INTEGRATING DYNAMIC PLANT GROWTH MODELS AND MICROCLIMATES FOR SPECIES DISTRIBUTION MODELLING

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0.1 Abstract

Climate is a major factor determining the distribution of plant species. Correlative models are frequently used to model the relationships between species distributions and climatic drivers but, increasingly, their use for prediction in novel scenarios such as climate change is being questioned. Mechanistic models, where processes limiting plant distribution are explicitly included, are regarded as preferable but more challenging.

The availability of tools for simulating microclimates with high spatial and temporal definition has also opened new possibilities for simulating the limiting environmental stresses experienced by plant over their ontogeny. However, the field of mechanistic species distribution modelling is relatively new and the tools and theory for constructing these models are underdeveloped.

In this paper we explore the potential for using a Dynamic Energy Budget model of organism growth integrated with microclimate and photosynthesis models. We model the interactions of plant growth and microclimatic stressors over the life stages of plant growth, and scale them up to demonstrate predictions of distribution at the continental scale. We develop the model using Julia, a new language for scientific computing, as a set of generic modelling packages. These have a modular, toolkit structure that has the potential to increase the efficiency and transparency of developing mechanistic SDMs.

0.2 Introduction

The relationship between the growth and distribution of plants and environmental drivers is a fundamental concern of ecology (Billings 1952). Modern tools and datasets enable modelling of the dynamic interactions between organisms and the environment at the scale of the individual organism. This capability can be used to develop insights and hypotheses about the mechanistic drivers of plant growth and stresses that limit the distribution of plant species. The use of such a physiological approach may assist the prediction of species distributions in future climates, or novel conditions (Bozinovic & Pörtner 2015; Kearney & Porter 2009).

Species distribution models (SDMs) are often developed using correlative techniques, with coarse-grained environmental predictors. However, there is a growing consensus that ecological models need to incorporate more structural realism (Grimm & Berger 2016). For this reason process-based, mechanistic and hybrid models have been proposed as a more realistic alternative to correlative SDMs (Dormann et al. 2012; Kearney, Wintle & Porter 2010; Singer et al. 2016; Connolly et al. 2017). Practically, correlative and mechanistic models exist on a spectrum of increasing causal detail (Dormann et al. 2012),

where mechanistic models include explicit biophysical and physiological processes (Connolly et al. 2017).

However, choosing mechanistic models over correlative models is not simply a question of theoretical value, but also one of economy: mechanistic models are more difficult to construct, and more computationally intensive than correlative models (Dormann et al. 2012; Kearney, Wintle & Porter 2010). Improvements to mechanistic species distribution modelling require simultaneous development of theory and the practical tools for applying it efficiently (Briscoe et al 2019).

Mechanistic species distribution models for plants

Mechanistic SDMs have become more common for animals (Kearney & Porter 2009). Although mechanistic modelling has a longer history in plant biology (Grimm & Berger 2016), mechanistic SDMs remain less well-developed for plants. We follow Connolly et al. (2017) and distinguish mechanistic models from process-based models (PBMs), ignoring those that include only dispersal processes without specifying the components of plant growth (Merow et al. 2011).

A range of mechanistic models have been used to predict species distributions. These include phenological models that integrate environmental stress factors (Morin, Viner & Chuine 2008; Chuine & Beaubien 2001; Chapman et al. 2014) and models of environmental interactions with growth processes based on tree growth rings (Sánchez-Salguero et al. 2016). Other models have incorporated plant growth and C/N allocation in response to environmental drivers, to produce maps of relative growth potential (Higgins et al. 2012; Higgins & Richardson 2014; Moncrieff et al. 2016; Storkey et al. 2014; Nabout et al. 2012). Mechanistic growth models provide the most scope for capturing the interactions between plant ontogeny and the environment, as plant stresses can co-occur in sequential patterns with different effects across plant ontogeny (Niinemets 2010). They can also provide a base model that can integrate phenological components, or be used for truly mechanistic demographic and distribution models.

A key example of a mechanistic growth model used for SDMs is the Thornley Transport Resistance model (TTR) (Thornley 1972a), that tracks carbon and nitrogen budgets for roots and shoots. It has been used in hybrid mechanistic/fitted plant SDMs (Higgins et al. 2012; Higgins & Richardson 2014; Moncrieff et al. 2016). Additionally, Nabout et al. (2012) applied the Plantgro model to maize distribution, which uses growth response curves tuned to monthly conditions. Stratonovitch, Storkey & Semenov (2012) and Storkey et al. (2014) used climatic data with daily time-steps and incorporated ontogeny in a sophisticated plant SDM. However, the Sirius model (Jamieson et al. 1998) used in Storkey et al. (2014) is focused on agricultural plants, and its formulation was not made available.

Plant growth and Microclimate

Realism in growth models can be increased by modelling causal processes more explicitly. It can also be improved by using finer gained environmental variables, because the responses of organisms to changes at the macroclimate scale actually occur at the microclimate scale (Harwood, Mokany & Paini 2014).

Animals usually exercise some choice over the microclimates they are exposed to, but the life of a plant occurs in a fixed location: they must tolerate all environmental conditions that occur there over their lifespan. However, at a finer scale plants grow through vertical

climatic gradients over their ontogeny. They experience different conditions at different life-stages, and these differences can be critical in growth process (Niinemets 2010) and in constraining the boundaries of their distribution (Smith et al. 2009). To establish at a particular location, plants must experience a favourable sequence of microclimatic conditions that match the needs of all life stages – not simply favourable climatic averages.

Growth based plant SDMs have generally used long time-steps (i.e. monthly) and climatic, rather than microclimatic data (Nabout et al. 2012; Higgins et al. 2012; Higgins & Richardson 2014; Moncrieff et al. 2016). A general plant model suitable for SDMs – that can simulate complete plant ontogeny with realistic combinations of environmental stresses – remains to be demonstrated. Dynamic energy budget (DEB) growth models, coupled to mass and energy exchange between organisms and their microclimates, have achieved this for animal SDMs (Kearney 2012; Kearney et al. 2018).

Dynamic Energy Budget theory

Dynamic Energy Budget theory (DEB) generalises growth processes for all organisms and symbioses (Kooijman 2010). It is frequently used to model the transition from juvenile to adult in animals and bacteria (Sarà et al. 2013; Jager, Martin & Zimmer 2013) and can capture complete organismal ontogeny. It has been used to model animal species distributions (Kearney 2012; Kearney et al. 2018), and has been suggested as an alternative growth model for plant SDMs (Higgins et al. 2012).

DEB theory simplifies the metabolism of organisms to material fluxes of substrates in processes of assimilation, growth and dissipation (Lorena et al. 2010). From simple rules and feedbacks it can capture complex growth dynamics while being explicit about matter, energy and entropy balances (Sousa et al. 2010).

DEB models focus on the interactions of different abstract categories of biomass, namely: *structure* (V), that is produced by the growth process and requires ongoing maintenance, and *reserve* (E), that represents the pool into which assimilates flow, and does not require maintenance. An additional type is *product* (P), representing byproducts of the growth process. In animals these are often excreted, but in plants may be included in measured biomass as bark and heartwood. The simplifying assumption of this framework is that each category has fixed proportion of chemical constituents. This enables the closure of both mass and energy balances (Sousa et al. 2010).

For models with multiple reserve substrates, such as separate carbon and nitrogen reserves, "synthesizing units" (SUs) are used to model enzyme dynamics for reserve combination, giving smooth transitions between limiting resources (Ledder et al. 2019; Kooijman 2010, pp.99–105). Synthesizing units bind multiple substrates to synthesize compounds, depending on their availability. Using an SU, carbon and nitrogen pools can be combined into a general reserve to be used in growth and maintenance. Reserve mobilised in each simulation time-step is calculated from the ratio of reserve to structure, adjusting growth rates to match available resources.

A useful outcome of the reserve-structure dynamics of a DEB model that tracks nutrient state is the ability to model growth from embryo to mature organism, by initially allocating high reserve/structure ratios and small structural mass. This can produce smooth transitions from the embryo phase, dependent primarily on stored nutrients, to later phases where nutrients are assimilated from the environment. Previous models of plant ontogeny often start with a seedling (Levy et al. 2000). In DEB models, growth rates vary with temperature but also with the dynamics of the root and shoot reserves, the growth rate

being proportional to the density of the limiting reserve. This captures transient dynamics that drive, for example, rapid growth of seedlings or rapid shoot growth after a sudden loss of biomass from e.g. grazing events or fire.

The intrinsic generality and modularity of DEB theory means that, in principle, any number of structures can interact to exchange substrates, allowing simulations of single-celled heterotrophs, complex autotrophs, and even symbioses. This ability allows us to construct a DEB plant model, where at least root and shoot structures must considered explicitly to model asynchronous nutrient assimilation. It also means that a DEB model has the open-ended potential to model more or less complex dynamics, by adding or removing structures. We could represent stems, leaves and roots separately, or including substrate exchange between fine roots and soil symbionts – requiring few additional formulations or parameters.

DEB models for plants

While the DEB model was proposed as a framework for modelling all organisms, the majority of published DEB models have focused on heterotrophs. The literature for autotrophs remains sparse: Lorena et al. (2010), Kooijman (2010), Muller et al. (2009) Kooijman, Andersen & Kooi (2004); Livanou et al. (2018) and Ledder et al. (2019) are notable contributions. A simple, single-structure microalgae model was presented in Lorena et al. (2010), contrasting with most animal models by tracking separate reserves for carbon and nitrogen to model temporally separated uptake dynamics. The symbiosis of a simple heterotroph and photo-autotroph was also modeled by Muller et al. (2009).

Modelling plants requires multiple structures to capture the additional spatial separation of nutrient and carbon uptake that occurs in roots and shoots (Kooijman 2010, pp.201–206). Such a plant model was demonstrated by Kooijman (2010). However, it has not been widely tested or peer-reviewed and uses a large number of parameters. Recently Ledder et al. (2019) explored the dynamics of a simplified two-structured plant model, proposing "The local control theory of resource allocation". In this formulation, resource sharing between plant structures is similar to resource sharing in a holobiont: roots and shoots only translocate unused metabolites, without centralised coordination or fixed allocations to translocation. This simple formulation achieves optimal growth rates, while maintaining dynamic growth behaviour. It also requires fewer parameters and causal processes than either globally-optimised resource sharing or the fixed-proportion local control used in Kooijman (2010) and in the well known Thornley Transport Resistance plant growth model (TTR) (Thornley 1972a).

There are some differences in the strategies used to track carbon, nitrogen and general reserve state in DEB autotroph models. Kooijman (2010) tracked carbon reserve (C), nitrogen reserve (N) and general reserve (E), while Ledder et al. (2019) did not track reserves at all, instead generating general reserve from assimilated C and N for each time-step. Lorena et al. (2010) track C and N reserves. Despite structural differences, these models invariably track reserve and structure as abstract, but stoichiometrically fixed compounds measured in C moles and N moles.

Modelling Microclimates

Improvements in climatic datasets and downscaling methods have enabled detailed modelling of microclimate at the scale of individual organisms in any location. NicheMapR

(Kearney & Porter 2017) and the microclimate datasets (Kearney 2018) generated by it are tools that make detailed site-specific microclimates accessible over multiple decades, with the hourly resolution for multiple heights and depths at reasonable accuracy. They provide soil water potential (Kearney & Maino 2018), soil temperature (Kearney et al. 2014), incident radiation, air temperature, snow cover, relative humidity and wind-speed, enabling the modelling of finely detailed organism-environment interactions. Microclimate data are provided as hourly sequences of environmental variables in discrete spatial layers.

Connecting growth models and microclimates

DEB models do not represent organism growth spatially, besides simple surface area/mass relationships. But microclimates are fundamentally spatial. Water availability and soil temperature both vary with depth, while air temperature varies with height above ground. This means that a spatially-explicit model is required to integrate a DEB growth model with microclimate data.

The interactions of plant growth and microclimate could be most accurately modelled with three-dimensional models of root and shoot architecture (Vrugt et al. 2001). However, producing mapped species distributions imposes a number of practical constraints. There are limits to computing power when models may run over 8000 times for a year of growth at a single point. This can translate to the order of a billion runs to produce continent-scale maps on decennial timescales. Further, our ability to easily construct complex models and determine their parameters is limited by the availability of easily assembled modelling tools and data. The dimensionality and accuracy of the spatial transformation used must be some compromise between these factors.

Realistic behaviour of a DEB plant model

There are a number of requirements for our plant growth model. Generally, a plant model should to some extent balance the growth of roots and shoots to align with their relative needs for substrate assimilation. To enable the modelling of growth throughout life-stages, it should capture growth trajectories from seed to plant, switching smoothly between stored and assimilated resources.

Optimal partitioning

Optimal partitioning theory (Thornley 1972a; McCarthy & Enquist 2007a) describes how resources are optimally allocated between plant organs depending on relative availability; plants with adequate N supplies preferentially grow more shoots, instead of roots. This dynamic is a central component of many plant models (Cheeseman 1993; Ledder et al. 2019), although it is not without criticism (Lambers 1983; Müller, Schmid & Weiner 2000).

There are multiple methods for modelling optimal root/shoot ratios. Two alternatives are *central* (Perrin 1992) and *local* (Cheeseman 1993; Ledder et al. 2019) control of translocation. Cheeseman (1993) showed that simple local rules can lead to the emergence of balancing at the scale of the whole plant, without the need to invoke signalling or centralised control of allocation. However, they use fitted polynomial functions for growth rates, rather than bottom-up methods that could respond to hourly microclimate conditions. Ledder et al. (2019) recently demonstrated a local control model in a context of dynamic growth using the synthesising units of a two-substrate DEB model, where translocation of excess metabolites achieves optimal balanced growth.

Shoots low in C translocate less or no excess to roots, leading to more shoot growth than root growth, until balance is achieved. The inverse happens for N in roots. With parallel complementary SUs a proportion of each substrate is always translocated, and effectively cycled between structures. These dynamics can be fine-tuned by using k-family synthesizing units, where the overall proportions of used and rejected metabolites can be adjusted (Ledder et al. 2019).

One difference between local control theory and functional-balance theory is that root growth is not affected by low water availability in the version of local control presented in Ledder et al. (2019). Optimisation of water uptake is not always supported by experimental results (Metcalfe et al. 2008; McConnaughay & Coleman 1999a) and root/shoot ratios may be unaffected by water availability (McConnaughay & Coleman 1999b). However, other studies cite both water and nutrients as factors in optimal root/shoot scaling. (McCarthy & Enquist 2007b). In local control theory (Ledder et al. 2019) only substrate availability (generally C and N) affect root/shoot ratios. Water shortages may have indirect effects by limiting assimilation.

Seed/plant transitions

Modelling complete plant ontogeny and changes in relation to microclimatic stresses requires a smooth transition between seed and plant life-stages. However, this transition is not commonly modelled. Seeds are largely composed of reserves such as carbohydrate and lipids, and rapid initial growth can be driven by the high ratio of reserve to structural tissue. DEB theory is well suited to modelling these processes, because the reserve concept links the embryo to the life cycle through the transition from use of initial reserve to assimilation of additional reserve (Kooijman 1986). Periods of slowdown and readjustment of growth rates may occur in the transition between seed reserve and assimilated reserve when resources are limiting (Kitajima 2002). These can be captured by a DEB model.

Aims

In this paper, we aim to explore the potential for modelling plant distributions based on limits to plant growth caused by the specific sequence of stresses a plant experiences during its ontogeny. There are three components of this approach. First, developing practical modelling tools that support both our current aims and future research in the field; second, developing methods to a connect a mechanistic model of plant ontogeny to microclimate models; and third, assessing the behaviour of the model across plant ontogeny and varying environmental conditions and scenarios, up to the scale of continental distribution. Ultimately, these components are intended to collectively enable the parametrisation of species distribution models of plant species and functional groups.

To model plant ontogeny with fine spatial and temporal resolution, we use a DEB model and connect assimilation, growth and maintenance processes to the microclimOz microclimate data set (Kearney 2018) using temperature response curves and a photosynthesis/transpiration model. We develop model components as separate libraries that enable future adaption for use in a wide variety of SDMs, and in ecological models more generally.

0.3 Methods

We modelled a simple, generalised C3 grass or herb-like plant using a two-structure two-reserve DEB model. The DEB model is based on the plant model provided in Kooijman (2016) and Kooijman (2010) with simplifications outlined by Ledder et al. (2019) and Lorena et al. (2010). While the plant model in Kooijman (2016) specifies a photosynthesis component for C assimilation, it does not integrate environmental variables, stomatal conductance or the role of soil moisture in C uptake. Instead we use a Farquhar-von Caemmerer-Berry photosynthesis, stomatal conductance and soil moisture and model adapted from MAESPA (Duursma & Medlyn 2012).

We implemented the model in Julia (Bezanson et al. 2012), a programming language developed for scientific computing, that enables the performance of C or Fortran languages with the modularity and ease of use of Python or R. DEB, photosynthesis, and microclimate integration packages were implemented as the standalone, modular libraries DynamicEnergyBudgets.jl (https://github.com/rafaqz/DynamicEnergyBudgets.jl), Photosynthesis.jl (https://github.com/rafaqz/Photosynthesis.jl) and Microclimate.jl (https://github.com/rafaqz/Microclima These provide generalised interfaces that facilitate adaptation for many modelling purposes (including outside of SDMs and ecology). Julia's type-system and multiple-dispatch paradigm allowed us to include most components and parameters as interchangeable or optional. This improves interactive exploration, allowing easy reduction of model parameter number but also addition of components for alternate formulations. Model components are compiled together by Julia at run-time to produce computational performance in the order of lower-level languages like C or Fortran.

State variables

Tracking nutrient reserves allows modelling of seed reserve and scenarios with fluctuating assimilation rates, as are common with variable environmental conditions. To allow this, we followed the approach of Lorena et al. (2010), tracking structure V with C and N reserves, but calculating general reserve at each time-step. These three state variables for roots and shoots lead to a six-state model, consistent with traditional plant models such as TTR (Thornley 1972b) and SIMPLE (Cheeseman 1993).

The modular DEB formulation allows for inclusion of additional state variables such as P (production) and M (maturity). P can track the production of growth byproducts such as leaf litter, or bark and heartwood in woody plants, while M can track reproductive maturity and seed-set.

We allocate initial seed mass by assigning large C and N with small V (Table 1). If initial reserve masses assigned to shoot and root do not match the ratio of later assimilation rates, balancing oscillations occurred between root and shoot growth until a stable assimilation ratio is reached. These oscillations drove early model "death" in variable conditions. We therefore used an initial reserve structure ratio that matches later shoot/root ratio of 4:1, minimising early growth-rate oscillations. Plants were simulated to grow for six months starting at monthly intervals over the six year period from January 2005 to December 2010. We use microclimates simulated from historical climatic data from 2005-2011 (Kearney 2018), covering the 'millennium' drought (Dijk et al. 2013) and the return of wetter conditions from late 2009.

Table 1: Initial masses of reserve and structure

State	Symbol	Mass (mg)
Shoot Structure	V_S	0.2
Shoot C Reserve	C_S	5.0
Shoot N Reserve	N_S	0.2
Root Structure	V_R	0.04
Root C Reserve	C_R	1.0
Root N Reserve	N_R	0.04

Avoiding Over-parametrization

The usefulness of complex, over-parameterised ecological models is debatable (Reichert & Omlin 1997). The DEB plant model in Kooijman (2016)] has 60-80 parameters depending on the use case and interpretation, reflecting the potential biologically-relevant complexity in a multi-state model. Microclimate integration requires additional parameters, while the MAESPA photosynthesis model itself has many parameters (20-40). This combination could result in a model that is over-parametrized and difficult to reason about, to explore and ultimately to parametrize. However, a DEB plant model can be simplified in two ways: amalgamation of parameters across structures and substrates, and simplification of the formulation.

Amalgamation of parameters is possible if we assume that there are common parameters shared between root and shoot structures, and for rates of substrate turnover. Kooijman (2010) used three $\dot{k}$ parameters per structure for the turnover of each reserve. Lorena et al. (2010) used only a single $\dot{k}$ parameter, as mobilisation rates were deemed to be the same in algae. Practically, this simplifies interactive control over whole plant turnover rates, and reduces failure of simulations due to fluctuations induced by differences between $\dot{k}$ parameters. For similar reasons we also amalgamated parameters for maintenance, yield for conversion of reserve to structure, and N/C ratios of all reserve and structure state.

Performing sensitivity analysis on model components and parameters is an obvious analytical approach to parameter reduction. However, it did not prove to be as easy as typical sensitivity analysis of ecological models. The influence some parameters is highly dependent on microclimatic conditions; sensitivity can be calculated for one particular microclimatic context, but this may not be useful for understanding how the model behaves across a wider range of environments. Running sensitivity analysis across a dataset such as microclimOz is a potential solution, but is computationally intensive and was not attempted here.

Instead we focused on manual sensitivity analysis. To facilitate this we developed a user-interface that dynamically updates simulations as parameter values are changed. The modular formulation also allowed us to swap or remove whole components from the interface to compare their behaviour in different environments.

Table 2: Model Components

Component	Formulation(s)	Shared/Spec	Parameters
Core (inc. growth + maint)		Shared	7
SU	Parallel Complimentary	Shared	0
Product	None	Specific	Unused

Table 2: Model Components

Component	Formulation(s)	Shared/Spec	Parameters
Maturity	None	Specific	Unused
Resorption	Lossless	Shared	1
Rejected translocation	Lossless	Specific	0, 0
Fixed translocation	None	Specific	Unused
Assimilation	FvCB, Constant N	Specific	
Scaling	Plant Morph	Specific	2, 2
Allometry	Allometry	Specific	2, 2

Formulation changes achieved using this method included simplification of growth rate calculations to use only two reserve substrates, and removing proportional translocation, following Ledder et al. (2019). Additionally, for plants without bark or heartwood, product is not a component of measured biomass. Product is also inherently modular in DEB, as it is a proportion of otherwise lost reserves. It could thus be ignored. In our case the reproductive phase of the life cycle is of less interest, and maturity and reproduction was also be ignored. However, to allow the optional use of maturity and the fixed translocation of the original model, we redefined the fraction of available flux directed to growth κ_{soma}, as a function of the components of a structure s:

$$\kappa_{soma}(s) = 1 - \kappa_{maturity}(s) - \kappa_{translocation}(s) \tag{1}$$

In our simplified formulation, κ_{soma} is equal to 1.

For simplicity, we also ignore the complexities of nitrogen assimilation and scale N uptake on the basis of root mass, the minimum requirement to simulate root/shoot balancing dynamics.

Kooijman (2010) used parameters for germination size and switches that initiate C and N assimilation at some point after growth has begun. This produces switching artefacts in early growth dynamics, and requires a parameter for each structure. In our formulation, photosynthesis and nitrogen uptake began from the start of the simulation, when the plant is still a seed. The structural mass of a seed is small in proportion to the reserve mass, and assimilation in early growth is not significant in comparison to reserve mobilisation (Fig. 2).

In combination, these changes reduced DEB model parameters from approximately 70 to 13 (not including environment or photosynthesis components), and reduced complexity without significant loss of dynamic capability. This simplified exploration of the model's behaviour, while allowing flexibility to increase complexity where necessary. The final model configuration is demonstrated in fig. 1.

Microclimate integration

Integrating a DEB plant growth model with microclimate data requires connecting spatially implicit masses of the DEB structures to the spatial distribution of environmental conditions in the microclimate.

In this section we describe how we used allometric equations to connect plant structures to microclimates, and how temperature response and assimilation formulations were used to connect variables to growth processes. We also describe a resorption formulation to balance available reserve and maintenance requirements in fluctuating microclimatic conditions.

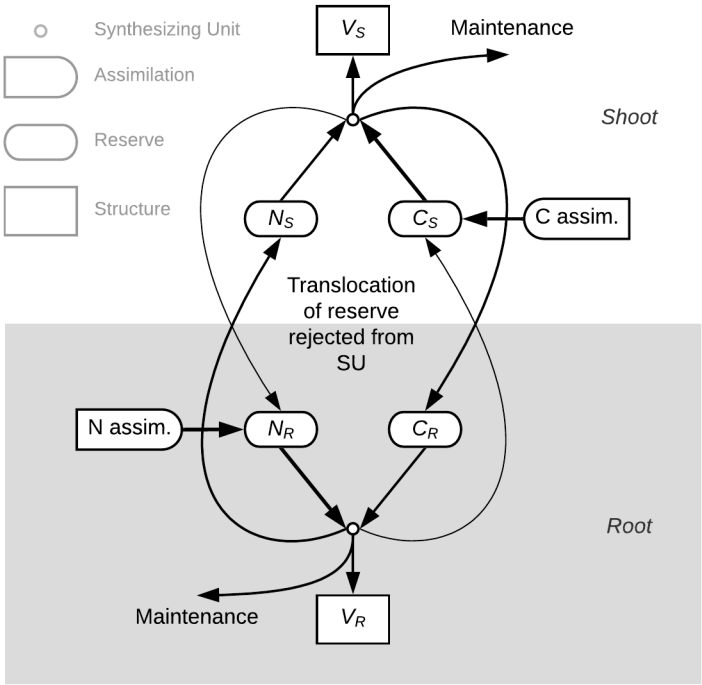

Figure 1: Diagram of the simplified DEB plant model. C and N are assimilated into C_S and N_R reserves using abstracted assimilation components. Mobilised reserves are incorporated into root and shoot structure, VR and VS, via synthesising units (circles). Substrate rejected from this process is translocated bidirectionally between roots and shoots. In practice far more N is translocated from root to shoot, and C from shoot to root, but cycling does occur.

Allometry

For any given geographic location, microclimOz data varies in only one (vertical) dimension at the microclimate scale, if variation in shade cover is ignored. We modelled only this vertical dimension, calculating the depth of roots and the height shoots for a given structural mass. To estimate these, a simple allometric equation was used:

$$\beta_1 \left(mass - \beta_0\right)^{\alpha} \tag{2}$$

Where β_0 is the intercept (mass at the soil surface), β_1 is a scalar and α the exponent. β_0 was set to the initial seed mass, for a seed close to the soil surface. Microclimate values used in the simulation are interpolated between available height/depth layers.

Photosynthesis

In DEB models each reserve requires an assimilation process (Kooijman 2010, p. 206). We defined assimilation processes as modular components external to the DEB framework, and used an external photosynthesis model to calculate C assimilation and modify shoot temperature.

The Farquhar-von Caemmerer-Berry (Farquhar, Caemmerer & Berry 1980; Caemmerer & Farquhar 1981) photosynthesis models are widely used in plant science, and an obvious

addition to a mechanistic plant model (Higgins et al. 2012). Developers of open-source models such as MAESPA (Duursma & Medlyn 2012) have put significant work into connecting Farquhar photosynthesis and Ball-Berry derived stomatal conductance to environmental drivers such as temperature and soil moisture. However, MAESPA was not written as a multi-purpose photosynthesis library. We adapted components of MAESPA into a modular, general purpose library of photosynthesis, stomatal conductance and plant heat balance formulations: Photosynthesis.jl. These formulations are extensive and will not be covered in this paper, but are available in the source of Photynthesis.jl, and covered in (Duursma & Medlyn 2012), noting that canopy and spatial components are not included in Photosynthesis.jl. We used the simple Ball-Berry stomatal conductance model, modified by an exponential response to soil water potential. Our choice of model components and parameters is essentially arbitrary and purely for demonstration. We also used a non-stomatal physiological response to soil water potential defined in (Zhou et al. 2013). Soil water potential was taken to be the maximum that the root system can access across its vertical extent. This formulation resulted in a 'Carbon Starvation' model of drought stress (O'Grady et al. 2013).

Temperature

Physiological processes in plants are reduced by temperatures above or below some optimum (Parent & Tardieu 2012). The plant model in Kooijman (2016) described 1, 3 and 5 parameter temperature response models. However, the lower parameter models do not capture decreasing growth rates above an optimum temperature. A simpler two-parameter model can adequately represent this temperature response for plants, and plant growth and maintenance processes are corrected by the formulation from Parent & Tardieu (2012). We used the provided parameter values for wheat.

Root temperature was taken as equal to the soil temperature at the midpoint of root depth. Above-ground microclimate variables were interpolated at the midpoint of shoot height. To calculate shoot temperature we include the effects of air temperature, relative humidity, wind-speed and soil water potential by iteratively solving the photosynthesis/stomatal conductance model, as in MAESPA.

For the present purpose, we ignored plant behaviours like changes in leaf angle (Karban 2008) or leaf thermoregulation (Michaletz et al. 2015).

Nutrient resorption

Plants regularly drop leaves and slough roots, with some resorption of nutrients (Wright & Westoby 2003). This may occur more rapidly in stressful conditions (Munné-Bosch & Alegre 2004). With highly variable microclimate data, simulations of a DEB plant model frequently ended in plant death when growth rates fell below zero, due to lack of reserves for structural maintenance. The capability to shed excess structure appears to be both mechanistically realistic and a practical requirement of modelling dynamic plant growth in variable microclimates.

The shedding of structure due to stress can be simulated by removing a proportion of structural and reserve mass as a function of growth rate. As growth rate is determined by resource availability after maintenance and temperature suitability, it is a reasonable indicator of stress. Our formulation uses the simplified assumption that if a leaf or branch is dropped, the reserve fraction is able to be reabsorbed, simply remaining in the reserve

state C and N, but structural components are not recoverable, and are subtracted from structural state V. We used a half-saturation point for metabolic rate that modulates the rate of resorption. Loss of mass is defined as:

$$jV = -V * \left(1 - \frac{1}{1 + \frac{h}{r}}\right) \tag{3}$$

where V is structure, j, change in structure, r is the growth rate, and h is the rate where half of the current structural mass will be lost per day. At $h = 0$ no loss of structure will occur, while at $h = \infty$ all structure will be lost for any rate r. The negative feedback induced by the dependency of the growth rate on the ratio of structure to reserve will mean r tends to remain significantly larger than h.

Plants often have imperfect and different rates of resorption of N and C (Vergutz et al. 2012). This formulation is available in DynamicEnergyBudgets.jl, but has two additional parameters, and was not used here.

Microclimatic Scenarios

For plotting simulations of plant ontogeny, we used three microclimate scenarios along a latitudinal transect from the east coast of Australia, moving west (Table 3).

Table 3: Transect

Location	Long	Lat
T1	148.92	-31.80
T2	145.92	-31.80
T3	142.92	-31.80

We utilised the 8-layer datasets from MicroclimOz for soil temperature and soil water potential and two-layer datasets for air temperature, relative humidity and wind speed. Single-layer data was used for incident solar radiation. The datasets for zero percent shade were used for all simulations.

Simulation

A numerical integration was used, with a fixed hourly time-step to include all available microclimate data. It was performed for a six month period to model the ontogeny of an annual plant. Plant death occurred when either root or shoot growth rate dropped below zero.

We ran this six month simulation in each transect location over the six year period from 2005 to 2010, starting at the beginning of each month. The model was then run for the entire grid of Australian microclimate data, starting at monthly intervals over the same six year period. The maximum shoot mass registered during each simulation was stored, and the mean taken from all simulations starting in each particular year.

Initially we plotted selected simulations at the first transect location, starting in August 2005, to demonstrate the dynamics of the model.

0.4 Results

The model smoothly simulated the early stages or plant ontogeny against a background of microclimatic variation (fig. 2), transitioning from dependence on stored seed reserves to assimilated reserves. A period of stalled growth and rebalancing was visible in late September when seed reserves became depleted, and low soil water potential limited assimilation and growth until late October. As N uptake is not mediated by soil water potential in the model, but C assimilation is, N assimilation was higher than C assimilation in dry times. This caused root growth to halt during water stress due to high availability of N.

Plant growth rates were corrected for the effects of temperature above or below the optimum (fig. 2). For roots this quickly stabilised as they grew to deeper soil levels with more stable temperature regimes. In contrast, leaf temperature, and consequently growth rate, fluctuated strongly throughout plant ontogeny.

Temporal variation along a transect

With increasing aridity moving inland along the transect between T1 and T3, the overall proportion of plants surviving decreased (fig. 3). The end of the millennium drought can be seen with improved recruitment rates in 2009 and 2010. At T2, A long sequence of high vapour pressure deficit and soil water potential combined with moderate soil temperature in 2010. This allowed simulations to accrue higher biomass than any simulations in T1. Simulations at T3 had a similar spike in 2010, but overall growth was more constrained by environmental stresses than at either T1 or T2.

Projected Australian distribution

The patterns seen in the transect are reflected across eastern Australia when simulated for the entire MicroclimOz dataset (fig. 4). Significantly broader distributions are visible in 2009 and 2010 with a marked inland shift in maximum growth rates, as would be expected with the end of the millennium drought. Fig. 4 also demonstrates that it is computationally tractable to produce distribution maps from this model, using a consumer desktop computer.

0.5 Discussion

In this paper we have demonstrated a proof of concept for a mechanistic, ontogenetically-explicit plant species distribution model. A simple DEB model of plant ontogeny, coupled to microclimatic drivers, can produce realistic plant growth dynamics from seed to maturity that respond to multiple environmental stresses and generate plausible spatial distributions.

Fundamental to the development of this model was component-based design methodology for mechanistic modelling. We have defined modular components that allowed us to iteratively simplify the model, and this should facilitate further development of mechanistic SDMs and other applications in the life-sciences.

However, it remains to be demonstrated that this class of models can fitted to specific species or functional groups with more predictive success than correlative models, or simpler process-based models. Model-fitting methods, mechanistic growth scaling and microclimate/plant interactions are avenues of further research.

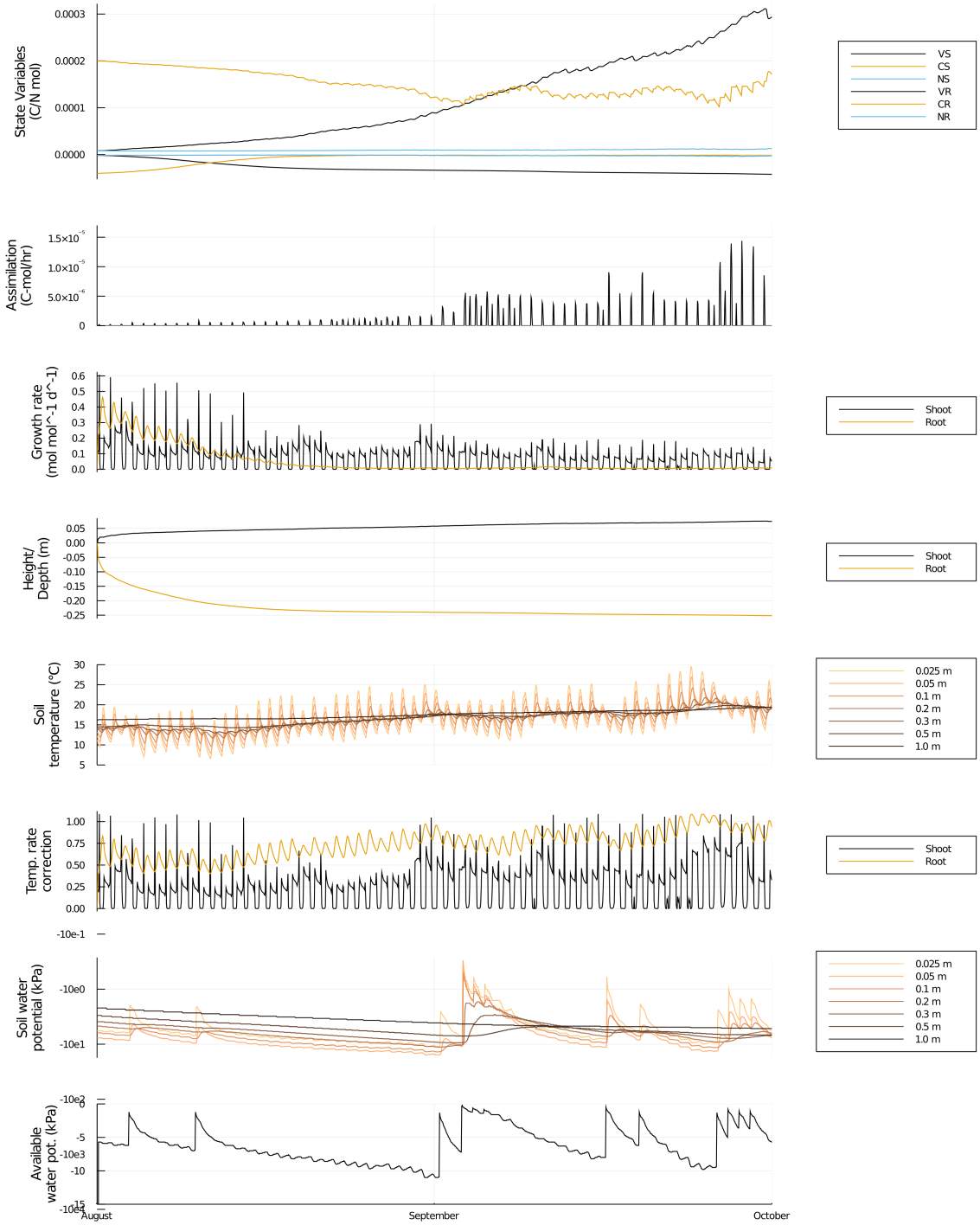

Figure 2: Early development in spring 2005 of at T1 in coastal NSW starting, showing detailed microclimate conditions and responses. Root state is shown as negative values. The calculated temperature correction factor and available soil water potential are shown in response to fixed environmental variables of soil temperature and water potential. This period demonstrates the transition between growth driven by seed reserve and by assimilated C and N.

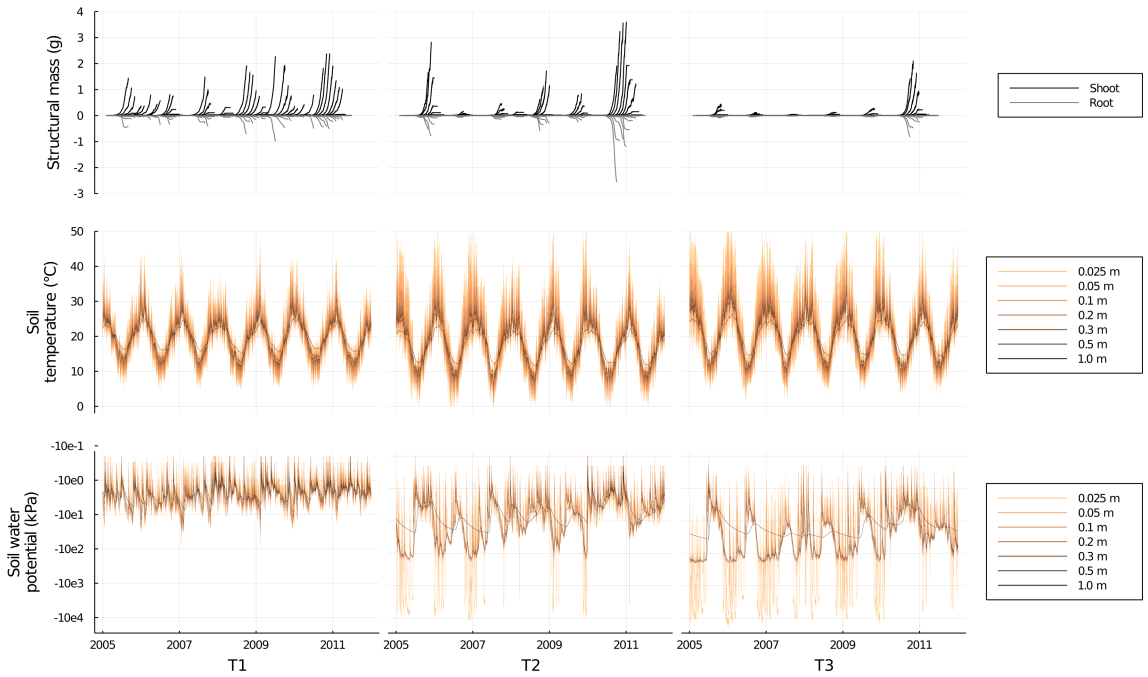

Figure 3: Six month simulations starting each month from 2001/2002 to 2010/2011, for all three locations. Growth plots show (dry) structural mass, here converted to grams. Root structural mass is shown as negative values. Soil water potential is shown on a log scale. A period of strong growth can be seen during 2010 in inland locations, coinciding with high soil water potential and moderate temperatures.

Extensible modelling tools

Mechanistic species distribution models are more difficult to build and more processor intensive than correlative models (Cabral, Valente & Hartig 2017; Connolly et al. 2017). The modelling packages that form the basis of this model outline a set of strategies for improving this situation. We have demonstrated two distinct methods for extending the presented model: extensible structure of the core DEB model, and interchangeable physiological and climatic components.

Modularity of structures and substrates in DEB

The number of structures and substrates of a DEB model can be flexibly extended to suit the requirements of a problem, allowing open-ended exploration using the same theoretical framework and modelling tools. This has been demonstrated for use in both single- or two-structured models, with one or two substrates. However, models used in plant SDMs (Stratonovitch, Storkey & Semenov 2012; Storkey et al. 2014) and other purposes (Falster et al. 2016) use additional structures to model plant growth. This is likely to be a common requirement. Despite the capacity for multiple structures in DEB theory (Kooijman 2010, pp.180–188), a generalised computational framework for chaining more than two structures has been lacking. Chained structures require methods for partitioning translocation between both adjacent structures, such as the case of stems translocating resources between leaves and roots.

Additional reserve substrates such as phosphorus may also be added and tracked to

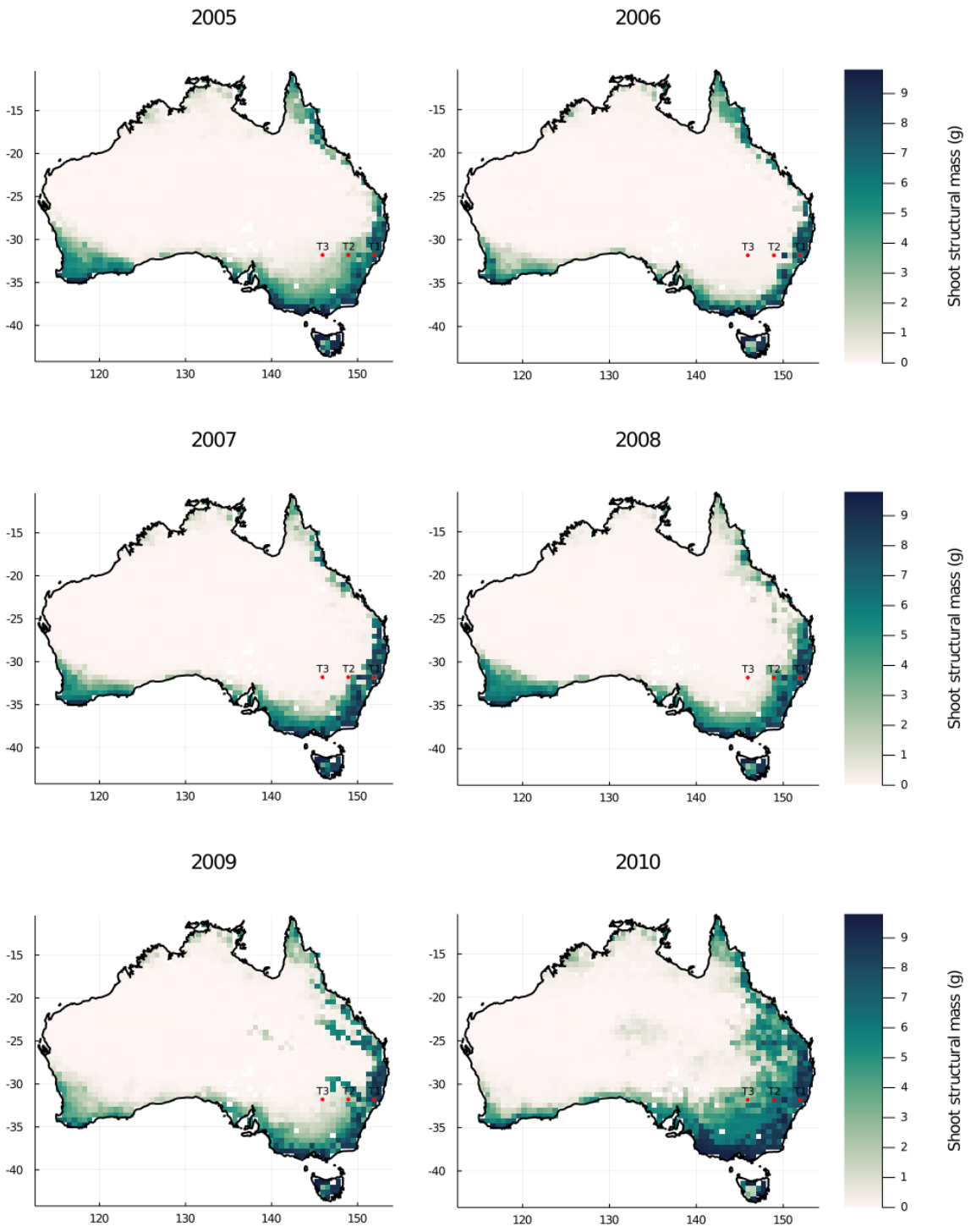

Figure 4: Distribution map of maximum plant growth. Maximum shoot mass from 12 six-month simulations, starting at the first day of each month, in each year. Simulations are run for the entire MicroclimOz dataset. The locations of T1, T2 and T3 are shown for reference.

model limitation of plant distribution by multiple nutrients. Again, methods for merging more than two reserves are less well-defined than the two-substrate synthesizing units used in this model.

Process modularity

The model presented in this paper is constructed from generic, open source Julia packages written for this task, but not limited to it. This demonstrates that a high-performance mechanistic model can be composed from generic library components, an approach that has a number of benefits. Common formulations and data sources can become well-tested and canonical, and easily re-purposed for SDMs and other uses. The modular structure also means that varying levels of process complexity can be used to match the processes critical to a particular research question. It can also resolve a criticism of fitted mechanistic models: the assumption that formulations are inherently correct (Dormann et al. 2012). These packages facilitate interactive and automated comparison of multiple formulation combinations, instead of just a single model.

The design and interfaces of these modelling tools need to be tested in practical applications and a broader range of contexts. The model as it stands may be useful for general models of the dynamics of vegetation where ontogenetically-explicit environmental responses are frequently limiting. But, an obvious next step is to fit a plant model to specific species or functional types.

Fitting models to species and functional types

Fitting SDMs for plant species of functional types is not without challenges. There is a shortage of suitable data, especially for rare species, and lack of methods for connecting available data and model parameters.

To deal with data shortages, it has been suggested that species distribution models should integrate both physiological and observation data into parameter fitting routines (Dormann et al. 2012). Fitting to observations has been demonstrated for mechanistic plant SDMs (Higgins et al. 2012), but methods for combining the uncertainties of observational data and physiological measurements need further work. Bayesian methods may be appropriate for this task (Dormann et al. 2012; Higgins et al. 2012).

Another avenue of research involves fitting models to databases of traits and trait-correlations, to specify plant functional types. Model parameters such as rates of reserve turnover, maintenance and resorption, are likely to be correlated with traits (Reich 2014), such as specific leaf area (SLA)). Leaf, stem and seed traits have been demonstrated to be effective species-level predictors of distributions in correlative models (Pollock et al. 2012). Mapping DEB model parameters to well-known trait correlations may simplify parameterisation of species-specific models (Wright et al. 2004; Falster et al. 2011).

Optional partitioning and scaling dynamics

In this paper, we have modelled the limitations to growth imposed by microclimatic stresses. But plant growth is also self-limited by changes in the ratio of mass to surface area, and other structural dynamics that cause shifting rates of assimilation, metabolism and translocation over plant ontogeny (Niklas & Hammond 2019). The model presented here used a simple curved response to capture the combined effects of competitively imposed and internal scaling dynamics (Kooijman 2010). This is far from a mechanistic approach, and has many

problems, and produces artefacts in root/shoot balance when used over longer lifespans and varying conditions.

Mechanistic scaling components such as those outlined in Niklas & Hammond (2019) may improve model behaviour by connecting size related growth dynamics to specific bottom-up processes, rather than top-down formulations imposed by the model. These additions could also include the effects of competition for resources, such as light, water and nutrients, which are not addressed in the model presented here.

Soil water and microclimatic feedbacks

The optimal partitioning dynamics in the model incorporated water availability in shoot assimilation via the stomatal conductance model. But there was no water-dependence for root growth. This may be a critical addition to accurately model optimal root/shoot partitioning for some plants McCarthy & Enquist (2007a).

The carbon starvation model of drought stress (O'Grady et al. 2013) was a convenient approach as DEB already tracks C reserves. However, mechanical responses such as hydraulic failure also contribute to plant mortality. In extreme conditions they may kill a plant without the presence of carbon starvation (Martinez-Vilalta et al. 2019). The interaction of both modes of drought-driven failure may be required for modelling plant distributions constrained by drought stress.

In our model, water uptake in photosynthesis and translocation did not strictly observe the conservation of matter: soil water potential in the microclimate is not affected by plant water use. There are multiple feedbacks between vegetation and environment (Billings 1952; D'Odorico et al. 2013), but modelling them is difficult. Microclimate calculations can be processor intensive, and introducing plant-environment feedbacks may greatly increase model run-time. The MAESPA model (Duursma & Medlyn 2012) has feedbacks between evapotranspiration and soil water potential, and ultimately radiation, temperature, relative humidity and wind speed should also be influenced by vegetation. Extending microclimate packages like NicheMapR to enable this flexibility while maintaining adequate performance is a challenge for future research.

0.6 Conclusions

In this paper we have shown that integrating mechanistic plant growth models with fine-grained microclimate data is a practical option for predicting environmentally forced plant growth dynamics, and ultimately distributions.

We have demonstrated methods for connecting dynamic energy budget growth models to microclimate datasets across plant ontogeny. This formulation can produce complex, realistic growth dynamics in response to multiple environmental stresses, and can be scaled up to produce mapped distributions using globally available microclimatic inputs (Kearney et al. 2020).

A set of practical modelling libraries has been developed that facilitate the open-ended development of mechanistic species distribution models. Modelling libraries such as these have the potential to make the process of model development more comparable to the effort of producing statistical SDMs.

0.7 Acknowledgements

We would like to thank James Maino, Jian Yen, Bas Kooijman, and Daniel Falster for feedback during the development of this manuscript, as well as the reviewers for the detailed feedback provided.

0.8 Appendix

The source code for generating the figures in this paper is available at https://github.com/rafaqz/DEBplant. The repository also contains a script to generate the user interface used to explore the model.

The final combination of model parameters are listed in Table. 4, Table. 5, Table. 6. Note that photosynthetic parameters and model combinations are not particularly meaningful, and serve only as a demonstration of potential to use Farquhar-derived models for this purpose.

Table 4: DEB parameters, components from DynamicEnergyBudgets.jl

Parameter	Value	Description	Software Component
N_{uptake}	$0.15\mu\mathrm{mol\,mol^{-1}\,s^{-1}}$	Constant rate of N uptake	ConstantNAssim
$y'V_E$	1.0	Yield of structural mass from reserve mass	DEBCore
$y'E_C$	0.9	Yield of general reserve from C-reserve	
$y'E_N$	30.0	Yield of general reserve from N-reserve	
$n'N_V$	0.03	Nitrogen per Carbon in structure	
$n'N_E$	0.025	Nitrogen per Carbon in reserve	
w_V	$25.0\mathrm{g\,mol^{-1}}$	Mol-weight of shoot structure	
$\dot{k}$	$0.6\mathrm{d^{-1}}$	Reserve turnover rate	CatabolismCNshared
$j'E_{mai}$	$0.01\mathrm{d^{-1}}$	Specific somatic maintenance costs	Maintenance
$MV_{ref}S$	0.02mol	Scaling reference for shoots	Plantmorph
$MV_{scaling}S$	0.3mol	Scaling mass for shoots	
$MV_{ref}R$	0.02mol	Scaling reference for roots	Plantmorph
$MV_{scaling}R$	0.3mol	Scaling mass for roots	

Table 5: Non-DEB parameters from DynamicEnergyBudgets.jl

Parameter	Value	Description	Software Component
$K_{resorption}$	1.0e-6	Half saturation metabolic rate for resorption of tissues.	StructuralLossResorption

Parameter	Value	Description	Software Component
ΔH_A	63.5kJ mol^{-1}	The enthalpy of activation of the reaction. Determines the curvature at low temperature	ParentTardieu
α	3.5	The ratio H_D $/H_A$	
T_0	300.0K	Reference temperature	
$\beta 1_S$	0.2m	Scalar for conversion to metres	Allometry
α_S	0.2	Exponent relating shoot mass to height	
$\beta 1_R$	1.0m	Scalar for conversion to metres	Allometry
α_R	0.2	Exponent relating root mass to depth	
SLA	24.0m^2 kg^{-1}	Specific leaf area	BallBerryPotentialCAssim

Table 6: C assimilation parameters in Photosynthesis.jl. Adapted from Duursma & Medlyn (2012) and Zhou et al. (2013).

Parameter	Value	Description	Software Component
rdfipt	1.0	Not documented in MAESPA	WangRadiationConductance
tuipt	1.0	Not documented in MAESPA	
tdipt	1.0	Not documented in MAESPA	
leafwidth	0.05 m	Mean width of leaves	BoundaryConductance
gsc	1.0mol m^{-2} s^{-1}	Stomatal conductance of the boundary layer to CO	
jmax25	184.0 mol m^{-2} s^{-1}	Maximum rate of electron transport at 25° C	Jmax
delsj	640.02J K^{-1} mol^{-1}	DELTAS in Medlyn et al. (2002)	
eavj	37259.0J mol^{-1}	Ha in Medlyn et al. (2002)	
edvj	200000.0J mol^{-1}	Hd in Medlyn et al. (2002)	
vcmax25	110.0μmol m^{-2} s^{-1}	Maximumrate rate of rubisco activity at 25° C	NoOptimumVcmax
eavc	47590.0J mol^{-1}	Ha Medlyn et al. (2002)	
s	2.836MPa^{-1}	Sensitivity parameter indicating the steepness of the decline	ZhouPotentialDependence
Ψ	-0.958MPa	The water potential at which $f(\Psi pd)$ decreases to half of its maximum value	
theta	0.4	Shape of light response curve	RubiscoRegen

Parameter	Value	Description	Software Component
ajq	0.324	Quantum yield of electron transport	
q10f	$0.67\mathrm{K}^{-1}$	Logarithm of the Q10	Respiration
dayresp	0.8	Respiration in the light as fraction of that in the dark	
rd0	$0.01\mu\mathrm{mol\,m^{-2}\,s^{-1}}$	Dark respiration at the reference temperature	
tbelow	173.15K	Temperature below which no respiration occurs	
tref	298.15K	Reference temperature at which rd0 was measured	
g0	$0.5\ \mu\mathrm{mol\,m^{-2}\,s^{-1}}$	Stomatal leakiness (gs when photosynthesis is zero)	BallBerryStomatalConductance
gamma	$0.0\ \mu\mathrm{mol\,mol^{-1}}$	Shape parameter of the light response of electron transport	BallBerryGSsubModel
g1	7.0	Slope parameter	
swpexp	$0.5\mathrm{kPa}^{-1}$	Exponent for soil water potential response of stomata	PotentialSoilMethod

0.9 Model Component Formulations

All formulation code can be found in DynamicEnergyBudgets.jl. The formulations here mirror the structure and syntax of the code as much as possible. Flux is tracked for each root and shoot organ as a matrix with axes state V, C, and N and transformations *assimilation*, *growth*, *maintenance*, *rejection*, and *resorption*, abbreviated in equations as *assim*, *grow*, *maint*, *rej* and *res*. Refer to the tables above for parameter descriptions.

Temperature correction

Formulation for from Parent & Tardieu 2012:

$$c = \frac{s_0 T e^{\frac{-\Delta H_A}{RT}}}{1 + \left[e^{\frac{-\Delta H_A}{RT}}\right]^{\alpha\left(1-\frac{T}{T_0}\right)}} \tag{4}$$

Where T is the current temperature, T_0 is the reference temperature equation, ΔH_A is the enthalpy of activation, α is the ratio H_D/H_A and R is the gas constant. s_0 is a normalising constant so that c at T_0 equals 1.

Synthesizing units

The parallel complementary *SU* is used in this model. See Ledder et al. (2019) for other possible SUs. k-family and minimum rule SUs are included in DynamicEnergyBudgets.jl.

$$SU_{pc}\,(v, w) = \frac{vw(v + w)}{v^2 + w^2 + vw)} \tag{5}$$

Growth Rate

We calculate the specific growth rate of structure $\dot{r}$ following Kooijman (2010):

$$\dot{r} = y'V, E(\kappa_{soma} \cdot j'E - j'E_{mai}) \tag{6}$$

Where:

$$j'E = SU\Big(\frac{y'E_C \cdot C(\dot{k}cS - \dot{r})}{V}, \frac{y'E_N \cdot N(\dot{k}cS - \dot{r})}{V}\Big) \tag{7}$$

Where $\dot{k}$ is the turnover rate, c is the temperature correction, S is the shape scaling factor and *SU* is a synthesizing unit function, in our case the Parallel Complimentary *SU*. This formulation is not analytically solvable, so a numerical root-finder is used.

Catabolism

Total catabolised general reserve, catabolised general reserve $J'_{E,cat}$ and rejected C and N reserves are calculated with:

$$
\begin{aligned}
catabolism(C, N) = & \\
J'_{C,cat} &= (\dot{k}Sc - \dot{r})C \\
J'_{N,cat} &= (\dot{k}Sc - \dot{r})N \\
J'_{E,cat} &= SU(J'_{C,cat}, J'_{N,cat}) \\
J_{C,rej} &= J'_{C,cat} - J'_{E,cat}/y'E_C \\
J_{N,rej} &= J'_{N,cat} - J'_{E,cat}/y'E_N
\end{aligned} \tag{8}
$$

where $J'_{C,cat}$ and $J'_{N,cat}$ are the flux of catabolised C and N reserves, and $J'_{E,cat}$ is the combined catabolised general reserve flux.

Growth

Determine growth fluxes $J_{X,grow}$:

$$
\begin{aligned}
growth(V, \dot{r}) = & \\
J_{V,grow} &= \dot{r} * V \\
J_{C,grow} &= \frac{-J_{V,grow}/y'V_E}{y'E_C} \\
J_{N,grow} &= \frac{-J_{V,grow}/y'V_E}{y'E_N}
\end{aligned} \tag{9}
$$

where $\dot{r}$ is the specific growth rate, V is structure, MV_{ref} is a reference mass and $MV_{scaling}$ the scaling mass.

Maintenance

Determine maintenance flux J given state V

$$
\begin{aligned}
maintenance(V) = & \\
J_{C,maint} &= \frac{j'E_{maint}Vc}{y'E_C} \\
J_{N,maint} &= \frac{j'E_{maint}Vc}{y'E_N}
\end{aligned} \tag{10}
$$

where c is the temperature correction factor.

Lossless Passive Translocation

Simply translocates the reserve rejected during catabolism between structures:

$$
\begin{aligned}
translocation_L(Jd, Js) = \\
Jd_{C,trans} &= -Js_{C,rej} \\
Jd_{N,trans} &= -Js_{N,rej}
\end{aligned} \tag{11}
$$

where Js and Jd represent shoot and root flux, then root and shoot flux for translocation in the reverse direction.

Dissipative Passive Translocation

This formulation adds parameters for yield of translocation of rejected C and N to reserves, to model overheads of translocation such as the carbon cost of phloem loading. It was not used in the final model, but is illustrative of the modularity of the formulation and ease of comparing parameter/behaviour trade-offs.

$$
\begin{aligned}
translocation_D(Jd, Js) = \\
Jd_{C,trans} &= -Js_{C,rej} * y'C_{C,trans} \\
Jd_{N,trans} &= -Js_{N,rej} * y'N_{N,trans}
\end{aligned} \tag{12}
$$

Carbon Assimilation

$$
J_{C,asi} = V_S w_V SA(e) \cdot SLA \tag{13}
$$

Where V_S is shoot structure in moles, w_V is the mass of structure in grams per mole, S is the scaling coefficient, e is the current microclimatic environment, and A is a function that returns the rate of C assimilation. SLA is the specific leaf area of the plant.

In this paper a Farquhar von-Caemerer Berry model is used for A. It must be noted that most photosynthesis models calculate the rate of uptake per area, usually extrapolated from total leaf mass. In the DEB formulation, reserve can vary independently to structure, so we use structural mass, not total mass in our calculations. This is because increasing reserve should not directly lead to increased assimilation.

Nitrogen Assimilation

Simple (temperature- and shape-scaled) constant nitrogen assimilation:

$$
J_{N,asi} = N_U V_R S \tag{14}
$$

where N_U is the rate of uptake of N-mols of nitrogen, V_R is root structure S is the shape scaling coeffient.

Organ Metabolism

$$
metabolism(V, C, N) = (catabolism \circ maintenance \circ growth \circ resorption)(V, C, N) \tag{15}
$$

Metabolism is calculated for state variables (V_S, C_S, N_S), then (V_R, C_R, N_R), for shoot and root organs, and assinged to the flux matrices J_S and J_R respectively.

Plant Model

We apply metabolism, translocation and assimilation functions to both root and shoot organs. This formulation allows for the addition of further organs if required.

$$
\begin{aligned}
J_{S1} &= metabolism(V_S, C_S, N_S) \\
J_{R1} &= metabolism(V_R, C_R, N_R) \\
J_{S2} &= translocation(J_{R1}, J_{S1}) \\
J_{R2} &= translocation(J_{S1}, J_{R1}) \\
J_{S3} &= assimilation_C(V_S, V_R) \\
J_{R3} &= assimilation_N(V_R, V_S)
\end{aligned} \tag{16}
$$

Where J_{SN} and J_{RN} are our flux matrices. Finally, state variables (V_S, C_S, N_S) are assigned the sums of all transformations in J_{S3}, and (V_R, C_R, N_R) the sums of all transformations in J_{R3}.

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