

## Research

### Temporal environmental variation may impose differential selection on both genomic and ecological traits

Ludwig Leidinger, Daniel Vedder and Juliano Sarmiento Cabral

L. Leidinger (<https://orcid.org/0000-0002-5008-683X>), D. Vedder (<https://orcid.org/0000-0002-0386-9102>) and J. S. Cabral (<https://orcid.org/0000-0002-0116-220X>) ✉ ([juliano.sarmiento\\_cabral@uni-wuerzburg.de](mailto:juliano.sarmiento_cabral@uni-wuerzburg.de)), Center for Computational and Theoretical Biology, Faculty of Biology, Univ. of Würzburg, Würzburg, Germany.

Oikos

130: 1100–1115, 2021

doi: 10.1111/oik.08172

Subject Editor: Justin Travis  
Editor-in-Chief: Dries Bonte  
Accepted 17 March 2021



The response of populations and species to changing conditions determines how community composition will change functionally, including via trait shifts. Selection from standing variation has been suggested to be more efficient than acquiring new mutations. Yet, studies on community trait composition and trait selection largely focus on phenotypic variation in ecological traits, whereas the underlying genomic traits remain understudied. Using a genome-explicit, niche- and individual-based model, we address the potential interactions between genomic and ecological traits shaping communities under an environmental selective forcing, namely temporal positively autocorrelated environmental fluctuation. In this model, all ecological traits are explicitly coded by the genome. For our experiments, we initialized 90 replicate communities, each with ca 350 initial species, characterized by random genomic and ecological trait combinations, on a 2D spatially explicit landscape with two orthogonal gradients (temperature and resource use). We exposed each community to two contrasting scenarios: without (i.e. static environments) and with temporal variation. We then analyzed emerging compositions of both genomic and ecological traits at the community, population and genomic levels. Communities in variable environments were species poorer than in static environments, and populations more abundant, whereas genomes had lower genetic linkage, mean genetic variation and a non-significant tendency towards higher numbers of genes. The surviving genomes (i.e. those selected by variable environments) coded for enhanced environmental tolerance and smaller biomass, which resulted in faster life cycles and thus also in increased potential for evolutionary rescue. Under temporal environmental variation, larger, less linked genomes retained more variation in mean dispersal ability at the population level than at genomic level, whereas the opposite trend emerged for biomass. Our results provide clues to how sexually-reproducing diploid plant communities might react to variable environments and highlights the importance of genomic traits and their interaction with ecological traits for eco-evolutionary responses to changing climates.

Keywords: environmental variability, genomic traits, mechanistic model, rapid evolution, standing variation



[www.oikosjournal.org](http://www.oikosjournal.org)

## Introduction

Communities of plant species are the result of different abiotic and biotic conditions (Huntley 1991). Changes in those conditions will therefore also reflect on communities and their trait composition. Response strategies that enable species survival under changing conditions may vary across species. They can, for instance, select for survival (Holt 1990), for lower body mass (Parmesan 2006), for dispersal (Berg et al. 2010) or for adaptation to new conditions (Joshi et al. 2001, Jump and Peñuelas 2005, Bell and Gonzalez 2009). Given enough time, this will result in the communities passing through ecological species successions (Huston and Smith 1987) and evolutionary taxon cycles (Ricklefs and Bermingham 2002). Even in short periods, populations within communities can change their traits in response to environmental variation via rapid evolution (Maron et al. 2004). In this case, selection on standing variation can be more efficient than acquiring novel mutations (Barrett and Schluter 2008, Bolnick et al. 2011). This standing variation can be both intraspecific and intra-individual, i.e. within-genome variation. A high standing variation thus provides a resource for populations to quickly respond to changing environments (Cochrane et al. 2015). However, the genomic traits which enable and maintain standing variation remain largely understudied in ecological and eco-evolutionary studies (but see Schiffers et al. 2013, Matuszewski et al. 2015).

Many functional species traits are quantitative and subject to genetic interactions, such as epistasis, pleiotropy and genetic linkage. To infer a direct connection between phenotype and genotype is therefore complex (Korte and Farlow 2013). Still, all this genomic background determines standing genetic variation, which in turn will constrain which individual phenotypes are possible and thus a population's evolutionary potential. With the increasing availability of exhaustive genetic data, considering detailed genetic factors in eco-evolutionary models has become more feasible, especially for model species (Exposito-Alonso et al. 2019, Frachon et al. 2019). Indeed, there is an increasing amount of genetic data at the population or even at the individual level (Domingues et al. 2012, Alonso-Blanco et al. 2016). Nevertheless, manipulating real-world systems to conduct meaningful experiments to isolate factors on both functional and genetic levels is difficult (but see Booth and Grime 2003). Thus, although the importance of genetic factors for ecological processes has long been recognised (Holt 1990), investigating its effects in real-world systems remains challenging (Hughes et al. 2008).

Simulation models provide a powerful alternative to overcome the practical challenges of empirically investigating and manipulating genetic traits and all the trait-mediated ecological functions they control. Modeling studies can cover any organisational level in biology, from genomes through species to communities (Münkemüller et al. 2012, Kubisch et al. 2014, Matuszewski et al. 2015, Saupé et al. 2019), and thus are suitable tools to explore potential eco-evolutionary regulations of species traits, particularly under

fluctuating environments. To generate realistic biodiversity dynamics in these conditions, key eco-evolutionary processes are necessary, namely local population dynamics, dispersal connecting populations, biotic interactions (in particular, niche preferences and resource competition), evolution and environmental dynamics (Urban et al. 2016, Vellend 2016, Cabral et al. 2019a). Considering that environmental heterogeneity and resource competition can be associated with niche differences among species (Maire et al. 2012) and that environmental dynamics may maintain species coexistence for longer (Zepeda and Martorell 2019), environmental fluctuations must pose some expected selective pressures on eco-evolutionary traits. For example, empirical evidence has shown that demographic rates decrease with body mass and increase with temperature (Brown et al. 2004, Savage et al. 2004), a decline in body mass might be advantageous in varying environments (Parmesan 2006), as a lower body mass reduces resource requirement (Savage et al. 2004) and increases evolutionary rates (Allen et al. 2006). Lower body sizes also increase reproductive rates (Savage et al. 2004) and thus more offspring dispersal can take place, further assisting species to respond environmental change via dispersal (Berg et al. 2010). Additionally, theoretical evidence has suggested that environmental fluctuations may select for intraspecific variation of dispersal ability (Mathias et al. 2001, Sieger and Hovestadt 2020), constituting bet-hedging strategies. Fluctuating environment may also select for increased niche tolerances to cope with varying conditions (Lynch and Gabriel 1987, Holt 1990), although this might be mostly relevant for larger species (due to longer generation times) and poor dispersers (reviewed by Sexton et al. 2017). All these trait selection can only be possible if genetic traits and standing genetic variation allow the selective pressure to act upon them. For example, genetic linkage can strongly decrease evolutionary rescue capabilities under climate change in heterogeneous landscapes (Schiffers et al. 2013). Therefore, species with less genetic linkage and larger standing variation might be in eco-evolutionary advantage in fluctuating environments (Cochrane et al. 2015), although the interplay between genetic and phenotypic traits remains largely understudied.

Given the above-mentioned expectations, we developed a genome-explicit metacommunity model (GeMM, Fig. 1) aimed at addressing the interplay of genomic and phenotypic traits in species communities under an environmental selective force, namely temporal stochastic auto-correlated environmental fluctuation (i.e. red noise; from now on 'temporal variation' or 'variable environments'). Specifically, we address the following questions. 1) Which phenotypic and genomic traits enable survival in temporally variable environments? 2) How do temporally variable environments shape standing variation (phenotypic and genetic)? We designed a simulation experiment under two different environmental scenarios, one with and one without temporal environmental variation (variable and static environments, respectively) and analyzed genomic and phenotypic trait characteristics of surviving communities. We expected communities in variable environments to select for higher tolerances, higher dispersal

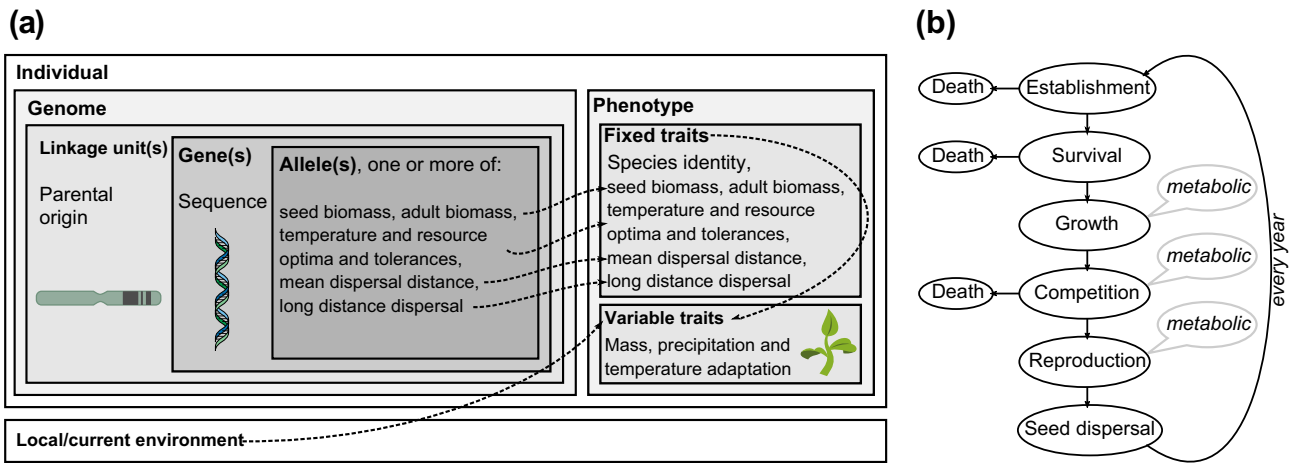


Figure 1. Schematic of the model. (a) Individuals represent the base agents in the model. They are comprised of a phenotype which interacts with other individuals and the environment, and a genome. The genome is diploid and consists of maternal and paternal sets of linkage units, which combine genes as one hereditary unit. Each gene may code for one or more alleles of functional traits. The expressed trait in the phenotype results as the average of all associated alleles in the genome. The expression of some of the traits ('variable traits') additionally depends on the local current environment and may change over time. (b) Flow of processes each individual passes every year. Some of the processes are dependent on the local temperature and individual biomass (marked 'metabolic'), while all processes depend on an individual's phenotypic traits (see (a)). The reproduction submodel further entails the processes of gametogenesis (including gene recombination), pollen movement and offspring production (see Supporting information for details). Dashed arrows represent influences, solid arrows represent sequence of events.

abilities and lower biomass and to exhibit increased standing variation, both phenotypic and genetic. While our expectations on trait responses were mostly confirmed, we find that standing variation decreases for all traits, although the relative loss in standing variation varied among traits and levels of organization. Our findings on virtual communities suggest how eco-evolutionary dynamics of real plant communities might unfold under changing environments.

## Material and methods

### The model

#### General structure

We use GeMM (ver. 1.0.0) – a genome- and spatially-explicit, niche- and individual-based model for plant metacommunities written in Julia (Bezanson et al. 2017, Fig. 1). A detailed model description with justification for assumptions, equations and parameter values can be found in the Supporting information (Grimm et al. 2006, 2010). Model parameters are summarized in Table 1 and in the Supporting information. The model generates metacommunity dynamics (Hanski 2001, Leibold et al. 2004) and it considers explicit local population and community assembly dynamics emerging from genomic and individual level processes. The model simulates discrete time steps, which can be translated to one year. In the model, individuals belong to species, which are characterized by individuals with identical genomic architecture (i.e. genome size and

gene linkage), but with phenotypic traits coded by the individual's genomes (i.e. seed and adult body sizes, dispersal ability, environmental niche preferences) falling within a species-specific Gaussian trait distributions (Fig. 1a). Thus, individuals of the same species vary slightly in their phenotypes, depicting intraspecific phenotypic variation. Note that any phenotypic trait coded by the genome and used as parameter in an ecological process (e.g. function) is by definition also functional. Dispersal of individuals (i.e. seeds) interconnects grid cells, while the position of individuals is characterized by the grid cell coordinates, i.e. all individuals are concentrated in the center of the respective grid cell.

#### Eco-evolutionary processes

Like some previous ecosystem models (Harfoot et al. 2014, Cabral et al. 2019b, reviewed by Cabral et al. 2017), yearly vegetative growth in biomass, fertility and mortality rates in the model are controlled following the metabolic theory of ecology (MTE, Brown et al. 2004, Price et al. 2010). Accordingly, the model considers discrete yearly time steps. In MTE, a biological rate  $b$  depends on the temperature  $T$  and individual mass  $M$ , scaling a base rate  $b_0$  as:

$$b = b_0 M^c e^{-\frac{E_A}{k_B T}} \quad (1)$$

where  $E_A$  is the activation energy and  $k_B$  the Boltzmann constant. The exponent  $c$  is  $\frac{3}{4}$  for biomass growth and

Table 1. Overview of model parameters and variables with biological relevance. Phenotypic traits  $y$  ( $M_r$ ,  $M_s$ ,  $\mu$ ,  $s$ ,  $\bar{P}$ ,  $\sigma_p$ ,  $\bar{T}$ ,  $\sigma_T$ ) are always the average of all corresponding trait loci  $y_i$  in the genome. Several values are arbitrary, but within empirically or theoretically supported ranges as indicated in the column ‘Justification’ (see main text and the Supporting information for further details) and dimensionless unless otherwise specified. Note that the species- and genome-specific variables allowed species and individuals to vary over replicates and to undergo selective pressure. Hence, the trait composition emerging from surviving individuals and species shows how selection imposed by the environmental scenarios acts upon a wide range of initialized species and individuals. The variability column describes whether and how values might change. Constant: values are global constants across scenarios; genome: values might differ within an individual’s genome, potentially giving rise to different phenotypes; scenario: values differ between scenarios, but stay constant within scenarios; species: values might differ between species, but stay fixed within species. SD: standard deviation.

Parameter	Value/range	Justification	Variability
Boltzman constant ( $k_B$ )	$1.38 \times 10^{-23} \text{ J K}^{-1}$	Brown et al. 2004	Constant
Activation energy ( $E_A$ )	$1 \times 10^{-19} \text{ J}$	Adapted from Brown et al. 2004	Constant
Base fecundity ( $r_0$ )	$1.4 \times 10^{12}$	Modified after Brown et al. 2004	Constant
Base growth rate ( $g_0$ )	$8.8 \times 10^{10}$	Modified after Brown et al. 2004	Constant
Base mortality rate ( $m_0$ )	$1.3 \times 10^9$	Modified after Brown et al. 2004	Constant
Carrying capacity ( $K$ )	100 kg	ca 1000 m <sup>2</sup> of grassland constant, Deshmukh 1984, Bernhardt-Römermann et al. 2011	Constant
Temporal resource SD ( $\delta_p$ )	0.0 or 0.2	Fung et al. 2018	Scenario
Temporal temperature SD ( $\delta_T$ )	0°C or 0.2°C	Fung et al. 2018	Scenario
Number of loci ( $n_l$ )	1 to 20	Fournier-Level et al. 2011, Schiffers et al. 2013	Species
Number of linkage units ( $n_u$ )	1 to $n_l$	From one single chromosome for all loci to one chromosome per locus, Schiffers et al. 2013	Species
SD among trait loci ( $\sigma_l$ )	0 to $0.1 \times$ mean of trait	Arbitrary, allowing intragenomic genome variability	Genome
Adult biomass ( $M_r$ )	$e^3$ – $e^{14}$ g	Arbitrary, allowing a large pool genome from herbs to trees, Brown et al. 2004, Cabral and Kreft 2012	Genome
Seed biomass ( $M_s$ )	$e^{-2}$ – $e^{10}$ g ( $< M_r$ )	Arbitrary, allowing a wide range of seed (or propagule) sizes	Genome
Dispersal kernel mean ( $\mu$ )	0–1 grid cells	Arbitrary, encompassing entire spectrum of possible short-distance dispersal (implicitly 0–30 m, given $K$ , covering the majority of empirically measured values, Thomson et al. 2011)	Genome
Dispersal kernel shape ( $s$ )	0–1	Arbitrary, allowing no to global long-distance dispersal	Genome
Resource optimum ( $\bar{P}$ )	0 to 10	Arbitrary, allowing a species pool beyond landscape limits to avoid pre-selection mid-domain effects, Colwell and Lees 2000	Genome
Resource tolerance ( $\sigma_p$ )	0–1	Arbitrary, allowing up to several grid cells in all directions beyond optimum	Genome
Temperature optimum ( $\bar{T}$ )	10–40°C	Arbitrary, allowing a species pool beyond landscape limits to avoid pre-selection mid-domain effects, Colwell and Lees 2000	Genome
Temperature tolerance ( $\sigma_T$ )	0–1°C	Arbitrary, allowing up to several grid cells in all directions beyond optimum	Genome

reproduction, and  $-\frac{1}{4}$  for mortality (Brown et al. 2004). This results in smaller individuals having a higher mortality than bigger ones, while individuals in cooler conditions have a lower mortality than those in warmer conditions. Using the MTE means reduced parameterization effort, since  $b_0$  values for the different processes are global constants and thus identical for every species. Additionally, the emerging longevity-fecundity tradeoff that comes with mass-regulated rates has been shown to inherently suppress the evolution of ‘super-species’ (Cabral et al. 2019b).

Over the course of a simulation, individuals thus grow in size, passing three life stages: 1) seed, 2) juvenile and 3) adult. Individuals disperse as seeds, establish, grow and become reproductive adults (Fig. 1b). Both seed biomass and adult biomass, i.e. the threshold biomass where individuals become reproductive, are two of the central, genetically-coded traits that define individuals (Fig. 1a, Table 1).

Adults are monoecious and reproduce sexually with a random adult of the same species within the same grid cell to produce new seeds (i.e. local mating). This process can be interpreted as

search of mating partner or as pollen movement, which is the term used from now on. We opted for local pollen movement for computational efficiency and to focus on gene flow only via seeds (but see the Supporting information for explorative scenarios with global pollen movement).

Seed dispersal follows a logistic dispersal kernel with genetically-coded mean dispersal distance and shape parameter  $\mu$  and  $s$ , respectively (Bullock et al. 2017). In our discrete landscapes, dispersal is modeled as centroid-to-area, with expected mean dispersal distances usually around equal to the length of the grid cells (cf. Chipperfield et al. 2011).

For establishment, all individuals have fundamental preferences concerning two different environmental measures: the first, temperature, has a direct effect on biological rates, as described by the MTE (Brown et al. 2004) and affects density-independent mortality, while the second axis is a surrogate for environmental resource niche axes, e.g. nutrients or precipitation. From here on this second axis is called ‘resource’ for simplicity. Individuals’ adaptation to resource conditions determine their competitive abilities. Both these preferences are characterized by an optimum and a tolerance,



which are represented as mean and standard deviation of a Gauss curve, respectively. The degree of mismatch between an individual's preference optimum with the local environment (i.e. within the grid cell) determines its adaptation value (i.e. environmental fitness). Near their optimum, individuals with a greater niche tolerance have lower adaptation values than individuals with narrower tolerance (i.e. specialists, Griffith and Sultan 2012). During establishment, the adaptation values toward temperature and resource are calculated for each new seed based on the local conditions and phenotypic traits (Fig. 1b).

Furthermore, each time environmental conditions change, all individuals in the affected grid cell pass establishment again to re-calculate their adaptation values. These adaptation values are functional for two different subsequent processes. First, individuals experience a metabolic, density-independent mortality (Brown et al. 2004). This mortality further scales with individual temperature adaptation, so that mortality is higher for individuals which are poorly adapted to the surrounding temperature (Cook 1979). Second, all individuals in a cell compete for the limited available space in the grid cell, i.e. total sustainable biomass. If the combined biomass of all individuals in a cell exceeds the grid cell's carrying capacity biomass, individuals are removed from the community until biomass is within grid cell limits. The choice of which individuals to remove is based on pair-wise comparisons of random pairs of individuals. From any of such two individuals, the individual less adapted to local resource conditions is removed. The function of this axis as competition axis meets the criteria of resources in general (aboveground competition for light and/or belowground competition for nutrient and water). Because small species and juveniles are more numerous, there is a higher chance of excluding smaller individuals, thus also implicitly accounting for self-thinning, which is a common phenomenon in plant communities, but difficult to model (Reynolds and Ford 2005, Wiegand et al. 2008). Moreover, this random pair lottery further allows small-sized species to persist longer in the community, as additional coexistence mechanisms are not implemented in the model (e.g. small-scale perturbations, pathogens, herbivores).

### **Genetic architecture**

All of the aforementioned traits (Table 1) are coded by one or more genes in an individual's diploid genome (polygenes). Single genes can also be associated to several traits at the same time (pleiotropy, Solovieff et al. 2013). Thus, each trait can be represented more than once in the genome (i.e. through different genes at different loci). Since trait representations are subject to species-specific variation, they can constitute different alleles – both within the haploid genome at different loci, but also between the maternal and paternal haploid genomes or between individuals (cf. Nevo 1978). Realized functional traits  $y$ , i.e. phenotypic traits, are then determined quantitatively by considering all respective loci  $y_i$  within an individual's genome and taking their average. This results in a random degree of species-specific phenotypic and genetic, i.e. intra-individual or intra-genomic, trait variation (cf. Mackay

2001). Lastly, genes may be combined to form a linkage unit, which represent a set of spatially close genes within the same chromosome arm. Linkage units thus comprise the smallest hereditary entities (Lande 1984, Hermann et al. 2013). Haploid gametes receive a complete random set of those linkage units following a recombination process, where each linkage unit can originate from either the paternal or maternal chromosomal complement of the individual producing the gamete. During reproduction, the gametes of two mating individuals thus form an offspring's (i.e. seed) genome. The phenotypic trait values of each offspring are then calculated on the basis of its recombined genome and local environmental conditions (Fig. 1a). Genetic architecture does not evolve, but initial species have different genetic architectures within the ranges shown in Table 1.

## **Experimental design**

### **Simulation arena**

We set our simulation experiments in a rectangular landscape of a grid of 5 by 7 grid cells, with periodic boundaries (closed torus). Each grid cell had a carrying capacity of 100 of total biomass, which approximately relates to 1000 m<sup>2</sup> of grassland (Deshmukh 1984, Bernhardt-Römermann et al. 2011). This comparison to a grassland was helpful to parameterize this key parameter (carrying capacity), but we did not focus on any particular grassland type, species pool or trait composition. Landscape size was arbitrary but ensured computational feasibility – higher values will allow a higher number of individuals, which will at least linearly increase the total run time of the simulations. Two perpendicular environmental gradients (temperature and resource) ran along the long and short axis of the landscape, respectively. The rectangular shape of our simulation arena provided a longer gradient in the physiologically important temperature direction.

### **Initialization**

We initialised each grid cell of the landscape with a different local community of random species. The species characteristics (i.e. genomic and phenotypic traits) as well as local abundances were chosen randomly from large ranges of uniform-distributed values. On the genomic level, species differed by the number of loci,  $n_l$  (maximum = 20, cf. Fournier-Level et al. 2011, Schiffers et al. 2013), intragenomic variation between trait values, i.e. genetic variation,  $\sigma_l$  (maximum =  $0.1 \times$  trait value), and number of linkage units,  $n_u$  (between one and  $n_p$ , Table 1). To obtain the phenotypic characteristics of a species, first an average phenotype was defined by randomly selecting a value for each phenotypic trait. These traits, more specifically, the adult biomass trait, were then used to calculate the number of offspring a single individual of this species would have. Given an already determined genetic architecture (i.e.  $n_p$ ,  $n_u$  and  $\sigma_l$ ), each individual of a species was then initialized as follows. For each trait representation (i.e. gene) within the genome, the associated trait value was chosen randomly following a Normal distribution

with the trait value of the average phenotype as mean and standard deviation the product of  $\sigma_i$  and the trait value (Table 1). Afterwards, the initial phenotype for each individual was calculated based on all genes in the genome. This resulted in varying degrees of intragenomic and intraspecific standing variation. We disabled mutations in our experimental design so that this standing variation was the only resource for selection. Grid cells were then filled with populations of several species until carrying capacity was reached. Because species vary randomly in their traits, including biomass, initial grid cell communities varied in richness. This resulted in initial communities with on average 10 species per grid cell and a total of 350 species in the landscape.

Values for simulation, global and species-specific parameters that were not varied in the different experimental scenarios were chosen to ensure plausible patterns, most importantly to achieve species co-existence by adjusting the mortality-to-fecundity ratio. Species-specific parameter values were drawn at random from a range that extended beyond what would be realisable in simulations to reduce geometric artifacts within the parameter space (Table 1). This also kept the need for additional assumptions at a minimum, since viable species emerged via environmental filtering and ecological interactions. Global parameter values were either adapted from the literature (Brown et al. 2004, Fournier-Level et al. 2011) or fine-tuned via trying out a range of realistic values.

### Scenarios

For investigating our general study question about the interplay of environmental variation and phenotypic and genomic traits, we designed two scenarios. In the first, temperature and resource gradients ranged through (arbitrary) constant values of 16.85–22.85°C (290–296 K) and 3–7 (arbitrary quantity), respectively, during the entire simulation run ('static environment'). In the second, initial temperature and resource values were the same as in static environments, but could change at each year ('variable environment'). The change followed a gaussian random-walk trajectory to yield positive auto-correlation (Fung et al. 2018). The amount of change ( $\delta_p$  and  $\delta_r$ , Table 1) was drawn randomly from a Normal distribution with a standard deviation of 0.2. This value corresponds to a moderate rate of change of no more than 0.5 degrees per year in the majority (ca 99%) of cases, which we found by trying different values to produce notable environmental change that did not kill all individuals in a short amount of time. Since our simulation arena represents a small spatial scale, all grid cells changed always by the same value at each timestep. The change of temperature was independent from that of resource and vice versa. Confounding effects, such as landscape configuration, different temporal dynamics, the role of both pollen- and seed-mediated gene flow, complex dispersal behavior and macro-evolutionary processes (e.g. clade diversification) have been studied elsewhere and were thus not included in the present study (Kremer et al. 2012, Münkemüller et al. 2012, Kubisch et al. 2014, Helsen et al. 2016, Aguilée et al. 2018). Table 1 contains the parameters which were varied for the scenarios, their

meaning and their values. Nevertheless, explorative simulations with global pollen movement, which might be still reasonable at least for some species due to the relatively small landscape area, generated qualitatively similar results (shown in the Supporting information). Deviations are in accordance for what is expected from global pollen movement, namely slightly more gamma richness in variable environments possibly due to increased mating success, loss of selective pressure on genetic linkage and overall slightly better maintenance of standing variation at both phenotypic and genetic levels possibly due to prolonging the presence of genotypic variants that would have been otherwise filtered out at environmental limits (Supporting information). Although empirical and modelling comparisons between pollen- and seed-mediated gene flow is scarce for herb species, pollen-mediated gene flow seems indeed to maintain genetic variation (for single herb species see Helsen et al. 2016, Gonçalves-Oliveira et al. 2020). Hence, the small differences observed in these explorative simulations indicate promising research directions. We also performed explorative scenarios with alternative boundary conditions (reflecting and absorbing), which generated very similar diversity and selection relationships between environmental scenarios (Supporting information). Explorative simulations with smaller grid sizes (3 × 5 grid cells) supported also similar relationships between scenarios, but with overall lower richness, as expected for smaller areas (Supporting information).

We started 100 different replicates which were simulated for 750 years. Each replicate, i.e. each unique initial community, was subjected to both scenarios. This yielded 200 simulation runs in total. From the 100 replicates, 95 reached the final time step in both scenarios with surviving species and were retained for the analyses (i.e. 190 runs). The duration of 750 years was adequate to allow quasi-equilibrium and short enough to warrant our selection-on-standing-variation rationale (Hermisson and Pennings 2005). The amount of replicates was sufficient to integrate most variation emerging from the model stochasticity as shown by the stabilizing trends of standard deviations of trait data obtained already after ca 40 replicates (Supporting information).

It is possible to increase the temporal, spatial and ecological (i.e. number of populations or species) extents, but runtime increases at least linearly up to quadratically with the number of individuals. For comparison, our scenarios took ca 2–5 days per simulation, with temporally varying environments and global pollen movement taking the longest (up to a week per simulation). In particular, pollen movement and seed dispersal are computationally intensive submodels, hence our simplifications for pollen movement in the main experiments. Genome size did not strongly impact runtime.

We recorded population-level statistics of the individuals in our simulation world at the start and every 50 years of a simulation run. The model does also allow yearly data recording but we chose 50-year intervals to speed up runtime (recording data to file is computationally demanding) and to reduce overall data size without compromising our analyses. This data encompassed individual phenotypic and genotypic

values. Thus, for each of these points in time, we tracked the state of local species populations including location, abundance, demographics, mean adaptation and trait values for all phenotypic and genomic traits.

## Analyses

To make the individual information more accessible, we calculated summary statistics at the population level. We defined a population as a group of conspecific individuals co-occurring in the same grid cell. For each population, we then calculated mean values of each phenotypic trait, the variance of each phenotypic trait (phenotypic intraspecific variation), and means of the individual genetic variation in each trait. We scaled all variance values by the respective population-specific means to get coefficients of variation. To compare emerging ecological patterns and identify when equilibrium is reached, we calculated a set of ecological metrics, namely species-richness, i.e. the average number of species per grid cell,  $\alpha$  ( $\alpha$ -diversity), the total number of species across the landscape,  $S$  ( $\gamma$ -diversity),  $\beta$ -diversity,  $\beta = S/\alpha - 1$  (Whittaker 1960), population demographic structure (i.e. number of juveniles and number of adults) and range-filling from the data on surviving communities. For diversity indices, we converted our data to community matrices and analyzed them using *vegan* (Oksanen et al. 2018) in R (<[www.r-project.org](http://www.r-project.org)>). To assess demographic structure within communities, we analyzed average numbers of juveniles and adults. Range-filling was calculated as the fraction of grid cells that was occupied by a species over all the grid cells that were potentially suitable for the given species. Suitability was asserted as an arbitrary cut-off where environmental parameters (temperature and resource) fell within a species' tolerance (optimum  $\pm$  tolerance).

For our study questions, we analyzed the trait composition of surviving communities genomic trait composition (study question 1), and differences in phenotypic and genetic standing variation (study question 2) between environments. Since we were interested in general patterns of the effect of environmental variability, rather than the effects of warming or cooling trends, we excluded resource and temperature optimum traits from our analyses. We transformed trait and variation distributions before analysis and visualization using a  $\log(x+1)$  transformation, because values were strongly right-skewed and were frequently  $< 1$ . Additionally, we calculated the degree of genetic linkage as  $n_f/n_u$ , because due to our method of initializing species,  $n_u$  directly depended on  $n_f$ .

To ascertain whether and how trait composition differs between environmental conditions (study question 1), we first compared species numbers and identities. Because each community is subjected to both environments, we analyzed what proportion of species was shared by both environments, and which were unique to one of the environments. To assess how phenotypic and genomic traits respond to variable environments, we compared trait characteristics between scenarios by performing principal component analyses on the population trait data. This way, we were able to describe general patterns in trait space between scenarios by relating the total

trait space shift to the principal components and correlated trait axes. Additionally, we compared community trait distributions pairwise between environments to identify trends in traits specific to the environments. For this, we calculated linear mixed models using the R package *lme4* (Bates et al. 2015) with trait as response, environment as fixed effect and replicate as random effect.

To find out whether there is a selective force on standing variation (both phenotypic and genetic) specific to environmental conditions (study question 2), we compared the phenotypic and genomic trait variances of surviving communities between scenarios for all traits separately. We again calculated linear mixed models, with trait variances as response, environment as fixed effect and replicate as random effect.

The model code, experiment definition files and analysis scripts are available at Github (<<https://github.com/CCTB-Ecomods/gemm>>). Albeit reporting of significance values is generally inappropriate for simulation models (White et al. 2014), we use significance here to identify which responses are stronger than others.

## Results

### Differences of ecological patterns between environments

Surviving communities in our simulation experiments (Fig. 1) differed in a number of ecological characteristics. Compared to communities in static environments, communities in variable environments were only about half as species-rich on a local level ( $\alpha$ -diversity, Fig. 2a) and exhibited less  $\beta$ -diversity (Fig. 2b), which resulted in decreased species richness on a regional scale ( $\gamma$ -diversity, Fig. 2c). Summing over all replicates, a total of 121 species survived in both environments, while 588 and 58 surviving species were unique to static and variable environments, respectively. For communities in variable environments, emerging functional differences comprised higher total abundances in all demographic stages (Fig. 2d–e) and decreased range filling (Fig. 2f). While all aforementioned metrics were constantly changing during the entire simulation course in the variable environments, in static environments they reached a quasi-equilibrium by year 500.

### Response of phenotypic and genomic traits

Surviving communities showed subtle differences in their trait syndromes combining all traits in a PCA (Fig. 3). In the first two principal components (40% of the variance explained), populations from variable environments occupied for the most part a subset of the trait space of populations from static environments (mostly overlapping ellipses in Fig. 3). Nevertheless, the trait space of variable environment communities was shifted towards increased environmental tolerances and decreased genetic linkage and number of genes (negative direction of second principal component

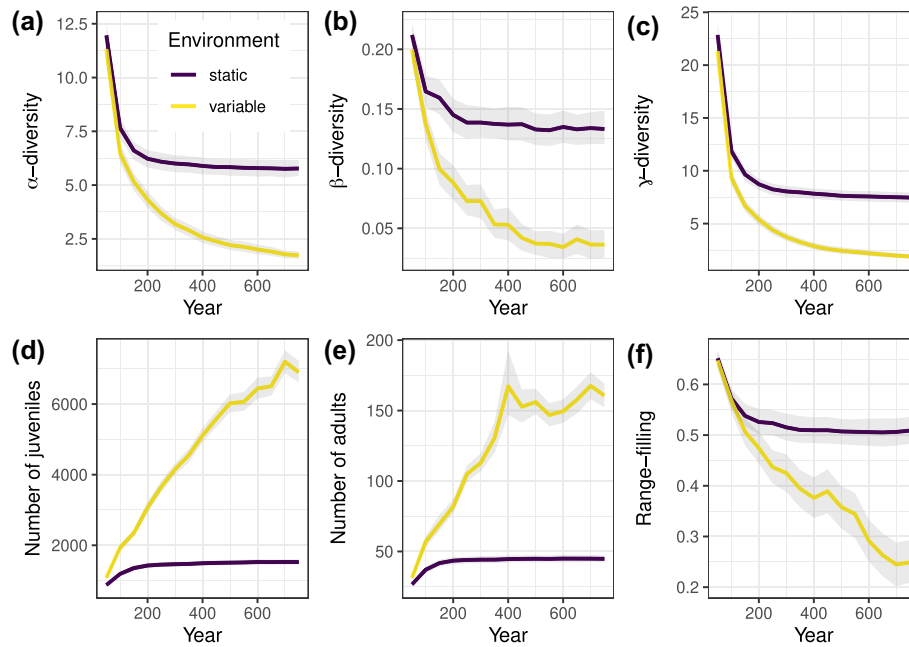


Figure 2. Averaged ecological patterns across the entire simulation arena over time after initialisation. Dark/violet: static environment, light/yellow: variable environment. Grey ribbons represent 95% confidence intervals. (a) Local species richness ( $\alpha$ -diversity) as numbers of species, (b)  $\beta$ -diversity (Whittaker 1960), (c) total species richness ( $\gamma$ -diversity) as numbers of species, (d) mean number of juveniles, (e) mean number of adults, (f) range-filling, i.e. the percentage of potentially suitable habitat that is actually occupied. Spikes are due to single replicates with extreme values.

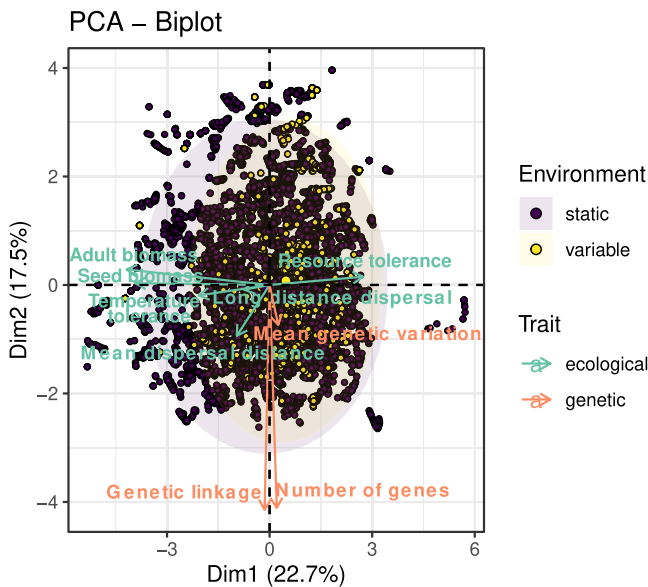


Figure 3. Principal component analysis (PCA) showing trait space characteristics (phenotypic and genomic) of surviving populations. Biplot of surviving populations and trait axes along the first two principal components. Populations without temporal environmental variation (dark/violet) versus with temporal environmental variation (light/yellow). Shaded ellipses highlight areas of 95% confidence.

– Fig. 3). With the exception of these first two axes, the following seven principal components contributed similarly to the overall explained variance (contribution of each trait to each principal component in the Supporting information).

Focusing on single traits, communities showed several differences between the two types of environments (Fig. 4a, Supporting information). Compared to static environments, surviving communities in variable environments showed on average significantly increased mean dispersal distance ( $\mu$ ), resource and temperature tolerances ( $\sigma_p$  and  $\sigma_T$ , respectively), decreased long distance dispersal ( $s$ ), decreased adult ( $M_a$ ) and seed biomasses ( $M_s$ ), decreased mean genetic variation ( $\sigma$ ) and strongly decreased genetic linkage ( $n_u$ ). Number of genes ( $n$ ) showed a positive trend, but exhibited no significant difference (Supporting information). These trait differences are robust over time, as mean trait values remained fairly stable in the static environments already from year 100 on (period necessary for the metacommunity to reach quasi-stationary dynamics from initial conditions), whereas resource tolerance and biomasses continued to change directionally in variable environments (time-series of mean traits and in trait shifts in the Supporting information).

### Differences in standing variation (phenotypic and genetic)

Additionally to differences in the trait composition at the community level, we found that phenotypic (between individuals) and genetic (between genes) trait variation



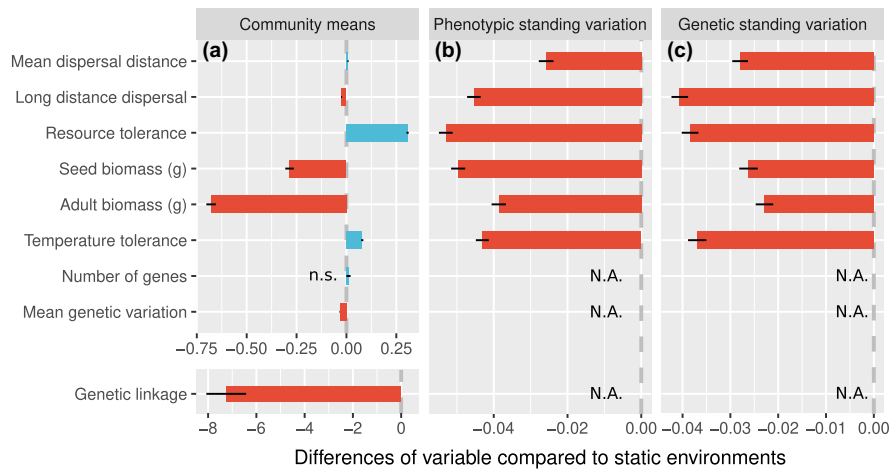


Figure 4. Community trait responses to temporal environmental variation along three organisational levels. (a) Differences in trait means in variable environments compared to static environments. (b) Differences in phenotypic standing variation (i.e. trait variances between conspecific individuals), and (c) differences in genetic standing variation (i.e. trait variances between genes or loci) in variable environments compared to static environments. Error bars show standard errors. Red and blue colors indicate negative and positive differences, respectively. Note the different axis scales. The abbreviation ‘n.s.’ denotes differences that are not significant ( $p > 0.05$ ). ‘N.A.’ marks trait differences that are not available at the given level.

significantly decreased for the variable environments in all traits (Supporting information), although the degree of decrease varied among the traits and type of standing variation (Fig. 4b–c). While long-distance dispersal and mean dispersal distance decreased comparatively less at the phenotypic than at the genetic standing variation, both adult and seed biomasses showed a stronger decrease at the phenotypic than at genetic standing variation. The decreasing trends of both temperature and resource tolerances were very similar at the phenotypic and genetic levels.

## Discussion

### General differences between scenarios

Our results show how community trait composition of plant metapopulations may differ between static and temporally variable environments in a genomically-explicit eco-evolutionary model. The changing abiotic conditions in variable environments act as a constant environmental filtering mechanism (Kraft et al. 2015), where only those species survive that are able to adapt to or track environmental changes. As a result, communities are poorer in species (Menge and Sutherland 1976). The decreased  $\beta$ -diversity suggests that these fewer species in variable environments are rather generalists, in comparison to static environments where species seem more specialized to local environmental conditions (cf. Gilchrist 1995). Furthermore, the reduced range-filling in variable environments is likely a mid-domain-like effect (cf. Colwell and Lees 2000), where due to the ongoing temporal variability, the margins of a potential range will often become unsuitable quickly, impeding establishment and survival. Moreover, because the environmental fluctuations in our

simulations were stochastic rather than periodical or directional, the probability for species to find alternating suitable conditions is low. This alternating suitability, however, is the prerequisite for temporal environmental variability to favor species co-existence and increased species richness (cf. Tilman and Pacala 1993, Descamps-Julien and Gonzalez 2005). In contrast, most communities in static environments reached a quasi-equilibrium already after the first 200 years.

### Study question 1. Which phenotypic and genomic traits enable survival in temporally variable environments?

The trait characteristics of communities in the respective environments represent successful strategies in surviving random environmental variation. The decreased values of resource tolerance in communities in static environments indicate increased environmental specialization. This is in contrast to communities in variable environments, where the variability in resource conditions favors species with higher tolerance values (i.e. specialization to local conditions are maladaptive in variable environments, Gilchrist 1995, Kassen 2002). Additionally, temperature tolerance directly affects individual survival due to metabolic constraints (Fig. 2d). Since a high temperature tolerance decreases fitness, species are selected to keep tolerances low if they occur at their respective environmental optimum. In variable environments, this environmental optimum is hardly met. As a consequence, selection acts rather on enhancing temperature tolerance to gain long-term fitness. Therefore, our experimental design captures the evolution towards bet-hedging strategies in terms of adaptation to variable environments (Slatkin 1974).

The second aspect of survival strategies lies in the biomass patterns. In general, species in variable environments were smaller than in static environments. Since growth rates and

fecundity follow MTE, smaller species are more fecund than bigger species at the expense of survival. A higher and more frequent number of offspring will spread the risk over time in variable environments (McGinley et al. 1987, Philippi and Seger 1989). Additionally, the larger range of different biomasses in static environments can be interpreted as temporal partitioning (Pronk et al. 2007), because it means that co-occurring species will reproduce at different times and intervals. This allows species to alternate dominance and thus produce temporally variable biotic conditions (cf. Olf et al. 2000, Wilson and Abrams 2005). Furthermore, both biomass and tolerance patterns suggest that specialization to avoid competitive exclusion plays a larger role in shaping communities in static environments, while communities in variable environments are primarily shaped by generalism and environmental filtering (cf. Menge and Sutherland 1976, Hulshof et al. 2013).

To track suitable conditions, dispersal abilities are crucial in changing environments (Bourne et al. 2014). While mean dispersal distances in our simulations showed little differences between scenarios, long-distance dispersal decreased and mean dispersal distance increased in variable environments. This selects for dispersal into rather neighboring grid cells than at longer distances, which could cause loss of seeds to unsuitable conditions. Besides primary dispersal traits, the dispersal rate also increased in variable environments via the indirect effect of metabolic rates: the high demographic turnover that comes with higher fecundity due to decreased biomass leads to more frequent dispersal. This further explains why the change in dispersal traits between environment was small. With the rate of change in our simulations and the small spatial extent of our landscape, dispersal distance (which is what is controlled by dispersal traits) is less important than dispersal rate (cf. Johst et al. 2002). However, this might change in fragmented landscapes, where dispersal distance is critical to connect habitable patches (Bacles et al. 2006, Boeye et al. 2013, Bonte et al. 2010).

Lastly, species may survive by adapting to changing conditions (Jump and Peñuelas 2005). This constant adaptation requires an appropriate genetic architecture: we expected genomes to contain a high variation of alleles (Holt 1990) which can be recombined to quickly respond to novel conditions (Schiffers et al. 2013, Matuszewski et al. 2015) by producing new phenotypes. Indeed, we found increased, albeit not significant, gene numbers in variable environments, but a strong significant selection towards lower genetic linkage. This combination of genetic traits allows more recombination potential. The decrease in genetic linkage for similar or slightly higher number of genes means an increase in linkage units. In our simulations, selection acted upon standing interspecific variation, as genetic architecture did not evolve. In nature, however, increased number of linkage units (e.g. chromosomes) can indeed emerge from chromosome fissions (a cause of ascendant dysploidy) or polyploidization followed by diploidization (exclusion of redundant gene copies). In fact, polyploidisation correlates with latitude and, arguably, with environmental stress

(Rice et al. 2019), but direct tests of this are difficult due to low feasibility (Van de Peer et al. 2017). Moreover, increased fecundity also increases adaptation potential as it leads to more recombination events. According to our results, the ecological adaptation response to variable environments also involved increasing environmental tolerances. However, the selection on genomic traits did not prevent the general decrease of mean genetic variation in variable conditions, which contradicts results from a previous modeling study (Matuszewski et al. 2015). With more detailed data on the levels of variation, we explain this contradiction in the following section.

## **Study question 2. How do temporally variable environments shape phenotypic and genetic standing variation?**

Having identified survival strategies on a population phenotypic level, we addressed selection patterns on the standing variation within the populations – both at the phenotypic intraspecific (i.e. between individuals) and genetic (i.e. between genes) levels. This addressed differential selection depending on the level of standing variation. All traits were more specialized, i.e. had lower variation, in variable environments at both phenotypic and genetic levels. In fact, standing variation significantly decreased over time in both scenarios for most traits, but in particular in variable environments (Supporting information), which is expected due to the lack in metacommunity dynamics at larger scales. However, it appears to be beneficial for species to maintain more plasticity in dispersal ability between individuals, as evidenced by the more moderate loss of variation at the phenotypic than at the genetic level when coping with temporal environmental variation.

Since variation in our experiments could be increased neither by mutation (Josephs et al. 2017), nor by external gene flow (Cornetti et al. 2016), selection could only act on standing variation. Under these conditions, high gene linkage preserves variation in the linked traits (cf. Teotónio et al. 2009), while low gene linkage allows faster specialization or adaptation of unlinked traits simultaneously. Indeed, the latter showed to be strongly selected in variable environments (Fig. 3). Ecological specialization can also be facilitated by low numbers of loci (Schiffers et al. 2014). In contrast, phenotypic uniformity might arise from increased number of loci which stabilize variation (Fraser and Schadt 2010). In our simulation experiments this phenotypic uniformity seems to be achieved by rather decreasing linkage, which makes loci to specialize independently. Moreover, our results of increased linkage units accompanied by decrease in standing variation further suggest these trends as stabilizing coexistence mechanisms by promoting intraspecific competition caused by phenotypic uniformity. Our explorative scenarios with global pollen movement also shows that increased gene flow across the landscape (via pollen additionally to seeds) can assist in maintaining genetic linkage and standing

variation, although the latter most notably for genetic standing variation in variable environments (Supporting information). Species richness was slightly higher for global pollen movement (Supporting information), and thus this increased standing variation enhanced coexistence. Future experiments could focus in which circumstances of gene flow phenotypic variation indeed impacts species coexistence negatively (Hart et al. 2016) or if low species numbers first allow higher phenotypic variation (Hulshof et al. 2013).

Our results furthermore exemplify that phenotypic and genetic variation do not need to be correlated, at least not for all traits (Fig. 4b–c; see the Supporting information for global movement). In the case of mean dispersal distance, the loss of phenotypic variation in variable environments was relatively lower than the loss of genetic variation (Fig. 4b–c). Hence, the retained phenotypic variation in mean dispersal distance is due to survival of different phenotypes, which, in turn, exhibit relatively specialized genotypes. However, the opposite happened for biomasses, with more specialized phenotypes but with more diverse genotypes. Such differential specialization of standing variation depending on trait, level and environment further stresses the essential role of ecotypes and different routes to achieve bethedging for species survival under changing environments.

## Limitations and perspectives

The fact that our simulations produced low coexistence across the landscape might result from too large a trait space in the initial species pool, most of which would be filtered by the relatively narrow environmental conditions. Since the initial species pool totaled on average 350 species, the probability is also high for it to contain a few strong generalist species, which outcompete other species. Moreover, an average initial number of 10 species per grid cell means a low probability for any species to be adapted to the local conditions. Nevertheless, the coexistence level obtained is also in accordance with theoretical expectations, considering that a niche partitioning along the two gradients would explain the average of a bit more than five species in static environments (i.e. at least one specialized species per environmental gradient combination, Armstrong and McGehee 1980). The filtering is also evidenced by the reduction of trait value ranges over all traits after simulation initialisation (Supporting information). In fact, additional post hoc simulations with more constrained initial communities (temperature and resource niche optima matching landscape limits) resulted in higher surviving species numbers, particularly in  $\alpha$ -diversity (Supporting information). Small-scale disturbance or trophic interactions, e.g. herbivory could further increase coexistence, as theoretical and empirical studies suggest (Roxburgh et al. 2004, Shea et al. 2004, Chesson and Kuang 2008). However, since these processes likely produce additional confounding effects, they were excluded at this stage, although they constitute directions for further model development. Trophic and others interactions, such as mutualism, can affect species survival under climate change (Berg et al. 2010) and even lead

to extinction cascades if keystone species are lost (Brook et al. 2008). Since keystone species would be affected by genetic factors as any other species, our experiments likely underestimates net species loss effects mediated by genetic factors.

Further model development could make some model assumptions species-specific parameters (i.e. genomically coded), e.g. pollen movement ability, number of mates per pollination event, self-compatibility, dioecious reproduction, clonal reproduction. These specifications could be aimed at experiments focusing either on the role of these assumptions or on particular real-world communities for which such species-specific information is available. Some of these traits are particularly relevant for grasslands, such as self-compatibility and clonality. In fact, recent model application to mimic calcareous grassland communities could integrate self-compatibility as species-specific, with self-compatibility promoting evolutionary rescue in species undergoing habitat loss and temperature warming (Figueiredo 2021). Still, the current mechanistic complexity of GeMM is already useful for various questions. For example, when applying GeMM to assess different scenarios promoting species invasions on oceanic islands, we confirmed the empirical evidence that propagule pressure is the key mechanism promoting island invasions, but could further show that invasive species have higher niche tolerances and dispersal ability than native species (Vedder et al. 2020). In such model applications, the resulting model runtimes must be considered during experimental design, as runtime increases with the number of individuals. For example, spatial extents larger than simulated here would need to be compensated by shorter temporal frameworks or by focusing on single species, whereas larger extents (e.g. for studying macroevolutionary dynamics) should rather focus on shorter spatial extents or smaller number of individuals. Nevertheless, in principle, our experiments demonstrate that GeMM can already be applied to the study of plant communities and, as long as the processes are similar, potentially to other organisms (e.g. maybe terrestrial invertebrates). Applying the model to other organisms may require adapting parameter settings and processes.

Another limitation relates to the genomic traits. Our model simplifies complex genetic factors and dynamics which could potentially have confounding effects on resulting patterns. For instance, linkage between genes in reality is not a binary decision, but rather a consequence of the physical distance between those genes. The larger the distance, the higher the probability of crossing over during meiosis. Additionally, genetic architecture is dynamic, especially in plants. Genomes can grow, e.g. by polyploidisation (Van de Peer et al. 2017), and shrink in size, both of which affects genetic linkage and potentially genetic variation. Since polyploidisation is often a stress response in plants it will arguably affect survival (Rice et al. 2019). Subsequent gene loss may then even initiate speciation (Albalat and Cañestro 2016). Our model hence represents the effects of genetic linkage and genome sizes without explicitly considering their genetic origins. Nevertheless, our findings on the interaction between genetic and phenotypic traits call for empirical

works identifying the factors that trigger these genomic processes and assessing their evolutionary relevance (Van de Peer et al. 2017).

To make our model and the findings on genomic and phenotypic traits under temporal environmental variation more applicable and relevant to real-world systems, the model could be constrained by real data in further studies. For instance, simulation arenas can be directly derived from actual landscapes, including environmental conditions (Karger et al. 2017). Species-specific parameters could be taken from databases for phenotypic traits (Kattge et al. 2011) and occurrence records (GBIF - <www.gbif.org/>) and enriched by genomic information (Dong et al. 2004, Howe et al. 2020) to constrain initial parameter space for the creation of random communities. Thus, our model represents an opportunity to integrate different types of datasets in a unifying mechanistic framework.

Even in the current state, our model addresses a number of eco-evo-environmental phenomena (cf. Govaert et al. 2019). The emerging patterns under randomly fluctuating environments can inspire new hypotheses which can be used to guide fieldwork and experimental studies, thus serving as null expectations to empirical studies. In this respect, the model realism lies on the explicit connection between genomic and ecologically functional traits. The consideration of genomic traits opens up new perspectives on biodiversity dynamics during impending climate change (Fig. 5). For scenarios of short-term change of environmental conditions, i.e. warming, lower or increased resource and more frequent extreme events, adaptation can only exploit standing intraspecific or genetic variation, rather than novel mutations. Species with enough phenotypic variation will likely have good adaptive potential, regardless of genetic characteristics. For species with low phenotypic variation, adaptive potential depends on genomic traits. Species that have highly specialized, i.e. uniform, phenotypes and show little or no genetic variation will only be able to survive rapidly changing conditions by tracking their specific favourable conditions. Fragmented environments or poor dispersal abilities therefore will likely

lead to the extinction of those species. Even if species have high genetic variation, genetic architecture is crucial for their performance. With a high degree of genetic linkage, species might not be able to adapt critical traits in time to react to changing conditions, since a beneficial trait allele might be linked to other disadvantageous alleles of other traits. Thus, net fitness is unlikely to increase. Low linkage, on the contrary, might enable rapid evolution to new environments, as genetic hitchhiking becomes less relevant. However, if linkage is too low, species can quickly lose genetic variation, rendering them unfit to react to subsequent change. Ideally, conservation measures targeted at particular species should thus consider population structure and genomic traits of species. The importance of genetic and functional diversity for species survival is already acknowledged in conservation biology (Díaz and Cabido 2001, Rao and Hodgkin 2002). Our results now imply that genomic diversity, i.e. the genetic architecture, can be central to species' adaptive success under impending environmental change.

When investigating real-world communities, differences from the expectations provided by our results in communities responding to warming temperatures may be highly informative to disentangle the effects of climate change compared to those of background environmental oscillations. Moreover, it should be possible to investigate how different combinations of environmental drivers may lead to different trends in both genomic and phenotypic traits. In fact, current human-driven changes form spatially-structured anthropogenic threat complexes (Bowler et al. 2020). Simulation experiments combining habitat loss and climate change have already suggested potentially disastrous consequences for species survival in both hypothetical (Travis 2003) and real-world (Sarmiento Cabral et al. 2013) systems. However, previous modelling studies have focused mostly on ecological processes and patterns, but eco-evolutionary models may allow explicitly integrating genetic patterns (Urban et al. 2016, Malchow et al. 2020). Hence, quantifying genetic diversity and functional patterns of empirical communities and matching these empirical patterns with simulation results varying in environmental

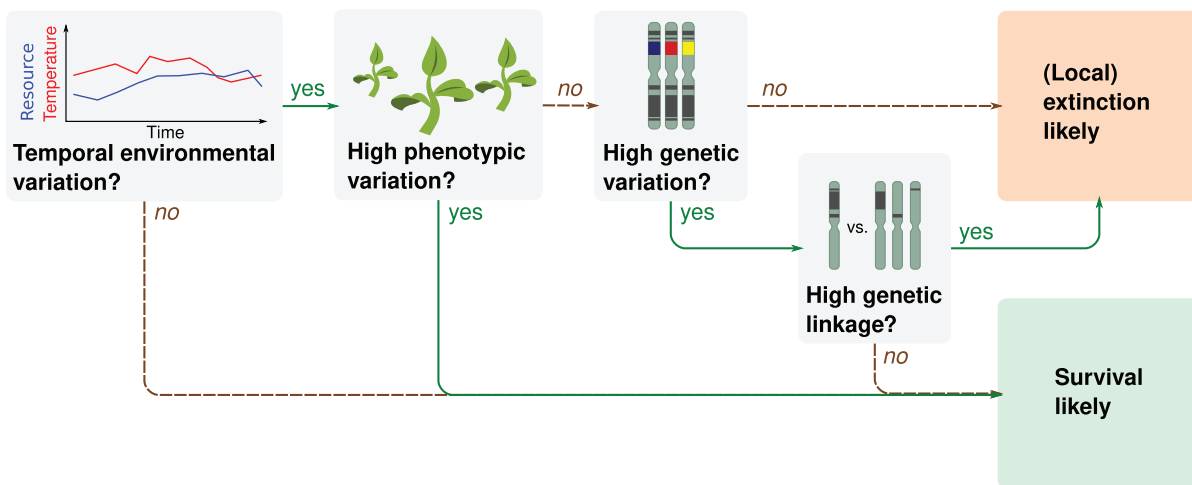


Figure 5. Phenotypic and genomic factors influencing species survival under variable environmental conditions.



scenarios could indicate the most likely scenario that the empirical community is undergoing (Overcast et al. 2019 for genetic and ecological patterns compared to biogeographical scenarios). Hence, quantification of community-wide, species-specific genetic and ecological patterns of real-world communities might be used to contrast competing hypotheses explaining empirical patterns (McGill et al. 2019 for interesting questions to be answered with eco-evolutionary models).

## Conclusion

We demonstrated complex interactions between genetic and ecological traits by using a simulation model that explicitly considers genetic architecture of plant communities in changing environments. These eco-evolutionary feedbacks broaden our understanding of the role of trait-specific standing variation in species survival and adaptation (Fig. 5). This enabled identifying ecological strategies of species to survive variable environmental conditions. Variable environments select species with higher tolerances and faster life cycles while species are selected to maintain more phenotypic variation of dispersal abilities. These adaptations are, however, mostly enabled by increasing the number of linkage units. Furthermore, we could show that selection pressure differs between traits and that there might be selection pressure to maintain higher phenotypic variation for dispersal traits and genetic variation of biomass traits.

Our findings suggest that genomes are subject to opposing forces – especially under changing conditions. While constant environmental filtering impoverishes genomes, populations and communities, there is a selective force to maintain variation at least at one organizational level for particular traits to adapt for future change. This conflict can be mediated to a certain degree by genetic architecture, namely a higher number of linkage units which allows rapid evolution based on standing variation. Additionally, traits that need quick specialization might require keeping or reducing the number of loci while reducing linkage between them. These complex interdependencies of genomic traits may further promote the high diversity in genetic architecture and ecological strategies in real-world species.

Additionally, our theoretical approach provided potential mechanisms responsible for the incongruence of phenotypic and genetic variation, which is sometimes found in nature. A mechanistic link between differential selection in those types of variation means that special care is called for when inferring genetic variation from phenotypic variation and vice versa.

In summary, this study highlights the importance of genomic traits for the functional assessment of local populations, species and metacommunities. We hope that conservation studies make more use of these characteristics to prioritize conservation efforts and expect future studies to investigate the genetic architecture of specific traits in natural populations.

## Data availability statement

Data, model code, experiment definition files and analysis scripts are available from the Github Repository <<https://github.com/CCTB-Ecomods/gemm>>.

*Acknowledgements* – Open Access funding enabled and organized by Projekt DEAL.

## Author contributions

**Ludwig Leidinger:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Daniel Vedder:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Software (supporting); Visualization (equal); Writing – review and editing (supporting). **Juliano S. Cabral:** Conceptualization (equal); Data curation (supporting); Investigation (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (supporting).

## References

- Aguilée, R. et al. 2018. Clade diversification dynamics and the biotic and abiotic controls of speciation and extinction rates. – *Nat. Comm.* 9: 3013.
- Albalat, R. and Cañestro, C. 2016. Evolution by gene loss. – *Nat. Rev. Genet.* 17: 379–391.
- Allen, A. P. et al. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. – *Proc. Natl Acad. Sci. USA* 103: 9130–9135.
- Alonso-Blanco, C. et al. 2016. 1135 genomes reveal the global pattern of polymorphism in *Arabidopsis thaliana*. – *Cell* 166: 481–491.
- Armstrong, R. A. and McGehee, R. 1980. Competitive exclusion. – *Am. Nat.* 115: 151–170.
- Bacles, C. F. E. et al. 2006. Effective seed dispersal across a fragmented landscape. – *Science* 311: 628–628.
- Barrett, R. D. H. and Schluter, D. 2008. Adaptation from standing genetic variation. – *Trends Ecol. Evol.* 23: 38–44.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bell, G. and Gonzalez, A. 2009. Evolutionary rescue can prevent extinction following environmental change. – *Ecol. Lett.* 12: 942–948.
- Berg, M. P. et al. 2010. Adapt or disperse: understanding species persistence in a changing world. – *Global Change Biol.* 16: 587–598.
- Bernhardt-Römermann, M. et al. 2011. Explaining grassland biomass the contribution of climate, species and functional diversity depends on fertilization and mowing frequency. – *J. Appl. Ecol.* 48: 1088–1097.
- Bezanson, J. et al. 2017. Julia: a fresh approach to numerical computing. – *SIAM Rev.* 59: 65–98.

- Boeye, J. et al. 2013. More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance. – *Evol. Appl.* 6: 353–364.
- Bolnick, D. I. et al. 2011. Why intraspecific trait variation matters in community ecology. – *Trends Ecol. Evol.* 26: 183–192.
- Bonte, D. et al. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. – *Oikos* 119: 560–566.
- Booth, R. E. and Grime, J. P. 2003. Effects of genetic impoverishment on plant community diversity. – *J. Ecol.* 91: 721–730.
- Bourne, E. C. et al. 2014. Between migration load and evolutionary rescue: dispersal, adaptation and the response of spatially structured populations to environmental change. – *Proc. R. Soc. B* 281: 20132795.
- Bowler, D. E. et al. 2020. Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. – *People Nat.* 2: 380–394.
- Brook, B. W. et al. 2008. Synergies among extinction drivers under global change. – *Trends Ecol. Evol.* 23: 453–460.
- Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – *Ecology* 85: 1771–1789.
- Bullock, J. M. et al. 2017. A synthesis of empirical plant dispersal kernels. – *J. Ecol.* 105: 6–19.
- Cabral, J. S. and Kreft, H. 2012. Linking ecological niche, community ecology and biogeography: insights from a mechanistic niche model. – *J. Biogeogr.* 39: 2212–2224.
- Cabral, J. S. et al. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. – *Ecography* 40: 267–280.
- Cabral, J. S. et al. 2019a. Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco-evolutionary model for plants. – *J. Biogeogr.* 46: 1569–1581.
- Cabral, J. S. et al. 2019b. Interactions between ecological, evolutionary and environmental processes unveil complex dynamics of insular plant diversity. – *J. Biogeogr.* 46: 1582–1597.
- Chesson, P. and Kuang, J. J. 2008. The interaction between predation and competition. – *Nature* 456: 235–238.
- Chipperfield, J. D. et al. 2011. On the approximation of continuous dispersal kernels in discrete-space models. – *Methods Ecol. Evol.* 2: 668–681.
- Cochrane, A. et al. 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? – *Global Ecol. Biogeogr.* 24: 12–24.
- Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – *Trends Ecol. Evol.* 15: 70–76.
- Cook, R. E. 1979. Patterns of juvenile mortality and recruitment in plants. – In: Solbrig, O. T. et al. (eds), – *Topics in plant population biology*. Macmillan Education UK, pp. 207–231.
- Cornetti, L. et al. 2016. Higher genetic diversity on mountain tops: the role of historical and contemporary processes in shaping genetic variation in the bank vole. – *Biol. J. Linn. Soc.* 118: 233–244.
- Descamps-Julien, B. and Gonzalez, A. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. – *Ecology* 86: 2815–2824.
- Deshmukh, I. K. 1984. A common relationship between precipitation and grassland peak biomass for East and southern Africa. – *Afric. J. Ecol.* 22: 181–186.
- Diáz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Domingues, V. S. et al. 2012. Evidence of adaptation from ancestral variation in young populations of beach mice. – *Evolution* 66: 3209–3223.
- Dong, Q. et al. 2004. PlantGDB, plant genome database and analysis tools. – *Nucleic Acids Res.* 32: D354–D359.
- Exposito-Alonso, M. et al. 2019. Natural selection on the *Arabidopsis thaliana* genome in present and future climates. – *Nature* 573: 126–129.
- Figueiredo, L. 2021. Extinction debt of plants, insects and biotic interactions: interactive effects of habitat fragmentation and climate change. – PhD thesis, Univ. of Würzburg, Germany.
- Fournier-Level, A. et al. 2011. A map of local adaptation in *Arabidopsis thaliana*. – *Science* 334: 86–89.
- Frachon, L. et al. 2019. Adaptation to plant communities across the genome of *Arabidopsis thaliana*. – *Mol. Biol. Evol.* 36: 1442–1456.
- Fraser, H. B. and Schadt, E. E. 2010. The quantitative genetics of phenotypic robustness. – *PLoS One* 5: e8635.
- Fung, T. et al. 2018. Quantifying species extinction risk under temporal environmental variance. – *Ecol. Complex.* 34: 139–146.
- Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. – *Am. Nat.* 146: 252–270.
- Gonçalves-Oliveira, R. C. et al. 2020. Genetic structure and gene flow among populations of *Encholirium magalhaesii*, a rocky grassland fields bromeliad. – *Braz. J. Bot.* 43: 283–290.
- Govaert, L. et al. 2019. Eco-evolutionary feed-backs – theoretical models and perspectives. – *Funct. Ecol.* 33: 13–30.
- Griffith, T. and Sultan, S. E. 2012. Field-based insights to the evolution of specialization: plasticity and fitness across habitats in a specialist/generalist species pair. – *Ecol. Evol.* 2: 778–791.
- Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based models. – *Ecol. Model.* 198: 115–126.
- Grimm, V. et al. 2010. The ODD protocol: a review and first update. – *Ecol. Model.* 221: 2760–2768.
- Hanski, I. 2001. Spatially realistic theory of metapopulation ecology. – *Naturwissenschaften* 88: 372–381.
- Harfoot, M. B. J. et al. 2014. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. – *PLoS Biol.* 12: e1001841.
- Hart, S. P. et al. 2016. How variation between individuals affects species coexistence. – *Ecol. Lett.* 19: 825–838.
- Helsen, K. et al. 2016. A direct assessment of realized seed and pollen flow within and between two isolated populations of the food-deceptive orchid *Orchis mascula*. – *Plant Biol.* 18: 139–146.
- Hermann, K. et al. 2013. Tight genetic linkage of prezygotic barrier loci creates a multifunctional speciation island in *Petunia*. – *Curr. Biol.* 23: 873–877.
- Hermisson, J. and Pennings, P. S. 2005. Soft sweeps: molecular population genetics of adaptation from standing genetic variation. – *Genetics* 169: 2335–2352.
- Holt, R. D. 1990. The microevolutionary consequences of climate change. – *Trends Ecol. Evol.* 5: 311–315.
- Howe, K. L. et al. 2020. Ensembl genomes 2020 – enabling non-vertebrate genomic research. – *Nucleic Acids Res.* 48: D689–D695.

- Hughes, A. R. et al. 2008. Ecological consequences of genetic diversity. – *Ecol. Lett.* 11: 609–623.
- Hulshof, C. M. et al. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. – *J. Veg. Sci.* 24: 921–931.
- Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. – *Ann. Bot.* 67: 15–22.
- Huston, M. and Smith, T. 1987. Plant succession: life history and competition. – *Am. Nat.* 130: 168–198.
- Johst, K. et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. – *Oikos* 98: 263–270.
- Josephs, E. B. et al. 2017. What can genome-wide association studies tell us about the evolutionary forces maintaining genetic variation for quantitative traits? – *New Phytol.* 214: 21–33.
- Joshi, J. et al. 2001. Local adaptation enhances performance of common plant species. – *Ecol. Lett.* 4: 536–544.
- Jump, A. S. and Peñuelas, J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. – *Ecol. Lett.* 8: 1010–1020.
- Karger, D. N. et al. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 1–20.
- Kassen, R. 2002. The experimental evolution of specialists, generalists and the maintenance of diversity. – *J. Evol. Biol.* 15: 173–190.
- Kattge, J. et al. 2011. TRY – a global database of plant traits. – *Global Change Biol.* 17: 2905–2935.
- Korte, A. and Farlow, A. 2013. The advantages and limitations of trait analysis with GWAS: a review. – *Plant Methods* 9: 29.
- Kraft, N. J. B. et al. 2015. Community assembly, coexistence and the environmental filtering metaphor. – *Funct. Ecol.* 29: 592–599.
- Kremer, A. et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. – *Ecol. Lett.* 15: 378–392.
- Kubisch, A. et al. 2014. Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. – *Oikos* 123: 5–22.
- Lande, R. 1984. The genetic correlation between characters maintained by selection, linkage and inbreeding. – *Genet. Res.* 44: 309–320.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Lynch, M. and Gabriel, W. 1987. Environmental tolerance. – *Am. Nat.* 129: 283–303.
- Mackay, T. F. C. 2001. The genetic architecture of quantitative traits. – *Annu. Rev. Genet.* 35: 303–339.
- Maire, V. et al. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. – *New Phytol.* 196: 497–509.
- Malchow, A.-K. et al. 2020. Rangeshiftr: an R package for individual-based simulation of spatial eco-evolutionary dynamics and species' responses to environmental change. – *bioRxiv* <<https://doi.org/10.1101/2020.11.17.384545>>.
- Maron, J. L. et al. 2004. Rapid evolution of an invasive plant. – *Ecol. Monogr.* 74: 261–280.
- Mathias, A. et al. 2001. Divergent evolution of dispersal in a heterogeneous landscape. – *Evolution* 55: 246–259.
- Matuszewski, S. et al. 2015. Catch me if you can: adaptation from standing genetic variation to a moving phenotypic optimum. – *Genetics* 200: 1255–1274.
- McGill, B. J. et al. 2019. Unifying macroecology and macroevolution to answer fundamental questions about biodiversity. – *Global Ecol. Biogeogr.* 28: 1925–1936.
- McGinley, M. A. et al. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. – *Am. Nat.* 130: 370–398.
- Menge, B. A. and Sutherland, J. P. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. – *Am. Nat.* 110: 351–369.
- Münkemüller, T. et al. 2012. From diversity indices to community assembly processes: a test with simulated data. – *Ecography* 35: 468–480.
- Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. – *Theor. Popul. Biol.* 13: 121–177.
- Oksanen, J. et al. 2018. – *Vegan: community ecology package.* – <<https://cran.r-project.org/web/packages/vegan/index.html>>.
- Olf, H. et al. 2000. Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. – *Oecologia* 125: 45–54.
- Overcast, I. et al. 2019. An integrated model of population genetics and community ecology. – *J. Biogeogr.* 46: 816–829.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Philippi, T. and Seger, J. 1989. Hedging one's evolutionary bets, revisited. – *Trends Ecol. Evol.* 4: 41–44.
- Price, C. A. et al. 2010. The metabolic theory of ecology: prospects and challenges for plant biology. – *New Phytol.* 188: 696–710.
- Pronk, T. E. et al. 2007. Coexistence by temporal partitioning of the available light in plants with different height and leaf investments. – *Ecol. Model.* 204: 349–358.
- Ramanatha Rao, V. and Hodgkin, T. 2002. Genetic diversity and conservation and utilization of plant genetic resources. – *Plant Cell Tissue Organ Culture* 68: 1–19.
- Reynolds, J. H. and Ford, E. D. 2005. Improving competition representation in theoretical models of self-thinning: a critical review. – *J. Ecol.* 93: 362–372.
- Rice, A. et al. 2019. The global biogeography of polyploid plants. – *Nat. Ecol. Evol.* 3: 265–273.
- Ricklefs, R. E. and Bermingham, E. 2002. The concept of the taxon cycle in biogeography. – *Global Ecol. Biogeogr.* 11: 353–361.
- Roxburgh, S. H. et al. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. – *Ecology* 85: 359–371.
- Sarmento Cabral, J. et al. 2013. Impacts of past habitat loss and future climate change on the range dynamics of south african proteaceae. – *Divers. Distrib.* 19: 363–376.
- Saupe, E. E. et al. 2019. Spatio-temporal climate change contributes to latitudinal diversity gradients. – *Nat. Ecol. Evol.* 3: 1419–1429.
- Savage, V. M. et al. 2004. Effects of body size and temperature on population growth. – *Am. Nat.* 163: 429–441.
- Schiffers, K. et al. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. – *Phil. Trans. R. Soc. B* 368: 20120083.
- Schiffers, K. et al. 2014. Landscape structure and genetic architecture jointly impact rates of niche evolution. – *Ecography* 37: 1218–1229.

- Sexton, J. P. et al. 2017. Evolution of ecological niche breadth. – *Annu. Rev. Ecol. Evol. Syst.* 48: 183–206.
- Shea, K. et al. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. – *Ecol. Lett.* 7: 491–508.
- Sieger, C. S. and Hovestadt, T. 2020. The degree of spatial variation relative to temporal variation influences evolution of dispersal. – *Oikos* 129: 1611–1622.
- Slatkin, M. 1974. Hedging one's evolutionary bets. – *Nature* 250: 704–705.
- Solovieff, N. et al. 2013. Pleiotropy in complex traits: challenges and strategies. – *Nat. Rev. Genet.* 14: 483–495.
- Teotónio, H. et al. 2009. Experimental evolution reveals natural selection on standing genetic variation. – *Nat. Genet.* 41: 251–257.
- Thomson, F. J. et al. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. – *J. Ecol.* 99: 1299–1307.
- Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. – In: *Species diversity in ecological communities*. Univ. of Chicago Press, pp. 13–25.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. – *Proc. R. Soc. B* 270: 467–473.
- Urban, M. C. et al. 2016. Improving the forecast for biodiversity under climate change. – *Science* 353: aad8466.
- Van de Peer, Y. et al. 2017. The evolutionary significance of polyploidy. – *Nat. Rev. Genet.* 18: 411–424.
- Vedder, D. et al. 2020. Effects of species traits and abiotic factors during the stages of plant invasions. – *BioRxiv* <<https://doi.org/10.1101/2020.04.20.050278>>.
- Vellend, M. 2016. *The theory of ecological communities* (mpb-57). – Princeton Univ. Press.
- White, J. W. et al. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. – *Oikos* 123: 385–388.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – *Ecol. Monogr.* 30: 279–338.
- Wiegand, K. et al. 2008. The role of size inequality in self-thinning: a pattern-oriented simulation model for arid savannas. – *Ecol. Model.* 210: 431–445.
- Wilson, W. G. and Abrams, P. A. 2005. Coexistence of cycling and dispersing consumer species: armstrong and mcgehee in space. – *Am. Nat.* 165: 193–205.
- Zepeda, V. and Martorell, C. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. – *Ecology* 100: e02726.