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Quantifying the Environmental Determinants of Plant Demography

S. S. Aujla

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Simran Singh Aujla

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Statement of contributions

The personal pronoun ‘we’ is used in each research chapter of this thesis. All chapters benefited from the help of collaborators. Nevertheless, the vast majority of ideas, analysis and writing in this thesis are exclusively the candidate’s work. Contributions to the chapters are listed below.

SSA – Simran S Aujla (Candidate)
RSG – Roberto Salguero-Gómez
MR – Mark Rees
DZC – Dylan Z Childs
MP – Maria Paniw

Chapter 1: SSA.

Chapter 2: MP collected data. MP and SSA wrote code; MP produced spatial data set using a combination of ArcMap, Python and R. MP created R script to calculate spatial autocorrelation. SSA wrote R scripts for the neighbourhood analysis, variable/model-selection, statistical analyses and data visualisation. SSA devised study design (of the analysis) with support from MR and RSG. SSA devised crowding indices with support from MR and RSG. SSA wrote manuscript with feedback from MR, MP and RSG.

Chapter 3: SA conducted data collection and experiments. SSA, RSG, MR and DZC designed study. SA carried out analyses with support from MR. SA wrote manuscript with feedback from MR.

Chapter 4: SSA conducted data collection. SSA, and MR designed study. SSA carried out analyses with support from MR. SSA wrote manuscript with feedback from MR.

Chapter 5: SSA carried out analyses with support from MR. SSA wrote manuscript with feedback from MR.

Chapter 6: SSA

Declaration by author

This thesis contains original work and does not contain material previously published or written by other persons, except where due reference has been made in the text. The contribution of collaborators to the conceptualisation, data collection, statistical analysis, authorship, and editing of this thesis has been clearly stated. This thesis content results from work I have undertaken since starting my research higher degree and includes no work submitted to qualify for any other degree or diploma in any university or other institution. I acknowledge that copyright of the thesis content resides with the copyright holder(s) of that material.

Abstract

The environment dictates population growth rates (λ). Rapid global change makes quantifying the roles of environmental stressors on populations a priority. We can scale from environmental effects on individuals to the consequences for λ by using structured population models. However, collecting the data population modelling is resource intensive. I illustrate how data-driven approaches and experiments can be used to understand the consequences of environmental variation for individual performance and λ, reducing fieldwork demands. First, I show that crowding effects and habitat quality can be approximated through model-selection and spatial autocorrelations of vital rates respectively. My crowding analysis shows that good habitat quality can mask strong intraspecific competition for the critically endangered carnivorous plant, *Drosophyllum lusitanicum*. I study the negative responses of British *Drosera rotundifolia* populations to experimental nitrogen addition. This peatland indicator species varied in responses to treatments and vital rates across sites, highlighting the need to spatially replicate demographic studies. I go on to apply retrospective decompositions to a range of ecological systems, comparing the functional decomposition approach with more common decomposition analyses of life table response experiments. I demonstrate that the functional decomposition approach is a simple, precise way to quantify the contribution of environmental variation and treatments on observed differences in λ. I build site-specific integral projection models of *D. rotundifolia* and show that treatment-induced changes in vital rates can have strong interactive effects on λ. Moreover, treatments that affect single vital rates can have non-additive effects. I use functional decompositions to understand multiple treatment effects on vital rates as an aggregate contribution to a change in λ. I explain how retrospective decompositions have a useful role in informing population management strategies. This thesis illustrates how we can quantify and disentangle various environmental determinants of vital rates and their contributions to λ across a range of ecosystems.

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Chapter 1: Thesis introduction

Background

We depend on stable populations for ecosystem function and harvestable resources (Ellner *et al*., 2016). However, human activity is altering species ranges and population growth rates (Walther, 2002; Parmesan, 2006, Grimm *et al*., 2008; Bobbink *et al*., 2010). For example, pollution from agriculture and industry changes the community composition of nutrient limited environments (Bobbink, 1991; Gunnarsson *et al*., 2004; Phoenix *et al*., 2006; Bubier *et al*., 2007). Anthropogenic climate change, habitat loss and their interactions cause population declines (Walther, 2002; Warren *et al*., 2001; Jetz *et al*., 2007). Humans also affect disturbance regimes, causing shifts in population growth directly or through changes to the outcomes of biotic interactions (Smith *et al*., 2005; Cahill *et al*., 2013; Paniw *et al.,* 2015). It is crucial that we find ways to quantify the importance of the biotic and abiotic environment for individual performance and the finite population growth rate, λ.

We may expect environmental change to affect some subsets of a population strongly, or exclusively. However, even strong effects on one transition in a life cycle or particular vital rate (survival, size transitions and reproductive output) do not always translate into strong effects on λ (Caswell, 1989). Fortunately, developments in population modelling to include structural information like the sex, age and size distribution of individuals have immense practical and theoretical utility for answering ecological and applied questions (Griffith *et al*., 2016). The flexibility of these population models has led to widespread use for a range of organisms in varied ecosystems (Salguero-Gómez *et al*., 2015). Moreover, accounting for structure in the models allows for a better understanding of the structure of projected populations and key transitions in the life cycle that cannot be inferred from vital rate models alone (Caswell, 1989; Merow *et al*., 2014).

Structured population models are parameterised from census data and link individual performance to population outcomes (Morris & Doak, 2002; Ellner *et al*., 2016). The data is used to describe the transitions of individuals over time through statistical models. Specifically, the statistical models describe how vital rates are related to a structuring characteristic like size (Caswell, 2001; Morris & Doak, 2002; Ellner & Rees, 2006; Ellner *et al*., 2016). Collecting the individual level data required for a size-structured population model is time and resource intensive. Consequently, researchers may not have the means to quantify the biotic and abiotic conditions associated with the individuals they measure, despite the value of such information in light of environmental change (Merow *et al*., 2014).

We can address a lack of information about environmental factors influencing population ecology by using experimental approaches. Integral projection models (IPMs) can be parameterised with data for individuals under different conditions (Dahlgren & Ehrlén, 2011). The different conditions can be the result of experimental manipulation. Such experiments are useful when it is difficult to record the exact environmental conditions when sampling, or if we intend to compare λ under current and projected conditions.

We may also want to quantify the importance of biotic interactions for individual performance. An example is competition, which is a key mechanism by which environmental change leads to extinction (Cahill *et al*., 2013). However, experimental approaches like neighbour removal studies can be highly invasive and resource intensive. Data-driven approaches may allow us to quantify the effect of species-specific crowding without necessarily making strong assumptions about how competition or facilitation operate. Flexibility around assumptions is useful because the size, distribution and species identity of neighbouring plants are all potentially important components of crowding (Tielbörger & Kadmon, 2000; Grant *et al*., 2014). Furthermore, statistical techniques to quantify spatial autocorrelation (Augustin *et al*., 1996; Bivand & Gomez-Rubio, 2013; Bardos *et al*., 2015) may have utility as a proxy for habitat quality. Crowding estimates may be biased by habitat quality because the success of individuals depends on habitat quality, and successful neighbours should be strong competitors. Consequently, these new statistical tools offer a way to quantify complex environmental factors and their influence on demographic processes.

Structured population models can include the environmental effects on vital rates, which allows a number of questions to be investigated (Dahlgren & Ehrlén, 2011). Firstly, the consequences for λ of a particular treatment can be compared directly with a control. These results can be decomposed; we may be interested in whether a treatment primarily affected λ through a particular vital rate. Furthermore, there could be multiple treatments or forms of variation in the environment, and we may wish to quantify the respective contributions of those environmental factors and their interactions to λ. The standard approach to decompose the observed variation in λ is a decomposition analysis of a life table response experiment (LTRE) (Caswell, 2001). However, Ellner *et al*. (2019) outline an alternative to the LTRE that does not require estimates of sensitivity. This functional decomposition approach provides an exact breakdown of the contributions of sources of variation to observed variation in λ. Applying retrospective decompositions to experimental demographic studies may help guide the management of populations.

Thesis outline

In this thesis, I investigate three perennial species that are susceptible to different environmental effects: *Drosera rotundifolia*, a small carnivorous rosette endemic to peatland (Crowder *et al*., 1990); *Drosophyllum lusitanicum*, a fire-adapted carnivorous subshrub found in arid regions of the Mediterranean (Müller & Deil, 2001; Correia & Freitas, 2002);

and *Actaea spicata*, a flowering forest herb found across Europe and some parts of Asia (Dahlgren & Ehrlén, 2011) (*Drosera, Drosophyllum* and *Actaea* hereafter). *Drosera* and *Drosophyllum* population sizes depend upon interspecific competition, which is mediated by nutrient availability (Crowder *et al*., 1990; Redbo-Torstensson,1994; Svensson, 1995) and the time since a fire disturbance and livestock browsing respectively (Ojeda *et al*., 1996; Calvo *et al*., 2002; Paniw *et al*., 2017). Individuals of *Actaea* grow at different rates across the soil nutrient gradients across their range, and their seeds are predated by the specialist moth, *Eupithecia immundata* (Dahlgren & Ehrlén, 2011). The population dynamics of these species are contingent on a wide array of environmental factors; these environmental determinants of population growth can be challenging to measure directly, but it is useful to quantify individual and non-additive effects of this kind of environmental variation on population growth.

Firstly, I investigate *Drosophyllum* vital rates, demonstrating how competitive effects on performance can be understood through data-driven approaches. I acknowledge that habitat quality is a multidimensional, complex metric that can bias estimates of crowding. Consequently, I account for habitat quality by calculating the spatial autocorrelation of vital rates, again being guided by the data, and find that good habitat quality ameliorates estimates of intraspecific competition.

Next, I quantify the negative effect of experimental *in-situ* ammonium nitrate addition on *Drosera* vital rates. I also acknowledge the importance of censusing individuals across sites/populations, despite the general lack of spatial replication in demographic studies Crone *et al*., 2011; Salguero-Gómez *et al.,* 2015). Notably, there were great differences in size-specific vital rates amongst the different populations.

In the next chapter I produce IPMs for *Drosera* with site-specific vital rate and nitrogen effects. I show that nitrogen primarily affected λ through induced changes to survival or growth depending on site. I separate the contribution of nitrogen-induced changes to vital rates to λ by using a functional decomposition and compare the results with those from the standard LTRE decomposition approach. Moreover, I simulate multiple treatment-induced changes to vial rates to show non-additive effects are important for λ; this includes interactions between treatment effects acting on the same vital rate, and even up to four-way interactions between treatment-induced changes to multiple vital rates.

Finally, I apply the functional decomposition on *Drosophyllum* and *Actaea*, showing evidence of strong site-specific, non-additive effects between environmental effects on λ. I propose that retrospective decompositions can offer useful information to conservationists/land managers when coupled with controlled experiments, and give an example based on analysis of the *Drosophyllum* observational study.

Environmental change has and will continue to cause species loss. As we become more aware of these projected changes, we become better equipped to design experiments to test the consequences of these changes for how organisms perform. This thesis illustrates how we can quantify and disentangle various environmental determinants of population processes and growth across a range of ecosystems.

References

1.

Augustin, N. H., Mugglestone, M. A. & Buckland, S. T. An Autologistic Model for the Spatial Distribution of Wildlife. *The Journal of Applied Ecology* **33**, 339 (1996).

2.

Bardos, D. C., Guillera-Arroita, G. & Wintle, B. A. Valid auto-models for spatially autocorrelated occupancy and abundance data. *Methods Ecol Evol* **6**, 1137–1149 (2015).

3.

Bivand, R. & Gomez-Rubio, V. *Applied spatial data analysis with R, Second edition*. (Springer, 2013).

4.

Bobbink, R. Effects of Nutrient Enrichment in Dutch Chalk Grassland. *The Journal of Applied Ecology* **28**, 28 (1991).

5.

Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* **20**, 30–59 (2010).

6.

Bubier, J. L., Moore, T. R. & Bledzki, L. A. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biol* **13**, 1168–1186 (2007).

7.

Cahill, A. E. *et al.* How does climate change cause extinction? *Proc. R. Soc. B.* **280**, 20121890 (2013).

8.

Calvo, L., Tárrega, R. & De Luis, E. The dynamics of mediterranean shrubs species over 12 years following perturbations. *Plant Ecology* **160**, 25–42 (2002).

9.

Caswell, H. Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling* **46**, 221–237 (1989).

10.

Caswell, H. *Matrix population models: construction, analysis and interpretation*. (Sinauer Associates, 2001).

11.

Chase, J. & Leibold, M. *Ecological Niches: Linking Classical and Contemporary Approaches*. (University of Chicago Press, 2003).

12.

Correia, E. & Freitas, H. Drosophyllum lusitanicum, an endangered West Mediterranean endemic carnivorous plant: threats and its ability to control available resources. *Botanical Journal of the Linnean Society* **140**, 383–390 (2002).

13.

Crone, E. E. *et al.* How do plant ecologists use matrix population models?: Matrix population models for plants. *Ecology Letters* **14**, 1–8 (2011).

14.

Crowder, A. A., Pearson, M. C., Grubb, P. J. & Langlois, P. H. Drosera L. *Journal of Ecology* **78**, 233–267 (1990).

15.

Dahlgren, J. P. & Ehrlén, J. Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology* **97**, 666–674 (2009).

16.

Ellner, S. P. & Rees, M. Integral Projection Models for Species with Complex Demography. **167**, 410–428 (2006).

17.

Ellner, S. P., Childs, D. Z. & Rees, M. *Data-driven Modelling of Structured Populations: A Practical Guide to the Integral Projection Model*. (Springer International Publishing, 2016). doi:10.1007/978-3-319-28893-2.

18.

Ellner, S. P., Snyder, R. E., Adler, P. B. & Hooker, G. An expanded modern coexistence theory for empirical applications. *Ecol Lett* **22**, 3–18 (2019).

19.

Grant, K., Kreyling, J., Heilmeier, H., Beierkuhnlein, C. & Jentsch, A. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecol Res* **29**, 991–1001 (2014).

20.

Griffith, A. B., Salguero-Gómez, R., Merow, C. & McMahon, S. Demography beyond the population. *J Ecol* **104**, 271–280 (2016).

21.

Grimm, N. B. *et al.* The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment* **6**, 264–272 (2008).

22.

Gunnarsson, U., Granberg, G. & Nilsson, M. Growth, production and interspecific competition in Sphagnum: effects of temperature, nitrogen and sulphur treatments on a boreal mire. *New Phytol* **163**, 349–359 (2004).

23.

Hutchinson, E. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**, 415–427 (1957).

24.

Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. *PLoS Biol* **5**, e157 (2007).

25.

Merow, C. *et al.* Advancing population ecology with integral projection models: a practical guide. *Methods Ecol Evol* **5**, 99–110 (2014).

26.

Morris, W. F. & Doak, D. F. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. (Sinauer Associates, 2002).

27.

Müller, J. & Deil, U. Ecology and structure of Drosophyllum lusitanicum (l.) Links populations in the south-west of the Iberian Peninsula. 47–68 (2001).

28.

Ojeda, F., Marañón, T. & Arroyo, J. Patterns of ecological, chorological and taxonomic diversity at both sides of the Strait of Gibraltar. *Journal of Vegetation Science* **7**, 63–72 (1996).

29.

Paniw, M., Quintana-Ascencio, P. F., Ojeda, F. & Salguero-Gómez, R. Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant. *Journal of Applied Ecology* **54**, 1884–1894 (2017).

30.

Paniw, M., Salguero-Gómez, R. & Ojeda, F. Transient facilitation of resprouting shrubs in fire-prone habitats. *Journal of Plant Ecology* 9 (2017).

31.

Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).

32.

Phoenix, G. K. *et al.* Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. *Global Change Biol* **12**, 470–476 (2006).

33.

Redbo-Torstensson, P. The demographic consequences of nitrogen fertilization of a population of sundew, Drosera rotundifolia. *Acta Botanica Neerlandica* **43**, 175–188 (1994).

34.

Salguero-Gómez, R. *et al.* The COMPADRE Plant Matrix Database: an open online repository for plant demography. *J Ecol* **103**, 202–218 (2015).

35.

Smith, M., Caswell, H. & Mettler-Cherry, P. STOCHASTIC FLOOD AND PRECIPITATION REGIMES AND THE POPULATION DYNAMICS OF A THREATENED FLOODPLAIN PLANT. *Ecological Applications* **15**, 1036–1052 (2005).

36.

Svensson, B. M. Competition between Sphagnum fuscum and Drosera rotundifolia: A Case of Ecosystem Engineering. *Oikos* **74**, 205 (1995).

37.

Tielbörger, K. & Kadmon, R. TEMPORAL ENVIRONMENTAL VARIATION TIPS THE BALANCE BETWEEN FACILITATION AND INTERFERENCE IN DESERT PLANTS. *Ecology* **81**, 1544–1553 (2000).

38.

Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).

39.

Warren, M. S. *et al.* Rapid responses of British butter¯ies to opposing forces of climate and habitat change. **414**, 5 (2001).

Chapter 2: Habitat quality masks competition

2.1 Abstract

Environmental change can lead to extinction by affecting the outcomes of biotic interactions. Therefore, quantifying the role of facilitation/competition for vital rates is a crucial precursor for accurately modelling populations. However, inferring a generalisable inter/intraspecific crowding effect from observational data is problematic because individuals are distributed in accordance with their realised niche, where they are dominant competitors. We use a data-driven model selection approach to quantify crowding and use the spatial autocorrelation of vital rates as a proxy of habitat quality for the fire-disturbed carnivorous subshrub, *Drosophyllum lusitanicum*. Accounting for habitat quality is essential, as without it we would mistake strong intraspecific competition for facilitation. We also find that intraspecific competition is stronger than interspecific competition in *D. lusitanicum*. We suggest that habitat quality is important to quantify in crowding studies because intraspecific competition and individual performance are contingent on habitat quality.

2.2 Introduction

Changes in the biotic and abiotic environment will affect species interactions, individual performance, and jeopardise coexistence (McKinney & Lockwood, 1999; Wiegmann & Waller, 2005; Kawai & Tokeshi, 2007; Rader *et al*., 2014), resulting in losses of biodiversity and ecosystem function (Balvanera *et al.,* 2006; Isbell *et al.,* 2011; Duncan *et al.,* 2015, Eisenhauer *et al*., 2016). There are many explanations for coexistence (Silvertown, 2004), and anthropogenic effects can destabilise communities by various mechanisms. For example, agriculture and industry can alter nutrient limited environments (Bobbink, 1991; Phoenix *et al.,* 2006), introduced non-native species may have a competitive advantage owing to few natural enemies (Mitchell & Power, 2003; DeWalt *et al*., 2004), and disturbance regimes can be supressed or imposed, affecting species with certain life-history strategies or physiological adaptations (Smith *et* al., 2005; Paniw *et al.,* 2015).

Given the global threats to biodiversity, we may be interested in the likelihood of a species persisting over its current range, or in the population growth rate of an invasive species. Models can be used to answer questions about a population's trajectory, and these may rely on measurements of individuals taken over time (Ellner & Rees, 2006; Crone *et al*., 2013; Rees *et al*., 2014). However, measurements of individual performance such as growth, survival, and reproductive output depend upon interactions with neighbouring individuals (Tielbörger & Kadmon, 2000; Grant *et al*., 2014). For plants, it would be useful to quantify the importance of interspecific and intraspecific crowding for these performance measures.

Estimating crowding effects from observational data collected in wild populations is challenging due to statistical issues. Error in a crowding measurement can cause regression tools to detect competitive effects when none exist (Detto *et al*., 2019), and measurement error is a certainty given how definitions of crowding are simplified proxies by necessity (Weiglet & Jolliffe, 2003). The best approach for estimating crowding is likely dynamic, monitoring individual performance over time (Freckleton *et al*., 2009; Damgaard & Weiner, 2017) as in Adler *et al*. (2010) and Teller *et al*. (2016). Moreover, demographic studies are less prone to biases that result in false positive findings of density dependence (Detto *et al*., 2019).

Competitive effects estimated from observational studies are prone to biases because of ecological sorting processes. Individuals are unlikely to be randomly distributed in space because biotic interactions result in individuals occupying positions in their realised niche, rather than their fundamental niche (Hutchinson, 1957; Chase & Leibold, 2003; Adler *et al.*, 2018). Niche based spatial aggregation can to the detection of weak interspecific effects at the population level because most individuals will not experience competition from heterospecific neighbours (Rees *et al.*, 1996; Tuck *et al.*, 2018); heterospecifics are competitively excluded from the realised niche of the dominant competitor. Similarly, we expect that individual level measurements of performance will also be biased by aggregation of a species based on high site quality. We may underestimate intraspecific competition because both conspecific density and performance are emergent results of site quality.

Here we investigate potential causes of variation in individual performance for *Drosophyllum lusitanicum* (*Drosophyllum* hereafter). *Drosophyllum* is an endangered carnivorous plant and post-fire specialist found in Mediterranean heathland communities (Müller & Deil, 2001; Correia & Freitas, 2002; Garrido *et al.*, 2003; Heubl *et al.*, 2006). The *Drosophyllum* system is an interesting case study as it features competition between newly emerged individuals post-fire (Preston & Baldwin, 1999; Quintana-Ascencio *et al.*, 2007), and the growing competition from dominant shrubs that are later to emerge (Ojeda *et al.*, 1996; Calvo *et al.*, 2002; Yates & Ladd, 2010). We focus on the roles of fire disturbance, habitat quality, and con/heterospecific plant interactions in determining plant growth, survival and reproductive output.

We use a spatially explicit demographic data set to test: 1) what variables most parsimoniously explained *Drosophyllum* performance; 2) whether crowding effects helped explain variation in performance; 3) whether there are differences between intra/interspecific crowding effects; 4) how the inclusion of spatial autocorrelation variables for *Drosophyllum* performance would affect estimates of crowding.

2.3 Methods

2.3.1 Study system

Drosophyllum is a geographically and taxonomically rare carnivorous subshrub, endemic to heathlands in the south-western Iberian Peninsula and north-western tip of Morocco (Garrido *et al*., 2003; Heubl *et al*., 2006). Moreover, natural populations of *Drosophyllum* are in stark decline due to heathland afforestation (Andrés & Ojeda, 2002) and fire suppression (Müller & Deil, 2001; Garrido *et al*., 2003).

Drosophyllum is part of a low scrub heathland community that is shaped by fire (Ojeda *et al*., 2000; Garrido *et al*., 2003). *Drosophyllum*, other subshrubs, and short-lived herbs emerge after fires in the low plant-density period before dwarf shrubs dominate (3-5 years) (Ojeda *et al*., 1996; Calvo *et al*., 2002; Yates & Ladd, 2010). Shrub dominance is clear in mature heathland communities, where prolific species include *Erica australis, Pterospartum tridentatum, Quercus lusitanica, Calluna vulgaris* and *Halimium lasianthum* (Müller & Deil, 2001; Paniw *et al*., 2015). Populations of early successionals benefit post-fire as light competition is alleviated, and potentially allelopathic leaf litter is burned away (Preston & Baldwin, 1999; Quintana-Ascencio *et al*., 2007; Gómez-Gonzáles *et al*., 2018). Additionally, mature shrub species facilitate *Drosophyllum* seedling survival in this transient post-fire window likely by blocking wind and intense UV radiation (Goméz-Aparicio *et al*., 2004; Adlassnig *et al*., 2006). Consequently, fire plays a key role in altering plant density, and therefore the importance of facilitative and competitive interactions that govern demography.

Drosophyllum persists in its community due to its fire-suited phenology. For example, reproductive individuals of *Drosophyllum* contribute a permanent soil seed bank (Correia & Freitas, 2002; Paniw *et al*., 2017a); germination from the seed bank is triggered by fire-related cues, presumably heat shock and increased light availability (Correia & Freitas, 2002; Cross *et al*., 2017). The species is iteroparous and individuals can start reproducing in their second year, though not clonally. An individual can develop 1-2 leaf rosettes each growing season, each containing 3 to >20 leaves that expand by unrolling from the base of the rosette (Ortega-Olivencia *et al*., 1995, Garrido *et al*., 2003). The maximum observed lifespan of individuals is 10 years (Juniper *et al*., 1989) and rosette number is a good proxy for age in natural heathland habitats (Paniw *et al*., 2015). However, most individuals die after one reproductive event (Paniw *et al*., 2017a).

2.3.2 Data collection

We censused *Drosophyllum* individuals through time at multiple locations, along with time since fire (TSF), browsing level and spatial information of *Drosophyllum* and shrub neighbours. Four locations within the southern Aljibe Mountains were selected as study sites (Paniw *et al*., 2017a). This region is characterised by a mild Mediterranean climate (*ca.* 18 °C mean annual temperature and *ca.* 1200 mm annual rainfall) and a rough topography dominated by Oligo-Miocene sandstone, which produces acidic, nutrient-poor soils in ridges and upper slopes (Ojeda *et al*., 2000). We used satellite imagery (Arino *et al*., 2011), public historical records (Junta de Andalucía, 2013), and visual clues (*i.e.*, fire scars on mature scrubs) to determine the post-fire stage of each site.

To measure crowding, we collected spatial data for *Drosophyllum* and neighbouring shrubs. The sampling was done every April between 2012 and 2015, coinciding with the peak of *Drosophyllum* flowering. At each study site, we established ten 1 × 1 m^2 quadrats along four permanent line transects of 10 m each, resulting in 40 quadrats. The four transects were located 3 m from each other and perpendicular to the main slope. We recorded the Cartesian coordinates of individuals of *Drosophyllum* within the quadrats and neighbouring shrubs.

Shrubs that grew adjacent (< 5 cm away) to Drosophyllum plants but were not located within the quadrats were also measured. Length and width measurements were taken for each shrub.

We collected individual-level *Drosophyllum* data relating to size and reproductive features to describe the species' population dynamics. We quantified individual size as the number of leaf rosettes, number of leaves per rosette, and the length of the longest leaf. We quantified reproductive status as whether or not the individual was flowering, and if so, the number of flowers it produced. Survival was inferred directly by the presence of an established individual from its previously recorded coordinates, since this species does not undergo vegetative dormancy. Similarly, new recruits were defined as new appearances at a given Cartesian coordinate of individuals with < 9 leaves and a maximum leaf length of 11 cm.

2.3.3 Spatial analyses

We produced a crowding index

$$W_{i,t} = \sum_{k} e^{-\alpha_m d_{ik}} V_{ik,t} \qquad (eqn. 1)$$

to describe the effects of crowding based on three assumptions; the crowding intensity, W, a *Drosophyllum* individual, i, experiences at time t depends upon: the distance, d, between centres of the *Drosophyllum* and a neighbour, k, the volume, V, of that neighbour, and whether the neighbour is a conspecific or heterospecific denoted by m. α determines the spatial scale over which neighbours influence crowding. Crowding values were based on a neighbourhood; a circular area with a radius of 20cm centred on a *Drosophyllum*.

Additionally, volume of neighbours is specifically the volume that intersects with the neighbourhood. We also considered a 20 cm (equal to neighbourhood radius) buffer zone in plots and did not include *Drosophyllum* within the buffer as focal individuals in the crowding analysis but did include them as neighbours (Fig. 1).

Our rationale for using volume rather than basal area (Teller *et al*., 2016) was that the vertically heterogeneous vegetation structure in the study system has importance for both competition and facilitation. Light is regarded as the primary source of competition between *Drosophyllum* and its neighbours (Correia & Freitas, 2002), and shrubs may also block strong coastal winds, providing facilitative effects on *Drosophyllum* performance (Paniw *et al*., 2017b). Moreover, volume may better describe competitive ability of conspecifics in capturing prey.

To calculate volumes, we considered plants to be cylindrical (Fig. 1). For heterospecifics, the average of an individual's length and width were used as its diameter, and the associated radius used for height (heterospecific shrubs have short robust growth forms). For conspecifics, we used a linear regression to test the relationship between number of *Drosophyllum* rosettes and basal area occupied from a separate analysis (rosette number and basal areas were obtained for 208 *Drosophyllum*; Gómez-Gonzáles *et al*., 2020; Supp. 1). Our *Drosophyllum* data included rosette number, so we estimated their logged basal areas by multiplying rosette number by the slope and adding the intercept from the regression model from the previous analysis. We considered the estimated basal areas to be circles, and the leaf length measurement was used for *Drosophyllum* height.

Numerous environmental factors for which we have little information (soil moisture, porosity, pH etc.) likely affect the performance of *Drosophyllum* individuals. Moreover, the factors are likely spatially correlated, and this causes statistical dependence between observations, violating generalised linear model assumptions (Bardos *et al*., 2015). Autocovariate regressions enable us to account for structure in the data caused by spatial dependency between observations (Augustin *et al*., 1996; Bardos *et al*., 2015). We created spatial autocorrelation variables using the autocov_dist function from the sp_dep R package (Bivand & Gomez-Rubio, 2013). The autocorrelation values were calculated by summing the inversely distance weighted vital rate responses of neighbours within a 50 cm radius for individual *Drosophyllum*, and then scaled (mean subtracted from value then divided by standard deviation). We calculated separate values for autocorrelation associated with size, probability of flowering and survival. We considered autocorrelation of flowering probability rather than total flowers because counts cannot be positively correlated in an auto-Poisson model (Besag, 1974). ~5% of *Drosophyllum* were not included in the analysis of performance as they had no neighbours within 50 cm; neighbourhood radii would need to be increased by meters to satisfy the function condition that each individual had at least one neighbour.

2.3.4 Model comparison

We established 'base models' that did not include crowding, and most parsimoniously explained variation in four performance metrics: growth, survival probability, flowering probability and number of flowers in R (4.0.1) (R Core Team, 2020). To identify the base models, we first ran models including a spatial autocorrelation main effect (either for size, survival probability or flowering probability), and each combination of variable interactions of size (the log of leaf length x leaf number), TSF and the presence/absence of livestock; we did not include both TSF and livestock in a single model for probability of flowering due to a lack of observations. For our size metric we multiply leaf length (cm) by leaf number and take the natural log. This size metric is different to our volumetric consideration of size for crowding but has been a good predictor of vital rates (Paniw *et al*., 2017a). We used general linear models for growth, binomial generalised linear models for survival and flowering and negative binomial generalised linear models (due to overdispersion in Poisson models) for number of flowers. Next, we carried out type II ANOVAs on these models to identify the significant variables and interactions, and ran simplified models with these significant terms, retaining spatial autocorrelation in each case. The simplified models were compared using AIC and BIC to identify the most parsimonious base models for each vital rate (Table 1).

2.3.5 Crowding intensity

To compare base models with equivalent models plus crowding we first needed to describe the most likely way crowding operates. We used a data-driven approach to approximate the spatial scale, α, as in equation 1, over which neighbours influenced crowding. We added crowding indices to base models and allowed both inter/intraspecific α values to vary; then we selected the combination of α values yielding the lowest AIC. An α pair was obtained for every performance metric with and without spatial autocorrelation in the model. Our crowding indices were then scaled (mean subtracted from value then divided by standard deviation). The relationship between α and crowding is illustrated in supplementary 2.

2.3.6 Crowding comparison

Firstly, we added our optimised crowding indices to base models to test whether the explanatory power of the models would improve. Model parsimony was assessed using AIC and BIC. Next, we compared the relative importance of intra/interspecific crowding in affecting each vital rate by comparing their coefficients. We demonstrated the effects of statistically significant forms of crowding by simulating a competitor removal experiment (where crowding variables are set to 0) and comparing these results to performance in observed crowding conditions. Lastly, we investigated how excluding spatial autocorrelation from models of *Drosophyllum* performance would affect the estimated sizes and directions of crowding effects.

2.4 Results

2.4.1 Explaining performance

Our base models (Table. 1) suggest that *Drosophyllum* individuals experienced the greatest changes in size immediately after a fire event and browsing reduced growth at this stage more than any other covariate (Fig. 2). Survival probability was also high immediately after a fire, and larger individuals were more likely to survive (Fig. 3). *Drosophyllum* were more likely to reproduce at larger sizes and when more than two years had elapsed since a fire event (Fig. 4). Moreover, larger individuals produced more flowers especially when livestock were absent (Fig. 5).

2.4.2 Crowding effects

Adding crowding variables to base models improved the growth, probability survival and flowering model, but not the total flowers model (Table. 1) based on AIC and BIC. We detected competitive intraspecific effects for growth, survival and flowering probability but not number of flowers. Interspecific effects were weaker, with no significant effects on survival or flowering probability, but a small negative effect on growth (Fig. 6, 7, 8 & 9). The neighbour removal simulations show that most *Drosophyllum* would experience more growth if either intraspecific or interspecific competition were removed (Fig. 10). Interspecific crowding was unimportant for survival for the majority of *Drosophyllum*. In contrast, intraspecific crowding was of considerable importance; simulated intraspecific crowding removal increased survival by an absolute value of 8.7% on average with a median improvement of 6.6% (Fig. 11). Similarly, we detected significant effects of intraspecific but not interspecific crowding on *Drosophyllum* flowering probability. Simulated intraspecific removal experiments increased the absolute probability of flowering by 5.4% on average, with a median improvement of 2% (Fig. 12). Moreover, *Drosophyllum* across the range of observed sizes experienced crowding (Supp. 3), and large changes in *Drosophyllum* growth survival and flowering probability were predicted across the size range (Supp. 4, 5 & 6). Crowding models also had better explanatory power when base models used to find optimal α values included spatial autocorrelation (AIC differences >2).

2.4.3 Spatial autocorrelation effects

Estimates of intraspecific crowding were more negative for total flowers, survival and flowering probability when spatial autocorrelation was included in models. Estimates of intraspecific crowding were more positive for the growth model (Fig. 13). For interspecific crowding, changes in effect size when comparing models with and without spatial autocorrelation were marginal, but the direction of change was opposite to those observed for intraspecific crowding (Fig. 13).

2.5 Discussion

Drosophyllum is thought to rely on a post-fire window because sub-shrubs dominate as TSF increases (Ojeda *et al*., 1996; Calvo *et al*., 2002; Yates & Ladd, 2010). Our results suggest that intraspecific competition was stronger than interspecific competition, which is similar to the findings from another crowding analysis in a shrub dominant system (Adler *et al*., 2010). These results are consistent with general patterns found in competition studies (Adler *et al*., 2018) and theories of species coexistence (Chesson, 2000; Gotelli, 2001). Intraspecific competition could be stronger because of competition for limited prey. Drosophyllum relies heavily on prey capture to obtain nutrients (as opposed to soil nutrients; Skates *et al*., 2019), and nutrient acquisition may be critical for growth at early life stages (Thorén & Karlsson, 1998) where *Drosophyllum* density is highest.

Our estimates of minor negative effects of interspecific crowding on Drosophyllum survival are likely due to slower heterospecific emergence. The appearance of heterospecific dominance in the field may largely be due to a combination of slower heterospecific emergence and strong, early intraspecific competition post-fire. However, the reduction in growth due to interspecific competition (Fig. 13) may be down to investment into stem elongation rather than leaf growth to avoid being shaded out by young shrubs (Brewer *et al*., unpublished data).

TSF is an aggregate of biotic and abiotic factors, including the density of neighbouring seedlings, the size of heterospecific competitors, soil composition and even the aging of focal individuals (Supp. 10). Consequently, TSF could be a constraint on vital rates for multiple non-exclusive reasons, including competition, and a shift to investment in reproduction. Preliminary analyses do not suggest strong growth-reproduction trade-offs (Paniw, *pers. commun.*), but the species life cycle does suggest a prioritisation of reproduction because of the importance of seed bank dynamics for species persistence.

Intraspecific crowding estimates varied depending on the inclusion of spatial autocorrelation in performance models (Fig. 13). We expected that estimates of intraspecific competition would be more severe (-) with the inclusion of autocorrelation because both conspecific density and performance are emergent results of site quality. Therefore, accounting for site quality should reveal a generalisable strength of interaction across sampled observations. Crowding estimates for growth are inconsistent with our prediction, but in this case the crowding and spatial autocorrelation variables are correlated (Supp. 7). Generally, if neighbours are relatively successful, local conditions should be good for a focal individual. However, positive neighbour performance in the case of growth is tightly coupled with increased crowding. Strikingly, the direction of crowding effect can invert depending on whether or not spatial autocorrelation is included – for example we detect facilitation between *Drosophyllum* for fertility and flowering probability, but this is nullified and even inverted (to very strong competition) when spatial autocorrelation is accounted for (Fig. 13).

We accounted for habitat quality of *Drosophyllun* with spatial autocorrelation proxies for vital rates. The spatial autocorrelation values are based on relative performance from observed *Drosophyllum*, so relatively poorly performing *Drosophyllum* may still be on decent quality habitat relative to their entire fundamental niche. Good conditions for *Drosophyllum* should generally be good for their competitors (acidic soils and low livestock disturbance), but there may be additional species-specific conditions that may bias our estimates of interspecific crowding. These potential niche differences warrant investigation into how the spatial autocorrelation of heterospecific neighbours might change estimates of interspecific crowding.

Our results show that measurements of performance can respond to interspecific and intraspecific crowding differently. Moreover, we found spatial autocorrelation to be highly significant in models of *Drosophyllum* performance, and a useful proxy to account for variation within a site. Accounting for environmental variation shows that high site quality can ameliorate estimates of intraspecific competition. However, care must be taken in choosing the right metric of performance as the basis for the spatial autocorrelation proxy, as neighbour performance may not be independent of focal individual performance, as in the case of neighbour growth and crowding. System specific knowledge is also useful when defining a crowding index and understanding to what extent individuals in a population are in transient positions or are likely dominant competitors at a location. Conclusions about interspecific competition may benefit from a similar habitat quality proxy being applied to heterospecifics, and a consideration of their species identities. Finally, time series data can help us identify indirect effects of competition on some aspects of performance, such as competition reducing flower production by reducing individual growth.

2.6 Figures

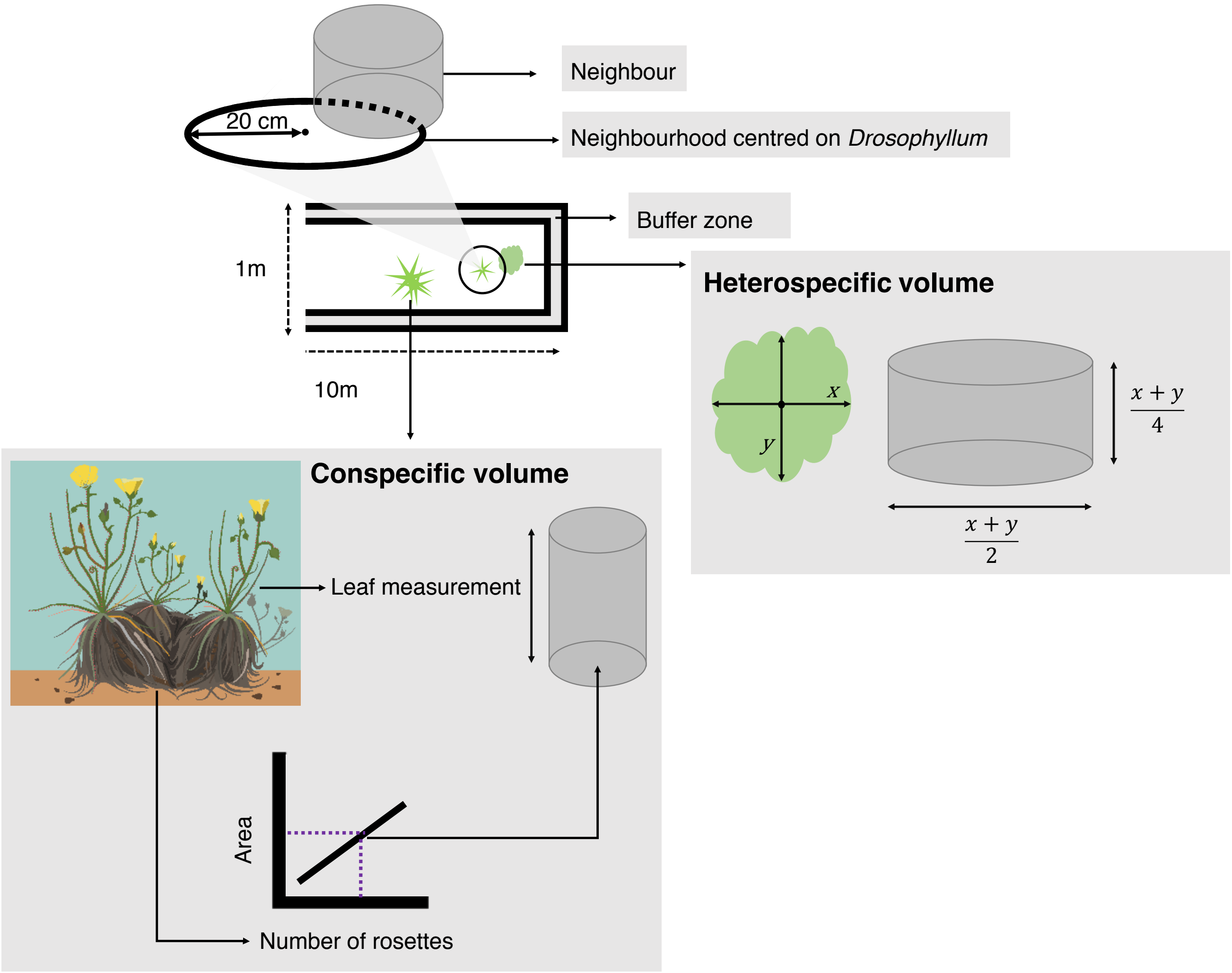


Figure 1. Illustration of how *Drosophyllum lusitanicum* neighbourhoods are considered in the spatial analysis. *Drosophyllum* individuals within the 10 x 1 m plot but outside the buffer zone have a 20 cm radius neighbourhood. Neighbours are treated as cylinders based on heterospecific width and length or conspecific leaf length and a known number of rosettes and basal area relationship.

Table 1. The models used to describe *Drosophyllum lusitanicum* performance, their associated AIC and BICs (lowest values in bold) and the optimal scaling parameters, αs, for intra/interspecific competition. TSF, AC and W signify time since fire, autocorrelation and crowding respectively. Pairwise interactions between variables in parentheses are signified by an exponent of two.

Model	Structure	Intra α	Inter α	AIC	BIC
Growth base	Ln($size_{t+1}$) ~ (ln(size) + TSF + browsing)^2 + scaled AC for ln(size)			1275.78	1342.70
Growth W	Ln($size_{t+1}$) ~ (ln(size) + TSF + browsing)^2 + scaled AC for ln(size) + scaled intra W + scaled inter W	15.76	-0.11	**1264.96**	1340.81
Growth W no AC	Ln($size_{t+1}$) ~ (ln(size) + TSF + browsing)^2 + scaled intra W + scaled inter W	12.75	0.38	1266.96	**1338.34**
Survival base	Survival ~ ln(size) + TSF + scaled AC for survival			1307.91	1338.31
Survival W	Survival ~ ln(size) + TSF + scaled AC for survival + scaled intra W + scaled inter W	1.95	9.65	**1275.27**	**1315.81**
Survival W no AC	Survival ~ ln(size) + TSF + scaled intra W + scaled inter W	-2.17	6.22	1300.88	1336.35
Flowering base	Flowering ~ ln(size) * TSF + scaled AC for flowering incidence			650.31	683.65
Flowering W	Flowering ~ ln(size) * TSF + scaled AC for flowering incidence + scaled intra W + scaled inter W	-25.97	1.10	**638.67**	**681.53**
Flowering W no AC	Flowering ~ ln(size) * TSF + scaled intra W + scaled inter W	28.02	-11.58	670.01	708.19

Total flowers base	Total flowers ~ (ln(size) + TSF + browsing)^2 + scaled AC for flowering incidence			**1164.08**	**1206.15**
Total flowers W	Total flowers ~ (ln(size) + TSF + browsing)^2 + scaled AC for flowering incidence + scaled intra W + scaled inter W	-6.43	1.80	1167.74	1216.81
Total flowers W no AC	Total flowers ~ (ln(size) + TSF + browsing)^2 + scaled intra W + scaled inter W	24.59	-14.09	1174.65	1220.22

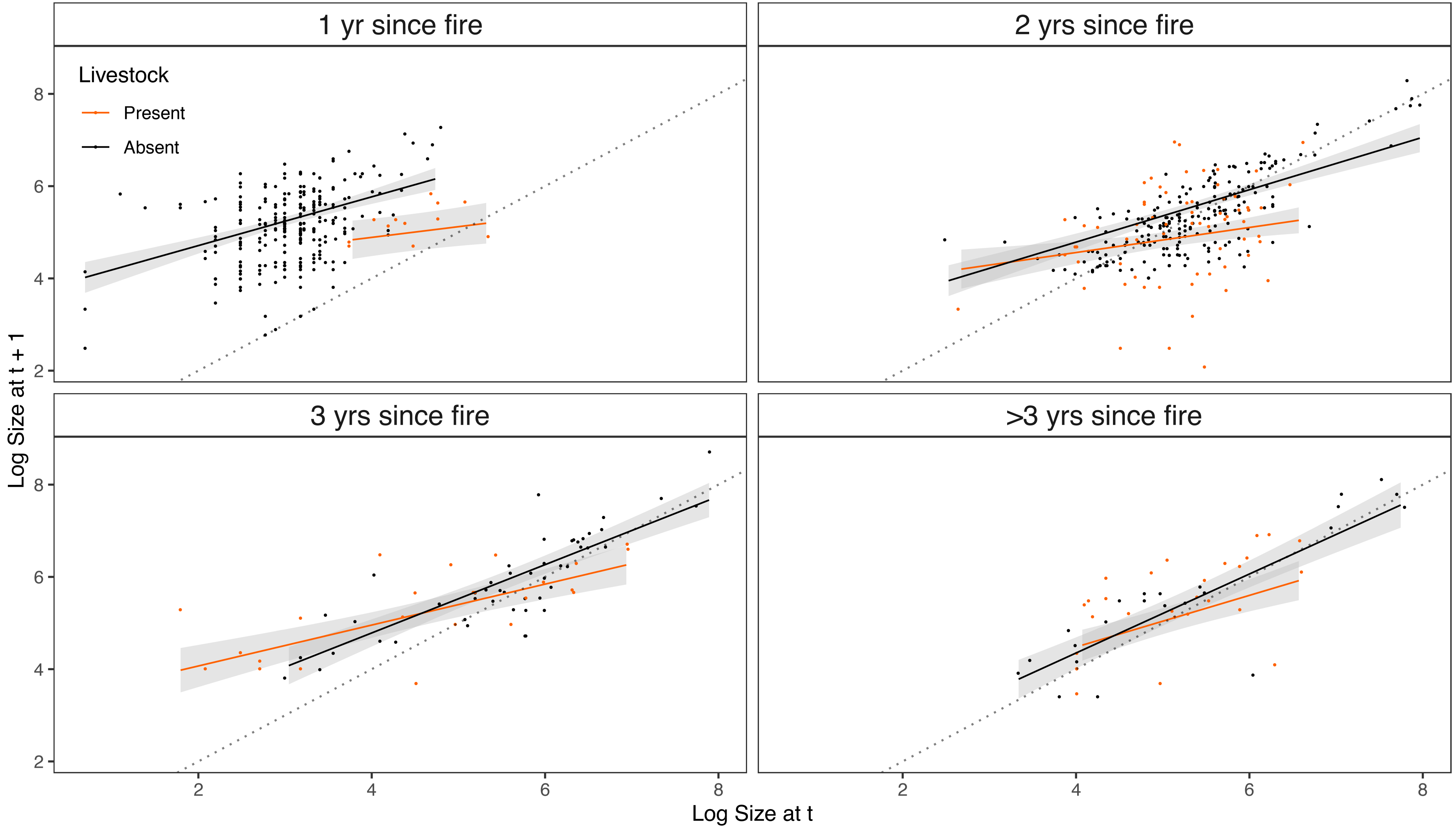


Figure 2. *Drosophyllum lusitanicum* changes in natural logged size categorised by years since a fire disturbance event under median levels of inter/intraspecific crowding and spatial autocorrelation for size. The fitted lines correspond to a general linear model. Colour corresponds to the presence or absence of browsing livestock. The shaded area around regression lines represent 95% confidence intervals of the predictions. The dashed line has a slope of 1 – points above it are individuals that grew.

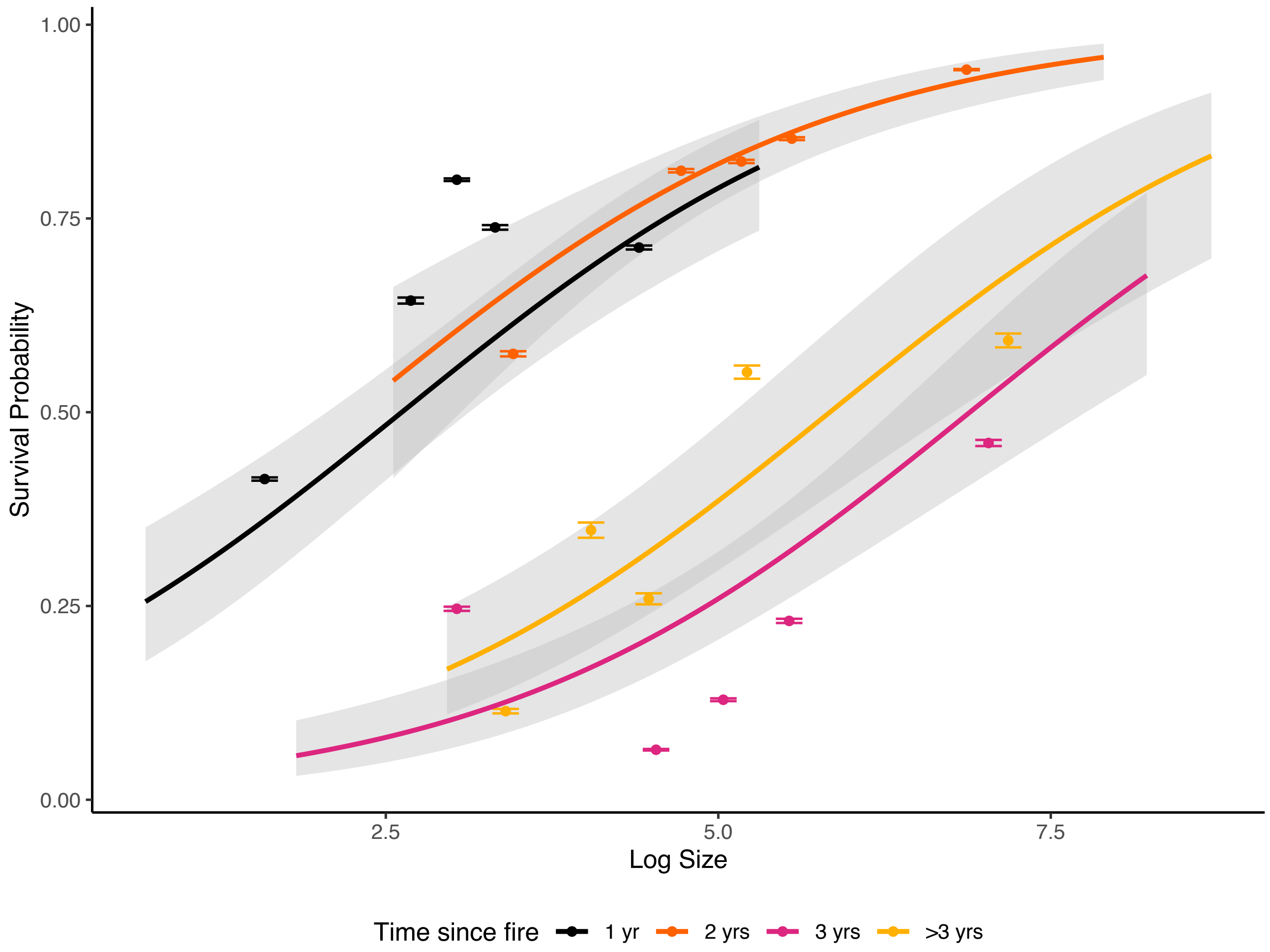


Figure 3. *Drosophyllum lusitanicum* survival probability against natural logged size under median levels of inter/intraspecific crowding and spatial autocorrelation for survival. The fitted lines correspond to a binomial generalised linear model and the shaded areas represent 95% confidence intervals of the predictions. Colour corresponds to the number of years since a fire disturbance event. Points are the average survival for individuals in each size pentile with associated standard error.

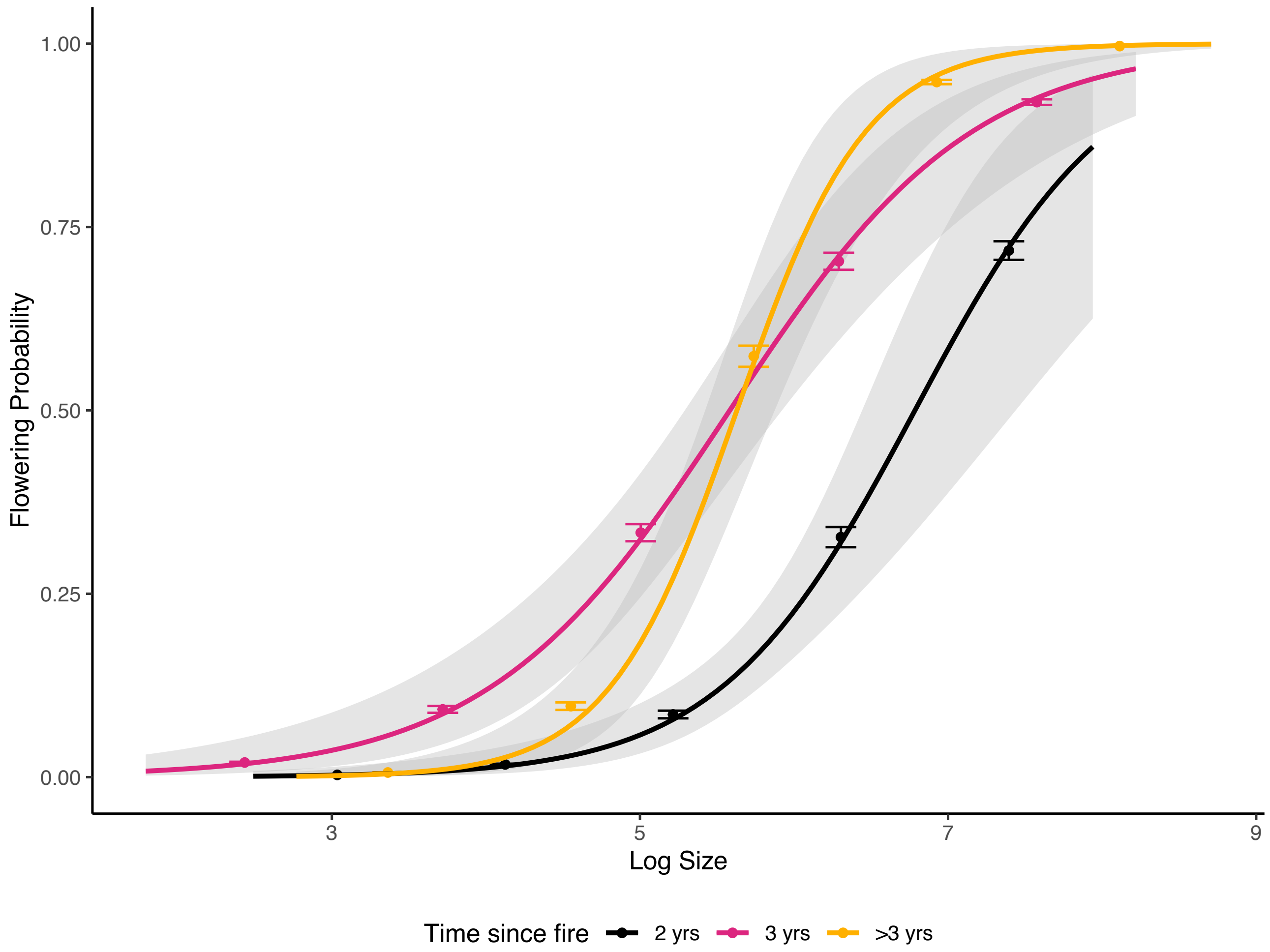


Figure 4. *Drosophyllum lusitanicum* flowering probability against natural logged size under median levels of inter/intraspecific crowding and spatial autocorrelation for flowering probability. The fitted lines correspond to a binomial generalised linear model and the shaded areas represent 95% confidence intervals of the predictions. Colour corresponds to the number of years since a fire disturbance event. Points are the average survival for individuals in each size pentile with associated standard error.

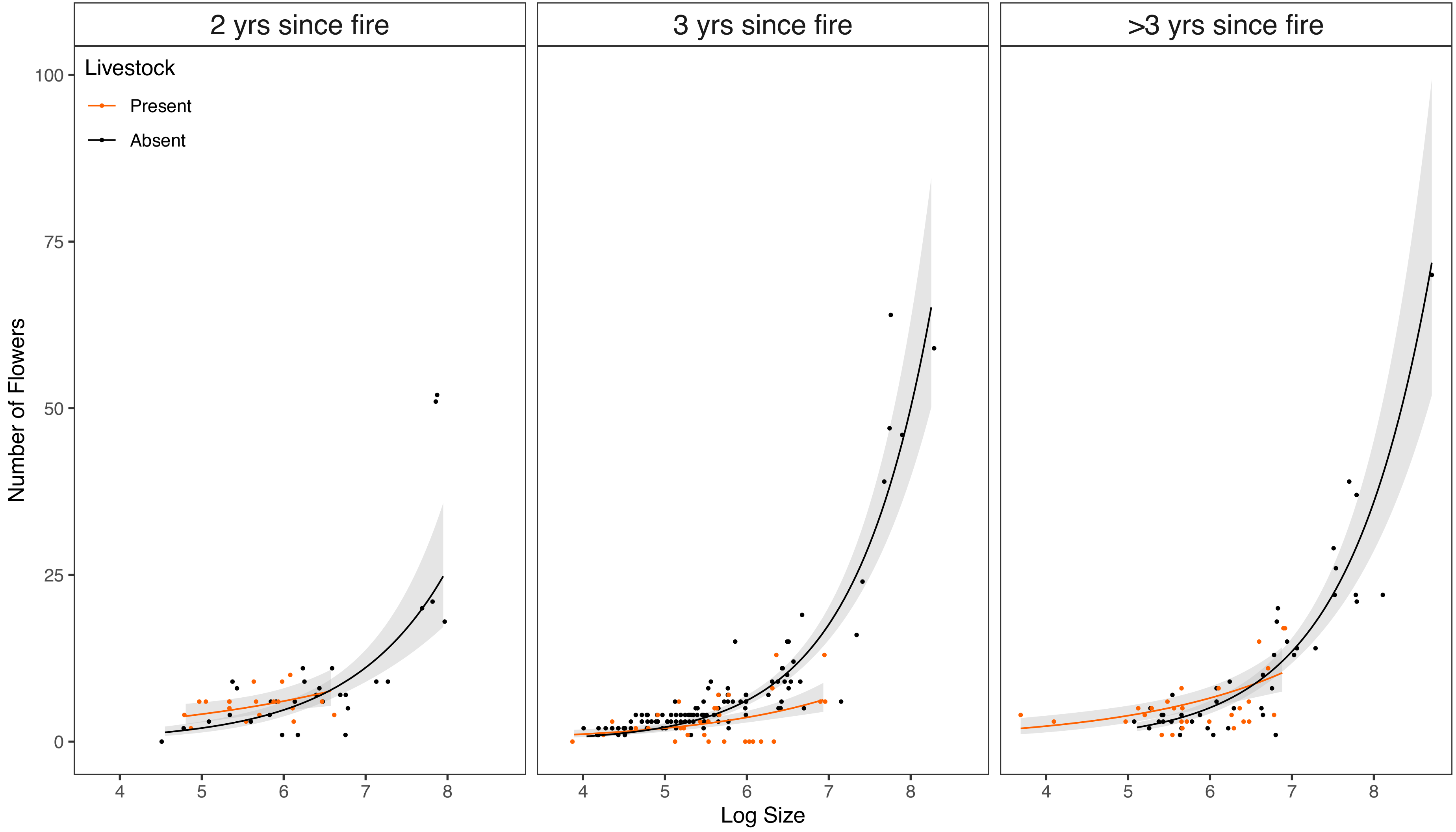


Figure 5. *Drosophyllum lusitanicum* fertility against natural logged size categorised by years since a fire disturbance event under median levels of spatial autocorrelation for flowering probability. Colour corresponds to the presence or absence of browsing livestock. The fitted lines correspond to a negative binomial generalised linear model and the shaded areas represent 95% confidence intervals of the predictions.

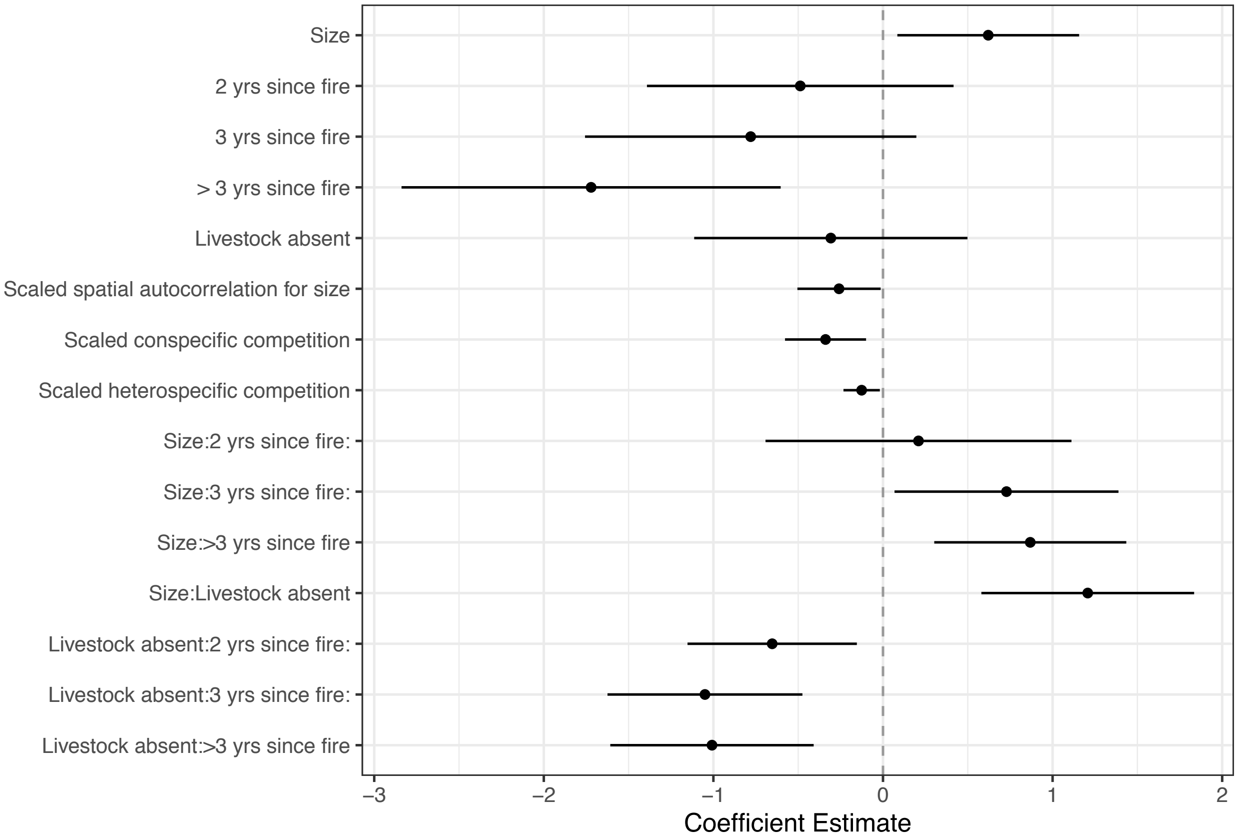


Figure 6. Coefficient plot with standard errors of the full base general linear model for *Drosophyllum lusitanicum* growth including interspecific and intraspecific competition. If a variable or interaction has an estimate greater than 0 it had positive effects on growth.

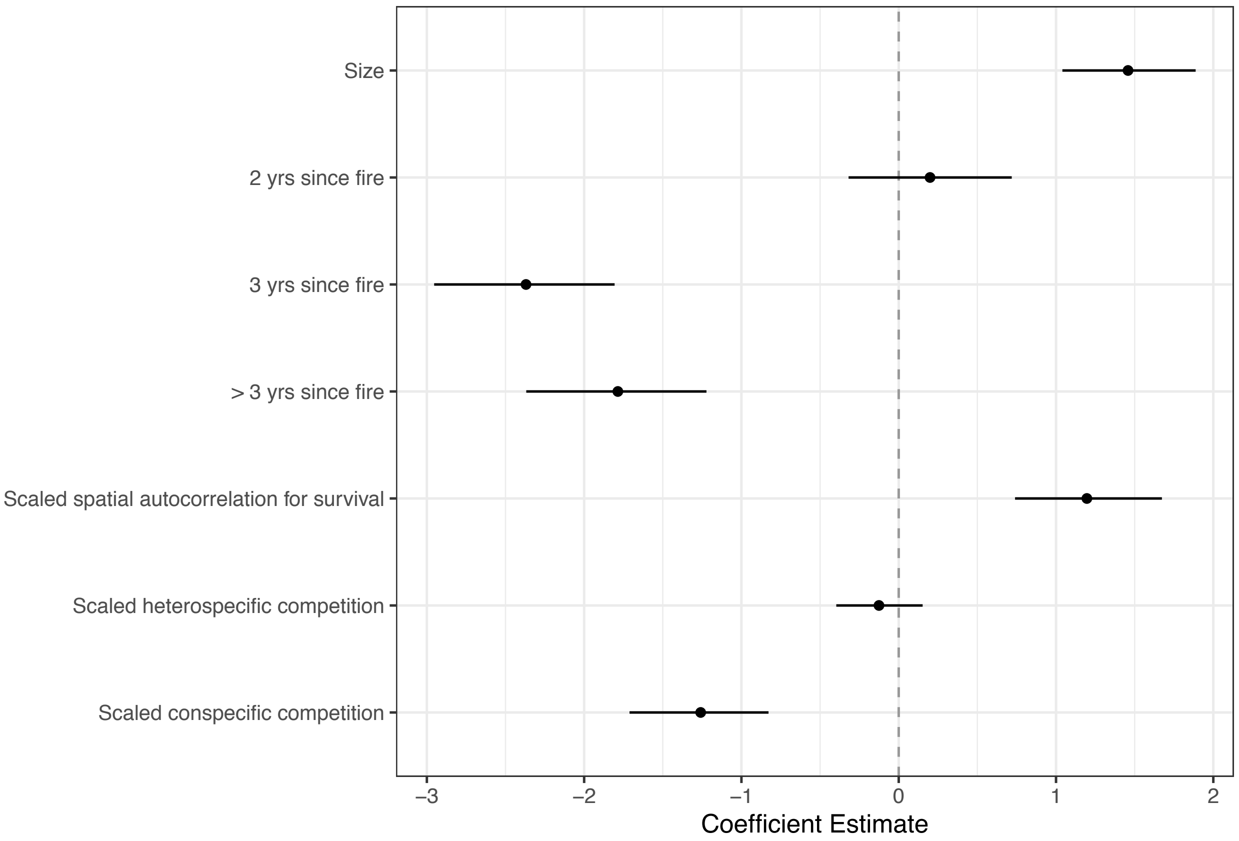


Figure 7. Coefficient plot with standard errors of the full base binomial generalised linear model for *Drosophyllum lusitanicum* probability of survival including interspecific and intraspecific competition. If a variable or interaction has an estimate greater than 0 it had positive effects on survival.

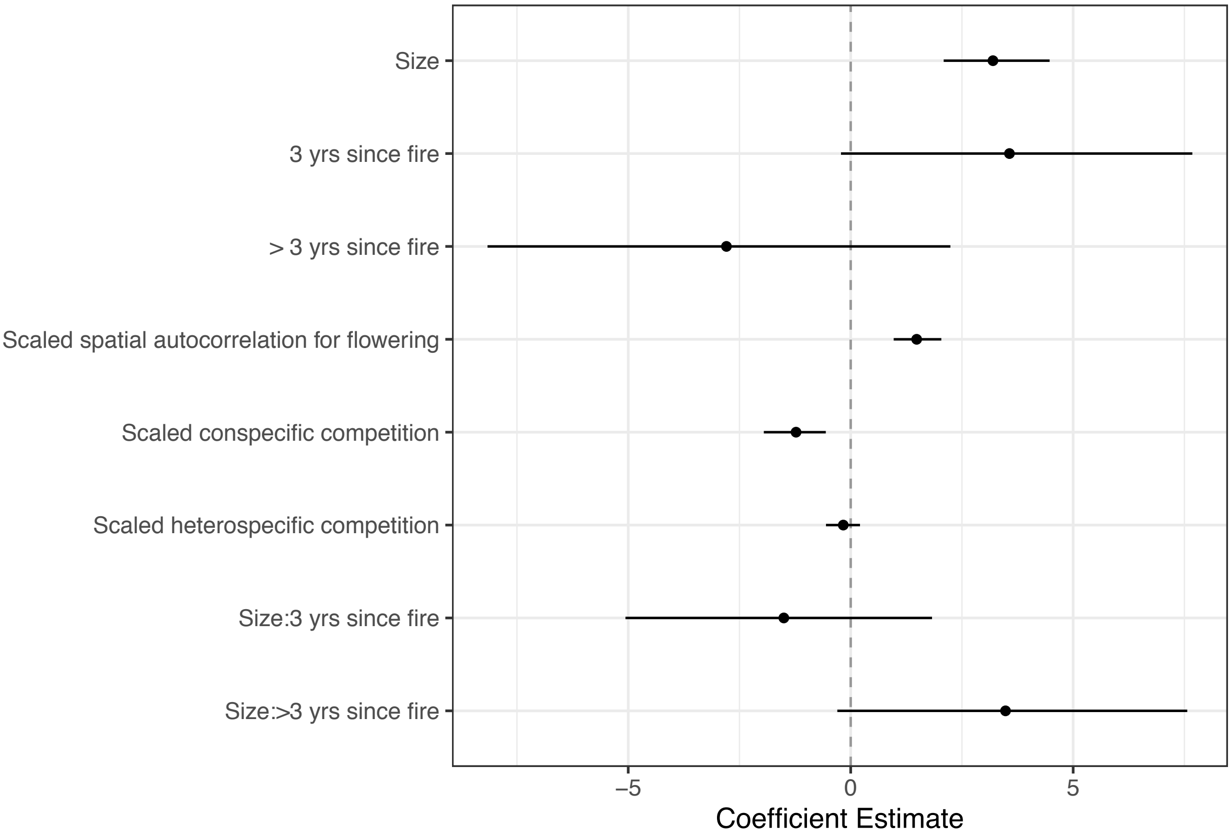


Figure 8. Coefficient plot with standard errors of the full base binomial generalised linear model for *Drosophyllum lusitanicum* probability of flowering including interspecific and intraspecific competition. If a variable or interaction has an estimate greater than 0 it had positive effects on survival.

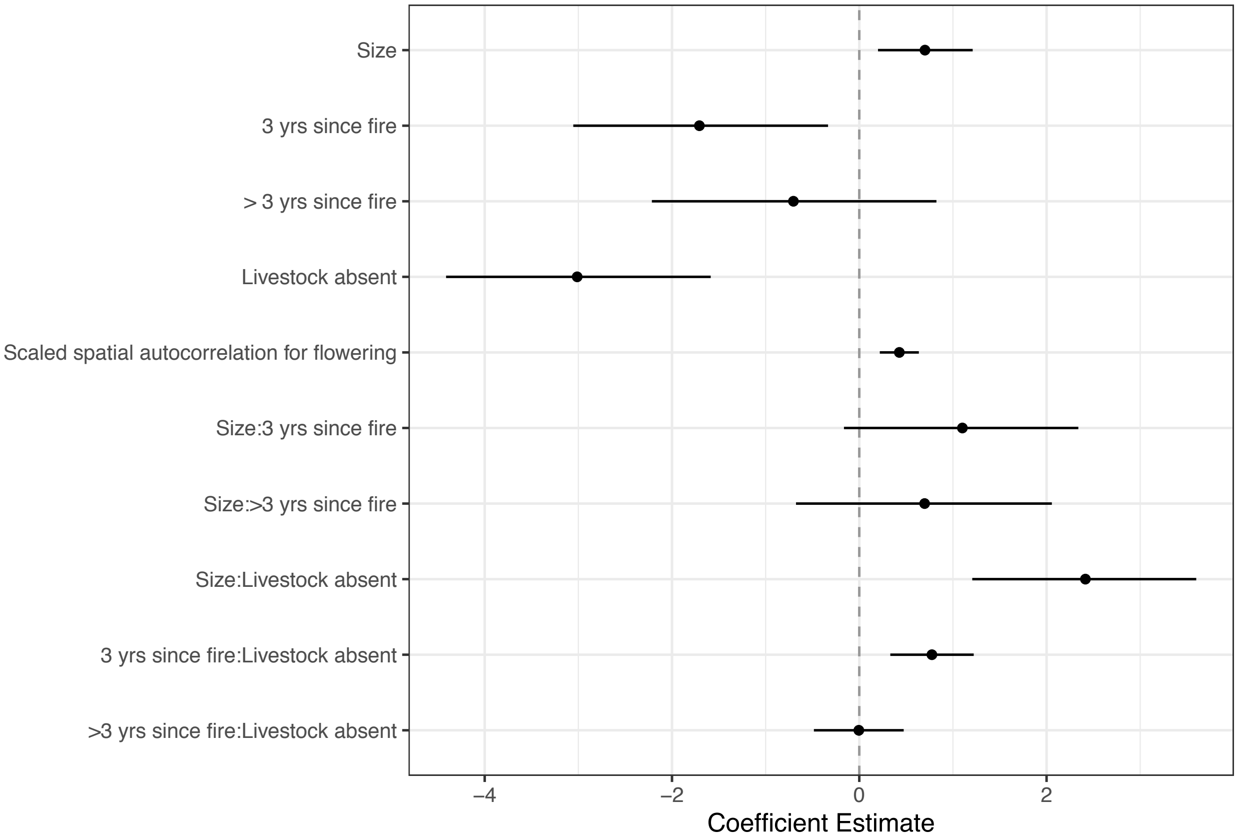


Figure 9. Coefficient plot with standard errors of the full base negative binomial generalised linear model for *Drosophyllum lusitanicum* total flower production. If a variable or interaction has an estimate greater than 0 it had positive effects on flower production.

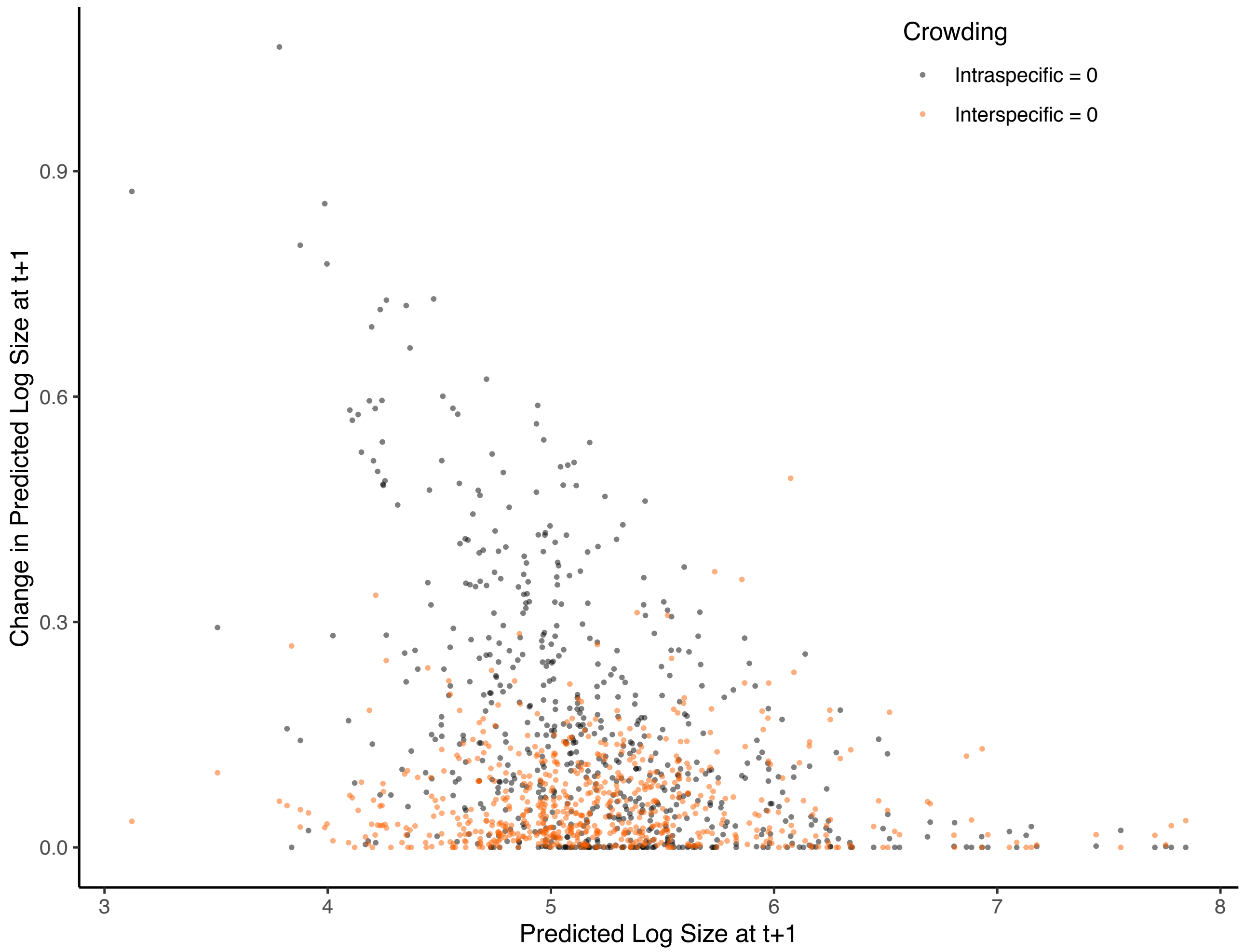


Figure 10. Changes in predicted *Drosophyllum lusitanicum* growth in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis corresponds to how large an individual is expected to become based on a general linear model including competition. Either interspecific or intraspecific crowding is set to 0, and the effects on growth estimates are presented on the y-axis.

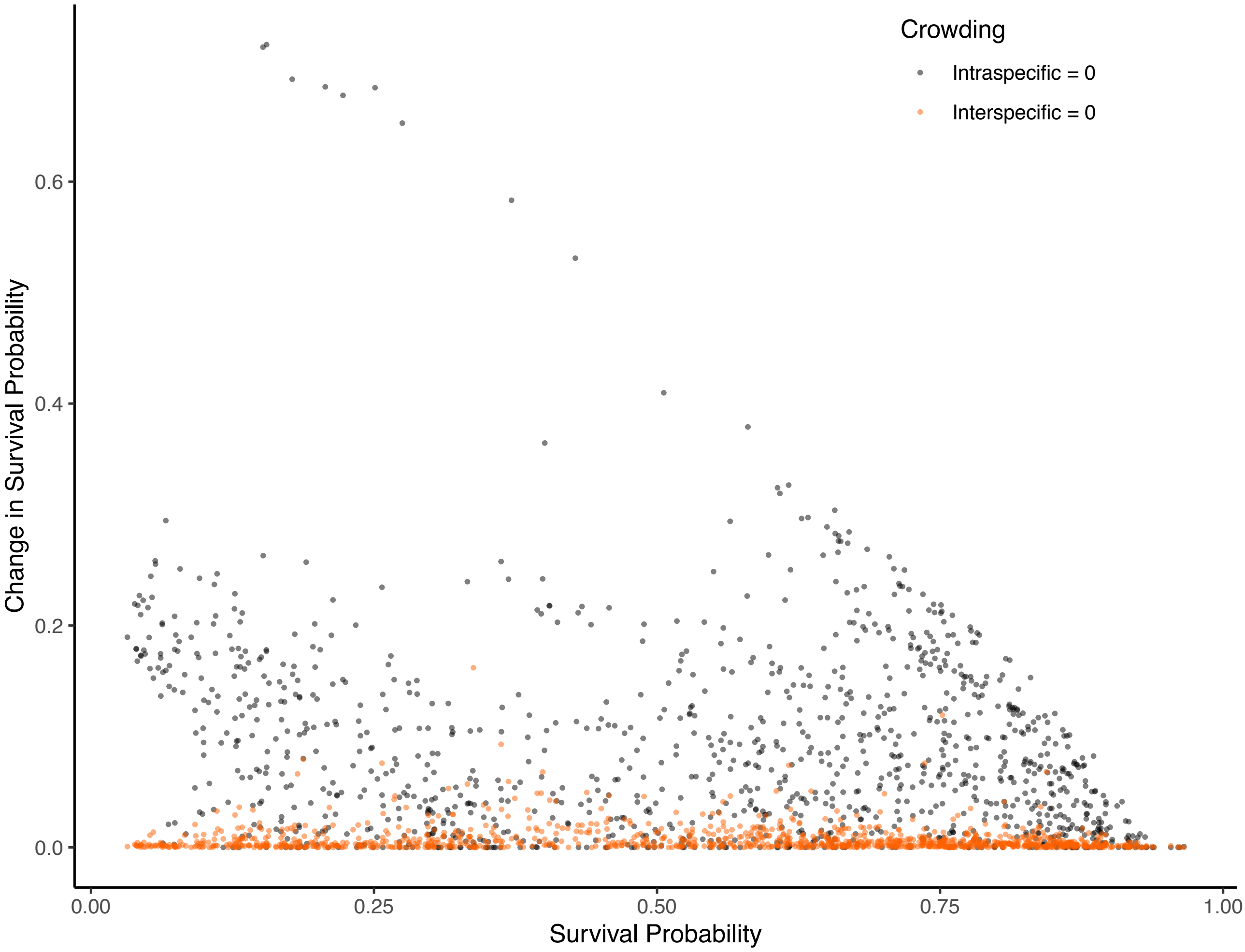


Figure 11. Changes in predicted *Drosophyllum lusitanicum* survival probability in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis corresponds to how likely an individual is to survive to next year based on a binomial generalised linear model including competition. Either interspecific or intraspecific crowding is set to 0, and the effects on survival probability estimates are presented on the y-axis.

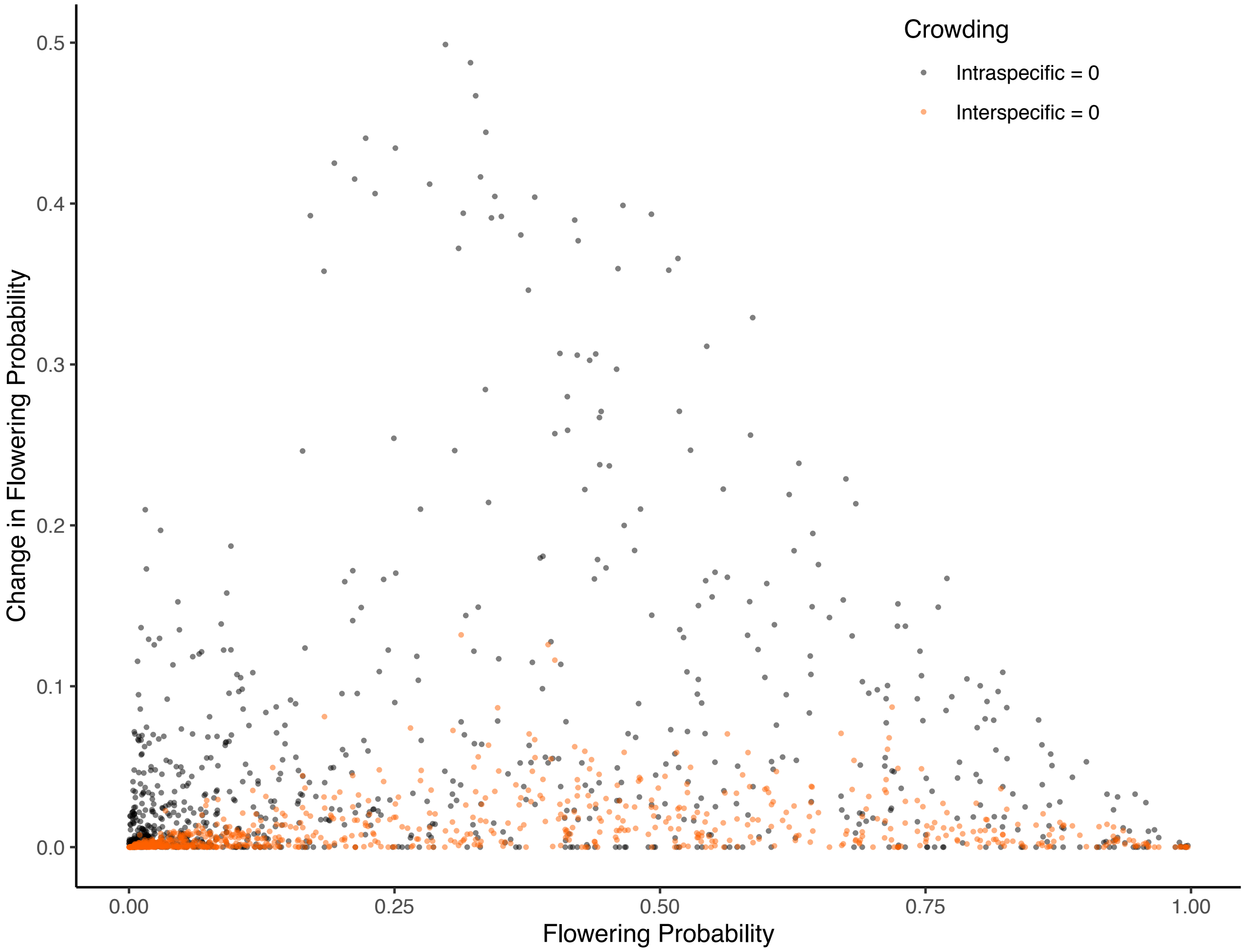


Figure 12. Changes in predicted *Drosophyllum lusitanicum* flowering probability in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis corresponds to how likely an individual is to flower to next year based on a binomial generalised linear model including competition. Either interspecific or intraspecific crowding is set to 0, and the effects on flowering probability estimates are presented on the y-axis.

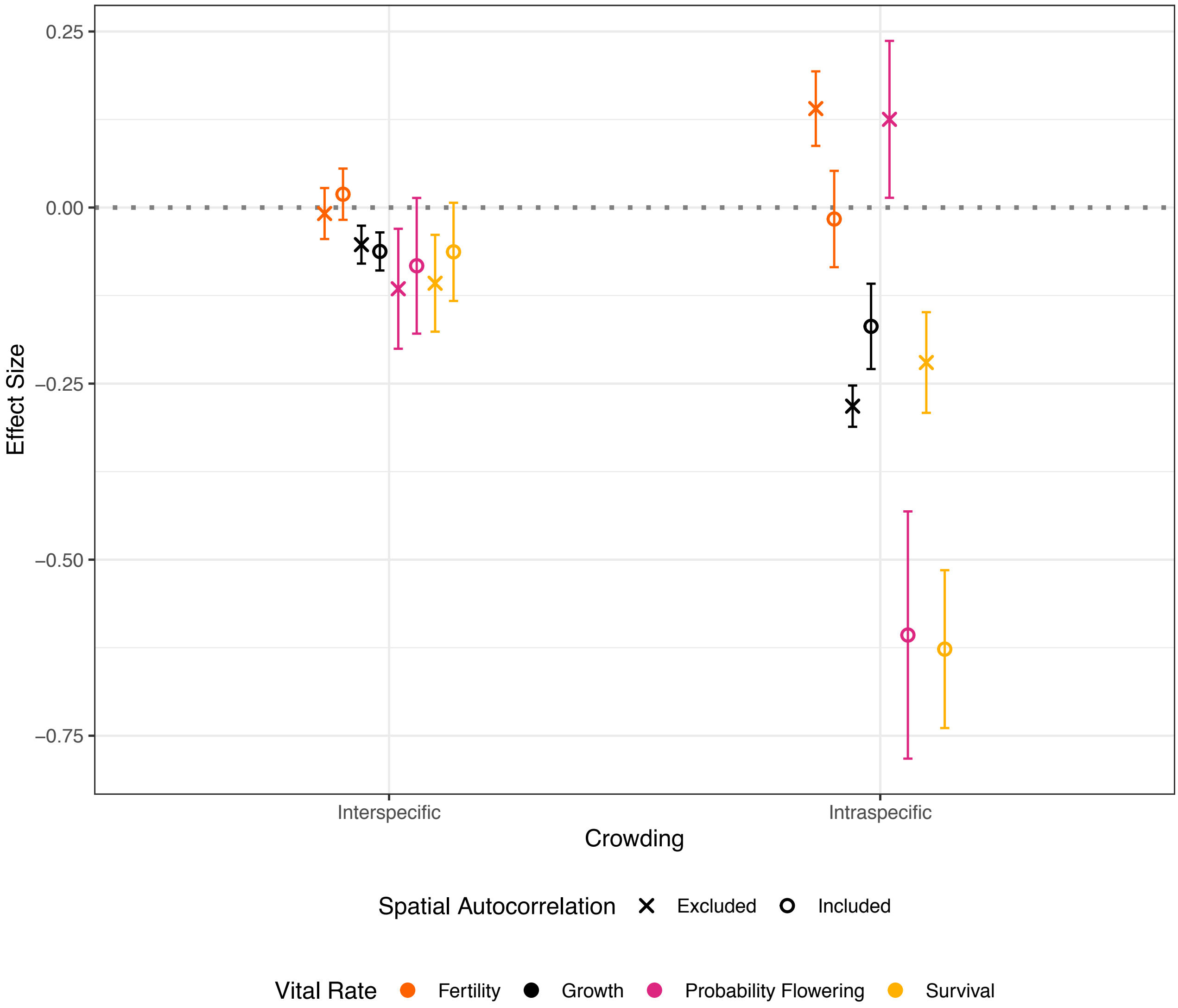


Figure 13. Estimated crowding effect sizes and standard errors for models of *Drosophyllum lusitanicum* performance where spatial autocorrelation was either included or excluded. The sign indicates competition (-) or facilitation (+).

2.7 References

1.

Adlassnig, W. *et al.* Endocytotic uptake of nutrients in carnivorous plants. *The Plant Journal* **71**, 303–313 (2012).

2.

Adler, P. B., Ellner, S. P. & Levine, J. M. Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters* **13**, 1019–1029 (2010).

3.

Adler, P. B. *et al.* Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecol Lett* **21**, 1319–1329 (2018).

4.

Andrés, C. & Ojeda, F. Effects of afforestation with pines on woody plant diversity of Mediterranean heathlands in southern Spain. *Biodiversity and Conservation* **11**, 1511–1520 (2002).

5.

Arino, O., Casadio, S. & Serpe, D. Global night-time fire season timing and fire count trends using the ATSR instrument series. *Remote Sensing of Environment* **116**, 226–238 (2012).

6.

Augustin, N. H., Mugglestone, M. A. & Buckland, S. T. An Autologistic Model for the Spatial Distribution of Wildlife. *The Journal of Applied Ecology* **33**, 339 (1996).

7.

Balvanera, P. *et al.* Quantifying the evidence for biodiversity effects on ecosystem functioning and services: Biodiversity and ecosystem functioning/services. *Ecology Letters* **9**, 1146–1156 (2006).

8.

Bardos, D. C., Guillera-Arroita, G. & Wintle, B. A. Valid auto-models for spatially autocorrelated occupancy and abundance data. *Methods Ecol Evol* **6**, 1137–1149 (2015).

9.

Besag, J. Spatial Interaction and the Statistical Analysis of Lattice Systems. *Journal of the Royal Statistical Society: Series B (Methodological)* **36**, 192–225 (1974).

10.

Bivand, R. & Gomez-Rubio, V. *Applied spatial data analysis with R, Second edition*. (Springer, 2013).

11.

Bobbink, R. Effects of Nutrient Enrichment in Dutch Chalk Grassland. *The Journal of Applied Ecology* **28**, 28 (1991).

12.

Calvo, L., Tárrega, R. & De Luis, E. The dynamics of mediterranean shrubs species over 12 years following perturbations. *Plant Ecology* **160**, 25–42 (2002).

13.

Chase, J. & Leibold, M. *Ecological Niches: Linking Classical and Contemporary Approaches*. (University of Chicago Press, 2003).

14.

Chesson, P. Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).

15.

Correia, E. & Freitas, H. Drosophyllum lusitanicum, an endangered West Mediterranean endemic carnivorous plant: threats and its ability to control available resources. *Botanical Journal of the Linnean Society* **140**, 383–390 (2002).

16.

Crone, E. E. *et al.* Ability of Matrix Models to Explain the Past and Predict the Future of Plant Populations: Forecasting population dynamics. *Conservation Biology* **27**, 968–978 (2013).

17\.

Cross, A. T. *et al.* Defining the role of fire in alleviating seed dormancy in a rare Mediterranean endemic subshrub. *AoB PLANTS* **9**, (2017).

18\.

Damgaard, C. & Weiner, J. It's About Time: A Critique of Macroecological Inferences Concerning Plant Competition. *Trends in Ecology & Evolution* **32**, 86–87 (2017).

19\.

Detto, M., Visser, M. D., Wright, S. J. & Pacala, S. W. Bias in the detection of negative density dependence in plant communities. *Ecol Lett* **22**, 1923–1939 (2019).

20\.

DeWalt, S. J., Denslow, J. S. & Ickes, K. NATURAL-ENEMY RELEASE FACILITATES HABITAT EXPANSION OF THE INVASIVE TROPICAL SHRUB CLIDEMIA HIRTA. *Ecology* **85**, 471–483 (2004).

21\.

Duncan, C., Thompson, J. R. & Pettorelli, N. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. *Proc. R. Soc. B* **282**, 20151348 (2015).

22\.

Eisenhauer, N. *et al.* Biodiversity-ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. *J Veg Sci* **27**, 1061–1070 (2016).

23\.

Ellner, S. P. & Rees, M. Integral Projection Models for Species with Complex Demography. **167**, 410–428 (2006).

24.

Freckleton, R. P., Watkinson, A. R. & Rees, M. Measuring the importance of competition in plant communities. *Journal of Ecology* **97**, 379–384 (2009).

25.

Garrido, B., Hampe, A., Marañón, T. & Arroyo, J. Regional differences in land use affect population performance of the threatened insectivorous plant Drosophyllum lusitanicum (Droseraceae). *Diversity and Distributions* **9**, 335–350 (2003).

26.

Gómez-Aparicio, L. *et al.* Applying Plant Facilitation to Forest Restoration: A Meta-Analysis of the Use of Shrubs as Nurse Plants. *Ecological Applications* **14**, 1128–1138 (2004).

27.

Gómez-González, S., Paniw, M., Antunes, K. & Ojeda, F. Heat shock and plant leachates regulate seed germination of the endangered carnivorous plant <i>Drosophyllum lusitanicum</i> *Web Ecol.* **18**, 7–13 (2018).

28.

Gómez-González, S. *et al.* Mediterranean Heathland as a Key Habitat for Fire Adaptations: Evidence from an Experimental Approach. *Forests* **11**, 748 (2020).

29.

Gotelli, N. J. *A primer of ecology*. (Sinauer Associates, 2001).

30.

Grant, K., Kreyling, J., Heilmeier, H., Beierkuhnlein, C. & Jentsch, A. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecol Res* **29**, 991–1001 (2014).

31.

Heubl, G., Bringmann, G. & Meimberg, H. Molecular Phylogeny and Character Evolution of Carnivorous Plant Families in Caryophyllales — Revisited. *Plant Biology* **8**, 821–830 (2006).

32.

Hutchinson, E. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**, 415–427 (1957).

33.

Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).

34.

Juniper, B., Robins, R., & Joel, D. *The Carnivorous Plants*. (Academic Press, 1989).

35.

Junta de Andalucía, Consejería de Medio Ambiente. *Plan de Prevención y Extinción de Incendios forestales de Andalucía (INFOCA)*. (2013).

36.

Kawai, T. & Tokeshi, M. Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proc. R. Soc. B* **274**, 2503–2508 (2007).

37.

McKinney, M. L. & Lockwood, J. L. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453 (1999).

38.

Mitchell, C. E. & Power, A. G. Release of invasive plants from fungal and viral pathogens. *Nature* **421**, 625–627 (2003).

39.

Müller, J. & Deil, U. Ecology and structure of Drosophyllum lusitanicum (l.) Links populations in the south-west of the Iberian Peninsula. 47–68 (2001).

40.

Ojeda, F., Marañón, T. & Arroyo, J. Patterns of ecological, chorological and taxonomic diversity at both sides of the Strait of Gibraltar. *Journal of Vegetation Science* **7**, 63–72 (1996).

41.

Ojeda, F., Marañón, T. & Arroyo, J. Plant diversity patterns in the Aljibe Mountains (S. Spain): a comprehensive account. *Biodiversity and Conservation* **9**, 1323–1343 (2000).

42.

Ortega-Olivencia, A., Claver, J. P. C. & Alcaraz, J. A. D. Floral and reproductive biology of Drosophyllum lusitanicum(L.) Link (Droseraceae). *Botanical Journal of the Linnean Society* **118**, 331–351 (1995).

43.

Paniw, M., Quintana-Ascencio, P. F., Ojeda, F. & Salguero-Gómez, R. Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant. *Journal of Applied Ecology* **54**, 1884–1894 (2017).

44.

Paniw, M., Salguero-Gómez, R. & Ojeda, F. Local-scale disturbances can benefit an endangered, fire-adapted plant species in Western Mediterranean heathlands in the absence of fire. *Biological Conservation* **187**, 74–81 (2015).

45.

Paniw, M., Salguero-Gómez, R. & Ojeda, F. Transient facilitation of resprouting shrubs in fire-prone habitats. *Journal of Plant Ecology* 9 (2017).

46.

Phoenix, G. K. *et al.* Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. *Global Change Biol* **12**, 470–476 (2006).

47.

Preston, C. A. & Baldwin, I. T. Positive and Negative Signals Regulate Germination in the Post-Fire Annual, Nicotiana Attenuata. *Ecology* **80**, 481–494 (1999).

48.

Quintana-Ascencio, P. F., Weekley, C. W. & Menges, E. S. Comparative demography of a rare species in Florida scrub and road habitats. *Biological Conservation* **137**, 263–270 (2007).

49.

R Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2020).

50.

Rader, R., Bartomeus, I., Tylianakis, J. M. & Laliberté, E. The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. *Diversity Distrib.* **20**, 908–917 (2014).

51.

Rees, M., Grubb, P. & Kelly, D. Quantifying the Impact of Competition and Spatial Heterogeneity on the Structure and Dynamics of a Four-Species Guild of Winter Annuals. *The American Naturalist* **147(1)**, 1–32 (1996).

52.

Rees, M., Childs, D. Z. & Ellner, S. P. Building integral projection models: a user's guide. *J Anim Ecol* **83**, 528–545 (2014).

53.

Silvertown, J. Plant coexistence and the niche. *Trends in Ecology & Evolution* **19**, 605–611 (2004).

54.

Skates, L. M. *et al.* An ecological perspective on 'plant carnivory beyond bogs': nutritional benefits of prey capture for the Mediterranean carnivorous plant Drosophyllum lusitanicum. *Annals of Botany* **124**, 65–76 (2019).

55.

Smith, M., Caswell, H. & Mettler-Cherry, P. STOCHASTIC FLOOD AND PRECIPITATION REGIMES AND THE POPULATION DYNAMICS OF A THREATENED FLOODPLAIN PLANT. *Ecological Applications* **15**, 1036–1052 (2005).

56.

Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G. & Ellner, S. P. Linking demography with drivers: climate and competition. *Methods in Ecology and Evolution* **7**, 171–183 (2016).

57.

Thorén, L. M. & Karlsson, P. S. Effects of supplementary feeding on growth and reproduction of three carnivorous plant species in a subarctic environment. *Journal of Ecology* **86**, 501–510 (1998).

58.

Tielbörger, K. & Kadmon, R. TEMPORAL ENVIRONMENTAL VARIATION TIPS THE BALANCE BETWEEN FACILITATION AND INTERFERENCE IN DESERT PLANTS. *Ecology* **81**, 1544–1553 (2000).

59.

Tuck, S. L., Porter, J., Rees, M. & Turnbull, L. A. Strong responses from weakly interacting species. *Ecol Lett* **21**, 1845–1852 (2018).

60.

Weigelt, A. & Jolliffe, P. Indices of plant competition. *Journal of Ecology* **91**, 707–720 (2003).

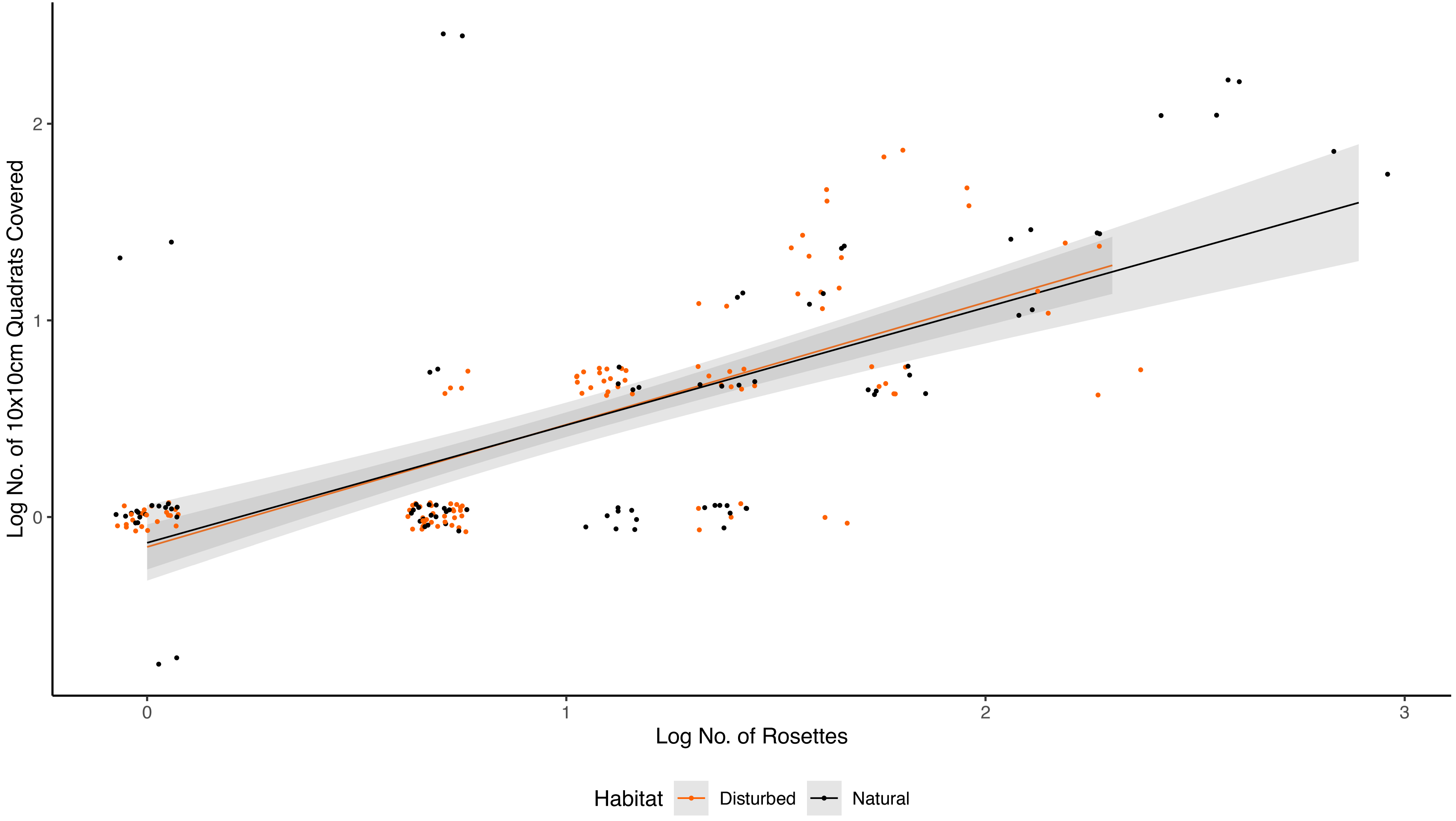
61.

Wiegmann, S. M. & Waller, D. M. Fifty years of change in northern upland forest understories: Identity and traits of “winner” and “loser” plant species. *Biological Conservation* **129**, 109–123 (2006).

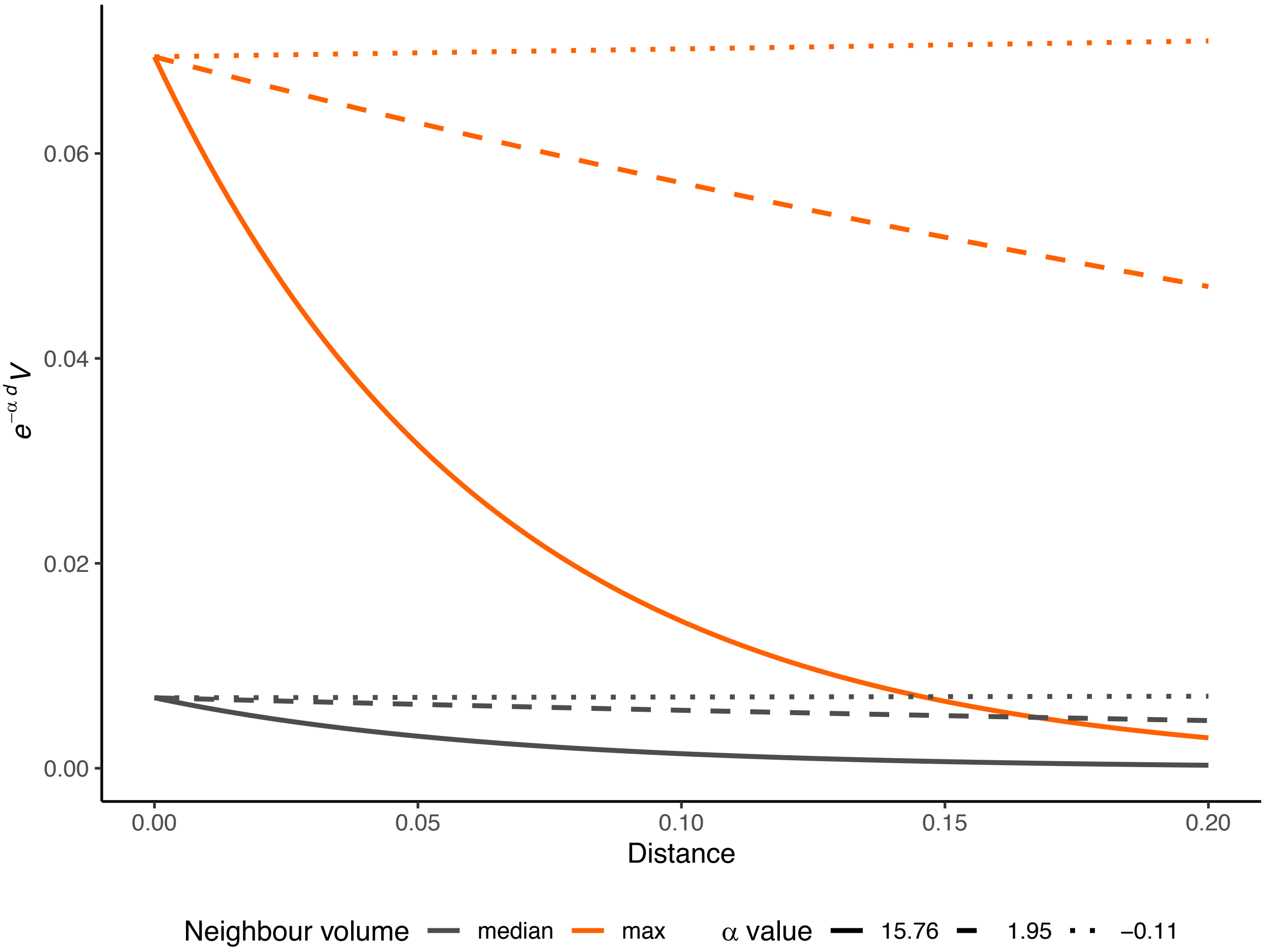
62.

Yates, C. J. & Ladd, P. G. Using population viability analysis to predict the effect of fire on the extinction risk of an endangered shrub Verticordia fimbrilepis subsp. fimbrilepis in a fragmented landscape. *Plant Ecol* **211**, 305–319 (2010).

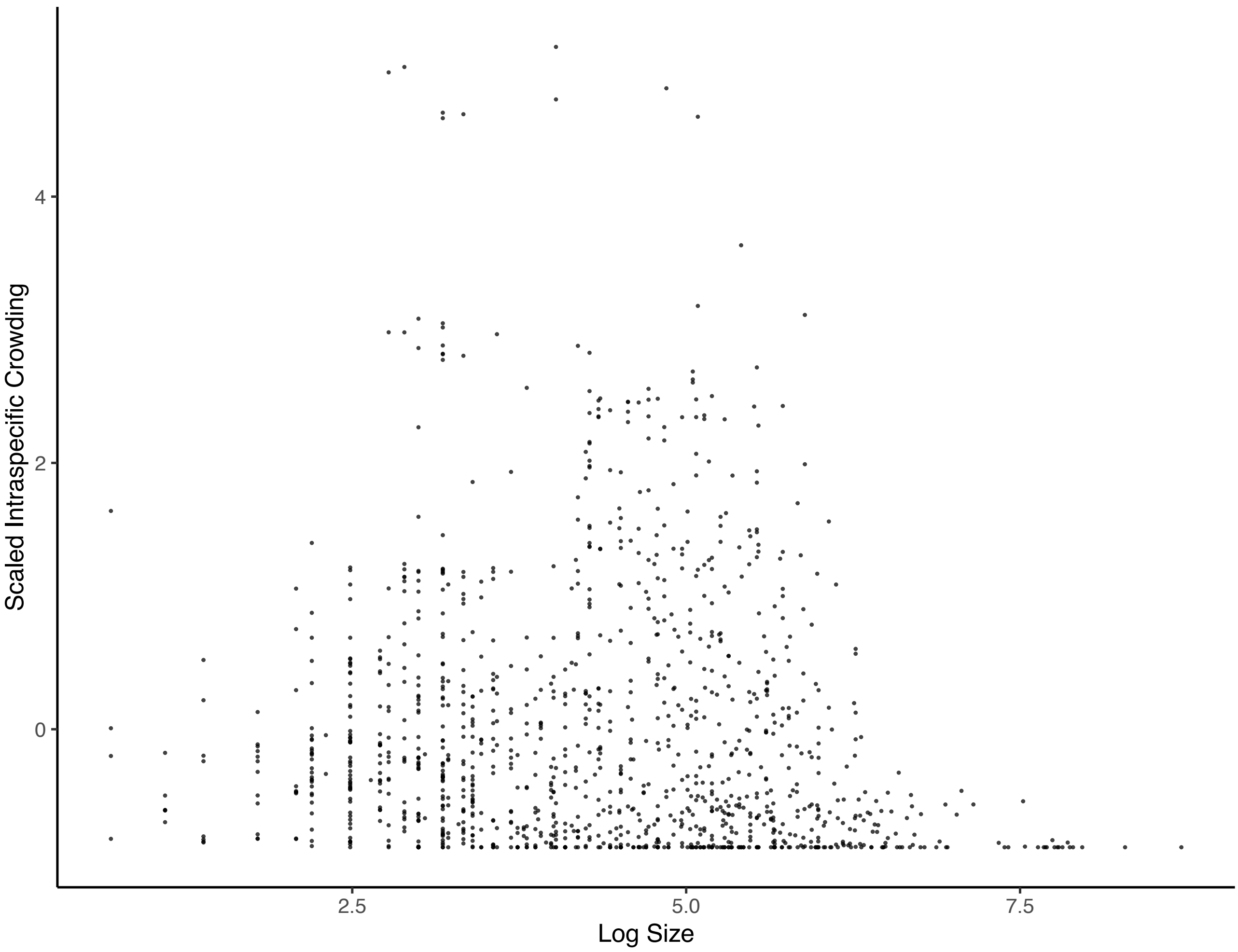
2.8 Supplementary information



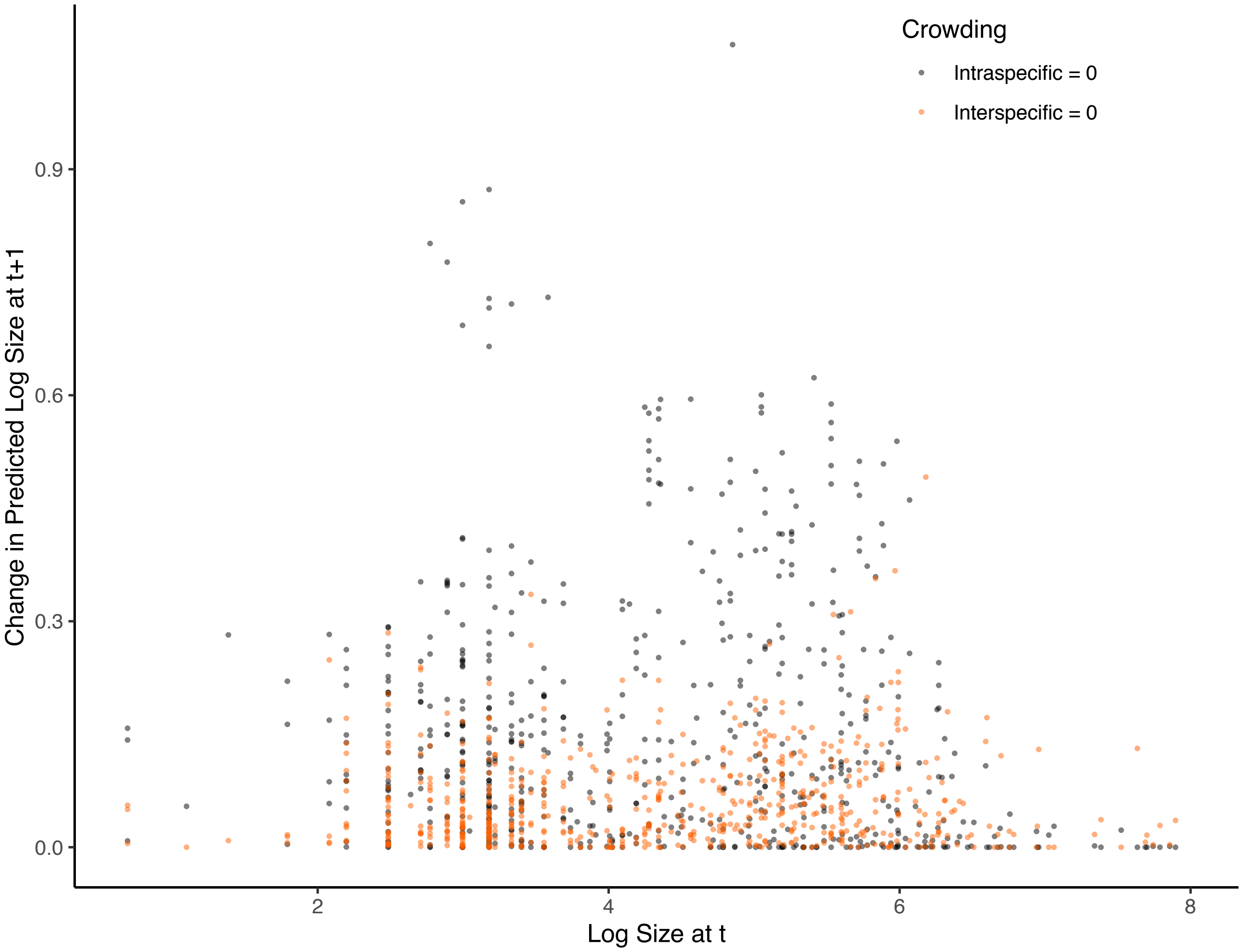
Supplementary 1. The area occupied by individuals of *Drosophyllum lusitanicum*, noting the number of basal rosettes each individual possesses. Colour corresponds to whether the individual is from disturbed or natural settings. Points are jittered horizontally and vertically to minimize overlap.



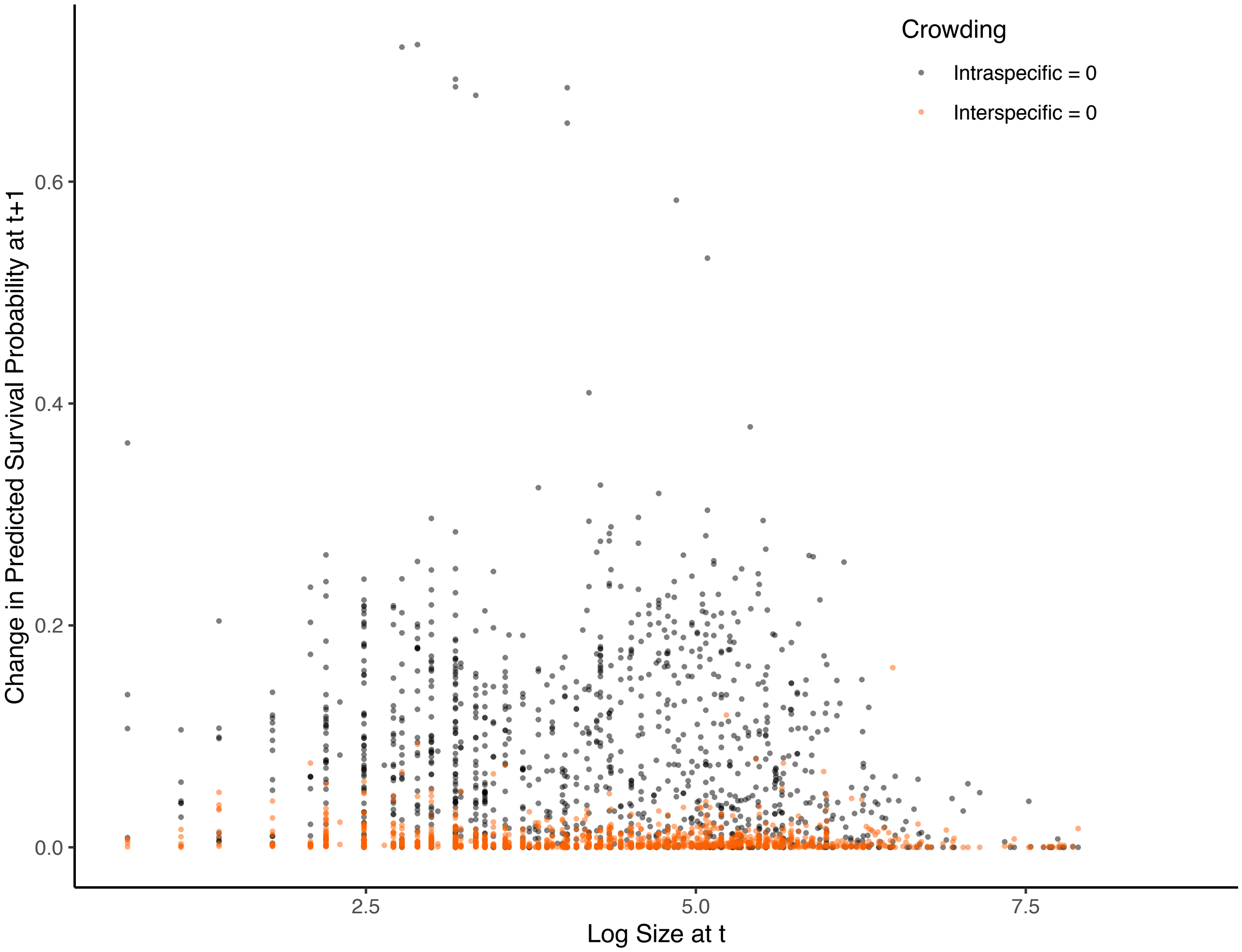
Supplementary 2. The crowding an individual of *Drosophyllum* experiences depending on α and distance to neighbour volume. The α values presented improved model parsimony in vital rate models when they were incorporated into crowding indices (Table. 1). Neighbour volumes are the median or maximum observed in the dataset.



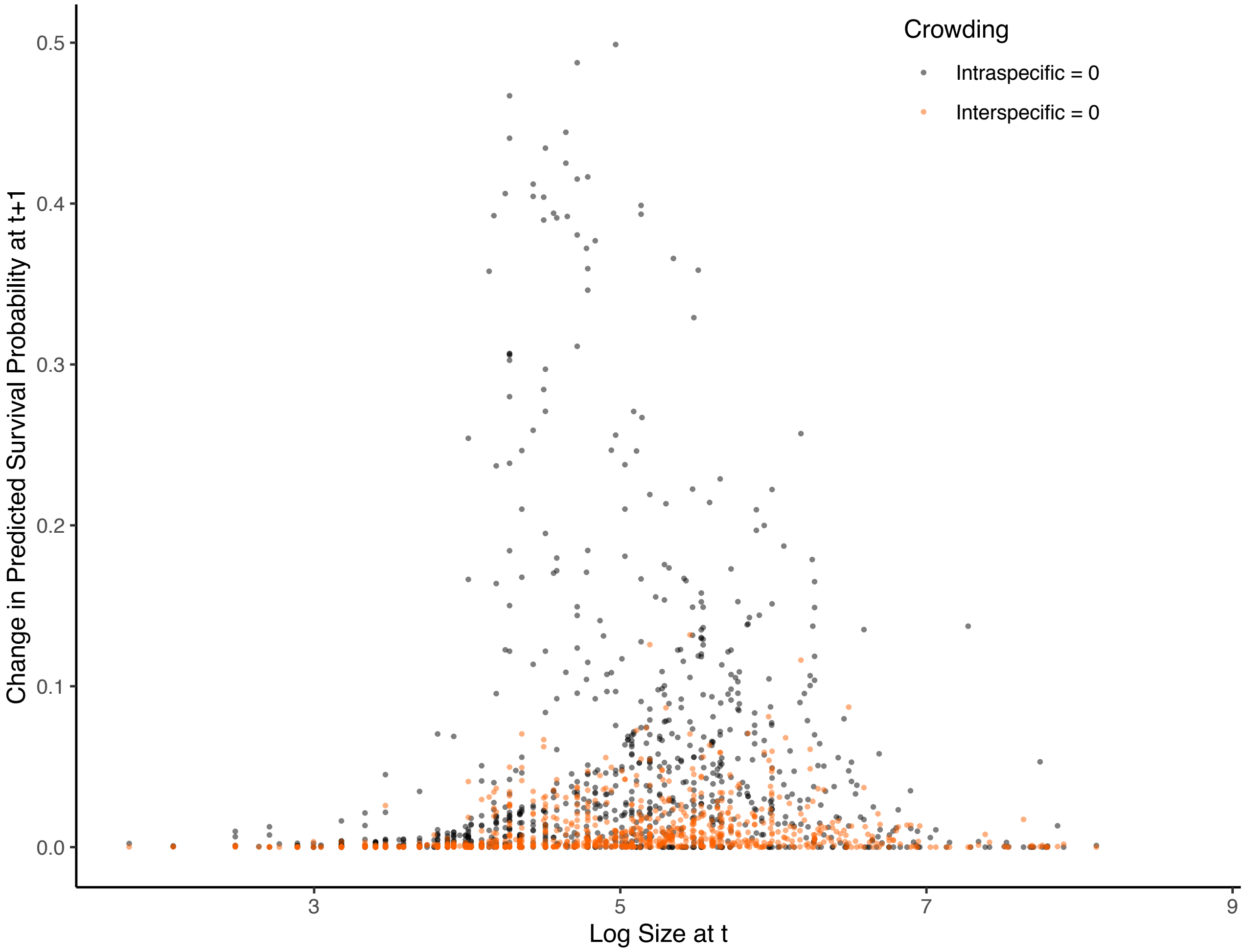
Supplementary 3. The intraspecific competition experienced by individuals of *Drosophyllum lusitanicum* across a range of sizes. Points represent an individual in a given year.



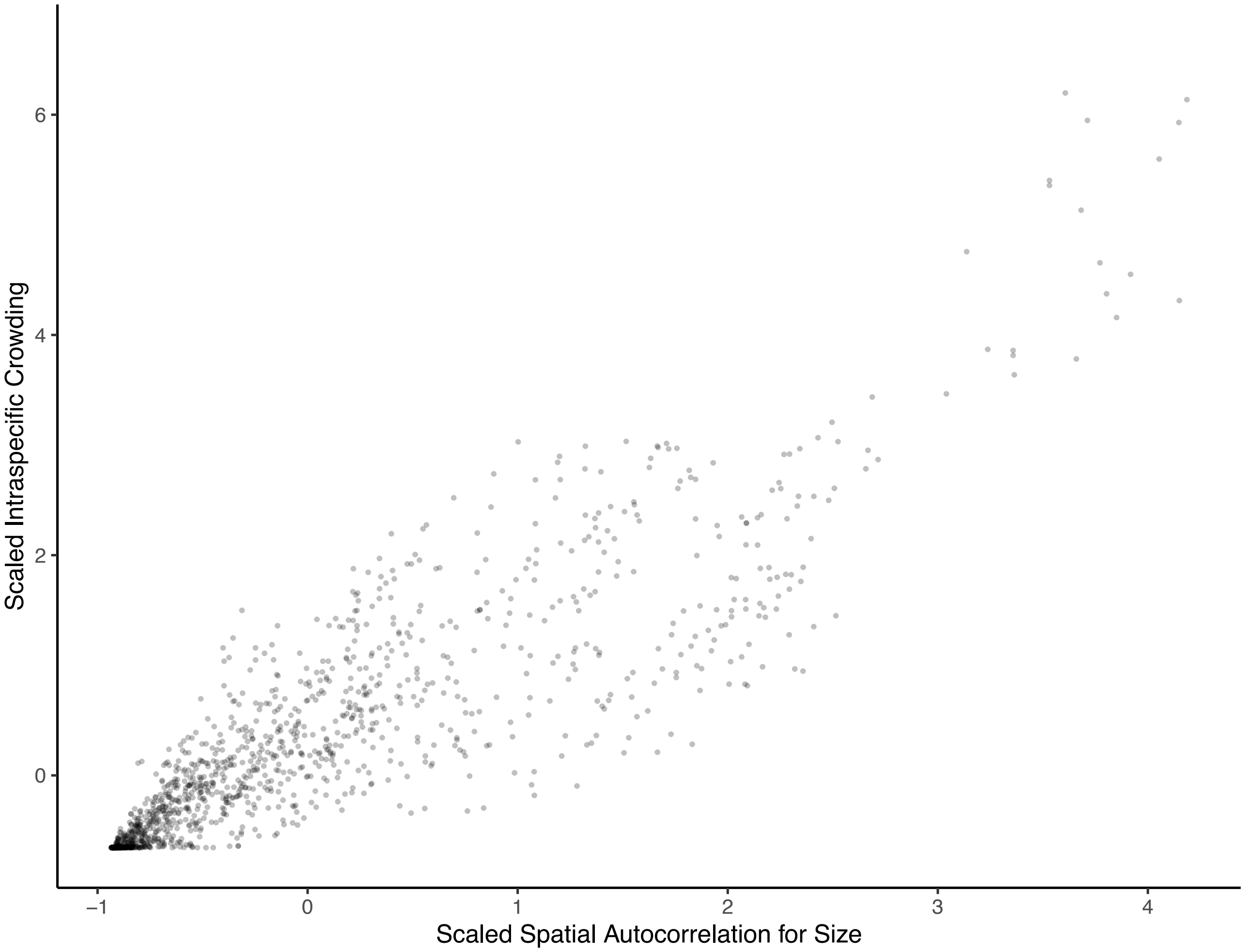
Supplementary 4. Changes in predicted *Drosophyllum lusitanicum* growth in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis indicates how large an individual is. Either interspecific or intraspecific crowding is set to 0, and the effects on growth estimates are presented on the y-axis.



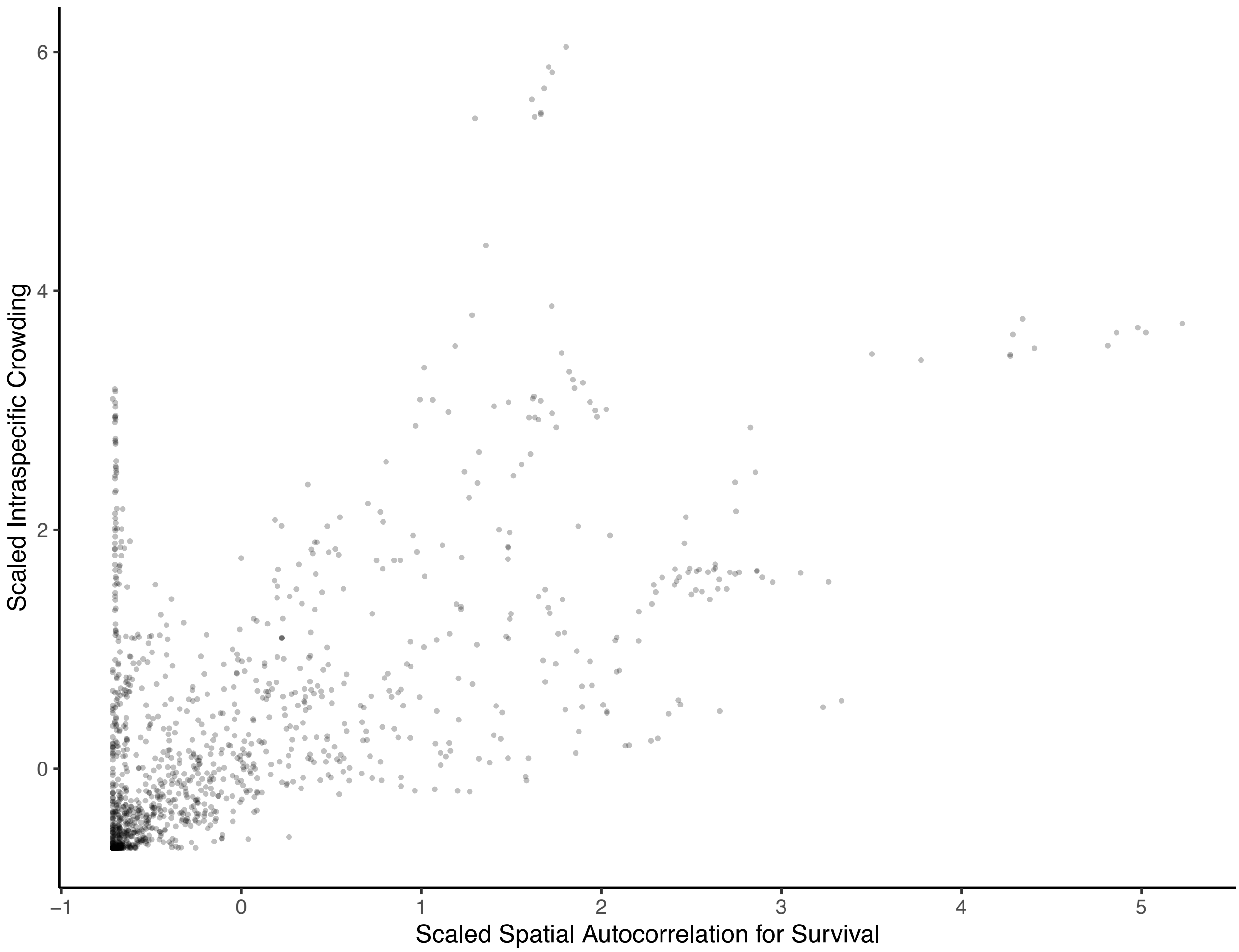
Supplementary 5. Changes in predicted *Drosophyllum lusitanicum* survival probability in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis indicates how large an individual is. Either interspecific or intraspecific crowding is set to 0, and the effects on growth estimates are presented on the y-axis.



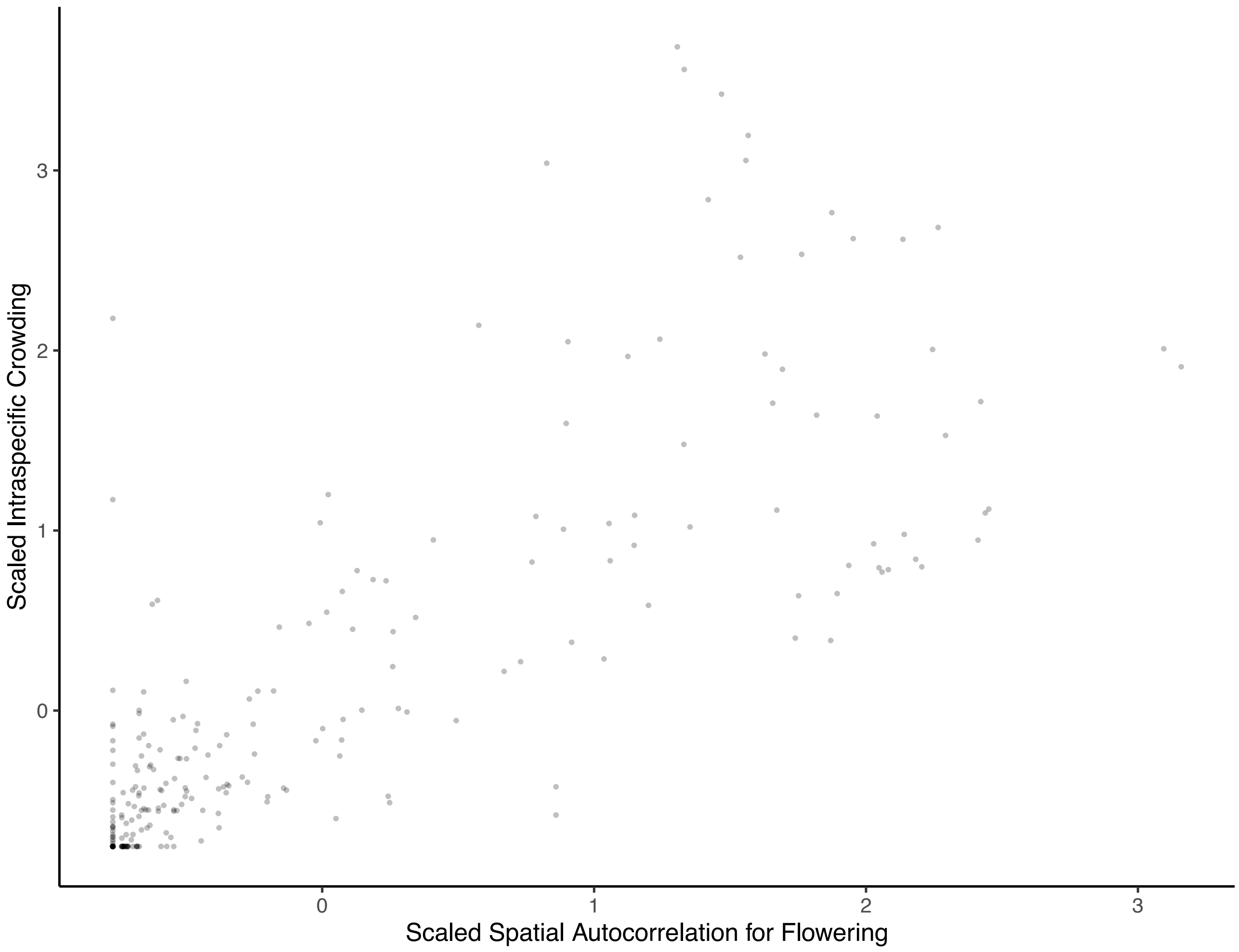
Supplementary 6. Changes in predicted *Drosophyllum lusitanicum* survival probability in a neighbour exclusion simulation. Points represent individual *Drosophyllum*. Position on the x-axis indicates how large an individual is. Either interspecific or intraspecific crowding is set to 0, and the effects on growth estimates are presented on the y-axis.



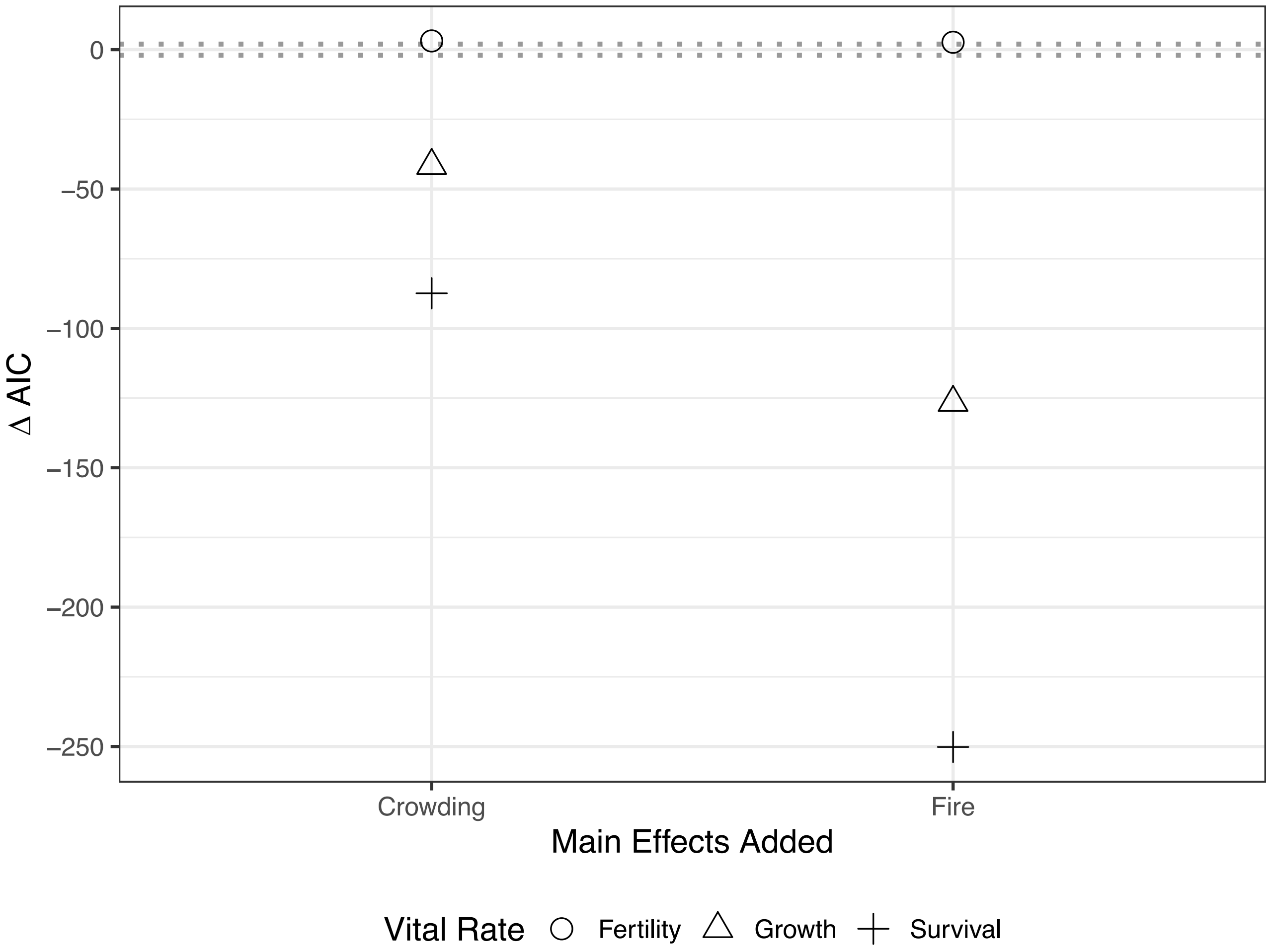
Supplementary 7. The relationship between the intraspecific crowding experienced by an individual of *Drosophyllum lusitanicum* and spatial autocorrelation for neighbour size. Points are scaled; mean of variable is subtracted from each value, and then divided by the standard deviation.



Supplementary 8. The relationship between the intraspecific crowding experienced by an individual of *Drosophyllum lusitanicum* and spatial autocorrelation for neighbour survival. Points are scaled; mean of variable is subtracted from each value, and then divided by the standard deviation.



Supplementary 9. The relationship between the intraspecific crowding experienced by an individual of *Drosophyllum lusitanicum* and spatial autocorrelation for neighbours flowering. Points are scaled; mean of variable is subtracted from each value, and then divided by the standard deviation.



Supplementary 10. Changes in *Drosophyllum* vital rate model parsimony when either time since fire disturbance or crowding variables are added to a model not containing either. The dashed zone covers 2 above and below 0, a range suggesting negligible changes in parsimony. The crowding indexes included α values that were optimised using base models that did not include time since fire terms. Time since fire could be a proxy for crowding since vegetation structure changes upon the disturbance, but the additional explanatory power above the more granular crowding metrics suggest it encompasses other determinants of *Drosophyllum* performance.

Chapter 3: Site-specific vital rate responses to nitrogen addition

3.1 Abstract

Peatlands host unique communities and sequester carbon but are vulnerable to nutrient pollution. Nitrogen inputs affects individual performance, resulting in changes to population size, community composition, and thus ecosystem function. *Drosera rotundifolia* is a potential indicator of peatland health and useful case study of how plants invest resources under changing conditions; most of these processes are observable above-ground, owing to its carnivorous habit and reduced root system. We test how the vital rates of British *D. rotundifolia* populations respond to a doubling of site-specific ambient nitrogen deposition. Nitrogen reduces individual growth and has site-specific negative effects on survival. Nitrogen will have a negative effect on flowering probability and seed capsule production because these vital rates are size-dependent. We note differences in size-specific vital rates amongst the different populations, highlighting the need to replicate demographic studies to understand how environmental change will affect species.

3.2 Introduction

Environmental degradation is a globally significant issue. Both changing climate and land use affect ecosystem function, community composition, species ranges and individual performance (Walther, 2002; Parmesan, 2006; Bobbink et al., 2010). Peatlands are particularly important for their unique species assemblages and carbon storage (Gorham, 1991; Clymo et al., 1998; Page et al., 2011; Page & Baird, 2016; Harenda et al., 2018). A key characteristic of peatlands is limited nutrient availability (Bobbink et al., 1998; Lovett et al., 2009) but increasingly intensive farming practices and industrial pollution are major sources of nitrogen pollution in these habitats (Galloway et al., 2008; Bobbink et al., 2010; Phoenix et al., 2012).

Community composition of bogs is likely to shift in response to increased deposition of nitrogen (Gunarsson et al., 2004; Bubier et al., 2007). The short-term morphological and life history related responses of peatland plants suited to low nitrogen are less well understood. Greater awareness of species responses could lead to the identification of new indicator species to assess bog health (Jennings & Rohr, 2011). Environmental change and variability can change plant morphology and functioning (Cheng et al., 2005; Latimer & Jacobs, 2012), but this may not be easy to monitor in wild populations over multiple years without considerable disturbance. This is most clearly the case for assessing differences in root systems where morphology will change in response to varying nutrient availability (Pregitzer et al., 1993).

Many carnivorous plant species possess root characteristics that make them ideal study systems to test plant responses to experimental treatments in the field. Carnivorous plants use their modified leaves to meet nutrient demands (Karlsson *et al*., 1996), rather than their often-diminished roots. It is therefore possible to measure carnivorous plant morphology as an indicator of resource availability (Ellison & Gotelli, 2002) and/or understand how individuals allocate their resources for nutrient acquisition.

The round-leaved sundew, *Drosera rotundifolia* (*Drosera* hereafter), is an ideal carnivorous species to study the effects of nitrogen on plant functioning. *Drosera* has a broad geographical range (Crowder *et al*., 1990). Populations of *Drosera* found in small fragments of peatland habitat may be at risk due to pollution, bog drainage and climate change affecting the habitat broadly (Crowder *et al*., 1990; Redbo-Torstensson, 1994). However, while there may be some declines in range or threats to individual populations, the conservation status of the species has been assessed and officially classified as of “least concern” according to the IUCN Red List (Maiz-Tome, 2016), the foremost source of information on extinction risk. A low extinction risk classification is rare amongst carnivorous plant species (Jennings & Rohr, 2011). Therefore, *Drosera* is a good candidate for spatially replicated experimental work given its ability to persist at high densities and under disturbance (Crowder *et al*., 1990).

In a previous experimental study, Redbo-Torstensson (1994) identified that increasing ammonium nitrate deposition treatments increased *Drosera* mortality in a south central Swedish bog, over 4 years. Additionally, low dosages of nitrogen (0.5g m^{-2}) increased the proportion of individuals that flowered, though the number of flowers produced on average did not differ significantly. Redbo-Torstensson suggested nitrogen fertilisation effects were mediated by interactions with *Sphagnum* moss; Svensson (1995) demonstrated such competition between *Drosera* and *Sphagnum fuscum* experimentally.

In this study we investigate the relationships between *Drosera* size and performance/vital rates (whether an individual survived, reproduced, changed in size, and how many flowers it produced) across multiple sites. Moreover, we test the effects of increased nitrogen inputs on performance across these sites. We also analyse the importance of past reproductive effort on future performance. These observed patterns and experimental effects can then be considered in future analyses of *Drosera* population viability in current and projected conditions using structured population models, for which carnivorous plants and spatial replication are underrepresented (Crone *et al*., 2011; Salguero-Gómez *et al.,* 2015).

3.3 Methods

3.3.1 Study sites

Four populations of *Drosera* were selected across three national parks. The sites were selected based on their suitability for multiple years of census-based data collection, and large population size to minimise population impacts from experimental manipulation. We monitored single populations in the Peak District, Loch Lomond and the Trossachs, and two populations from Snowdonia.

The study sites had some notable differences. The Peak District 1 and Snowdonia 1 sites were most similar, with populations distributed around a small bog pool. Both of these sites were dominated by *Sphagnum* moss, with some emerging grasses, sedges and shrubs. Saturated growing media is essential for *D.* rotundifolia, and the water level at Peak District 1 and Snowdonia 1 increases between spring and summer. In Snowdonia 1, previously dormant *Sphagnum* becomes saturated by water that is channelled down nearby mountains, coinciding with most *Drosera* growth. In contrast at the Peak District 1 site a desiccated surface layer of patches of dormant *Sphagnum* remained, and this was more common away the central pool at the site. The Snowdonia 2 site is covered by a matt of *Sphagnum*, and this is further overtopped by an abundance of grasses and heather. *Drosera* occurred in locations where other vascular plants were in low densities. In fact, *Drosera* was most prevalent on sheep disturbed tracks. Finally, the Loch Lomond site was characterised by a manmade (~20 years old) rockface resulting from the construction of a path. The exposed rock face supports a very shallow layer of soil, sufficient for *D.* R*otundifolia* but little else. A constant stream of water from higher ground maintains soil moisture. There is a more typical sphagnum bog habitat <100m from the rock face uphill, but *D. rotundifolia* density and abundance was substantially lower. Population coordinates are presented in Table 1 (photographs; Supp. 1, 2, 3 & 4).

3.3.2 Sampling methods and measurements

Plants were given an identity through one of two methods depending on their local habitat: 1) an A3 acetate sheet was placed above a plot. The position of each plant was marked on the sheet, along with a unique ID. 2) A bamboo skewer attached to a unique plastic bead was placed into the ground near each plant, within a 25 x 25 cm plot. Plots were marked with tent pegs at corners so as to not be conspicuous. A bead was threaded onto one of the tent pegs for plot identification purposes.

Data were recorded for 1512 *D. rotundifolia* individuals between July and mid-September 2017. Measurements were taken including leaf length (centre of rosette to trichome tip), petiole length, the number of living leaves, whether an individual flowered, the number of flowering stalks/inflorescences, stalk lengths, whether those stalks bifurcated (Supp. 5), the number of seed capsules, and how many leaves were engaged in carnivory (based on leaf curling). During the same period in 2018 we attempted to identify previously marked plants and took repeat measurements.

3.3.3 Nitrogen treatments

The sites varied in annual atmospheric nitrogen deposition rates. The nitrogen deposition rates associated with each population based on Air Pollution Information System records (APIS, 2017) are presented in Table 1. 720 of the plants in the census were exposed to a nitrogen treatment. The treatment consisted of a single sprayed application of ammonium nitrate solution on plots after all measurements had been taken at the site. The nitrogen addition was site specific, with the amount applied being equivalent to the ambient deposition the area would ordinarily receive, meaning treated individuals were exposed to double the levels of annual deposition. The range of control and treatment nitrogen exposure was within the range of values in the Swedish study by Redbo-Torstensson (1994).

3.3.4 Analysis

For each vital rate we fitted models including all interactions between the explanatory variables: size, site, and nitrogen addition. Additionally, we included whether an individual produced any bifurcating inflorescences when analysing number of flowers. Analyses were carried out using general linear models for growth, binomial generalised linear models for survival and probability of reproduction, and negative binomial regression for number of flowers, after Poisson generalised linear models for flowers failed to meet test assumptions. We then carried out type II ANOVAs on these models to filter non-significant predictors of performance and compared the AIC of candidate models to identify the most parsimonious. Finally, we added an additional main effect of whether an individual flowered the previous year to models of survival and growth to test whether accounting for prior reproductive effort helped explain performance. All analyses were carried out in R (4.0.3) (R Core Team, 2020).

3.4 Results

Drosera size is positively related to size in the previous year (general linear model: F= 33.70, df=1,572, p<0.01), is negatively related to nitrogen (F=7.61, df=1,562, p<0.01) and there is a significant effect of site (F=81.88, df=3,572, p<0.01) and a site size interaction (F=5.1, df=3,572, p<0.01) (Fig. 1). Reproductive status last year did not improve the model (t=1.51, df=1,571, p>0.05).

Survival was positively related to an individual's size the previous year (binomial generalised linear model: $\chi^2=18.48$, df=1,571, p<0.01) (Fig. 2). There was a significant site-nitrogen interaction ($\chi^2=10.15$, df=3,571, p<0.02), with the treatment having a negative effect on survival at Snowdonia 1, but not at other sites. Livestock interference reduced the number of monitored individuals at Snowdonia 2, hence the large degree of error. When reproductive status last year was added to the model, it was identified as a significant predictor of survival (z=2.15, df=1,883, p<0.05).

Larger individuals produced more flowers (negative binomial generalised linear model: $\chi^2=133.89$, df=1,317, p<0.01), and site was also a significant factor ($\chi^2=36.13$, df=3,317, p<0.01). Individuals at Loch Lomond 1 were capable of reproducing at smaller sizes and a plant of a given size at Loch Lomond 1 was more productive than equivalently sized plants in Snowdonia or the Peak District 1. Moreover, some individuals at Peak District 1 and Loch Lomond 1 produced bifurcating inflorescences, and these individuals were more productive ($\chi^2=69.75$, df=1,317, p<0.01) (Fig. 3).

Size was significantly positively related to the probability of reproduction (binomial generalised linear model: $\chi^2=242.05$, df=1,888, p<0.01) (Fig. 4). Additionally, site was important for probability of reproduction ($\chi^2=146.47$, df=3,888, p<0.01), and there was a significant interaction with size ($\chi^2=15.17$, df=3,888, p<0.01). Individuals at Loch Lomond 1 had a significantly higher likelihood of reproducing at a given size compared with the other.

3.5 Discussion

Nitrogen addition had a negative effect on plant growth (Fig. 1) probably due to increased growth of competitors that are better able to utilise it (Redbo-Torstensson, 1994; Svensson, 1995). We did not see significant effects of nitrogen on reproduction directly. However, nitrogen may have indirect negative effects on reproduction since both the number of flowers produced and probability of reproduction are size dependent (Fig. 3 & 4), and nitrogen influences growth (Fig. 1). Our nitrogen treatment was informed by rainfall-based deposition and applied by spraying affected *Drosera*. We should expect stronger negative effects on *Drosera* performance in the future because of the additional nitrogen inputs from livestock and runoff (Galloway *et al*., 2008; Bobbink *et al*., 2010).

Site was an important determinant of reproductive output and mortality (Fig. 2, 3 & 4). At Loch Lomond plants have relatively high reproductive output given their size (Fig. 4). A possible explanation is that individuals on a rock face habitat can invest more in reproduction due to a lack of competition. A *Drosera* leaf is comprised of a thin tube beginning at the centre of the plant (petiole) and ends with a carnivorous disc. The petiole lengthens when there is little light availability (Hatcher, 2019), so with little competition established *Drosera* individuals can remain compact. Crowder *et al*. (1990) also noted that shade is related to longer leaf length, and plants on exposed peat faces were smaller on average. Sites where *Drosera* recruitment is possible but interspecific competition is minimal, like Loch Lomond 1, could be important population reservoirs and sources of colonisers as nitrogen addition increases.

Drosera at Snowdonia 1 had lower survival when exposed to nitrogen (Fig. 2). The Peak District and Snowdonia 1 field sites appeared similar, but the differences in nitrogen effects on survival may be due to water availability. Mosses at Snowdonia 1 were constantly saturated, whereas at Peak District the top layer of *Sphagnum* was often desiccated. It could be that the drier conditions buffer *Drosera* mortality because the mosses are incapable of exploiting the added resources and growing while desiccated (Titus & Wagner, 1984).

Finally, we investigated whether reproduction in a previous year was a significant predictor of survival and growth. This was not the case for growth, and so it seems growth is dictated by conditions within the current growing season. In contrast, survival was positively related to prior reproduction. It seems reasonable that reproduction would have a negative effect on future performance, since resources are being allocated towards something with no immediate benefit to the individual. However, it is also likely that reproduction occurs in microhabitats that are conducive towards general *Drosera* success. Therefore, we may have seen a relationship due to habitat quality rather than trade-offs. It may be favourable for *Drosera* to reproduce rather than store excess resources for subsequent years since peatland *Sphagnum* topography can be dynamic, and desiccation and competitive exclusion are persistent threats even to established *Drosera*. Moreover, *Drosera* is often successful on disturbed ground (Crowder *et al*., 1990), and so a strategy of front-loading reproductive investment and short generation times may allow for substantial population increases over short periods.

3.6 Figures

Table 1. Locations of studied British *Drosera rotundifolia* populations. Annual N deposition rates are the mean based on 3 years of data between 2010-2012 from Air Pollution Information System records (http://www.apis.ac.uk/ accessed 01/02/2016).

Population	**Latitude/ Longitude**	**OS Grid Reference**	**N deposition / Kg N ha^{-1} yr^{-1}**	**No. plants given extra N**	**No. plants measured**
Loch Lomond (Inversnaid)	56°15'5.65"N 4°40'4.05"W	NN 34814 09762	17.08	202	467
Peak District (Rocher Bog)	53°26'7.23"N 1°36'24.84"W	SK 26213 93245	27.30	205	433
Snowdonia 1 (Llyndy Isaf	53° 1'16.86"N 4° 3'31.82"W	SH 620 491	12.04	126	237
Snowdonia 2 (Llyn Barfog)	52°34'13.31"N 3°59'24.46"W	SN 6522 9881	8.26	187	375
			Total:	**720**	**1512**

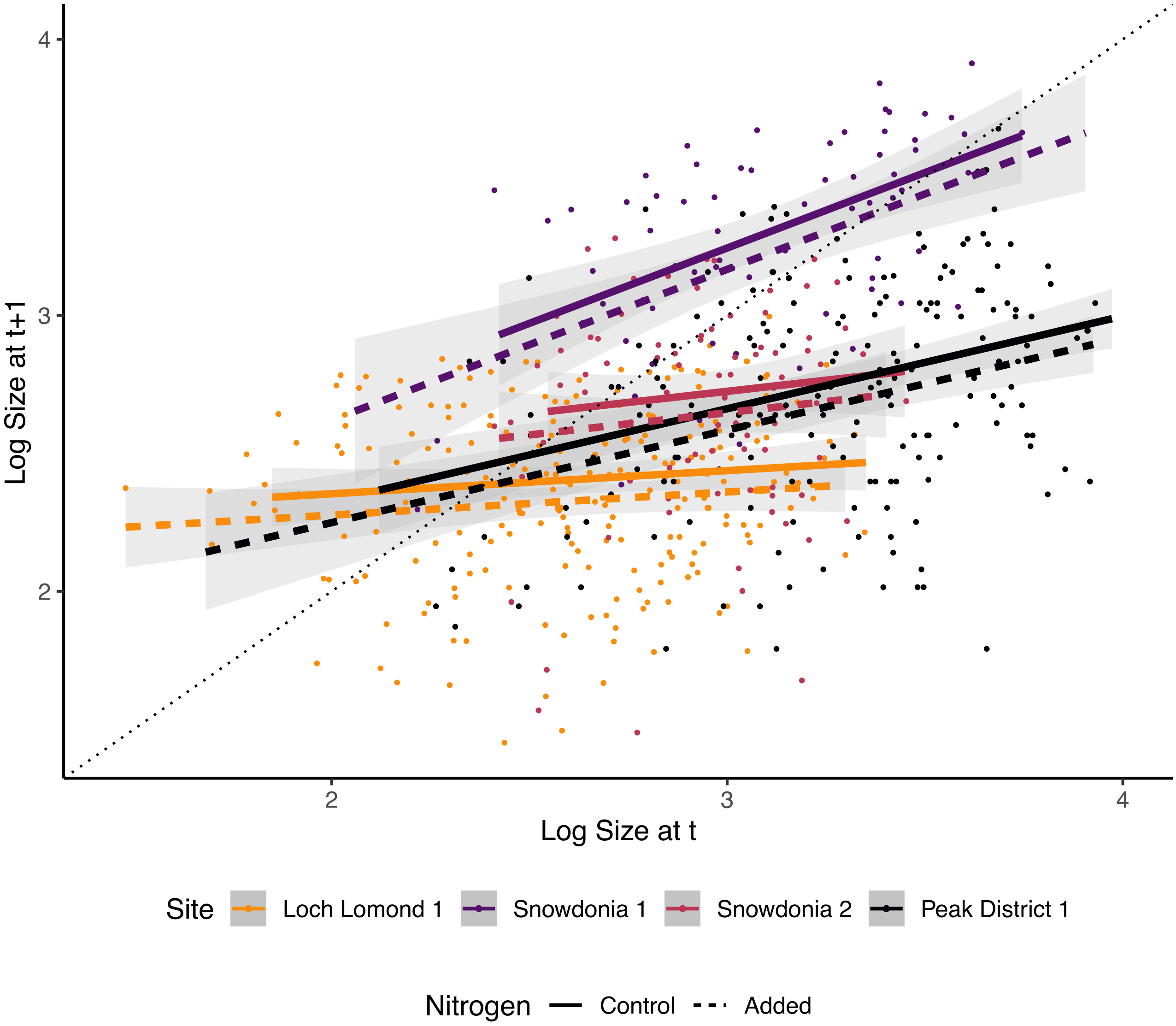


Figure 1. *Drosera rotundifolia* changes in natural logged size over a year, categorised by site and experimental addition of nitrogen. The fitted lines correspond to a general linear model. The shaded area around regression lines represent 95% confidence intervals. The dotted line has a slope of 1, representing stasis.

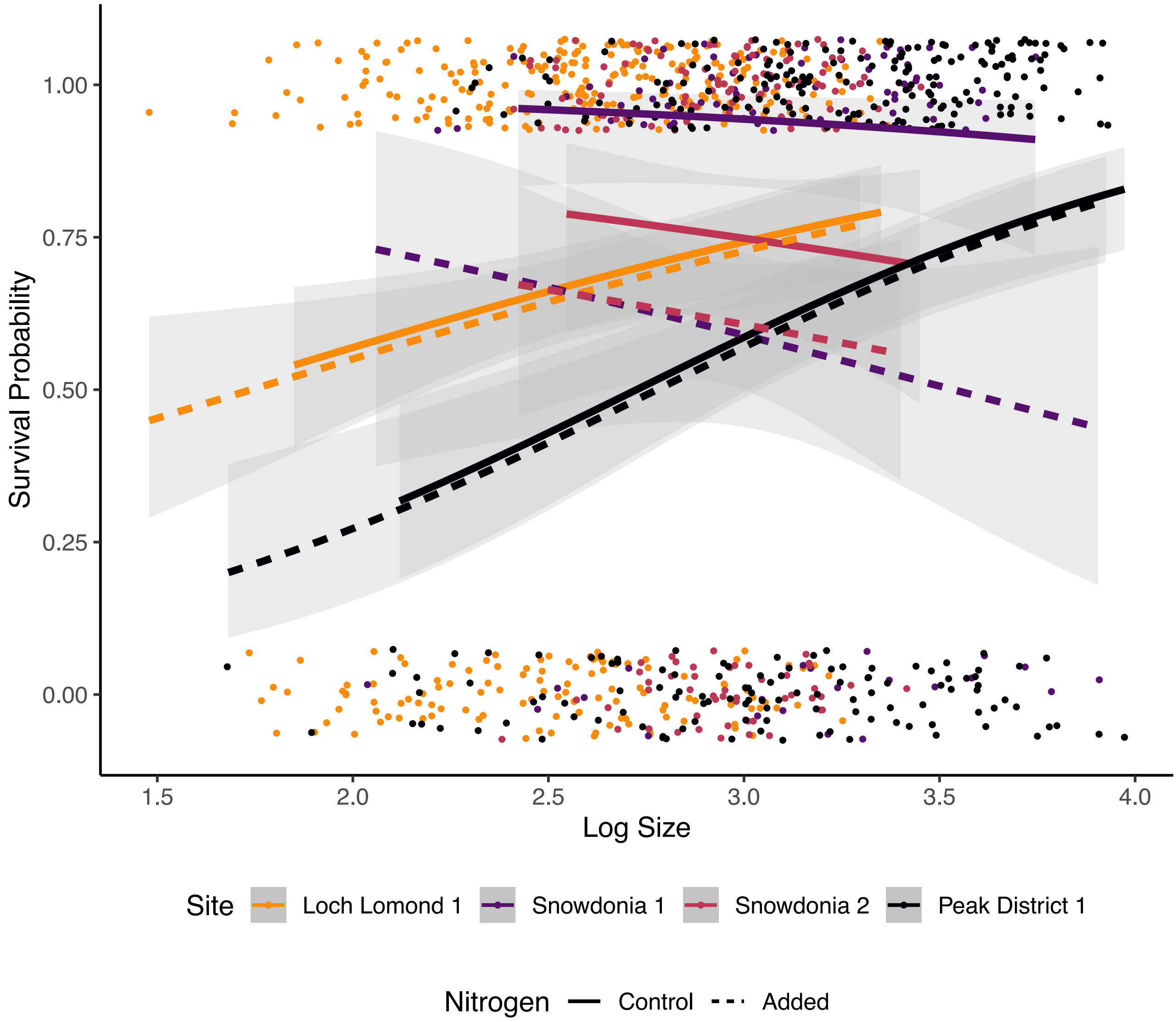


Figure 2. *Drosera rotundifolia* survival probability in relation to size (log transformed) and categorised by site and experimental addition of nitrogen. The fitted lines correspond to a binomial generalised linear model. The shaded area around regression lines represent 95% confidence intervals. Points have been jittered about 0 and 1.

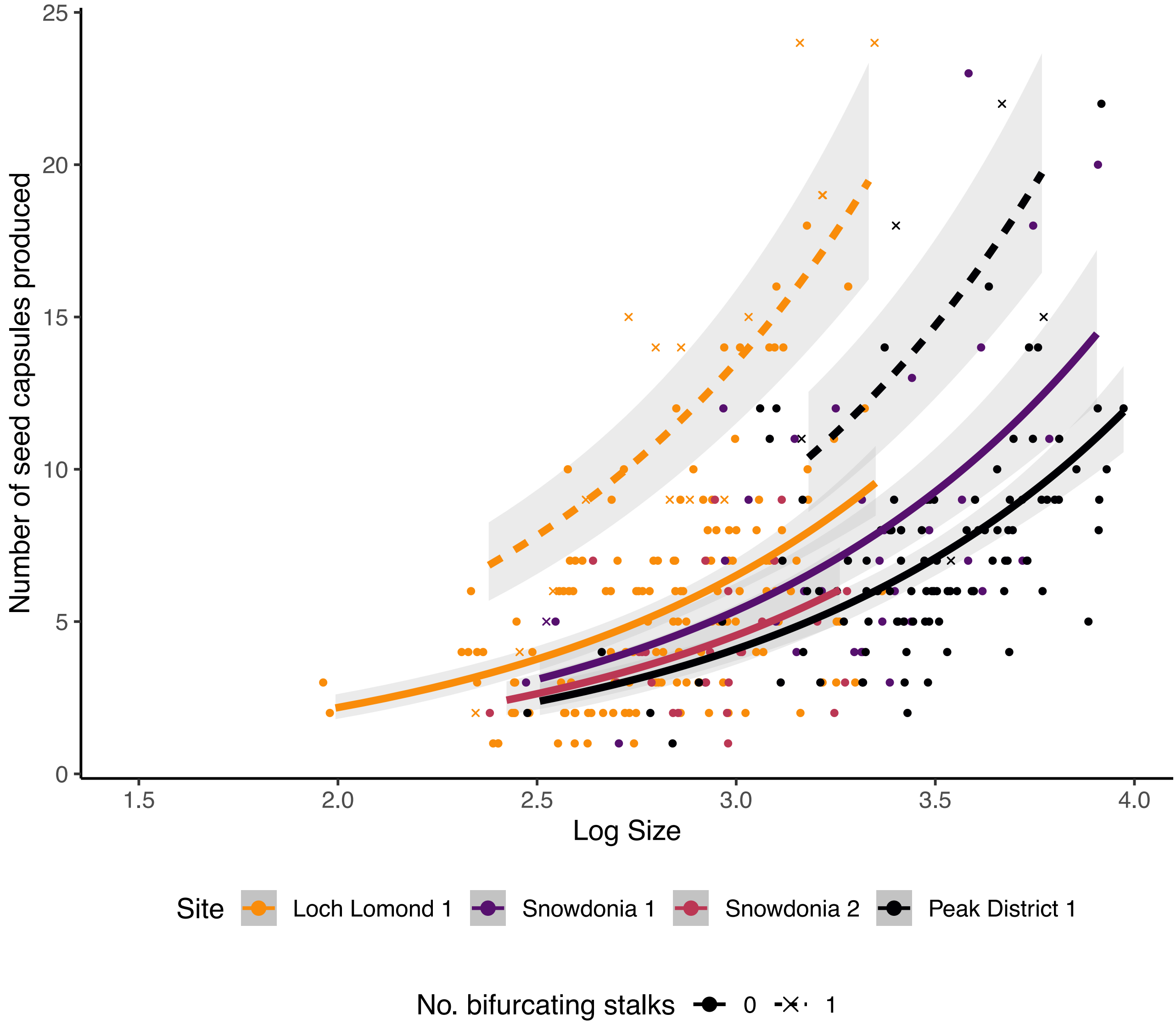


Figure 3. *Drosera rotundifolia* reproductive output in relation to size (log transformed) and categorised by site and whether an individual produced a bifurcating inflorescence. The fitted lines correspond to a negative binomial generalised linear model. The shaded area around regression lines represent 95% confidence intervals.

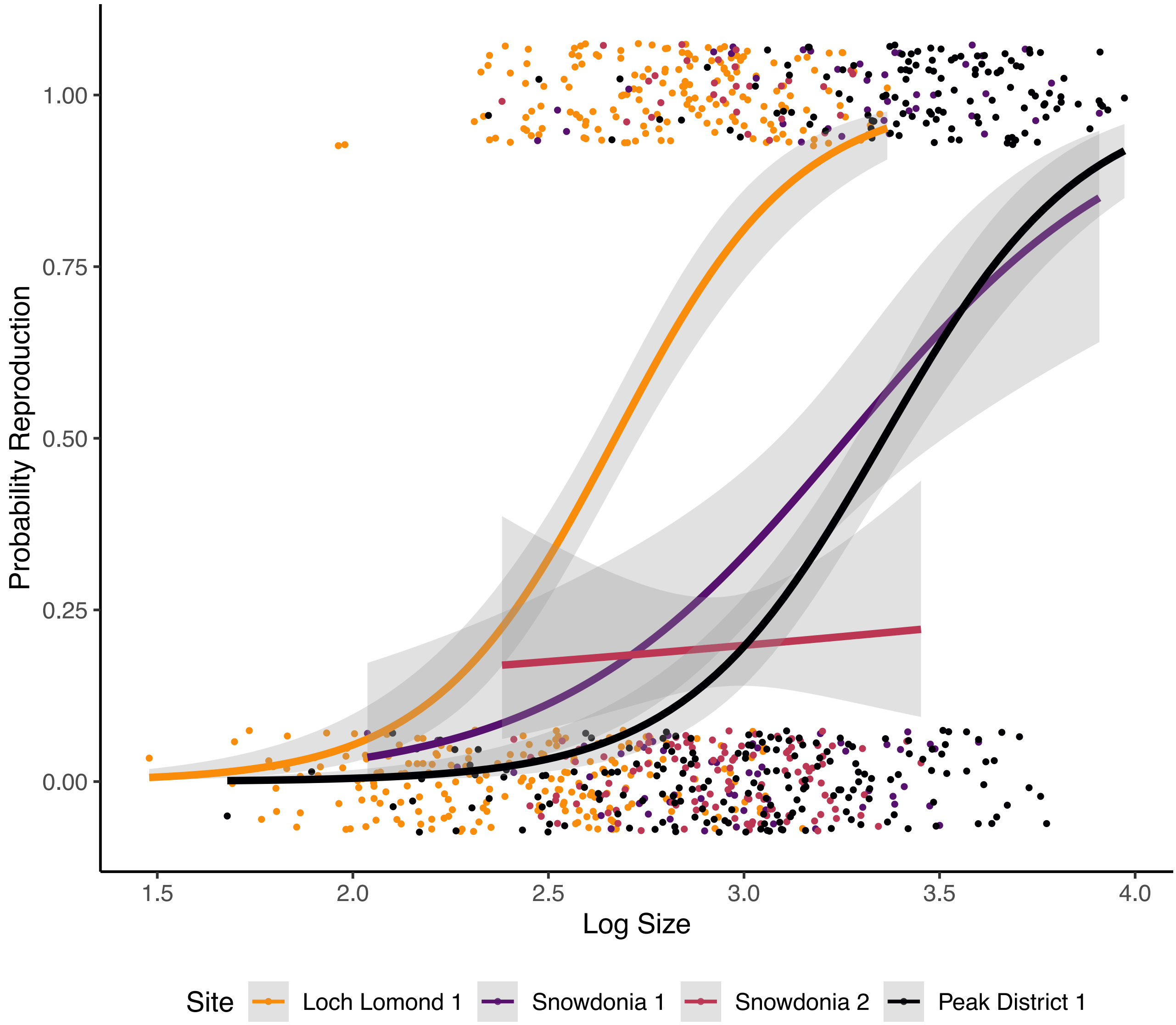


Figure 4. Drosera rotundifolia reproductive probability in relation to size (log transformed) and site. The fitted lines correspond to a binomial generalised linear model. The shaded area around regression lines represent 95% confidence intervals. Points have been jittered about 0 and 1.

3.7 References

1.

Air Pollution Information System. Simple site-based assessment result for total N deposition (wet and dry) from 2010-2012 (3 year average). http://www.apis.ac.uk/search-location.

2.

Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* **20**, 30–59 (2010).

3.

Bobbink, R., Hornung, M. & Roelofs, J. G. M. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J Ecology* **86**, 717–738 (1998).

4.

Bubier, J. L., Moore, T. R. & Bledzki, L. A. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biol* **13**, 1168–1186 (2007).

5.

Chen, S., Bai, Y., Zhang, L. & Han, X. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. *Environmental and Experimental Botany* **53**, 65–75 (2005).

6.

Clymo, R. S., Turunen, J. & Tolonen, K. Carbon Accumulation in Peatland. *Oikos* **81**, 368 (1998).

7.

Crone, E. E. *et al.* How do plant ecologists use matrix population models?: Matrix population models for plants. *Ecology Letters* **14**, 1–8 (2011).

8.

Crowder, A. A., Pearson, M. C., Grubb, P. J. & Langlois, P. H. Drosera L. *Journal of Ecology* **78**, 233–267 (1990).

9.

Ellison, A. M. & Gotelli, N. J. Nitrogen availability alters the expression of carnivory in the northern pitcher plant, Sarracenia purpurea. *Proceedings of the National Academy of Sciences* **99**, 4409–4412 (2002).

10.

Galloway, J. N. *et al.* Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science* **320**, 889–892 (2008).

11.

Gorham, E. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* **1**, 182–195 (1991).

12.

Gunnarsson, U., Granberg, G. & Nilsson, M. Growth, production and interspecific competition in Sphagnum: effects of temperature, nitrogen and sulphur treatments on a boreal mire. *New Phytol* **163**, 349–359 (2004).

13.

Harenda, K. M., Lamentowicz, M., Samson, M. & Chojnicki, B. H. The Role of Peatlands and Their Carbon Storage Function in the Context of Climate Change. in *Interdisciplinary Approaches for Sustainable Development Goals* (eds. Zielinski, T., Sagan, I. & Surosz, W.) 169–187 (Springer International Publishing, 2018). doi:10.1007/978-3-319-71788-3_12.

14.

Hatcher, C. Carnivorous plant responses to resource availability: environmental interactions, morphology and biochemistry. (Loughborough University, 2019).

15.

Jennings, D. E. & Rohr, J. R. A review of the conservation threats to carnivorous plants. *Biological Conservation* **144**, 1356–1363 (2011).

16.

Karlsson, P. S. & Svensson, B. M. The Significance of Carnivory for Three Pinguicula Species in a Subarctic Environment. 7 (2020).

17.

Latimer, A. M. & Jacobs, B. S. Quantifying how fine-grained environmental heterogeneity and genetic variation affect demography in an annual plant population. *Oecologia* **170**, 659–667 (2012).

18.

Lovett, G. M. *et al.* Effects of Air Pollution on Ecosystems and Biological Diversity in the Eastern United States. *Annals of the New York Academy of Sciences* **1162**, 99–135 (2009).

19.

Page, S. E. & Baird, A. J. Peatlands and Global Change: Response and Resilience. *Annu. Rev. Environ. Resour.* **41**, 35–57 (2016).

20.

Page, S. E., Rieley, J. O. & Banks, C. J. Global and regional importance of the tropical peatland carbon pool: TROPICAL PEATLAND CARBON POOL. *Global Change Biology* **17**, 798–818 (2011).

21.

Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).

22.

Phoenix, G. K. *et al.* Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Glob Change Biol* **18**, 1197–1215 (2012).

23.

Pregitzer, K. S., Hendrick, R. L. & Fogel, R. The demography of fine roots in response to patches of water and nitrogen. *New Phytol* **125**, 575–580 (1993).

24.

R Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2020).

25.

Redbo-Torstensson, P. The demographic consequences of nitrogen fertilization of a population of sundew, Drosera rotundifolia. *Acta Botanica Neerlandica* **43**, 175–188 (1994).

26.

Salguero-Gómez, R. *et al.* The COMPADRE Plant Matrix Database: an open online repository for plant demography. *J Ecol* **103**, 202–218 (2015).

27.

Svensson, B. M. Competition between Sphagnum fuscum and Drosera rotundifolia: A Case of Ecosystem Engineering. *Oikos* **74**, 205 (1995).

28.

Titus, J. E. & Wagner, D. J. Carbon Balance for Two Sphagnum Mosses: Water Balance Resolves a Physiological Paradox. *Ecology* **65**, 1765–1774 (1984).

29.

Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).

3.8 Supplementary information

Supplementary 1. *Drosera rotundifolia* at Loch Lomond 1, by Inversnaid. Photograph is representative of the habitat in most plots. *D. rotundifolia* occurred in high densities with negligible competition with mosses, but some shading from other vascular plants.

Supplementary 2. *Drosera rotundifolia* at Peak District 1, a *Sphagnum* bog site near High Bradfield. *D. rotundifolia* occurred in high densities across the site. *D. rotundifolia* was absent amongst dense tufts of forbes and grasses but occurred on water saturated *Sphagnum* and on the more peripheral, drier patches of *Sphagnum*, further from the central bog pool.

Supplementary 3. *Drosera rotundifolia* at Snowdonia 1, a *Sphagnum* bog site on Llyndy Isaf Mountain. *D. rotundifolia* occurred in high densities across the site amongst grasses but were mainly sampled near the pool. The *Sphagnum* across the site was saturated throughout the growing season, owing to runoff from neighbouring mountains.

Supplementary 4. *Drosera rotundifolia* at Snowdonia 2, Llyn Barfog, a site dominated by grasses and forbs. *D. rotundifolia* mainly occurred on patches of *Sphagnum*, in low densities amongst other vascular plants, but were most abundant on the edges of sheep tracks.

Supplementary 5. *Drosera rotundifolia* inflorescences. On the left is an inflorescence that is bifurcating/forking. On the right is an inflorescence that is singular. The inflorescence on the right is more mature, and seeds likely dispersed. The flowers on the tips of the bifurcating inflorescence are unopened; flowers open in sequence from the lowest to highest position, as the inflorescence develops and unfurls.

Chapter 4: Treatment-induced changes to vital rates can have non-additive effects

4.1 Abstract

Environmental change will affect population growth by affecting one or more vital rates. It would be useful to quantify how treatment-induced changes to vital rates and their interactions contribute to the finite population growth rate, λ. We decompose the effects of experimental nitrogen addition on λ for four *Drosera rotundifolia* populations, comparing the estimates from the standard approach, a life table response experiment decomposition analysis (LTRE), with the exact values from a functional decomposition. We identify that nitrogen primarily affected λ through induced changes to survival or growth depending on site. The LTRE produced good estimates for the relative, but not absolute contribution of treatment-induced changes to λ. We conduct treatment simulations to show the potential for strong interactions between treatment-induced changes to vital rates; we show four-way interactions between affected vital rates, and non-additive effects of multiple treatments that affect a single vital rate. The functional decomposition is a useful tool that can clarify how environmental variation or treatment induced changes to vital rates contribute to population size.

4.2 Introduction

Peatland ecosystems cover ~3% of the Earth's land surface, but their vast carbon stocks make them a conservation priority (Gorham, 1991; Clymo *et al*., 1998; Page *et al*., 2011; Harenda *et al*., 2018). Nitrogen deposition is a growing problem for peatland habitats due to industrial and intensive agricultural practices (Galloway *et al*., 2008; Bobbink *et al*., 2010; Phoenix *et al*., 2012). Increased nitrogen deposition can cause plant community composition to change (Gunnarsson *et al*., 2004; Bubier *et al*., 2007; De Vries *et al*., 2010), with potential consequences for biodiversity and carbon storage (Bobbink & Roelofs, 1995; Page & Baird, 2016).

Bog plants are underrepresented amongst plant demographic studies, but previous work generally shows worse outcomes as a result of nitrogen deposition (Press *et al*., 1986). Redbo-Torstensson (1994) identified that increasing ammonium nitrate deposition treatments increased *Drosera rotundifolia* mortality in a south central Swedish bog, over 4 years. In a study on *Sarracenia purpurea*, another carnivorous bog plant, experimental additions of nitrogen were projected to cause population declines (Gotelli & Ellison, 2002). Spatially replicated demographic studies are also underrepresented (Crone *et al*., 2011; Salguero-Gómez *et al.,* 2015), and this is pertinent given the increasing fragmentation of bog habitats (Raeymaekers, 2000; Wilson & Provan, 2003).

Nitrogen deposition has clear implications for finite population growth rate, λ, but it is useful to consider how changes in size, survival and reproduction (vital rates) resulting from nitrogen addition translate into changes in λ. It is important to understand the relative effect of vital rate change on λ because: 1) Interactions between several treatment affected vital rates may be the main driver of changes in λ; 2) Relatively weak effects of a treatment on a vital rate may have unexpectedly large consequences for λ; 3) It may help in generating or validating hypotheses for which mechanisms are driving population trends.

A robust modelling framework is needed to answer how a treatment affects λ through a particular vital rate. Longitudinal data for individuals can be used in statistical models to describe relationships between vital rates and a population-structuring variable like size. These data can be used to parameterise an integral projection model (IPM) (Ellner & Rees, 2006; Crone *et al*., 2013; Rees *et al*., 2014), and we can compare the outputs of IPMs when a treatment effect is or is not included. The standard approach for understanding how treatment-induced changes in vital rates influence λ is via a life table response experiment decomposition analysis (LTRE) (Caswell, 2001). This approach is widely used and assumes approximately linear relationships between the parameter of interest and λ, and that the all effects are additive (i.e. there are no interactions). Non-linearity and interactions can both be accounted for through the standard LTRE approach; it would be useful to compare the results of the standard and more comprehensive LTRE against an exact partitioning of the effects of a treatment on λ. The functional decomposition (Ellner *et al*., 2019) approach can be used to identify exactly how treatment-induced changes in vital rates influence λ.

Drosera rotundifolia (*Droesra* herefter) has a global distribution (Maiz-Tome, 2016), and has been the subject of several demographic studies (Redbo-Torstensson, 1994; Nordbakken *et al*., 2004). *Drosera* may have value as an indicator species of peatland health because carnivorous plant morphology can be sensitive to nutrient availability (Gotelli & Ellison, 2002). Nordbakken *et al*. (2004) used matrix population models and found highly variable population growth rates from year to year. Nitrogen is a limiting factor for *Drosera* but predicting population responses to nutrient inputs is challenging because of complex interactions between *Drosera* and *Sphagnum (*Svensson, 1995; Nordbakken *et al*., 2004). It would be useful to test the effects of nitrogen on *Drosera* dynamics in the field, across different sites, given the complex mixture of competition and facilitation between plant functional groups in peatland communities (Oke and Hager, 2020).

Here we predict the consequences of an experimental treatment of ammonium nitrate on λ for four distinct *Drosera* populations using IPMs. We carried out a functional decomposition to identify how nitrogen treatments impact λ through vital rates and their interactions at the different sites. Furthermore, we compared the results of this decomposition analysis with the results of the standard approach (1^{st} order LTRE), and an LTRE including vital rate interactions and non-linearity (2^{nd} order LTRE). Finally, we simulate treatment effects to test the potential importance of interactions between treatment-induced changes to a single, or multiple vital rates.

4.3 Methods

4.3.1 Study system

Four populations of *Drosera* were selected across three national parks for multiple years of sampling. We monitored single populations in the Peak District, Loch Lomond and the Trossachs, and two populations from Snowdonia. The sites were selected based on their suitability for multiple years of census-based data collection, and large population size to minimise population impacts from experimental manipulation.

The study sites had some notable differences. The Peak District and Snowdonia 1 sites were most similar, with populations distributed around a small bog pool. Both of these sites were dominated by *Sphagnum* moss, with some emerging grasses, sedges and shrubs. Saturated growing media is essential for *Drosera*, and the water level at Peak District and Snowdonia 1 increases between spring and summer. In Snowdonia 1, previously dormant *Sphagnum* becomes saturated by water that is channelled down nearby mountains, coinciding with most *Drosera* growth. In contrast, at the Peak District site a desiccated surface layer of patches of dormant *Sphagnum* remained, and this was more common away from the central pool at the site. The Snowdonia 2 site is covered by a matt of *Sphagnum*, and grasses and heather further overtop this. *Drosera* occurred in locations where other vascular plants were in low densities. Furthermore, *Drosera* was most prevalent on sheep disturbed areas. Finally, the Loch Lomond site was characterised by a manmade (~20 years old) rockface resulting from the construction of a path. The exposed rock face supports a very shallow layer of soil, sufficient for *Drosera* but little else. A constant stream of water from higher ground maintains soil moisture. There is a more typical sphagnum bog habitat <100m from the rock face uphill, but *Drosera* density and numbers were substantially lower. Population coordinates are presented in Table 1 (photographs; Chapter 3, Supp. 1, 2, 3 & 4).

4.3.2 Field data

We measured *Drosera* individuals between July and mid-September 2017-19 over three field seasons. Plants were given an identity through one of two methods depending on their habitat: 1) an A3 acetate sheet was placed above a plot. The position of each plant was marked on the sheet, along with a unique ID. 2) A bamboo skewer attached to a unique plastic bead was placed into the ground near each plant, within a 25 x 25 cm plot. Plots were marked with tent pegs at corners so as to not be conspicuous. A bead was threaded onto one of the tent pegs for plot identification purposes. It was possible for individuals to go ‘missing’ when their associated marker was displaced; in this analysis missing markers were not assigned into the dead category. All plants had an accompanying marker and individuals were either noted as new recruits, survivors, or dead, inferred by the absence of *Drosera* next to a firmly planted marker.

Plots were assigned a nitrogen treatment so that the number of control and treated individuals was similar, and to avoid spatial aggregation of one treatment (Table. 1). Treated plots were sprayed with ammonium nitrate solution after data collection. The same plots were sprayed with the solution on year 1 and 2. Nitrogen dosage was site-specific, equal to the annual ambient nitrogen deposition at the site. The nitrogen deposition rates associated with each population based on 2016 Air Pollution Information System records (APIS, 2017) are presented in Table 1. The range of control and treatment nitrogen exposure was within the range of values in the Swedish study by Redbo-Torstensson (1994).

4.3.4 Experimental data

In the Loch Lomond field site, the lack of *Sphagnum* moss and plant competition allowed us to identify and measure all recruits in a plot. This was not possible at other sites, and so a seed sowing experiment was conducted at the Arthur Willis Environment Centre at The University of Sheffield to collect recruit size information. 56 37x24 cm trays were filled with *Sphagnum* moss, with a minimum depth of 3 cm. ~200 seeds were sown in each tray in early August 2018 after a 5-week cold stratification period. 18 trays contained Peak District 1 seeds, 18 for Snowdonia 1. No germination occurred in 2018 despite the cold stratification. Germination occurred in 2019 and 43 individuals were measured in early September, the back end of field-census data collection in the field.

4.3.5 Parameterising IPMs

We produced two sets of IPMs for each site, one set included nitrogen effects and the other did not. The IPM kernel is based on our pre-reproductive census data (Rees *et al.* 2013) and is defined as

$$K(z',z) = s(z)G(z',z) + Pb(z)b(z)PrC_1(z')$$

where $s(z)$ is the probability of surviving, $G(z',z)$ describes size transitions, $Pb(z)$ is the probability of reproducing, *b* is the number of seed capsules produced, Pr is the probability of a capsule producing a recruit and $C_1(z')$ is the size distribution of recruits a year after emergence. z and z' refer to logged longest leaf values at a point in time and a year later respectively.

The functions that constitute the kernel come from statistical models. All analyses were carried out in R (4.0.3) (R Core Team, 2020). Model selection was carried out for *Drosera* growth, flowering probability, number of seed capsules and survival in Chapter 2. These models were applied to our three-year dataset, where data was aggregated to a single year transition; coefficients for vital rate models can be found in the supplementary information. We modelled *Drosera* vital rates to depend on size in the previous year, and site. Moreover, we included an interaction between size and site for all vital rates except for total capsule production. Nitrogen effects were modelled as a main effect for growth and survival, and we included a nitrogen x site interaction for survival. The one difference is that we removed whether flowering stalks were bifurcating as a model factor for total capsule production, as the antecedent factors causing this morphology are unknown. Significant effects of nitrogen on survival were only detected at Snowdonia 1 in the analysis in Chapter 2, but all site-specific nitrogen coefficients were included for the purposes of comparing methods for decomposing the effects of treatments on λ in the next section.

For recruitment we calculated a per capsule recruitment number by dividing the total number of recruits observed in Loch Lomond 1 by the total number of seed capsules at the site. We chose to use Loch Lomond 1 per capita recruitment because germination rates in the experiment may have been affected by an irregular cold stratification process. We had two different recruitment size distributions, the field measurements for Loch Lomond 1, and a distribution from AWEC to represent recruitment at sites with a *Sphagnum* growing medium.

4.3.6 Parameter sensitivity analysis

We expected that nitrogen addition would affect population growth rates. A functional decomposition (Ellner *et al.*, 2019) enabled us to quantify how much of the discrepancies between λ values are due to the effects of nitrogen on either survival, or growth, or an interaction between the two. We carried out the functional decomposition and compared the results to the standard LTRE approach. The functional decomposition involved a comparison of λ values based on different sets of conditions. We first obtained 'null' λ values from site-specific IPMs

$$\epsilon^0 = \lambda(p_1, p_2, \dots p_n) \qquad (eqn. 1)$$

where model parameters, p, did not include nitrogen effects. Nitrogen effects were then included in these models sequentially, as having an effect on growth, or survival. Subtracting the null λ from the λ including a nitrogen effect on a parameter, δp_1, gives the contribution to λ of the nitrogen effect so for p_1 we have

$$\epsilon^{p_1} = \lambda(p_1 + \delta p_1, p_2, \dots p_n) - \epsilon^0 \qquad (eqn. 2)$$

Finally, we tested whether nitrogen effects on parameters have an additive effect on population growth, or an interaction emerges.

$$\epsilon^{p_1 p_2} = \lambda(p_1 + \delta p_1, p_2 + \delta p_2, \dots p_n) - \epsilon^0 - \epsilon^{p_1} - \epsilon^{p_2} \qquad (eqn. 3)$$

If $\epsilon^{p_1 p_2}$ is not 0 there is evidence of an interaction. The decomposition approach exactly quantifies how a treatment (nitrogen) effect on a vital rate affects λ. Values of ϵ can be compared to test if nitrogen affects population growth primarily through a certain vital rate or an interaction.

The standard approach has been to approximate sensitivities from an LTRE by testing the effects of small perturbations to the underlying parameters (Caswell, 2001), in this case nitrogen effects. We compared the results of the functional decomposition with the approximations from the standard LTRE approach. λ can be written to 1st order as

$$\lambda(p_1+\delta p_1, p_2+\delta p_2, \dots p_n+\delta p_n) \approx \lambda(p_1, p_2, \dots p_n) + \frac{\partial\lambda}{\partial p_1}\delta p_1 + \frac{\partial\lambda}{\partial p_2}\delta p_2 + \cdots + \frac{\partial\lambda}{\partial p_n}\delta p_n (eqn. 4)$$

and rearranging allows us to partition the effects of the experimental treatments on λ.

$$\lambda(p_1+\delta p_1, p_2+\delta p_2, \dots p_n+\delta p_n) - \lambda(p_1, p_2, \dots p_n) \approx \frac{\partial\lambda}{\partial p_1}\delta p_1 + \frac{\partial\lambda}{\partial p_2}\delta p_2 + \cdots + \frac{\partial\lambda}{\partial p_n}\delta p_n (eqn. 5)$$

We can approximate the contribution to λ of the nitrogen effect on a given parameter by calculating the product of the parameter sensitivity and the value of its nitrogen coefficient. Here we are approximating the functional decomposition as follows,

$$\epsilon^{p_1} \approx \frac{\partial\lambda}{\partial p_1}\delta p_1 \qquad (eqn. 6)$$

Writing λ to 2nd order we can account for possible non-linearity in the relationship between the parameter and λ. In this case we approximate the functional decomposition as

$$\epsilon^{p_1} \approx \frac{\partial\lambda}{\partial p_1}\delta p_1 + \frac{\partial^2\lambda}{2\partial p_1^2}(\delta p_1)^2 \qquad (eqn. 7)$$

The 2nd order approximation contains a cross derivative that can be used to approximate the interaction from the functional decomposition

$$\epsilon^{p_1 p_2} \approx \frac{\partial^2 \lambda}{\partial p_1 \partial p_2} \delta p_1 \delta p_2 \qquad (eqn. 8)$$

In what follows we compare the three different approaches to determine if the standard 1st order LTRE approach is accurate, and if not where the inaccuracy comes from (i.e., is it due to non-linearity or interactions).

4.3.7 Simulated treatment effects

We tested the importance of interactions between simulated changes in vital rates on λ. We incorporated site-specific treatment effects on growth, survival, probability of reproduction and capsule number into our control IPMs. Treatment effect size is equal to negative standard error of the respective vital rate model intercepts. This effect size is based on the site-specific nitrogen effects on survival and the effect of nitrogen on growth, since on average these nitrogen coefficients were -1.20 times their respective model intercept standard error.

We investigated how changes in vital rates induced by two separate treatments might affect λ. In this case both treatment effects were artificial and site-specific. The treatments effects were equal to the negative standard error of the intercept of each vital rate model. We conducted functional decompositions to see how the importance of treatment interactions varied by vital rate and site. Finally, we compared the predicted survival of individuals under conditions of control, single treatment, both treatments, and both treatments operating additively.

4.4 Results

Our IPMs suggest that most sampled populations are in decline (Fig. 1). Declines at Loch Lomond 1, Peak District 1, and Snowdonia 2, and the increase at Snowdonia 1 are all extreme trajectories (>10% annual changes in population size). Effects of nitrogen on λ vary considerably across sites. For example, Loch Lomond 1 varies relatively little between treatments, while Snowdonia 1 experiences over a 30% decline with nitrogen addition.

The relationship between the nitrogen coefficient for size change and λ were fairly linear across a range of realistic values and including the potential for positive effects (Fig. 2). There was a more pronounced non-linear relationship between the nitrogen coefficient for survival and λ, particularly for Snowdonia 1 and 2 (Fig. 3). Simulated nitrogen effects on capsule production had a relatively linear relationship with λ (Fig. 4), but effects on probability of reproduction showed a high degree of non-linearity (Fig. 5).

The approximations from the 1st and 2nd order LTRE approaches were similar to the functional decomposition when it came to the proportional influence of nitrogen affected vital rates on λ (Fig. 6 & 7). The functional decomposition and 2nd order LTRE decomposition showed that the vital rate interaction had marginal influence on λ (Fig. 7). Moreover, even the standard approach (1st order LTRE) would provide a fairly accurate representation of how nitrogen influences λ through each vital rate, given the unimportance of the interaction (Fig. 6).

Nitrogen affected λ at Loch Lomond 1 predominantly by affecting growth (Fig. 7). We stress that there were no statistically significant effects of nitrogen on survival for all sites other than Snowdonia 1 (though it appears that this is only the case for Snowdonia 2 due to smaller sample sizes). However, the small effect sizes of nitrogen on survival probability at

Loch Lomond 1 and Peak District 1 are evident in the decomposition as survival was relatively less important than at the Snowdonia sites. The interaction between growth and survival was relatively unimportant at all sites.

We compared the results of the functional decomposition with the 2nd order LTRE approach. Results were similar (Fig. 8); half the estimates were almost identical to the exact values acquired through the functional decomposition, and all but one estimate were out by <3.5%.

Strong interactions, up to and including four-way interactions, between treatment-induced changes in vital rates affected λ (Fig. 9). Interactions involving the probability of survival or reproduction had the greatest effects on λ for our simulated treatments.

Lastly, we detected interactive effects for λ when two simulated experimental treatments were assigned effects on a single vital rate (Fig. 10). Interactive effects could be small even when the treatment effects were large. There were differences in size-specific survival between additive treatment effects and interactive treatment effects, demonstrated in Figure 11 (2 and B).

4.5 Discussion

Our population modelling suggested extreme projected changes in population size (Fig. 1). A highly variable λ is consistent with extreme year-to-year variation identified by Nordbakken *et al*. (2004). We suspect that these patterns are due to *Drosera* populations consisting of ephemeral pockets of individuals that thrive after small-scale disturbance events. It may be more appropriate to study such population dynamics with more extensive sampling of individuals but with less granularity than in our data collection. Nevertheless, individual level census data is very useful when assessing the impact of an experimental treatment. We detected that additional nitrogen deposition negatively affects population trajectories (Fig. 1), which is consistent with other studies (Redbo-Torstensson, 1994; Gotelli & Ellison, 2002). All populations suffer with the addition of nitrogen, though this effect is small at the site with very little plant competition, Loch Lomond 1. The negative effects of nitrogen may primarily be due to interactions with *Sphagnum* (Svensson, 1995). The Loch Lomond 1 site is a human-made rock-face with very shallow, wet soil; as nitrogen pollution increases such locations may become important reservoirs of *Drosera* because of the reduced competition with *Sphagnum* and vascular plants.

We identified some non-linearity in projected λ values in response to varying treatment parameters (Fig. 2 & 3). However, the relative importance of treatment-induced main effects on growth and survival (Fig. 6) were quite accurate when compared with the functional decomposition, which includes non-linearity and interactions (Fig. 7). Nitrogen effects on survival caused most of the difference in projected λ's between treated and control populations (Fig. 7). Growth was relatively more important in Loch Lomond 1 and Peak District 1. This may be because of the smaller effects of the nitrogen treatment on survival at these sites and the fact both featured individuals with bifurcating flowering stalks, leading to a steeper positive size-fecundity relationship. The unimportance of the interaction is also noteworthy; many sensitivity analyses that rely on the 1st order LTRE approach assume there are no interactions, and here we see that excluding the interaction has little impact on our inferences.

The LTRE approach has the benefit of the user knowing sensitivity values, allowing them to identify to whether changes in λ are due to a relatively large coefficient, or the sensitivity of λ to a particular parameter. Our analysis shows that the approximations are sometimes prone to errors (Fig. 8), despite their very accurate relative absolute size (Fig. 6 & 7).

Treatments that affect one vital rate can affect other population processes, causing changes in λ. For example, treatments that influence size transitions affect λ because of the importance of size for vital rates that directly affect the total number of individuals (survival and recruitment). We can see simulated treatments that affect changes in size were important for λ at Loch Lomond 1 and Peak District 1 (Fig. 9). Interestingly, the most important treatment effect interactions included probability of survival or reproduction, even when changes in size were important.

Finally, we identified that treatments affecting a single vital rate can have interactive effects on λ (Fig. 10). The difference between vital rate predictions under conditions of no treatment and one treatment is not equal to the difference in prediction between conditions of one treatment and two identical treatments (Fig. 11). Consequently, interactive treatment effects can be important because small changes in outcomes for one vital rate can have large consequences for λ. Potential examples where interactive effects may be more prevalent include where there is strong non-linearity between size and reproduction and survival, and/or there are age-dependent processes that make survival even more important.

To summarise, we were able to detect the negative consequences of applying small doses of nitrogen to a population by taking individual-level measurements and using them to parameterise integral projection models. Our simulation suggests that treatments that affect a single vital rate can have important interactive effects on λ. We found that the standard LTRE approach was sufficient in explaining how changes in vital rates resulting from nitrogen addition translate into changes in λ. However, we would encourage the functional decomposition approach as it is simple to implement and gives an exact breakdown of treatment effects.

4.6 Figures

Table 1. Locations of studied British *Drosera rotundifolia* populations. Annual N deposition rates are the mean based on 3 years of data between 2010-2012 from Air Pollution Information System records (http://www.apis.ac.uk/ accessed 01/02/2016).

Population	**Latitude/ Longitude**	**OS Grid Reference**	**N deposition / Kg N ha^{-1} yr^{-1}**	**# Control, # treated plots**	**# Control, # treated plants**
Loch Lomond 1	56°15'5.65"N 4°40'4.05"W	NN 34814 09762	17.08	6, 6	496, 514
Peak District 1	53°26'7.23"N 1°36'24.84"W	SK 26213 93245	27.30	9, 11	288, 322
Snowdonia 1	53° 1'16.86"N 4° 3'31.82"W	SH 620 491	12.04	4, 6	94, 96
Snowdonia 2	52°34'13.31"N 3°59'24.46"W	SN 6522 9881	8.26	9, 12	106, 182
				Total:	**984, 1114**

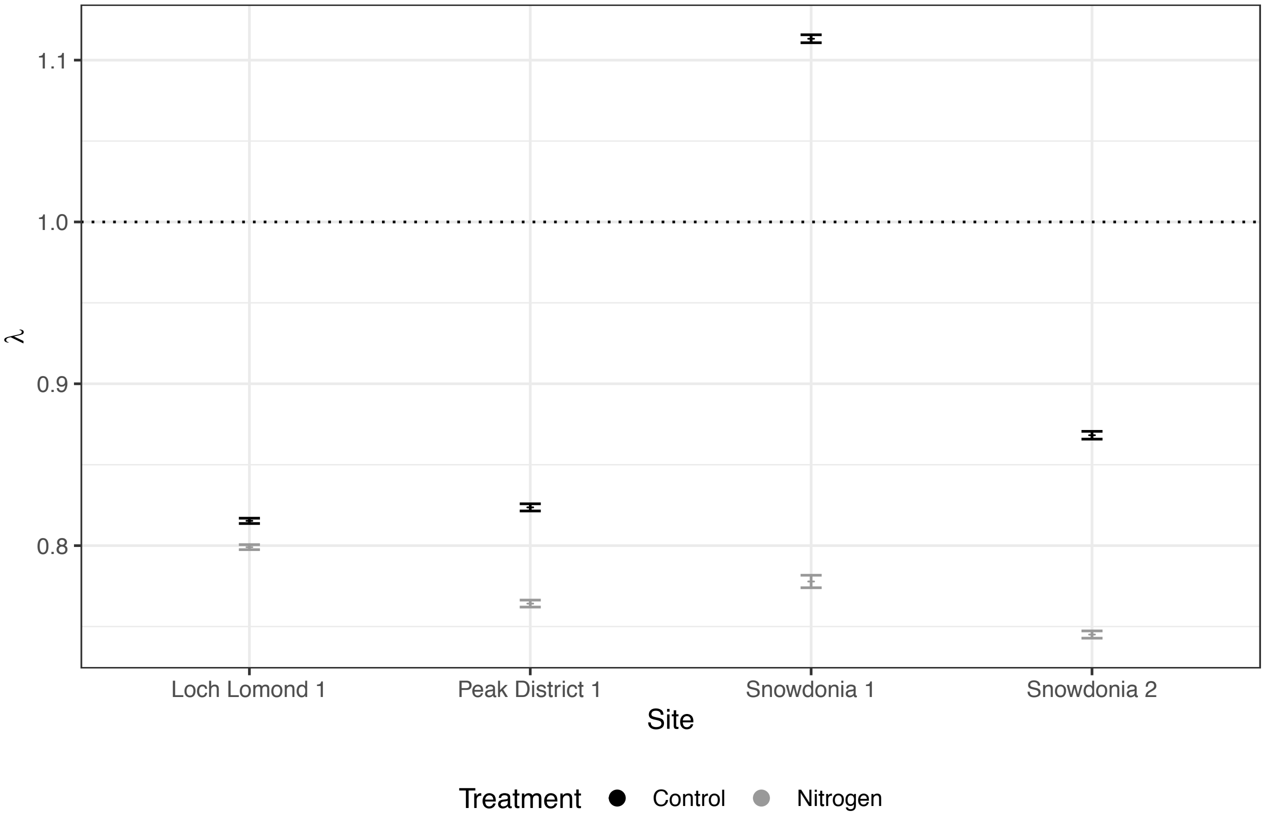


Figure 1. *Drosera rotundifolia* site-specific finite population growth rates, obtained from integral projection models. Values for nitrogen are based on the inclusion of a a nitrogen effect on changes in individual size, and site-specific effects on survival. Points are the mean of the population growth rate after bootstrapping 2000 times, with error bars for the 99% confidence intervals. Points below the dashed line are experiencing declines.

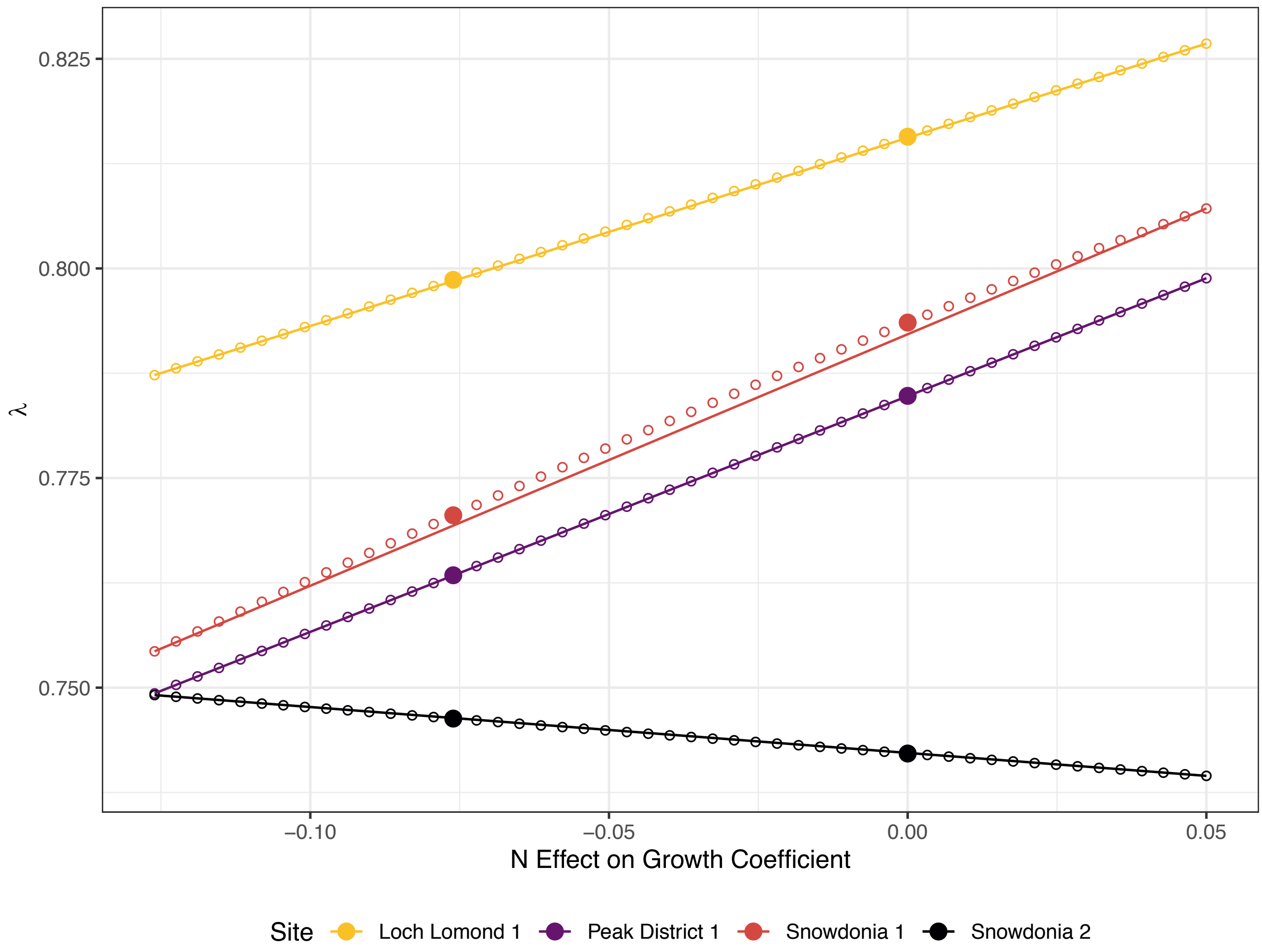


Figure 2. The relationship between *Drosera rotundifolia* finite population growth rate and a varying nitrogen on growth coefficient. All points are obtained from site-specific integral projection models where the nitrogen on survival coefficient is a fixed value based on modelling the field data. Solid points are placed at a coefficient value of 0, and at the value obtained from modelling the data. Straight lines are plotted for each site between an upper and lower value coefficient value to help identify non-linearity.

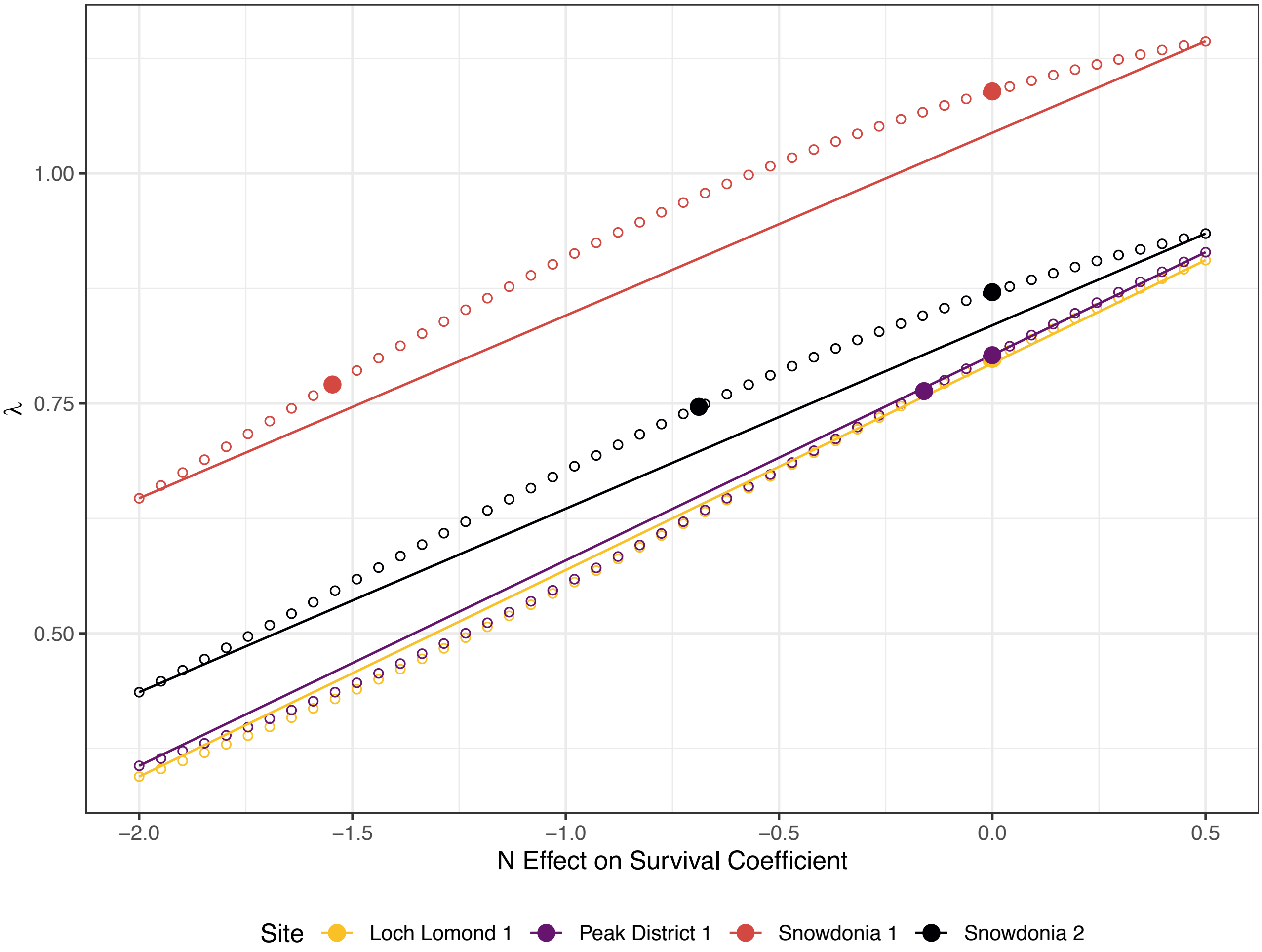


Figure 3. The relationship between *Drosera rotundifolia* finite population growth rate and a varying nitrogen on survival coefficient. All points are obtained from site-specific integral projection models where the nitrogen on growth coefficient is a fixed value based on modelling the field data. Solid points are placed at a coefficient value of 0 (the control treatment), and at the value obtained for each site. Straight lines are plotted for each site between an upper and lower value coefficient value to help identify non-linearity.

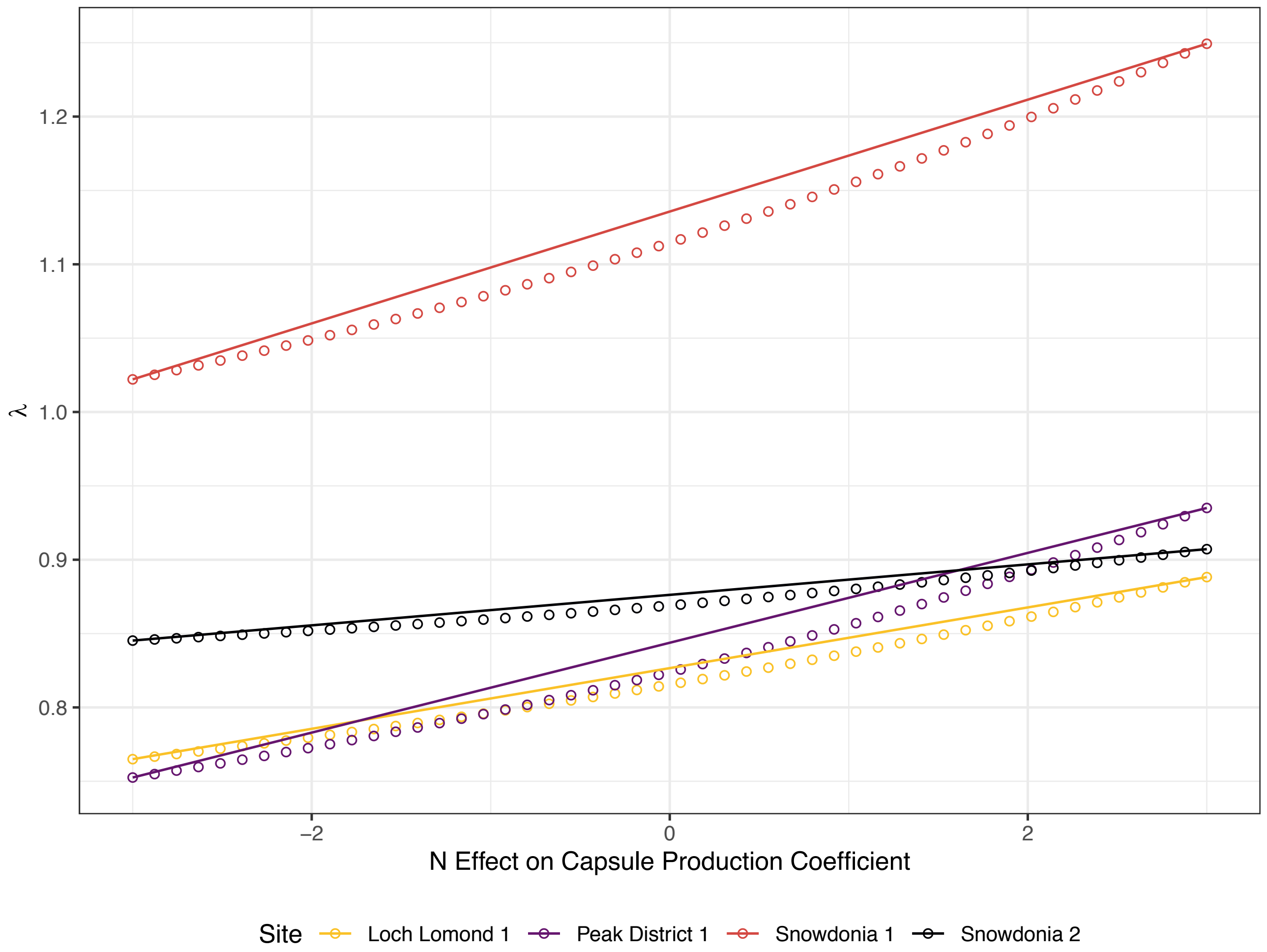


Figure 4. The relationship between *Drosera rotundifolia* finite population growth rate and a varying nitrogen on capsule production coefficient. Values on the x-axis are multiples of the standard error of site-specific capsule production model intercepts. All points are obtained from site-specific integral projection models where the nitrogen on growth, survival and probability of reproducing coefficients are set to 0. Straight lines are plotted for each site between an upper and lower value coefficient value (-3 and 3 times standard error) to help identify non-linearity.

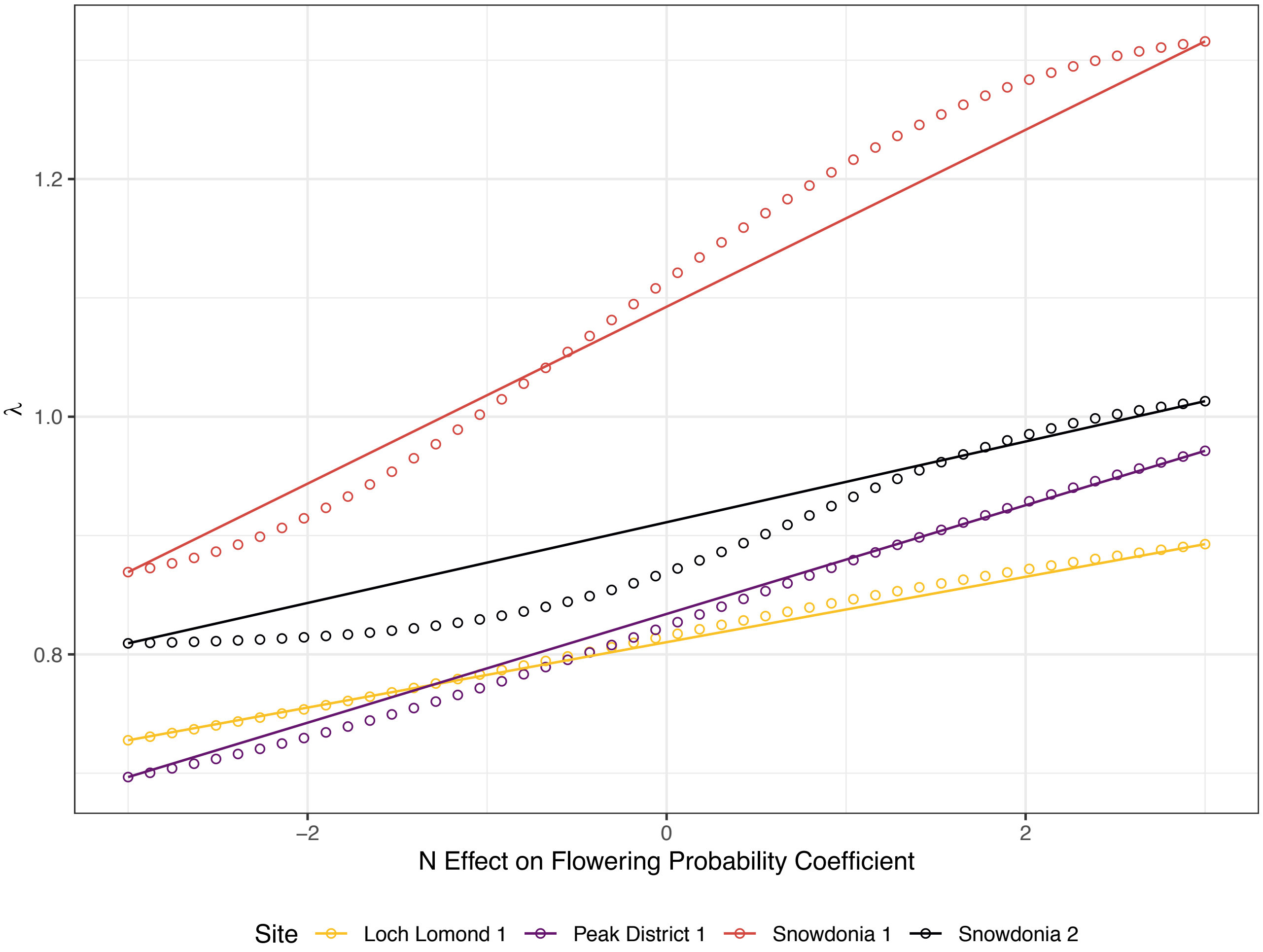


Figure 5. The relationship between *Drosera rotundifolia* finite population growth rate and a varying nitrogen on reproduction probability coefficient. Values on the x-axis are multiples of the standard error of site-specific probability reproduction model intercepts. All points are obtained from site-specific integral projection models where the nitrogen on growth, survival and capsule production coefficients are set to 0. Straight lines are plotted for each site between an upper and lower value coefficient value (-3 and 3 times standard error) to help identify non-linearity.

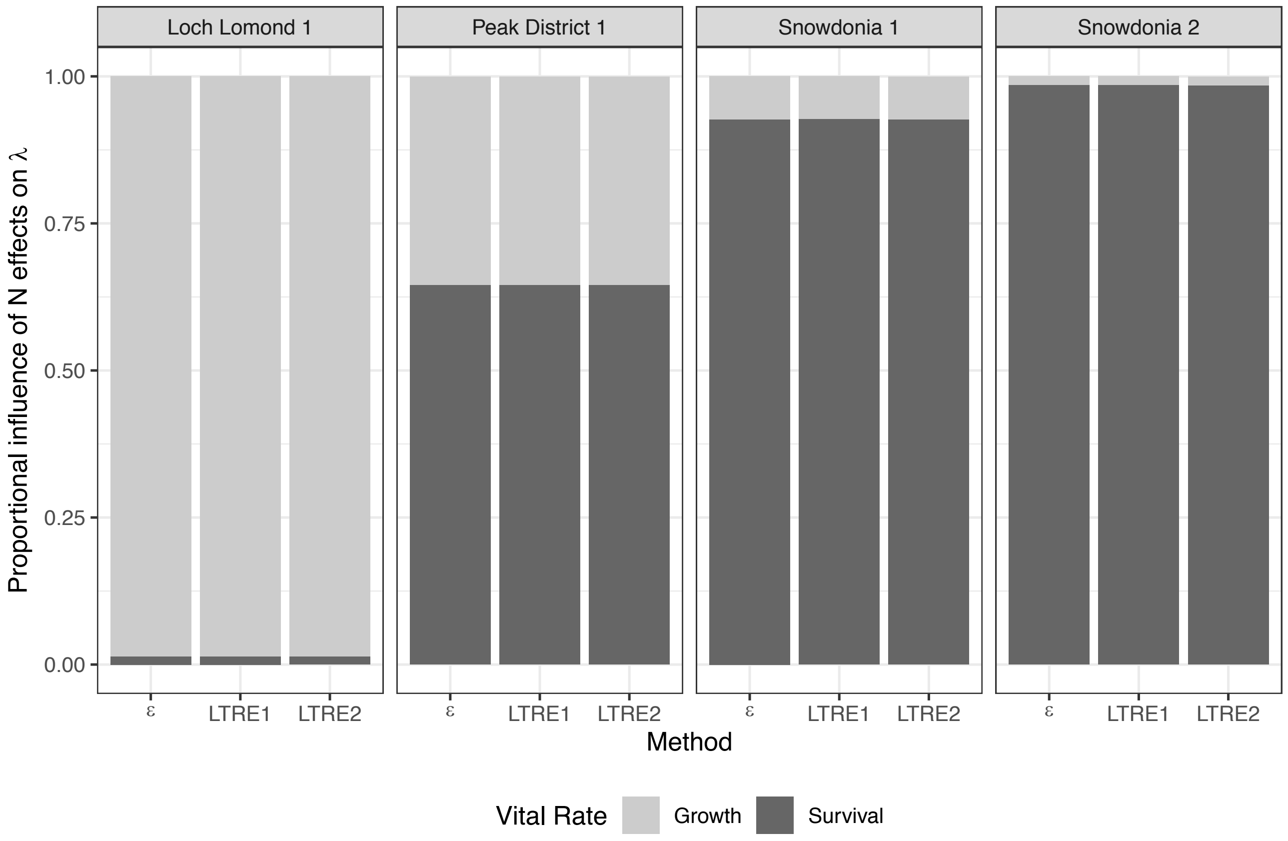


Figure 6. Site-specific breakdowns of how treatment-induced changes in *Drosera rotundifolia* vital rates influence the finite population growth rate, λ. The greater the proportion of a bar is taken by one vital rate, the more important the nitrogen effect on that vital rate was in influencing population growth. The columns represent three methodologies: ε is the functional decomposition. LTREs are results from a decomposition of life table response experiments, where LTRE1 involves taking the first order derivative, and LTRE2 involves the first and second order derivatives. Absolute values of sensitivities and nitrogen coefficients were used to ensure the sum of proportions is 1.

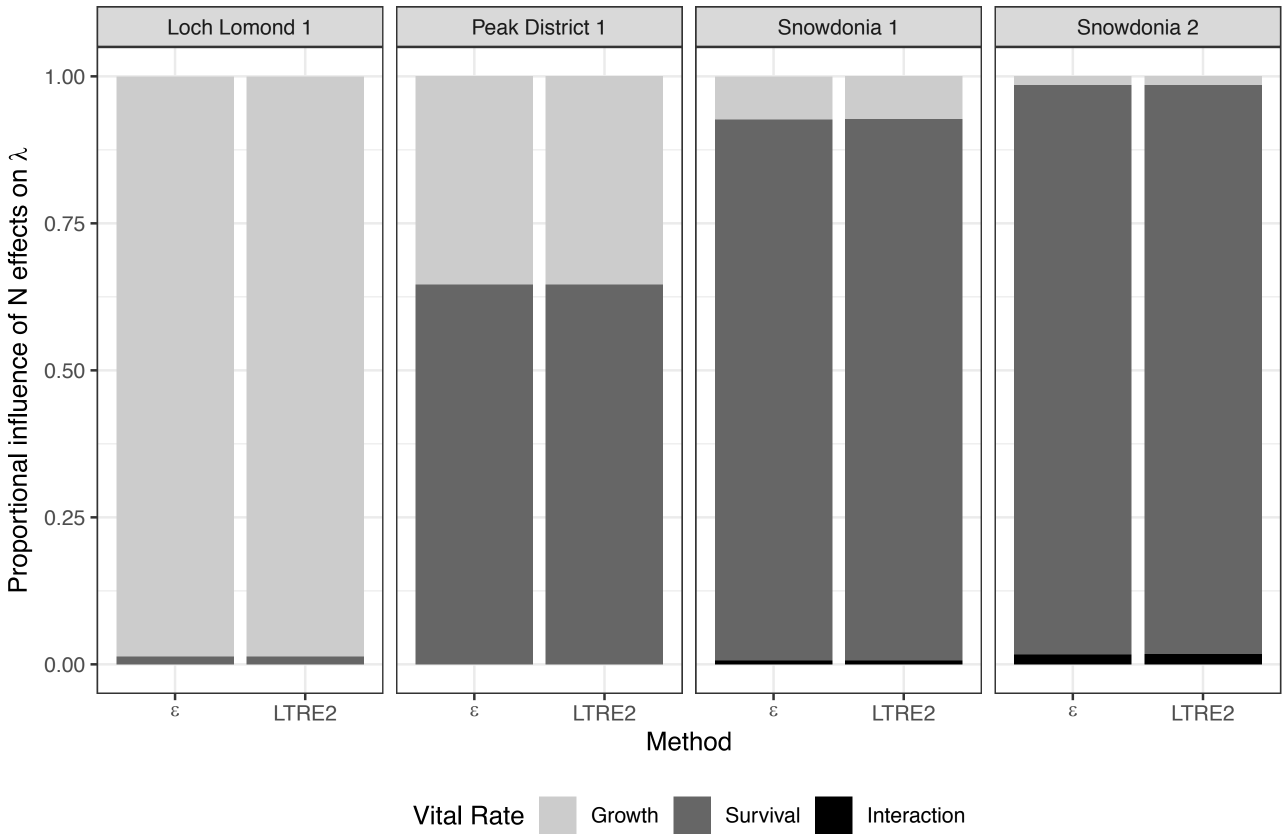


Figure 7. Site-specific breakdowns of how treatment-induced changes in *Drosera rotundifolia* vital rates influence the finite population growth rate, λ. The greater the proportion of a bar is taken by one vital rate, the more important the nitrogen effect on that vital rate was in influencing population growth. The columns represent the functional decomposition, ε, or the 2nd order decomposition of a life table response experiment (*i.e.* including the first and second order derivatives and the cross derivative), LTRE2. Absolute values of sensitivities and nitrogen coefficients were used to ensure the sum of proportions is 1.

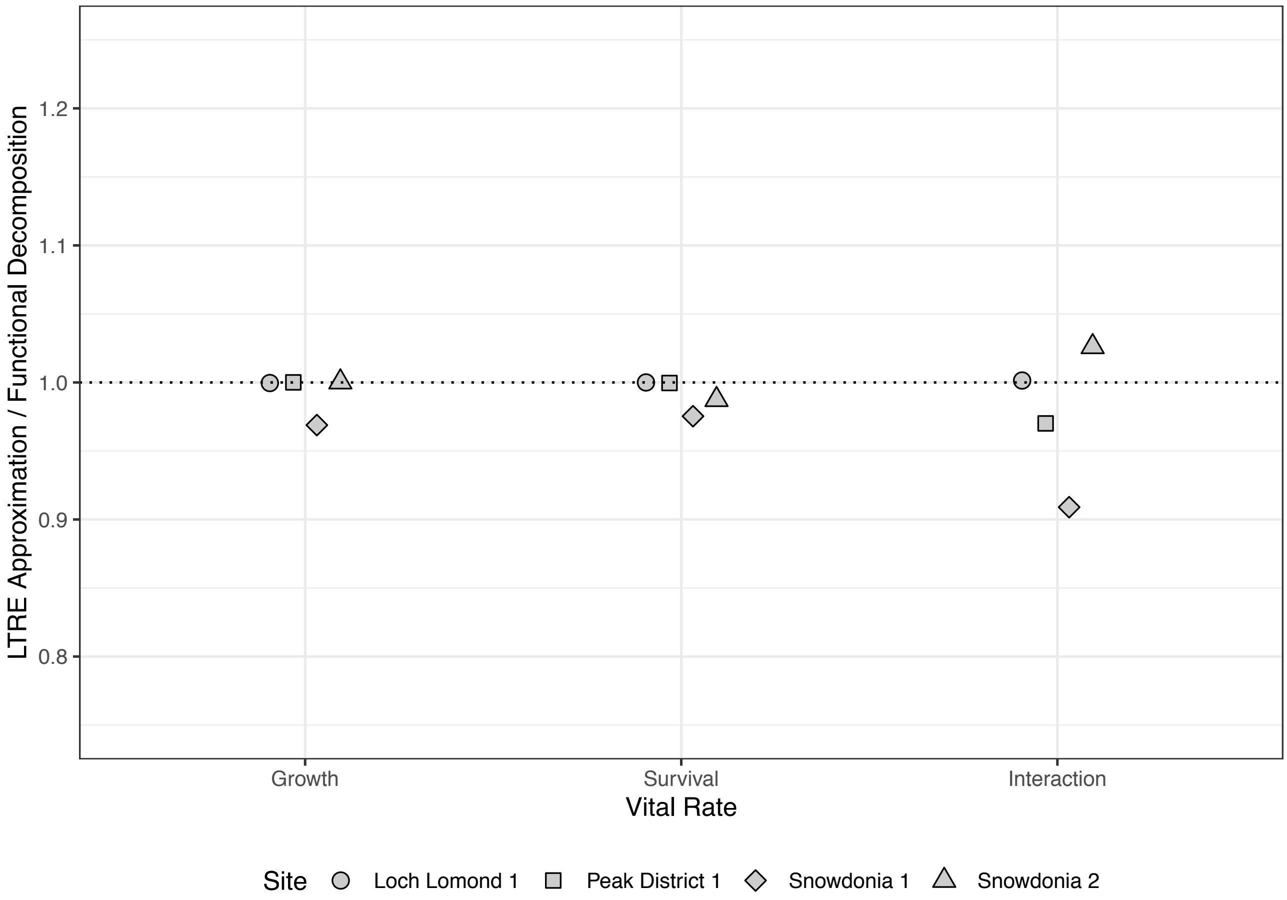


Figure 8. A comparison between functional decompositions and the product of 2nd order decomposition of life table response experiments (*i.e.,* including the first and second order derivatives and the cross derivative) sensitivity approximations and nitrogen effect coefficients. If points are close to the dashed line, the approximations are close to the exact values. The life table response experiment involved taking the first and second order and cross derivatives.

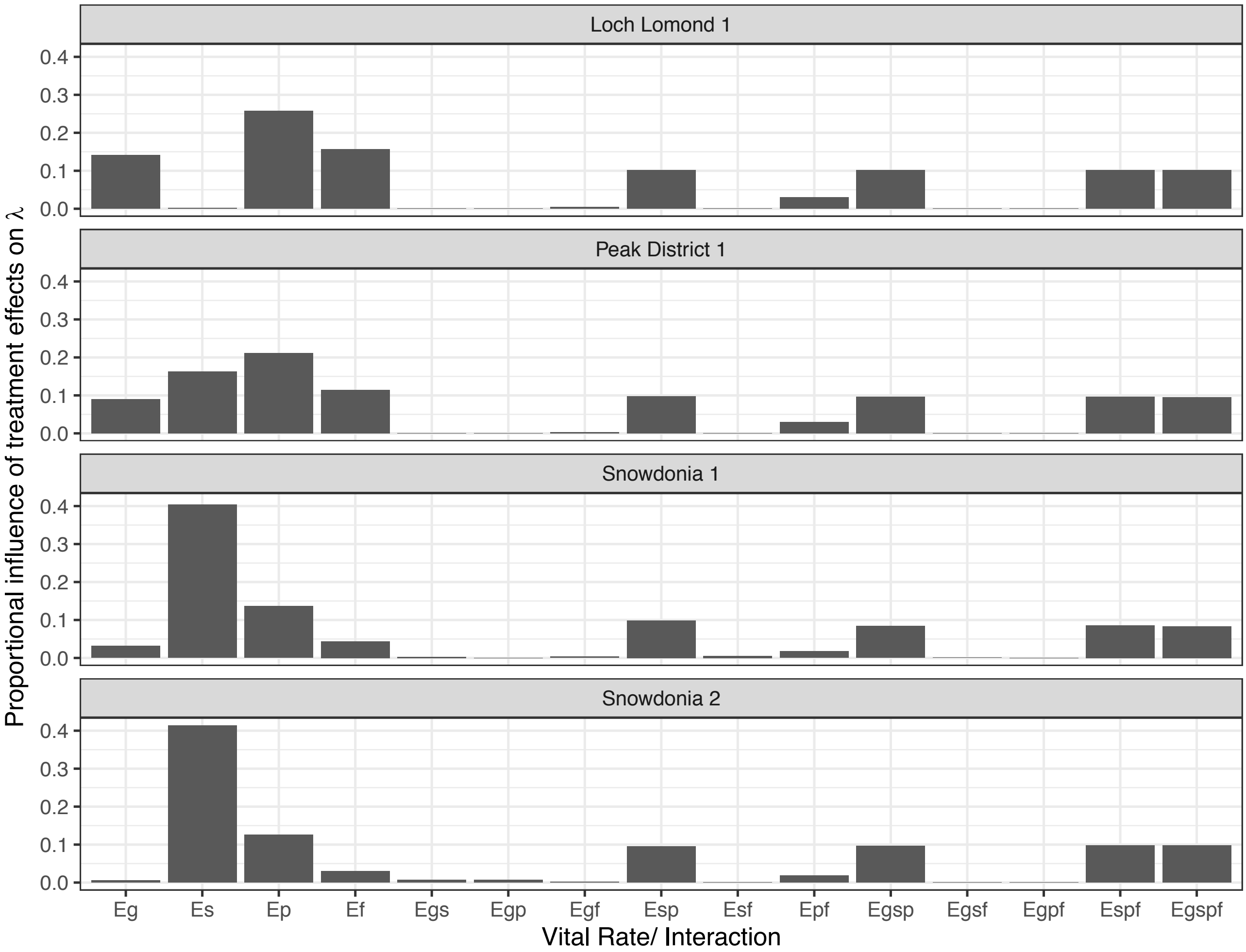


Figure 9. How artificial treatment-induced changes in *Drosera rotundifolia* vital rates influence the finite population growth rate, λ. Bars represent the relative contribution of a treatment-induced change to a vital rate, or non-additive effects of changed vital rates, on λ. The letters g, s, p and f refer to changes in growth, survival probability, probability of reproduction, and capsule production respectively. Multiple letters represent the non-additive effect of several treatment-induced changes of corresponding vital rates. Larger values indicate that the treatment affected λ more through these vital rates or interactions. Values are from a functional decomposition, and the absolute contribution of main and interactive effects on λ are divided by their sum to give their proportional influence on λ. All simulated treatment effects are site-specific, equal to the negative standard error of their respective vital rate models.

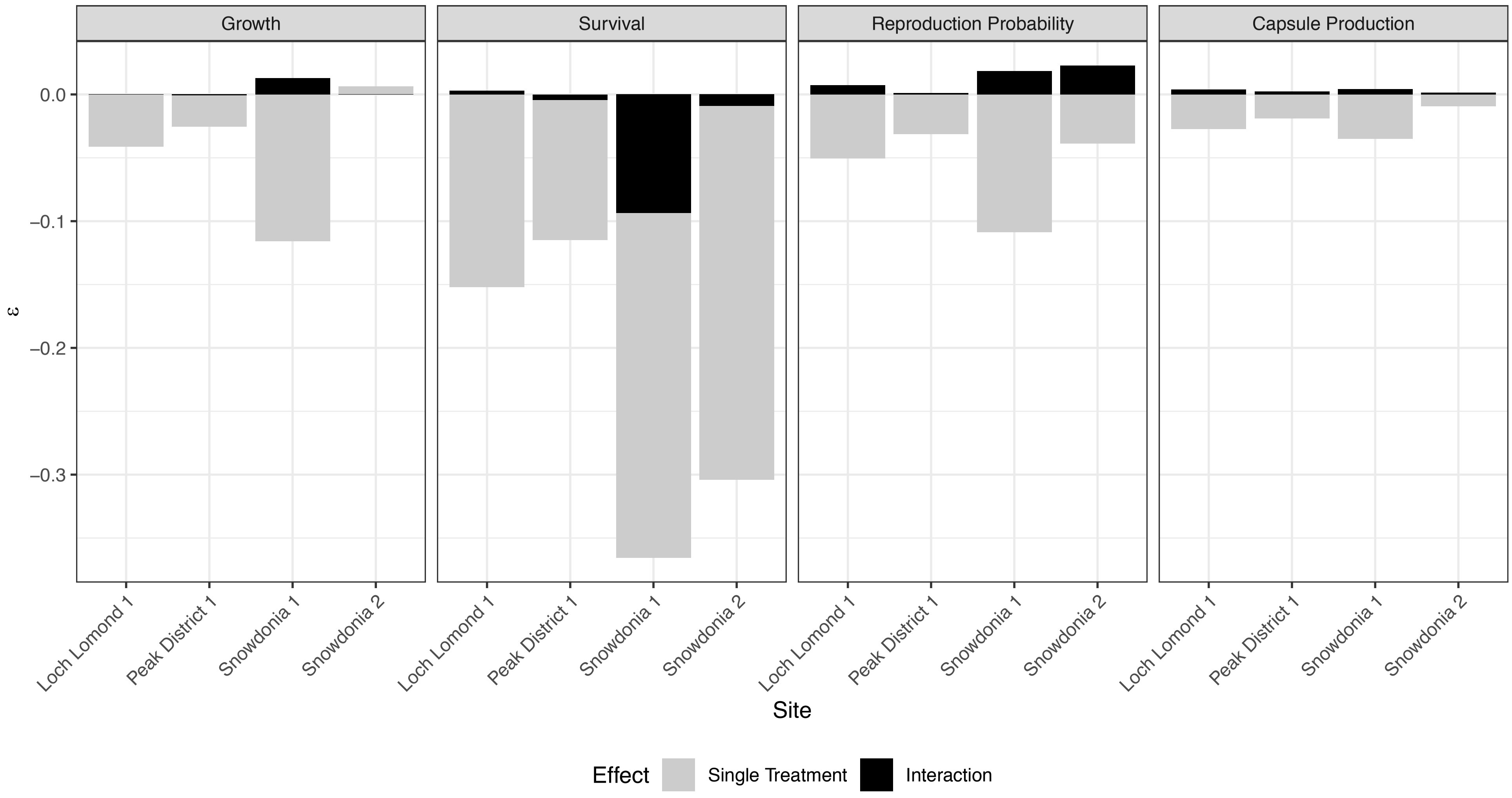


Figure 10. How the finite population growth rate, λ, of *Drosera rotundifolia* under control conditions change in response to a treatment effect, and the non-additive effect of two treatment effects. The treatment effects are identical artificial site-specific effects equal to the negative standard error of their respective vital rate models. A larger absolute value indicates the treatment or interaction had a greater effect on λ. Positive interactions reflect cases where the two treatments have an effect on λ that is smaller than their combined individual effects.

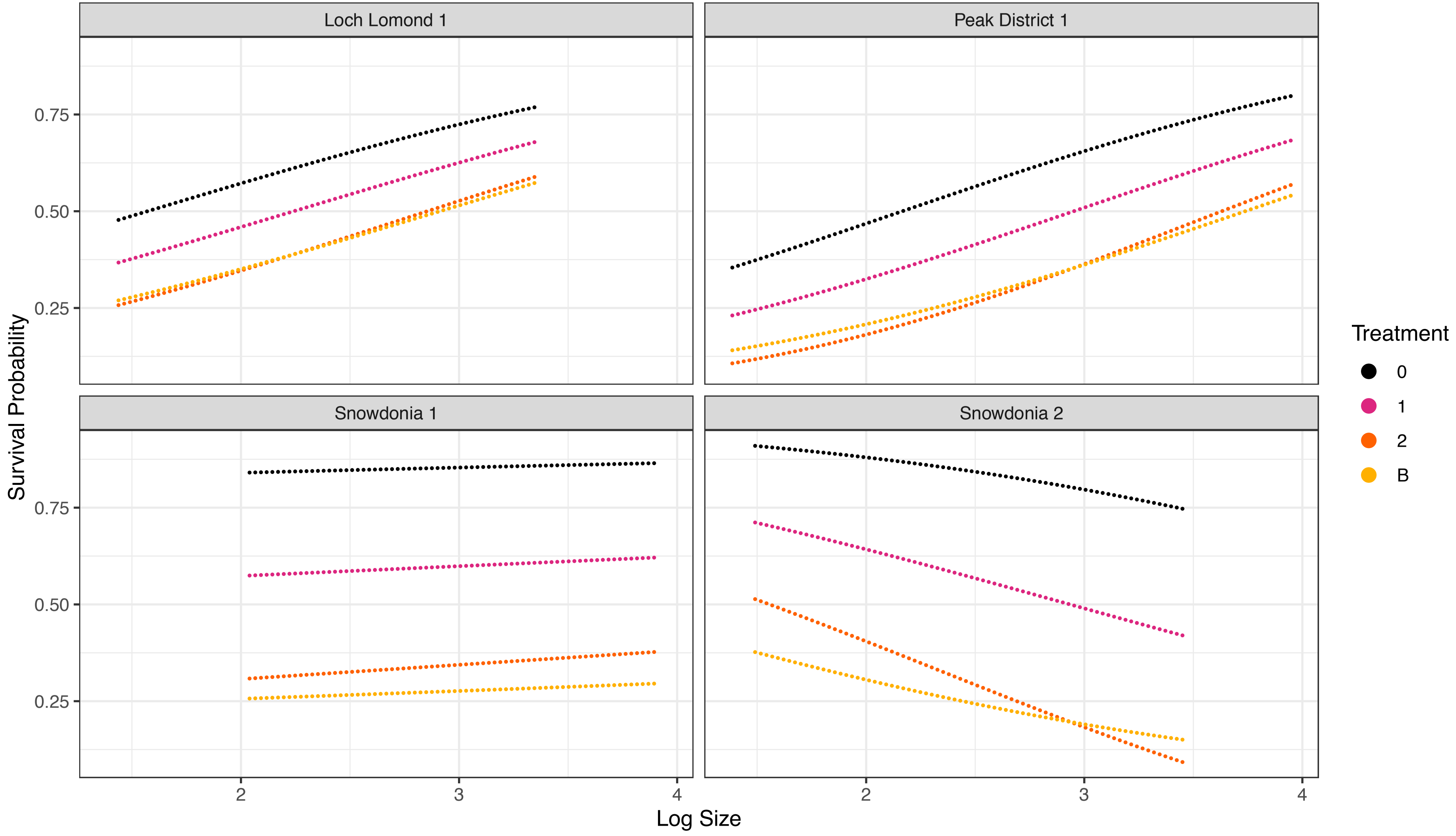


Figure 11. How size-specific *Drosera rotundifolia* survival probabilities under control conditions (0) change with a treatment (1) and two treatments (B), where all described treatments have identical effect sizes. 2 shows an additive treatment effect, double the difference between 0 and 1. Points are plotted across the range of observed non-seedling sizes at each site.

4.7 References

1.

Air Pollution Information System. Simple site-based assessment result for total N deposition (wet and dry) from 2010-2012 (3 year average). http://www.apis.ac.uk/search-location.

2.

Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* **20**, 30–59 (2010).

3.

Bobbink, R. & Roelofs, J. G. M. Nitrogen critical loads for natural and semi-natural ecosystems: The empirical approach. *ACID REIGN '* **4**, 6 (1995).

4.

Bubier, J. L., Moore, T. R. & Bledzki, L. A. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biol* **13**, 1168–1186 (2007).

5.

Caswell, H. *Matrix population models: construction, analysis and interpretation*. (Sinauer Associates, 2001).

6.

Clymo, R. S., Turunen, J. & Tolonen, K. Carbon Accumulation in Peatland. *Oikos* **81**, 368 (1998).

7.

Crone, E. E. *et al.* Ability of Matrix Models to Explain the Past and Predict the Future of Plant Populations: Forecasting population dynamics. *Conservation Biology* **27**, 968–978 (2013).

8.

Crone, E. E. *et al.* How do plant ecologists use matrix population models?: Matrix population models for plants. *Ecology Letters* **14**, 1–8 (2011).

9.

Ellner, S. P. & Rees, M. Integral Projection Models for Species with Complex Demography. **167**, 410–428 (2006).

10.

Ellner, S. P., Snyder, R. E., Adler, P. B. & Hooker, G. An expanded modern coexistence theory for empirical applications. *Ecol Lett* **22**, 3–18 (2019).

11.

Galloway, J. N. *et al.* Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science* **320**, 889–892 (2008).

12.

Gorham, E. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* **1**, 182–195 (1991).

13.

Gotelli, N. J. & Ellison, A. M. NITROGEN DEPOSITION AND EXTINCTION RISK IN THE NORTHERN PITCHER PLANT, SARRACENIA PURPUREA. *Ecology* **83**, 2758–2765 (2002).

14.

Gunnarsson, U., Granberg, G. & Nilsson, M. Growth, production and interspecific competition in Sphagnum: effects of temperature, nitrogen and sulphur treatments on a boreal mire. *New Phytol* **163**, 349–359 (2004).

15.

Harenda, K. M., Lamentowicz, M., Samson, M. & Chojnicki, B. H. The Role of Peatlands and Their Carbon Storage Function in the Context of Climate Change. in *Interdisciplinary Approaches for Sustainable Development Goals* (eds. Zielinski, T., Sagan, I. & Surosz, W.) 169–187 (Springer International Publishing, 2018). doi:10.1007/978-3-319-71788-3_12.

16.

Maiz-Tome, L. Drosera rotundifolia: The IUCN Red List of Threatened Species 2016: e.T168798A1232630. (2015) doi:10.2305/IUCN.UK.2016-1.RLTS.T168798A1232630.en.

17.

Nordbakken, J.-F., Rydgren, K. & Økland, R. H. Demography and population dynamics of *Drosera anglica* and *D. rotundifolia*: Drosera anglica *and D* . rotundifolia. *Journal of Ecology* **92**, 110–121 (2004).

18.

Oke, T. A. & Hager, H. A. Plant community dynamics and carbon sequestration in *Sphagnum* -dominated peatlands in the era of global change. *Global Ecol. Biogeogr.* **29**, 1610–1620 (2020).

19.

Page, S. E. & Baird, A. J. Peatlands and Global Change: Response and Resilience. *Annu. Rev. Environ. Resour.* **41**, 35–57 (2016).

20.

Page, S. E., Rieley, J. O. & Banks, C. J. Global and regional importance of the tropical peatland carbon pool: TROPICAL PEATLAND CARBON POOL. *Global Change Biology* **17**, 798–818 (2011).

21\.

Phoenix, G. K. *et al.* Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Glob Change Biol* **18**, 1197–1215 (2012).

22\.

Press, M. C., Woodin, S. J. & Lee, J. A. THE POTENTIAL IMPORTANCE OF AN INCREASED ATMOSPHERIC NITROGEN SUPPLY TO THE GROWTH OF OMBROTROPHIC SPHAGNUM SPECIES. *New Phytol* **103**, 45–55 (1986).

23\.

R Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2020).

24\.

Redbo-Torstensson, P. The demographic consequences of nitrogen fertilization of a population of sundew, Drosera rotundifolia. *Acta Botanica Neerlandica* **43**, 175–188 (1994).

25\.

Rees, M., Childs, D. Z. & Ellner, S. P. Building integral projection models: a user's guide. *J Anim Ecol* **83**, 528–545 (2014).

26\.

Salguero-Gómez, R. *et al.* The COMPADRE Plant Matrix Database: an open online repository for plant demography. *J Ecol* **103**, 202–218 (2015).

27\.

Svensson, B. M. Competition between Sphagnum fuscum and Drosera rotundifolia: A Case of Ecosystem Engineering. *Oikos* **74**, 205 (1995).

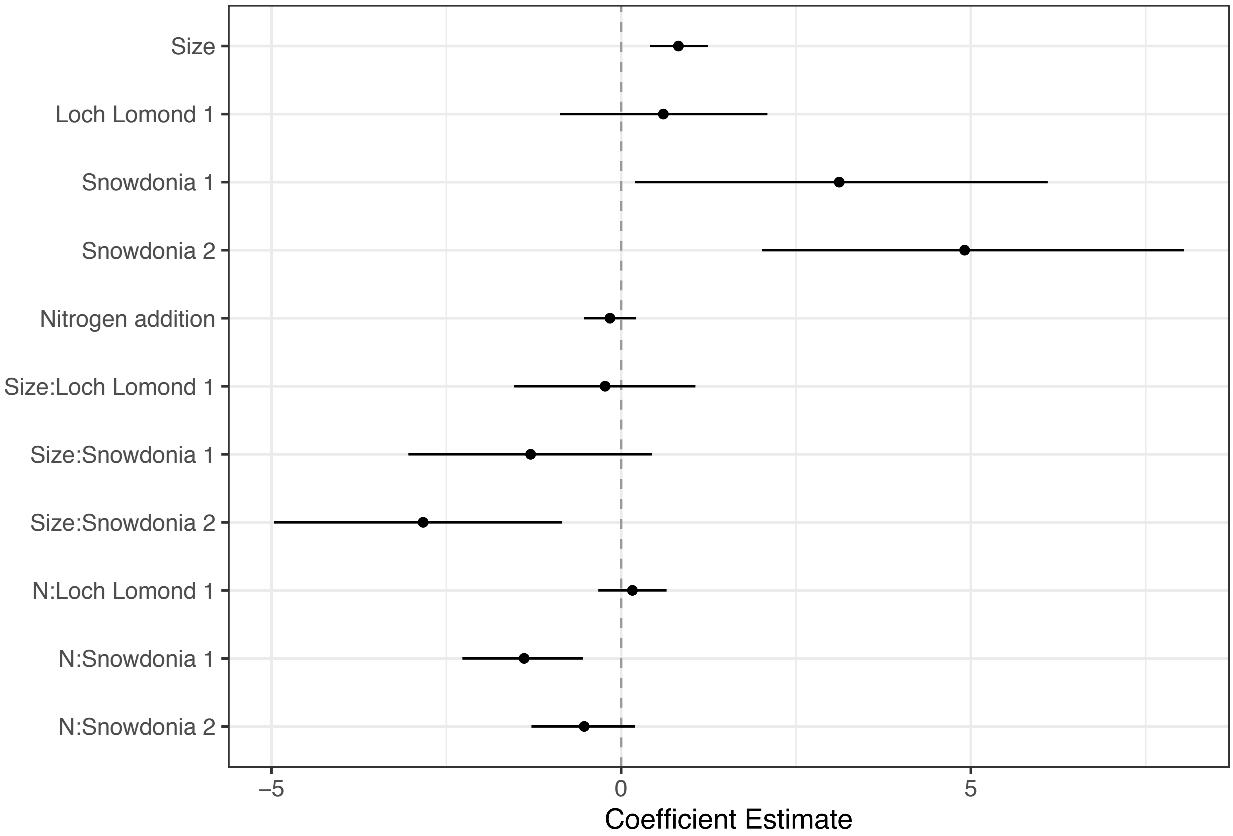
28\.

Vries, W. D. *et al.* Use of dynamic soil–vegetation models to assess impacts of nitrogen deposition on plant species composition: an overview. *Ecological Applications* **20**, 60–79 (2010).

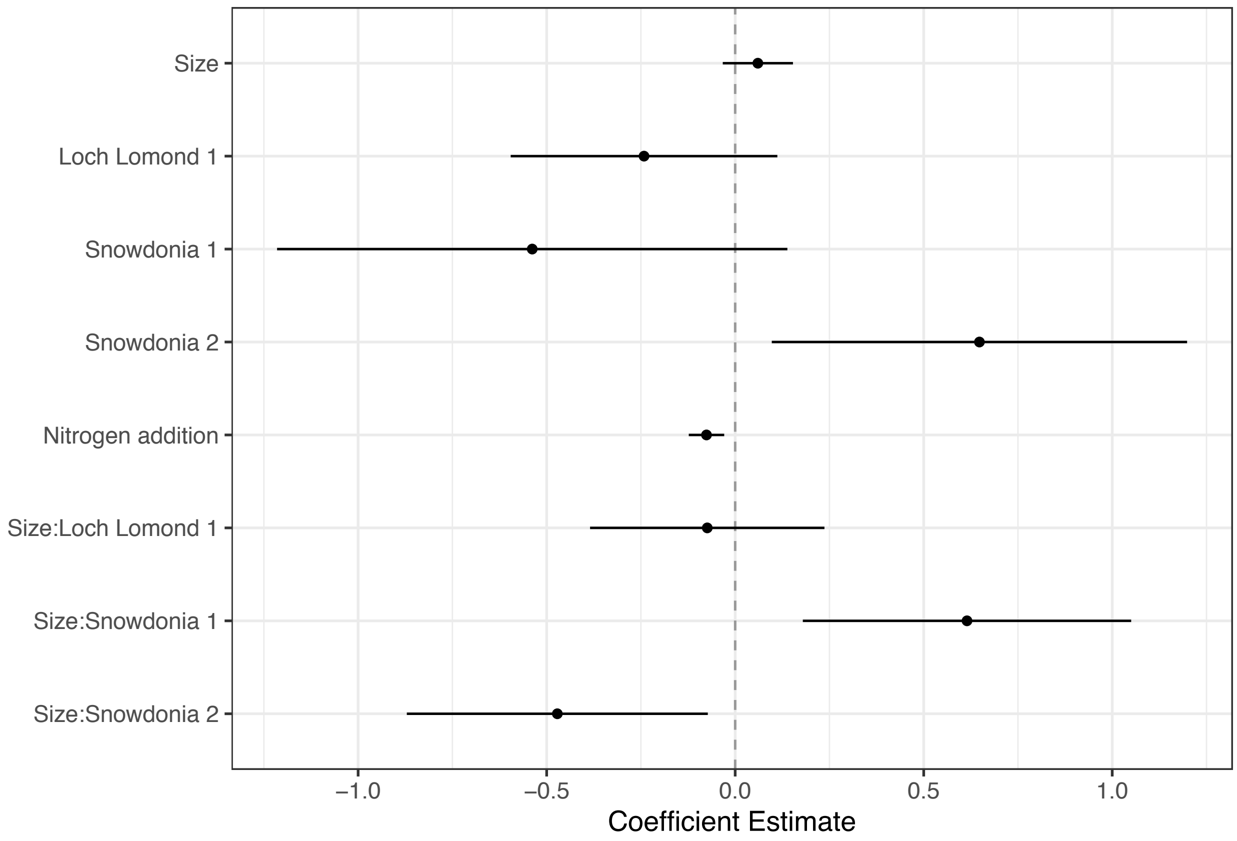
29\.

Wilson, P. J. & Provan, J. Effect of habitat fragmentation on levels and patterns of genetic diversity in natural populations of the peat moss *Polytrichum commune*. *Proc. R. Soc. Lond. B* **270**, 881–886 (2003).

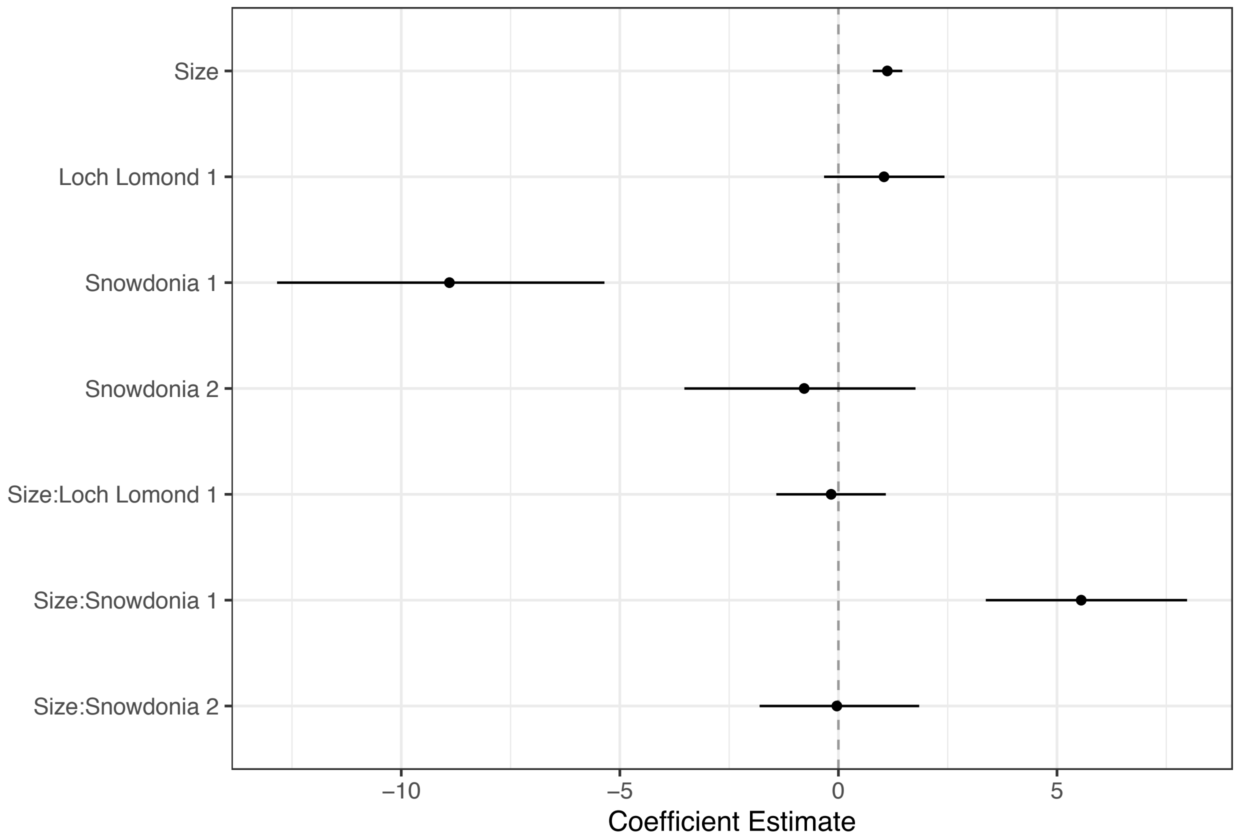
4.8 Supplementary information



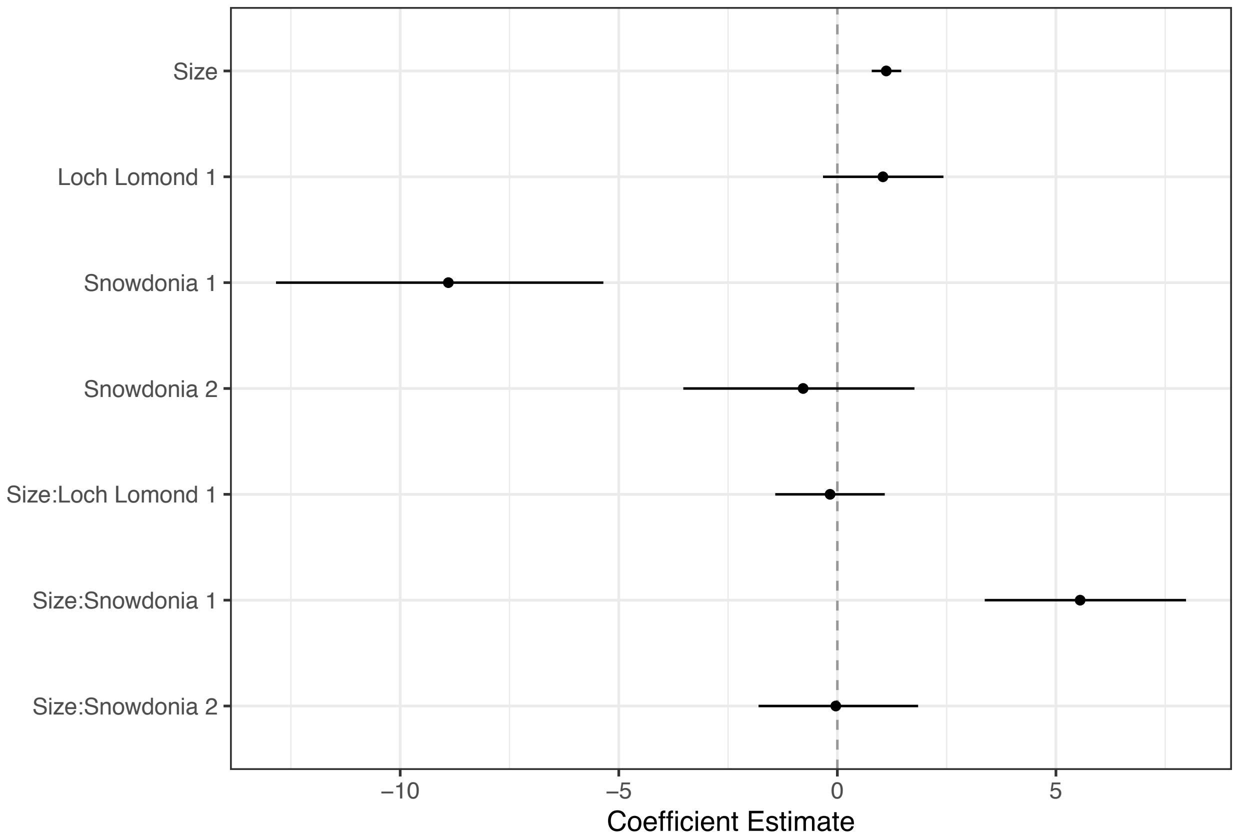
Supplementary 1. Coefficient plot of a binomial generalised linear model for *Drosera rotundifolia* survival probability. Points greater than 0 indicate the variable or interaction had a positive effect on survival. Size is the natural log of leaf length. N represents the experimental addition of nitrogen effect.



Supplementary 2. Coefficient plot of a general linear model for *Drosera rotundifolia* change in size. Points greater than 0 indicate the variable or interaction had a positive effect on survival. Size is the natural log of leaf length.



Supplementary 3. Coefficient plot of a binomial generalised linear model for *Drosera rotundifolia* flowering probability. Points greater than 0 indicate the variable or interaction had a positive effect on survival. Size is the natural log of leaf length.



Supplementary 4. Coefficient plot of a negative binomial generalised linear model for *Drosera rotundifolia* the number of seed capsules produced. Points greater than 0 indicate the variable or interaction had a positive effect on survival. Size is the natural log of leaf length.

Chapter 5: Retrospective decompositions can inform population management interventions

5.1 Abstract

Understanding the environmental drivers of population growth is critical given the scale of anthropogenic change in many ecosystems. The effects of experimental treatments or environmental variation on observed differences in population growth can be decomposed to inform management interventions. We conduct a functional decomposition on *Actaea spicata* and *Drosophyllum lusitanicum* populations, which are known to be affected by nutrient availability and seed predation, and fire disturbance and livestock respectively. This retrospective analysis shows that an environmental effect on multiple vital rates can be understood as an aggregate effect on population growth. We show that livestock exclusion in the *D. lusitanicum* system can be positive or negative depending upon time since fire, demonstrating how a decomposition analysis can inform management. We also find that multiple environmental changes can produce large non-additive effects on population growth. Coupling retrospective decompositions with experiments has great potential to guide future population management strategies.

5.2 Introduction

Stable populations contribute to ecosystem function, provide value in harvestable resources, and may be desirable to conserve according to public will (Ellner *et al*., 2016). However, climate and land use change threaten the stability of populations by restricting species ranges and diminishing the lifetime reproductive success of individuals (Walther, 2002; Parmesan, 2006, Grimm *et al*., 2008; Bobbink *et al*., 2010). Anthropogenic effects play a large role in (local) extinction events (Morris *et al*., 2020), but it can be difficult to disentangle the roles of individual anthropogenic stressors on population decline as their effects can interact (Niinemets, 2010; Cahill *et al*., 2013).

The composition of a population can be more important for long-term viability than population size; characteristics of individuals like age, sex and size determine their contribution to the finite population growth rate, λ, (Crouse *et al*., 1987). Furthermore, environmental change can apply different pressures to demographic subsets within a population. However, strong effects of treatments the environment on individual performance/ vital rates like survival, growth and reproductive success do not necessarily contribute much to λ (Caswell, 1989). Structured population models bridge the gap between individual performance and population outcomes (Morris & Doak, 2002; Ellner *et al*., 2016), with the benefit of understanding the structure of projected populations and key transitions in the life cycle (Caswell, 1989; Merow *et al*., 2014).

Perturbation analyses of structured population models can help to make informed management choices in light of environmental change (Morris & Doak, 2002; Ellner *et al*., 2016). Sensitivity and elasticity analyses have been the go-to approaches to inform management strategies (Mills *et al*., 1999), as they identify the vital rates that λ is most dependent upon (Caswell, 2000). These prospective analyses have a lot of utility for conservation (Silvertown *et al*., 1996; Ehrlén *et al*., 2001), and even an approach to integrate sensitivities and management costs has been developed (Baxter *et al*., 2006). However, we feel the use of retrospective analyses to inform conservation management has been undervalued.

Retrospective approaches such as life table response experiments (LTREs) help identify how the observed variation in λ depends upon observed variation in vital rates (Horvitz *et* *al*., 1997; Caswell, 1989; 2000). A problem with using retrospective analyses to inform management is that the variables that contribute most to differences in λ may not have acted upon the vital rates λ is most sensitive to (Caswell, 1989), leading to an inferior intervention choice. However, a retrospective decomposition of the vital rate contributions to λ can be informative when populations undergo experimental treatments or environmental variation is known (Horvitz *et al*., 1997). We often know the anthropogenic effects that are likely to affect ecosystems and individual populations (Lande, 1998; Morris *et al*., 2020). Therefore, we can identify how variation in λ depends upon nuanced effects of future change by carrying out spatially replicated experiments (Jentsch *et al*., 2007). Consequently, an LTRE can be considered a useful empirical extension of sensitivity analysis (Hamda *et al*., 2012), where future management strategies can be based on the decomposed observed variation in λ due to ecologically relevant treatments.

The standard approach for decomposing the treatment or vital rate contribution to λ is through decomposition analysis of an LTRE (Caswell, 1989). The functional decomposition approach is an alternative to an LTRE that does not require sensitivity estimates (Ellner *et al*., 2019). In chapter 3 we show that the standard approach (an approximation) produces values for the relative contributions to λ from treatment affected vital rates that are similar to the exact values from a functional decomposition. However, the absolute contributions of treatment affected vital rates were error prone, particularly for interactive effects. The interactive effects of treatments/environmental factors can be negligible (Smith *et al*., 2005; Elderd & Doak, 2006) or important in explaining variation in λ (Schleuning *et al*., 2008). In chapter 3 we note that interactions between nitrogen affected growth and survival were unimportant for λ, but simulated treatments for other vital rates showed that even four-way interactions could have large effects on λ. Ultimately, interactive effects of realistic changes to vital rates may result in strong observable declines in λ; this could be more informative to land managers than the knowledge that proportionate changes in those vital rates have relatively weak effects on λ. Consequently, it is important to accurately quantify the roles of an environmental gradient or treatment induced changes to vital rates and their interactions in determining variation in λ (Elderd & Doak, 2006; Schleuning *et al*., 2008).

We look at two studies, one for *Actaea spicata* and another for *Drosophyllum lusitanicum*, where statistical parameters for vital rates are from Dahlgren and Ehrlén (2009) and Paniw *et al*. (2018) respectively. In both cases these parameters inform structured population models, integral projection models (IPMs), that produce values for λ under different conditions. We consider how variation in seed predation intensity, soil potassium concentration, and their interactions contribute to variation in λ for *A. spicata*. We consider how variation in time since a fire disturbance event (TSF) and the presence of browsing livestock contribute to variation in λ for *D. lusitanicum*. We conduct retrospective analyses to understand the importance of interactions between environmental effects in these systems and compare the results of a standard approach (LTRE decomposition) with a functional decomposition.

5.3 Methods

We investigated how the environment affected the population growth of *A. spicata*, a flowering forest herb. Data for *A. spicata* were collected from four sites in Tullgarn natural reserve, Sweden, with 200 non-seedling individuals recorded at each site at the first census. Four annual censuses were taken from 2004–2007 between June–July, including information about plant size, and the number of fruits and seeds produced. Individuals were also assigned plot quadrant level environmental information, including edaphic factors, interspecific density, canopy cover and seed predation. Further details of the system, sampling and modelling can be found in Dahlgren and Ehrlén (2009), and commented code for IPM construction in Merow *et al*. (2014) Appendix A. Vital rate modelling showed that soil K significantly increased plant size. Furthermore, seed predation by a specialist moth, *Eupithecia immundata*, was thought to cause the observed variation in seeds per fruit, rather than other environmental variables (Dahlgren & Ehrlén, 2009).

We compared the results from two retrospective analyses, the standard LTRE decomposition approach and a functional decomposition: the standard approach (Caswell, 2001) involved testing the effects of small perturbations to the underlying parameters of the IPM; the functional decomposition (Ellner *et al*., 2019) involved a comparison of λ values obtained from IPMs that were based on different sets of conditions (parameter values). Chapter 3 contains more detail about how both of these approaches are applied to population models, and how the standard approach can deal with possible non-linearity in the relationship between a parameter and λ, and interactions between parameters.

For *A. spicata* we created IPMs with varying seed predation and soil K parameters, taking the minimum (0 for predation), mean and maximum observed values for these environmental variables. We considered the λ from a model with minimum seed predation and soil K to be a ‘null’ λ. Our retrospective analyses describe how changing parameter values to mean or max observed values contributes to changes from this null λ.

In our analysis we compare the approximations from the 1st order LTRE with the exact values of parameter main effects from the functional decomposition. Next, we assess the accuracy of the 2nd order LTRE and estimated interactive effects. Finally, we compare the relative importance of the parameters and their interactions on influencing the observed variation in λ.

We investigated how the environment affected the population growth of *D. lusitanicum*, a post-fire specialist carnivorous subshrub. Data for *D. lusitanicum* were collected from eight populations that had experienced a recent fire event. 2378 individuals were recorded across the eight populations, along with livestock pressure (high or low) and TSF (0, 1, 2, 3 or >3 years). Paniw *et al*. (2017) describe multiple effects of livestock and TSF on vital rates; vital rate models describing how survival, size transition, probability of flowering, and number of flowering stalks vary by size have different intercepts and slopes depending on TSF and livestock level. TSF and livestock level also affect intercepts in vital rate models for the number of flowers per stalk and the seedling size distribution. Finally, the interaction between TSF and livestock levels affect the intercepts of all vital rate models already described. Further details of the system, sampling and modelling can be found in Paniw *et al*. (2017).

We used a retrospective decomposition to quantify the effects of environmental variation on *D. lusitanicum* populations. The standard approach is to calculate sensitivity of λ to changes in a parameter and multiply that sensitivity by the observed value of the parameter. This should be done for each parameter affected by an environmental effect and summed in order to calculate an aggregate contribution of that environmental effect on λ. Instead we use the functional decomposition approach to quantify the exact contribution of environmental effects on λ. We compared the λ values generated by IPMs under different livestock and TSF conditions. We created IPMs specific to the eight sites with varying TSF and livestock browsing parameters. Our null λ was based on conditions of no browsing, and 2 years after a fire event. We selected 2 years post-fire because flowering individuals occur, and seed bank dynamics play a smaller role in population growth by that point. We investigated how changes to 3 or >3 years since fire, livestock pressure and their interactions contributed to changes in growth rate from the null λ.

5.4 Results

For *A. spicata* the standard approach did not estimate the contribution of variation in parameters to λ accurately (Fig.1). For example, the estimate for the contribution of going from low to mean soil K was 36% greater than the exact value obtained from the functional decomposition.

The 2nd order LTRE did not offer much more accuracy than estimates from the 1st order (Fig. 2). However, there was little curvature to account for between changing parameters and λ (Fig. 3).

Interactions between increasing seed predation and soil K had strong negative effects on λ (Fig. 1). The interactions between seed predation and soil K accounted for between 3.9 to 13.6% of the changed parameters total effects on λ (Fig. 4).

For *D. lusitanicum* we found that greater browsing intensity or increasing TSF generally corresponded with lower λ values (Fig. 5). However, the interactive effects of greater browsing with either increase in TSF increased λ. Interactive effects had a greater relative contribution to deviations from the null lambda than either main effect for 6/8 sites (Fig. 6).

5.5 Discussion

A functional decomposition can quantify how a treatment or a deviation from a baseline condition contributes to λ. For *D. lusitanicum*, substantial observed variation in λ corresponds to factors that can be controlled by humans *e.g.,* fire suppression and livestock browsing. Quantifying the contribution of this environmental variation to λ provides clear information that can be useful to land managers. For example, livestock have negative effects on λ early after fire but are beneficial 3 or more years after fire (Fig. 5).

Environmental variation can affect multiple vital rates, which was the case for *D. lusitanicum*. We were interested in the collective effects of fire, livestock, and their interactions on λ (Fig. 5), but there can be cases where researchers want a more nuanced understanding of how environmental effects contribute to λ. In other systems we may want to investigate how environmental variation affects λ through a particular vital rate, rather than its aggregate effects on all vital rates. In this case we can apply a functional decomposition where a null model is compared to models including some treatment-induced changes to vital rates, but not others.

Our results support the need to investigate non-additive effects of environmental changes (Elderd & Doak, 2006; Jetz *et al*., 2007; Niinemets, 2010; Hof *et al*., 2011; Cahill *et al*., 2013). In 6/8 cases the non-additive effect of the fire state and browsing combination were responsible for more variation in *D. lusitanicum* λ than the main effects (Fig. 6). Similarly, for *A. spicata* interactive predation and soil K effects were about as important as predation when predation was high (Fig. 4). Interactive effects can be small (Schleuning *et al*., 2008), but a simple management intervention dealing with a main effect contributing little to variation in λ may have greater value when we acknowledge the presence of multiple interactions.

The relative importance of environmental variation and interactions differed across all eight sites for *D. lusitanicum*. Evidence for compensatory variation in vital rates across species ranges (Villellas *et al*., 2015) and the potential for labile traits amongst some species but not others (McDonald *et al*., 2017) highlight the need to spatially replicate demographic experiments (Crone *et al*., 2011; Salguero-Gómez *et al.,* 2015). Conserving some populations may be untenable as the environment continues to change (Hossell *et al*., 2003). Functional decompositions can aid in selecting sites where interventions will yield the desired result.

Retrospective decompositions and prospective analyses both have their place in informing the methods to control population size. Management options based on, say increasing the vital rate with the highest elasticity may be impossible (Horvitz *et al*., 1997), have disproportionately large costs, or non-linearly increasing costs (Baxter *et al*., 2006). Consequently, the efficacy of an intervention based on prospective analysis still requires quantification of how costly proportionate changes in vital rates are to make. In contrast, a functional decomposition only quantifies the contribution to λ of observed variation in vital rates. We can quantify the cost of an experimental treatment, or its mitigation, and relate that to the contribution to λ obtained through a decomposition analysis. A mixed approach where elasticity analysis informs the types of interventions to test through experiments and subsequent decomposition may be a way to utilise the strengths of both approaches.

In summary, we show how observed variation in *A. spicata* and D. *rotundifolia* λ can be attributed to different sources of environmental variation. We see discrepancies between the results of the standard LTRE decomposition approach and the exact values from the functional decomposition. Furthermore, we note strong interactive effects and the potential for interactions to be important when considering population management interventions, such as for livestock and time since fire disturbance. Applying functional decompositions to spatially replicated experiments including reasonable intervention treatments or projected environmental changes may offer insights into the best ways to manage populations in light of global change.

5.6 Figures

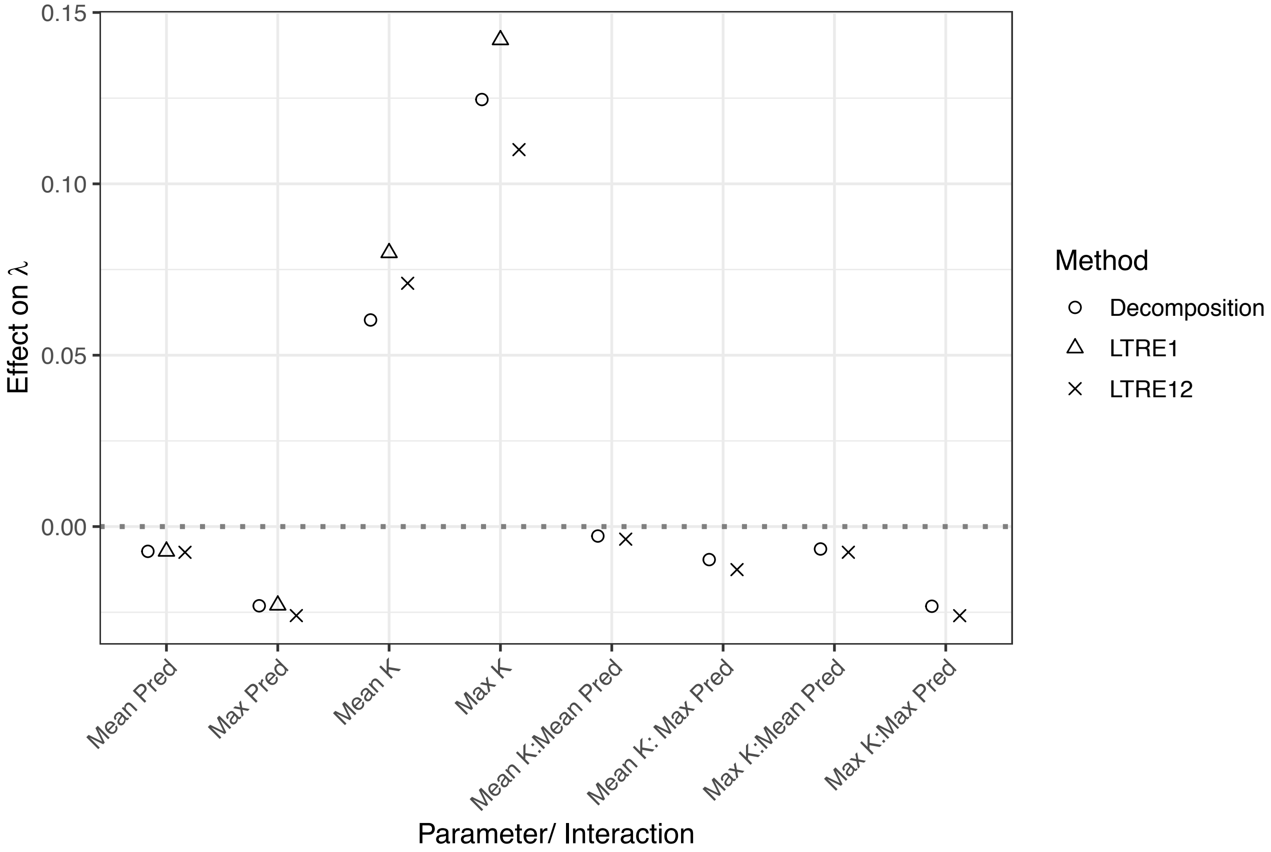


Figure 1. How population growth of *Actaea spicata* changes when soil potassium and seed predation change from their minimum to mean and maximum observed levels. The exact effect of the environmental change is given by the (functional) decomposition. LTREs are results from life table response experiment decompositions, where parameter sensitivities are multiplied by corresponding parameter values. LTRE1 involves taking the first order derivative, and LTRE12 involves the first and second order derivatives for main effects, and the cross derivative for the interactive effect of two altered parameters.

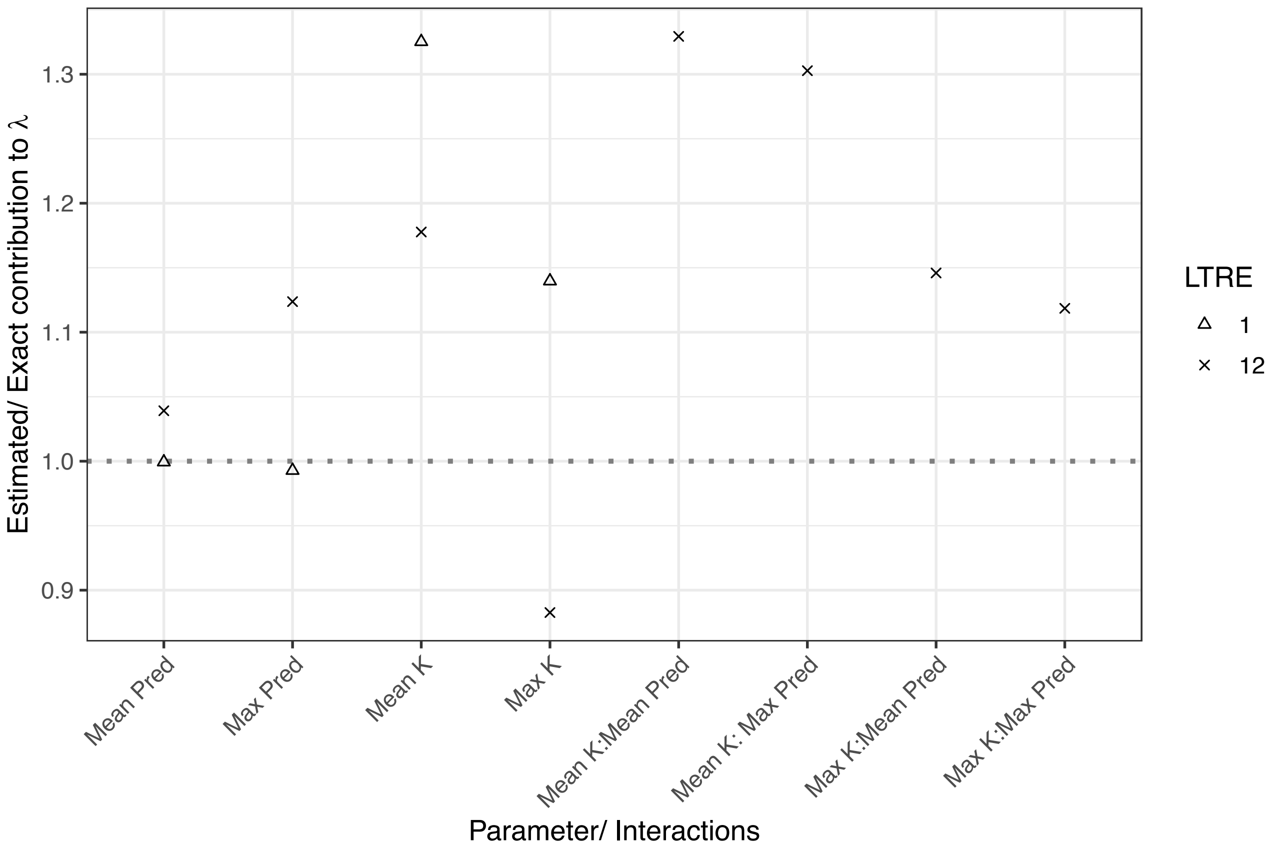


Figure 2. The accuracy of life table response experiment (LTRE) decompositions at estimating how environmental variation contributes to *Actaea spicata* population growth. 1 refers to an LTRE where only the first order derivative was taken. 12 refers to an LTRE where the first and second order derivatives were taken to estimate the main effects, and the cross derivative for the interactive effect of two altered parameters. Results of LTRE decompositions are compared with the exact contributions to population growth obtained from a functional decomposition. Points closer to 1 are more accurate.

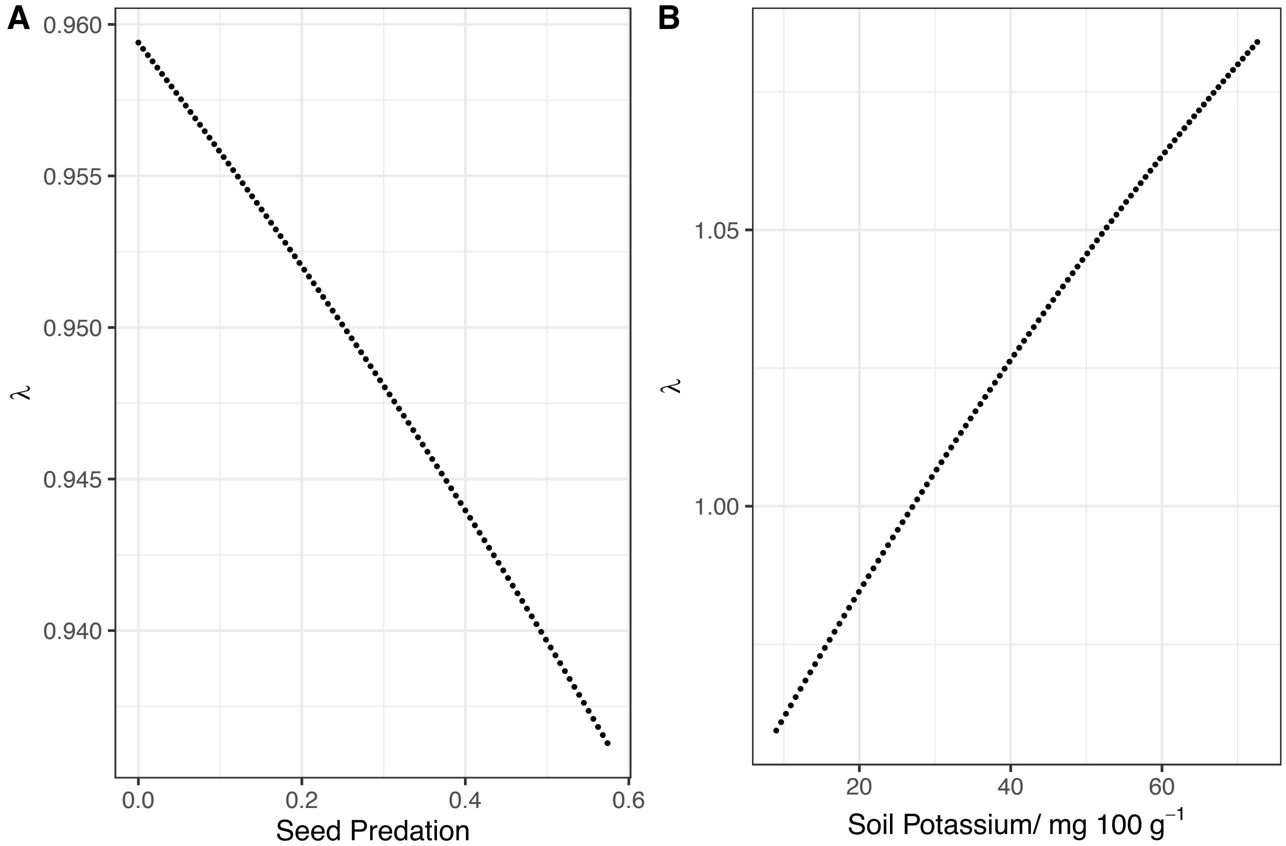


Figure 3. The relationship between changing environmental parameters and *Actaea spicata* population growth rate. Points are obtained from integral projection models where parameter values are set between minimum and maximum observed values: A) seed predation between 0 and 0.57; B) soil potassium between 9 and 72.6.

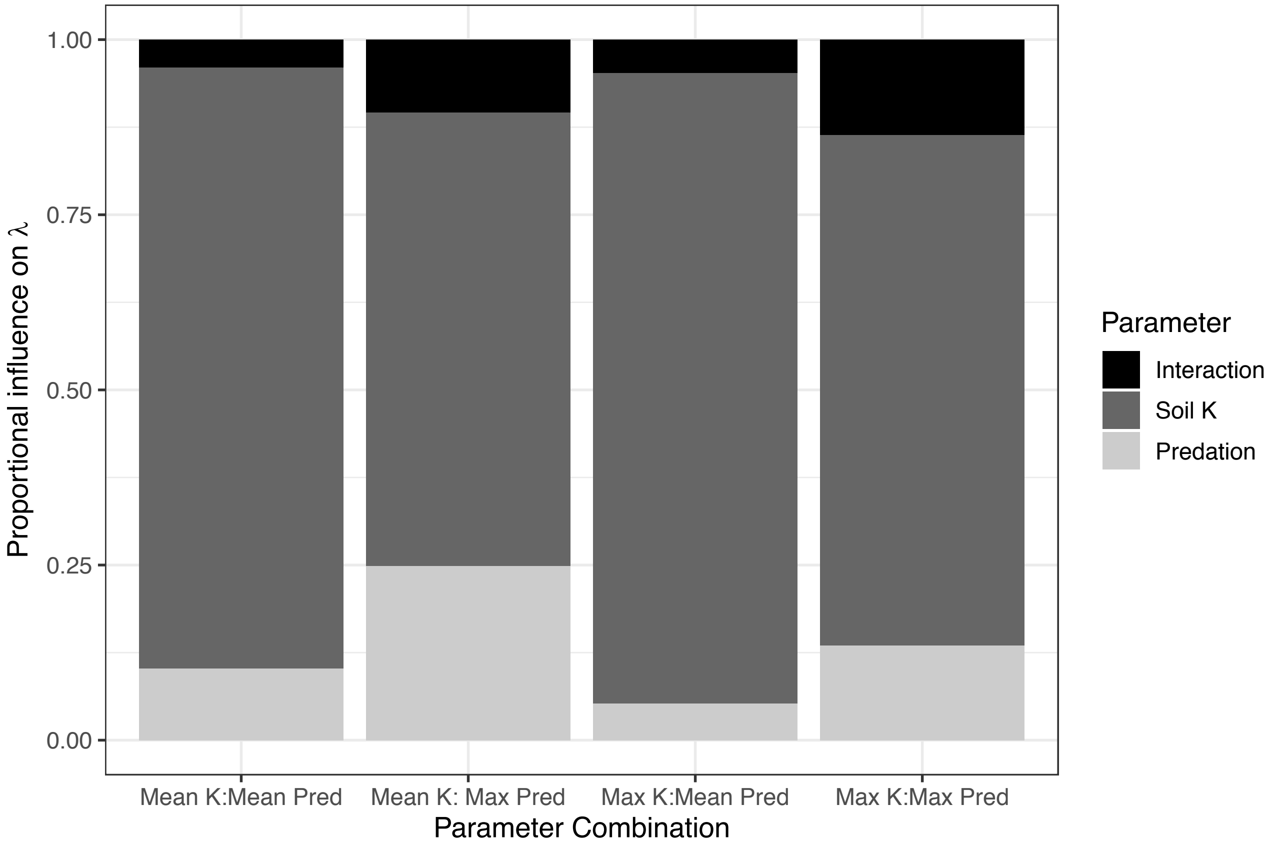


Figure 4. The relative contribution of environmental effects on *Actaea spicata* population growth. Each column represents a combination of two environmental effects; changing from minimum observed soil potassium concentration and seed predation to a combination of mean and or max observed values. Changes in population growth rate caused by changes to each environmental variable, and the non-additive effect of changing both variables (interaction) were calculated using a functional decomposition. The absolute change in population growth caused by each main/individual effect or interaction is divided by their sum to give their relative contributions to population growth.

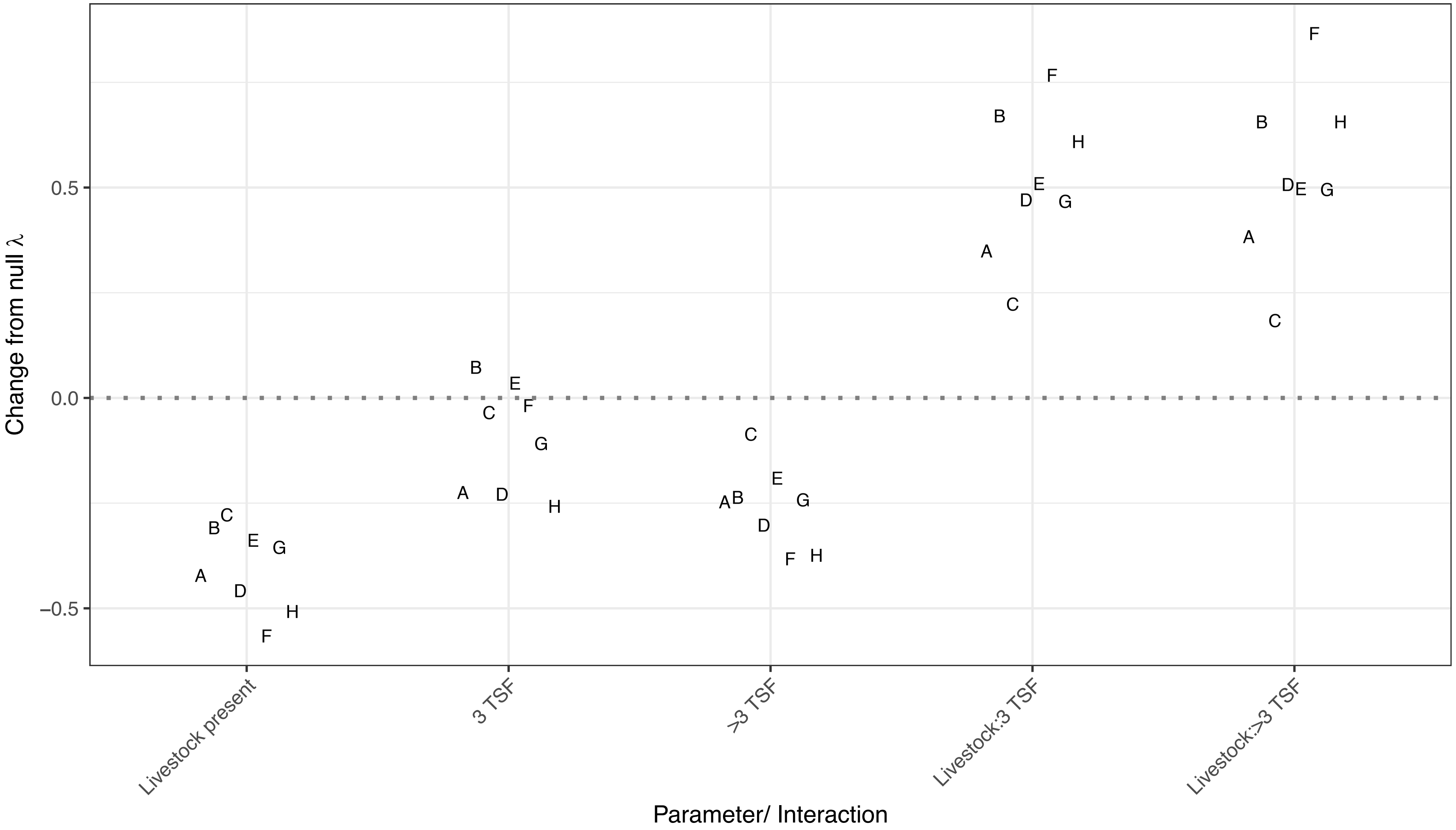


Figure 5. The contribution of environmental effects on *Drosophyllum lusitanicum population* growth rate. Letters represent eight different sites. Livestock, TSF3 and TSF>3 correspond to changes in population growth rate when changing from low to high livestock intensity, or from 2 years since fire to 3 or >3 years respectively. Colon separated factors represent interactions – the non-additive effect on population growth when increasing both livestock intensity and time since fire (to either 3 or >3).

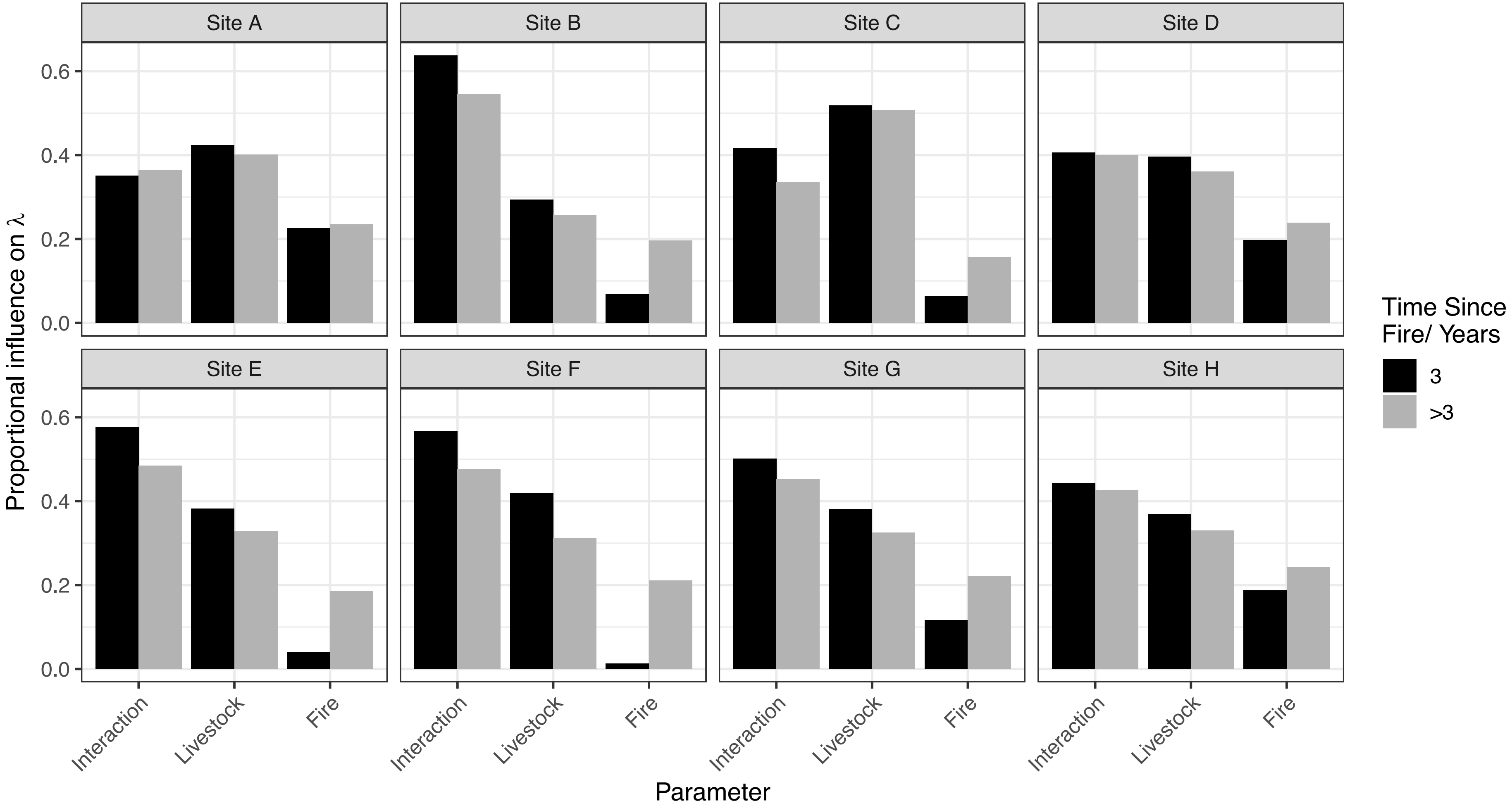


Figure 6. The site-specific relative contribution of environmental effects on *Drosophyllum lusitanicum population* growth. Columns represent the relative absolute effect of changing livestock intensity, time since fire disturbance, and the non-additive effect of changing both (interaction) on population growth rate. Changes are from low to high livestock intensity, and from 2 to 3 or >3 years since fire. The main/individual and interactive environmental effects on population growth rate are from a functional decomposition, and their absolute values are divided by their sum to give their relative contributions to population growth.

1.

5.7 References

Baxter, P. W. J., McCARTHY, M. A., Possingham, H. P., Menkhorst, P. W. & McLEAN, N. Accounting for Management Costs in Sensitivity Analyses of Matrix Population Models. *Conservation Biology* **20**, 893–905 (2006).

2.

Cahill, A. E. *et al.* How does climate change cause extinction? *Proc. R. Soc. B.* **280**, 20121890 (2013).

3.

Caswell, H. Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling* **46**, 221–237 (1989).

4.

Caswell, H. PROSPECTIVE AND RETROSPECTIVE PERTURBATION ANALYSES: THEIR ROLES IN CONSERVATION BIOLOGY. *Ecology* **81**, 619–627 (2000).

5.

Caswell, H. *Matrix population models: construction, analysis and interpretation*. (Sinauer Associates, 2001).

6.

Crone, E. E. *et al.* How do plant ecologists use matrix population models?: Matrix population models for plants. *Ecology Letters* **14**, 1–8 (2011).

7.

Crouse, D. T., Crowder, L. B. & Caswell, H. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* **68**, 1412–1423 (1987).

8.

Dahlgren, J. P. & Ehrlén, J. Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology* **97**, 666–674 (2009).

9.

Ehrlén, J., Groenendael, J. V. & de Kroon, H. Reliability of Elasticity Analysis: Reply to Mills et al. **15**, 4 (2001).

10.

Elderd, B. D. & Doak, D. F. Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and Mimulus guttatus: Flooding and plant population dynamics. *Journal of Ecology* **94**, 656–669 (2006).

11.

Ellner, S. P., Childs, D. Z. & Rees, M. *Data-driven Modelling of Structured Populations: A Practical Guide to the Integral Projection Model*. (Springer International Publishing, 2016).

12.

Ellner, S. P., Snyder, R. E., Adler, P. B. & Hooker, G. An expanded modern coexistence theory for empirical applications. *Ecol Lett* **22**, 3–18 (2019).

13.

Grimm, N. B. *et al.* The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment* **6**, 264–272 (2008).

14.

Hamda, N. T., Jevtić, D. M. & Laskowski, R. Decomposition analysis of LTREs may facilitate the design of short-term ecotoxicological tests. *Ecotoxicology* **21**, 1504–1512 (2012).

15.

Hof, C., Araújo, M. B., Jetz, W. & Rahbek, C. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* **480**, 516–519 (2011).

16.

Horvitz, C., Schemske, D. W. & Caswell, H. The Relative ‘Importance’ of Life-History Stages to Population Growth: Prospective and Retrospective Analyses. in *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems.* vol. 18 247–271 (Springer, 1997).

17.

Hossell, J. E., Ellis, N. E., Harley, M. J. & Hepburn, I. R. Climate change and nature conservation: Implications for policy and practice in Britain and Ireland. *Journal for Nature Conservation* **11**, 67–73 (2003).

18.

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* **5**, 365–374 (2007).

19.

Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. *PLoS Biol* **5**, e157 (2007).

20.

Lande, R. Anthropogenic, ecological and genetic factors in extinction and conservation. *Res Popul Ecol* **40**, 259–269 (1998).

21.

McDonald, J. L. *et al.* Divergent demographic strategies of plants in variable environments. *Nat Ecol Evol* **1**, 0029 (2017).

22.

Merow, C. *et al.* Advancing population ecology with integral projection models: a practical guide. *Methods Ecol Evol* **5**, 99–110 (2014).

23.

Mills, L. S., Doak, D. F. & Wisdom, M. J. Reliability of Conservation Actions Based on Elasticity Analysis of Matrix Models. *Conservation Biology* **13**, 815–829 (1999).

24.

Morris, W. F. & Doak, D. F. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. (Sinauer Associates, 2002).

25.

Morris, W. F., Ehrlén, J., Dahlgren, J. P., Loomis, A. K. & Louthan, A. M. Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proc Natl Acad Sci USA* **117**, 1107–1112 (2020).

26.

Niinemets, Ü. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* **260**, 1623–1639 (2010).

27.

Paniw, M., Quintana-Ascencio, P. F., Ojeda, F. & Salguero-Go, R. Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant. *Journal of Applied Ecology* 11 (2017).

28.

Paniw, M., Quintana-Ascencio, P. F., Ojeda, F. & Salguero-Gómez, R. Data from: Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant. *Dryad* (2018) doi:https://doi.org/10.5061/dryad.40qt2.

29.

Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).

30\.

Salguero-Gómez, R. *et al.* The COMPADRE Plant Matrix Database: an open online repository for plant demography. *J Ecol* **103**, 202–218 (2015).

31\.

Schleuning, M., Huamán, V. & Matthies, D. Flooding and canopy dynamics shape the demography of a clonal Amazon understorey herb: Demography of an Amazon herb. *Journal of Ecology* **96**, 1045–1055 (2008).

32\.

Silvertown, J., Franco, M. & Menges, E. Interpretation of Elasticity Matrices as an Aid to the Management of Plant Populations for Conservation. *Conservation Biology* **10**, 591–597 (1996).

33\.

Smith, M., Caswell, H. & Mettler-Cherry, P. STOCHASTIC FLOOD AND PRECIPITATION REGIMES AND THE POPULATION DYNAMICS OF A THREATENED FLOODPLAIN PLANT. *Ecological Applications* **15**, 1036–1052 (2005).

34\.

Villellas, J., Doak, D. F., García, M. B. & Morris, W. F. Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecol Lett* **18**, 1139–1152 (2015).

35\.

Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).

Thesis discussion

The aim of this thesis was to understand the roles of environmental variation in determining the performance of individuals and population growth. This objective can be broken into component questions. Firstly, how can we quantify the role of complex forms of environmental variation on performance? In Chapters 2 and 3 I show how data-driven statistical approaches and simple experiments can be used to better understand how biotic and abiotic factors affect plant performance. Secondly, by what mechanisms does environmental variation affect λ? In Chapters 4 and 5 I use retrospective decompositions to show how environmental variation and observed/ simulated treatments affect λ, demonstrating how treatment-induced changes to vital rates have non-additive effects on λ. Thirdly, how does variation in the environmental contribute to λ? In chapter 5 I show that environmental effects on multiple vital rates can be understood as an aggregate effect on λ, and compare the roles of different forms of environmental variation.

In Chapter 2 I present evidence of strong negative intraspecific competition for *Drosophyllum* vital rates. This finding is consistent with general patterns of intraspecific competition being stronger than interspecific competition. I speculate that competition for prey is particularly important for small/young *Drosophyllum.* The crowding indices I used were optimised using the whole *Drosophyllum* population, but if intraspecific competition is prey-based and disproportionately affects recruits it may be worth considering the population as a spectrum of competition susceptible individuals. In general, the suspected mechanism of competition should inform both the assumptions of crowding indices and the data chosen when running an optimisation procedure to arrive at the best parameter values for the indices. Notably, I ran an optimisation procedure to generate the scaling parameters (α) for intra/interspecific competition indices. Consequently, the statistical significance of crowding effects that were incorporated into base models must be cautiously interpreted.

Including spatial autocorrelation in vital rate models offers a way to account for habitat quality, but this requires careful consideration. Firstly, not every dependent variable performance metric can have its own specific spatial-autocorrelation metric. For example, I used autocorrelation of flowering probability rather than total flowers as a predictor of total flower production because counts cannot be positively correlated in an auto-Poisson model. Furthermore, the researcher must be aware of correlations associated with a given performance metric if they are assuming neighbour success is a proxy of habitat quality. An example is growth, where large neighbour size may indicate good habitat quality, but more successful neighbours also exert greater competitive effects on the focal individual, muddying the association. Two ways to deal with these correlations are either to use a performance metric where neighbour performance has negligible effects on focal individual performance, or to account for the correlating variable prior to including the autocorrelation variable in the statistical model.

Interspecific effects were fairly unimportant in determining *Drosophyllum* success, but I suggest that additional steps could be used in future analyses. Firstly, distinguishing between species may show great variation in competitive effects. Secondly, the approach to quantify habitat quality can be applied heterospecifics. I only considered habitat quality in terms of suitability for *Drosophyllum*. However, interspecific competition estimates may not be generalisable to the entire fundamental niche of the focal species because interspecific interactions may only be occurring at locations of middling quality. Using spatial autocorrelation for competing neighbouring species as a proxy for habitat quality from ‘their perspective’ may be a way to account for this limitation of an observational dataset.

In Chapter 3 there is evidence of great differences between *Drosera* populations in terms of size-specific survival, reproduction and growth. Additionally, the nitrogen treatment I applied had negative effects on *Drosera* vital rates. *Sphagnum* may have exerted greater competitive effects under treated conditions generally, but the Scottish population (Loch Lomond 1) had minimal sphagnum in plots, suggesting other interspecific interactions may be important.

Fine scale environmental variation is likely important for *Drosera* for several reasons. Firstly, a single neighbouring plant can drastically affect light availability. Secondly, S*phagnum* growth results in complex topography and hydrology across the site. I speculate that *Drosera* are recruited where conditions are highly favourable, often after disturbances. Heterospecifics may colonise plots or increase in size at a much greater rate than *Drosera b*y the second round of census data collection, having negative effects on *Drosera* size in subsequent years. The observed prevalence of retrogression in *Drosera* may result from such changes in competitive landscape, following disturbance events.

I did not detect trade-offs in *Drosera*, and environmental variation could be one of the main reasons. In fact, analysis showed that a previous reproduction event positively correlated with survival. Therefore, it is far more likely that a good local environment determines both survival and reproductive success. One future consideration is utilising proxies of habitat quality like the spatial autocorrelation of vital rates used in the previous chapter. The complexity of quantifying quality at such fine scales in bog habitats combined with high plant densities make the spatial autocorrelation approach an appealing option.

In Chapter 4 I parameterise IPMs with three years of field data to test the effects of nitrogen on λ for *Drosera* at four British sites. I carried out retrospective decomposition analyses to identify which vital rate responses to nitrogen were most important in influencing population growth rate. Decomposing observed variation in λ across sites showed that the effects of a treatment can primarily affect λ through different vital rates, highlighting the need to assess multiple populations to identify general strategies to control population growth.

Simulating treatment effects on *Drosera* vital rates revealed the importance of non-additive effects on λ. It is therefore important to quantify treatment interactions, and I recommend wider use of functional decompositions by demographers. Conservationists may reprioritise population interventions or the vital rates they wish to change in light of the non-additive effects of multiple environmental factors.

In Chapter 5 I conduct retrospective decomposition analysis on *Actaea* and *Drosophyllum* populations. The studies these analyses are based on were observational, but the approach to decomposing observed variation is the same as for a highly controlled experiment. I demonstrate how we can understand multiple environmental effects on multiple vital rates as an aggregate environmental effect on λ. I identify very strong non-additive effects of environmental variation on variation in λ. I did not quantify the uncertainty in the contributions of environmental variation to λ, as this analysis was based on statistical model parameters and not the raw data. However, I would recommend quantifying uncertainty in a treatment's contribution to λ as an extra step in the workflow before implementing any population management strategy.

I do not advocate always using retrospective decomposition analyses as an alternative to more often used elasticity analyses to inform population management. Elasticities offer great utility when we have an incomplete understanding of the existing or future drivers of population decline; elasticities do not depend on understanding how those drivers affect vital rates. The more information we have about future environmental effects on vital rates, and the costs to mitigate them, the more useful functional decompositions will be in informing conservation management practices.