particularly common for climate variables (Fig. 4.5; see also Table S4.1).

DISCUSSION

We used data-driven population viability analyses to assess spatial variation in wildflower harvesting across the global geographical distributions of 26 serotinous Proteaceae species. We found that harvesting 50% of the seed crop compromised population viability and increased the extinction risk of populations. We detected considerable spatial variation in sensitivity to harvesting across species' geographical distributions (Figs 4.2-4.4) with a large degree of intra- and interspecific variation in sensitivity, notably for nonsprouters (Figs 4.2, 4.3 and S4.1). Range-wide intraspecific variation in sensitivity to harvesting was associated with large-scale environmental variation (Fig. 4.5). The predominantly u-shaped responses that we found show that populations at the periphery or environmental extremes are more sensitive to harvesting than populations in more optimal environments across the range. Our study presents a case study demonstrating the importance of combining large-scale demographic data and

environmental variation when studying the ecological impacts of harvesting across species' geographical ranges.

Our study greatly extends the taxonomic and geographical scale of previous investigations that assessed the sensitivity of plant species to harvesting. The high sensitivity to harvesting of certain species generally concurs with previous studies that focused on some of these species (Mustart & Cowling, 1992; Maze & Bond 1996; Cabral *et al.* 2011). The high differentiation in sensitivity to harvesting that we detected among species and populations (Fig. 4.2, 4.3, S4.1) provides evidence for range-wide variation in seed-limitation (Maze & Bond 1996). High sensitivity to harvesting notably arises from seed-limitation (i.e. an insufficient seed crop to promote recruitment owing to low seed production; Nathan & Muller-Landau 2000). For example, at high population densities, fewer flowers are produced due to overcrowding which limits total seed production (Maze & Bond 1996). Low sensitivity to harvesting suggests that certain species can sustain substantial amounts of seed removal (as found for *P. neriifolia* which can tolerate 85% flower removal; Maze & Bond 1996). The indifferent responses to harvesting that we found were particularly apparent for nonsprouters with large geographical ranges (*L. rubrum*, *P. repens* and *P. neriifolia*) indicating consistent seed-saturation across the ranges of these species. Seed saturation occurs if successful germination and recruitment are limited more by post-fire habitat conditions than by the availability of seeds (Lamont, Witkowski & Enright 1993).

The high degree of intraspecific variation in sensitivity to harvesting across species ranges ultimately results from intraspecific variation in key demographic rates of reproduction and survival (Treurnicht *et al.* 2016, Chapter 2). Moreover, the varying degrees of intraspecific variation in sensitivity that we detected may arise from 'demographic compensation', i.e.

alternating responses of individual demographic rates to spatial or environmental gradients, a phenomenon known to determine species' range sizes (Doak & Morris 2010; Villellas *et al.* 2015). Demographic compensation reduces variation in population growth. However, this may not necessarily reduce variation in seed limitation and sensitivity to harvesting. In fact, variation in harvesting sensitivity should increase when demographic compensation results from opposing environmental responses of fecundity (seed production) and per-seed recruitment probability. High sensitivity to harvesting may arise when fecundity is low and recruitment probability is high, whereas populations with high fecundity and low recruitment should be more insensitive to harvesting.

The population-level responses of sensitivity to harvesting are shaped by geographical location and environmental variation, which provide insights for understanding the ecological process that drive variation in sensitivity across geographical ranges. The distinct geographical patterns of high sensitivity at range edges (e.g. *L. rubrum*, *P. repens* in Fig. 4.4) can be explained by the fact that range limits often coincide with climatic niche limits which constrain individual growth and reproduction (Holt 2003; Sexton *et al.* 2009). Species with more restricted ranges showed an opposite pattern of higher sensitivity to harvesting in the centre of their geographical distributions (e.g. *L. xanthoconus*, Fig. 4.4; *L. modestum*, Fig. S4.2). These species may already experience climatic limits throughout their relatively small geographical distributions. In turn, some species had nearly uniform sensitivity across their ranges. Notably, high-altitude occurring species had >10% of their populations at high risk of extinction even under 0% harvesting (e.g. *L. album*, *P. punctata*; Fig. 4.4c, S4.1). These high-altitude species are likely more constrained across their range by slow growth associated with short growing seasons, harsh climatic conditions and specific germination requirements needed for recruitment (e.g. Mustart *et al.* 2012; Treurnicht *et al.* 2016, Chapter 2). Overall, resprouters were less sensitive

to harvesting (Fig. S4.2) explained by their ability to establish persistent adults and therefore being less seed limited (Bond & Midgley 2001; Higgins, Flores & Schurr 2008). Interestingly, one resprouter (*L. salignum*) was sensitive to harvesting throughout a large part of its range (Fig. S4.2) likely owing to the slightly lower fire survival rates observed for this species (Treurnicht *et al.* 2016, Chapter 2).

In light of the fire-driven life cycle of our study species (e.g. Treurnicht *et al.* 2016, Chapter 2), we implemented the effect of harvesting as a proportional reduction of seeds in species' canopy seedbanks. There are, however, ample opportunities for further studies of harvesting impacts. For example, extensive, multigenerational experiments across species' geographical distributions could help to reduce uncertainty on the impacts of harvesting (Ticktin 2004). Wildflower harvesting is also spatially and temporally heterogeneous which may alleviate the impact of harvesting on population dynamics at large spatial extents (Freckleton *et al.* 2003), while certain Proteaceae species may compensate for flower removal by reallocating resources to increase seed production in remaining inflorescences (Stock *et al.* 1989). Once these factors are included in long-term monitoring protocols it will be possible to include these factors when studying harvesting impacts on future population persistence. Furthermore, harvesting guidelines suggest no harvesting in young and juvenile stands until at least 50% of plants have flowered, while no harvest is recommended one year before a scheduled burn to allow accumulation of seedbanks (Van Wilgen & Lamb 1986; Mustart & Cowling 1992). However, burning usually happens when stands are older and more prone to senescence. The "resting" of these stands may thus contribute insignificantly to seed crops (>15 years; Treurnicht *et al.* 2016, Chapter 2). Finally, future studies should consider the spatial scaling of harvesting impacts since metapopulation structure may be more affected by seed crop harvesting via effects on long distance dispersal and recolonization ability (Cabral *et al.* 2011). Our study is

complementary to such spatially-explicit models. To consider both local and metapopulation approaches would provide future directions for understanding the effects of harvesting at large spatial extents.

A key goal of demographic analyses is to understand harvesting impacts by evaluating population persistence across geographical extents and multiple species to inform conservation management (Ticktin 2004; Crone *et al.* 2013; Frederiksen *et al.* 2014). Our range-wide approach provides an opportunity to develop species- and region-specific priorities for management. The differentiated responses of sensitivity to harvesting, often associated with geographical and climate niche limits (e.g. Fig. 4.3-4.5), caution against the application of uniform management guidelines across species' ranges. In particular, range-restricted species had a large proportion of populations at high risk of extinction without harvesting and were more vulnerable to harvesting (e.g. *L. modestum*; *P. compacta*; Figs S4.2, 4.3). These findings are congruent with the species' current endangerment status (Raimondo *et al.* 2009) and climate change is expected to impact significantly on the range sizes of these particular species (e.g. Cabral *et al.* 2013). For these species close monitoring is needed, especially since they contribute substantially to the economic market (D'Alton *et al.* 2015). To inform long-term experiments on harvesting impacts, we have identified areas where the 26 study species are likely more vulnerable to harvesting (Fig. S4.3). Overall, the differentiated intra- and interspecific responses that we found imply that generalisation on the impacts of harvesting may be challenging, but it is this level of understanding that is important for conservation (Hampe & Petit 2005) as "early-detection" tools for systematic conservation planning (Pressey *et al.* 2007; McIntosh *et al.* 2017). Applying large-scale demographic analyses to model organisms for biodiversity research is also increasingly recognised owing to ongoing global change (Schurr *et al.* 2012; Forest 2017).

Global change is a major driver of population declines, biodiversity loss and species range shifts (Sala *et al.* 2000; Urban 2015; Pecl *et al.* 2017), yet local population extinctions are often overlooked in these forecasts. The geographical patterns of sensitivity to harvesting that we detected in the north-western CFR (e.g. Fig. 4.4) coincides with regional assessment of climate change vulnerability owing to decreasing precipitation and shorter fire intervals in these locations of the study biome (Midgley *et al.* 2003; Yates *et al.* 2010; Wilson, Latimer & Silander 2015). The consistent relationships of high sensitivity to harvesting and climatic extremes that we detected (e.g. Fig. 4.5) also stresses the urgency to jointly consider the potential impacts of both harvesting and climate change in future investigations. Such joint analyses are invaluable to evaluate the future persistence of species (e.g. Bomhard *et al.* 2005; Cabral *et al.* 2013). Although serotiny may respond adaptively to gradual shifts in fire frequency, this requires favourable post-fire recruitment conditions (Lamont & Enright 2000) and meeting these criteria seems unlikely given the changing climate and fire regimes of our study region (Wilson, Latimer & Silander 2015; Van Wilgen *et al.* 2016). In summary, our findings show that harvesting compromises future persistence across species' ranges with concomitant implications for conservation management in a rapidly changing world.

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FIGURES

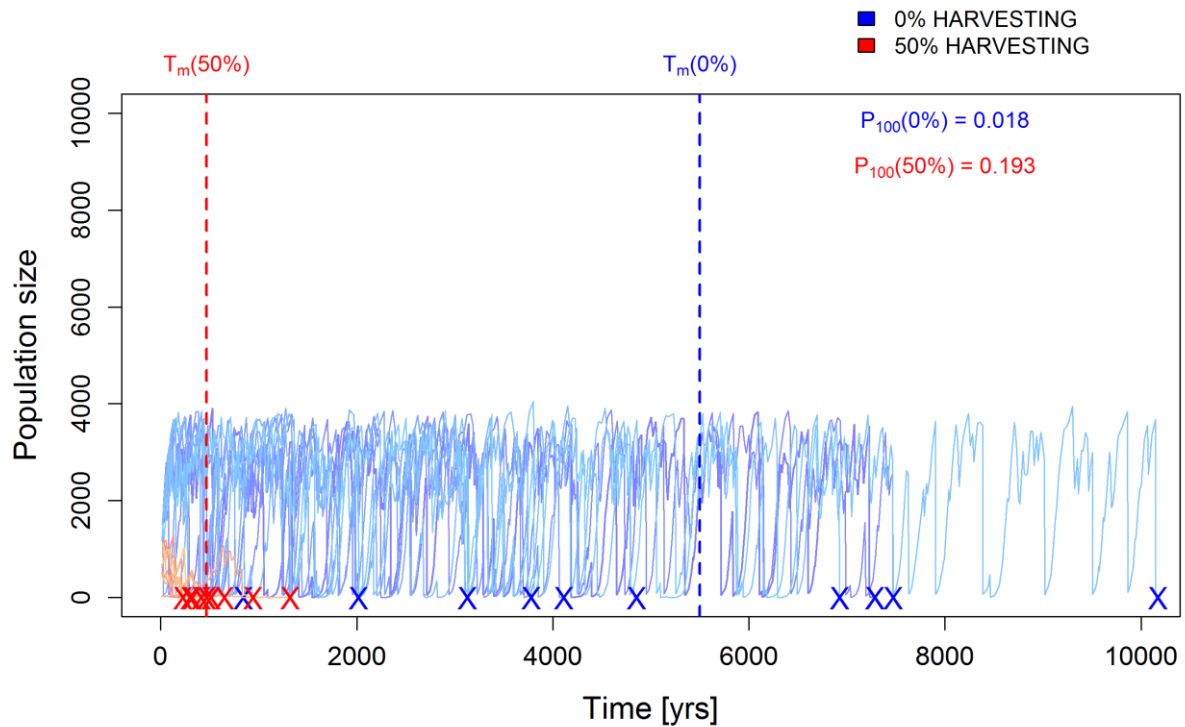


Fig. 4.1. Example of the stochastic extinction analyses showing simulated population dynamics over time for the persistence of one population (*P. repens*) in response to 0% (blue lines) and 50% (red lines) wildflower harvesting, respectively. Multiple extirpation events (X; years) are recorded per simulation. The intrinsic mean time to extinction (T_m ; following Grimm & Wissel 2004) and the probability of extirpation over 100 years (P_{100}) are recorded as measures of population viability per harvesting scenario. Note that only a subset ($n=10$) of the total replicated simulations are depicted. Full simulations specified a maximum time horizon of 100 000 years, ran 10 000 time step replications and included 26 serotinous Proteaceae species (see Methods for details).

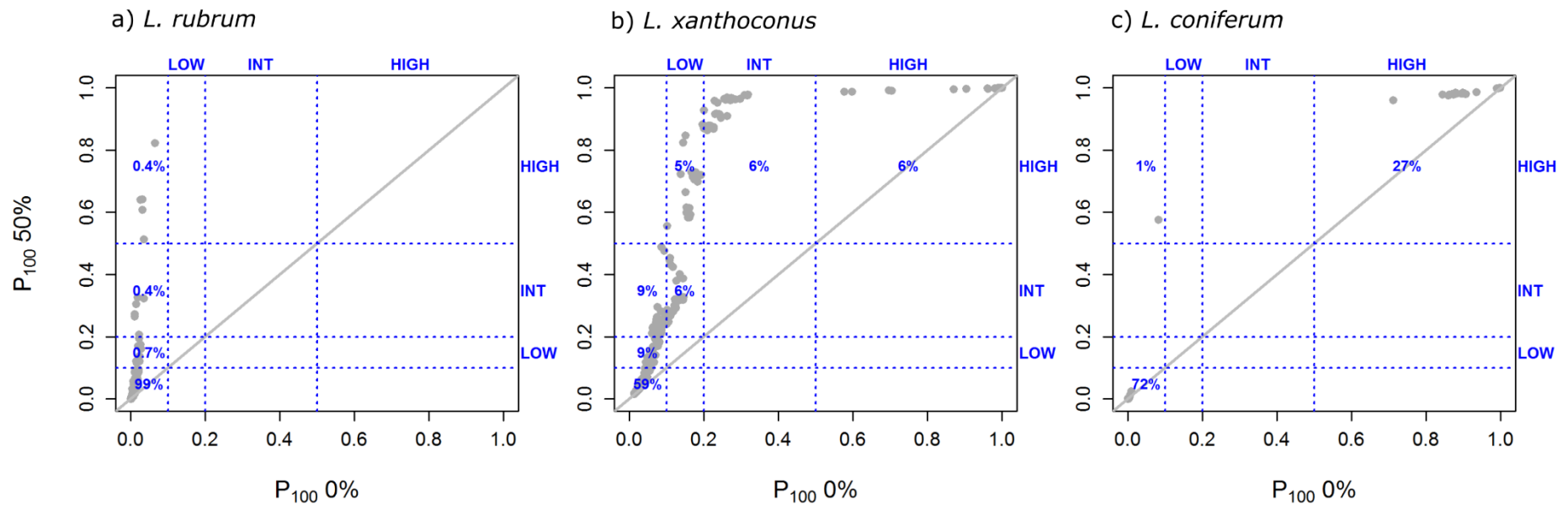


Fig. 4.2. Intraspecific variation in sensitivity to wildflower harvesting across the geographical distributions of three *Leucadendron* species, (a) *L. rubrum*, (b) *L. xanthoconus*, (c) *L. coniferum*. $P_{100} 0\%$ (x-axis) and $P_{100} 50\%$ (y-axis) are estimated probabilities of extirpation (or extinction) over 100 years in response to two harvesting scenarios, respectively, derived from stochastic extinction analyses. Horizontal and vertical dashed [blue] lines indicate ‘extinction risk categories’ of ‘LOW’, ‘INT’ and ‘HIGH’ that correspond to the extinction probability thresholds of the IUCN (method E. Quantitative Analysis; IUCN 2001). Species arranged (left to right) according to increasing proportion (%) of populations sensitive to harvesting. For example, the bottom-left quadrat (no label) indicates the percentage of populations per species at ‘very low risk’ in response to harvesting whereas the upper-right quadrat (‘HIGH’) indicates the percentage of populations at ‘high’ risk of extinction. See Fig. S4.1 for all 26 serotinous Proteaceae study species.

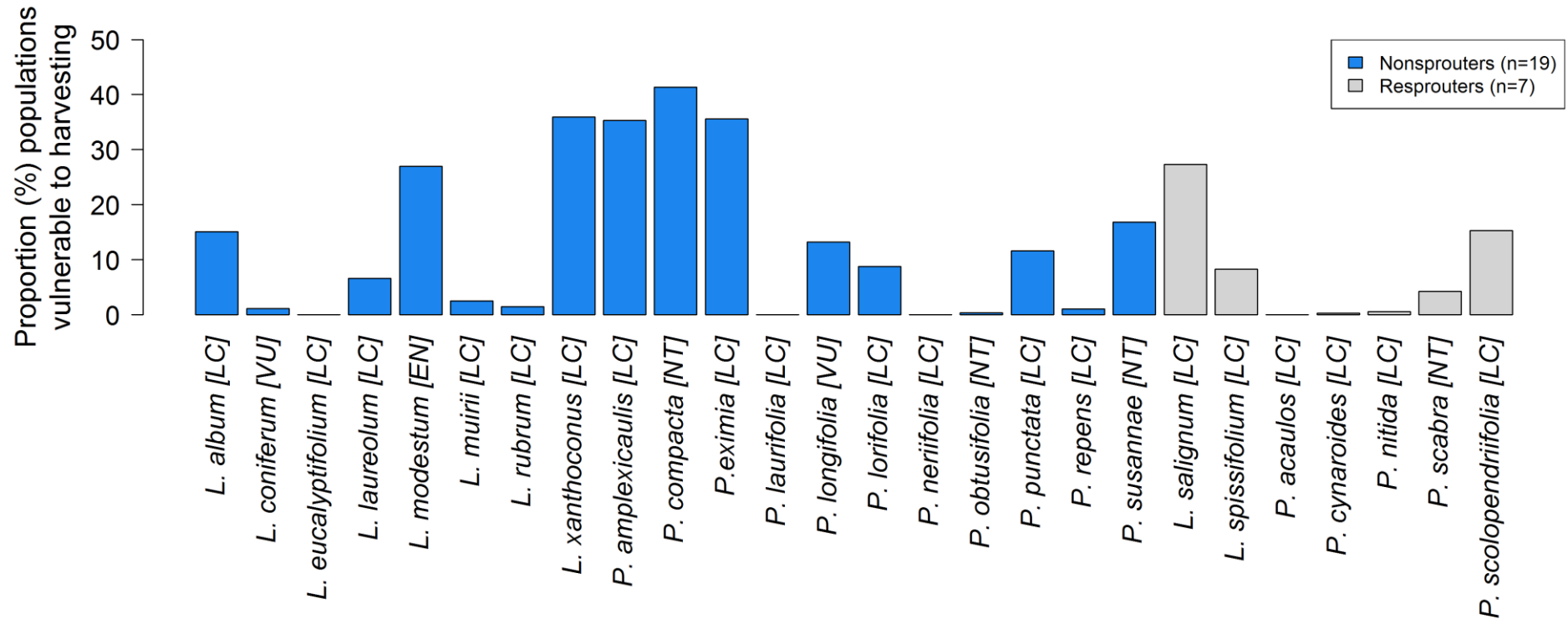


Fig. 4.3. Interspecific variation in sensitivity to wildflower harvesting across the geographical distributions of 26 serotinous Proteaceae species. Individual bars [blue: nonsprouter (n=19); grey: resprouters (n=7)] show the mean proportion of populations per species that increase in sensitivity, i.e. shift from a no/low risk category to a higher risk category (LOW, INT or HIGH), due to harvesting. Across all species, the mean proportion of populations that increased in response to harvesting was 12% (n=26). See also Figs 4.2 and S4.1. Square brackets [] after species names indicate the National Red List Status (Raimondo *et al.* 2009; Red List of South African Plants 2017) per species.

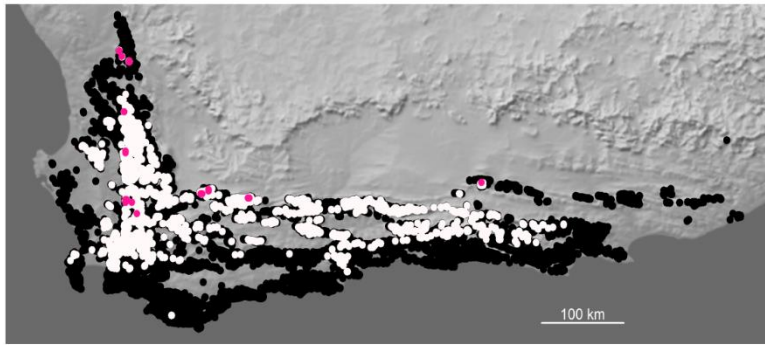
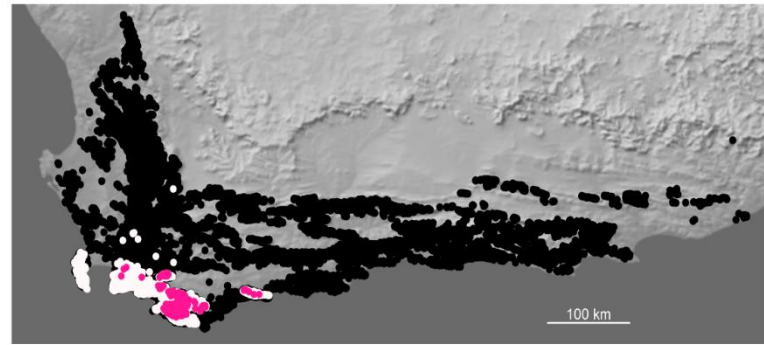
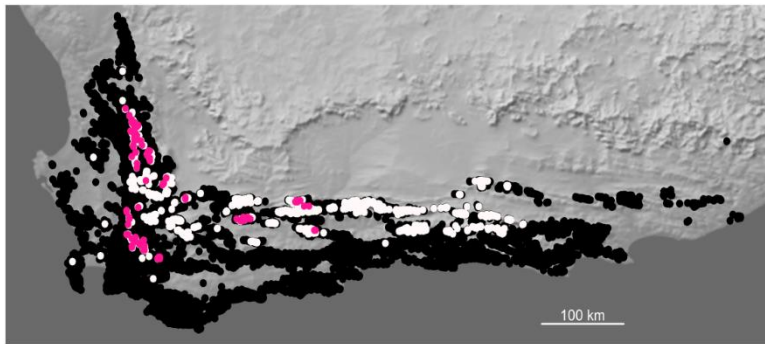
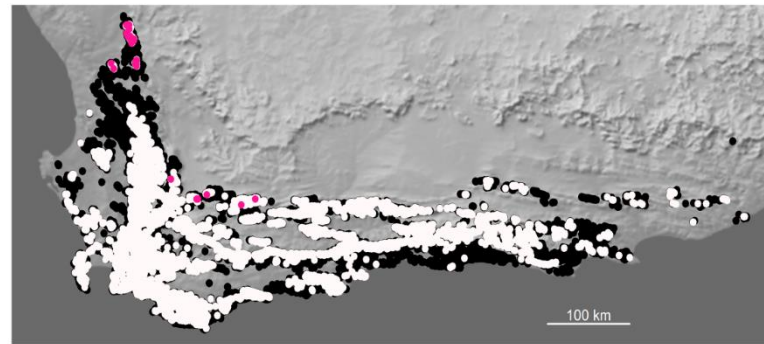
a) *L. rubrum*b) *L. xanthoconus*c) *P. punctata*d) *P. repens*

Fig. 4.4. Range-wide variation and geographical patterns in sensitivity (P_{abs}) to wildflower harvesting for four serotinous Proteaceae species in the study region (Cape Floristic Region, South Africa). Pink dots indicate grid cells ($1' \times 1'$) within the range of a species (white area; presence records from Rebelo 2001) where the absolute change in extirpation probability (P_{abs} ; i.e. the difference between 0% and 50% harvesting) is > 0.1 (10%). Black area depicts the geographical distribution of CFR Proteaceae (Rebelo 2001). The four species include: (a) *L. rubrum*, (b) *L. xanthoconus*, (c) *P. punctata* and (d) *P. repens*. See Fig. S4.2 for all 26 study species.

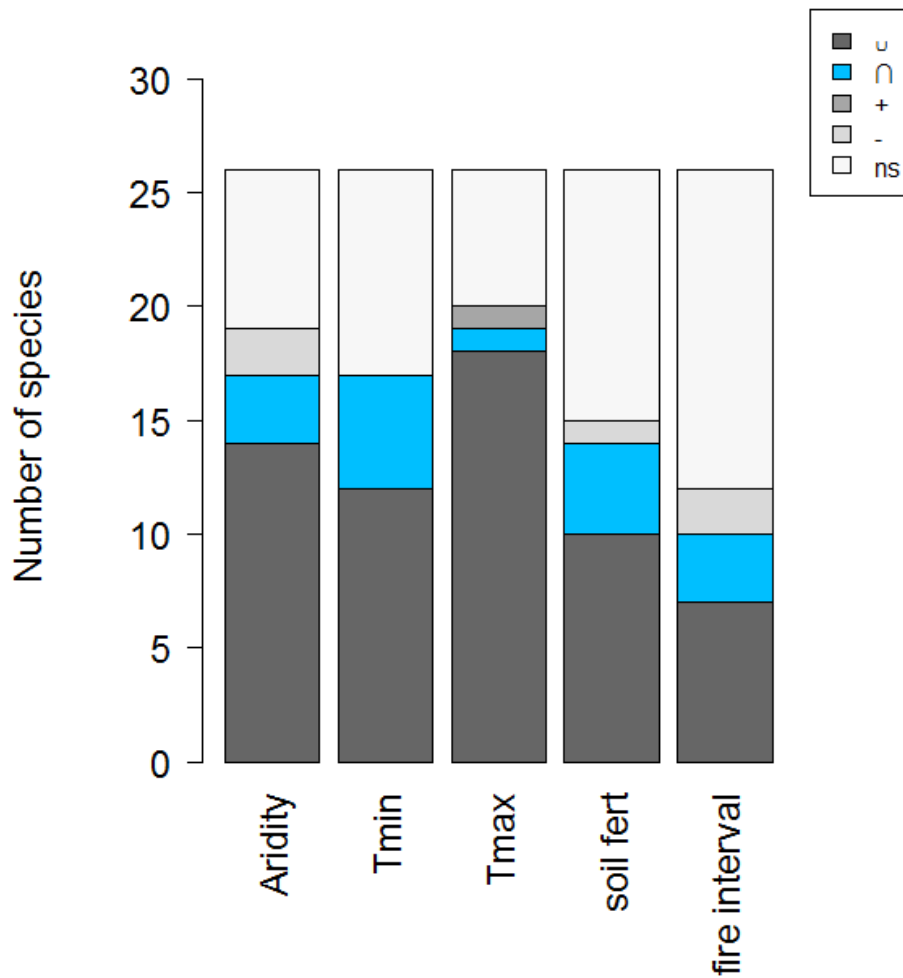


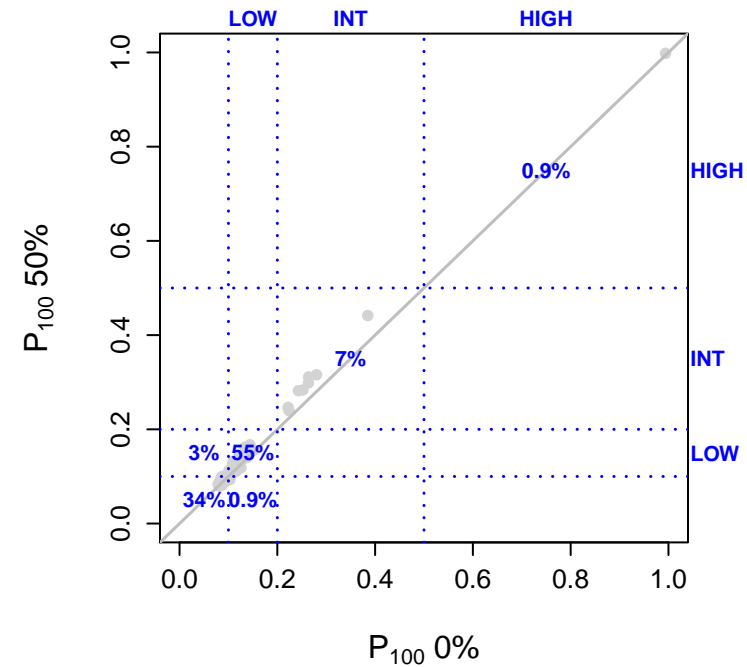
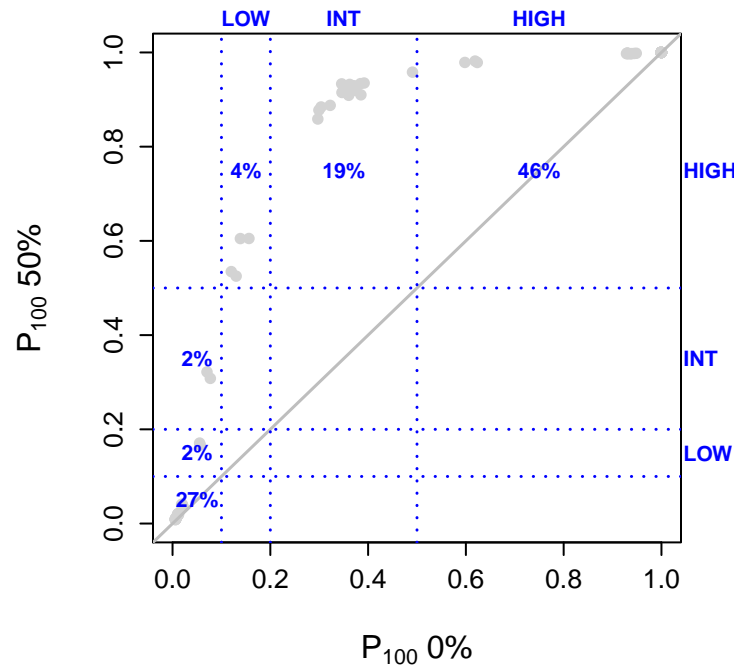
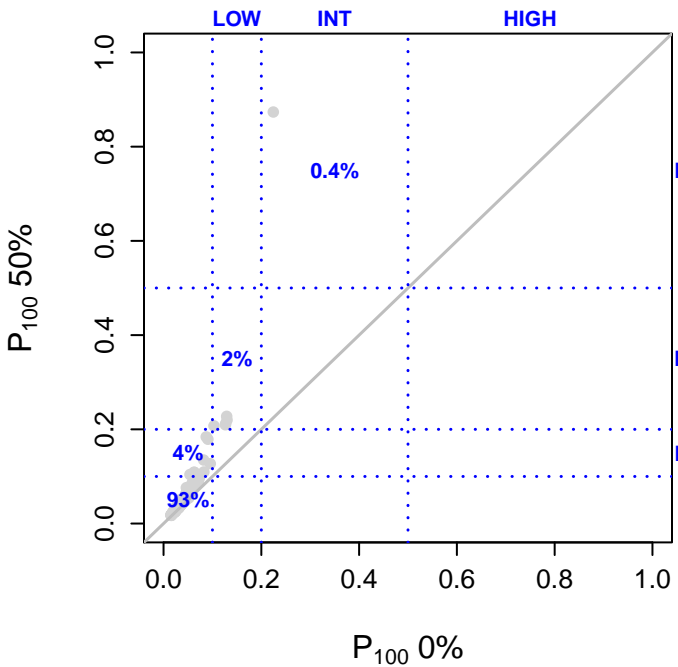
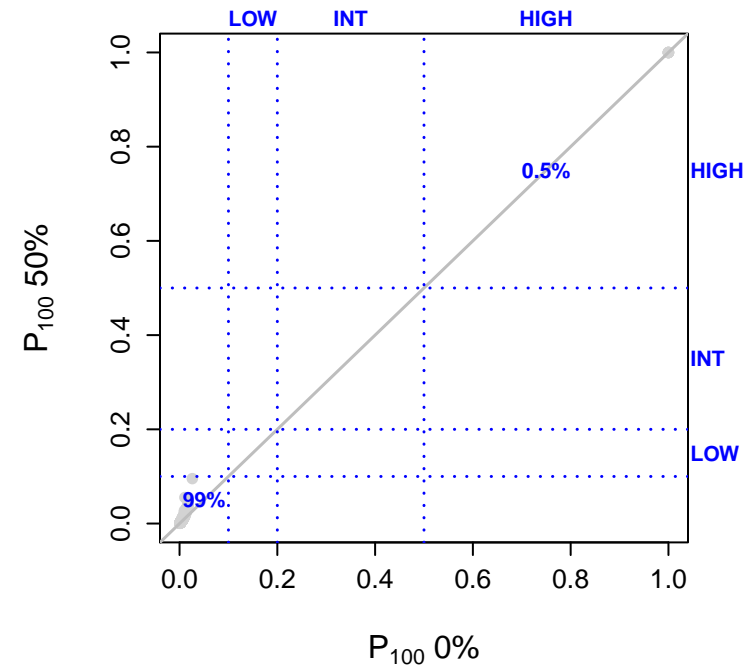
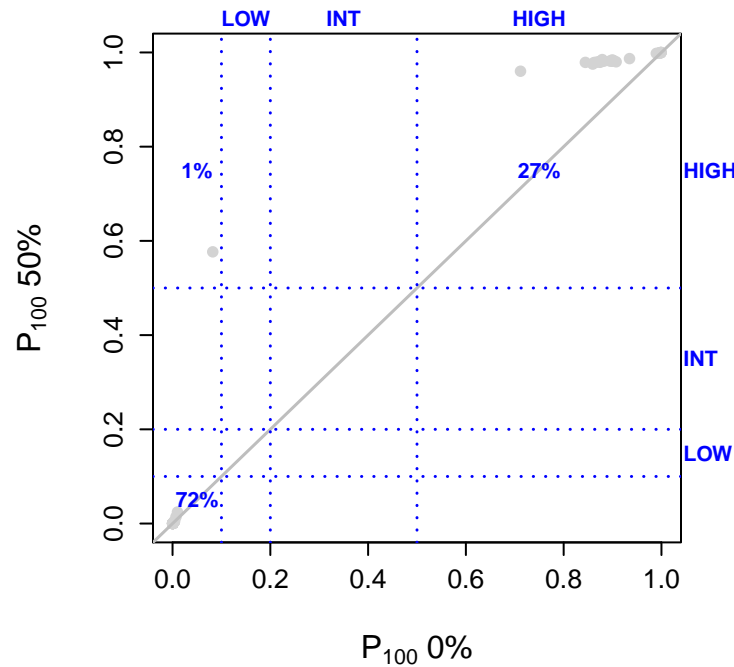
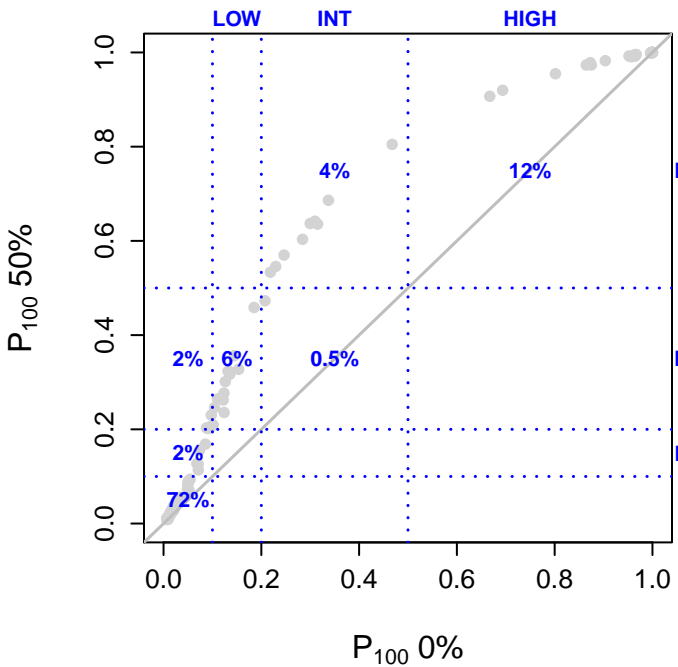
Fig. 4.5. Shape of relationships between sensitivity to wildflower harvesting across species' geographical ranges and environmental variation of the study region (CFR, South Africa) for 26 serotinous Proteaceae species (see also Table S4.1). Barplot shows the number of species for which an environmental effect was detected. The shape of environmental responses was specified as either: positive ("+"), negative ("-"), unimodal [negative quadratic; "∩"], u-shaped [positive quadratic; "∪"] or no effect ("ns"). Responses were quantified from the best model per species that describe the response of P_{abs} (sensitivity to harvesting; log-transformed) to these multiple environmental variables in linear regressions and a model selection approach. Environmental variables include: climate variables (summer aridity index (aridity), winter minimum temperature in the month of July (Tmin; °C), summer maximum temperature in the month of January (Tmax; °C)), soil nutrient status (index; soil fert) and fire return interval (years).

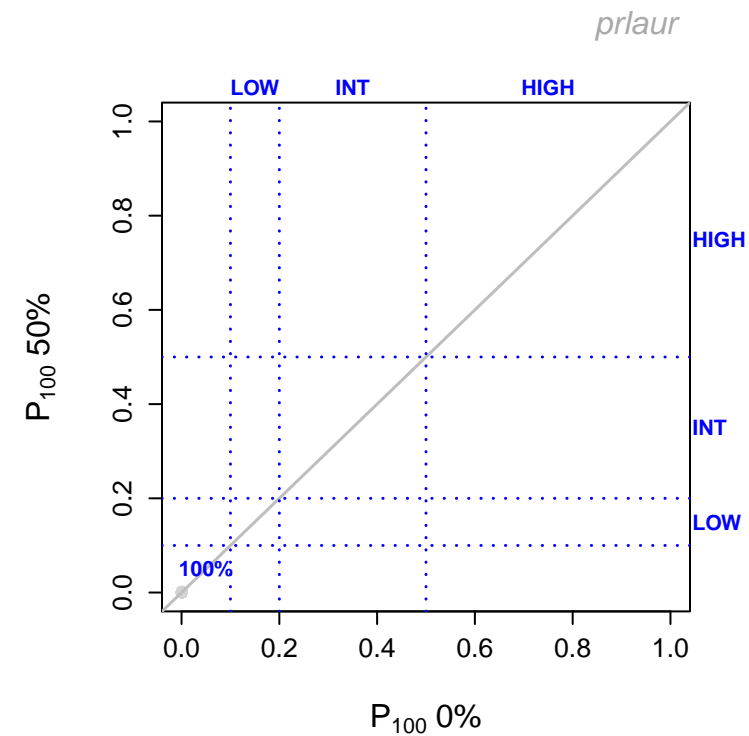
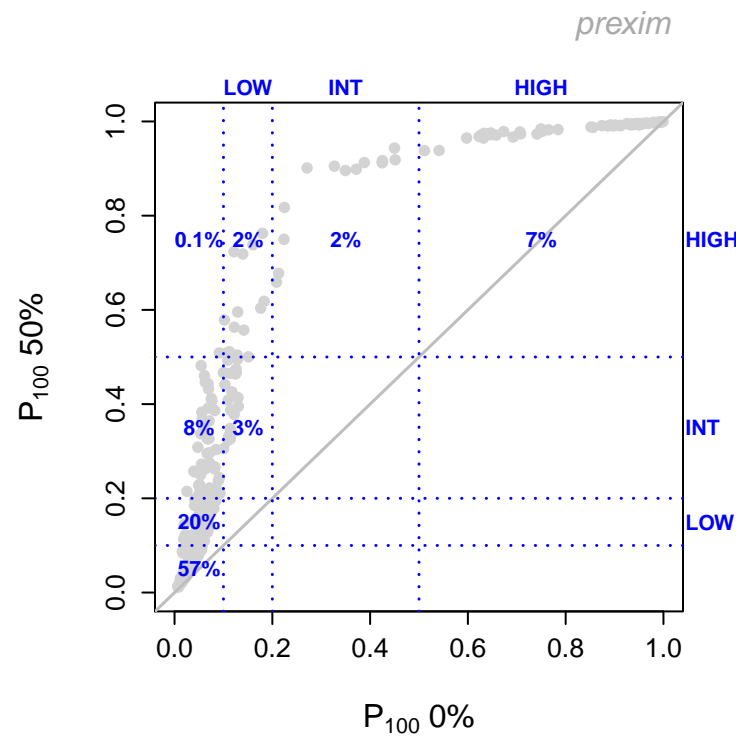
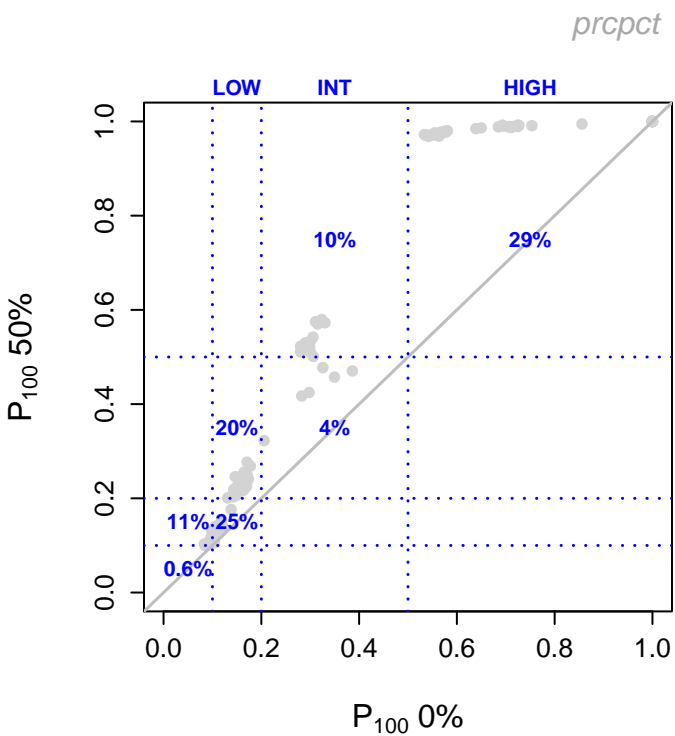
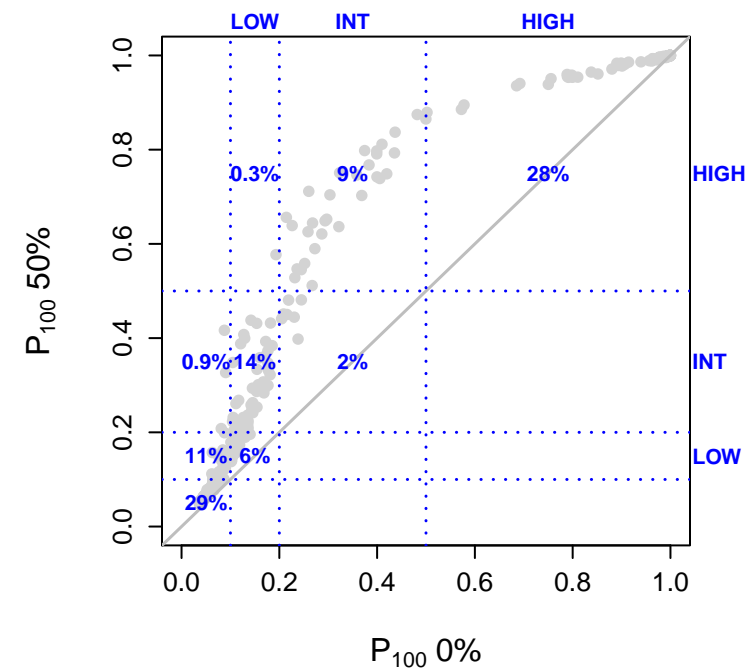
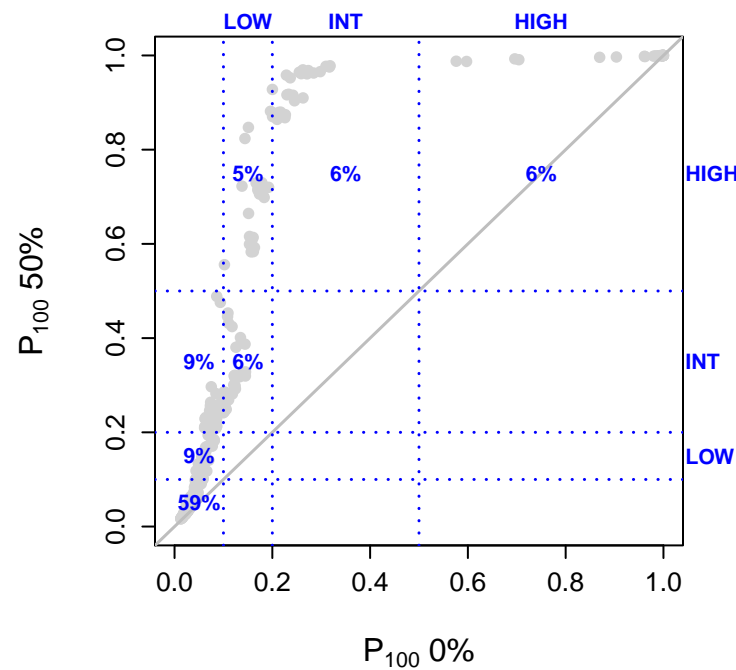
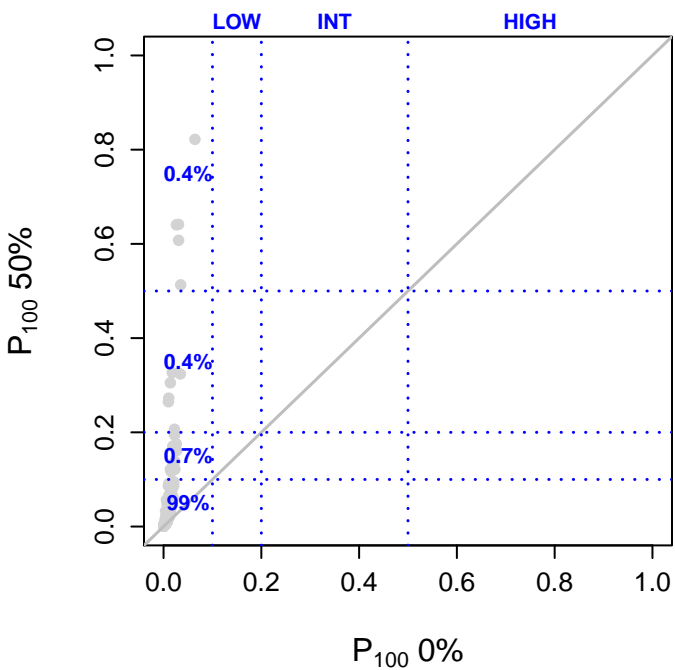
CHAPTER 4

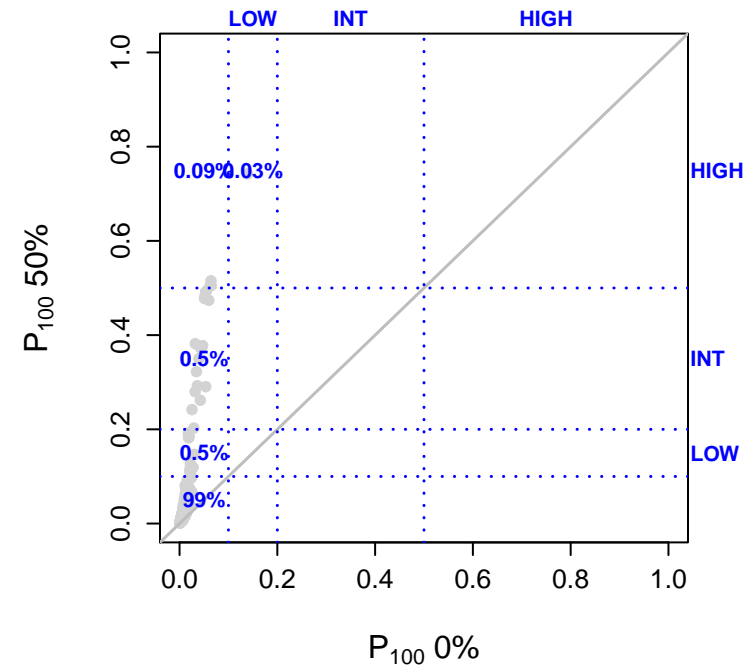
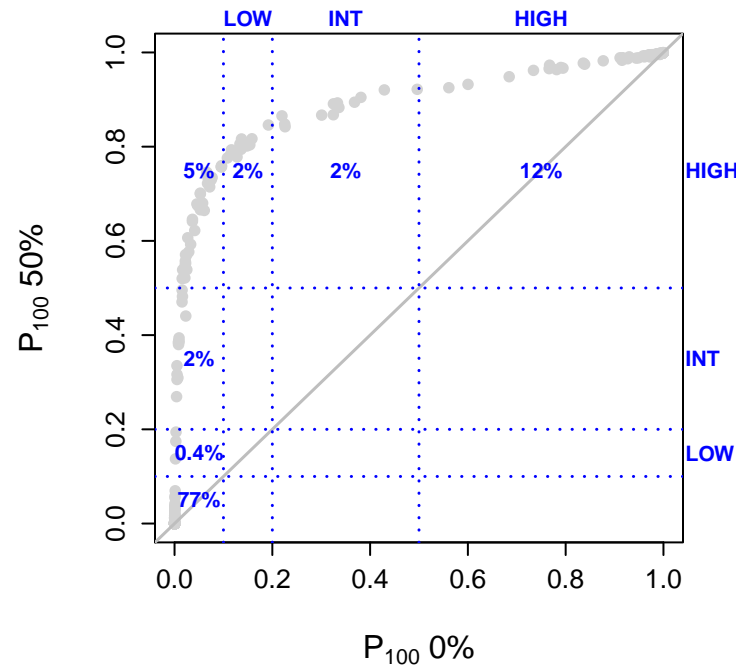
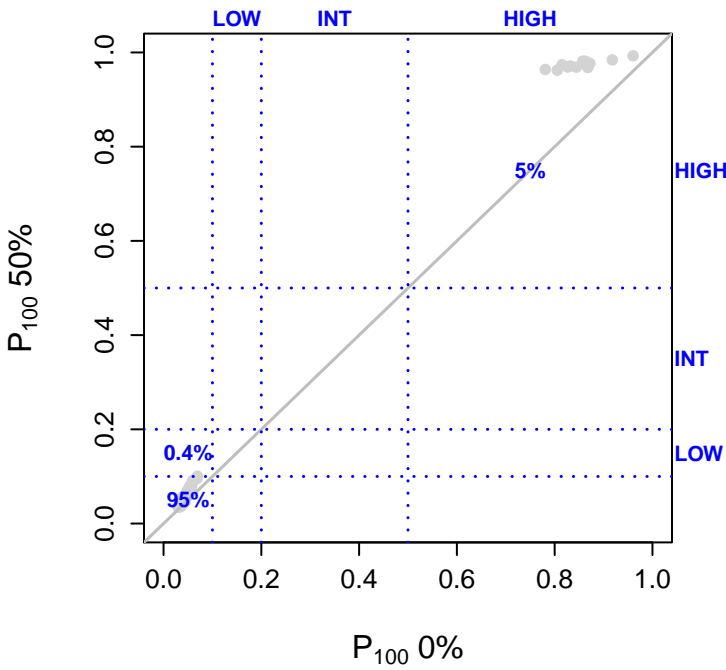
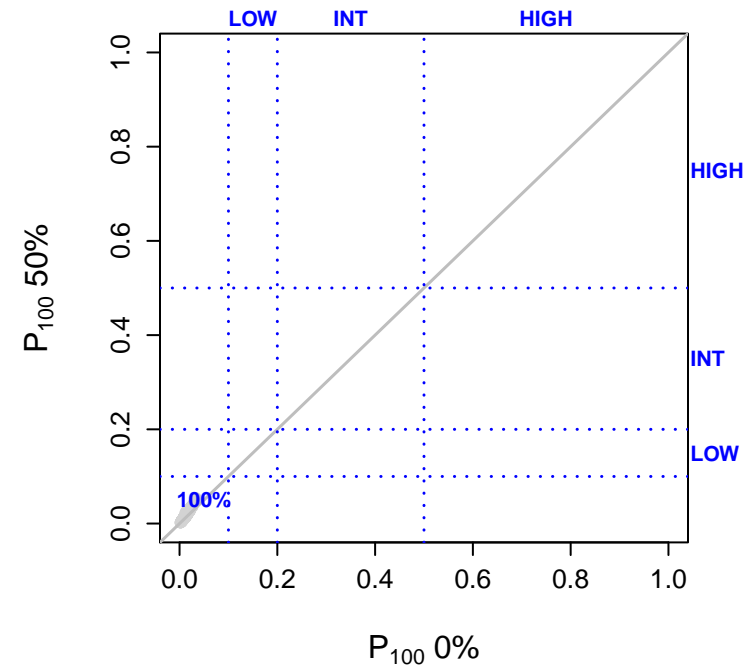
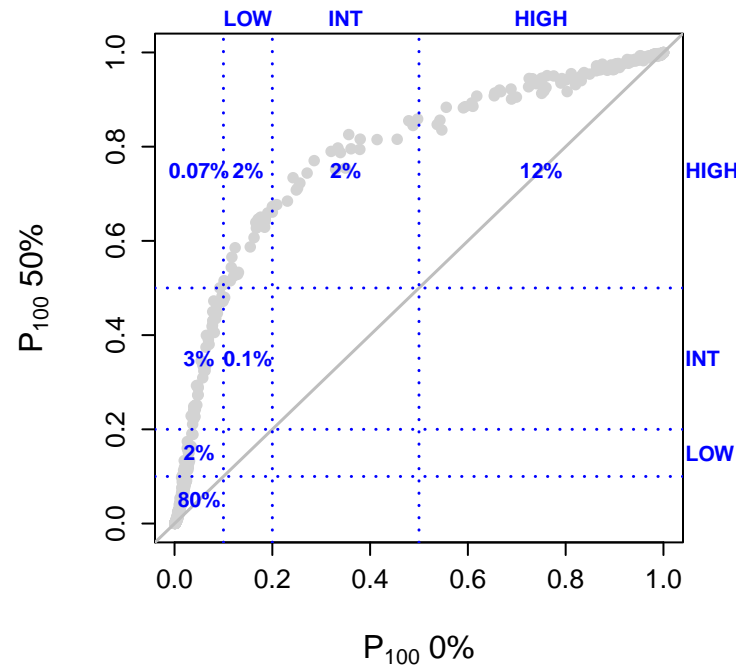
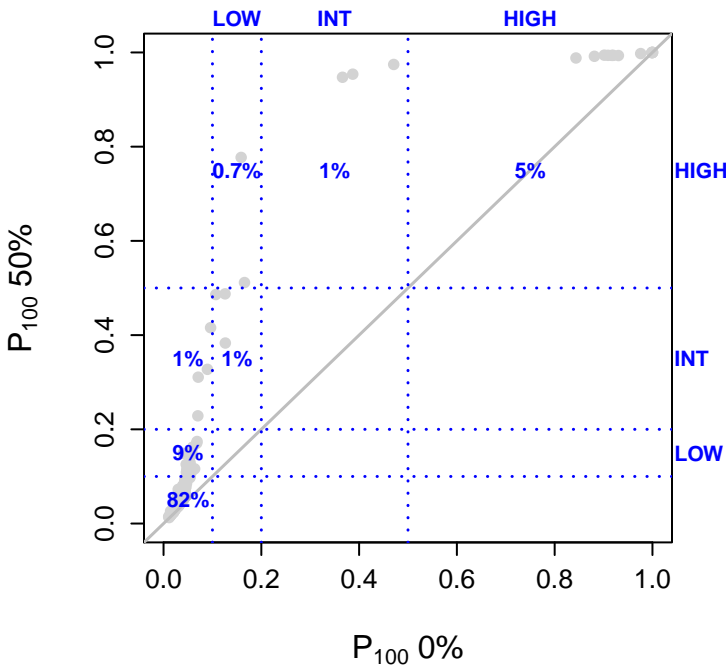
Supporting Information:

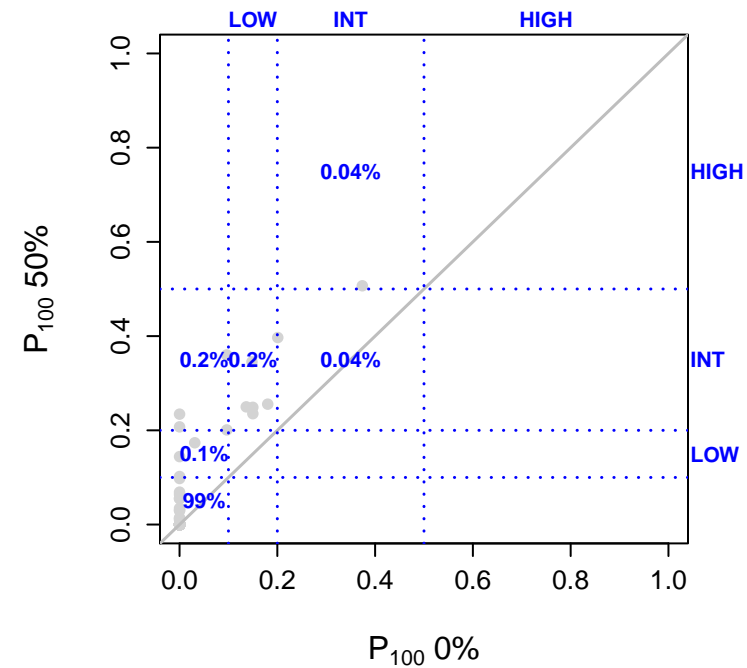
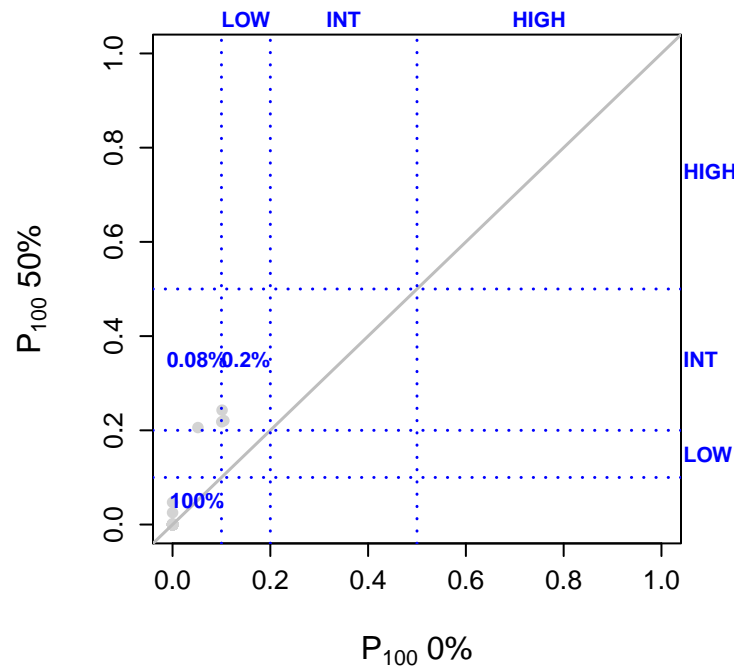
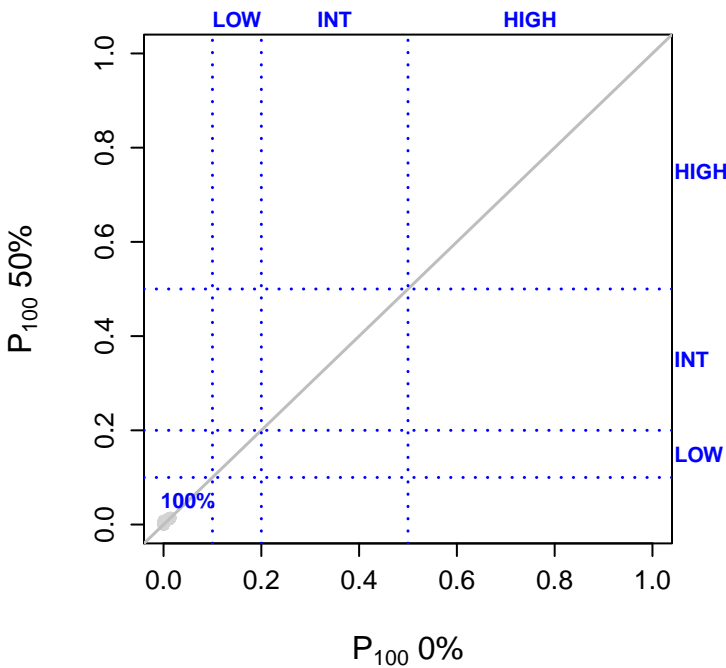
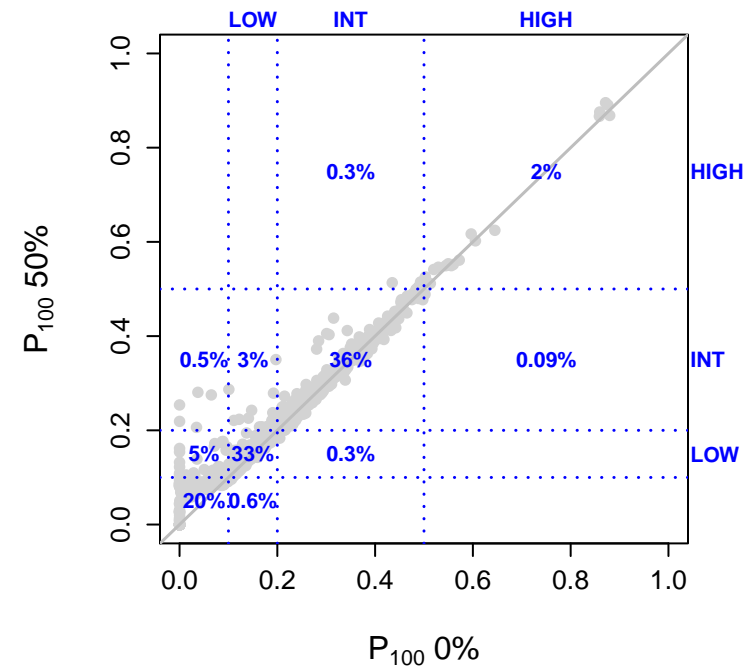
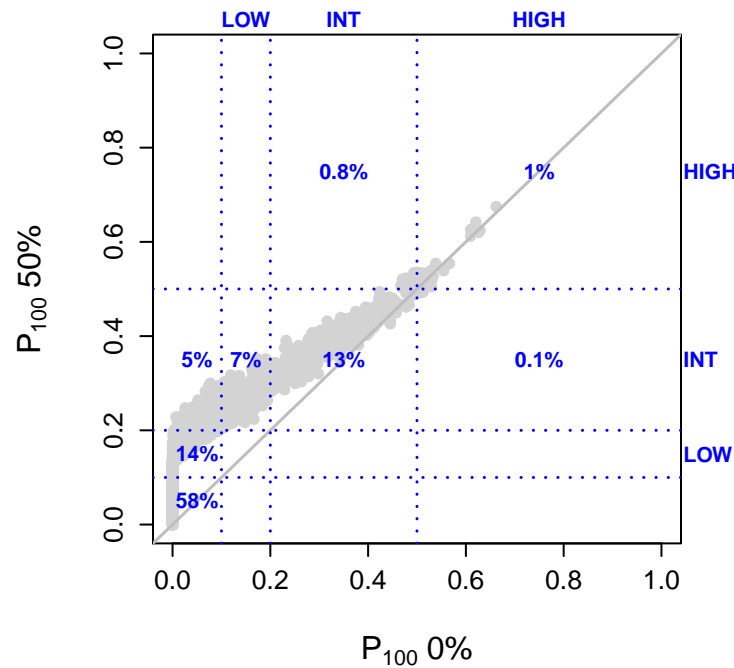
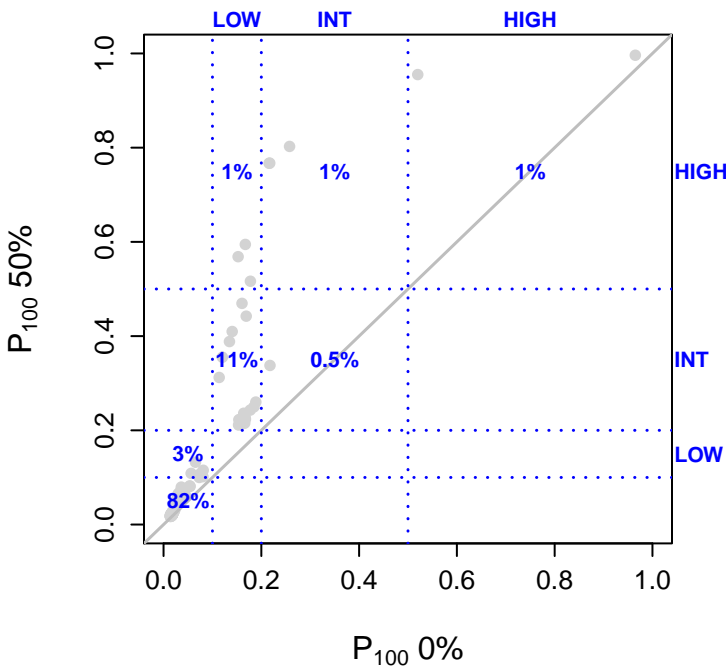
GEOGRAPHICAL VARIATION IN SENSITIVITY TO WILDFLOWER HARVESTING INFERRED FROM RANGE-WIDE DEMOGRAPHIC DATA FOR 26 PROTEACEAE SPECIES

Fig. S4.1 (continued on next page). Intraspecific variation in sensitivity to wildflower harvesting across the global geographical distributions of 26 serotinous Proteaceae species. P_{100} 0% (x-axis) and P_{100} 50% (y-axis) are estimated probability of extirpation over 100 years in response to two harvesting scenarios, respectively, derived from stochastic extinction analyses (described in main text). Horizontal and vertical dashed [blue] lines indicate ‘extinction risk categories’ of ‘LOW’, ‘INT’ and ‘HIGH’ that correspond to the extinction probability thresholds of the IUCN (method E. Quantitative Analysis; IUCN 2001). Per species, the bottom-left quadrat (no label) indicates the percentage (%) of populations per species at ‘very low risk’ in response to harvesting whereas the upper-right quadrat (‘HIGH’) indicates the percentage of populations at ‘high’ risk of extinction. The diagonal [solid grey] line indicates the 1:1 association that would be expected if 50% harvesting had no impact on population viability and sensitivity. See also Fig. 4.2 in main text.









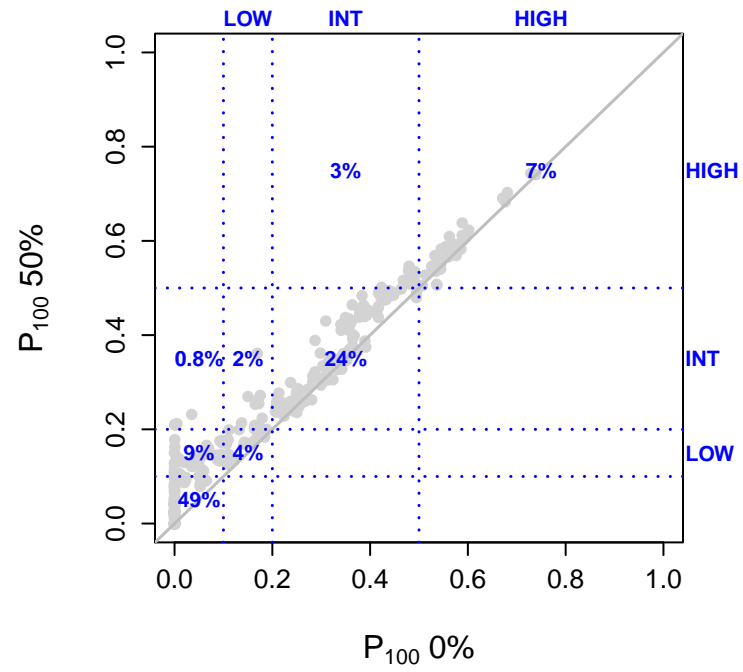
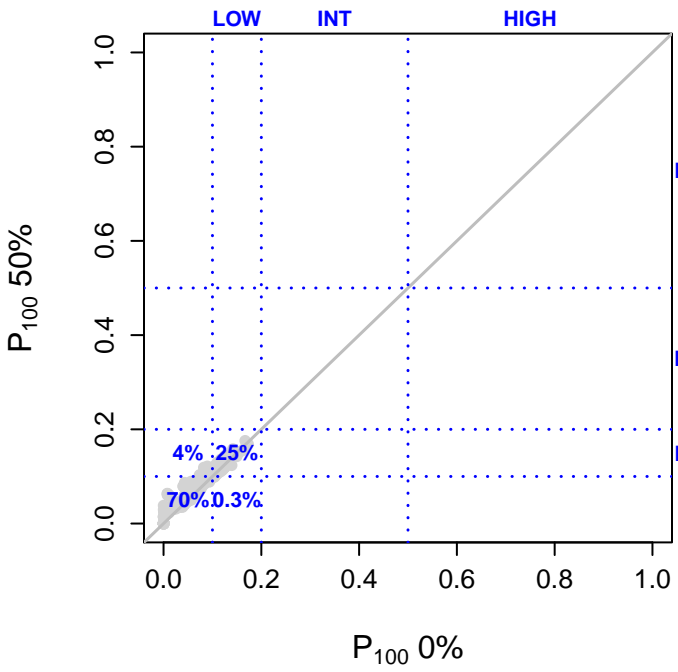
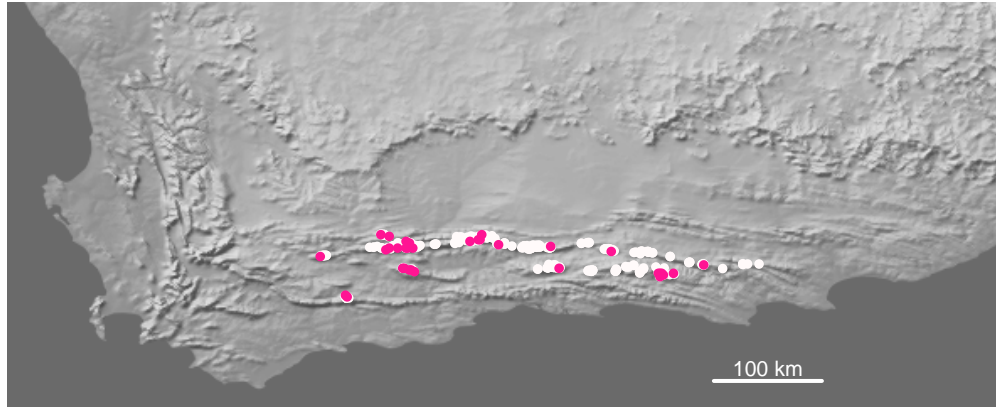
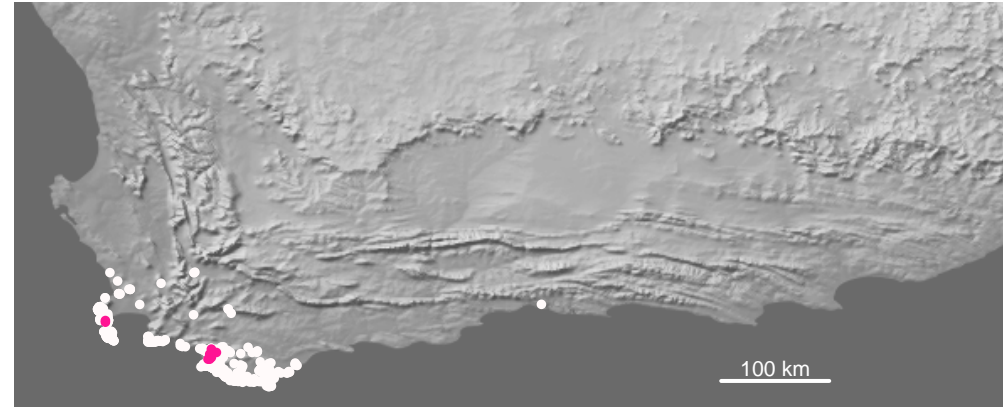


Fig. S4.2 (continued on next page). Range-wide variation and geographical patterns in sensitivity (P_{abs}) to wildflower harvesting for 26 serotinous Proteaceae species in the Cape Floristic Region (South Africa). Pink dots indicate grid cells ($1' \times 1'$) within the range of a species (white area; presence records from Protea Atlas Project; Rebelo 2001) where the absolute change in extirpation probability (P_{abs} ; i.e. the difference between 0% and 50% harvesting) is > 0.1 (10%). Species name abbreviations follow Rebelo (2001), see Table S4.1 for full names.

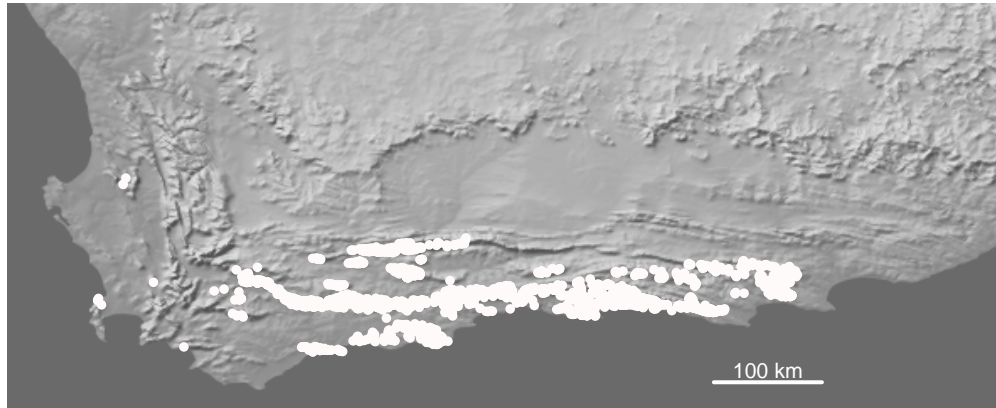
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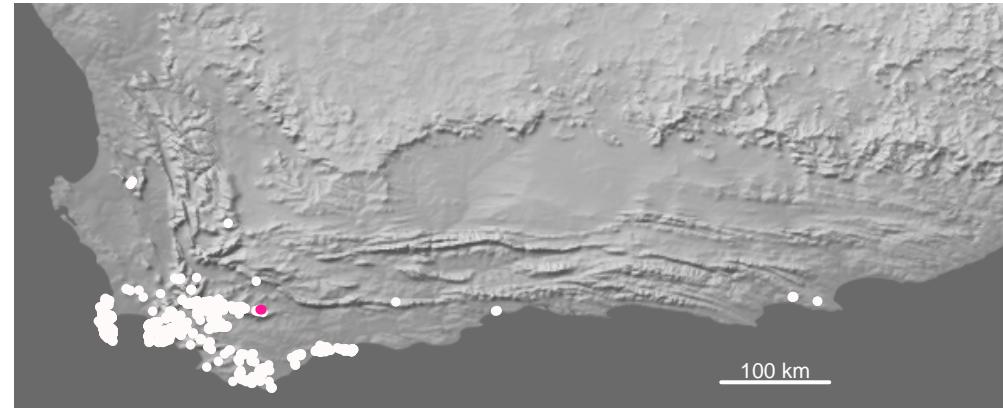
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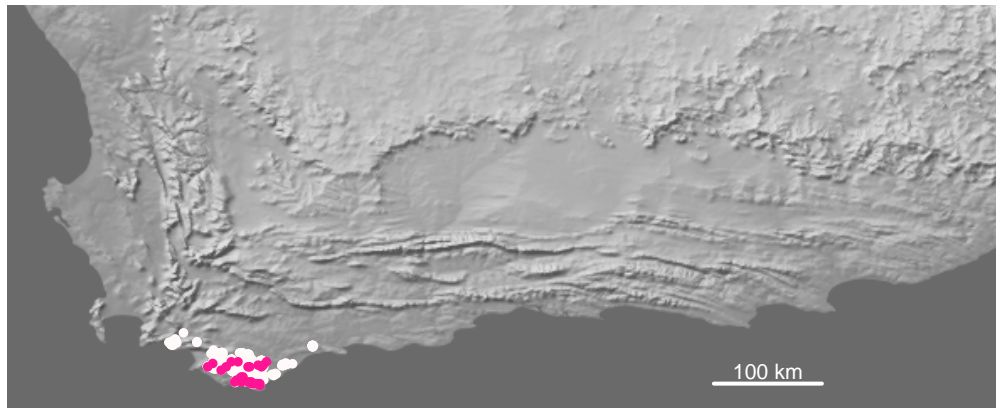
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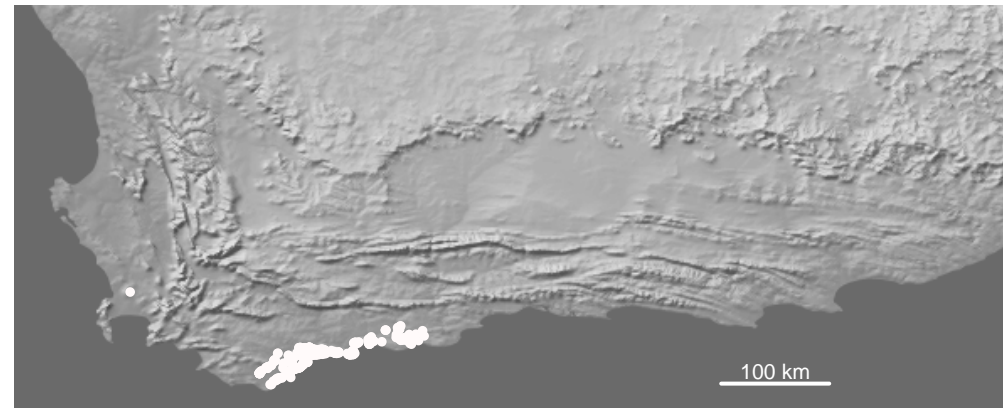
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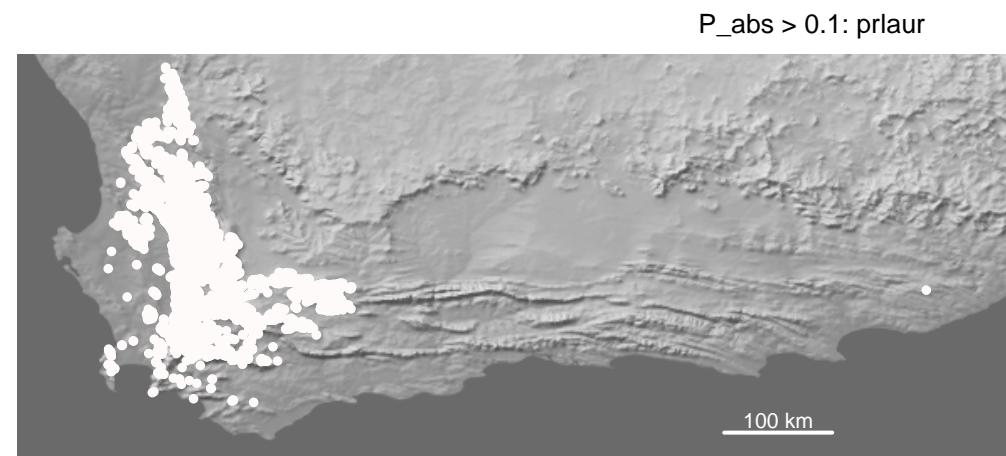
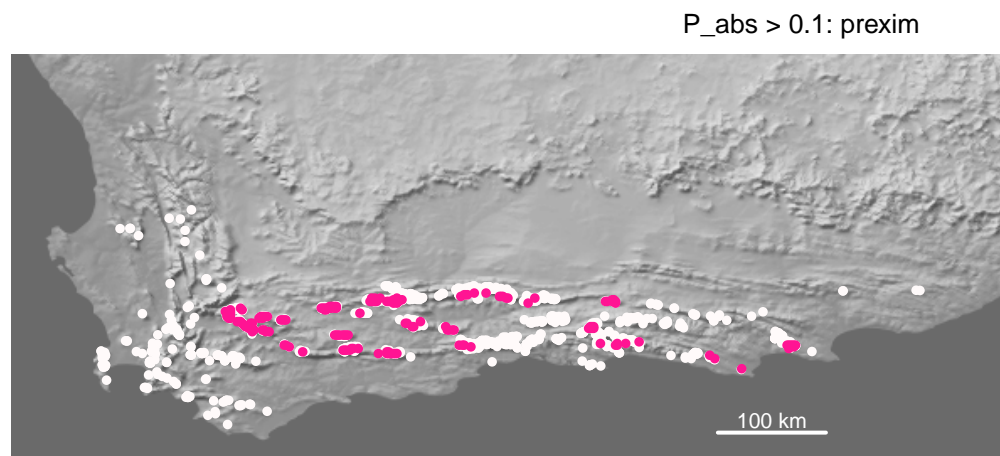
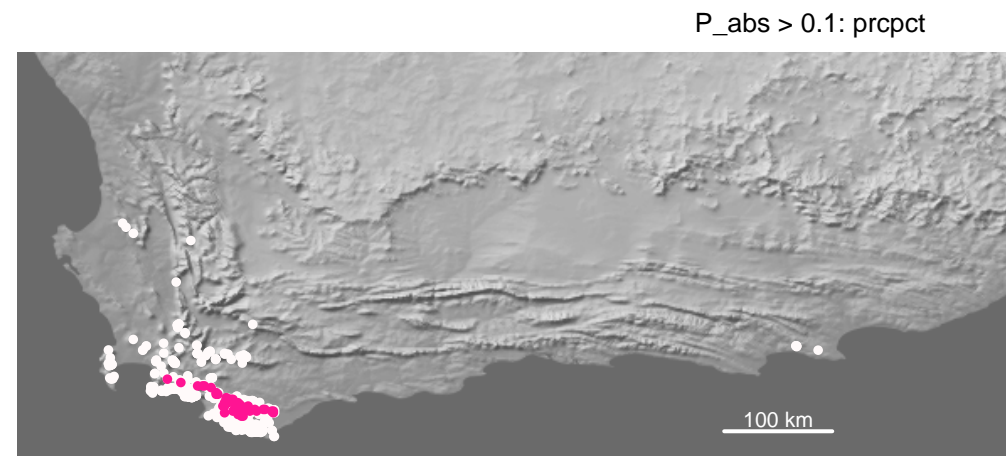
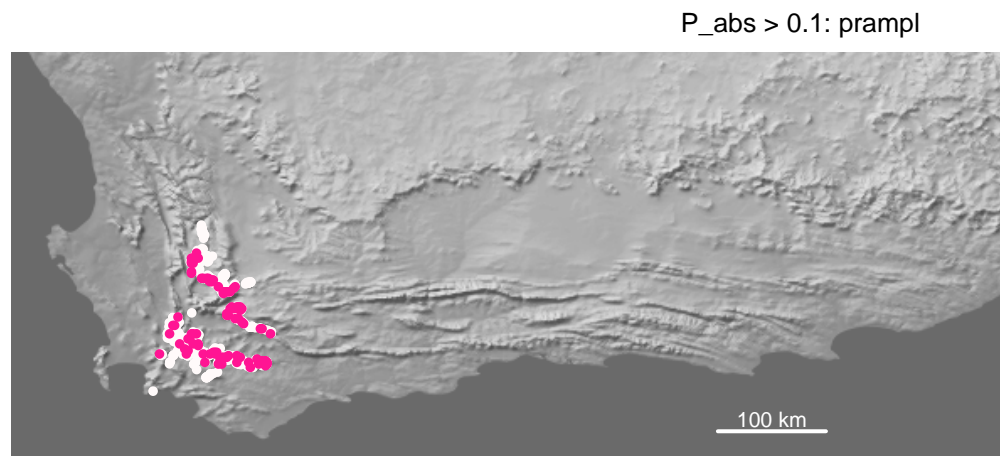
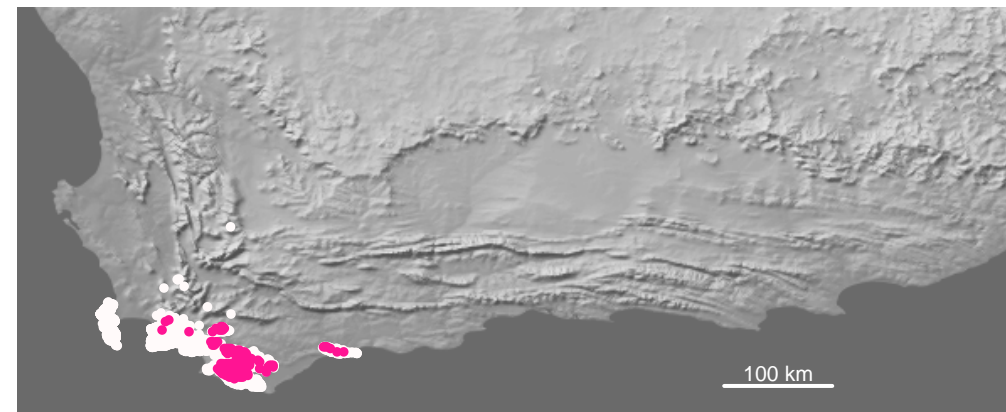
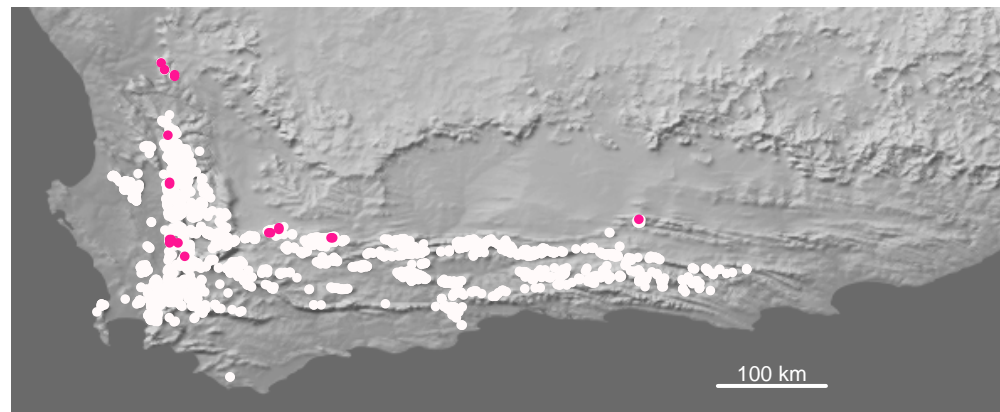


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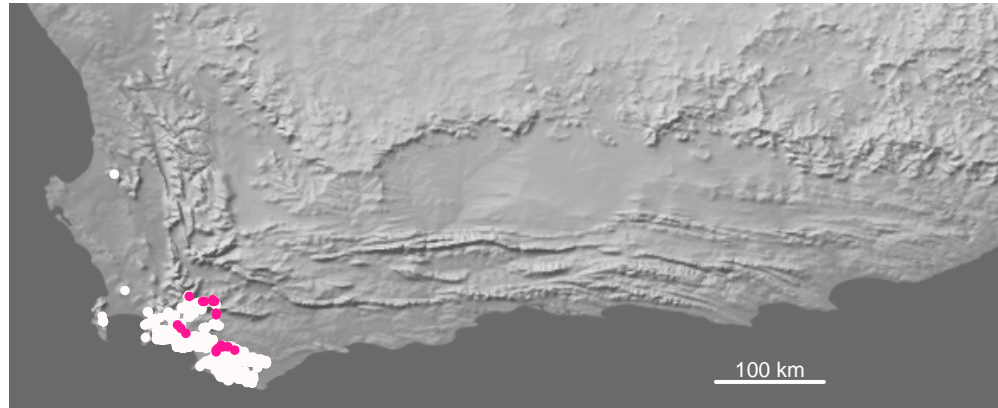


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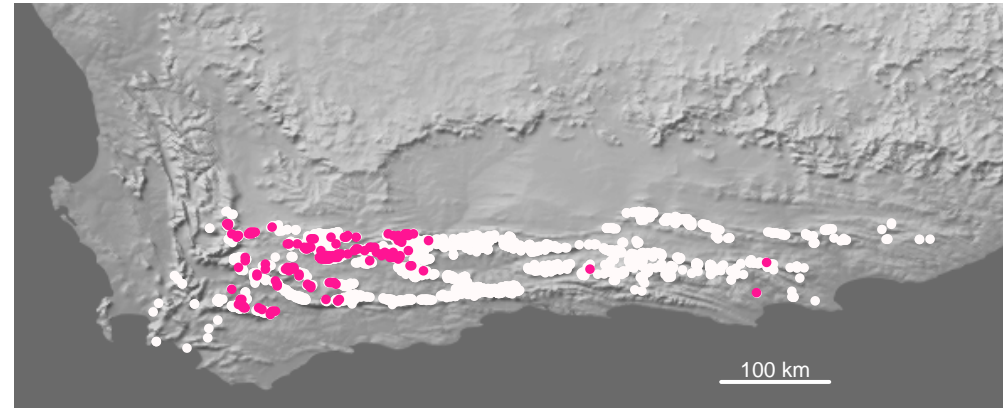




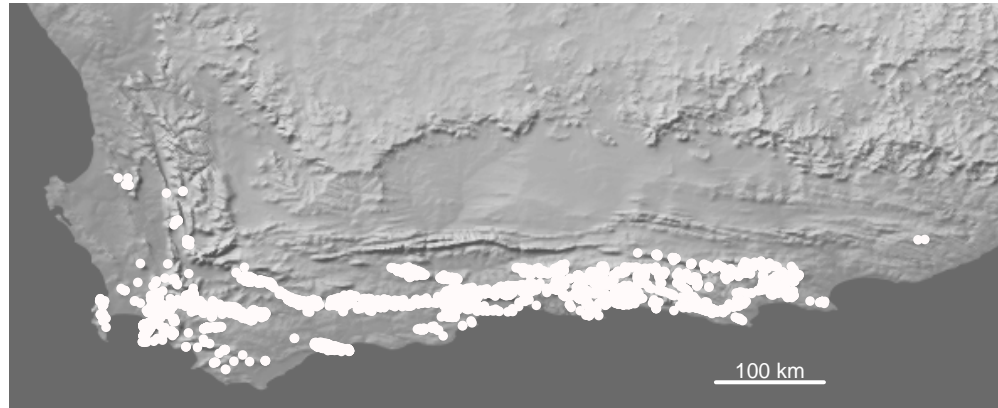
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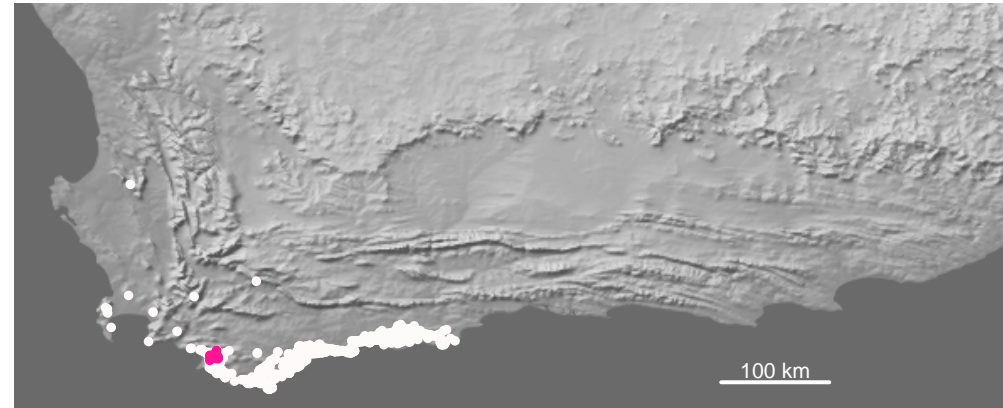
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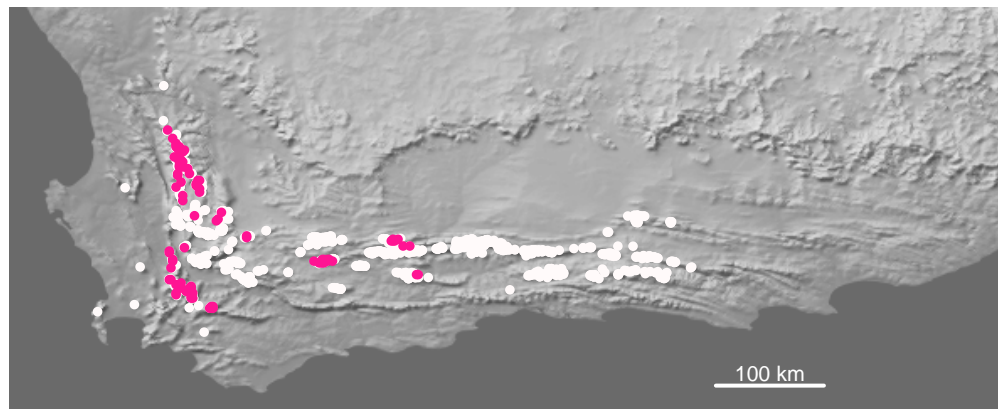
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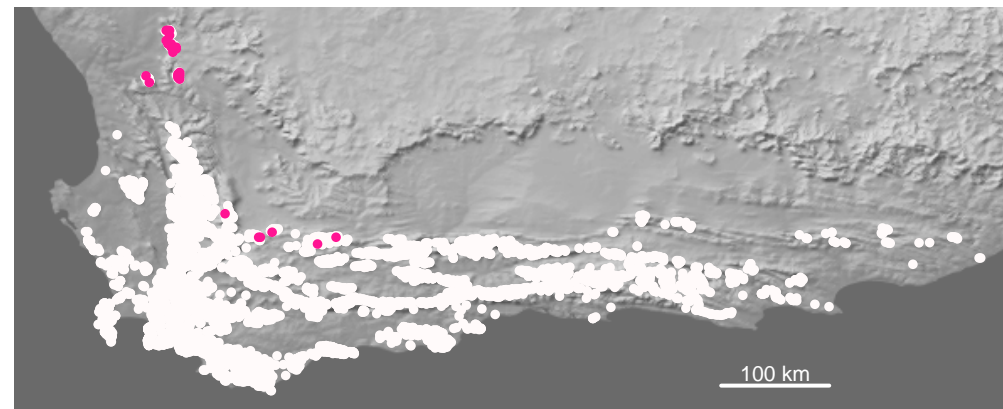
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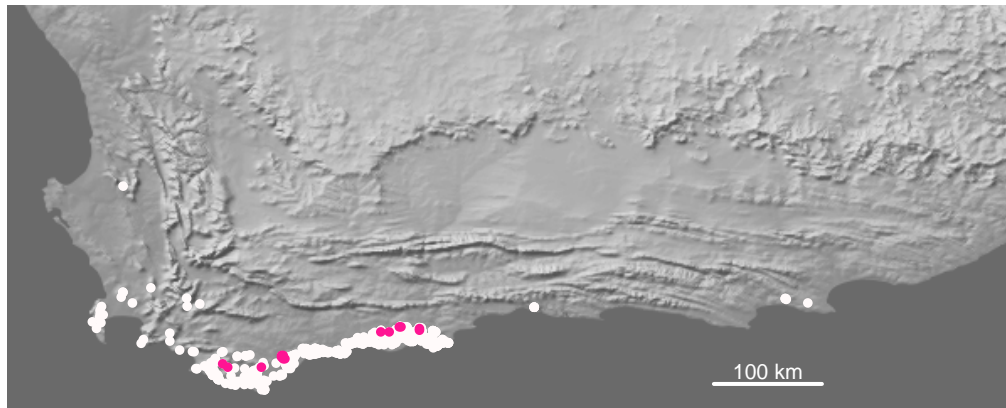
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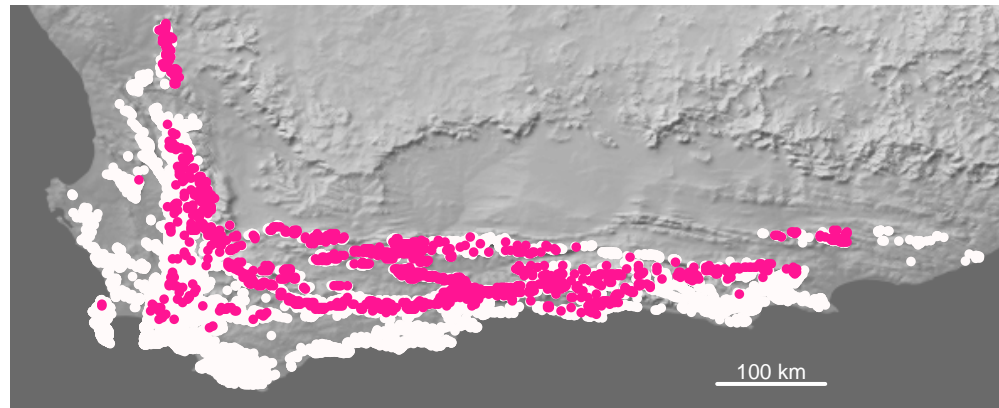
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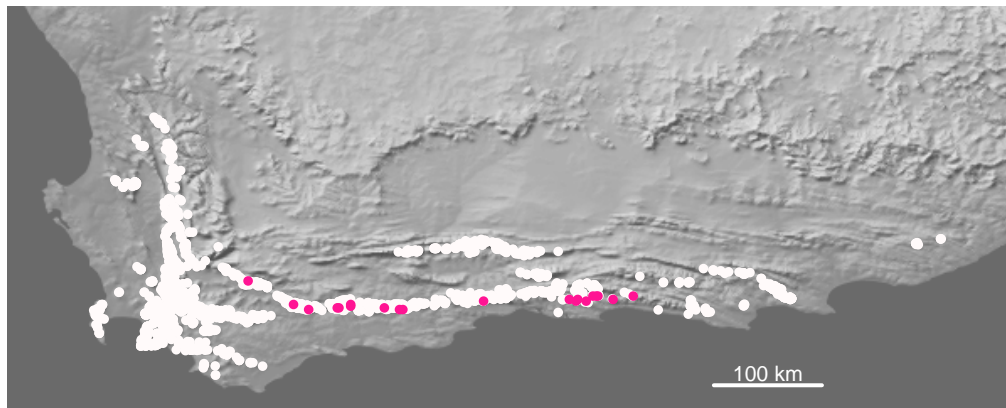
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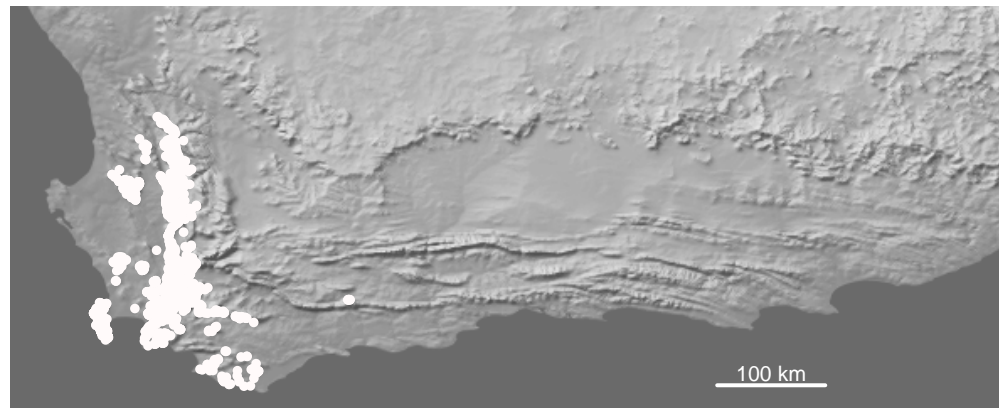
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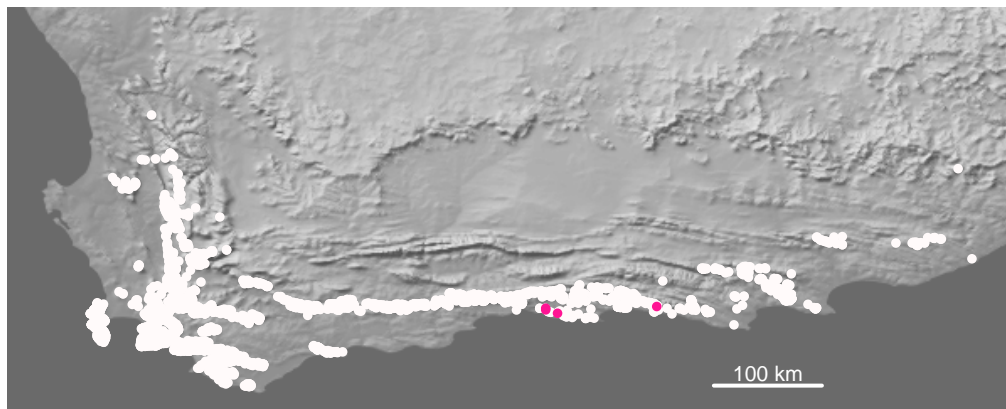
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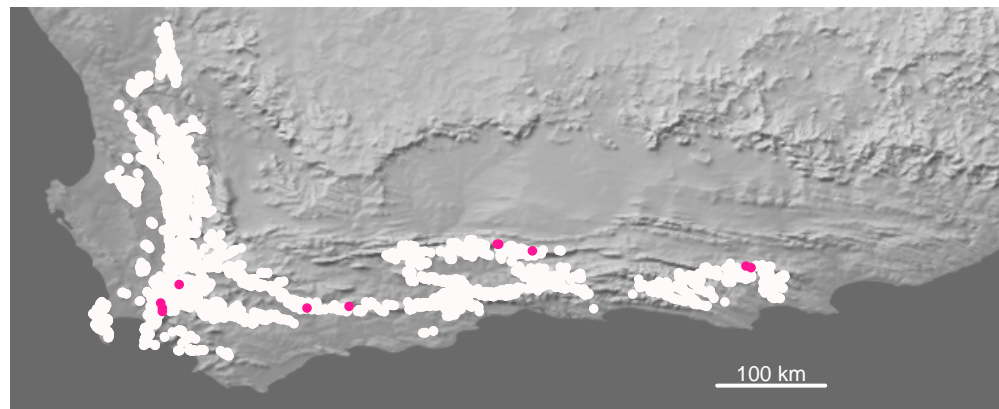
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P_abs > 0.1: prcyna



P_abs > 0.1: prniti



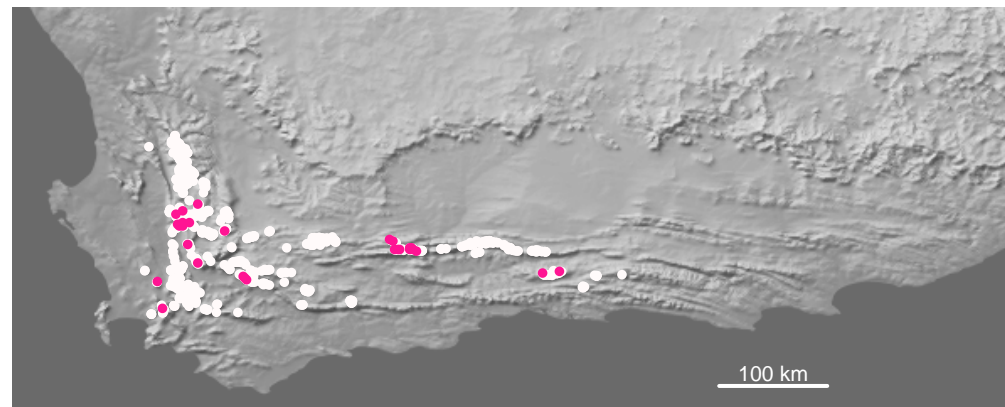
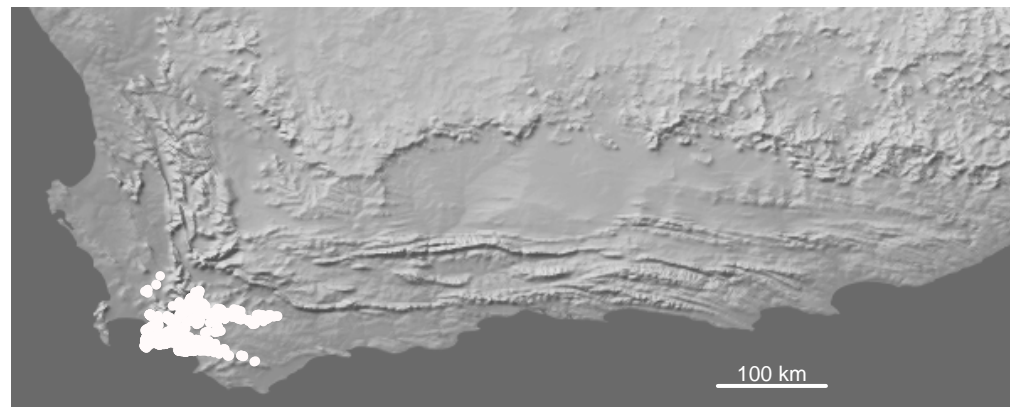


Table S4.1 (continued on next page). Relationships of range-wide sensitivity to wildflower harvesting and large-scale environmental variation for 26 serotinous Proteaceae species (with abbreviations, range size; Rebelo 2001 and National Red List status (Red List of South African Plants 2017)). Environmental variables include: climate variables of drought, cold and heat stress [i.e. an aridity index (Aridity), winter minimum temperature in the month of July (Tmin; °C), summer maximum temperature in the month of January (Tmax; °C)], soil nutrient status (index; soil fert) and fire return interval (years; fire interval). The shape of environmental responses was specified as either positive (“+”), negative (“-”), unimodal [negative quadratic; “∩”] or u-shaped [positive quadratic; “U”]. Responses were quantified from the best model per species from linear regressions that describe the response of P_{abs} (sensitivity to harvesting; log-transformed) to multiple environmental variables in a model selection approach. Bottom panel of the table summarises the number of species for which a particular environmental effect (or shape) was detected. See also Fig. 4.5.

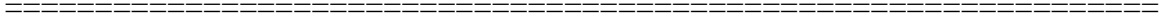
Table S4.1 (continued)

Species name	Abbreviation (Rebelo, 2001)	Range size (1' × 1' grid cells)	IUCN Red List status	AI	Tmin	Tmax	Soil fert	Fire interval
<i>Leucadendron album</i>	ldalbu	213	LC	na	"∩"	"U"	"∩"	"U"
<i>L. coniferum</i> Δ	ldcfrm	287	VU	"U"	"∩"	na	"U"	na
<i>L. eucalyptifolium</i>	ldeuca	1407	LC	"U"	"U"	"U"	"_"	na
<i>L. laureolum</i>	ldlaur	458	LC	na	"U"	"U"	na	"U"
<i>L. modestum</i>	ldmode	223	EN	na	na	"U"	"∩"	na
<i>L. muirii</i>	ldmuir	203	LC	"U"	na	na	na	na
<i>L. rubrum</i>	ldrubr	1538	LC	"U"	"U"	"U"	"U"	"U"
<i>L. xanthoconus</i>	ldxant	891	LC	na	na	"U"	"U"	na
<i>Protea amplexicaulis</i>	prampl	377	LC	"∩"	na	"U"	na	na
<i>P. compacta</i> #	prcpct	391	NT	"U"	"∩"	"∩"	"U"	na
<i>P. eximia</i>	prexim	840	LC	"∩"	na	"U"	"∩"	"∩"
<i>P. laurifolia</i>	prlaur	2752	LC	"_"	na	"+"	na	"_"
<i>P. longifolia</i>	prlong	453	VU	"U"	"U"	"U"	na	"U"
<i>P. lorifolia</i>	prlori	1469	LC	"U"	"U"	"U"	na	"∩"
<i>P. neriifolia</i> #¶	prneri	1811	LC	"U"	"U"	"U"	"U"	"U"
<i>P. obtusifolia</i> Δ	probtu	470	NT	"U"	na	na	"U"	na
<i>P. punctata</i>	prpunc	707	LC	"U"	"U"	"U"	"U"	na
<i>P. repens</i> #¶	prrepe	4070	LC	"U"	"U"	"U"	"U"	"U"

Table S4.1 (continued)

Species name	Abbreviation (Rebelo, 2001)	Range size (1' × 1' grid cells)	IUCN Red List status	AI	Tmin	Tmax	Soil fert	Fire interval
<i>P. susannae</i> Δ	prsus	359	NT	"U"	na	"U"	na	na
<u><i>L. salignum</i></u>	ldsgnm	6007	LC	"U"	"∩"	"U"	na	"U"
<u><i>L. spissifolium</i></u>	ldspis	1338	LC	"∩"	na	na	na	na
<u><i>P. acaulos</i></u>	pracau	891	LC	"_"	"∩"	"U"	na	"_"
<u><i>P. cynaroides</i></u>	prcyna	1719	LC	na	"U"	"U"	"U"	na
<u><i>P. nitida</i></u>	prniti	2727	LC	"U"	"U"	"U"	"U"	"∩"
<u><i>P. scabra</i></u>	prscbr	476	NT	na	"U"	na	na	na
<u><i>P. scolopendriifolia</i></u>	prsrfl	484	LC	na	"U"	na	"∩"	na
	"U"			14	12	18	10	7
	"_"			2	0	0	1	2
	"+"			0	0	1	0	0
	"∩"			3	5	1	4	3
	na			7	9	6	11	14

Underlined = resprouter; Symbols indicate species previously investigated as per: # Cabral et al (2011): *P. repens*, *P. neriifolia* and *P. compacta*; ¶ Maze & Bond (1996): *P. repens*, *P. neriifolia*; Δ Mustart & Cowling (1992): *P. obtusifolia*, *P. susannae*, *L. coniferum*.



CHAPTER 5:
CONCLUSION & SYNTHESIS

In the 21st century, global change is expected to have detrimental effects on biodiversity by causing shifts in abundance, distributions and extinction rates of organisms (Urban *et al.* 2015; Scheffers *et al.* 2016; Pecl *et al.* 2017). To understand the resilience and tolerance limits of species to such ongoing change, we require an integrative understanding of the environmental drivers and underlying functional determinants of species' ecological performance, population dynamics and niches (McGill *et al.* 2006; Schurr *et al.* 2012a; Violle *et al.* 2014; Nadeau, Urban & Bridle 2017). Studying the demographic responses of species and populations across different environments and disturbance regimes offer a means to assess the importance of these drivers for ecological performance (Schurr *et al.* 2012a; Ehrlén & Morris 2015). In turn, how variation in traits define ecological niches provides a more general understanding of the inherent tolerance limits of different species (Williams *et al.* 2008; Araújo *et al.* 2013; Moran, Hartig & Bell 2016). These approaches are also considered useful to understand the drivers of species' geographical ranges and range limits, and may help to project the effects of changing environmental conditions on species (Schurr *et al.* 2012a; Ehrlén & Morris 2015; Estrada *et al.* 2016). Beyond these scientific merits, such an understanding is also important for conservation planning and management recommendations to mitigate the impacts of climate change on biodiversity (Araújo *et al.* 2004; Hampe & Petit 2005; Dawson *et al.* 2011). Only when we understand the environmental context where species currently persist and identify where they are likely to occur in future, can we develop effective strategies to conserve biodiversity in a rapidly changing world.

In this dissertation, I used 26 serotinous Proteaceae species with fire-dependent life cycles in the Cape Floristic Region (CFR, South Africa) as 'model organisms' (Schurr *et al.* 2012b) to investigate how environmental variation and functional traits affect demography, population dynamics and species' ecological niches. Specifically, demographic and functional perspectives

were used to address fundamental and applied objectives relevant to ecology and conservation biogeography. From a fundamental perspective, my research in Chapter 2 showed how key demographic rates (or vital rates) of reproduction and survival are shaped by environmental variation and population density across species' geographical distributions. This range-wide demographic study highlighted an important interplay between drivers of fire and climate that differentially shape species' population dynamics at large spatial extents. It further showed high intraspecific variation in key demographic rates, notably fecundity and recruitment. In Chapter 3, I showed how variation in functional traits explains variation in the demographic performance and thereby the Hutchinsonian niches of species. This investigation revealed strong relationships between traits and characteristics of species niches and thus provides a novel framework for resolving relationships between trait variation, performance and the abiotic environment across species' geographical distributions. Finally, from an applied perspective, I showed in Chapter 4 how range-wide demographic data can be integrated into population viability analyses to assess geographical variation in sensitivity to wildflower harvesting. Wildflower harvesting compromised population viability across the geographical distributions of species. Population-level sensitivity to harvesting was associated with geographical location and environmental variation, notably sensitivity increased towards the environmental extremes of species' ranges. These findings illustrate the importance of jointly considering range-wide demographic and environmental variation when studying population responses to harvesting, and provide insights for the sustainable management of species across their geographical distributions.

Together, the demographic and functional investigations of this dissertation significantly extend the taxonomic and geographical cover of previous studies in plant ecology. In terms of the fundamental and applied ecological aspects encompassed in this dissertation, the following

perspectives are highlighted to provide guidelines for prospective studies and insights for global change.

Throughout my investigations, I found that resprouter species (i.e. species having fire-protected traits, such as buds or underground meristems; Clarke *et al.* 2013) were more tolerant to fire disturbance. Resprouters showed very high fire survival rates (Chapter 2) and their fire niches were defined by a strong effect of resprouting ability (i.e. resprouters can tolerate both shorter and more variable fire intervals; Chapter 3). These species were generally also less sensitive to wildflower harvesting (Chapter 4). Resprouters are known to have distinct fitness advantages since they possess the ability to rapidly recover after fire and establish long-lived, persistent adults (Higgins, Flores & Schurr 2008; Clarke *et al.* 2013; Pausas *et al.* 2016). In contrast to these persistence strategies of resprouters, nonsprouters (i.e. fire-killed species without fire protected buds; Clarke *et al.* 2013) were more susceptible to fire disturbance with very high fire mortality rates (Chapter 2). These obligate seeders rely entirely on their canopy seedbanks to regenerate after fire and face so-called ‘immaturity risk’ if fire intervals are short (Zedler 1995; Kraaij *et al.* 2013), whereas they are prone to senescence at long fire-free intervals (>15 years, Treurnicht *et al.* 2016, Chapter 2 of this dissertation). There are certain functional traits (notably variation in leaf N, leaf longevity and SLA) that depicted nonsprouters as species that are “fast” reproducing and rapid colonisers (Chapter 3). It would be interesting to study how these traits respond, and whether species respond differentially, to the changing fire regimes of the study biome (e.g. Wilson, Latimer & Silander 2015). Considering other fire regime variables, such as fire season and the intensity of fires, on the population dynamics of species also requires further investigation (cf. Kraaij *et al.* 2014; 2017).

Although adult resprouters are able to survive fire, their post-fire survival ability may be compromised under increasingly arid climates (Enright *et al.* 2014). This may likely be due to variation in the hydraulic and bud protection strategies of newly formed shoots which may be particularly vulnerable in the immediate post-fire environment (Clarke *et al.* 2013; Pausas *et al.* 2016). I, however, found that resprouters are able to persist under a broader range of cold-stressed environments (Chapter 3). This aligns with their ability to tolerate harsher climatic conditions (Clarke *et al.* 2013; Pausas *et al.* 2016) and supposes that they may be able to cope with more variable environments, indicating where resprouters may potentially persist (for example, the high altitude environments in the CFR often associated with colder winters). Interestingly, the recruitment rates of one resprouter (*P. cynaroides*) also responded positively to an increasing amount of frost days (Chapter 2). An understanding of how exactly changing environmental conditions, including both climate and fire regimes (and considering both in unison), will act on both resprouters and nonsprouters remains unclear and should provide a stimulus for further investigation. A combination of experimental approaches by studying post-fire germination responses of seedlings (cf. Mustart *et al.* 2012), adult resprouting responses (by marking individuals over several fire cycles), as well as manipulating environmental conditions *in situ* can be used to explore these aspects.

The demographic analyses in this dissertation considered interspecific competition only implicitly (e.g. by quantifying the realised or ‘post-interactive’ Hutchinsonian niche). Investigating the specific role of biotic interactions and their variation across species’ ranges thus remains a necessary step for future research. Notably, studies performed at more local scales have shown that Proteaceae communities are structured by direct competition and indirect (e.g. pollinator-mediated) biotic interactions, and potentially also community-level Allee-effects (Nottebrock *et al.* 2017a, Nottebrock *et al.* 2017b). The integration of data across large spatial scales would be a promising research agenda to better understand how the

interaction of community-level processes with species-specific demographic variation across environmental gradients shapes biodiversity dynamics.

Despite the range-wide data collection efforts of this dissertation, ongoing data collection and the long-term monitoring of species remains an imperative task in biodiverse regions. In the CFR biodiversity hotspot, plant ecologists are able to capitalise on “real-world” experiments brought about by changing environmental conditions throughout the region. The CFR thus provides ideal opportunities to monitor responses of species to ongoing global change. It is also timeous to consider joint research agendas by integrating existing range-wide demographic datasets, along with transplant experiments and regional abundance data (Latimer *et al.* 2009). This research agenda may provide a more comprehensive approach to climate change forecasts and the adaptive capacity of species (Dawson *et al.* 2011; Thuiller *et al.* 2014). Such an integration of approaches can also be used to test the assumptions from species distribution models (Guisan & Thuiller 2005). Furthermore, the integration of wildflower harvesting experiments under different post-fire ages, population densities and environmental conditions is needed (cf. Chapter 4). Moreover, a proper regional (geo-referenced) inventory and resource-based assessment of wildflower harvesting in the CFR is currently lacking (Van Wilgen *et al.* 2016).

Globally, fire regimes and climate are expected to change in future (IPCC 2013). In particular, the CFR faces an uncertain future in the face of global change (Midgley & Bond 2015; Wilson, Latimer & Silander 2015; Slingsby *et al.* 2017). It is therefore crucial to consider both fire and climate in biodiversity research and conservation planning. Variation in fire and climate played a pronounced role in determining the demography and population dynamics of the 26 study species and, ultimately, will jointly determine the future persistence of species in the face of

global change. Demographic responses to variation in climatic conditions and fire regime, and responses to wildflower harvesting were strongly differentiated among the study species. The individualistic responses to global change will therefore likely result in large-scale reshuffling of species and communities in the CFR. Moreover, habitat loss is expected to isolate populations, increase extinction risk and limit gene flow threatening the future persistence of many species (Davis & Shaw 2001; Cabral *et al.* 2013). Although predicting the impacts of climate change on biotic systems is a challenging task, the recent availability of comprehensive global databases (Kattge *et al.* 2011; Salguero-Gómez *et al.* 2015; Salguero-Gómez *et al.* 2016), novel computational models, as well as high resolution climate data (e.g. Karger *et al.* 2017) puts ecologists in a steady position to address this challenge.

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APPENDIX A

DESCRIPTION OF DEMOGRAPHIC NICHE MODELS

*This work is currently *in prep.* as: Pagel, J., Treurnicht, M. *et al.* Demographic niches as a basis to disentangle drivers of geographic range formation in plants.

Appendix A – Demographic niche models

This appendix describes the estimation of demographic niche models based on the data and analyses presented in chapter 2. The materials that are reproduced here have been prepared to appear as supplementary material in

Pagel, J., Treurnicht, M., *et al.* Demographic niches as a basis to disentangle drivers of geographic range formation in plants. *in prep.*

Study species and demographic data

Our study includes 26 species of the Proteaceae family, specifically of the genera *Protea* (16 species) and *Leucadendron* (10 species), that were chosen to represent variation in geographical distributions throughout the Cape Floristic Region (Rebello 2001) and in life-history traits like dispersal capability and resprouting ability. For each species we obtained data on between-population variation in key demographic rates across the plants' entire life cycle (Treurnicht *et al.* 2016; see Chapter 2 of this dissertation). Fecundity data was collected as the number of fertile seeds in the canopy seed bank (*#Seeds*) of each of five individuals per population. Data on post-fire recruitment was collected on transects in recently burned sites (one to three years after fire) by recording the numbers of post-fire recruits (*#Recruits*) and of potential pre-fire parents (*#Parents*, which for dioecious *Leucadendron* species includes only females). Counting pre-fire adults is possible, because the burned skeletons can still be identified also for plant individuals that died in the recent fire. Hence, also the total number of pre-fire adults (*#All.Adults*) and the number of individuals still alive after the fire (*#Survivors*) could be recorded to estimate fire survival rates. For further details on the field sampling protocol see Treurnicht *et al.* (2016). Study sites for demographic sampling were selected to cover major environmental gradients in the geographical distribution of each study species and the data from these sites was combined with existing datasets collected by CapeNature from 1979-2011 (CapeNature, unpublished data) and SANParks from 2007-2012 (Kraaij *et al.* 2013). Additionally, we also included post-fire recruitment data from Heelemann *et al.* (2008; 2011) and other unpublished data sources (W.J. Bond; R.M. Cowling; F.M. Schurr respectively).

Environmental variables

Climatic and edaphic variables expected to be main determinants of the performance and survival of serotinous Proteaceae were extracted from the South African Atlas of Climatology and Agrohydrology (Schulze 2007) as long-term averages (1950 – 2000) and with a spatial resolution of $1' \times 1'$ (c. $1.55 \text{ km} \times 1.85 \text{ km}$). We included July minimum daily temperature (*Tmin*), January maximum daily temperature (*Tmax*) and a *January aridity index* calculated as the ratio between the monthly mean values of precipitation *P* and temperature *T*: $AI = P / (T + 10^\circ\text{C})$ (De Martonne, 1926). As an edaphic variable, we used a *soil fertility index* that combines soil texture and base status and ranges from 0 to 10. Information on the fire regime, another important driver of the study species' demography, was obtained from both observational records and model predictions. For the demographic sampling sites, the fire

history (time since the last fires and length of the previous fire interval) was inferred from a combination of measured plant ages (based the number of branches and internodes on the tallest stem of Proteaceae shrubs), information from landowners and conservation managers, a historical fire database or from satellite observations (see Treurnicht et al. 2016, Chapter 2 for details).

Demographic niche model

The aim of the presented statistical analysis is to estimate how environmental conditions, fire return intervals and density dependence affect key demographic rates of each of our study species in order to quantify species' niches in terms of the predicted environmental response of population growth rates. The demographic rates of interest, which together describe the entire life cycle of serotinous Proteacea, are the total fecundity of individuals, the establishment rate per seed and the rate of adult fire survival. While the available demographic data is directly informative on total fecundities and fire survival rates, direct estimation of establishment rates in the field sites would require knowledge of the total number of shed seeds from which the observed recruits emerged. To address this data gap, we use a hierarchical modelling approach that integrates the different types of demographic data across the study sites. Specifically, the model jointly estimates predictors of fecundity and establishment rate from both the fecundity data and the recruitment data. In order to describe the recorded number of recruits after a fire as the combined outcome of pre-fire fecundity and post-fire establishment, the (unobserved) total size of the pre-fire canopy seed bank is included as a latent variable in the model. A graphical overview of the model structure is given in Fig. A.1 and in the following we describe the model components for each demographic rate.

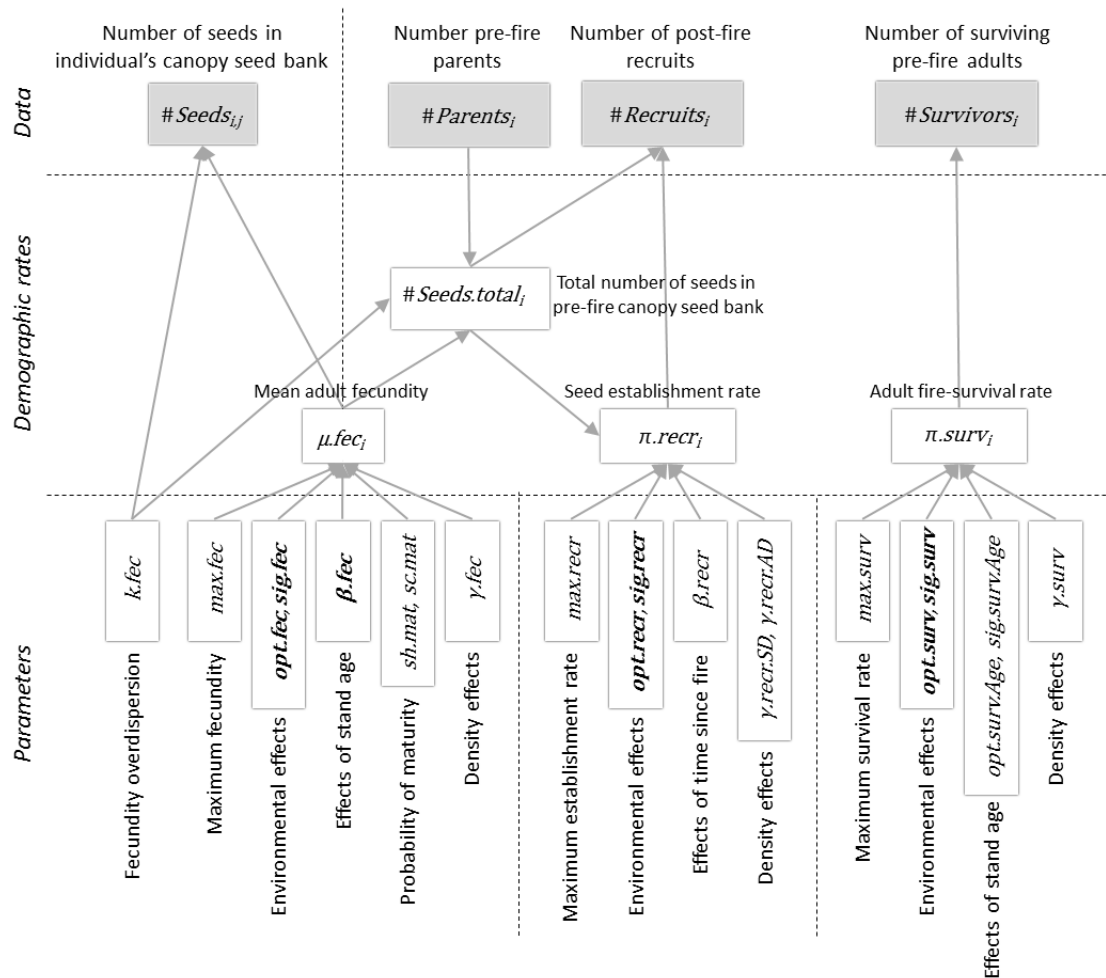


Figure A.1. Structure of the hierarchical model for inferring drivers of variation in key demographic rates from the different data types recorded across populations for each study species.

Fecundity

The recorded size of the canopy seed bank ($\#Seeds_{i,j}$) of plant j in population i is described by an overdispersed Poisson distribution

$$\#Seeds_{i,j} \sim \text{Poisson}(Fec_i)$$

$$Fec_i \sim \text{Gamma}\left(\frac{\mu.fec_i}{k.fec}, k.fec\right)$$

where the expected value of mean fecundity $\mu.fec_i$ is determined by limiting effects of post-fire stand age (Age_i), environmental covariates (\mathbf{X}_i) and population density (D_i):

$$\mu.fec_i = max.fec \cdot f(Age_i) \cdot g(\mathbf{X}_i) \cdot h(D_i)$$

Effects of stand age on fecundity arise from the time of maturation until the first flowering and cone production, increasing accumulation of standing cones on growing plants and possibly senescence of aged individuals:

$$f(\text{Age}_i) = M_i \cdot \exp(\beta \cdot \text{fec}_1 \cdot \text{Age}_i + \beta \cdot \text{fec}_2 \cdot (\text{Age}_i)^2)$$

where M_i is a binary random variable (0, 1) indicating maturity. The probability of population-level maturity is calculated from a Weibull distribution for the age ($t.mat$) of first cone production:

$$M_i \sim \text{Bernoulli}(p.mat_i)$$

$$p.mat_i = \text{Pr}(t.mat < \text{Age}_i)$$

$$t.mat \sim \text{Weibull}(sh.mat, sc.mat)$$

For nonsprouting species, the minimum time to reproductive maturity is in addition set to three years (Rebelo, 2001).

The effects of different environmental covariates $k = 1 \dots K$ are described by Gaussian demographic response functions:

$$g(\mathbf{X}_i) = \exp\left(\sum_{k=1}^K \frac{-(X_{i,k} - \text{opt.fec}_k)^2}{2 \cdot \text{sig.fec}_k^2}\right)$$

where the mean opt.fec_k denotes the optimal conditions and the inverse variance ($1/\text{sig.fec}_k^2$) measures the strength of the response to deviation from the optimum for each environmental factor k .

Density effects on seed production are described as exponential decline of fecundity with increasing population density (D_i):

$$h(D_i) = \exp(-\gamma \cdot \text{fec} \cdot D_i)$$

Establishment

Establishment is modelled as a binomial process for the number of recorded recruits ($\#Recruits_i$) in population i that depends on the total number of available seeds in the canopy seed bank at the time of the last fire ($\#Seeds.total_i$) and the establishment rate $\pi.rec_r_i$, which is the probability per seed to become an establish recruit:

$$\#Recruits_i \sim \text{Binomial}(\#Seeds.total_i, \pi.rec_r_i)$$

Since $\#Seeds.total_i$ is unknown for the recently burned sites where recruitment was recorded, it is modelled as a latent variable:

$$\#Seeds.total_i \sim \text{Poisson}(\#Parents_i \cdot \text{Fec}_i)$$

where $\#Parents_i$ denotes the number of pre-fire parents and Fec_i being dependent on environmental covariates (\mathbf{X}_i) as well as the stand age (Age_i) and the adult population density (D_i) at the time of the previous fire, as described above.

Recruitment rate $\pi.rec_r_i$ is affected by environmental covariates (\mathbf{X}_i) and density effects:

$$\pi.rec_r_i = \text{max.rec_r} \cdot g(\mathbf{X}_i) \cdot h(\text{SD}_i, \text{AD}_i, \text{Age}_i)$$

As for fecundity, the effects of different environmental covariates $k = 1 \dots K$ are described by Gaussian demographic response functions:

$$g(\mathbf{X}_i) = \exp\left(\sum_{k=1}^K \frac{-(X_{i,k} - \text{opt.recr}_k)^2}{2 \cdot \text{sig.recr}_k^2}\right)$$

Establishment is affected by density effects from other seedlings ($SD_i = \#Seeds.total_i / \text{Transekt.Area}_i$) as well as from fire-surviving adults ($AD_i = \#Survivors_i / \text{Transekt.Area}_i$):

$$h(SD_i, AD_i) = \frac{1}{1 + c_i(\gamma.recr.SD \cdot SD_i + \gamma.recr.AD \cdot AD_i)}$$

Here the multiplier c_i is included to account for differences in the time since fire (tsf_i) at which recruitment data were recorded on each side. It reflects higher expected seedling counts during earlier phases of ongoing self-thinning, which generally occurs within three years after fire in CFR Proteaceae (Manders & Smith 1992, Treurnicht *et al.* 2016):

$$c_i = \begin{cases} \left(\frac{tsf_i}{3}\right)^{\beta.recr} & \text{if } tsf_i < 3 \\ 1 & \text{if } tsf_i > 3 \end{cases}$$

Survival

Fire survival is modelled as a binomial process for the number of surviving pre-fire adults ($\#Survivors_i$) in population i that depends on the total number of pre-fire adults ($\#All.Adults_i$) and the fire survival rate $\pi.surv_i$:

$$\#Survivors_i \sim \text{Binomial}(\#All.Adults_i, \pi.surv_i)$$

Variation in fire survival rates are again modelled in response to the environmental covariates (\mathbf{X}_i) and depending on stand age (Age_i) and population density (D_i) similarly as for fecundity:

$$\pi.surv_i = \text{max.surv} \cdot f(Age_i) \cdot g(\mathbf{X}_i) \cdot h(D_i)$$

$$f(Age_i) = \exp\left(\frac{-(Age_i - \text{opt.surv.Age})^2}{2 \cdot \text{sig.surv.Age}^2}\right)$$

$$g(\mathbf{X}_i) = \exp\left(\sum_{k=1}^K \frac{-(X_{i,k} - \text{opt.surv}_k)^2}{2 \cdot \text{sig.surv}_k^2}\right)$$

$$h(D_i) = \exp(-\gamma.surv \cdot D_i)$$

Note that here the population density refers to the density of adults ($\#All.Adults_i / \text{Transekt.Area}_i$) that occurred before the recent fire after which survival data were recorded, and likewise stand age (Age_i) denotes the age at the time of this fire (i.e. the length of the previous fire interval).

Since variation in the very low survival rates of nonresprouting species was small (Treurnicht *et al.* 2016, Chapter 2), we modelled those as species-specific constants and considered effects of covariates only for the survival rates of resprouting species.

Table A.1. Overview of prior distributions for all model parameters

Model parameter	Description	Prior distribution	Prior parameters	
Fecundity	$\log(max.fec)$	maximum fecundity (log)	Normal	$\mu = 0, \sigma^2 = 10^4$
	$opt.fec_k$	environmental optima	Normal	$\mu = 0, \sigma^2 = 10^4$
	$1/sig.fec^2_k$	env. response strengths	Exponential	$\lambda = 1$
	$\beta.fec$	age effects	Double-Exponential	$\mu = 0, \lambda = 1$
	$sh.mat$	Weibull parameters describing age of maturity	Gamma	$\alpha = 0.01, \beta = 0.01$
	$sc.mat$		Gamma	$\alpha = 0.01, \beta = 0.01$
	$\gamma.fec$	strength of density effects	Exponential	$\lambda = 1$
	$k.fec$	overdispersion parameter	Gamma	$\alpha = 0.01, \beta = 0.01$
Establishment	$max.recr$	maximum establishment rate	Beta	$a = 1, b = 1$
	$opt.recr_k$	environmental optima	Normal	$\mu = 0, \sigma^2 = 10^4$
	$1/sig.recr^2_k$	environmental response strengths	Exponential	$\lambda = 1$
	$\beta.recr$	effect of time since fire	Exponential	$\lambda = 1$
	$\gamma.recr.SD$	strength of density effects from seeds	Exponential	$\lambda = 1$
	$\gamma.recr.AD$	strength of density effects from adults	Exponential	$\lambda = 1$
Survival	$max.surv$	maximum survival rate	Beta	$a = 1, b = 1$
	$opt.surv_k$	environmental optima	Normal	$\mu = 0, \sigma^2 = 10^4$
	$1/sig.surv^2_k$	environmental response strengths	Exponential	$\lambda = 1$
	$opt.surv.Age$	age optimum for survival	Normal	$\mu = 0, \sigma^2 = 10^4$
	$1/sig.surv.Age^2$	age response strengths	Exponential	$\lambda = 1$
	$\gamma.surv$	strength of density effects	Exponential	$\lambda = 1$

Bayesian parameter estimation

Parameters of the model were estimated independently for each study species. All environmental variables were scaled and centred. The aridity index (AI) and soil fertility index were also log-transformed before the analyses. The hierarchical model was formulated in a Bayesian framework and samples from the parameter posterior distribution were generated with Markov chain Monte Carlo (MCMC) methods in the software JAGS (Plummer 2003). An overview of parameter prior distributions is given in Tab. A.1. In three replicated MCMC chains, posteriors were sampled from 100,000 iterations after a burn-in period of 500,000 iterations. Convergence was checked by the multivariate scale reduction factor of Gelman & Rubin (1992) being smaller than 1.1. For all further analyses, the posterior samples were regularly thinned to a sample size of 1,000 for each chain resp. 3,000 samples in total.

Table A.2. Explained variance (Nagelkerke's R^2_N) for the different types of demographic data.

Species	Nagelkerke's R^2_N		
	Fecundity	Recruitment	Survival*
<i>Leucadendron album</i>	0.91	0.69	
<i>Leucadendron coniferum</i>	0.38	0.46	
<i>Leucadendron eucalyptifolium</i>	0.38	0.38	
<i>Leucadendron laureolum</i>	0.29	0.45	
<i>Leucadendron modestum</i>	0.43	0.84	
<i>Leucadendron muirii</i>	0.34	0.36	
<i>Leucadendron rubrum</i>	0.48	0.05	
<i>Leucadendron salignum</i>	0.69	0.26	0.52
<i>Leucadendron spissifolium</i>	0.80	0.45	0.52
<i>Leucadendron xanthoconus</i>	0.56	0.44	
<i>Protea acaulos</i>	0.53	0.32	
<i>Protea amplexicaulis</i>	0.81	0.53	
<i>Protea compacta</i>	0.59	0.66	
<i>Protea cynaroides</i>	0.71	0.61	0.64
<i>Protea eximia</i>	0.67	0.48	
<i>Protea laurifolia</i>	0.55	0.12	
<i>Protea longifolia</i>	0.48	0.36	
<i>Protea lorifolia</i>	0.62	0.30	
<i>Protea neriifolia</i>	0.44	0.38	
<i>Protea nitida</i>	0.70	0.23	0.41
<i>Protea obtusifolia</i>	0.51	0.50	
<i>Protea punctata</i>	0.53	0.47	
<i>Protea repens</i>	0.73	0.17	
<i>Protea scabra</i>	0.63	0.51	0.81
<i>Protea scolopendrifolia</i>	0.69	0.50	0.83
<i>Protea susannae</i>	0.60	0.46	

*Note that variation in survival rates was modelled only for resprouting species.

Model evaluation

For each species the model fit was assessed separately for each observed demographic variable by calculating the general R^2 of Nagelkerke (1991) :

$$R_N^2 = \left[1 - \left(\frac{L_0}{L_{\hat{\theta}}} \right)^{\frac{2}{n}} \right] / \left[1 - \left(\frac{L_0}{L_{sat}} \right)^{\frac{2}{n}} \right],$$

Here, $L_{\hat{\theta}}$ denotes the likelihood of the respective observed data given the mean posterior estimate of all model parameters, L_0 denotes the likelihood for a null model, where mean per-capita demographic rates ($\mu.fec$, $\pi.rec$, $\pi.surv$) are estimated as species-specific constants, and L_{sat} denotes the likelihood for a saturated model, where these demographic rates are estimated as free parameters for each populations. Explained variance in each demographic variable for each study species is shown in Tab. A.2.

Prediction of population growth rates for the estimation of species' niches

The estimated model parameters allow to predict per-capita rates of fire survival $\pi.surv$, fecundity (size of canopy seed bank) $\mu.fec$ and recruitment (per seed) $\pi.rec$ as functions of environmental covariates \mathbf{X} , fire interval T (defining *Age* at time of fire) and the adult resp. seed densities (D , AD , SD). Based on these rates the new population size N after one fire interval of length T can be calculated as the sum of fire survivors and new recruits:

$$N_{t+T} = N_t \cdot \pi.surv(\mathbf{X}, T, D) + N_t \cdot p.fem \cdot \mu.fec(\mathbf{X}, T, D) \cdot \pi.rec(\mathbf{X}, SD, AD)$$

For dioecious *Leucadendron* species the parameter $p.fem$ specifies the sex ratio (proportion of female individuals in a population) and accounts for the fact that fecundity rates $\mu.fec$ are defined per female.

The niche of a species is defined as the set of environmental conditions for which the intrinsic growth rate of small populations (r_0) is positive. To calculate r_0 we set all density variables to zero and first calculate the rate of change in population size per fire interval

$$\lambda_0(\mathbf{X}, T) = \frac{N_{t+T}}{N_t} = \pi.surv(\mathbf{X}, T) + \mu.fec(\mathbf{X}, T) \cdot \pi.rec(\mathbf{X}) \cdot p.fem$$

The intrinsic growth rate is then calculate on an annual basis as

$$r_0(\mathbf{X}, T) = \frac{\log[\lambda_0(\mathbf{X}, T)]}{T}$$

A complete overview of the predicted responses of r_0 as well as of the underlying demographic rates is presented for all study species in Fig. A.2.

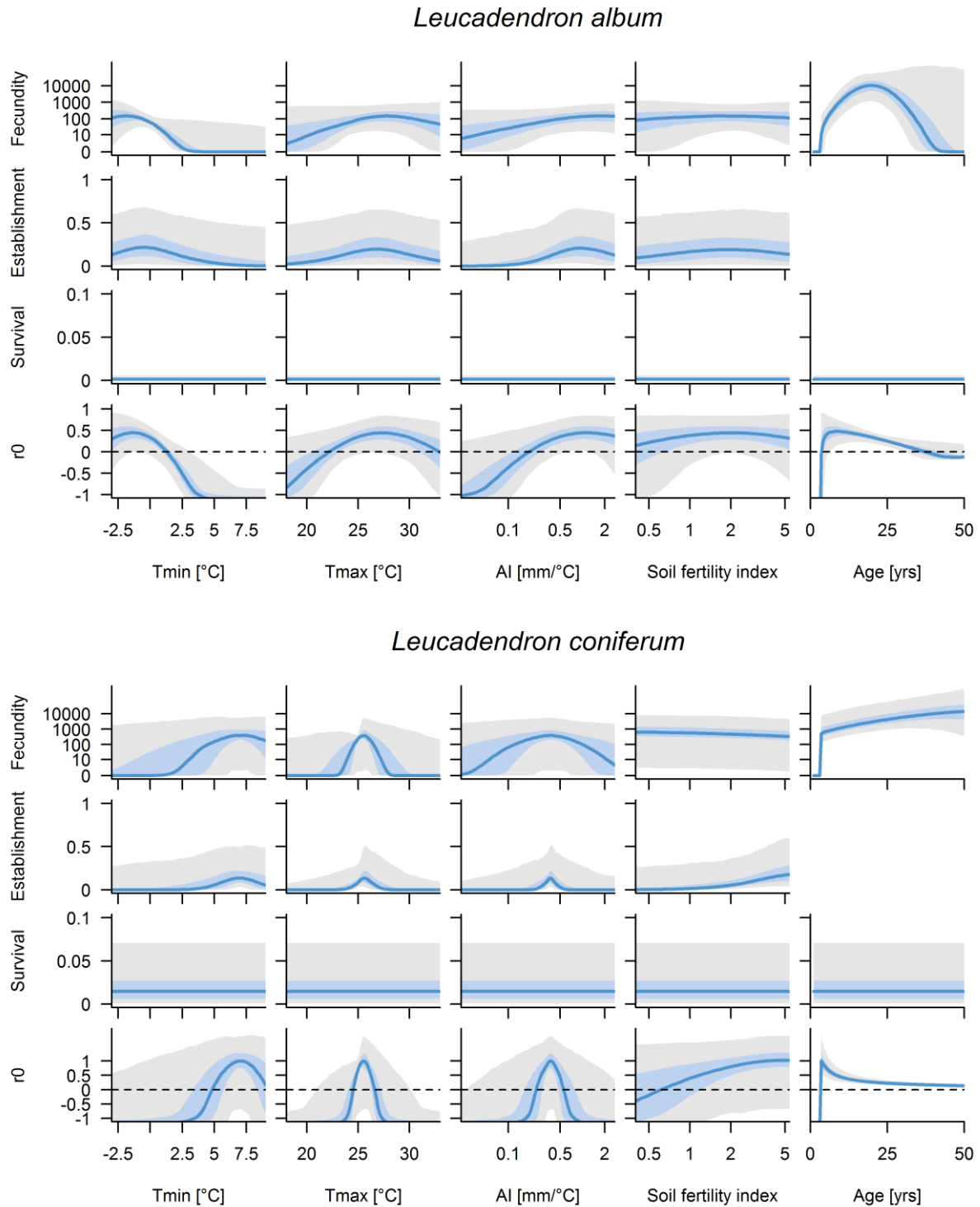


Figure A.2. Predicted responses of demographic rates ($\mu.fec$, $\pi.rec$, $\pi.surv$) and intrinsic population growth rate r_0 to environmental covariates and stand age at the time of fire (i.e. fire interval). Lines show the posterior median of predicted rates and the shaded areas the 50% (dark shading) resp. 95% (light shading) credibility intervals. Response curves were generated by varying each covariate over the range of environmental conditions in the study region (CFR) while keeping other covariates at the value that optimizes r_0 .

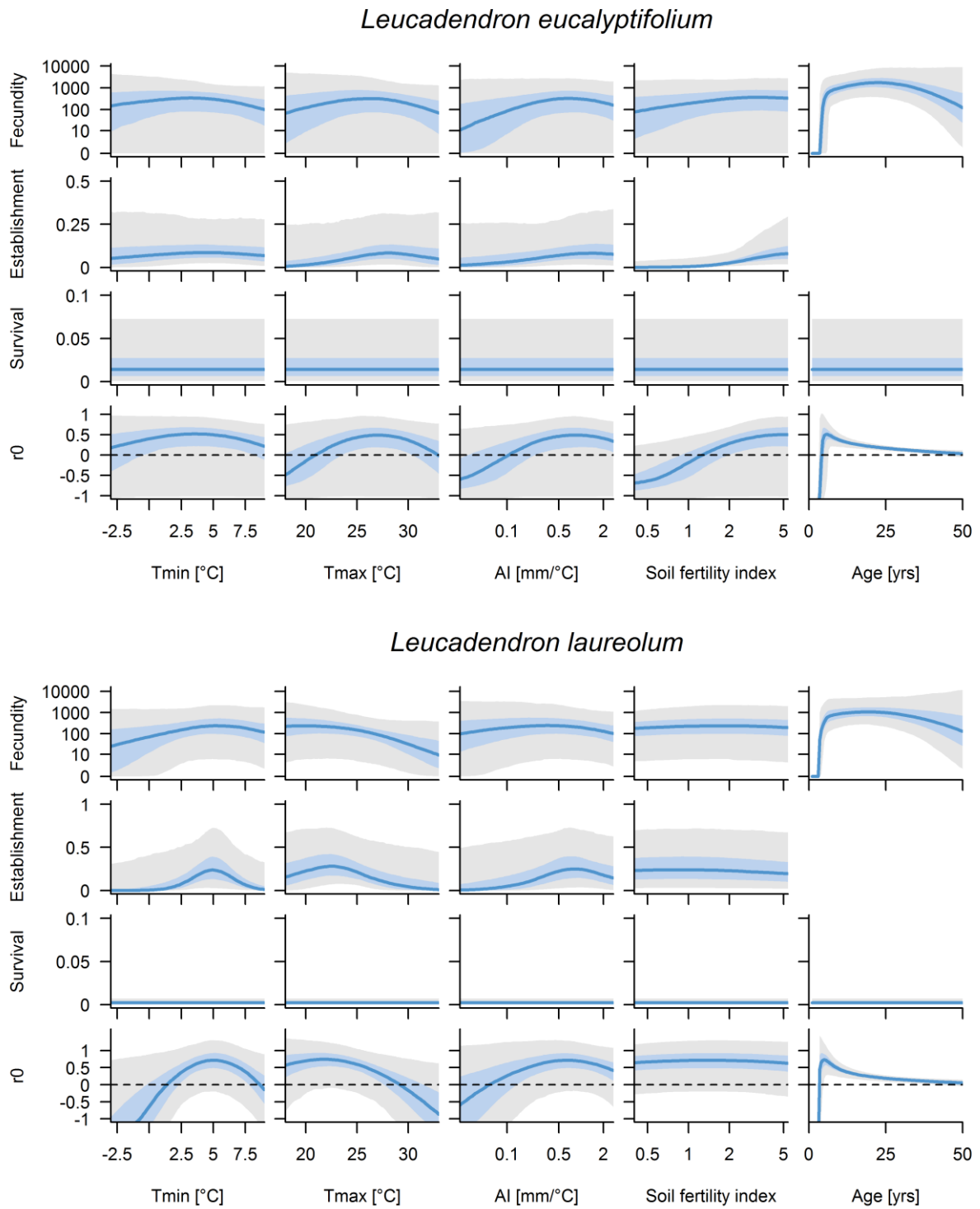


Figure A.2. (continued)

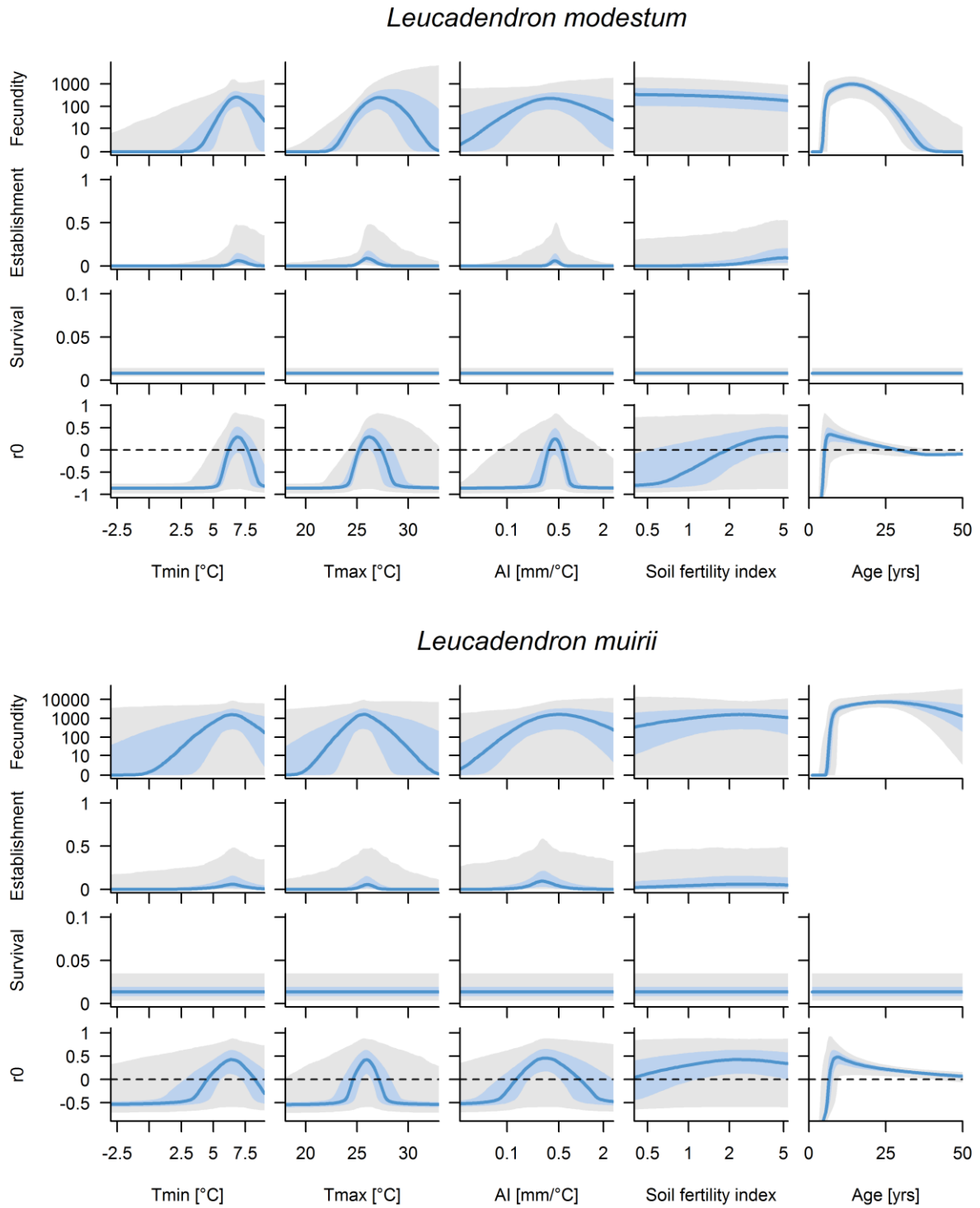


Figure A.2. (continued)

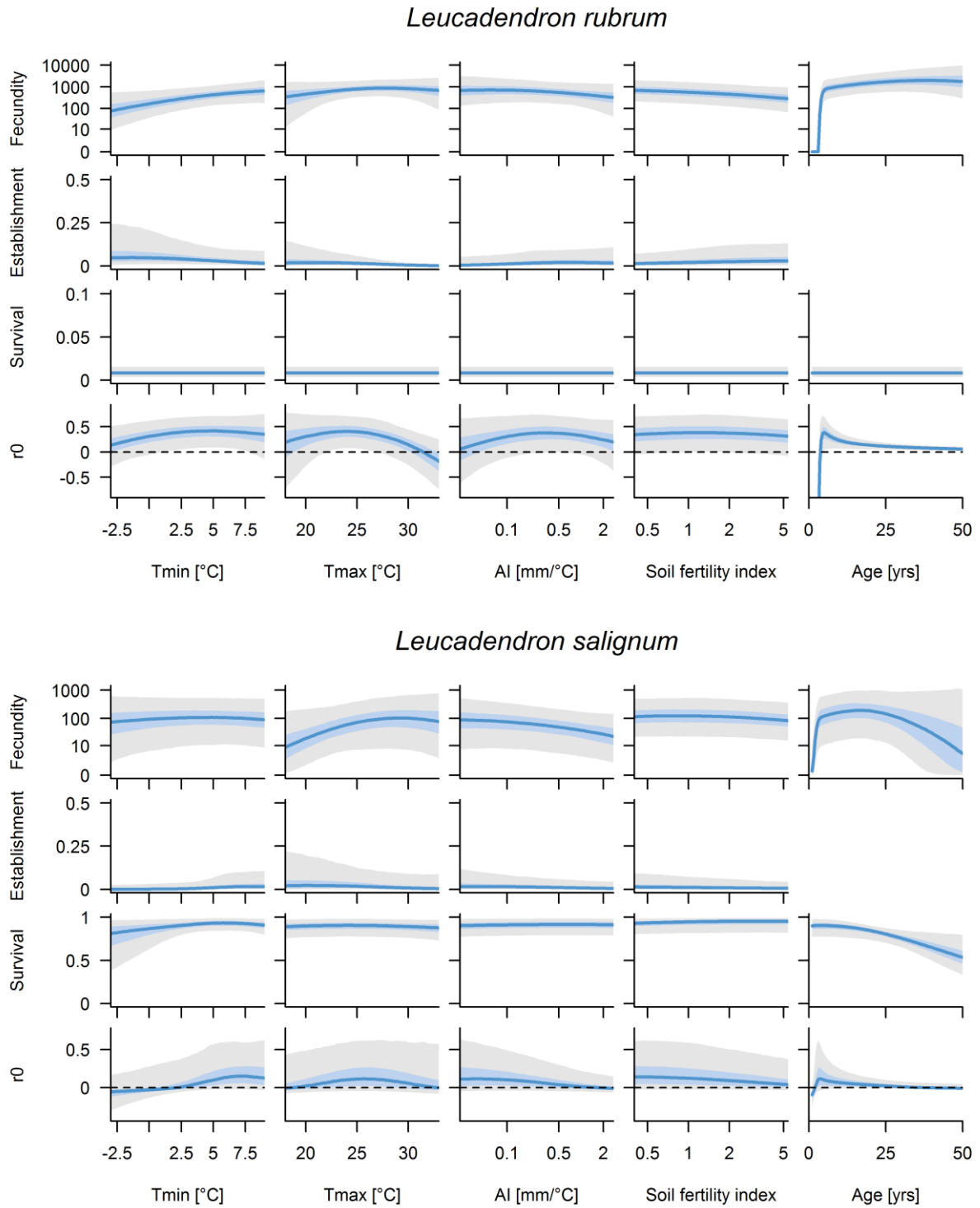
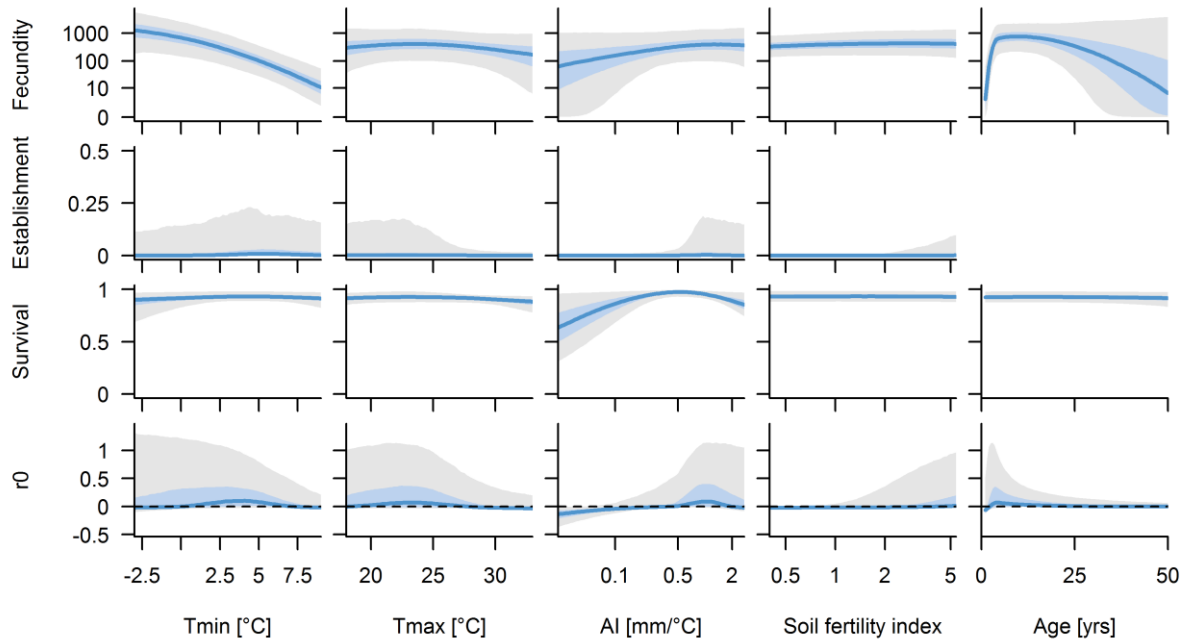


Figure A.2. (continued)

Leucadendron spissifolium



Leucadendron xanthoconus

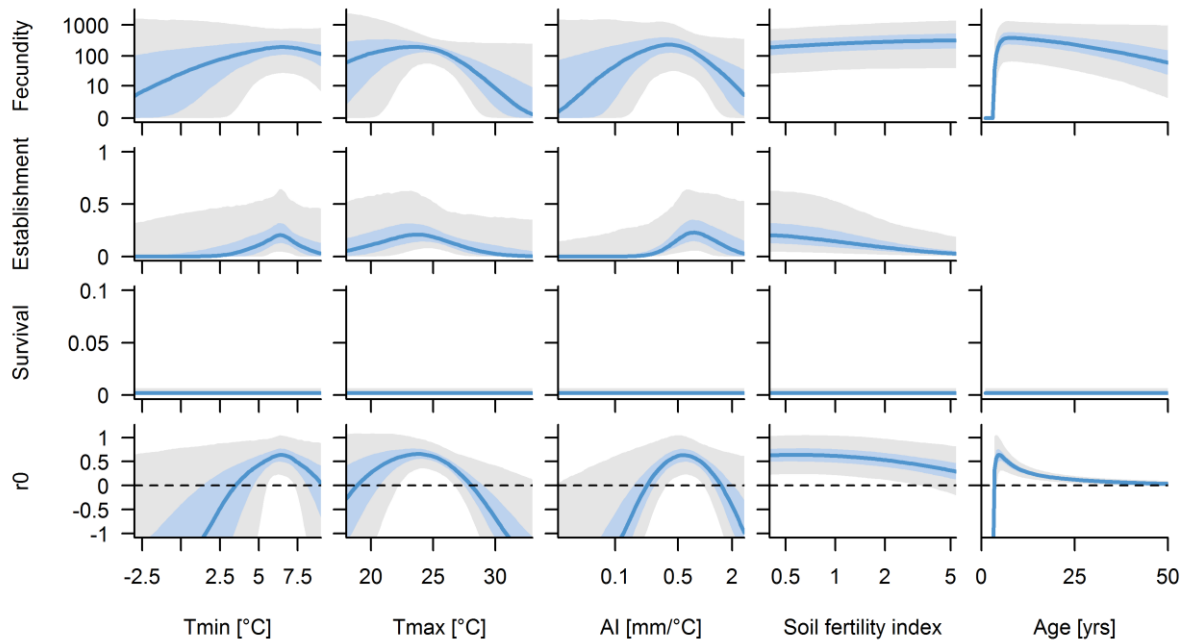


Figure A.2. (continued)

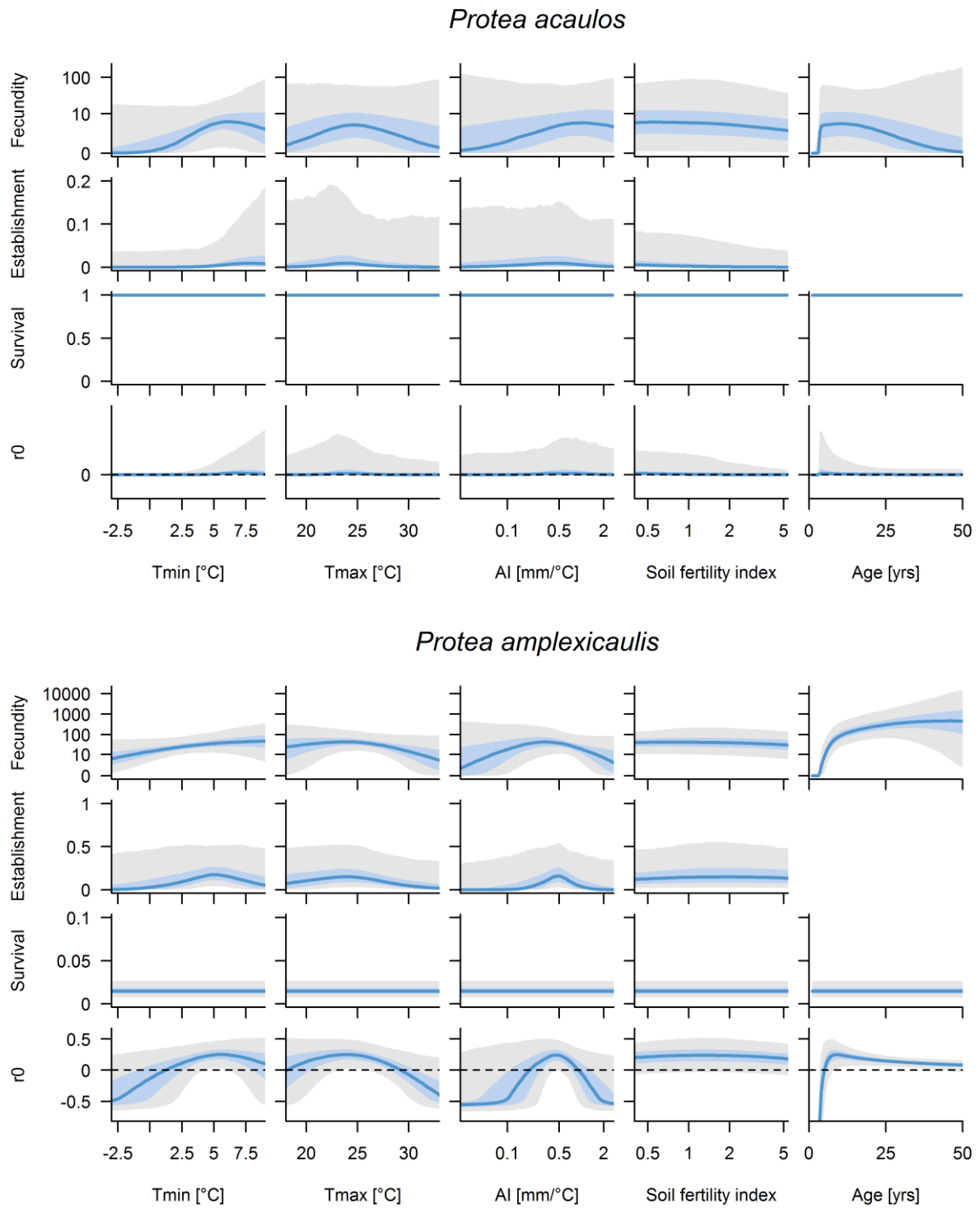


Figure A.2. (continued)

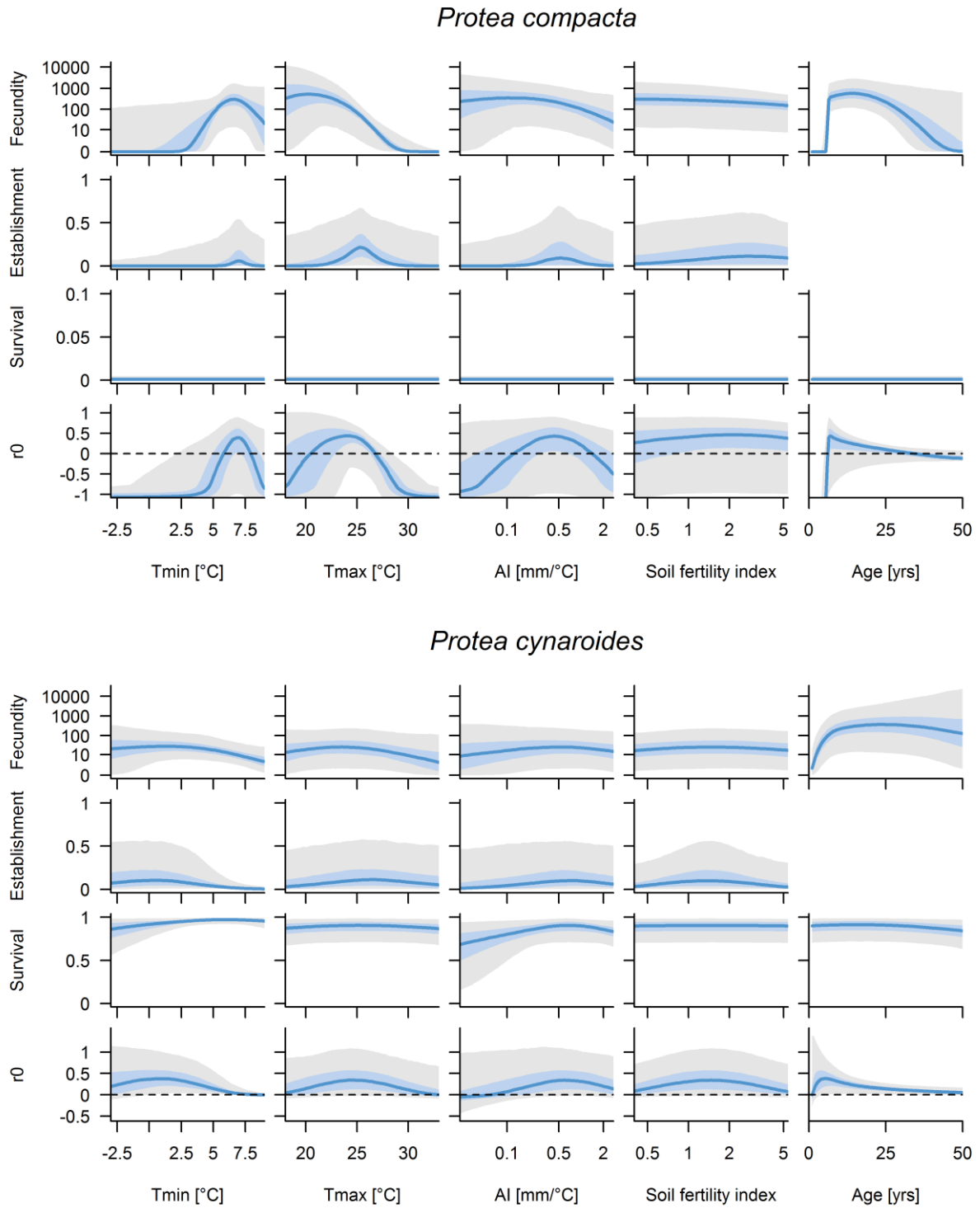


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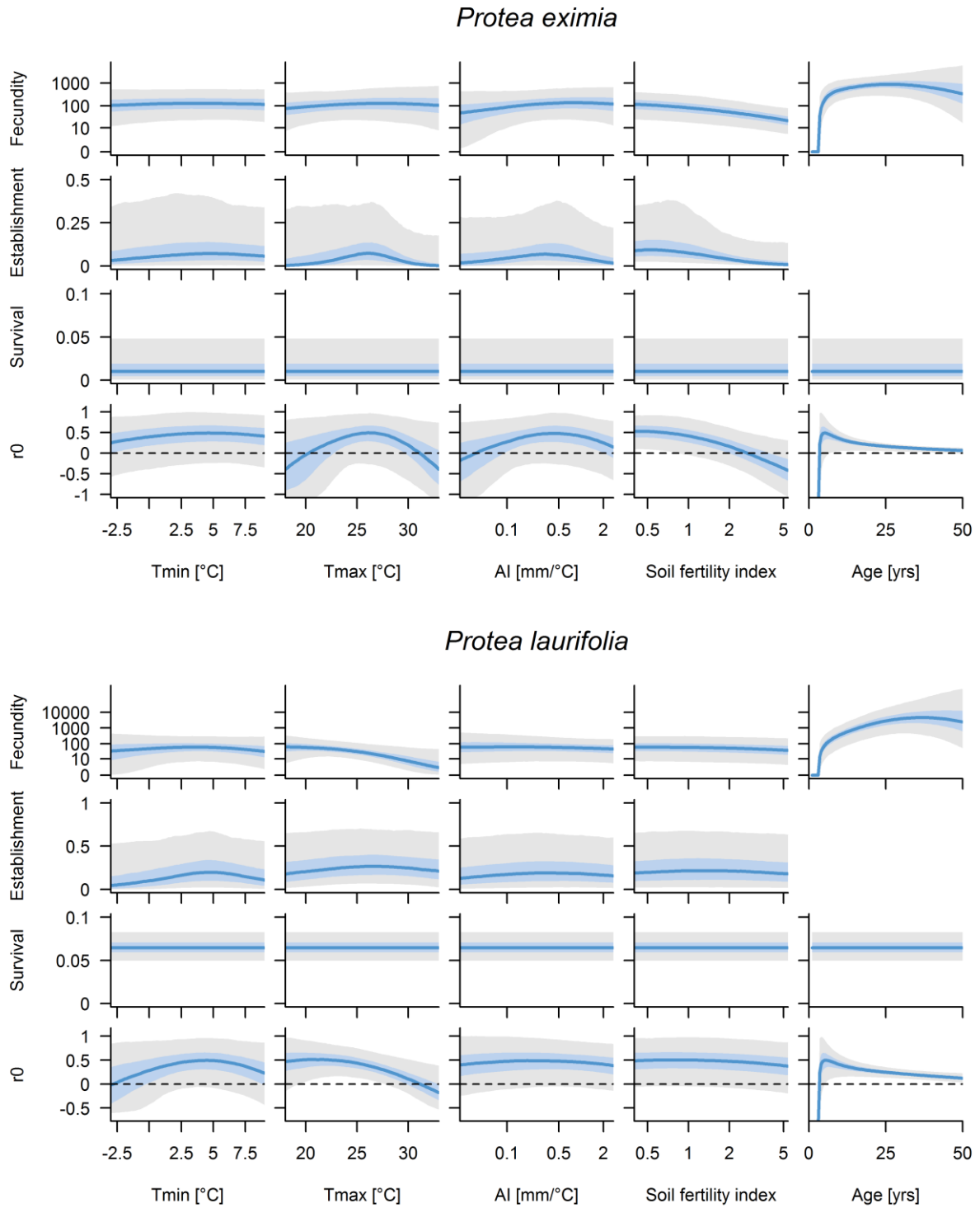


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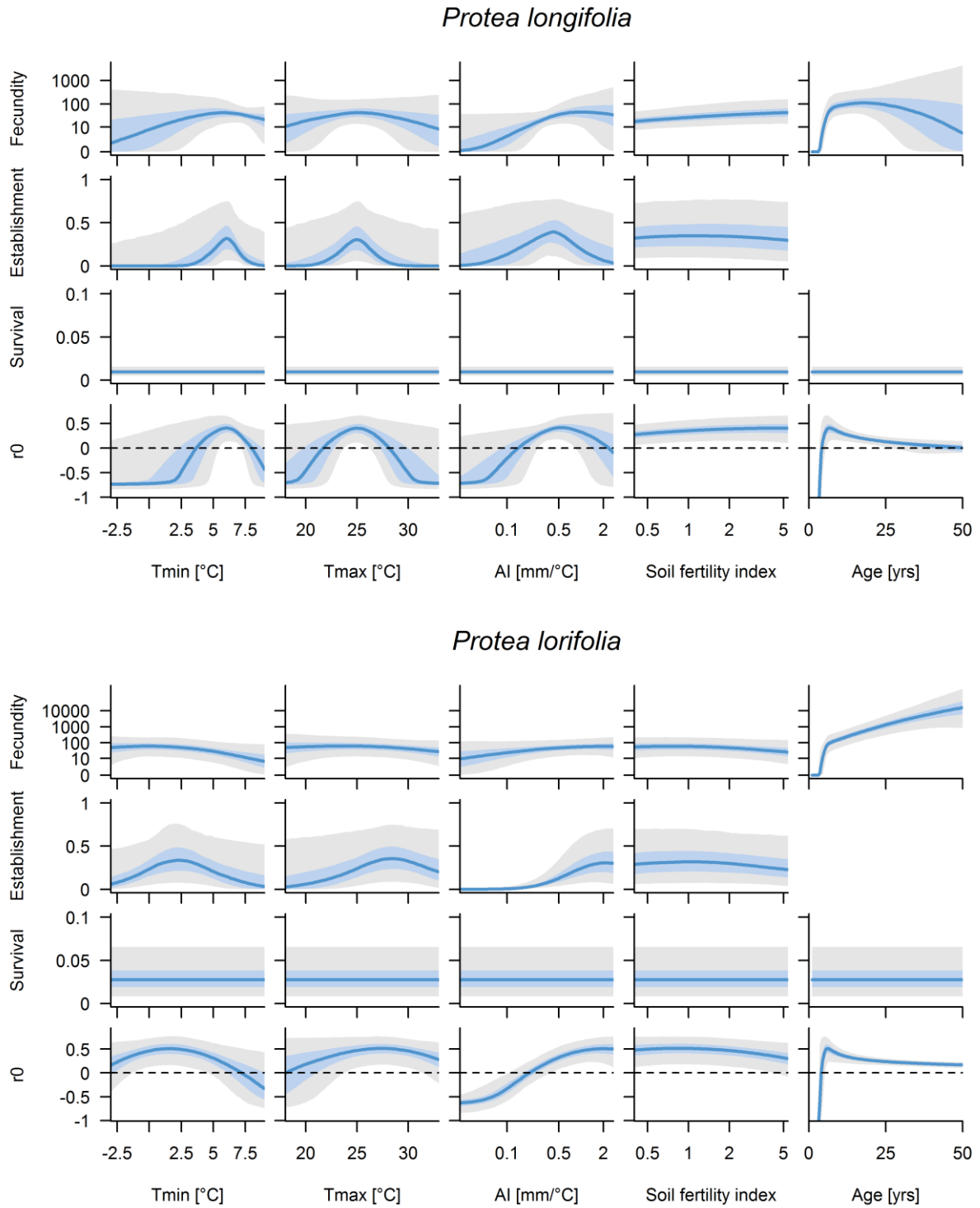


Figure A.2. (continued)

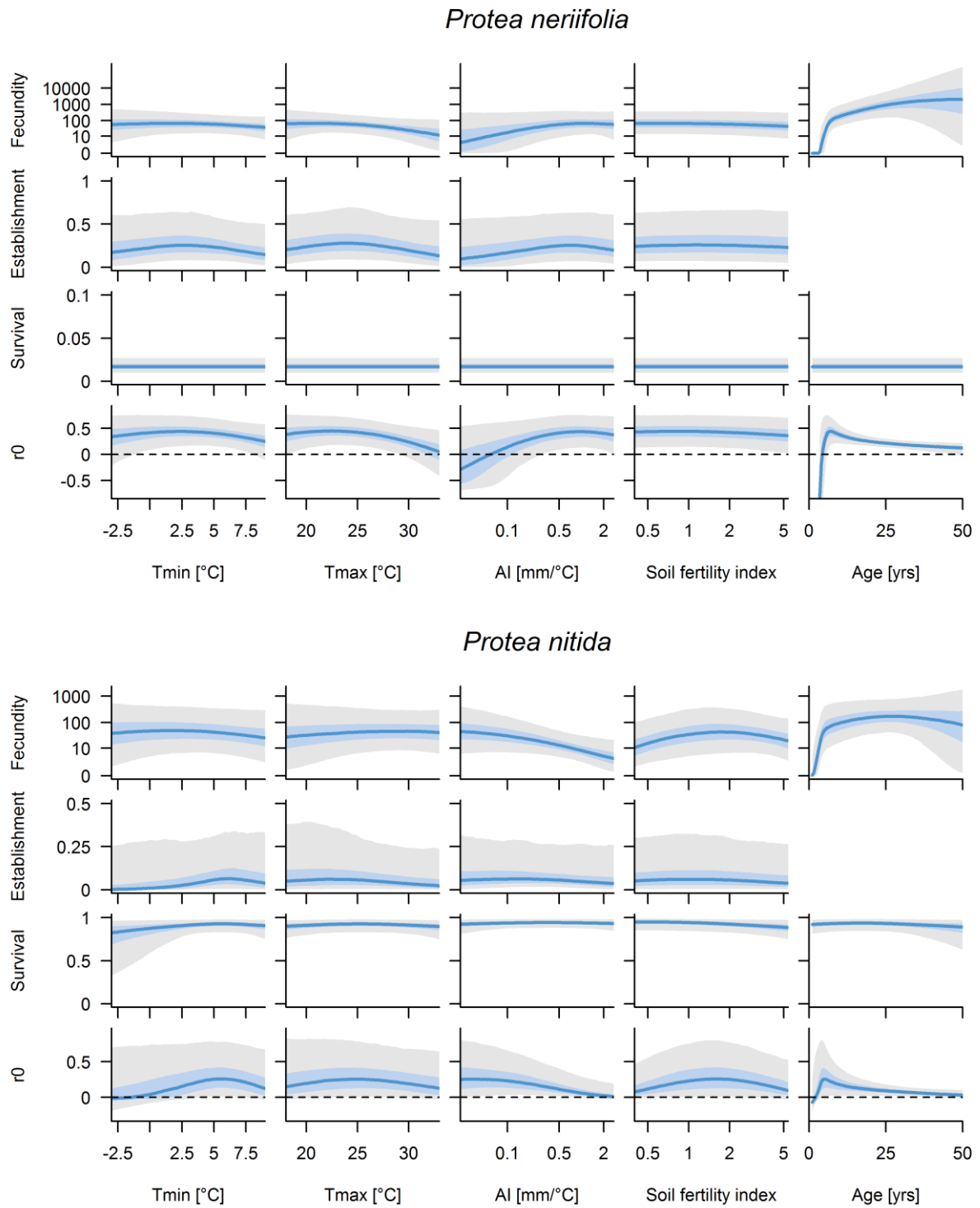


Figure A.2. (continued)

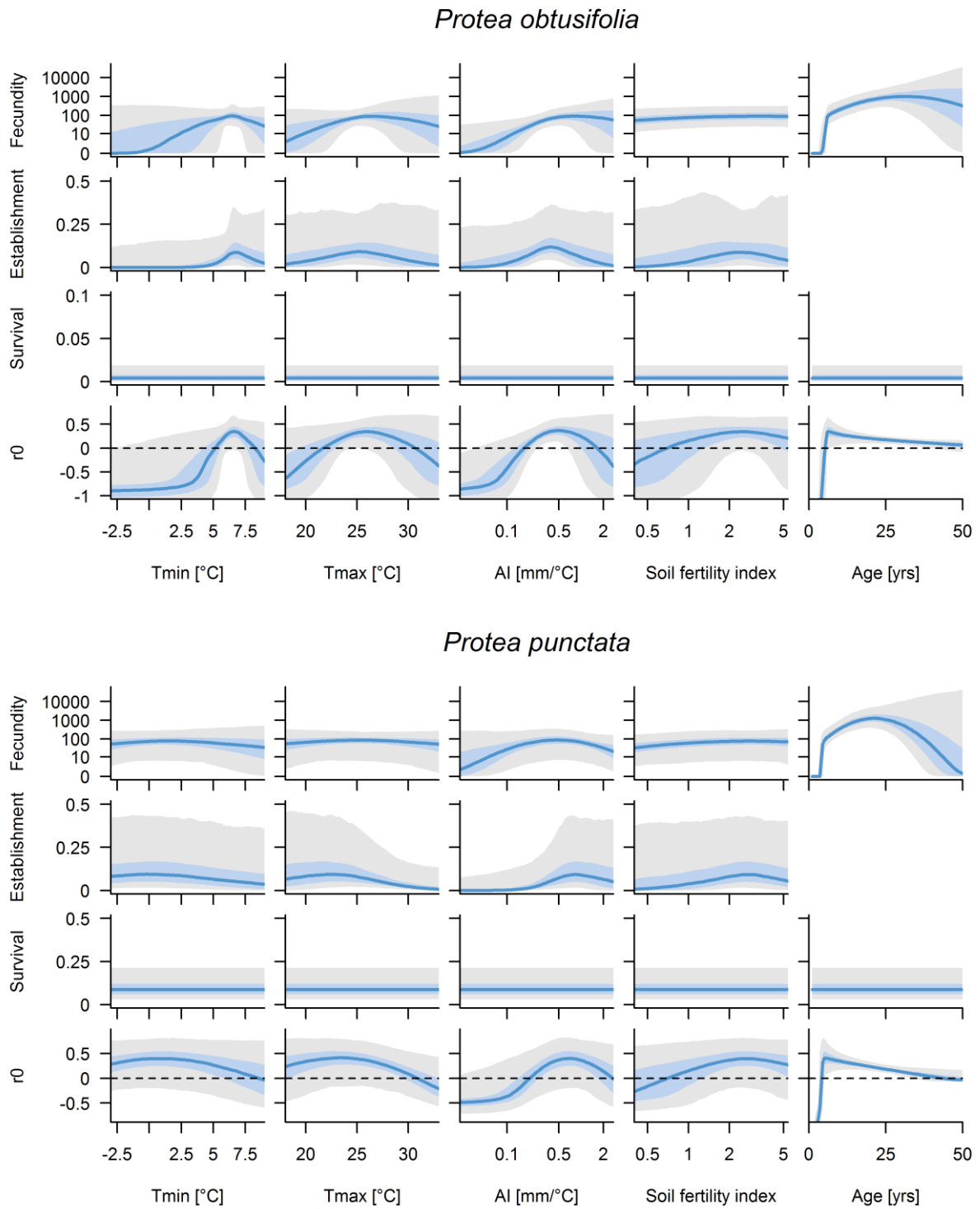


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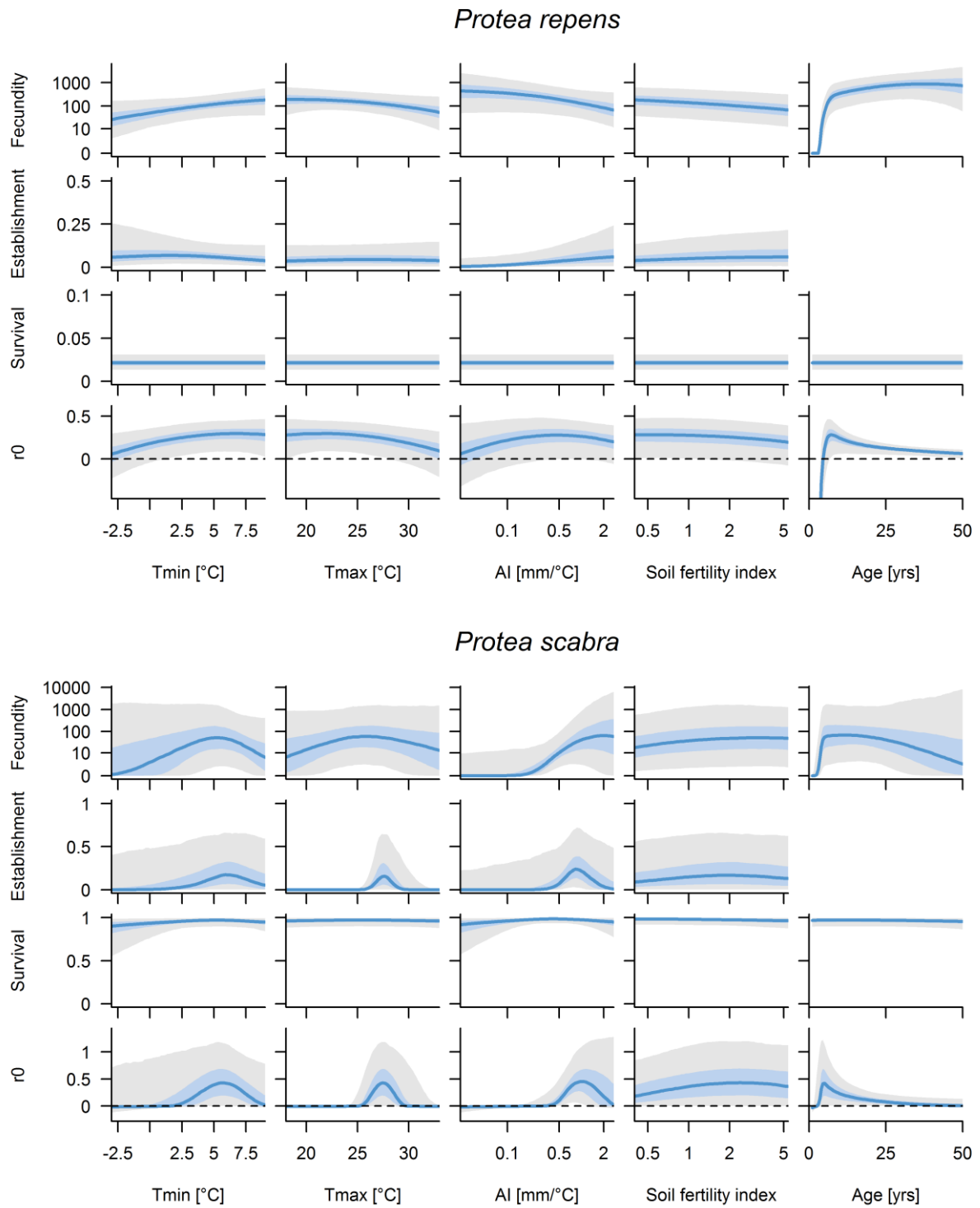


Figure A.2. (continued)

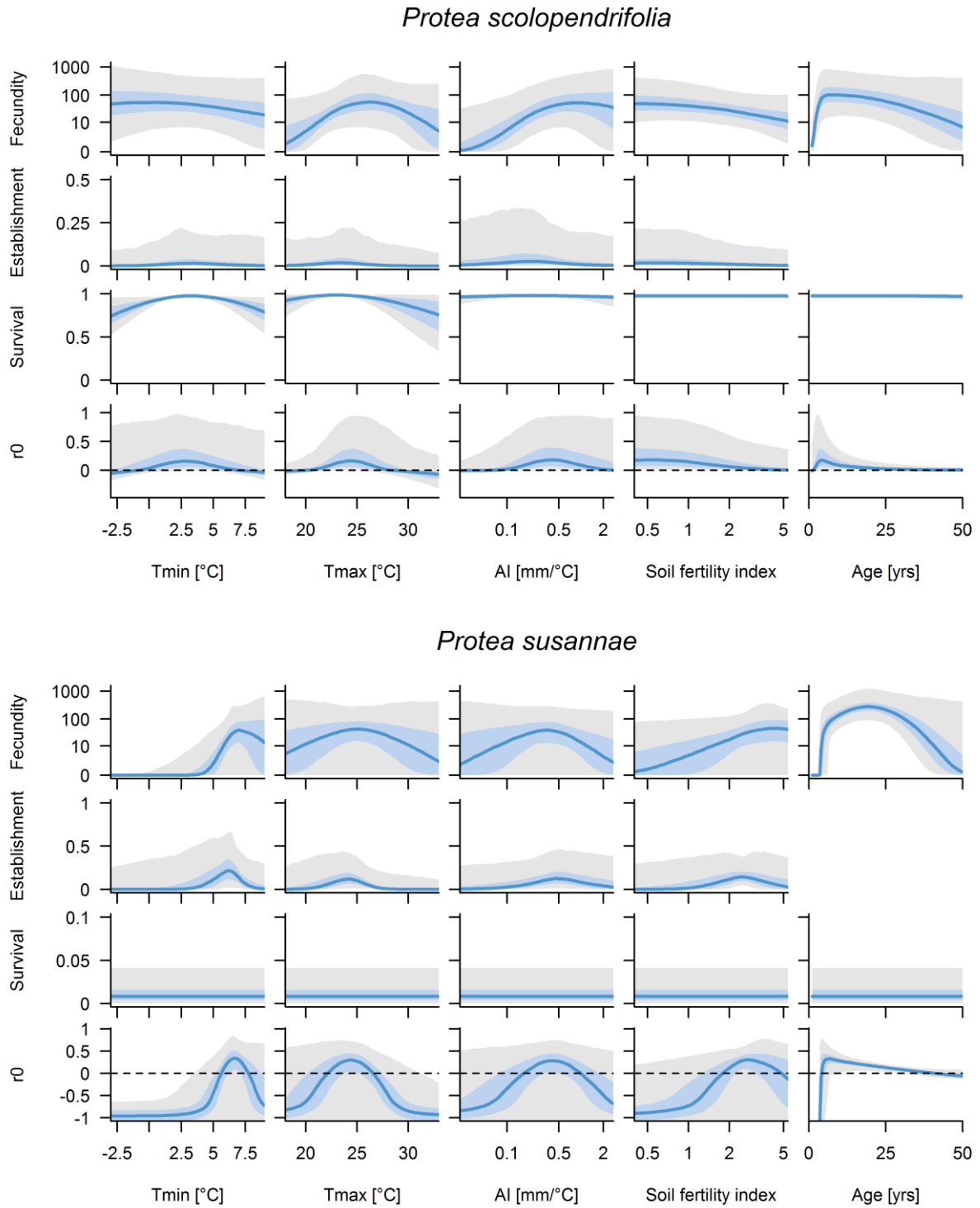


Figure A.2. (continued)

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