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# Towards a new generation of trait-flexible vegetation models

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## Abstract

Plant trait variability, emerging from eco-evolutionary dynamics that range from alleles to macroecological scales, is one of the most elusive but possibly most consequential aspects of biodiversity. Plasticity, epigenetics, and genetic diversity are major determinants of how plants will respond to climate change, yet these processes are rarely represented in current vegetation models. We provide an overview of the challenges associated with understanding the causes and consequences of plant trait variability, and review current developments to include plasticity and evolutionary mechanisms in vegetation models. We also present a roadmap of research priorities to develop a next generation of vegetation models with flexible traits. Including trait variability in vegetation models is necessary to better represent biosphere responses to global change.

## A short review of trait variability and its consequences for ecosystems

Plants are the main primary producers in the terrestrial biosphere and have major impacts on global biogeochemical cycles and climate (e.g. [1–3]). Plant ecosystems also maintain an astonishing amount of biological diversity and provide a multitude of services (e.g. [4]). They do so, at each location, through a mix of growth forms and physiological functions that is known as **phenotypic** or **trait variability** (Glossary) [5].

The study of trait variability has a long tradition in ecology. After all, selection on heritable **intraspecific trait variability** was the key idea for Darwin’s theory of evolution. In the 1970-80s, the emerging field of comparative ecology emphasized plant **ecological strategies** and analyses of **interspecific trait variability** and **trade-offs** between species [6–8]. Energetic organization of trait data during the last 20 years [9–14] has enabled broad-scale quantification of key traits and trade-offs across space and time, and across taxonomic and functional groups [15,16]. A fundamental insight is that certain combinations of traits jointly characterize plant life-histories and their ecological strategies [17,18]. Increasingly, the focus is shifting to the effects of both intraspecific variability [19–21] and **rapid evolution** [22] in the context of species and ecosystem **adaptation** to climate change.

Observed within- and between-species variability in **plant functional traits** can result from **plastic** responses to biotic and abiotic conditions, and from heritable genetic or **epigenetic** differences (e.g., [20,23–26] and Figure 1). Evidence for within-species variability from **provenance trials, common garden experiments** [27–30], and observations of rapid evolution [30–32] demonstrate that intraspecific phenotypic differences are often heritable and adaptive. This suggests that traits can evolve at ecological time-scales and that the concept of a species as a functionally static unit is an approximation at best.

A challenge for understanding the consequences of trait variability is that we seldom know if measured trait differences arise from **standing diversity**, plasticity, or both. There is hope that population genomics and next generation sequencing [33] could establish **genotype**-to-**phenotype** maps [34] and make it easier to decipher the genetic and plastic components of observed patterns of variation. Currently, however, most data only document existing patterns of trait variability, with no guarantee that this variability will persist over time, e.g. under changing climates.

Another key challenge is understanding the consequences of trait variability. Trait variability is often assumed critical for competition, **fitness,** adaptation and resilience in plant communities, particularly during rapid climatic change [35,36] – e.g. because trait variability likely increases **evolvability**, and buffers species and ecosystems against environmental fluctuations [20,23,26]. However, theoretical models show that trait variability is not always beneficial [37] and empirical studies often fail to demonstrate the expected links to fitness [38]. The consequences of trait variability thus seem more complex and context-dependent than commonly assumed. If true, an obvious and possibly the only route forward is to explore these questions with models that describe traits in a more quantitative and mechanistic way.

## Modelling the consequences and evolution of plant trait variability: the crucial role of vegetation models

Detailed **mechanistic models** already exist that describe communities of plant species in terms of their underlying biogeochemical and ecological processes (**Dynamic vegetation models** = DVM see Box 1, see also [39–41]). These models have been instrumental for understanding global biome distributions and for creating dynamic projections of plant ecosystems under global environmental change [41–44].

An increasingly noted shortcoming of these models, however, is their limited representation of phenotypic variability (e.g. [45,46]). Most DVMs operate with a fixed phenotype per species or represent the world's species via a small number of **Plant Functional Types** (PFTs). This simplistic representation largely neglects the complex patterns of trait variability within and between species. Such patterns occur at all ecological scales [18,20] and across ontogenetic stages. Fixed phenotypes do not account for changes in traits that may occur through plastic and **eco-evolutionary dynamics** [15,27]. Thus, most current models are ill-equipped to explore the consequences of trait variability for ecosystems dynamics or biosphere-atmosphere interactions [1,3]. The lack of processes responsible for trait variability (Fig. 1) increases the uncertainties in the predictions provided by DVMs.

In response to these issues, there have been several attempts to establish next-generation vegetation models, which here we summarize as *plastic*, *prescribed*, and *eco-evolutionary* models of trait variability (Box 2 and Supplementary material)

Plastic models of intraspecific variability emphasize functional plasticity and trade-offs within plants. In such models, plants can, for example, exhibit morphological and/or physiological changes (e.g. in leaf characteristics or allocation strategies) in response to environmental conditions [47–49]. However, these models are limited by the lack of heritable variability. For example, they assume that all individuals of a species in a given environment express the same phenotype and that the adaptation to changes in environmental drivers is instantaneous.

Models with prescribed intraspecific variability incorporate non-plastic trait variability into the modeled processes, but do not explain its origin. These models may help to understand the role of trait variability in structuring plant communities; however, their ability to correctly predict the re-assembly of communities after disturbance is being challenged. Mounting evidence suggests that evolutionary processes can happen on ecological time scales, in particular under strong selection [31,32].

Eco-evolutionary models address this shortcoming by simulating intraspecific variability as the result of ecological and evolutionary processes (in particular **natural selection**, e.g. [50]). Simple eco-evolutionary models draw new individuals from a given trait distribution and let selection act upon them. More sophisticated (and computationally costly) models draw new individuals from the current community following genetic inheritance rules, and via explicit models of genotype-phenotype relationships (see Box 3). By representing genetic processes, rapid evolution in response to climate change can be more reliably modeled.

## Research priorities for next-generation trait-flexible models

Despite encouraging progress, there is clear potential for a more robust representation of intraspecific trait variability and its genetic origin in DVMs. Below we outline what we see as research priorities and key challenges for creating a new generation of *trait-flexible* models that, in principle, would fully account for and predict observed variability and plasticity in plant traits and functions.

### Understanding plasticity, acclimation, and lagged effects

Current DVMs may include limited plasticity at the process-level, e.g. in allocation, phenology, photosynthesis and autotrophic respiration [51]. In working towards a more complete treatment of physiological and morphological plasticity a first challenge is to create appropriate empirical models. In particular, plasticity as a within-generation response to environmental variability needs to be disentangled from across-generation responses achieved either by epigenetic or genetic inheritance. Representing within-generation lagged effects is especially challenging, e.g. the effect of past stress (drought, starvation, etc.) on plant traits and future mortality rates. Lagged effects are observed in empirical studies but not well understood and thus rarely modeled [52]. A first step would be to incorporate some of these lagged effects through dynamic functions that relate disturbance events to physiological responses [52–54].

## Closing the demographic loop

For modelling eco-evolutionary dynamics, we also have to determine the fitness of any given phenotype or genotype. Many existing vegetation models are not particularly well-suited for this task [39] also due to a limited description of mortality and recruitment processes [39,55]. arguably because the primary focus of past model development has been on growth (individual-tree and stand-scale models), productivity, and carbon cycling (global models). Many widely-used models simulate recruitment via a constant seed rain, making reproduction independent from the performance of traits or species in the standing community (but see [56]). This is clearly inadequate to simulate evolution.

Moreover, a lot is known about variability in seed production and seed size and the implications for plant demography (e.g., [8,17,57]), yet relatively little use is made of this knowledge (but see [58,59]). Other entry points to simulate plasticity across life stages are changes in allocation to plant defenses [60] and ontogenetic shifts in leaf traits [61]. Ultimately, without realistic descriptions of all three demographic processes – reproduction, growth, and mortality (i.e., "closing the demographic loop") – we cannot generate realistic predictions about how selection influences the distribution of observed phenotypes at local scales, especially in variable environments.

## Space and dispersal

Evolutionary models often assume well-mixed populations but we know that genetic and phenotypic variation in plants show strong spatial structure. Few models incorporate key mechanisms for predicting shifts in species' range [62]. Further, spatial processes are needed to study plant responses when climatic and non-climatic agents of selection are decoupled [63]. When trying to represent these structures and processes in DVMs, we face the problem that most DVMs are not spatially explicit. Typically, they produce maps based on independently-simulated communities (e.g., from 25 x 25m up to several hectares), which are then averaged to create large-scale maps. In principle, the knowledge and data for a better representation of spatial processes is often available. Yet, it can be prohibitively complex to track pollen and seeds or to follow the germination and growth of a large number of offspring. However, recent examples show some solutions to implement spatial processes such as dispersal and pollination at various geographical scales (i.e., local to continental) [64–67].

### Trade-offs

Any eco-evolutionary model will have to define appropriate trade-offs to constrain species properties to eco-physiologically realistic values, and to avoid unbeatable (and unrealistic) "superspecies" (or supergenotypes) emerging and taking over. A pragmatic approach [46,56] is to represent key trade-offs using observed trait correlations (e.g., the leaf economics spectrum or LES: [13]). Another option is to incorporate theory for specific trade-offs, e.g. concerning seed and seedling competition vs. colonization abilities [57], water and nutrient use in photosynthesis [68], or biomass allocation to different plant parts (e.g., [69]). A further approach is to better define trait-climate relationships using combined trait and flux data, allowing one to develop dynamic **acclimation** functions [70]. Still, some fundamental questions remain; most notably the extent to which trade-offs among traits are general within species as well as across taxonomic groups, and independent of other plant parameters [19]. Increasingly detailed quantification of geographic trait variation (e.g. [71]) will facilitate a better representation of local adaptation [72] and overcome some of the limitations described in Box 2.

### Epigenetic inheritance

Current DVMs do not consider that plastic responses can be propagated across generations via epigenetic mechanisms [73]. These effects are probably more significant and have a shorter response time than genetically inherited effects [22,63,73] . The main challenge of implementing epigenetic processes is our lack of precise knowledge about them: there is abundant empirical evidence for epigenetic regulation in non-natural environments, but we lack data to make predictive models for natural situations. Limited knowledge of epigenetic mechanisms makes their implementation a low priority, until high-throughput sequencing provides sufficiently abundant quantitative data linking them to evolutionary processes [73].

### Genetic architecture and the genotype-phenotype link

Many eco-evolutionary models of trait evolution assume that mutations act directly on traits [56,74,75] . In reality, mutations act on genes and thus only indirectly on traits via genotype-phenotype links. Accounting for recombination, **genetic architecture** of traits**,** and any deviation from random mating can lead to important differences in the rate of adaptation simulated by gene-based-evolution models compared to trait-based-evolution models. In particular, recombination enables considerably faster creation of new phenotypes from an existing gene pool than does mutation. The ways in which genetic architecture drives trait evolution is still debated. However, enough knowledge is available to couple basic evolutionary models with explicit genetic structure to DVMs and other ecological models [50,67,76] (Box 3). Presumably, accounting for the rate of adaptation of traits is most important: 1) for short-lived plants; 2) in ecosystems with frequent generational changes due to high disturbance rates or forest management; and 3) for tree populations at the edge of their distributions [77]. Yet, a key problem in these models is predicting phenotypes from genotypes and environment; this requires data and knowledge still unavailable for many tree species and traits of interest, and is often population-specific. Another challenge is scaling up these processes to large spatial and time scales to understand adaptation processes such as gene flow and reproductive isolation across species' ranges (see also next section: *Efficient scaling*)

## Efficient scaling across several space or time scales

Implementing many of the processes described above invokes an old, but still unresolved issue in theoretical ecology: the problem of upscaling the effects of local or short-term processes (dispersal, microevolution) to large temporal and spatial scales [78]. Aside from the inevitable technical considerations, it is important to consider that patterns of trait variability might not hold across geographic and ecological scales ([19,79]). These findings have implications for DVMs because global trait parameters, even if flexible, might add uncertainty when upscaling local ecosystem properties. More fundamental research is needed on the subject. For now, a practical and partial solution would be to use georeferenced trait data when determining tradeoffs and, when available, local trait data (see Tradeoff section).

## Model-Data integration

Finally, a crucial point for the utility of new model structures is their ability to use and integrate existing data. General approaches for model-data integration have been discussed elsewhere (e.g. [40]). The core of this discussion is that data can enter the model at different levels - as inputs, as drivers, as prior information on **model parameters** or on model outputs, the latter requiring inverse modelling to back-propagate output data to infer model parameters or states. These general insights remain valid for the problem we tackle here, but in practice the question will be if sufficient data are available to constrain DVMs and where in these models are the data best placed to constrain key processes.

The most obvious data type to consider is trait data. For example, the TRY database (www.try-db.org) currently holds ca. 12 million trait records from 280000 species. For further trait databases see Schneider et al. 2019 [14], *eFlower* (http://eflower.myspecies.info/), and

*China Plant Trait Database* [80]. Not all trait records map 1:1 to model parameters, but these databases are clearly a key data source for creating priors on model parameters and trade-offs, or to obtain data on outputs for those model types in which trait distributions are emergent. There are many other, more specialized data types that are also interesting. Data from **provenance** experiments, for example, contain information about heritable intraspecific differences, in particular regarding leaf properties (morphology and chemistry), bud burst, phenology, photosynthetic and hydraulic physiology and other quantitative traits [81]. Both historical and current data from provenance trials are being used for quantitative genetic studies, but these data are underutilized for parameterizing models.

## Concluding remarks and future directions

Most current DVMs describe species or PFTs by a single set of properties that is static in space and time. Empirical data show this is a crude approximation at best, as genetic and phenotypic diversity allow for plastic responses and long-term adaptations to environmental conditions, also via epigenetic inheritance.

We suggest that a new generation of trait-flexible vegetation models is needed which embraces the variability and adaptability of functional traits in vegetated ecosystems. An ideal model would explicitly account for phenotypic plasticity as well as genetic and epigenetic mechanisms in a spatio-temporal context. Such a model would allow researchers not only to quantify the degree to which trait variability buffers diversity and ecosystem functioning against climate change, but also to improve our mechanistic understanding of the processes contributing to trait diversity, and thus biodiversity. Trait-flexible models could help separate the heritable components of trait variability from plastic components, across-generational trait variability, and the influence of biotic and abiotic factors. Inclusion of a wider range of flexible traits could further help determining the individual contribution of certain traits to plant fitness.

One risk of adding additional processes to existing models is that they become increasingly complex, difficult to parameterize, and thus be prone to higher uncertainty [82] [83]. Countering that is the potential to increasingly rely on optimality-based approaches in model components. In principle, these approaches should allow models to be at least as powerful as standard approaches but would require fewer inputs (e.g. [68,69,84,85]). In practice, compromises will have to be made between accuracy, realism, and generality [83] (see also Outstanding Questions), but we believe that immediate progress is possible in the areas that we have highlighted in this Opinion piece.

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## Figure legends

**Figure 1 - Conceptual figure of trait variability.** Rectangles represent states (genotype or phenotype) and ovals represent processes driving variability. The top half represents individual-level processes determining trait variability within a lifetime. The bottom half represents community- or population-level processes that influence variability between generations. Dashed arrows represent how genetic and plasticity can trigger changes in phenotype within a lifetime of an individual.

**Figure I Box 3**: **Physio-demo-genetic (PDG) models: outline and an application.** A) Conceptual framework of PDG models. PDG models couple: (i) a biophysical module to simulate carbon and water fluxes at the tree level using climate observations; (ii) a forest dynamics module to calculate demographic rates for adult trees (growth, mortality, and reproduction) based on carbohydrate reserves, and to simulate ecological processes across the life cycle; and, (iii) a quantitative genetics module relating genotype to the phenotype of one or more functional traits. B) (left) Latitudinal cline of chilling (i.e. low temperature) requirements ($Sc*$) and (right) dependency of forcing (i.e. high temperature) requirements ($Sf*$) on average temperature after 400 years of simulation. Initially, both $Sc*$ and $Sf*$ start with a single value at all locations. (reproduced from [76]).

## Additional material (3 text boxes, 1 table, and Glossary)

## Box 1 Dynamic vegetation models – an overview

The overarching goal of dynamic vegetation models is to describe the functioning of vegetated ecosystems by modelling the key processes that drive vegetation dynamics: primary production, competition, water and nutrient cycles (Figure I, see also [40,41]). These processes are simulated in response to abiotic and biotic drivers.

Models differ in their emphasis on different processes and scales. Some models concentrate on shorter time scales, with a focus on productivity and allocation as well as short-term feedbacks such as water and nutrients. Other models also consider succession and changes in community structure as a result of mortality, competition, and disturbances [55]. Global models are often used to study general patterns in vegetation composition or can be coupled to climate models to examine vegetation-atmosphere feedbacks [1]. At the local end of the spectrum, we find forest models focusing on ecophysiology, adaptation, and forest management [41,55]. Despite these differences in the scale of interest, most models create their predictions by simulating a local community or ecosystem, which is then upscaled to the desired resolution. As a result, most global models can and are also used to model stand-scale dynamics. Still, most models do not explicitly consider spatial feedbacks and dynamics. An exception are so-called landscape models, which are spatially explicit and can reproduce spatial processes such as fire or insect outbreaks [64].

Functional diversity is typically implemented by assigning different model parameters for each species or **plant functional type** (PFT). The main aim of the PFT concept is to reduce the, often large, taxonomic diversity to a small number of manageable vegetation types, such as deciduous temperate forests, evergreen boreal forests, continental grasslands, etc [86]. An alternative to this species or type-centered paradigm are trait-based models. These drop the species concept in favor of describing individual plants by a set of traits, emerging from general correlations and dependencies such as the leaf and stem economics spectra (e.g., [46,56,87]).

## BOX 2: State-of-the-art of models including intraspecific trait variability

Within the ecological modelling literature, we identified three main approaches for including plastic trait variability. See supplementary material for a complete list of models and methods.

| | |
|---|---|
| **1. Plastic models of intraspecific variability** | |
| **General approach** | Plasticity is described through equations of the physiological response to a change in environmental conditions. For example, acclimation of photosynthesis is described by an equation describing the response of maximum photosynthetic rate in relation to leaf nitrogen concentration [48]. |
| **Advantages** | - Allows plant responses to be simulated in different environments and ecosystems, as equations are used to describe the general functioning of plant ecophysiology. |
| **Limitations** | - Difficult to determine generalizable functions applicable to different plants and conditions.<br>- By describing only one plastic response, related counter-responses might be missing because physiological processes are interrelated. |
| **Examples** | PnET-CN [49]; IBM-Esther [47]; ORCHIDEE-NP [48] |
| **2. Models based on prescribed trait distributions** | |
| **General approach** | Well-established trade-offs (e.g., leaf- and wood-economic spectra) are used to assign and constrain trait values corresponding to model parameters. Trait values are sampled from empirical trait distribution generated from plant trait databases (e.g. [14]) or local measurements. Different trait values are assigned to individual plants. |

| | |
|---|---|
| **Advantages** | - No major modification of model structure necessary.<br>- Allows studying the effects of selection and trait variability.<br>- Many data are available for traits across the leaf and stem-economic spectrum. |
| **Limitations** | - Ongoing adaptation to changing local environmental conditions is not simulated, which implies no trait evolution.<br>- No trade-offs or constraints, potentially leading to unrealistic combinations of traits<br>- A more detailed description of intraspecific / interspecific variability is impossible due to the lack of a mechanistic underpinning corresponding to the real ecological processes. This limitation makes predictions from such a model somewhat questionable.<br>- Not bound to any particular spatial scale and can potentially represent a large number of combinations of traits but it is not clear if these combinations represent actual species. |
| **Examples** | ArcVeg [88]; Ecotone [89]; CABLE [90]. |
| **3. Eco-evolutionary models (species or trait-based)** | |
| **General approach** | Concepts from quantitative genetics are used to simulate adaptive evolution; trait values are determined by the genetic contribution of one to several loci associated with a particular trait. Trait distributions emerge from some or all of the following processes: heritability, mutation, gene flow. A detailed example is presented in Box 3. |
| **Advantages** | *Trait- and species-based models*:<br>- Simulates the rate of adaptation to changes of environmental drivers from first principles<br>- Allows simulating adaptive responses of plastic and non-plastic traits<br>- The equations controlling the quantitative genetics are first order algebraic |

| | |
|---|---|
| | (easily computable).<br>*Trait-based models only*:<br>- Avoids technical and data limitations associated with working at the species level. While species-level trait data are often difficult to obtain, community-level relationships are relatively well described.<br>- Inter- and intraspecific variability are both covered<br>- By applying selection on the initial trait space, functional diversity patterns at the macro scale emerge, e.g. observed clines in traits across environmental gradients. |
| **Limitations** | - Requires insight of genetic architecture of traits (distribution of allelic effects in the population, number of alleles and loci determining the trait, interactions between alleles and/or loci); Until now, only simple genotype-phenotype relationships are included (e.g., no epigenetics or gene activation)<br>- Requires knowledge on pollen and seed dispersal as well as mating system<br>- Because of computation costs, only a subset of traits can evolve, and need to be selected.<br>*Trait-based models only*:<br>- Plants are defined by sets of traits not directly attributable to any species, difficult to connect to species-specific data for validation and initialization purposes. |
| **Examples** | aDGVM [56]; FORGEM [76]; PDG [67]; Jedi-DGVM [87] |

## Box 3 - Integrating physiology, demography and genetics in forest trees with Physio-demo-genetic models

Physio-demo-genetic (PDG) models integrate physiological, demographic, and evolutionary processes. PDGs have been developed to better understand the interplay among plasticity and genetic adaptation and the effects of both processes on tree population dynamics under global change [67,76,91]. The advantage of PDG models is their ability to account for the variability in functional traits due to both standing genetic variation and evolutionary change in response to changing local environmental conditions.

In such models, trait values are modeled following a classical quantitative genetic model (Figure IA) and are thus inherited by a tree's offspring. As reproduction, growth, and survival of individual trees depend on their particular trait constellation, the interaction between the biophysical- and the demographic model results in a trait-fitness relationship for the particular environmental conditions. PDGs have been applied to examine the adaptation of the timing of budburst (TBB) along altitudinal or latitudinal gradients of *Fagus sylvatica* (the European beech). Simulations show that few generations were sufficient to develop non-monotonic genetic differentiation in the TBB along the local climatic gradient (Figure IB).

# Glossary Box

**Acclimatization/acclimation:** plastic response of an individual to environmental change within its lifetime, often important on short timescales (e.g., months/seasons). We consider the two terms as synonyms in the broadest sense, without distinction between natural or controlled environments.

**Adaptation:** genetic response to selection resulting in genetic and phenotypic changes tween generations. Natural selection relies on differential fitness of individuals with different phenotypes.

**Common garden experiment / provenance trial:** a classic experimental design to test for heritable differences between populations/provenances, consisting of planting seedlings or seeds of the same family or species, but from different geographical origin or context, in the same location.

**Dynamic vegetation models (DVM, related: land surface models, ecosystem models, process-based vegetation models, terrestrial biosphere models, etc.):** a group of models that dynamically simulate the succession, distribution, and structure of natural vegetation, using mostly mechanistic representations of large-scale vegetation processes.

**Eco-evolutionary dynamics:** the interplay of ecological and evolutionary processes at the same time scales.

**Ecological strategy**: the manner in which a species obtains and uses resources, interacts with other organisms, copes with (and is adapted to) environmental stresses and, in the end, ensures genetic continuity among generations.

**Epigenetic:** heritable changes in gene expression that are not caused by mutations of the DNA sequence. The induced phenotypic changes (due for instance to DNA methylation) are potentially reversible, and thus less stable than changes due to DNA sequence mutation.

**Evolvability**: the capacity of a biological system for adaptive evolution, and thus the ability to adapt to future environments through evolutionary processes.

**Fitness:** expected lifetime reproductive success of a phenotype or genotype, frequently expressed as a result of abiotic and biotic processes.

**Genetic architecture**: the number of loci determining a given trait and whether a locus acts on several traits (pleiotropy); the number of allele per loci and their effects on each trait, the degree of linkage between loci, and interactions between loci (epistasis).

**Genotype**: a set of genes that determine the phenotype.

**Mating system:** determines who mates with whom in a species or population, and includes the self-pollination rate, the rate of pollen immigration and the variances of individual fecundities. The mating system determines the level of genetic drift, the level of inbreeding of the offspring, and, through inbreeding depression, the dynamics of natural regeneration.

**Model parameter:** a variable in an equation or algorithm describing (part of) a mechanism or process. In dynamic vegetation models, parameters can define traits or properties of processes included in the model.

**Phenotype:** a set of traits

**Trait or phenotypic variability:** the variation in phenotypes between species (interspecific) or within and among populations of a species (intraspecific) which can arise from genetic and epigenetic variation, and/or from plastic responses to the environment.

**Plant functional traits:** observable characteristics of a plant, including morphological, physiological and phenological characteristics. Traits influence the demographic and reproductive performances or ecological functions of a plant.

**Plant Functional Type (PFT):** The PFT concept classically refers to aggregating functionally similar species into a single group (i.e., functional type). In principle, PFTs could also be defined to classify variability within a species.

**Plasticity**: the phenomenon of the same genotype producing different phenotypes in response to different environmental stimuli. Plasticity includes acclimatization/acclimation.

**Provenance:** variety of a tree species from a well-defined geographic area.

**Rapid evolution:** the response to selection within a few generations, e.g. through selection on **standing diversity** and recombination.

**(Natural) selection:** the main mechanism of evolution relying on differential survival and/or reproductive success of individuals with different phenotypes. Selection affects the standing diversity.

**Standing diversity:** existing genetic diversity within a population.

**Trade-off:** trade-offs describe situations where further investment of resources in some trait or process necessitates less investment in another trait or process.

**TABLE 1 - Traits with their reported sources of intraspecies variability categorized by class or process type, followed by key empirical correlations or constraints and DVMs including a trait-flexible implementation [a,b,c,d]. The full list of models and details on their implementation of flexible traits can be found in the supplementary material.**

| Class/ Process | Trait | Reported within-species variation: source not distinguished | Evidence for genetic/ epigenetic link to variation | Variation from plasticity | Empirical key correlations or constraints with other traits or processes | Trait variability in current models |
|---|---|---|---|---|---|---|
| **Photosynthesis** | Maximum photosynthetic rate, $V_{cmax}$ | [92] | [93] | [93–96] | Positively correlated with leaf nitrogen, phosphorous and specific leaf area [94,97–99] | LPJmL-FIT [46], MATEY [85] |
| | Leaf mass per area (g $m^{-2}$) or its inverse, specific leaf area ($cm^2g^{-1}$) | [100–103] | [27,104,104–107] | [95] | Correlated negatively with leaf lifespan, positively with leaf nitrogen, phosphorous and dark respiration [13,86]. Higher at more arid sites and higher irradiance | LPJmL-fit [46], MATEY [85], LM3-PPA [110] |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | | sites [108,109] | |
| | Nitrogen content (g m$^{-2}$) | [102,103] | [27,107,111] | [71] | Higher at more arid sites, higher irradiance [108,112] | CABLE [90], MATEY [85], TFS [113] |
| | Stomatal conductance (gw) | [114] | [27,115] | [116,117] | Assimilation rate higher at low soil phosphorus [118] | - |
| Respiration | Proportional change in respiration per 10 C increase in temperature ($Q_{10}$) | [119] | - | [120,121] | Two types of acclimation: 1- adjustments in the $Q_{10}$ and 2- changes in the enzymatic capacity of the respiratory system. | PnET-CN [49] |
| | Number of mitochondria per cell | [122] | - | [123] | Respiration, growth, acclimation at high CO$^2$ [123]. | - |
| | Leaf respiration in darkness and in the light | [103] | [27] | [95,120] | Leaf dark respiration varies in relation to site climate [124]. | LM3-PPA [110] |
| Wood/ leaf | Wood density | [125,126] | [104,127,128] | [129] | Connections to growth | LPJmL-FIT [46], |

| | | | | | | |
|---|---|---|---|---|---|---|
| structure | | | | | rate and mortality. Higher at more arid sites [125]. | aDGVM2 [56], TFS [113] |
| | Wood and sapwood hydraulic conductivity and anatomy (vessel Lumen area, ring-width). Hydraulic plasticity and P50[d] | [126,130] | [104,128] | [131–135] | Globally, higher at wetter sites, higher at warmer sites [136,137] | - |
| | Herbivory defense (plant secondary metabolites, spines) or serotiny (fire resistance) | [138] | [138–141] | [142] | Defense-growth trade-off influences allocation strategies [143]. | - |
| | Bark thickness | [144] | [145,146] | [145] | Thicker in sites with more frequent fire and/or more frequent/severe drought, and hotter sites [144,147,148] | LPX [149] |
| Phenology | Timing of budburst | [150] | [151–153] | [151] | constraints: duration | Forgem [76], PDG [67] |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | | growing season vs frost damage [24,153] | |
| | Timing of leaf fall / growth cessation | [154] | [24] | [155] | constraints: duration growing season vs frost damage [24,153]. Nutrient resorption [154] | - |
| | Frost hardiness | - | [27] | [156,157] | constraints: duration growing season vs frost damage [156] | Forgem, Forgro [76] |
| Allocation | Biomass compartments, allometries (leaf:fine root, diameter:height) | [158] | [27,105,111] | [111,159] | Growth, stem and leaf economics spectra | Jedi-DGVM [87], aDGVM2 [56] |
| | Leaf area / sapwood area ratio | [126] | [104] | [131,132] | Globally, lower at drier sites, and in species with smaller leaves and/or lower specific leaf | - |

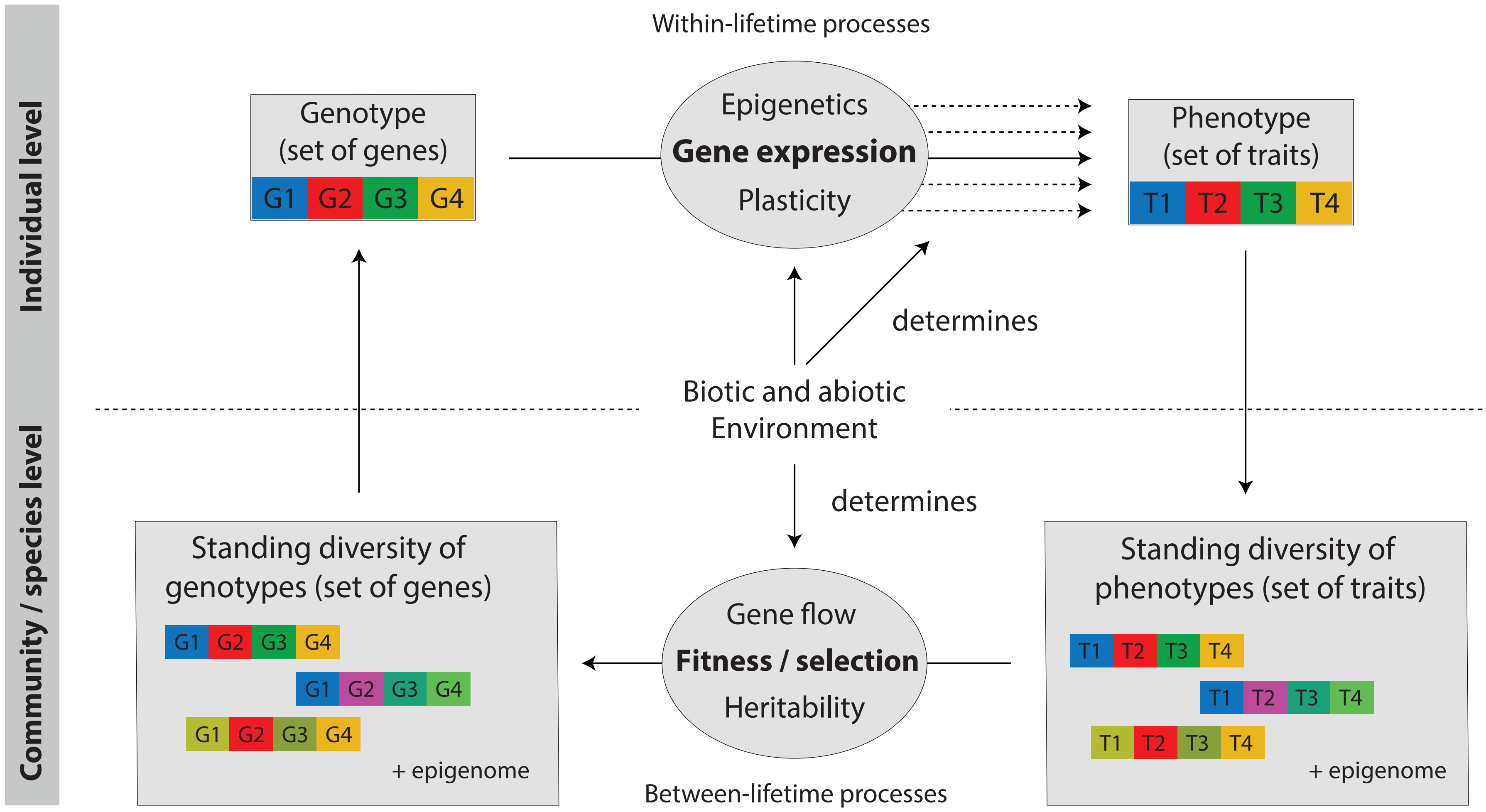
| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | | area [137] | |
| Reproduction | Seed size | [160,161] | [162] | [57,163] | Height, seedling survival, dispersal distance [8,160]. | hybrid-DVM [164], aDGMV2 [56] |
| | Germination rate | [161] | [27,105] | [165] | Recruitment | Esther IBM [47] |

[a] The source of variability, when determined, is classified as plastic or genetic or both. It also provides a brief description of key correlation with other traits and processes.

[b] A list of examples is presented in which dynamic vegetation models have implemented trait variability for the specified trait.

[c] This table is not an exhaustive list, thus more references in a cell do not necessarily imply a higher number of studies, when possible at least 2 examples per cell were included. Primary literature was preferred over review articles. The full list of models and reviewed articles can be found in the supplementary material.

[d] P50: water potential at which 50% of hydraulic conductivity is lost



Individual level

Community / species level

Within-lifetime processes

Genotype
(set of genes)

G1 G2 G3 G4

Epigenetics
**Gene expression**
Plasticity

Phenotype
(set of traits)

T1 T2 T3 T4

determines

Biotic and abiotic
Environment

determines

Standing diversity of
genotypes (set of genes)

G1 G2 G3 G4

G1 G2 G3 G4

G1 G2 G3 G4

\+ epigenome

Gene flow
**Fitness / selection**
Heritability

Standing diversity of
phenotypes (set of traits)

T1 T2 T3 T4

T1 T2 T3 T4

T1 T2 T3 T4

\+ epigenome

Between-lifetime processes