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

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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; Díaz *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, CO_2, water and nutrients. Implementation of the carbon economy allows FSP models to explore how changes in key climatic variables such as increased temperatures, elevated CO_2 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 (Dunbabin *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
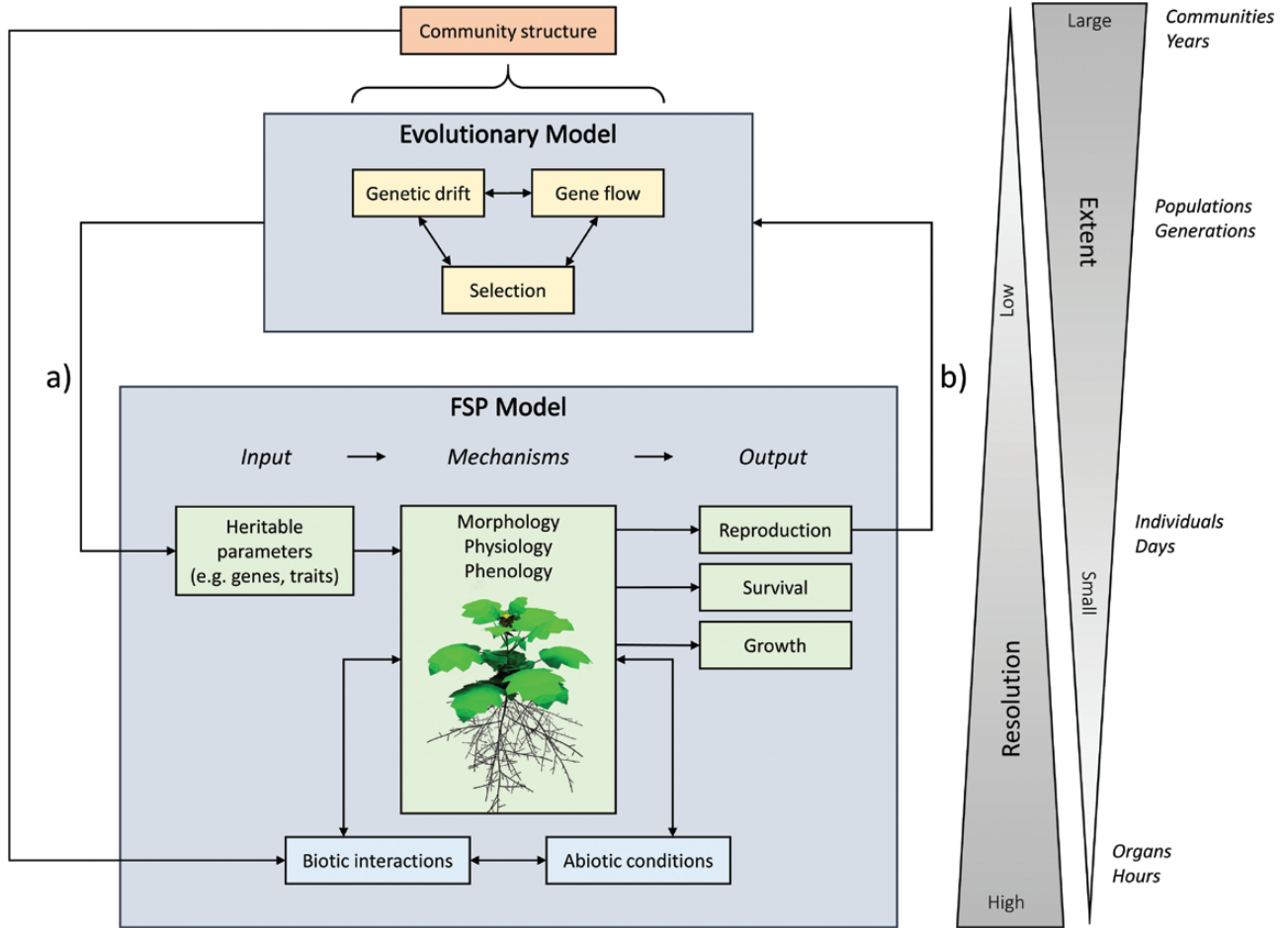
Figure 1. A visual summary of the processes and scale of evolutionary FSP modelling. The FSP model simulates the morphology, physiology and phenology of individually distinct plants in relation to their (a)biotic environment, which shapes individual vital rates (growth, reproduction and survival). The 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.

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,

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; Díaz *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 with peaks and valleys that is described by one or more trait axes, see Gavrilets 2010; Svensson and Calsbeek 2012; De Visser and Krug 2014). The computational benefits of this approach can be exemplified by the work of Renton and Poot (2014), who developed an evolutionary FSP model that simulated single root systems searching for bedrock cracks that would provide access to ground water and ensure their survival in the dry Australian summer. The model was used to simulate selection in a large and complex fitness landscape consisting of 16 trait axes, which would require 10^{16} simulations to explore using a full-factorial simulation design and 10 values for each trait. However, because an evolutionary algorithm was used to traverse evolutionary trajectories across the fitness landscape (rather than using a full-factorial simulation design), these potential 10^{16} simulations were reduced to a more manageable 800 000 simulations (2000 generations * 100 plants * four runs). The work by Renton and Poot (2014) also demonstrates that a large fitness landscape may have multiple local optima that will be missed when only traversing a single evolutionary trajectory through the fitness landscape. To identify the presence and locations of these local optima requires multiple, preferably randomly generated, initial conditions, both through an initial population of plants with randomly generated genotypes and through replication of the evolutionary runs. Although the fitness landscape investigated by Renton and Poot (2014) was both large and complex (i.e. consisting of many interacting trait axes), both the environment and the drivers of selection did not change between generations and the plants were simulated in isolation rather than in competition with other plants. This resulted in a static fitness landscape that did not change over time, contrasting the dynamic fitness landscapes that shape plant communities. Recent years have seen the development of three other evolutionary FSP models that simulated dynamic fitness landscapes driven by resource competition between plants (Yoshinaka *et al.* 2018; Bongers *et al.* 2019; de Vries *et al.* 2020), marking the first steps towards simulating selection in a dynamic environment.

6. PHENOTYPIC PLASTICITY AND SELECTION IN A DYNAMIC ENVIRONMENT

Plants live in dynamic environments where both abiotic conditions and biotic interactions vary over temporal and spatial scales, and

climate change is expected to increase the strength and frequency of environmental variation, and in particular the frequency of disturbances such as heat waves, droughts, pathogens or insect pests (Seidl *et al.* 2017). Plant populations can be seen as the combined results of selection pressures exerted by the environment over large temporal and spatial scales, as these environmental dynamics determine the dynamics of the fitness landscape (MacColl 2011). Therefore, a phenotype observed in a natural system is not necessarily optimized for the local environment in which it is observed, but rather optimized for the broader context of the temporal and spatial variation of the environment in which the plant occurs (Laughlin and Messier 2015). One way in which plants can adapt to this variation is through active plastic responses to environmental cues that aim to maximize their fitness in dynamic environments (Sultan 2000; Morel-Journel *et al.* 2020). However, a plastic response will not necessarily allow the plant to express the optimal phenotype in all possible environments that the plant might encounter (Bongers *et al.* 2019; Douma *et al.* 2019). Thus, plastic responses allow plants to scale between two extreme strategies: a Jack-of-all trades that is able to maintain fitness in unfavourable environments, versus a master-of-some that is able to maximize fitness in favourable environments (Richards *et al.* 2006). These strategies highlight that we must be cautious in assuming that a plant is expressing 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 a broad environmental context is essential to accurately predict 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.*

2018), and used to study how environmental variation drives selection for plastic responses. This goes beyond what is possible with experimental methods and is an important step towards understanding the role of phenotypic plasticity in the response of plant communities to the novel conditions caused by climate change. In particular, FSP models can shed light on the role of active plastic responses to cues that indicate environmental heterogeneity and mediate traits that vary on subindividual levels. Some examples that are relevant in the light of climate change include shade-avoidance responses to light cues that mediate novel or changing competitive interactions, plasticity in root and leaf traits in response to temporal and spatial heterogeneity in the availability of nutrients and water, phenological responses to temperature changes and defence responses to herbivore or pathogen attack (Nicotra *et al.* 2010).

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.

CONFLICT OF INTEREST

None declared.

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