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Linking plant ecophysiology to the dynamics of diverse communities

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Abstract

The local climate represents the primary selection pressure acting on vegetation, but competitive interactions between plant strategies determine their composition. We link growth and reproduction characteristics from different plant strategies, that emerge from climatic constraints, to their competitive abilities and calculate explicitly their spatial dynamics. DIVE (Dynamics and Interactions of VEgetation), a simple generic model is built, that calculates population dynamics in the presence of perturbations, seed and resource competition. To understand the impacts of competition and perturbations on the population dynamics, a range of sensitivity experiments are conducted. DIVE simulations feature successional dynamics from fast-growing towards slow-growing plant strategies and as such corresponds to widely observed characteristics of terrestrial vegetation. Perturbations, seed and resource competition were found to affect succession and diversity, with the community composition at steady state ranging from competitive exclusion to coexistence and total extinction. We conclude that linking ecophysiological characteristics of vegetation to competition is a valid approach to determine population dynamics. Furthermore, incorporating mechanisms of perturbations and competition may be essential in order to effectively predict the response of community dynamics to changing environmental conditions.

1 Introduction

The local climate represents the primary selection pressure acting on vegetation on the global scale (Woodward, 1987), determining the general performance of plants, such as biomass and seed production. At local scales the performance of plants affects competitive interactions (e.g. for resources or between seeds for bare soil) and determines plant species composition (e.g. a large tree can exclude small grasses by overshading and may dominate vegetation). Also perturbations such as fire, disease, abiotic stress, influence vegetation composition by increasing bare area (Sousa, 1984), i.e. if due to perturbations bare area increases, high seed producing fast colonising small grasses could rapidly establish and not be excluded by larger trees.

As environmental conditions change, plant species will respond with altered performance e.g. in growth and reproduction, resulting in changed competition for bare soil and for resources between plants (Grime, 1977; Raizada et al., 2009). Such dynamics in competitive interactions along with altered perturbations will affect plant composition (Hughes, 2000; Zavaleta et al., 2003; Parmesan and Yohe, 2003; Hoegh-Guldberg et al., 2008; Sandel et al., 2010) and also ecosystem processes such as carbon and nutrient cycling (Shaver et al., 2000; Bunker et al., 2005; Fisher et al., 2010). For example a big tree that is smaller in a dryer environment over shades less, allowing small grasses to be more abundant, additionally if due to perturbations many trees die, grasses might exclude trees.

Since it is expected that different plant species respond to altered environmental conditions differentially (e.g. Körner, 1998; Sandel et al., 2010), changes in performance and therefore competition may alter steady states (meant as equilibrium vegetation or climax, Clements, 1936) and succession. Thus it seems necessary to understand how plant species composition changes along with competitive interactions, performance and climate to be able to predict how vegetation responds to environmental change.

Existing models will typically either capture physiological processes but not population dynamics, or model population dynamics but with little physiological detail. One option would now be to create overarching models, i.e. to include population dynamics in vegetation models such as the Dynamic Global Vegetation Model (DGVM) LPJ (Sitch et al., 2003) at the cost of increased model complexity.

In this work, we link how individual plant strategies cope with the environment to their population dynamics in two steps (see Fig. 1). In the first step we run the JEna DIversity JeDi Model (Kleidon and Mooney, 2000), that selects successful plant strategies from random ones via an environmental filter. JeDi understands these strategies from trade-offs such as allocation between root and shoot (e.g. Tilman, 1990). In the second step, the dynamics of these plant population strategies (PPSs) is described based on the emergent growth and reproduction characteristics. The here presented model Dynamics and Interactions of VEgetation (DIVE) then applies a biotic filter to the different PPSs to calculate their spatial dynamics. The occupied area of each PPS is calculated due to its characteristics, that translate into key demographic processes such as establishment (increase of PPS in area on bare soil), mortality (decrease of PPS in area due to death), invasion and exclusion (increase of a PPS by decreasing another one). Seeds of the PPSs compete to establish on bare soil and larger PPSs (higher biomass per m^2) can exclude smaller ones by competition for resources under the presence of varying amounts of perturbations. Perturbations summarise abiotic disturbances such as fire, disease, herbivory. A PPS can be categorised into a coloniser (grow rapidly, unable to persist in a location for long time, early successional plants, MacArthur and Wilson, 1967; Odum, 1969) or competitor (persist in a location for long time, late successional plants, MacArthur and Wilson, 1967; Odum, 1969) based on its characteristics.

With our approach, population dynamics and competitive abilities emerge as the consequence of implicit demographic processes and competition for bare soil and resources. For example, an invasion rate does not need to be predefined but is the consequence of differences in plant population specific characteristics of biomass and productivity. While models that use rule-based competition would require new rules for each new PPSs or plant functional type (PFT), DIVE easily accommodates large increases in the number of PPS, because it does not need to categorise them a priori.

Our aims are (1) to model PPS dynamics by linking ecophysiological plant performance characteristics to competitive interactions and (2) to assess the role of perturbations, competition for bare soil and resources for steady and transient states of PPS composition. We apply our model for a hypothetical tropical site and test five different PPS. We will show that with our approach, PPS characteristics translate into realistic patterns of succession and steady states. Further we show how competition for bare soil and for resources affect not only the steady state but how such steady states are reached.

2 Methods

2.1 Model overview

DIVE explicitly calculates population dynamics as the consequence of the different characteristics of PPSs, which are: biomass per occupied m^2, seed flux (total seeds produced by a PPS per unit time), specific growth rate (how fast can a seedling reach adult size), specific mortality rate (how fast is an adult removed from the occupied area).

In a first step this input of PPS characteristics could be obtained by running a process-based vegetation model that then in a second step serves the input to run DIVE (see Fig. 1). We used the process-based Jena Diversity (JeDi) Model (Kleidon and Mooney, 2000) to generate different PPSs and assess in a second step their dynamics under different intensities of perturbations, seed and resource competition. JeDi models diverse vegetation from ecophysiological assumptions and has successfully reproduced global patterns of plant diversity, abundance distributions and biomes (Kleidon and Mooney, 2000; Kleidon et al., 2009; Reu et al., 2010).

All PPSs change in area in time within a homogenous grid. Each PPS is initialised with a small amount of seeds. PPSs increase in occupied area within a grid by seeding bare area (establishment) or invading the occupied area of other PPSs. Therefore decreases in area are due to exclusion and also death (mortality). Please note that an increase in area of PPSs has no effects on its characteristics, such as biomass per m^2, because these are input for DIVE. Table 1 lists all model parameters and variables.

2.2 Population dynamics

The PPS i occupies the fractional area A_i of a grid cell, that changes due to establishment on bare area S_i, mortality M_i, invasion I_i and exclusion E_i.

$$\frac{dA_i}{dt} = S_i - M_i + I_i - E_i \qquad (1)$$

The non vegetated area A_{bare} is given by subtracting the sum over fractional areas A_k of all PPSs from the total of 100%.

$$A_{\mathrm{bare}} = 1 - \sum_{k=1}^{n} A_k \tag{2}$$

2.3 Establishment and seed competition

Establishment of new individuals is modelled by assuming that all seeds from all PPSs are well mixed over the grid. PPSs establish on bare area A_{bare}, dependent on the germination fraction g_i and on the PPS's specific growth rate $\kappa_{\mathrm{grow},i}$.

$$S_i = g_i \cdot A_{\mathrm{bare}} \cdot \kappa_{\mathrm{grow},i} \tag{3}$$

From each PPS's seed flux $f_{\mathrm{seed},i}$, we calculate the germination fraction g_i, that describes the degree of seed limitation. A value of $g_i = 1$ corresponds to no seed limitation, a value of $g_i = 0$ to complete seed limitation.

$$g_i = 1 - e^{-c_{\mathrm{R1}} \cdot A_i \cdot f_{\mathrm{seed},i}} \tag{4}$$

We model the germination fraction g_i as a saturating function of numbers of seeds, so for a certain threshold of seed number, producing more seeds does not lead to an increase in establishment, Eq. (4). To investigate what effects seed competition might have, we introduce a factor for seed competition strength, c_{R1}, that changes seed saturation. For $c_{\mathrm{R1}} \rightarrow \infty$ seeds are not limiting. Therefore PPSs effectively do not differ in their degree of seed limitation and seed production rates are not relevant for establishment (neutral seed competition). Every PPS will have the same germination fraction as long as one seed is present. Establishment includes the increase in fractional coverage of new individuals as they grow towards their adult size, but not the increase in biomass per occupied m^2 (biomass per occupied m^2 is given with the input). This rate of increase in area is captured with a PPS specific growth rate, $\kappa_{\mathrm{grow},i}$. The growth rate is determined by the biomass per occupied square meter BM_i and the productivity of a seedling $f^0_{\mathrm{npp},i}$.

$$\kappa_{\mathrm{grow},i} = \frac{f^0_{\mathrm{npp},i}}{\mathrm{BM}_i} \tag{5}$$

Note that $\frac{1}{\kappa_{\mathrm{grow},i}}$ describes how long a seedling needs to become adult. Thus, the faster a PPS grows, and the more seeds it produces, the faster it establishes.

2.4 Mortality and perturbations

Mortality M_i of PPS i, the death of individuals resulting in bare area, is modelled as the loss of coverage due to a PPS specific mortality rate $\kappa_{\mathrm{mort},i}$.

$$M_i = A_i \cdot \kappa_{\mathrm{mort},i} \tag{6}$$

The PPS specific mortality rate $\kappa_{\mathrm{mort},i}$ depends on the PPS characteristics and on a factor that scales mortality: c_{Mort}. Fast growing PPSs usually have higher turnover rates, thus die faster, the faster the metabolism the sooner a plant dies. Thus we calculate the mortality rate dependent on a PPS's biomass (e.g., McCoy and Gillooly, 2008) in relation to its Carbon losses (respiration, r_i, and litter flux, l_i). In order to investigate the effects of perturbations, we incorporate the reaction of perturbations in altered mortality by the factor c_{Mort}, that scales mortality:

$$\kappa_{\mathrm{mort},i} = c_{\mathrm{Mort}} \cdot \frac{f_{\mathrm{res},i} + f_{\mathrm{lit},i}}{\mathrm{BM}_i} \tag{7}$$

Under low perturbations, mortality is low, producing ideal conditions where PPSs do only a very low coverage due to mortality. Increasing perturbations result in increased mortality e.g. due to grazing, herbivory, disease, harshness (e.g. Chesson and Huntly, 1997; Diaz et al., 2007). Note that mortality rates are calculated analog to growth rates (see Eq. 5).

2.5 Invasion and extinction resulting from resource competition

Competition for resources is modelled implicitly by biomass dominance. We assume that size matters, in that larger plants will typically out compete smaller ones. Therefore in DIVE a large (high biomass) PPS can invade the area of smaller PPSs. Smaller ones become excluded from the grid due to e.g. being a poorer competitor for light, water or others resources (e.g. Siemann and Rogers, 2003). We calculate the competitive dominance d_i of a PPS by normalising its biomass BM_i with the total sum of biomass of all PPSs:

$$d_i = \frac{\mathrm{BM}_i}{\sum_k \mathrm{BM}_\mathrm{k}} \tag{8}$$

Note that the terms d_i are normalised such that $\sum_k d_k = 1$. From the differences of dominances of two distinct PPSs i and j we obtain the competition coefficients α_{ij}. To influence the intensity of resource competition we introduce c_{R2}: PPS do not compete for resources when $c_{\mathrm{R2}} \rightarrow \infty$, because $(d_i - d_j)^\infty = 0$.

$$\alpha_{ij} = \begin{cases} 0 & \text{if } d_i \leq d_j \\ (d_i - d_j)^{c_{\mathrm{R2}}} & \text{otherwise} \end{cases} \tag{9}$$

The more dominant PPS i outcompetes the smaller one j proportional to its coverage. Therefore PPS i invades the area A_j of the less dominant PPS j with the invasion rate x_{ij}, proportional to their competition coefficient α_{ij} and dependent on the growth rate, $\kappa_{\mathrm{grow},i}$.

$$x_{ij} = A_i \cdot \alpha_{ij} \cdot A_j \cdot \kappa_{\mathrm{grow},i} \tag{10}$$

We assume that invasion into areas occupied by other PPSs does not depend on seed production. The sum of invasions of a PPS results in its total gain I_i, while the sum of all losses results in exclusion E_i.

$$I_i = \sum_{j=1}^{n} x_{ij} \tag{11}$$

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$$E_i = \sum_{j=1}^{n} x_{ji} \tag{12}$$

Note that the sum of invasions and exclusions in one grid is balanced, so that $\sum_{i=1}^{n} I_i + \sum_{i=1}^{n} E_i = 0$.

2.6 Model application

In principle DIVE could be coupled to a process-based model, but we do a simpler uncoupled setup here, because our focus is to understand the model behaviour and the role of perturbations and competition. Therefore simulations proceeded in two stages represented in Fig. 1. The first stage involved running the JeDi model (Kleidon and Mooney, 2000) for a particular, fixed climate in order to generate a number of PPSs that are viable under such climatic conditions. Of these viable PPSs, five were selected with their characteristics forming the basis for DIVE simulations. The second stage involved running the DIVE model with the five selected PPSs and calculating the rate of change of the occupied areas of these PPSs over different intensities of resource competition, seed competition and perturbations. We only use five different PPSs in order to demonstrate the dynamics.

The details for the JeDi first step are as follows. JeDi was run for one grid in a constant tropical like climate (precipitation: $1.4 \times 10^{-7}\,\mathrm{m\,s^{-1}}$, radiation: fRADs: $278\,\mathrm{W\,m^{-2}}$, temperature: 290 K). 500 PPSs were seeded, each grew, reproduced or died in isolation from all others. By 500 years, all PPSs were at equilibrium with 386 of the initial populations becoming extinct (having zero biomass and not producing any seeds). From the 114 viable populations, five were chosen that reflected the range of different growing strategies, such as coloniser or competitor. The five PPSs are shown in Fig. 2.

The values of the characteristics of the five PPSs can be seen in Table 2, and are compared to each other in Fig. 2. They are ordered by dominance from high to low and described in the follow: PPS 1 is the most dominant with very low seed flux, mortality and growth rate. It could be a very big tree with low seed production. PPS 2 is less dominant but has a high seed flux with low growth and mortality rate, e.g. a tree with high seed production. PPS 3 is low dominant with high seed flux and low growth rate, e.g. a shrub with low seed production. PPS 4 has a high growth rate but very small seed flux, e.g. a grass with low seed flux. Note that the ratio between specific growth and mortality rate is high. PPS 5 has the second highest growth rate and intermediate seed flux. It is not dominant, and might express a high seed producing grass.

The details for DIVE simulations, the second step, are as follows. Seeds from the five selected PPSs were planted by assuming that $A_i(t=0)=1$, in an initially bare area: $A_{\mathrm{bare}}=1$. The rate of change over daily time steps was recorded under different competition and perturbation conditions as detailed in the Methods section and described in the next paragraph.

To evaluate the role of resource, seed competition and perturbations for steady state of population dynamics and transient states with DIVE, we do different sensitivity analysis. For each different seed competition, resource competition and perturbation, a sensitivity simulation was conducted. First we varied the perturbing parameter, $c_{\mathrm{Mort}}=(0.001, 0.05, 0.1, 1, 10)$ when competition between PPSs is operating, in order to assess the impact of perturbations. Second, we assessed the impacts of seed and resource competition via sensitivity studies in which combinations of strong ($c_{\mathrm{R1}}=1$) or neutral seed competition ($c_{\mathrm{R1}}=10^9$) with strong ($c_{\mathrm{R2}}=1$) or neutral resource competition ($c_{\mathrm{R1}}=10^9$) under two values of perturbation, $c_{\mathrm{Mort}}=0.05$ and 1. Third, we vary the strength of both types of competition continually from strong to neutral to investigate the effects of competition on diversity. Diversity is measured as the Shannon index of biodiversity: $H=-\sum_{i=1}^{n}(\frac{A_i}{\sum_k A_k}\cdot\log(\frac{A_i}{\sum_k A_k}))$. Diversity is minimal ($H=0$) if not more than 1 PPS occupies an area $A_i>0$. Diversity is maximised ($H=1.61$) if all PPSs occupy equal areas.

3 Results

Below, we show the time-series of population dynamics using DIVE capturing sensitivities of perturbations, seed and resource competition. We found that the change in the area of PPSs in DIVE was similar to the successional dynamics observed in a wide range of ecosystems. Perturbations and competition were found to alter population dynamics in transient and steady states. Figures 3 and 4 show how successional dynamics alter with these factors. Table 3 summarizes how seed and resource competition under different intensities of perturbations affect the steady state of composition. Figure 5 shows the dependency of diversity on competition.

3.1 The role of perturbations

Successional stages range from fast growing, small adult sized PPSs (PPS 5 and 3) to slow growing, large adult sized PPSs (PPSs 2 and 1) (Fig. 3). Under conditions of low perturbations and with both seed and resource competition operating, the largest PPS (1) competitively excludes all others. The successional progression towards this steady state can be seen in Fig. 3a in which PPS 1 is the last to increase in area, but then excludes all other PPS. As the intensity of perturbations increases, the smaller, faster reproducing PPS 2 increases in area (Fig. 3b–d). For a wide range of intensity of perturbations two PPSs co-exist (1 and 2, then 2 and 3) with the selection for slow and fast growing PPSs changing as the intensity of perturbations increases.

3.2 The role of competition under different perturbations

Table 3 summarizes how competition and perturbations lead to the steady state, while Fig. 4 shows the successional dynamics. Under conditions of low to intermediate perturbations, turning off resource competition leads to high importance of seed flux. Initially PPS 5 is the only present population because it is able to rapidly colonise all available bare area (Fig. 4b). Later, PPSs 2 and 3 with the highest seed flux increase in area and stably co-exist while excluding all other PPSs. This situation is reversed by turning off seed competition, while resource competition is turned on. See Fig. 4c for the results of this strong selection for size or dominance, where PPS 1 almost covers the complete area in steady state. Primary succession also has changed, PPS 5 as most successful is replaced by PPS 4. However all five PPSs are present in early succession. Turning both forms of competition off leads to the emergence of PPS 4 (Fig. 4d); described as the G/M PPS in Table 3. In steady state all PPSs are present.

Increasing perturbations to intermediate and high levels leads to coexistence of at least two PPSs irrespective of strength of seed and resource competition (Fig. 4e–h). Under such conditions there are two main regimes in which either the PPS with greatest seed flux or best growth-mortality relationship will occupy most area. Seed competition always leads to PPS 2 with highest seed flux to occupy most area, co-existing with PPS 3 (Fig. 4e, f). PPS 4 with best growth-mortality relationship will be most successful when seed competition is off (Fig. 4g, h). As competition operates PPS 1 is still the second most successful PPS (Fig. 4h).

Even higher levels of perturbations leads to a decrease in total coverage of area and the effective extinction of those PPSs that do not have a high seed flux. Under such perturbations, only those PPS that are able to produce large numbers of seeds to colonise the large amount of bare area can persist (only shown for competition operating in Fig. 3e).

3.3 The role of competition and perturbations for diversity

The sensitivities of diversity, measured as Shannon Information Entropy, are shown in Fig. 5. Under low perturbations (Fig. 5a), high strength of both types of competition results in no diversity (bottom left). As competition strengths decrease, diversity increases, PPSs coexist. Under high resource competition, seed competition does only partly affect diversity in steady state, while varying resource competition for one strength of seed competition strongly affects diversity (Fig. 5a). Therefore, under low perturbations (low mortality), resource competition has a strong impact on population composition, while seed competition is less important. For high perturbations, it is the reverse (Fig. 5c): while resource competition has no effect, seed competition is very important. For intermediate perturbations, a shift between both happens (Fig. 5b). Consequently, under increasing perturbations, diversity is decreasingly affected by resources competition while increasingly by seed competition.

4 Discussion

We next review our results, to see if the model leads to a realistic behaviour. In the follow we talk about limitations in DIVE and benefits of DIVE compared to other model approaches. We conclude the section with a discussion of future developments and applications of the DIVE model.

4.1 Population dynamics

4.1.1 Succession

Communities in early succession are usually dominated by fast-growing species, while in later succession by slow-growing species (competitor) (Odum, 1969). DIVE successfully reproduced such successional dynamics. Fast growing species are represented in DIVE by PPSs that rapidly establish due to a high growth rate and high seed flux (colonisers). Competitive PPSs are large and represent slow growing species in the real world. In early succession in a DIVE simulation, colonisers are high abundant, competitors are at low abundance and so competition for resources plays a minor role in determining PPS composition. As bare area becomes limited, establishment decreases and colonisers are replaced by competitors as it is found in the real world (e.g. Huston and Smith, 1987). The role of invasion and exclusion (resource competition) increases in importance with respect to establishment. As PPSs compete for resources, large PPSs steadily invade the area occupied by smaller PPS, excluding them due that they e.g. capture most of available light (Tilman, 1990). When small PPSs are not able to compensate exclusion with establishment, they go extinct.

4.1.2 The role of perturbations

Consistent with Johst and Huth (2005) under low perturbations PPS composition was determined by late-successional strategies (competitors), while under high perturbations by early successional strategies (coloniser). The intensity of perturbations can affect how effective less dominant PPS are at reclaiming area via establishment and so can determine whether steady states of competitive exclusion or coexistence are achieved. This relationship between perturbation and coexistence may be seen as support for the Intermediate Disturbance Hypothesis (e.g. Grime, 1973; Connell and Fox, 1979), that proposes diversity is maximised over intermediate intensity of perturbations or disturbances.

While in the study of Fisher et al. (2010) altered mortality had no significant effects on the global scale for plant functional type composition, we found perturbations controlling mortality to be an important factor on the grid level of how and what steady states are reached. Diaz et al. (2007) also concluded, that grazing which expresses a perturbation interacts with species composition, suggesting that this is an important assumption that should be included in models. Also fire plays an important role for vegetation, because it resets succession. Consequently models that do not capture fire as a disturbance may fail to predict vegetation patterns for certain biomes such as savannahs (Thonicke et al., 2001).

4.1.3 The role of competition

Competition does matter for population dynamics. Using DIVE we are able to evaluate the role of competition for resources and bare soil independently. Different steady states are reached and the way towards these differ for varying strength of seed and resource competition. Arora and Boer (2006) obtained same results by changing one parameter that controlled seed limitation and resource competition. However, with DIVE we are able to distinguish resource from seed competition and can show that both processes have different effects, especially when perturbations come into play. For example, with no seed competition (seeds are effectively unlimited) diversity is high during succession before decreasing to the competitive exclusion steady state. Higher diversity at steady state requires intermediate levels of perturbations when there is no seed competition. However, realistic successional patterns were only obtained, when both resource and seed competition operate.

4.2 Benefits and limitation of the DIVE approach

DIVE links performance of PPSs under climatic conditions to the resulting competition between PPS. Such an approach allows that characteristics e.g. a species specific invasion rate or dominance do not need to be predefined, as it is done commonly in vegetation models (e.g. Arora and Boer, 2006; Cox, 2001), because they are emergent properties. This allows that such properties can change over time along with climate change, and may lead to better characterisation of vegetation composition under future climate. The DIVE approach could be used coupled to Global Vegetation Models (e.g., Box, 1981; Foley et al., 1996; Sitch et al., 2003; Woodward and Lomas, 2004), where each plant functional type (PFT) serves via the climatic filter the necessary information used in DIVE to calculate the occupied area of each PFT.

DIVE does not represent dynamics or competition of individual plants. It rather uses aggregated informations that describes a whole PPS by one set of characteristics. Space is considered to be homogeneous. These assumptions allow us to abstract spatially explicit dynamics of individuals into spatially implicit dynamics of well mixed PPSs, leading to an approach of intermediate complexity.

DIVE models competition implicitly by assuming that large PPS outcompete smaller ones that result in invasions. This assumption is to a first approximation reasonable, since differences in competitive ability result mainly on differences in size, because e.g. resource acquisition depends on size (Bengtsson et al., 1994; Keating and Aarssen,

2009) and smaller plants are over shaded by larger ones (Siemann and Rogers, 2003). DIVE does not use rules based on predefined characteristics as Dynamics Global Vegetation Models (DGVM) do, such as to predefine a PFT as tree-like that will excludes all shrub-like PFTs (e.g. Sitch et al., 2003; Arora and Boer, 2006; Cox, 2001). It rather uses emergent functional relationships, such as biomass or productivity, that then reflect a population's strategy in being a coloniser or competitor. The performance of a PPS directly affects these abilities via e.g. the intrinsic growth rate (Huston, 1979) or seed production (Angert et al., 2009).

In DIVE competition between plants is always considered as negative. However, interactions can also be positive, resulting in increased performance of neighbouring plants, e.g. a large plant shades a plant adapted to shade (Callaway et al., 2002). With our approach we do not address such facilitative interactions and assume that these are of secondary importance for community dynamics at larger scales.

The intensity of perturbation was shown to significantly affect population dynamics. The perturbation parameter c_{Mort} in DIVE implicitly models a range of different perturbations as a constant response, while they could be modelled also stochastically. Stochastic perturbation events have major impacts on vegetation dynamics (Johst and Huth, 2005), and could be further integrated in DIVE. However, perturbation rates are unknown and it might be needed to determine specific values for specific regions of the Earth. Going further, perturbation processes could be modelled explicitly within DIVE, e.g. also dependent on the current vegetation composition. It may also be necessary to introduce PPS specific perturbation parameters as not all PPSs will be affected by the same magnitude by the same perturbation. But then it is important that the response to a perturbation is reflected in a certain trade-off.

Strength of seed and resource competition are also difficult to determine. Since we showed that considering competition leads to plausible population dynamics, we suggest competition remains strong in DIVE simulations.

It was shown, that transient dynamics, where a system in equilibrium due to a disturbance or perturbation moves towards a new steady state, can be very complex

(Hastings, 2004; Stott et al., 2010). Ecological communities might never get into a steady state (Wallington et al., 2005) and time for response can be very different (Sandel et al., 2010). Models calculating vegetation dynamics should be aware of the importance of transient dynamics for vegetation composition. Especially when predicting biomass under climate change scenarios, estimates are uncertain (Rammig et al., 2010) and depend on vegetation composition (Fisher et al., 2010). With DIVE transient states are captured, because it does not assume steady states. In general, if we want to use DIVE in realistic vegetation simulations, it needs to be coupled to a vegetation model such as JeDi. In each time step JeDi would determine the performance and characteristics of each PPS, that would translate into the community dynamics. It will be necessary to choose values of the free parameters c_{Mort}, c_{R1} and c_{R2}. The model could be run with a certain setup. If e.g. the successional dynamics reproduce observations, some good estimates for the free parameters could be found. Then the model can be used for future climates.

5 Conclusions

In this work we introduced DIVE (Dynamic Interactions of VEgetation) a simple model that captures vegetation dynamics from perturbations and competition between plant population strategies (PPSs). DIVE is based on the fundamental assumption that vegetation is not necessarily at steady state. The motivation was to capture these assumptions by using emergent plant strategy specific growth and reproduction properties with an approach that would be scalable for producing predictions for vegetation response to both local and global changes. This study can be understood as a proof of concept for an approach to model competition and the effects of perturbations at a global scale by linking plant strategy performance to spatial dynamics.

We found that DIVE reasonably reproduces successional dynamics from fast to slow growing plant strategies. We have shown that competition between PPSs that compete for limited resources under the presence of a wide range of perturbations can have significant effects on the PPS composition in steady states and how such steady states are transited to. This suggests the when modelling vegetation at global scales, perturbation and competition need to be considered.

In future work DIVE can be coupled to other vegetation models to address vegetation dynamics and diversity issues. Coupled to a process-based diversity model such as JeDi (Kleidon and Mooney, 2000), would allow us to address how vegetation composition may shift under climate change and affect global vegetation pattern and carbon fluxes, because altered emergent characteristics of growth and reproduction will affect population dynamics. Especially when predicting current vegetation's response to future climates, it may be essential to capture competition not only for determining steady states, but how existent PPSs change over time towards steady states or more complex dynamics.

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Table 1. Model parameters used in DIVE.

Symbol	Meaning	Unit/Value
Input: PPS performance		
BM$_i$	total biomass of *i* per occupied m^2	gC m^{-2}
$f_{\mathrm{seed},i}$	seed flux of *i* per occ. m^2	gC m^{-2} d^{-1}
$f^0_{\mathrm{npp},i}$	seed productivity of *i* per occ. m^2	gC m^{-2} d^{-1}
$f_{\mathrm{lit},i}$	litter flux of *i* per occ. m^2	gC m^{-2} d^{-1}
$f_{\mathrm{res},i}$	respiration of *i* per occ. m^2	gC m^{-2} d^{-1}
Derived PPS characteristics		
d_i	dominance of *i*	
$\kappa_{\mathrm{grow},i}$	specific growth rate	d^{-1}
$\kappa_{\mathrm{mort},i}$	specific mortality rate	d^{-1}
g_i	germination fraction, seed limitation	
α_{ij}	competition coefficient	
x_{ij}	invasion rates	d^{-1}
State variables and area rates		
A_i	fractional coverage of PPS *i*	
S_i	rate of establishment of PPS *i*	d^{-1}
I_i	rate of invasion of PPS *i*	d^{-1}
E_i	rate of exclusion of PPS *i*	d^{-1}
M_i	rate of mortality of PPS *i*	d^{-1}
A_{bare}	fractional non covered area	
Parameters		
c_{R1}	seed competition strength	$[1,\infty]$ m^2 d gC^{-1}
c_{R2}	resource competition strength	$[1,\infty]$
c_{Mort}	perturbation factor	$[10^{-3},10^2]$

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Table 2. Values of PPS characteristics.

	d_i	$f_{\mathrm{seed},i}$ [gC m^{-2} d^{-1}]	$\kappa_{\mathrm{grow},i}$ [d^{-1}]	$\kappa_{\mathrm{mort},i}$ [d^{-1}]
PPS1	0.49672416	0.05936389	0.0003532702	0.0002462552
PPS2	0.36854641	1.45684800	0.0004131365	0.0003107458
PPS3	0.11228805	1.27272900	0.0012683940	0.0009588134
PPS4	0.01202068	0.04679167	0.0120577500	0.0017684150
PPS5	0.01042070	0.68838450	0.0051505500	0.0028644800

Table 3. Summary of impacts of competition and perturbations for steady state of population dynamics. The most important characteristic to be most abundant in steady state is given and if competitive exclusion (excl) or coexistence (coex) occur. If non of both types of competition operate, the ratio $\kappa_{\text{grow}}/\kappa_{\text{mort}}$ (G/M) is important for being abundant.

Seed comp	Res. comp	Most abundant	Result	Fig.
Low-intermediate perturbations				
on	on	size	excl or coex	4a
on	off	seed flux	coex	4b
off	on	size	excl or coex	4c
off	off	G/M	coex	4d
Intermediate-high perturbations				
on	on	seed flux	coex	4e
on	off	seed flux	coex	4f
off	on	G/M, size	coex	4g
off	off	G/M	coex	4h

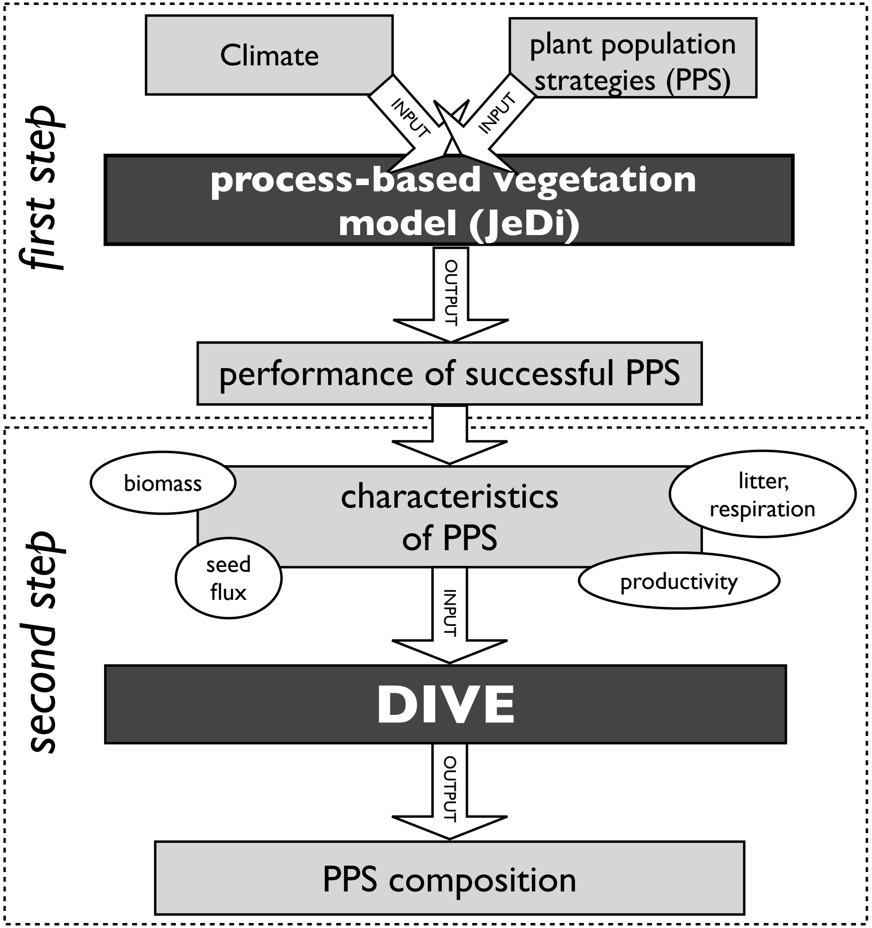

Fig. 1. Flow chart diagram of the model setup. First JeDi is run to produce the necessary input for DIVE (ellipses) to calculate population dynamics by competiton.

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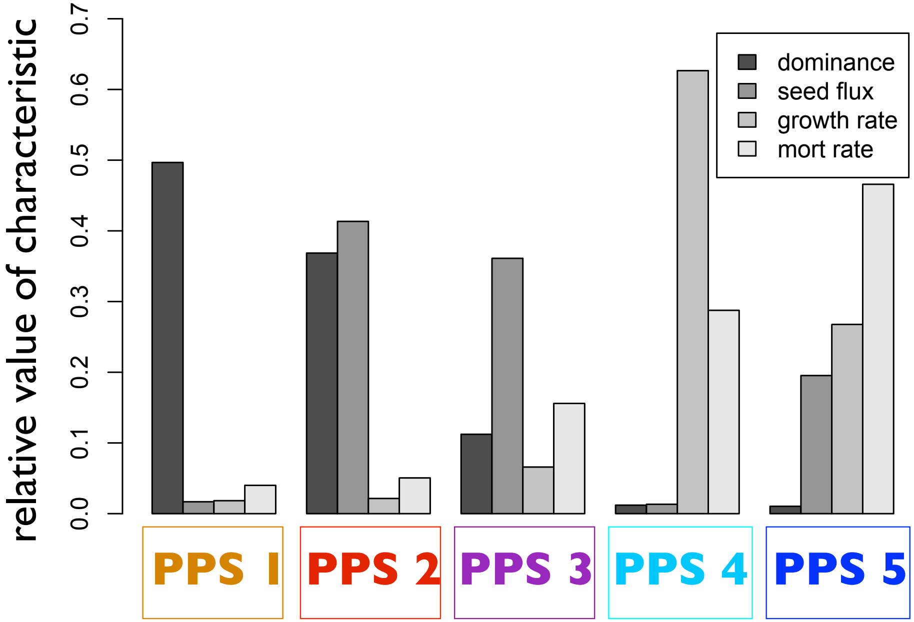

Fig. 2. The five PPSs, each expressed by a different colour with their four characteristics (dominance, seed flux, growth rate κ_{grow} and mortality rate κ_{mort}). The colours refer to the same PPSs in the following figures. Characteristic are normalised.

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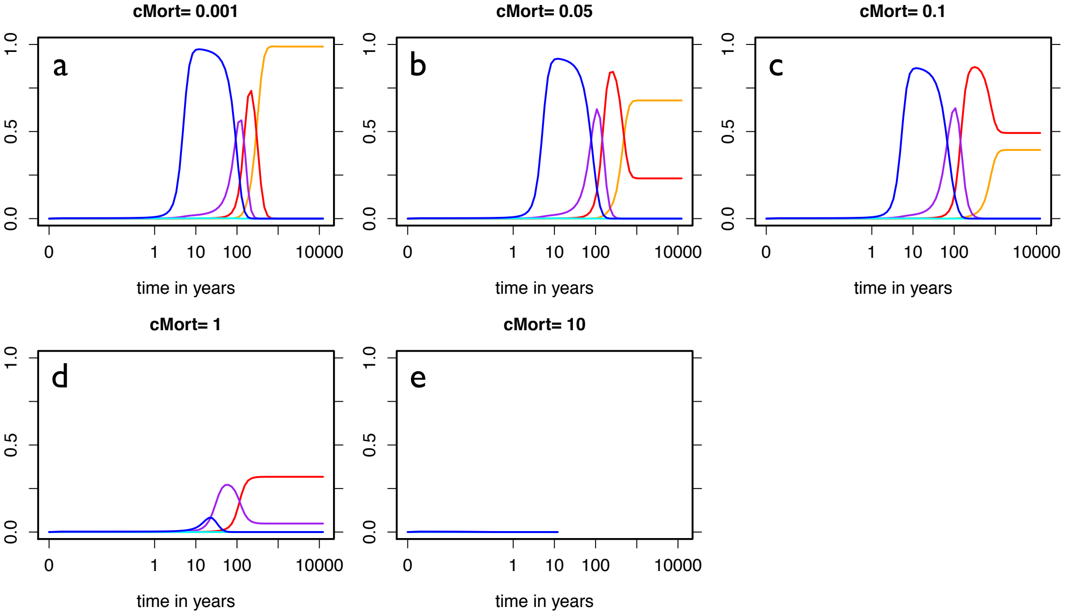

Fig. 3. Time-series of population dynamics under increased perturbations (c_{MORT}) from **(a** to **e)**. The time in years is on logarithmic scale, the *y*-axis shows the relative abundance or occupied area of each PPS. Colours refer to coloured PPSs in Fig. 2. PPSs interact between seeds and for resources.

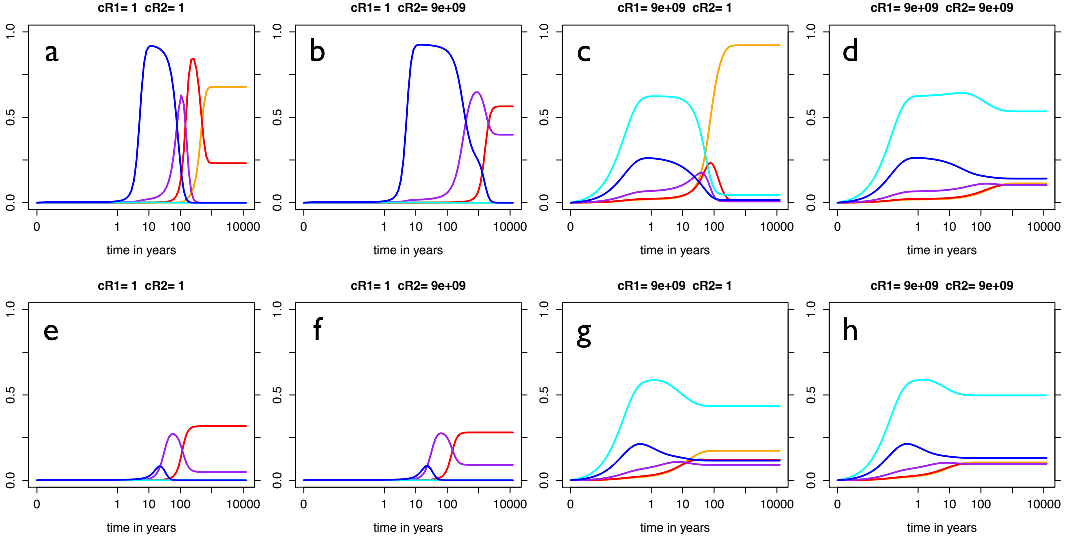

Fig. 4. Time-series of population dynamics for seed competition working (c_{R1}=1) or neutral (c_{R1}=9e+9), resource competition working (c_{R2}=1) or neutral (c_{R2}=9e+9) for c_{Mort}=0.05 **(a–d)** and c_{Mort}=1 **(e–h)**. Each colour represents the coverage of a PPS, corresponding to Fig. 2.

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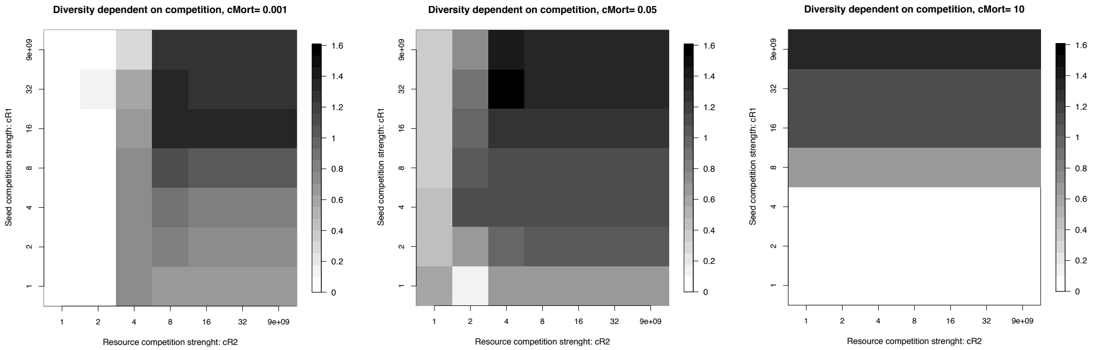

(a) low perturbations (b) intermediate perturbations (c) high perturbations

Fig. 5. Each point represents the diversity (Shannon Information Entropy) after 10 000 years of a DIVE simulation dependent on seed (y-axis) and resource competition (x-axis). Strength of seed competition decrease bottom to top, strength of resource competition decrease from left to right.

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