Using evolutionary functional–structural plant modelling to understand the effect of climate change on plant communities

Jorad de Vries*

ETH Zürich, Institute for Integrative Biology, Zürich 8092, Switzerland
*Corresponding author’s e-mail address: jorad.devries@usys.ethz.ch

ABSTRACT

The ’holy grail’ of trait-based ecology is to predict the fitness of a species in a particular environment based on its functional traits, which has become all the more relevant in the light of global change. However, current ecological models are ill-equipped for this job: they rely on statistical methods and current observations rather than the mechanisms that determine how functional traits interact with the environment to determine plant fitness, meaning that they are unable to predict ecological responses to novel conditions. Here, I advocate the use of a 3D mechanistic modelling approach called functional–structural plant (FSP) modelling in combination with evolutionary modelling to explore climate change responses in natural plant communities. Gaining a mechanistic understanding of how trait–environment interactions drive natural selection in novel environments requires consideration of individual plants with multidimensional phenotypes in dynamic environments that include abiotic gradients and biotic interactions, and their combined effect on the different vital rates that determine plant fitness. Evolutionary FSP modelling explicitly simulates the trait–environment interactions that drive eco-evolutionary dynamics from individual to community scales and allows for efficient navigation of the large, complex and dynamic fitness landscapes that emerge from considering multidimensional plants in multidimensional environments. Using evolutionary FSP modelling as a tool to study climate change responses of plant communities can further our understanding of the mechanistic basis of these responses, and in particular, the role of local adaptation, phenotypic plasticity and gene flow.

KEYWORDS: Climate change; ecology & evolution; functional traits; functional-structural plant modelling; local adaptation; phenotypic plasticity.

1. INTRODUCTION

The ’holy grail’ of trait-based ecology is to predict the fitness of a species in a particular environment based on its functional traits (Lavorel and Garnier 2002), which has become all the more relevant in the light of global change (Funk et al. 2017). The persistence of many plant species relies on their ability to either adapt to changing conditions in their current habitat range, or to track their climatic niche beyond their current range and into previously unoccupied habitats. Either way, these plant species will face an array of novel abiotic and biotic conditions that exert selection pressures not experienced within their current range (Franks et al. 2007; Franks and Weis 2008; Lustenhouwer et al. 2018). Predicting how plant populations and communities will respond to the novel conditions caused by climate change has thus far been challenging, because the roles of key eco-evolutionary mechanisms such as adaptive evolution, phenotypic plasticity and gene flow are still poorly understood (Anderson and Song 2020). Furthermore, current ecological models are ill-equipped to predict ecological responses to novel conditions due to their reliance on statistical methods and current observations (Pagel and Schurr 2012) rather than the mechanisms that determine how functional traits interact with the environment, thereby determining plant fitness (Williams and Jackson 2007; Angert et al. 2011; Alexander et al. 2016; Urban et al. 2016). This calls for the development of novel mechanistic modelling approaches designed to make predictions and formulate hypotheses on the adaptive value of
functional traits and life-history strategies in a changing world (Urban et al. 2016). Here, I will advocate the utilization of a 3D mechanistic modelling approach called functional–structural plant (FSP) modelling (Evers et al. 2018; Louarn and Song 2020), in combination with evolutionary modelling to explore climate change responses of natural plant communities. First, I will explain why understanding climate change responses of plant communities requires mechanistic modelling approaches. Second, I will introduce FSP modelling and discuss how FSP models can link individual plants to their (a)biotic environment to accurately simulate the trait–environment interactions that drive climate change responses of individual plants. Thirds, I will discuss how coupling FSP and evolutionary models allows scaling from individuals to communities through mechanistic simulation of demographic and evolutionary processes. Fourth, I will discuss how evolutionary FSP modelling can help explore the behaviour of complex systems with multidimensional plant phenotypes in multidimensional environments. Last, I will highlight the importance of considering the spatial and temporal dynamics of these multidimensional environments, their effects on selection and the role of phenotypic plasticity.

2. UNDERSTANDING CLIMATE CHANGE RESPONSES REQUIRES MECHANISTIC MODELLING APPROACHES

Climate change responses of plant communities are not dominated by any one trait or environmental factor, but rather, are the product of interactions between multiple traits, abiotic factors, biotic interactions and demographic processes (McGill et al. 2006; Laughlin and Messier 2015). Plant communities are complex mixtures of different species that represent a range of functional strategies. In turn, each species within a community has functional trait variation, which affects the different vital rates that determine the fitness of that species (Laughlin et al. 2020). While functional traits are a great tool to describe variation in functional strategies on the species and community levels (Wright et al. 2004; Diaz et al. 2016), they have proven to be poor predictors of ecosystem functioning (van der Plas et al. 2020). This indicates that species level functional trait variation may fail to capture the granularity required to accurately link traits to vital rates, and that traits taken out of the context of the individual lack predictive power (Yang et al. 2018). This is highlighted by two observations: first, the fact that multiple functional strategies can coexist in a given environment challenges the idea that traits can predict ecosystem level responses in a detailed way (Adler et al. 2014). Second, functional trait variation on the species level is often the result of multiple populations that have adapted to their local environmental conditions, showing that functional trait variation needs to be considered in the context of the local environment. This population level variation is important to consider in the context of climate change, as it can either improve or impede a species’ ability to track their environmental niche or adapt to local environmental change (Atkins and Travis 2010; Anderson and Song 2020; Anderson and Wadgymar 2020). Observed patterns of local adaptation along environmental gradients suggest that populations at the species’ cold range edge are generally adapted to abiotic conditions, while populations at the warm range edge are generally adapted to biotic interactions (Griffith and Watson 2005; Hargreaves et al. 2014). These observations are in accordance with ecological theory, which suggests that the selection pressures exerted by abiotic conditions play a larger role in environments that are abiotically stressful, while biotic interactions play a larger role in more benign environments (Louthan et al. 2015; Briscoe Runquist et al. 2020). However, how abiotic and biotic selection pressures interact to shape locally adapted phenotypes is not clear-cut (Briscoe Runquist et al. 2020; Hargreaves et al. 2020), yet these interactions are key to understanding climate change impacts on plant communities (HilleRisLambers et al. 2013). Therefore, understanding how plant communities respond to the novel conditions resulting from climate change requires a focus on the mechanisms that link the functional traits to fitness on the level of individual plants through interactions with their abiotic and biotic environment.

3. FSP MODELLING: LINKING THE PLANT TO THEIR (A)BIOTIC ENVIRONMENT

Perhaps the most important mechanism that links plant form and function to plant fitness in relation to its local (a)biotic environment is the acquisition of, and competition for resources such as light, water and nutrients, which shape plant communities through niche differentiation and competitive exclusion (Kunstler et al. 2016; Levine et al. 2017; Adler et al. 2018). Plant community structure is expected to change as a result of climate change, either through changes in the interactions between competitors that currently coexist, or through the introduction of novel competitors. This leads to major changes in the identity and strength of competitive interactions, as well as the environmental context in which these interactions occur (Alexander et al. 2015). Predicting how these changes in competitive interactions may affect future plant communities requires modelling approaches to simulate the mechanisms of resource acquisition and competition, and their effects on demographic processes (Alexander et al. 2016). Competitive interactions are strong drivers of selection, because traits that favour resource acquisition may allow pre-emptive access to that resource (i.e. a tall plant shades a short plant but not vice versa; Falster and Westoby 2003), and may lead to competitive asymmetry (i.e. a tall plant acquires a disproportionate share of resources compared to a small plant; Weiner 1990; McNickle and Dybzinski 2013). Integrating these mechanisms is key to understanding climate change responses of plant communities, but requires both a high spatial resolution that captures plant architecture and resource heterogeneity on the subindividual-level, as well as a community-level perspective that captures relative trait values of individually distinct plants.

To this end, I propose the use of FSP modelling, which is a mechanistic modelling approach that simulates the performance of individual plants through an explicit representation of plant structure in a 3D environment in combination with functional responses to that environment. Functional–structural plant modelling is a versatile toolbox that can integrate scales ranging from gene to community levels, represent a wide range of systems and answer a wide variety of questions (Evers et al. 2018; Louarn and Song 2020). Functional–structural plant modelling is an excellent tool to simulate climate change responses of plant communities because of their ability to simulate a high level of spatial detail, which allows simulation of the mechanisms that underly interactions between traits and the (a)biotic environment and from which relationships between traits and fitness emerge. Functional–structural plant models have widely adopted the carbon economy as the basis
to simulate the link between plant form and function and plant fitness in relation to the (a)biotic environment (Sterck and Schieving 2007; Evers et al. 2010; Gauthier et al. 2020). The carbon economy encompasses the assimilation of carbon through photosynthesis, the allocation of these assimilates to drive plant growth and development and the loss of these assimilates through respiration, tissue death or exudation. The carbon economy is strongly dependent on the abiotic environment, as both photosynthesis and plant development are temperature-dependent processes, and because photosynthesis requires the acquisition of light, CO₂, water and nutrients. Implementation of the carbon economy allows FSP models to explore how changes in key climatic variables such as increased temperatures, elevated CO₂ levels and altered water availability affect plant growth and development. To describe plant form and function, FSP models may take a trait-based approach that integrates a large variety of morphological, physiological and phenological plant traits, such as leaf shape (Schmidt and Kahlen 2018), plant height (Renton et al. 2005), leaf insertion angle (de Wit et al. 2012), root insertion angle (Postma et al. 2014), defence expression (de Vries et al. 2019) and flowering time (de Vries et al. 2018), among many others. Functional–structural plant modelling is then able to link these traits to the abiotic environment, including nutrients (Dunabin et al. 2004), water (Braghiere et al. 2020), light (Hitz et al. 2019) and temperature (Chen et al. 2014). Functional–structural plant models can capture the heterogeneity in resource availability, plant morphology and plant functional responses in a high level of spatial detail, thereby accurately simulating how these climatic variables drive plant growth and development, and mediate competitive interactions. Thus far, FSP models have mostly considered the acquisition and competition for different above- and below-ground resources in isolation (Postma and Lynch 2012; Evers and Bastiaans 2016; Bongers et al. 2018; de Vries et al. 2018), but recent developments have seen the integration of the two resource systems in whole-plant models that simulate both shoot and root architectures (Drouet and Pagès 2007; Louarn and Faverjon 2018; Zhou et al. 2020; de Vries et al. 2021). Such a whole-plant approach is imperative to simulating plant community dynamics, because competition for multiple resources drives niche differentiation and shapes different functional strategies (Kunstler et al. 2016; Levine et al. 2017; Adler et al. 2018). This highlights how the carbon economy is not only the foundational mechanism that links the plant to their abiotic environment, but also the link through which interactions between the plant and their biotic environment play out.

Functional–structural plant modelling is an excellent tool to simulate plants in a broad ecological context, and has been used to study a myriad of biotic interaction such as plant–plant (Bongers et al. 2014; Evers and Bastiaans 2016; Faverjon et al. 2019), plant–herbivore (de Vries et al. 2018), plant–pathogen (Robert et al. 2008; Garin et al. 2014; Streit et al. 2017) or plant–mycorrhizal interactions (Schnepf et al. 2016; de Vries et al. 2021). However, these biotic interactions are mostly simulated in isolation, and models that simulate interactions between biotic agents have only seen recent development (Douma et al. 2019; de Vries et al. 2021). These interactions between biotic agents are known play an important role in shaping climate change responses of plant communities (HilleRisLambers et al. 2013; Post 2013), which calls for the integration of multiple biotic interactions into FSP models designed to simulate climate change responses of plant communities. Similarly, FSP models that focus on natural systems are often used to simulate single plant species rather than diverse mixed-species communities, which have received only recent attention (Faverjon et al. 2019; Bongers 2020). Simulation of mixed-species plant communities is required to link variation in physiological, phenological and morphological traits to plant community structure (Zakharova et al. 2019), which is a strong driver of the competitive interactions among plants (Alexander et al. 2016; Adler et al. 2018), as well as interactions between plants and pollinators (Sargent and Ackerly 2008), soil microbes (Hodge and Fitter 2013), pests (Agrawal et al. 2006) and pathogens (Mordecai 2011). This calls for an increased focus on the development of FSP modelling tools designed to simulate mixed-species plant communities going forward.

4. COUPLING FSP AND EVOLUTIONARY MODELS

Understanding the full scope of the eco-evolutionary dynamics that drive climate change responses of plant communities requires explicit consideration of population level processes, both genetic and demographic, that drive evolution through selection, genetic drift and gene flow (Lowe et al. 2017). In particular, gene flow between populations is known to play a complex evolutionary role as it can either promote or constrain adaptation (Garant et al. 2007). Low amounts of gene flow ensure that beneficial alleles can spread across populations to maintain adaptive genetic variation (Slatkin 1987; Rieseberg and Burke 2001; Tallmon et al. 2004), while large amounts of gene flow can homogenize populations and work against the diversifying forces of mutation, genetic drift and directional selection that drive local adaptation (Haldane 1930; García-Ramos and Kirkpatrick 1997, but see Fitzpatrick et al. 2015). Because FSP modelling is a trait- and individual-based modelling approach, it can accommodate intraspecific trait variation (Zakharova et al. 2019), which is the basis of these eco-evolutionary processes and is therefore key to predict community responses to environmental change (Bolnick et al. 2011). To couple FSP and evolutionary models, one or more model parameters have to be made subject to selection, gene flow and genetic drift. This requires a definition of fitness to drive selection for these parameters, the incorporation of mechanisms that link these parameters to fitness and for these parameters to be heritable (Fig. 1). These heritable parameters will most commonly constitute a selection of functional traits (de Vries et al. 2020), but can also constitute genes or even the shape of a plastic response (Bongers et al. 2019), depending on the model. Similarly, plant fitness will most commonly be defined as reproduction, but, depending on the model, fitness can include male and female fecundity and survival. The combination of FSP and evolutionary modelling allows for the mechanistic simulation of demographic and evolutionary processes from which contrasting functional strategies along multiple environmental gradients emerge (Bornhofen et al. 2011; de Vries et al. 2020). Additionally, this mechanistic approach can simulate co-evolution between species and selection-driven changes in species interactions as emergent model behaviour, because the underlying mechanisms simulated by the FSP model are driven not only by absolute trait values, but also by trait values relative to those of neighbouring plants. Integrating physiological, demographic and evolutionary processes in the same model requires balancing the high temporal and spatial resolution required for physiological processes with the large temporal and spatial extend required.
for demographic and evolutionary processes (Fig. 1; Oddou-Muratorio et al. 2020; Zhang and DeAngelis 2020). This balancing of resolution and extent is also prevalent when comparing the simulation of small, short-lived plant species that allow for more spatial and temporal detail, to simulation of trees, which require sacrificing spatial and temporal detail to balance the increased computational demand inherent to simulating large, long-lived plant species. To deal with this constraint, evolutionary FSP models can represent a community of plants that stretches across an environmental gradient as a series of small, local communities consisting of tens to hundreds of individuals, depending on their size, to infer the selection pressure at discrete points along the environmental gradient (Bongers et al. 2019; de Vries et al. 2020). Subsequently, to simulate the larger spatial extent required for evolutionary processes such as gene flow, the evolutionary FSP models can be designed to simulate several of these small, local communities in parallel, and connect them through a submodel of pollen and seed dispersal (Colbach 2009). By striking this balance between the integration of detailed physiological processes and large-scale demographic and evolutionary processes, evolutionary FSP modelling offers a unique opportunity to unravel how climate change affects plant communities.

5. SIMULATING SELECTION OF MULTIDIMENSIONAL PHENOTYPES IN MULTIDIMENSIONAL ENVIRONMENTS

Plants exist in complex environments where multiple (a)biotic drivers of selection interact with multiple plant functional traits to determine the different vital rates that make up plants fitness; growth,

Figure 1. A visual summary of the processes and scale of evolutionary FSP modelling. The FSP model simulates the morphology, physiology and phenology of individually distinct plants in relation to their (a)biotic environment, which shapes individual vital rates (growth, reproduction and survival). The FSP model is coupled to the evolutionary model through a) one or more heritable parameters (e.g. genes, traits) that serve as input to the FSP model and are subject to selection, gene flow and genetic, and b) the fitness components that are the output of the FSP model and drive selection, gene flow and genetic drift. These population level processes in turn determine the community-level variation that determine what genotypes are present in the population, as well as the biotic interactions that these individuals experience. This coupling requires the model to balance the high spatial and temporal resolution required to simulate detailed physiological processes and the large extent required to simulate demographic and evolutionary processes that shape populations and communities.
reproduction and survival (Fig. 1; McGill et al. 2006; Laughlin and Messier 2015; Laughlin et al. 2020). Describing functional differences between species therefore requires consideration of multiple trait axes that differentiate between species in multiple ecological dimensions (Laughlin 2014; Kraft et al. 2015), and of the interactions between these trait axes that give rise to trade-offs, and define functional strategies (Wright et al. 2004; Sterck et al. 2011; Diaz et al. 2016; Züst and Agrawal 2017). However, integrating this multidimensionality in both the plant phenotypes and their environment leads to an exponentially increasing computational demand. This computational demand can be drastically reduced by using an evolutionary algorithm to explore the behaviour of complex FSP models that integrate multidimensional phenotypes and environments. This is achieved by the evolutionary model only simulating an evolutionary trajectory from a set of initial trait values to an optimal combination of trait values, rather than using a full-factorial simulation design to fully explore the fitness landscape (a conceptual representation of trait–fitness relationships as a surface) for all possible trait combinations. This computational demand can be drastically reduced by using an evolutionary algorithm to explore the behaviour of complex FSP models that integrate multidimensional phenotypes and environments. This is achieved by the evolutionary algorithm used to traverse evolutionary trajectories across the fitness landscape (rather than using a full-factorial simulation design) to find the optimal phenotype for the environment it is currently observed in, but rather consider the plant within the broader context of spatial and temporal variation in the environment. Understanding the role of phenotypic plasticity in plant population responses to climate change, both in the short and the long term (Nicotra et al. 2010; Valladares et al. 2014; Henn et al. 2018). Phenotypic plasticity is in itself a complex target of selection, and can play an important role in shaping evolutionary processes (Crispo 2008). On the one hand, phenotypic plasticity can dampen natural selection by allowing phenotypic divergence between populations without promoting genetic divergence. On the other hand, phenotypic plasticity may promote natural selection by allowing plant populations to adapt to, and persist in novel environments. However, phenotypic plasticity is often neglected in research on plant population responses to climate change (Matesanz and Ramírez-Valiente 2019), potentially because accurately measuring phenotypic plasticity requires elaborate experimental set-ups (Arnold et al. 2019). As a result, many outstanding questions regarding the role of phenotypic plasticity in plant population responses to climate change remain.

Functional–structural plant modelling has proven to be an excellent tool to evaluate the adaptive value of phenotypic plasticity (Bongers et al. 2019). In FSP models, phenotypic plasticity can be mechanistically represented as a dose–response curve that describes the expression of a trait in response to a particular environmental cue (Evers et al. 2007). The calibration of these response curves relies on experimental studies to elucidate the different components of the plastic response, such as the type of response curve (Poorter et al. 2010), the different cues involved in the response (Pierik et al. 2013), as well as the location of signal perception and integration (Pantazopoulou et al. 2017). When such detailed experimental data are available, the shape of the response curve can be implemented in an evolutionary FSP model as a functional trait that is subject to selection by the (a)biotic environment (Bongers et al. 2019).
7. CONCLUSIONS

Understanding climate change responses of plant communities requires consideration of functional trait variation at the individual level in relation to the local (a)biotic environment. These trait–environment interactions determine the individual vital rates that drive population level eco-evolutionary dynamics, which ultimately shape plant communities. Here, I have outlined how evolutionary FSP modelling can help understand climate change responses of plant communities by taking a mechanistic modelling approach that integrates processes from plant physiology to community scales. Evolutionary FSP modelling is a versatile tool to study interactions between traits and fitness and how plant physiology drives eco-evolutionary processes, and to unravel the mechanistic basis of species interactions.

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CONFLICT OF INTEREST

None declared.

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