Bridging ecophysiological trade-offs and population dynamics – How competition and climate shape community structure

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Summary

The regional climate is the primary selective factor for whether a plant species is successful or not. Under favorable climatic conditions more species can thrive than under unfavorable conditions. Furthermore, it is competitive interactions that strongly affect the relative abundances of plant species within communities through competition for light, water, or space. Additionally disturbances such as fire or wind throw can strongly affect community composition. Examine the abundances of plants in a realistic community therefore still remains as challenging. In my thesis I investigate the role of competition, disturbances and climate on the development of vegetation community structure and diversity patterns.

To answer these research questions the model DIVE (Dynamics and Interactions of VEgetation) has been developed. It determines population dynamics of plant communities while calculating the abundances of each plant species dependent on its establishment at open sites, competition for occupied sites and mortality in the presence of different rates of disturbances and strengths of r- and K-selection. Thereby r-selection favors the selection of colonizers that quickly establish on open sites and K-selection favors the selection of competitors that grow slowly but can exclude less competitive plants. As follows, r-selection influences establishment, K-selection competition and the disturbance rate mortality.

DIVE is a simple general model linking plant strategies to their competitive dynamics, using growth and reproduction characteristics. These characteristics serve as input information for DIVE. The input information for DIVE is gains from simulations with the JeDi (Jena Diversity) model. This model simulates a variety of hypothetical functional plant strategies that emerge from climatic constraints. Thereby our approach bridges from theoretical population dynamics models such as Lotka-Volterra to realistic vegetation models, which calculate biogeochemical exchange fluxes but usually simulate only a few so called plant functional types instead of diverse communities. In the first study of my thesis examined the dynamics of DIVE using a community out of 5 plant strategies under different sensitivities of strength of r- and K-selection and disturbances. The results show that the simulated successional dynamics are reasonable if K-selection is present. Under K-selection big competitive strategies slowly overgrow the smaller ones. The highest levels of diversity are found in simulations in the absence of selection. Under high levels of selection strength, intermediate levels of disturbances are required to obtain coexistence.

The second study investigates the relation of diversity to disturbances. The results show that, depending on the presence or absence of r- or K-selection, four different diversity-disturbance curves appear: flat under absence of selection, increasing under K-selection, decreasing under r-selection and hump-shaped under r- and K-selection. We show that these curves develop through the different realizations of the colonization-competition trade-off. This trade-off means, that either a plant strategy can quickly occupy open sites or it can competitively exclude smaller strategies.

The second study blocked out the role of climate, as simulation were done for a moist tropical climate only. But climate in fact represents a first filter that sorts out plant strategies, while competition can be seen as second additional filter. The third study therefore explores the effects of climate onto the relation of diversity to disturbances using four different climates: a moist and a dry tropical climate and a warm and a cold temperate climate. First of all, in absence of selection the model reproduces the observed diversity gradient from the poles towards the tropics. The temperate climates are more restricted to high disturbances than the tropical ones. Therefore in our simulations flat diversity-disturbance curves are only observed in the tropical climates. Nevertheless an additional increase in disturbances would also lead in the tropical climates to no strategies surviving. Further r- and K-selection show the same effects in the different climates, as already proposed in the second study. Interestingly the tropics are highly influenced by strong r-selection which means that diversity proportionally decreases while in the cold temperate climates r-selection takes the less influence. Remarkably under both strong r- and K-selection the warm temperate climate reach highest diversity.

My thesis shows the importance of competition for population dynamics. During this thesis the first model has been developed that independently controls strength of r- and K-selection. The results can help to explain found diversity-disturbance relations with strength of selection. Furthermore, because of the simplicity and generality of DIVE, it could be used to understand vegetation structure and functioning at the global scale and the response of vegetation to global change.

Zusammenfassung

Die klimatischen Bedingungen bestimmen in erster Linier, ob eine Pflanze in ihrer Umwelt überleben kann oder nicht. So existieren z.B. unter einem Klima mehr Arten als in einem anderen. Auf der anderen Seite, sind es die Interaktionen zwischen einzelnen Pflanzen, wie z.B. Wettbewerb um Raum, Licht oder Wasser, die die Häufigkeit der einzelnen Arten bestimmen. Weiterhin können Störungen, z.B. Feuer oder Dürren, die Artzusammensetzung stark beeinflussen. Der Erfolg einer Art hängt also von vielen verschiedenen Faktoren ab, wodurch es auch heutzutage noch sehr schwer ist, Artzusammensetzungen zu berechnen.

Die vorliegende Dissertation untersucht die Rolle von Wettbewerb, Störungen und Klima auf die Zusammensetzung der Pflanzengemeinschaften und auf Mustern von pflanzlicher Artenvielfalt.

Um die bestehende Frage anzugehen, wird als erstes ein Modell entwickelt (DIVE), welches Populationsdynamik von verschiedenen Artgemeinschaften berechnet. DIVE berechnet die Abundanz einer jeden Art in Abhängigkeit von ihrer Neuansiedlung und ihrem Sterben sowie dem Wettbewerb um bereits besetzten Raum. Diese drei Prozesse werden beeinflusst von drei Sensitivitätsparametern: der Stärke der r-Selektion, die die Neuansiedlungsrate verändert, der Stärke für K-Selektion, die die Stärke des Wettbewerb verändert, und die Störungsrate, die die Sterberate beeinflusst. Die Populationsdynamik, also z.B. Sukzession, verändert sich in Abhängigkeit der gewählten drei Sensitivitätsparameter.

Wie jedes Populationsmodell, benötigt auch das Modell DIVE Parameter der modellierten Arten, um die Populationsdynamik zu berechnen, wie z.B. Wachstumsrate, Sterberate, Samenproduktion und Biomasse. Wir benutzen das Model Jena Diversity (JeDi) - DGVM um diese Daten zu erzeugen. JeDi-DGVM, ein Vegetationsmodell, wendet einen klimatischen Filter auf hypothetische funktionelle pflanzliche Wachstumsstrategien an, übrig bleiben die Typen, die das Klima überleben. Damit schließt unser Ansatz eine Brücke zwischen den sehr theoretischen Populationsmodellen, wie z.B. Lotka-Volterra, und den realistischen Vegetationsmodellen, die zwar biogeochemische Kreisläufe berechnen, aber Vielfalt kaum beachten.

Die erste Studie dieser Arbeit untersucht die Dynamik des Modells DIVE mithilfe einer 5-Arten Gemeinschaft mit unterschiedlichen Stärken von r- und K-Selektion und Störungen. Die Sukzessionsdynamik ist plausibel unter K-Selektion, denn dann überwachsen größere Arten langsam die kleineren. Die höchste Artenvielfalt wird in Simulationen erzeugt, in der r- und K-Selektion sehr schwach ist. Wenn r- und K-Selektion stark sind, führen mittlere Störungen zur Koexistenz von verschiedenen Pflanzenstrategien. Dieses Szenario bestätigt damit die Hypothese, die sagt, dass Diversität am höchsten ist unter mittleren Störungen.

Die zweite Studie untersucht die Beziehung von Diversität zu Störungen in einem feucht tropischen Klima. Es wird festgestellt, dass je nach dem ob r- oder K-Selektion wirkt, sich vier Beziehungen ergeben: eine flache Kurve ohne Selektion, eine ansteigende Kurve unter ausschließlich K-Selektion, eine abnehmende Kurve unter ausschließlich r-Selektion und eine buckelartige Kurve unter r- und K-Selektion. Wir zeigen den Grund dafür auf, nämlich dass r- und K-Selektion jeweils unterschiedliche Pflanzenstrategien fördern. Strategien, die eher schnell freie Flächen besiedeln werden durch r-Selektion gefördert, während K-Selektion solche fördert, die wettbewerbsfähig sein aber langsam wachsen (colonization-competition trade-off).

In der dritten Studie untersuchen wir die Auswirkungen des Klimas auf die Beziehung von Diversität zu Störungen, denn in der zweiten Studie wurde die Bedeutung des Klimas ausgeblendet. Wobei das Klima ja eine Schlüsselrolle spielt, denn es wirkt wie ein erster Filter, der pflanzliche Strategien aussortiert, die hier nicht überleben können. Wettbewerb wirkt dann als ein zweiter Filter. In dieser Studie wurden vier verschiede Klimate untersucht: immerfeuchte Tropen, wechselfeuchte Tropen, warmgemäßigte Zone und kaltgemäßigte Zone. In erster Linie stellen wir fest, dass wir ohne Selektion die typische Diversitätsreihenfolge von den Tropen zu den Polen erhalten. Die gemäßigte Zone ist stärker von hohen Störungen limitiert als die Tropen, daher ist die Beziehung zwischen Diversität und Störungen nur in den tropischen Klimaten eine flache Kurve. Nichtsdestotrotz, würde man den gleichen Effekt in den Tropen erwarten, unter noch höheren Störungen. Ansonsten haben r- und K-Selektion die gleichen Auswirkungen in alles Klimaten auf die Beziehung von Diversität zu Störungen. Bemerkenswert ist, dass in den Tropen r-Selektion besonders starke Auswirkungen auf die Diversität hat, also die Diversität besonders stark erniedrigt. Während in der kaltgemäßigten Zone r-Selektion weniger Einfluss hat. Interessanterweise erreicht unter starker r- und K-Selektion die warmgemäßigten Zone die höchste Diversität.

Diese Dissertation zeigt auf, wie wichtig Wettbewerb für die Populationsdynamik ist. Es wird zum ersten Mal ein Modell konstruiert, dass r- und K-Selektion in unterschiedlichen Stärken und unabhängig voneinander testen kann. Unsere Ergebnisse können helfen gefundene Beziehungen von Diversität zu Störungen anhand von möglichen Stärken für Selektion zu erklären. Weiterhin können wir mit unserem Modell gekoppelt an Globale Vegetationsmodelle untersuchen wie Klimaveränderungen Vegetation, Diversitätsmuster und Kohlenstoffausstausch beeinflussen.

Chapter 1

Introduction

The coexistence of different species from a limited number of resources has long been a scientific question. For example, the competitive exclusion principle of Gause (1934) states, that the number of limiting resources restrict the number of coexisting species. This means, if two species compete for the same resource, one will go extinct. Nevertheless, in nature, many species can coexist while competing for only a few limited resources (e.g. Hutchinson, 1961). Furthermore, at different geographic regions, a different number of species coexist, so diversity varies over the globe. Many hypotheses have been developed to answer this paradox of coexistence and to investigate the drivers of the diversity gradient (see e.g. Huston, 1979; Palmer, 1994; Willig et al., 2003). Three important factors that shape diversity and coexistence are: climate, competition and disturbances. In this thesis, we investigate the role of these three factors in influencing plant diversity patterns across the global land surface.

The first step toward understanding plant diversity pattern requires the development of a model of interacting plants. Although the theoretical knowledge about why species coexist has increased (e.g. Willig et al., 2003), it is still quite difficult to simulate species coexistence in order to realistically reproduce community processes. Computer models are currently used from simulating species coexistence (theoretical models), forest dynamics (gap models), and simulating global vegetation and biogeochemical fluxes (vegetation models). In this way, different applications require different model approaches. Our desire to simulate species coexistence will need to utilize components of each of the model types. These model types will first be described, and then summarized based on how they will utilized in this thesis.

Theoretical models

Theoretical models can simulate the growth of single species (e.g. Verhulst's equation, 1838) or how different species interact (e.g. predator-prey dynamics, (Lotka, 1920; Volterra, 1926)). Later, space was included in models and provided a solution for Hutchinson's problem. Different spatial models have been developed, leading to coexistence of many different species (see Tilman and Kareiva, 1997, for examples). For example, Tilman (1994) developed a spatial model, where individual species interact through competition. This model is characterized by an hierarchical order of competing plant species. Each competitor can only invade areas, that are occupied by less competitive plants. Additionally, each plant is characterized by a mortality and a colonization rate. The rates of mortality and colonization, under which coexistence is possible, can be gained by solving the model analytically. This represents a common feature of theoretical models. So, plants coexist if the loss of area of less competitive species is balanced by a lower mortality and higher colonization rate. This reflects a trade-off in the competitive versus the colonizing ability, which is a critical component of our study. This fundamental trade-off has been explored in different forms. For example, MacArthur and Wilson (1967) described a colonizers as r-strategist and a competitor as K-strategist.

Vegetation models

Global vegetation models simulate vegetation based on a few plant functional types and are able to simulate global biogeographical and biogeochemical patterns (e.g. Woodward and Lomas, 2004; Foley et al., 1996; Hughes et al., 2006; Sitch et al., 2003). The usage of a few fixed prescribed plant functional types (Box, 1996) has its limitations. Global vegetation models predict the amazon dieback (Betts et al., 2004). Such big vegetation changes can happen, if only one plant functional type goes extinct. Since this might be unrealistic, a better representation of the diverse vegetation is strongly needed. Additionally, community composition of the few plant functional types is often derived from empirical data, but not mechanistically calculated. Rates of dominance of plant functional types are usually prescribed and fixed, while they could vary due to temporal climatic variability. Therefore, rather than being fixed parameters such values should ideally emerge from plant growth and seed production.

The JeDi-DGVM model, developed from the former KM2000 model here can help (Kleidon and Mooney, 2000; Pavlick et al., 2012). It simulates many so called plant strategies and their growth driven by climate data. Each plant strategy consists of a set of random parameters, that influence plant ecophysiology in form of trade-offs. For example the total carbon allocation needs to be parted in allocation to roots versus leaves. Allocating into roots gives the plant more available water, and allocation into leaves more light for photosynthesis. However, death will result from, for example, only allocating into roots as well as only allocating into leaves. Therefore, a trade-off is needed. Furthermore, JeDi-DGVM simulates the growth and death of all these plant strategies, but does not consider competition. Still, it leads to realistic diversity pattern, biome maps, but can also reflect biogeochemical fluxes (Kleidon and Mooney, 2000; Reu et al., 2011; Pavlick et al., 2012).

Summary of different model approaches

We have shown, that theoretical model approaches are able to reproduce community dynamics out of the idea of trade-offs, but they still need more realism in the representation of species. Traits, such as mortality or colonization rate, naturally emerge out of the performance of a plant in its environment and may change with climatic changes. In theoretical models these traits are fixes and gained by solving the model analytically. Using vegetation models, such traits could be dynamically simulated out of the performance of the plant types forced by realistic climate data. Still, we want to model plant diversity. The JeDi-DGVM here gives us the possibility of simulating diversity.

1.1 Our DIVE approach to model community structure

Here, we will combine the advantages of theoretical and vegetation models to build a realistic community model. Thereby we use the concept of theoretical models to simulate population dynamics considering strength of r- and K-selection, and disturbances. The species specific information is gained by the JeDi-DGVM, which calculates the performance of different plant strategies under their climatic conditions.

1.1.1 Strength of r- and K-selection

Colonization and competition are important processes that control community structure. The differences in the ability of species to colonize and to compete are important for their survival. That means, if a plant grows high in biomass and produces only a few seeds, than its colonization rate might be low, but its competitive ability high (colonization-competition trade-off (e.g. Tilman, 1990). Dependent on the environment and the current situation of the neighboring plants, these abilities lead to the success or failure of a plant. In contrast to this Niche Theory (Hutchinson, 1957), the Neutral Theory of Biodiversity (Hubbell, 2001) states that species differences are not important, and only ecologic drift leads to realistic diversity patterns. Considering the importance of competition, both theories reflect the extremes. Still it is unclear, how strength of competition might be distributed geographically.

Following MacArthur and Wilson (1967), we use the concept of r- and K-selection for the DIVE model. An r-strategist is a colonizer, and lacks a good competitive ability. A K-strategist is a competitor, with a low colonizing ability. The species interact to colonize open areas (r-selection) and to compete for occupied areas (K-selection). Hence, species survive by successfully colonizing or out-competing other species. Therefore, in the DIVE model we will include the strength of r-selection and the strength of K-selection, that modulate the effectiveness of interactions to colonize and to compete. Thereby, we can investigate the role of r- and K-selection for community composition.

1.1.2 Disturbances

Disturbances are an important factor that influence plant communities (e.g. Sousa, 1984). Disturbances destroy vegetation, such as due to fire, herbivory, or wind throw. In these ways, disturbances leave open spaces that allow plants to invade or to colonize. The role of disturbances for diversity has been described by the Intermediate Disturbance Hypothesis (IDH) that states, that diversity is highest under intermediate disturbance (Connell and Fox, 1979; Grime, 1973). Under low disturbance the best competitor has sufficient time to exclude all other plants. Increasing disturbances can lead to coexistence, because they open space for new plant species. Under high disturbances, the slow growing competitors are not able to reproduce as fast as they die through disturbances, so only colonizers ultimately survive.

Although there are many studies that try to verify the IDH, several disturbance-diversity curves have been found, such as increasing, decreasing, U-shaped, and nonsignificant (see summary by Mackey and Currie, 2001). Different reasons of why these curves look as they are have been put forward, but a general theory is still missing. Fox (2012) even suggested the abandonment of the IDH, because so many different factors seem to control the pattern, that it does not lead to new insights. However, it has been found that disturbance frequency and intensity interact and can shape diversity-disturbance relationships (Miller et al., 2011). We want to look for generalities in diversity-disturbance relationships shaped by r- and K-selection.

1.1.3 Climate

Climate shapes the environmental conditions on the plants. Therefore climate influences plant diversity patterns, for example tree species diversity is shaped by the mean annual evapotranspiration (Currie and Paquin, 1987). In a moist tropical climate, where drought and temperature do not limit growing conditions, we expect and observe the highest number of species. While in a less favorable climate, such as a tundra climate, where the summer is short and the winter long, just a few species survive (Barthlott et al., 1999; Kleidon and Mooney, 2000).

Climatic conditions also shape the traits of plant strategies. In favorable environments, a plant can have a high productivity and grow tall, while in a non-favorable environment, this same plant's productivity will be low. If the plant is adapted to cold environments, this relation could be reversed. Such trait variation might be reflected in trade-offs such as the colonization competition trade-off. Therefore, we want to investigate how, in different climates, this tradeoff is reflected in the surviving plant species and how disturbances and the strength of r- and K-selection influence plant diversity.

1.2 Research questions

In this dissertation, we evaluate the role of disturbances, competition, and climate for simulated diversity patterns. To do so, as described in the first research paper (p. 3), we first develop the DIVE model that simulates community structure from the sensitivities of strength of r- and K-selection and the level of disturbances. The input data for the DIVE model is derived from simulations with the JeDi-DGVM. JeDi-DGVM simulates the performance of many plant strategies forced by climate data. While at first, both models run independently, in further steps, DIVE is interactively coupled to the JeDi-DGVM (see Fig. 1.1 next page). Applying this approach, we will investigate the following research questions:

- How do the dynamics of community structure (e.g. succession) change with different strengths of competition and the levels of disturbance?
- How do different strengths of r- and K-selection and the levels of disturbances shape the colonization-competition trade-off?
- How do the strengths of r- and K-selection shape diversity-disturbance relationships?
- Does climate influence the effects of r- and K-selection?

The next chapter summarizes the three research papers included in this thesis, while also describing their connection. We close this chapter with a brief general outlook of promising research topics for the future. The third chapter encompasses the three research papers.

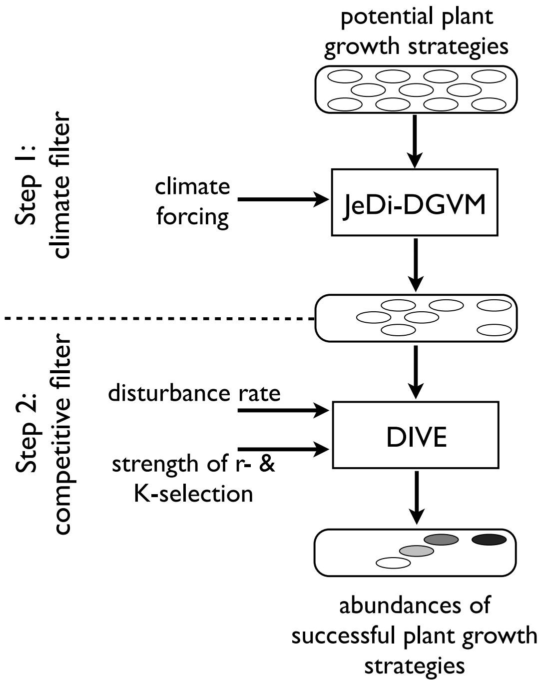

Figure 1.1: Schematic diagram of our model approach, in which we use two simulation models. In step 1, the JEDI model applies a climatic filter to the simulated plant growth strategies and results in survival or death. In step 2, the DIVE model simulates the population dynamics of the survived plant growth strategies and represents a competitive filter. Thereby, the strengths of r- and K-selection and the rate of disturbance are simulated as sensitivity parameters. The DIVE model simulates thereby the abundances (grey shade) of the surviving plant strategies, which is then used for further analysis (figure and caption adopted from research paper 2).

Chapter 2

Synopsis

In this dissertation a new model for community composition is described and analyzed. The DIVE model (Dynamics and Interactions of VEgetation) simulates whole populations of plant strategies in a homogenous area. DIVE calculates population dynamics based on three distinct processes: establishment on bare space, invasion and exclusion of occupied space, and mortality. Establishment is influenced by the strength of seed competition, also referred to as of r-selection (MacArthur and Wilson, 1967). Invasion and exclusion is affected by the strength of resource competition, also referred to as K-selection (MacArthur and Wilson, 1967). Mortality depends on the level of disturbances, also referred to as perturbations. Thereby the strength of seed competition, resource competition, and disturbances are sensitivity parameters which do not depend on each other.

Establishment on bare area depends on the germination fraction, which accounts for seed competition and on the growth rate (e.g. illustrated in Fig. 2 p. 18). Without seed competition, the total seed production does not matter for establishment, as long as a minimal seed mass is produced. Under high seed competition, the plant strategy with the highest seed production leads to a high germination fraction (e.g. illustrated in Fig. 3 p. 18).

Competition for resources is modeled implicitly via biomass dominance, as the potential to compete can be modeled proportional to biomass (Siemann and Rogers, 2003; Bengtsson et al., 1994; Keating and Aarssen, 2009). If resource competition is off, this potential is zero, and invasion and exclusion do not occur. Under high resource competition, the full potential is taken to calculate invasion and exclusion. Further invasion and exclusion dynamics depend on the growth rate of the invading plant strategy.

Mortality of a plant strategy depends on its specific mortality rate and perturbations such as grazing, harshness, disease (Chesson and Huntly, 1997; Diaz et al., 2007). In the DIVE model, perturbations are modeled continuously, while disturbances such as fire or wind throw are discrete spatial and temporal events. We do so in order to sum up different types of disturbances into one rate (Fig. 4 p. 19 illustrates the effect of perturbations, and section 5.1.3. p. 25 discusses this limitation).

For input, the DIVE model needs different characteristics of plant strategies: biomass, seed production, growth rate, and mortality rate. In this way the performance of a plant strategy directly affects the characteristics (Angert et al., 2009; Huston, 1979). These characteristics are derived from the JeDi-DGVM (Kleidon and Mooney, 2000; Kleidon et al., 2009; Pavlick et al., 2012; Reu et al., 2011). The JeDi-DGVM is run in a hypothetical constant tropical climate into steady-state, so that these performance traits reflect equilibrium populations of plant strategies. Then, the performance traits are used to calculate the plant strategy characteristics. Growth rate results from productivity versus biomass. The mortality rate is calculated from carbon losses (respiration and litter) versus biomass. To analyze the model behavior, five plant strategies in steady-state were selected. These plant strategy represent different types: high biomass but low seed production, intermediate biomass but high seed production, low biomass and high seed production, low biomass with a very high growth rate but low seed production, and high mortality and growth rate with high seed production but very low biomass (Fig. 5 p. 20). DIVE was then run using these five strategies (Fig. 1, p. 17 illustrated the model setup). These offline simulations with constant characteristics of plant strategies were used to analyze the model behavior quantitatively, without having feedbacks between JeDi-DGVM and DIVE.

2.1 The importance of strength of seed and resource competition, and perturbations for community structure

High competition strength required intermediate levels of perturbations to obtain coexistence (see Fig. 6 p. 22). This result is consistent with the Intermediate Disturbance Hypothesis (Connell and Fox, 1979; Grime, 1973). Only in the presence of resource competition were reasonable successional dynamics observed (Fig. 7 p. 22). The highest community diversity was achieved without competition and when perturbations were not too high (Fig 7 d,h p. 22). Interestingly, this model setup resulted in the most successful plant strategy being derived from a high growth rate. While this seems unrealistic for a natural setting, it may represent the present-day management of crop lands. In a crop land, seed input is high and competition is minimized by management. Without seed competition but with resource competition, diversity was high during succession, but finally competitive exclusion happened under low perturbations. The absence of seed competition allowed all strategies to exist at a minimal level. Only seed competition led to a steady-state community dominated by the highest seed producing strategy, which also seems unrealistic (Arora and Boer, 2006). Diversity in steady-state was strongly influenced by the strength of resource competition under low perturbations, while under higher perturbations, the strength of seed competition was more important (see Fig. 8 p. 24).

2.2 How the strength of r- and K-selection shape diversity-disturbance-relationships

In this part of the study, the DIVE model was developed further. We coupled the JeDi-DGVM to the DIVE model. This allowed the use of all simulated plant strategies from JeDi-DGVM, while forcing the coupled model with a realistic moist tropical climate (model setup is illustrated in Fig. 2, p. 34). This results in an ability to model diverse plant communities, where climatic changes directly influence the plant performance, and thus reflect changes in community composition and successional dynamics (Grime, 1977; Hoegh-Guldberg et al., 2008; Hughes, 2000; Parmesan and Yohe, 2003; Raizada et al., 2009; Sandel et al., 2010; Zavaleta et al., 2003). The effects of strength of r-selection, K-selection, and disturbances is then analyzed through the use of sensitivity simulations for each parameter. The simulated communities are analyzed in steady-state in terms of their diversity, the range of the colonization-competition trade-off, and the abundances of colonizers versus competitors to understand their role for diversity-disturbance relationships (see Fig. 1 p. 31).

Selection constrains the range of viable plant strategies through the colonization-competition trade-off (Fig. 4, p. 38). Strong r-selection favors colonizers and strong K-selection favors competitors. Furthermore, the success of colonizers and competitors depends on the level of disturbances. This interplay leads to different shapes of diversity-disturbance curves, as illustrated by Fig. 2.1 on the next page (and Fig. 6, p. 40). Without r/K-selection, neither the abundance of colonizers nor competitors depends on disturbance, leading to a flat curve (Fig. 5a, p. 39 and Fig 6a, p. 40). In the cases with only r-selection, the most abundant strategies are still competitive species, which also show a relatively high colonizing ability (Fig 4b, p. 38). This does not agree with our hypothesis, that colonizers will be most successful in this case. The possible reason is, that the model does not distinguish between individual seed mass and seed number; it only simulates summed seed mass. Therefore, high competitive strategies with high biomass also have a high seed mass and are thus successful through r-selection (see discussion, p. 41). Still the achieved diversity-disturbance curve decreases, because r-selection limits diversity through the importance of seeds (Fig. 6c, p. 40). Strong K-selection shifts the abundance of competitors towards colonizers with increasing disturbances (Fig 5c, p. 39), reflecting a increasing diversity-disturbance curve (Fig 6g, p. 40). Under low disturbances, the best competitor is most abundant but cannot completely exclude all others since the absence of r-selection leaves the other strategies little space to develop. So, under both r- and K-selection, the abundance of competitors decreases with disturbances and colonizers increase (Fig 5d, p. 39). This results in the hump-shaped diversity-disturbance curve (Fig 6i, p. 40), proposed by the Intermediate-Disturbance Hypothesis (Connell and Fox, 1979; Grime, 1973).

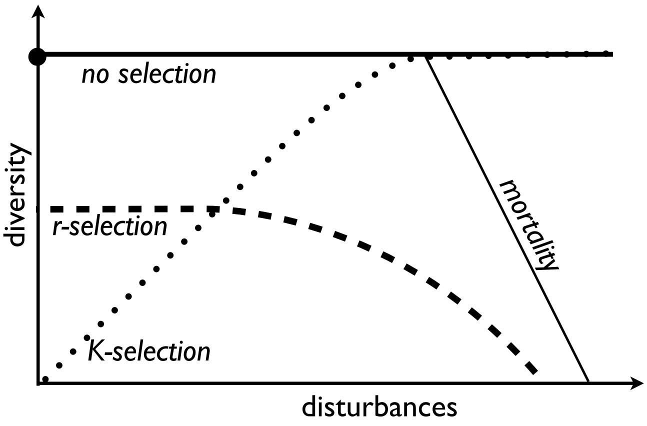

Figure 2.1: Schematic figure of the relationship between diversity and disturbances dependent on r- and K-selection. Under no selection diversity is only limited by mortality at very high disturbances. Increasing r-selection decreases diversity in general through the importance of seeds. But further limits diversity under high disturbances. Increasing K-selection leads to competitive exclusion under low disturbances. With increasing disturbances diversity can increase until its capacity, set by no selection. Under both r- and K-selection diversity is hump-shaped related to disturbances.

2.3 The effects of climate on diversity-disturbance relationships

In this part of the study, we again used the coupled DIVE model to the JeDi-DGVM. This time though, applying different sensitivities of disturbance level, strength of r- and K-selection, we forced the coupled model by four representative climates: a moist tropical, a dry tropical, a warm temperate, and a cold temperate. This allows us to investigate the effects of climate on the range of the colonization-competition trade-off, and the further restrictions of this trade-off by r- and K-selection. This might results in different diversity-disturbance relationships (DDRs) in different climates, and the strength of the effects or selection on diversity may vary in different climates (Fig. 1, p. 51).

The climates differ in temperature, precipitation, and the length and severity of a dry season (Fig 3, p. 55). Accordingly the length of the growth period differs in between these climates. With our simulations we see two effects of climate without considering competition: diversity and plant strategy richness decreases from the moist tropics towards the cold temperates (Fig 4, p. 56), and the colonization-competition trade-off is more restricted in the less favorable climates (Fig. 5 orange line, p. 58). Both of these results were expected, as diversity decreases from the tropics towards the poles (e.g. Barthlott et al., 1999). However, the effects of r- and K-selection are different in different climates.

K-selection is less strong in the moist tropics than in the other climates (Fig. 6, red line, p. 59). That means that with K-selection, diversity is proportionally more reduced in the temperate zone. This effect is probably because in the simulations in the moist tropics, more species exist with equal biomass (Fig. 4a, p. 56). This might lead to more equally distributed competition.

If there are only a few species with high competitive ability, then these species have a better chance to outcompete all others. Therefore, with K-selection, we still simulate the expected diversity gradient.

Increasing r-selection strength reduces diversity and the length of the trade-off axis (Fig. 5, p. 58 and 6 blue line, p. 59). R-selection is strongest in the moist tropics and weakest in the cold temperates. This means, that r-selection reduces diversity mostly in the favorable tropical climates with. If we do the same analysis for the seed production as done for the biomass above, we find that there is no climate where many species have a high seed production. Still, in the cold temperates, short growth periods lead to less time to colonize open areas, so more species that are adapted to a cold climate may persist.

To come back to the simulated DDRs, a flat DDR is only found in the tropical climates (Fig 7, p. 61). The reason might be, that the unfavorable temperate climate is earlier limited by increasing mortality due to disturbances, leading to partly decreasing curves. In all climates, selection had qualitatively the same effects. K-selection led to competitive exclusion under low disturbances. R-selection led to an overall decrease in diversity, and further decreased diversity under high disturbances. A hump-shaped relationship was reached under r- and K-selection in all climates. Interestingly, under strong r- and K-selection, the warm temperate climate allows for the highest diversity (Fig. 7, p. 61).Our results suggest, that global rates of r- and K-selection might be geographically distributed differently.

2.4 Concluding remarks and outlook

In this dissertation, we presented a new vegetation model that couples its population dynamics model framework to a Dynamics Global Vegetation Model (DGVM). This is based on the idea of using a theoretical model to simulate the dynamics of community structure but force it with realistic characteristics of diverse plant strategies. Thereby, changes in climate can be reflected in the change of the community. A particular strength of the model is that it considers seed (r-selection) and resources competition (K-selection) as distinct processes. This is important, as the strength of r- and K-selection is presently unknown, yet both influence community composition in different ways in different climates.

Our results help to quantify the strength of selection. Having for example field data on the abundance of colonizers versus competitors, overall diversity and disturbance rate can reveal r- and K-selection strength. To try to mechanistically explain why a certain DDR is observed, this study suggests that field studies should measure many different factors, and should not just try to verify the proposed unimodal relationship of the Intermediate-Disturbance Hypothesis (Fox, 2012).

Quite early, Dobzhansky (1950) reasoned that the tropics are more influenced by competition and other species interactions then the temperates. The result of our third study show the same effects. Diversity is most reduced with increasing r/K-selection in the favorable tropical climate, so that diversity under highest competition would be lowest in the tropics. This obviously is unrealistic based on the existing global diversity pattern. However, it increases our knowledge about the possible strength of selection. In the tropics, selection strength might be lower than in the temperates.

Our results highlight the importance of species interaction which results in the simulated plant community structure. Especially under climate change, community structure may change. These changes will be reflected in the abundances of present species (Hoegh-Guldberg et al., 2008; Parmesan and Yohe, 2003; Zavaleta et al., 2003). Furthermore, biogeochemical fluxes such as productivity or net carbon uptake can change (Fisher et al., 2010). Therefore, when modeling global vegetation, it is important to consider species interaction and diversity, while most global vegetation models do not include this mechanistically. Applying the approach presented here as the coupled DIVE-JeDi-DGVM on the global scale allows to simulate effects of climate change on functional diversity, different ecosystem services, and biogeochemical exchange fluxes.

Chapter 3

Research Papers

Summary of the contributions of the research articles:

Paper I

Title:	The relative importance of seed competition, resource competition and perturbations on community structure
Authors:	K. Bohn, J. G. Dyke, R. Pavlick, B. Reineking, B. Reu and A. Kleidon
Status:	published in Biogeosciences 2011
Contribution:	model development: K. Bohn with help of A. Kleidon, B. Reineking; simulation runs and analysis: K. Bohn; paper concept: K. Bohn with help of J. G. Dyke, A. Kleidon; writing: K. Bohn with help of J. G. Dyke; comments: all coauthors; english editing and polishing: A. Kleidon

Paper II

Title: The strengths of r- and K-selection shape diversity-disturbance relationships
Authors: K. Bohn, R. Pavlick, B. Reu and A. Kleidon
Status: submitted to Ecology Letters
Contribution: design of the study: K. Bohn by discussion with A. Kleidon;
model coupling, simulation runs and analysis: K. Bohn;
writing: K. Bohn wrote the first version, all coauthors contributed to revisions;
english editing and revising the text: A. Kleidon with K. Bohn

Paper III

Title: Contrasting the effects of climate versus competition on diversity-disturbance relationships
Authors: K. Bohn, R. Pavlick, B. Reu and A. Kleidon
Status: to be submitted
Contribution: design of the study: K. Bohn;
paper concept, simulation runs, writing: K. Bohn
discussions on concept: A. Kleidon, R.Pavlick, B.Reu
english editing and revising the text: A. Kleidon

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Biogeosciences

The relative importance of seed competition, resource competition and perturbations on community structure

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Abstract. While the regional climate is the primary selection pressure for whether a plant strategy can survive, however, competitive interactions strongly affect the relative abundances of plant strategies within communities. Here, we investigate the relative importance of competition and perturbations on the development of vegetation community structure. To do so, we develop DIVE (Dynamics and Interactions of VEgetation), a simple general model that links plant strategies to their competitive dynamics, using growth and reproduction characteristics that emerge from climatic constraints. The model calculates population dynamics based on establishment, mortality, invasion and exclusion in the presence of different strengths of perturbations, seed and resource competition. The highest levels of diversity were found in simulations without competition as long as mortality is not too high. However, reasonable successional dynamics were only achieved when resource competition is considered. Under high levels of competition, intermediate levels of perturbations were required to obtain coexistence. Since succession and coexistence are observed in plant communities, we conclude that the DIVE model with competition and intermediate levels of perturbation represents an adequate way to model population dynamics. Because of the simplicity and generality of DIVE, it could be used to understand vegetation structure and functioning at the global scale and the response of vegetation to global change.

1 Introduction

Plant community dynamics are largely determined by the interrelated effects of climate, competition and perturbations. Climate represents the primary selection pressure for vegetation at the global scale (Woodward, 1987), and determines the general performance of plants, such as biomass and seed production. At local scales, general plant performance affects competitive interactions for resources and space and thereby determines plant species composition. For instance, a large tree can exclude small grasses by over-shading and may thus dominate the community. Perturbations, such as fire, disease or abiotic stress, influence community composition by increasing available space (Sousa, 1984). With higher levels of perturbations, available space increases, allowing fast growing small grasses with high seed production to rapidly establish and escape competitive exclusion by larger trees.

The interplay of competition and perturbations in shaping community structure is altered when environmental conditions change. Since plant species respond differentially to altered environmental conditions (e.g. Körner, 1998; Sandel et al., 2010), competition for space and resources is affected (Grime, 1977; Raizada et al., 2009). These changes in performance and therefore competition may alter succession and steady states (in the sense of equilibrium or climax vegetation, Clements, 1936), with consequences for plant composition (Hughes, 2000; Zavaleta et al., 2003; Parmesan and Yohe, 2003; Hoegh-Guldberg et al., 2008; Sandel et al., 2010) and ecosystem processes such as carbon and nutrient cycling (Shaver et al., 2000; Bunker et al., 2005; Fisher et al., 2010). For example, water stress may reduce tree shading and allow for an increase in coverage of smaller

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grasses. Consequently, in order to predict how vegetation will respond to environmental change, both, the performance of individual species and their competitive interactions need to be adequately considered in vegetation models.

A range of models has been developed to simulate the dynamics of species composition and its response to environmental change. These can broadly be classified into three groups. First, several theoretical models exist to explain the coexistence of species in plant communities based on colonisation, competition and mortality (e.g. Tilman, 1994; Tilman and Kareiva, 1997). However, rates of colonisation and mortality are represented by aggregated parameters and are not related to underlying mechanisms. Consequently, there is no explicit link to plant ecophysiology. Second, gap models simulate competition between individual plants, e.g. for water and light, in a process-based fashion based on plant geometry (e.g. Bugmann, 2001). However, this group of models requires empirical parameterisation of plant geometry, e.g. how crown area depends on individual tree growth (e.g. Badeck et al., 2001). In addition, these models are computationally expensive to run, and are thus usually only applied on local or regional scales. Third, Dynamic Global Vegetation Models (DGVMs) calculate population dynamics but use only a few plant functional types (PFT) to simulate global biogeography and biogeochemical patterns (e.g. Box, 1981; Foley et al., 1996; Sitch et al., 2003; Woodward and Lomas, 2004). Coexistence of different PFTs in DGVMs is often empirically prescribed. For instance, grasses are always present with a minimum fractional coverage or only when the soil water content is above a certain threshold (e.g. Sitch et al., 2008; Haxeltine and Prentice, 1996). Some DGVMs need to predefine e.g. species specific invasion rates or dominances of PFTs to calculate population dynamics (Cox, 2001; Arora and Boer, 2006). However, due to climatic change as well as spatial and temporal climate variability, such parameters could vary. Therefore, such values should rather be emergent properties from plant growth or seed production. To overcome some of these limitations, some global approaches have integrated gap model ideas into DGVMs to get a more realistic and process-based vegetation composition (e.g. ED – Moorcroft et al., 2001; Fisher et al., 2010, SEIB-DGVM – Sato et al., 2007, LPJ-GUESS – Hickler et al., 2004). These new models still require intensive empirical parameterisations and are very complex because they consider a large number of processes at a high level of detail.

In this study, we seek a less complex approach in which population dynamics is still process-based by relating individual plant population performance to the emergent community structure. We developed the model DIVE (Dynamics and Interactions of VEgetation) that simulates whole populations of plant strategies (PPS), rather than individuals. DIVE calculates population dynamics based on establishment, mortality, invasion and exclusion as distinct processes that are shaped by competition between seeds for available space, competition for resources and perturbations. The rates of establishment, mortality, invasion and exclusion are linked to the modelled emergent performances of different plant strategies derived from an individual-based plant model (Kleidon and Mooney, 2000; Reu et al., 2011), that covers how individual plant strategies cope with their environment without considering interspecies competition. By doing so, we do not need to predefine the dominance or the colonization rates of the PFTs. Furthermore, we implement competition in a way, such that we can separately control not only the strength of seed competition (Arora and Boer, 2006), but also resource competition and perturbations.

We used the DIVE model and applied it to a hypothetical tropical environment. To understand the effect and role of different types of competition and perturbations on community structure and dynamics, we performed several sensitivity simulations in which we varied the strength of seed competition, resource competition and perturbations. We analysed the simulations in terms of their temporal dynamics and the resulting diversity in the climax state. Thereby we can relate different strength of competition and perturbation to the emergent successional dynamics and coexistence in the model. The results are discussed in terms of the plausibility of the dynamics, inherent limitations and potential application of the model in further studies.

2 Model description

2.1 Overview

The purpose of DIVE is to capture population dynamics from perturbations and competition between different plant population strategies (PPSs). DIVE calculates population dynamics as the consequence of different characteristics of PPSs in terms of their biomass, seed flux, growth and mortality rate. These characteristics are derived from the output of the Jena Diversity (JeDi) model (Kleidon and Mooney, 2000; Reu et al., 2011). This model filters many random plant strategies that grow independently from each other to yield those, that can cope with the climate from the fundamental assumption of unavoidable ecophysiological trade-offs. We used the following mean output from JeDi that describes mean population characteristics without considering the number of individuals in a population: biomass, seed flux, litter flux, respiration and productivity of a seedling (see Fig. 1 and Table 1). This constant set of output data was used as input for all DIVE simulations. The stocks and fluxes are calculated per unit occupied area (gC m^{-2} or gC m^{-2} d^{-1}, respectively).

DIVE calculates the change in occupied area in fractions of all PPSs in time within a homogenous area on a daily time step. Each PPS is initialised with an amount of seeds. PPSs increase in covered area by establishment (seeding bare area) or invading area covered by other PPSs. Decreases in area are due to exclusion and mortality (death). Competition of seeds to establish and competition for resources to invade are

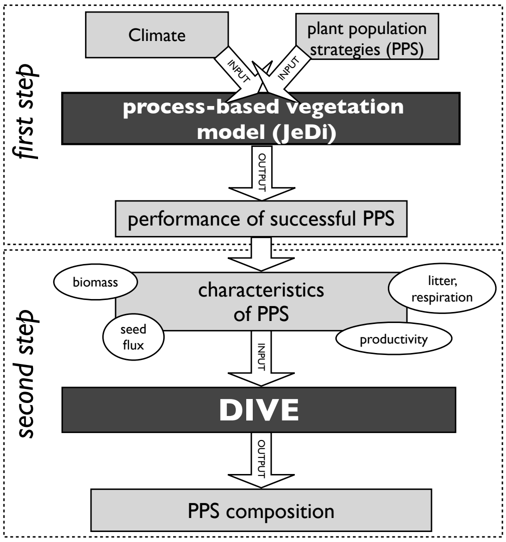


Fig. 1. Flow chart diagram of the model setup. First JeDi is run to produce the necessary input for DIVE (ellipses) to calculate population dynamics by competition.

controlled by two independent parameters. A third parameter controls perturbations that result in low or high mortality. Table 1 lists all model parameters and variables.

2.2 Population dynamics

The fractional area A_i occupied by PPS i changes due to four processes:

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

with establishment S_i [$\mathrm{m^2\,m^{-2}\,d^{-1}}$] on the fraction of bare area, mortality M_i [$\mathrm{m^2\,m^{-2}\,d^{-1}}$], which includes the effect of disturbances, invasion I_i [$\mathrm{m^2\,m^{-2}\,d^{-1}}$] into area occupied by other PPS and exclusion E_i [$\mathrm{m^2\,m^{-2}\,d^{-1}}$] by other PPS. Bare, i.e. non vegetated, fractional area A_{bare} is given by subtracting the sum over fractional areas A_i of all PPSs from the total of 100 %.

$$A_{\text{bare}} = 1 - \sum_{i=1}^{n} A_i \qquad (2)$$

2.3 Establishment and seed competition

Establishment describes how much bare area can be covered by each PPS by germination of the seeds in one time step (see Fig. 2a–d). We assume that all seeds from all PPSs are well mixed and that establishment happens only on bare ground and not in shade below existing populations. Establishment depends on the germination fraction of a PPS g_i [frac.], the bare area A_{bare} and on the growth rate $\kappa_{\text{grow},i}$ [$\mathrm{d^{-1}}$]. The germination fraction g_i describes how much of the total area could be occupied by the actual seed flux per PPS. Since we do not consider different age classes, incorporating the growth rate $\kappa_{\text{grow},i}$ allows us to model the effective area gain by the whole population rather than the area that seedlings would cover. The inverse of the growth rate describes the time that a seedling needs to reach adult size.

Table 1. Model variables and parameters used in DIVE.

Symbol	Meaning	Unit/Value
Output of JeDi, Input to DIVE: PPS performance		
BM_i	biomass of PPS i per $\mathrm{m^2}$ of occupied (occ.) area	$\mathrm{gC\,m^{-2}}$
$f_{\text{seed},i}$	seed flux of i per $\mathrm{m^2}$ of occ. area	$\mathrm{gC\,m^{-2}\,d^{-1}}$
$f^0_{\text{npp},i}$	seedling net primary productivity of PPS i per $\mathrm{m^2}$ of occ. area	$\mathrm{gC\,m^{-2}\,d^{-1}}$
$f_{\text{lit},i}$	litter flux of PPS i per $\mathrm{m^2}$ of occ. area	$\mathrm{gC\,m^{-2}\,d^{-1}}$
$f_{\text{res},i}$	respiration of PPS i per $\mathrm{m^2}$ of occ. area	$\mathrm{gC\,m^{-2}\,d^{-1}}$
n	number of PPS	
PPS Characteristics derived form JeDi output		
d_i	dominance of i	
$\kappa_{\text{grow},i}$	growth rate	$\mathrm{d^{-1}}$
$\kappa_{\text{mort},i}$	mortality rate	$\mathrm{d^{-1}}$
g_i	germination fraction	frac.
α_{ij}	competition coefficient	
x_{ij}	invasion rates	$\mathrm{d^{-1}}$
State variables and area rates		
A_i	fractional coverage of PPS i	$\mathrm{m^2\,m^{-2}}$
S_i	rate of establishment of PPS i	$\mathrm{m^2\,m^{-2}\,d^{-1}}$
I_i	rate of invasion of PPS i	$\mathrm{m^2\,m^{-2}\,d^{-1}}$
E_i	rate of exclusion of PPS i	$\mathrm{m^2\,m^{-2}\,d^{-1}}$
M_i	rate of mortality of PPS i	$\mathrm{m^2\,m^{-2}\,d^{-1}}$
A_{bare}	fractional non covered area	$\mathrm{m^2\,m^{-2}}$
Parameters		
c_{R1}	seed competition strength	$[1,\infty]\ \mathrm{m^2\,d\,gC^{-1}}$
c_{R2}	resource competition strength	$[1,\infty]$
c_{Mort}	perturbation factor	$[10^{-3}, 10^2]$

$$S_i = g_i \cdot A_{\text{bare}} \cdot \kappa_{\text{grow},i} \qquad (3)$$

From each PPS's seed flux $f_{\text{seed},i}$ [$\mathrm{gC\,m^2\,d^{-1}}$], we calculate the germination fraction g_i as a saturating function of numbers of seeds, so for a certain threshold of seed number,

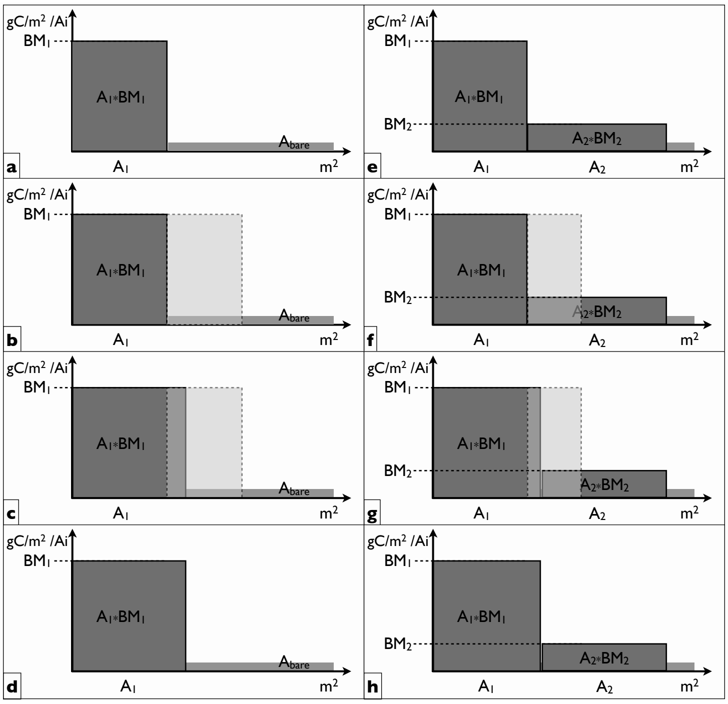


Fig. 2. Illustration of how area is gained via establishment **(a–d)** and invasion **(e–h)**. PPS 1 occupies the area A_i **(a)**. The germination fraction would results in a large increase of area covered with seedlings **(b)**. The actual gain in area by the average population is then determined by the growth rate (**c** and **d**). If competition happens, the PPS with the higher biomass per occupied area (equivalent to dominance) can invade in the area of smaller PPS (**e** and **f**). Again here the growth rate determines how much the average population would gain in area (**g** and **h**).

producing more seeds does not lead to an increase in establishment:

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

A value of $g_i = 1$ describes that a PPS has produced sufficient seeds to germinate on the whole area, a value of $g_i = 0$ means that the seed flux is too low to start germination. If different PPSs have a different seed flux, then some will have the potential to gain more area than others. This will affect the establishment in future time steps via the available bare area. Therefore, seeds from different PPSs compete for bare area indirectly but do not have a direct effect on each other. To investigate what effects seed competition might have, we introduce a factor for seed competition strength, c_{R1}, that changes seed saturation (see Fig. 3). For $c_{\mathrm{R1}} = 1$, the seed flux is very important for establishment. If a PPS has a low seed flux, its germination rate and establishment will be low. For $c_{\mathrm{R1}} \to \infty$, the seed flux becomes irrelevant for establishment (neutral seed competition). Then, every PPS will have the same germination fraction as long as one seed is produced.

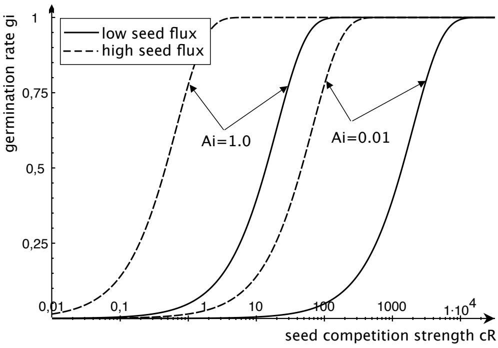


Fig. 3. Qualitative behavior of Eq. (4) with increasing seed competition for low and high seed flux PPS that occupy a low or high fraction of area.

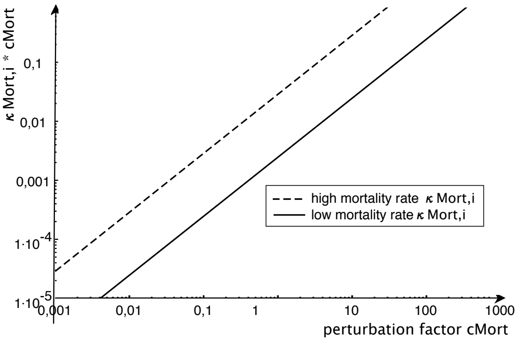


Fig. 4. The effect of perturbations on mortality (see Eq. 6) for a PPS with low and high mortality rate.

The growth rate $\kappa_{\mathrm{grow},i}$ is determined by the biomass per m^2 of occupied area of i 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 the biomass is given per m^2 of occupied area, and therefore the total biomass per m^2 of the community is determined by $\sum_{k=1}^{n} \mathrm{BM}_k \cdot A_k$.

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's mortality rate $\kappa_{\mathrm{mort},i}$ [d^{-1}] and on a factor that scales mortality: c_{Mort}.

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

We explore the effects of different intensities of perturbations via the use of c_{Mort}, a parameter that alters the mortality rate. Higher values for c_{Mort} would correspond to more severe perturbations that would lead to an increase in mortality, e.g. due to grazing, herbivory, disease or harshness (e.g. Chesson and Huntly, 1997; Diaz et al., 2007). Low values of c_{Mort} correspond to low intensity of perturbations and consequently lower mortality (see Fig. 4).

The PPS's mortality rate $\kappa_{\mathrm{mort},i}$ depends on the PPS characteristics. 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 [$\mathrm{gC\,m^{-2}\,d^{-1}}$].

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

In many cases, fast-growing plants live shorter, because they have higher metabolic rates, while slow-growing plants show the opposite pattern (e.g. Gillooly et al., 2001; Ricklefs, 1998; McCoy and Gillooly, 2008). With Eq. (7) we can distinguish the turnover time of slow versus fast-growing PPS. For example, a slow and a fast-growing PPS might have the same biomass, but will differ in their gross primary production (GPP). Since in steady state GPP equals the sum of litter fall and respiration, different mortality rates will result. We divide by biomass because mortality rates are predicted to be proportional to body size (Brown et al., 2004; Gillooly et al., 2001). We use biomass as a surrogate for body size, although they are decoupled by plant density, because our simplistic approach has no notion about individuals and the biomass of each PPS describes a whole population per m^2 of occupied area. Therefore Eq. (7) allows abstraction from the carbon losses of a PPS into the loss of area. Note that mortality rates are calculated in an analogous manner 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 outcompete smaller ones. Therefore, in DIVE a large (high biomass) PPS can invade the area of smaller PPSs. Smaller PPSs become excluded 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 and, respectively, the relative size d_i of a PPS by normalising its biomass per m^2 of occupied area BM_i with the sum of biomass of all n PPSs:

$$d_i = \frac{\mathrm{BM}_i}{\sum_{k=1}^{n} \mathrm{BM}_k} \tag{8}$$

From the differences in dominance between two distinct PPSs i and j we obtain the competition coefficients α_{ij}. To influence the intensity of resource competition we introduce a parameter c_{R2}:

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

With this formulation, PPS do not compete for resources when $c_{\mathrm{R2}} \to \infty$, because $(d_i - d_j)^{\infty} \to 0$. 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, $\kappa_{\mathrm{grow},i}$ (analogous to establishment, Fig. 2e–h).

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

We assume that invasions into areas occupied by other PPSs do 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.

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

Table 2. Values of PPS characteristics calculated in DIVE from the output of JeDi: dominance d_i, seed flux $f_{\mathrm{seed},i}$, growth rate $\kappa_{\mathrm{grow},i}$ and mortality rate $\kappa_{\mathrm{mort},i}$.

	d_i	$f_{\mathrm{seed},i}$	$\kappa_{\mathrm{grow},i}$	$\kappa_{\mathrm{mort},i}$
PPS 1	0.497	0.059	0.035×10^{-2}	0.246×10^{-2}
PPS 2	0.369	1.457	0.041×10^{-2}	0.311×10^{-2}
PPS 3	0.112	1.273	0.127×10^{-2}	0.959×10^{-2}
PPS 4	0.012	0.047	1.206×10^{-2}	1.768×10^{-2}
PPS 5	0.010	0.688	0.515×10^{-2}	2.864×10^{-2}

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

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

3 Simulation setup

Because our focus is to understand the model behaviour of DIVE and the role of perturbations and competition for population dynamics, we use a simple setup (Fig. 1). In this setup we use a constant tropical climatic forcing to first derive a set of feasible plant population strategies and their growth characteristics. Then we select five strategies from this set and use them for the DIVE simulations.

3.1 Climatic forcing

We consider in the following a constant tropical-like climate. We prescribe a daily precipitation rate of $12\,\mathrm{mm\,d^{-1}}$, a mean incoming flux of solar radiation of $278\,\mathrm{W\,m^{-2}}$ and a near surface air temperature of 290 K. We use the constant climate to explicitly avoid the effects of climatic variability on population dynamics.

3.2 Selection of PPS

We used the JeDi model (Kleidon and Mooney, 2000; Reu et al., 2011) to generate the performances of a whole range of PPSs. JeDi models diverse vegetation from ecophysiological assumptions based on trade-offs. JeDi uses climate data (see previous section) and a large set of vectors with randomly assigned traits, that describe characteristics such as allocation, phenology, light use efficiency and senescence. These traits correspond to ecophysiological properties. JeDi then models the growth, reproduction and death of these trait vectors, calculates land surface fluxes and C-fluxes. The JeDi model and has successfully reproduced global patterns of plant diversity, abundance distributions and biomes (Kleidon and Mooney, 2000; Kleidon et al., 2009; Reu et al., 2011).

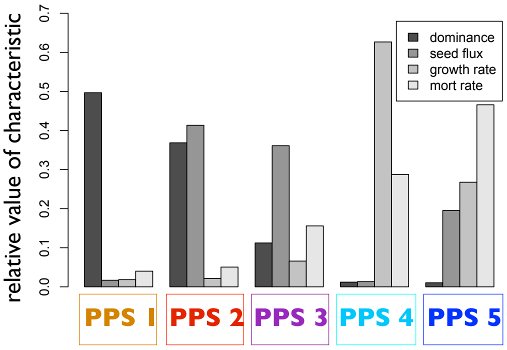


Fig. 5. The five PPSs, each expressed by a different colour with their four characteristics (dominance d_i, seed flux $f_{\mathrm{seed},i}$, growth rate $\kappa_{\mathrm{grow},i}$ and mortality rate $\kappa_{\mathrm{mort},i}$). The colours refer to the same PPSs in the following figures. Characteristic are normalised by their sum, see Table 2 for specific numeric values.

We ran JeDi in order to generate a number of PPSs that are viable under such climatic conditions. 500 PPS were seeded, each grew, reproduced or died in isolation from all others. After 500 yr, all PPS were at equilibrium with 386 of the initial populations becoming extinct, having zero biomass and not produced any seeds. From the 114 viable populations, five were chosen that reflected a range of different growing strategies, such as coloniser or competitor.

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

3.3 Setup of DIVE simulations

We ran the DIVE model with the five selected PPSs and calculated the rate of change of the occupied areas of these PPSs over different intensities of resource competition, seed competition and perturbations.

DIVE simulations started from bare area, i.e. $A_{\mathrm{bare}}(t=0)=1$ and $A_i(t=0)=0$. When $A_i=0$, the actual seed flux is given by $A_i \cdot f_{\mathrm{seed},i}=0$ and the rates of establishment are zero. Therefore it is necessary to start with an initial actual seed flux for the five selected PPSs. This is implemented in the first time step by setting $A_i \cdot f_{\mathrm{seed},i} = f_{\mathrm{seed},i}$ in Eq. (4). All simulation were run for 10 000 yr with a daily time step.

To evaluate the role of resource and seed competition as well as perturbations for steady states and transient states of population dynamics, we conducted a series of sensitivity analysis experiments:

- to assess the impact of perturbations, we used the following values for the perturbation parameter: $c_{\mathrm{Mort}}=(0.001, 0.05, 0.1, 1, 10)$ in scenarios with seed and resource competition, $c_{\mathrm{R1}}=1$ and $c_{\mathrm{R2}}=1$
- to assess the impacts of seed and resource competition we used 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 perturbation scenarios, $c_{\mathrm{Mort}}=0.05$ and 1.
- to investigate the effects of competition on diversity, we changed the strength of both types of competition from strong to neutral, $c_{\mathrm{R1,2}}=(1, 2, 4, 8, 16, 32, 10^9)$. We used three different values for $c_{\mathrm{Mort}}=(0.001, 0.05, 10)$.

3.4 Analysis

To assess the quality of the simulated succession for the sensitivities to perturbation and competition, we plot time-series of the occupied areas A_i. The effects of perturbations and competition on diversity were evaluated using the Shannon Index of biodiversity. This index is defined by

$$H=-\sum_{i=1}^{n}\left(\frac{A_i}{\sum_{k=1}^{n} A_k}\cdot\log\left(\frac{A_i}{\sum_{k=1}^{n} A_k}\right)\right) \quad (13)$$

This diversity index is minimal with $H=0$ if not more than 1 PPS occupies an area $A_k>0$. Diversity is at a maximum with $H=1.61$, if all PPSs occupy equal areas.

4 Results

4.1 The role of perturbations

Different values of perturbations under high resource and seed competition lead to different successional patterns and to steady states of competitive exclusion, coexistence and total extinction (Fig. 6). The first PPS to increase is the fast-growing grass-like PPS 5, followed by the shrub-like PPS 3 to slow-growing tree-like PPS 2 and 1. Under conditions of low perturbations and with both seed and resource competition operating, the largest PPS 1 is the last to increase in area, but then competitively excludes all others (Fig. 6a). As the intensity of perturbations increases, the successional order does not change, but the fast reproducing tree-like PPS 2 increases in area and coexists with the most dominant PPS 1 (Fig. 6b–c). For higher levels of perturbations, occupied areas of all PPSs decrease and PPS 1 is not able to exist, but still PPS 2 and 3 coexist (Fig. 6d). Under further increased levels of perturbation, none of the PPS can sustainable exist, all go extinct (Fig. 6e). Hence, under high resource and seed competition, intermediate perturbations are required to obtain coexistence. The successional patterns seem reasonable, because they range from fast-growing PPSs towards slow-growing PPSs similar to observed successions in a wide range of ecosystems (MacArthur and Wilson, 1967; Odum, 1969).

4.2 The role of competition under different perturbations

We obtained different successional patterns and steady states when resource and seed competition were strong or neutral (Fig. 7). Under conditions of low to intermediate perturbations, turning off resource competition leads to high importance of seed flux (compare Fig. 7a and b, see Table 3). Initially, only the high seed-producing grass-like PPS 5 is present, because it is able to rapidly colonise all available bare area (Fig. 7b). Later, the tree-like PPSs 2 and shrub-like PPS 3 with a high seed flux increase in area and stably coexist while excluding all other PPSs. This situation is reversed when seed competition is turned off and resource competition is turned on, representing a strong selection for size or dominance (see Table 3): PPS 1 almost covers the complete area in steady state (Fig. 7c). Primary succession also has changed, and the low seed-producing grass-like PPS 4 replaces PPS 5 as the most successful strategy. However, all five PPSs are present in early succession. Turning both forms of competition off leads to the emergence of the grass-like PPS 4 with best growth-mortality relationship (Fig. 7d, Table 3). In steady state all five PPSs coexist.

Increasing perturbations to intermediate and high levels leads to coexistence of at least two PPSs, irrespective of strength of seed and resource competition (Fig. 7e–h). Under such conditions there are two main regimes in which either the PPS with greatest seed flux or the one with best growth-mortality relationship will occupy most area (Table 3). Seed competition always leads to PPS 2 with highest seed flux to occupy most area, coexisting with PPS 3 (Fig. 7e and f). PPS 4 will be most successful when seed competition is turned off (Fig. 7g and h). This pattern is independent from resource competition, but as resource competition operates, the most dominant PPS 1 is still the second most successful PPS (Fig. 7h).

Hence, we obtain coexistence of all five PPS when resource and seed competition are neutral. But to reproduce successional dynamics ranging from fast-growing toward slow-growing PPS, resource competition needs to be considered.

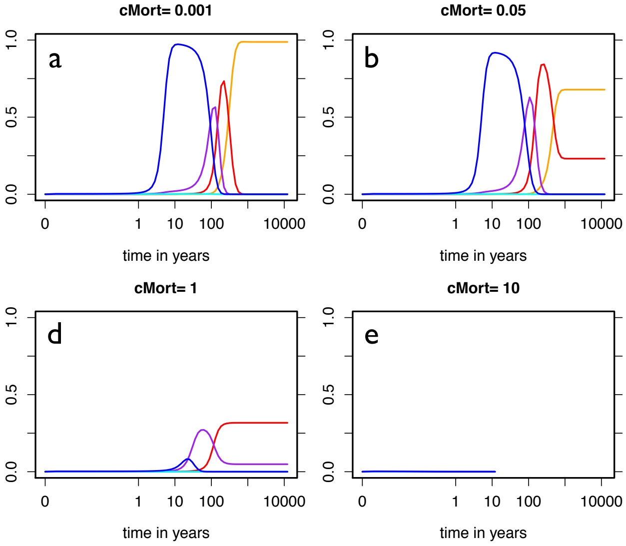


Fig. 6. Time-series of population dynamics under five increasing values for perturbations (c_{Mort}) from **(a)** to **(e)**. The time in years is on logarithmic scale, the y-axis shows the relative abundance or occupied area of each PPS. Colours refer to coloured PPSs in Fig. 5. PPSs interact between seeds and for resources.

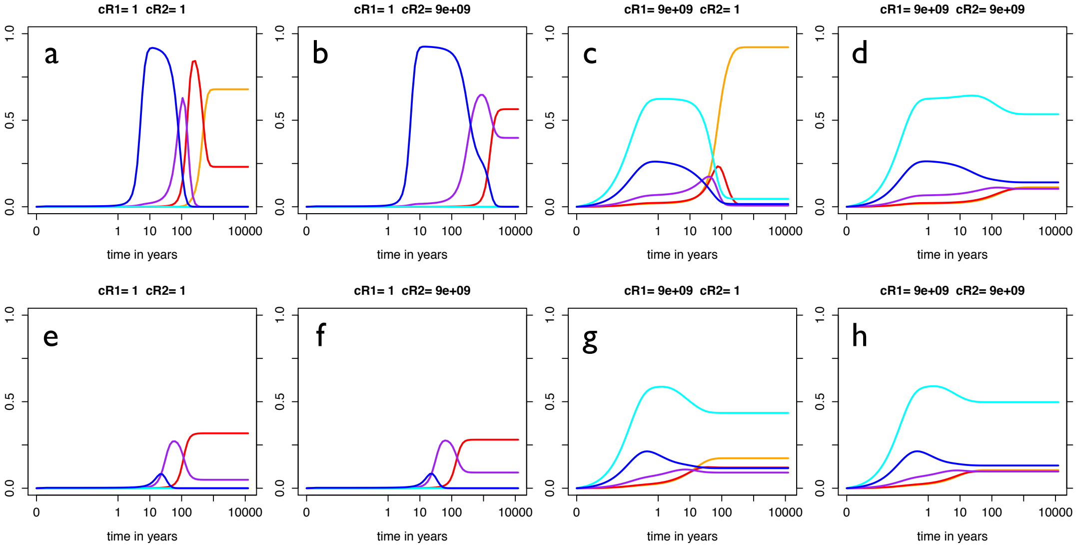


Fig. 7. Time-series of population dynamics for seed competition working (c_{R1}=1) or neutral (c_{R1}=9e+9), resource competition working (c_{R2}=1) or neutral (c_{R2}=9e+9) for c_{Mort}=0.05 **(a–d)** and $c_{\mathrm{Mort}} = 1$ **(e–h)**. Each colour represents the coverage of a PPS, corresponding to Fig. 5.

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 neither seed or resource competition operate, the ratio $\kappa_{\mathrm{grow}}/\kappa_{\mathrm{mort}}$ (G/M) is important for being abundant.

Seed comp	Res. comp	Most abundant	Result	Fig.
Low-intermediate perturbations				
on	on	size	excl or coex	7a
on	off	seed flux	coex	7b
off	on	size	excl or coex	7c
off	off	G/M	coex	7d
Intermediate-high perturbations				
on	on	seed flux	coex	7e
on	off	seed flux	coex	7f
off	on	G/M, size	coex	7g
off	off	G/M	coex	7h

4.3 The role of competition and perturbations for diversity

Diversity is strongly influenced by perturbations and the strength of competition. Under low perturbations, high strength of both types of competition results in no diversity (Fig. 8a, bottom left). As the values of competition strengths decrease, diversity increases. Under conditions of high resource competition, seed competition plays only a minor role in affecting species diversity at steady state, while under conditions of high seed competition, resource competition can strongly affect diversity (Fig. 8a). Therefore, under low perturbations, resource competition has a strong impact on population composition, while seed competition is less important. For high perturbations, it is the reverse, while resource competition has no effect, seed competition is very important (Fig. 8c). For intermediate perturbations, a shift between both happens (Fig. 8b). Consequently, under increasing perturbations, diversity is decreasingly affected by resources competition while increasingly by seed competition.

5 Discussion

We first discuss the limitations of DIVE and then interpret the results in terms of our goal to better understand the interplay and relative importance of perturbations and competition in shaping the diversity of communities. We then discuss possible extensions of the model and potential future applications of DIVE.

5.1 Limitations

The limitations we discuss in the following concern the structure of the model in terms of how populations and their dynamics are represented in DIVE as well as the setup of the model. Even though DIVE is designed to represent population dynamics in a very general way and thereby minimize the number of free parameters, it is nevertheless necessary to choose values of the free parameters c_{R1}, c_{R2}, and c_{Mort} that are associated with competition and mortality.

5.1.1 Representation of populations

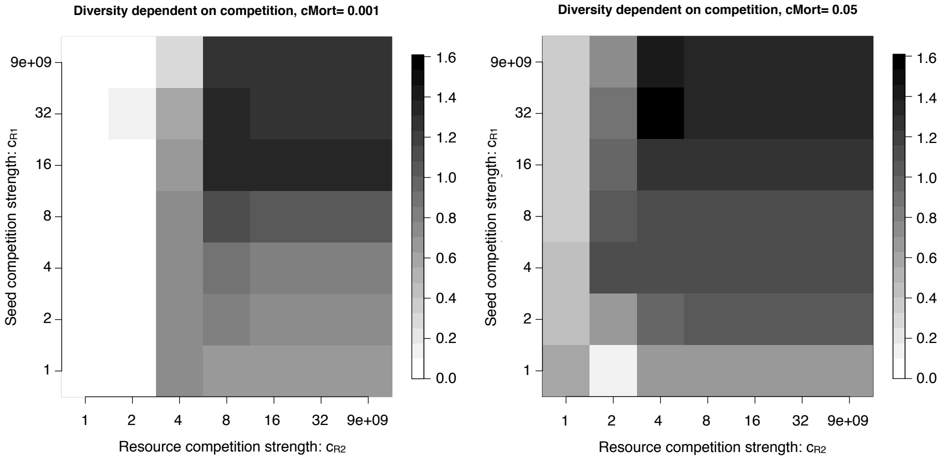
DIVE models populations dynamics of different PPSs rather than at the level of individual plants, age or height classes. There are models that explicitly represent these population aspects (e.g. Moorcroft et al., 2001; Fisher et al., 2010, represents different height classes). Since mortality may be different at different ages within a population of one PPS, populations may be more adaptive and respond differently to perturbations when different age classes are represented. This effect is not captured by DIVE. A good justification for not including different classes is that this makes the DIVE model much less computationally expensive while potentially allowing for the representation of a greater diversity of PPS in the model.

Populations also do not explicitly compete for resources such as light, water, nutrients etc., and space is considered to be homogeneous. This limitation could be addressed, but it would require a joint representation of the ecophysiological processes of the PPS, which is currently calculated in the JeDi model, and the resulting population dynamics, which is simulated separately by DIVE.

However, despite the simplicity of our approach, we are able to investigate the influence of perturbations, seed and resource competition. As competition might be influenced also by environmental and biological heterogeneity, the inclusion of strength of competition in individual-based spatially explicit models, could lead to even more complex model with more unknown parameters.

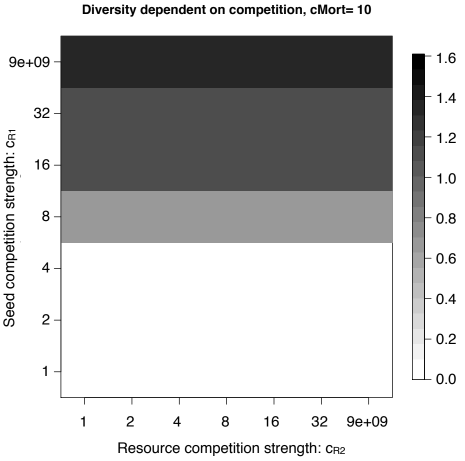
5.1.2 Representation of competition

DIVE models competition implicitly by assuming that populations with a higher biomass outcompete ones with lower biomass. This assumption is to a first approximation reasonable, since differences in competitive ability result mainly on differences in size. For instance, the acquisition of light depends on size (Bengtsson et al., 1994) such that, for example smaller plants are over-shaded by larger ones (Siemann and Rogers, 2003). But smaller sized plants could also have higher competitive abilities than bigger ones (Keating and Aarssen, 2009). However, to account for different types of resource competition within one model equation, it makes sense to incorporate resource competition and its strength by



(a) low perturbations

(b) intermediate perturbations



(c) high perturbations

Fig. 8. Each point represents the diversity (Shannon Information Entropy) after 10 000 yr of a DIVE simulation dependent on seed (y-axis) and resource competition (x-axis). The values for the strength of seed competition decrease bottom to top and for the strength of resource competition decrease from left to right.

using a simple approach, because larger plants are likely to be better competitors (Keating and Aarssen, 2009). DIVE uses plant strategy parameters that emerge from functional relationships and climatic constraints, such as growth rate and seed production, 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, only competitive interactions between plants are considered that are detrimental to the abundance of a population. 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. This could potentially be implemented in the model if resource competition is represented in a more process-based way, as discussed above. We may, however, assume that these are of secondary importance for community dynamics at larger scales.

5.1.3 Representation of mortality

We model mortality in a simple way dependent on each PPS characteristics (e.g. biomass) and a PPS-independent perturbation parameter c_{Mort}. While our formulation (see Eq. 6) seems adequate to work for different plant strategies, if we were to use DIVE to analyze specific biomes such as the tropics, in the light of Wright et al. (2010) a better parameterisation could be needed. They concluded e.g. that mortality rates of tropical tree species are in general independent of the maximum height, while wood density was found to be a more important aspect. However, we want to use not only trees but also grasses and shrubs and therefore need a more general parameterisation.

The perturbation parameter c_{Mort} plays a critical role in affecting the mortality of a PPS. This parameter is introduced to capture the many different types of perturbations in one term, e.g. disease, herbivory, grazing or disturbances such as fire and windfall. We use a constant value for this parameter, even though many disturbances are stochastic and to some extent dependent on the climatic conditions – as is the case for fire – or on the composition of the community – as is the case for herbivory. Stochastic perturbation events have major impacts on vegetation dynamics (Johst and Huth, 2005), and different PPSs may respond differentially to perturbations. Diaz et al. (2007), for instance, concluded that grazing, which expresses a form of perturbation, interacts with species composition. This deficit could be addressed by modeling the value of c_{Mort} stochastically, and by modeling the associated processes that represent perturbations more explicitly.

While there has been progress in understanding mortality, disturbances and perturbations (e.g. Negrón-Juárez et al., 2010; Lines et al., 2010; Chao et al., 2008), challenges still remain with respect to the quantification of perturbation rates, as these values might differ in specific regions of the Earth. Given these limitations, we chose this parameter to be fixed, because we wanted to include perturbations in a simple and transparent way. A better representation of the different forms of perturbations at the global scale for many different PPSs is a great challenge and it is a parsimonious assumption that, in sum, its effects might be equal to all species.

5.1.4 Choice of PPS

The choice of the five PPS was somewhat arbitrary. This was done to be able to clearly analyze the dynamics of DIVE and attribute these to the choice of the three open parameters. In future applications, there is in principle no limit to the number of interacting populations. This is particularly important when we want to use DIVE to better understand diversity patterns in terms of the associated coexistence of PPSs as well as their geographical variation. For this we would need to represent many more PPS in DIVE.

Also, the selected PPS are not based on observed characteristics, so it may seem that the simulated dynamics are somewhat artificial. In principle one could use empirical data of ecological succession to determine realistic parameter values for each ecosystem to tune the dynamics of DIVE. This would then, however, remove the general nature of the DIVE approach. By using the simulated characteristics from the JeDi model, one captures the generality of the range of PPSs that can cope with the climatic conditions within a region. An alternative strategy for improving the representation of plant function might be to concentrate on the depiction of ecophysiological trade-offs within JeDi (or similar models).

5.1.5 Constant climatic forcing

We used a hypothetical tropical climatic forcing in the simulations. This was done to avoid the effects of climatic variability on population dynamics so that the simulated population dynamics could be more easily attributed to the choice of parameters c_{R1}, c_{R2}, and c_{Mort}. This tropical forcing provides the conditions under which the greatest diversity of PPS's can survive.

Under different climatic settings, e.g. seasonal or interannually varying climates, the population dynamics would clearly be affected by the seasonality, and the sensitivities to the free parameters would possibly be different to some extent. This potential limitation could easily be addressed in the future by prescribing realistic climatic forcing.

5.2 Interpretation

Despite its simplicity and potential limitations, DIVE is able to capture the essential basics of population dynamics. With an adequate choice of the three open parameters c_{R1}, c_{R2}, and c_{Mort}, it is able to represent realistic successional dynamics as well as their sensitivity to the intensity of perturbation.

The successional dynamics in DIVE are consistent with the general observed pattern of succession. Communities in early succession are usually dominated by fast-growing species (colonisers), while in later succession by slow-growing species (competitor) (Odum, 1969). Fast growing species are represented in DIVE by PPSs that rapidly establish due to a high growth rate and high seed flux (colonisers). Competitors are represented in DIVE by PPSs that are slow growing and gain a high biomass, thereby able to exclude others. In early succession in a DIVE simulation, colonisers are highly abundant, competitors are at low abundance and competition for resources plays a minor role in determining the PPS composition at this stage. As time progresses and bare area becomes limited, establishment decreases and colonisers are replaced by competitors, consistent with the real world (e.g. Huston and Smith, 1987). At this stage, the role of invasion and exclusion, i.e. resource competition, is more import than establishment in shaping community composition. As PPSs compete for resources, PPSs with high biomass steadily invade the area occupied by PPS with lower biomass by capturing more of the available space (Tilman, 1990). When small PPSs are not able to compensate exclusion with establishment, they become extinct. Hence, these dynamics in DIVE are fully consistent with observations and established ecological theory.

The sensitivity of the simulated population composition to the strength of perturbations is also consistent with observations. We found that under low perturbations, the composition was determined by late-successional strategies (competitors), while under high perturbations it was determined by early successional strategies (coloniser). These outcomes are consistent with Johst and Huth (2005). Furthermore, the intensity of perturbations affects how effective less dominant, i.e. PPS with small biomass, are at reclaiming area via establishment and so can determine whether steady states of competitive exclusion or coexistence are achieved. We found that under high levels of competition, intermediate levels of perturbations were required to obtain coexistence. This relationship is consistent with the Intermediate Disturbance Hypothesis (e.g. Grime, 1973; Connell and Fox, 1979), which proposes diversity is highest at intermediate intensity of perturbations. In summary, we conclude that the DIVE model adequately represents population dynamics in a simple way.

To get back to our main motivation of understanding the relative importance of competition and perturbations on community structure, we found that diversity is highest without competition as long as mortality was not too high. However, in the absence of competition, we found that a PPS dominated the steady state which had a low dominance, low seed production, but a high growth rate (Fig. 5d and h). This outcome of population dynamics seems unrealistic in terms of natural settings, but could represent a human managed crop land. In a crop land the seed input is high and competition is minimized by management. However, in the presence of seed competition, this PPS was absent, and in the presence of only resource competition, it was less dominant in the community. This would suggest that at least resource competition needs to be considered to obtain reasonable community dynamics in DIVE.

In the presence of resource competition, but no seed competition, we found high diversity during succession, but a final state of competitive exclusion by the most dominant PPS with the highest biomass under low perturbations. The absence of seed competition allowed for all PPS to exist at a minimal level so that diversity can result during succession. To obtain higher levels of diversity in the final state, higher levels of perturbations or a lower strength of resource competition are required.

When only seed competition is considered, we found that this also led to unrealistic outcomes. In this case, we found coexistence, but the steady state community was dominated by the PPS with the highest seed production, and not by the PPS with the highest dominance (Fig. 5b and f). This finding is consistent with Arora and Boer (2006), who found that strong seed competition leads to unrealistic patterns of competitive exclusion within their model that is based on Lotka-Volterra equations. We also found that while the relative abundances were affected by the prescribed intensity of mortality (c_{Mort}), the relative dominance was not affected. This result suggests that resource competition seems to be more important in shaping realistic community dynamics than seed competition.

When investigating the diversity of the final state (Fig. 6), we found that resource competition played the more important role than seed competition in the case of low perturbations. At the other extreme of high perturbations, the diversity was shaped by the strength of seed competition and the intensity of resource competition had no effect. Intermediate levels of perturbations led to coexistence and high diversity for the widest range of the strengths in resource and seed competition.

Given that succession and coexistence is observed in plant communities, we conclude that at least resource competition and intermediate levels of perturbation are required to simulate the dynamics of diverse populations.

5.3 Potential extensions and applications of DIVE

Current models that attempt to simulate vegetation dynamics, including composition or coexistence of different plants types, do not take into account that the strength of competition can be different in different environments, and for different plant types. Hence, current approaches impose assumptions about the strengths of competition and their effect on community structure. We have shown that the strength of competition and perturbation are critical in determining community structure. Therefore including the effects of resource and seed competition in the current generation of dynamics vegetation models could yield different results.

Thus, as a next step, it would seem important to find out the effects of competition and perturbations on the dynamics and diversity of communities across a range of realistic climates. This can easily be done using global climatologies and by including many more of the simulated PPSs from the JeDi model. This would require to couple the DIVE and JeDi models, as the plant properties needed as an input for DIVE would no longer be constant. Such an investigation would allow us to understand how reasonable the assumption of uniform, constant values for the three open parameters of DIVE are.

DIVE could also be improved by a better representation of perturbations, such as fire, herbivory, and windfall. For some forms of perturbations, process-based models exist, e.g. for fire (Thonicke et al., 2001). Also, competition can be represented in more detail, as discussed above.

Such a model would have a great potential use as it would allow us to investigate not just the role of population dynamics and functional diversity on the mean climate, but also the transient dynamics under global changes.

6 Conclusions

Understanding how diverse vegetation communities may change and interact with environmental change remains a key scientific challenge. Here we present a simple and general model DIVE that provides an adequate way to model plant population dynamics that could be used for global investigations concerning diversity and global change.

A particular strength of DIVE is that it considers seed competition and resource competition as distinct processes. This is important, because each of them influences population dynamics in a different way, and differently under different intensities of perturbations. We found that, diversity is highest under neutral seed and resource competition. However, to obtain reasonable successional dynamics, at least resource competition needs to be considered. Intermediate levels of perturbations are required to achieve coexistence under high strength of competition, which is consistent with the Intermediate Disturbance Hypothesis. In conclusion, at least resource competition and intermediate levels of perturbation are required to simulate realistic dynamics of diverse populations.

A promising next step will be to investigate how the strengths of seed and resource competition affect population dynamics in different climatic settings and what effect this may have for diversity patterns. In the future, an integration of the DIVE into the JeDi model can be used to study how global change affects global vegetation, diversity patterns and surface exchange fluxes of water and carbon in a process-based way.

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The strengths of r- and K-selection shape diversity-disturbance relationships

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Abstract

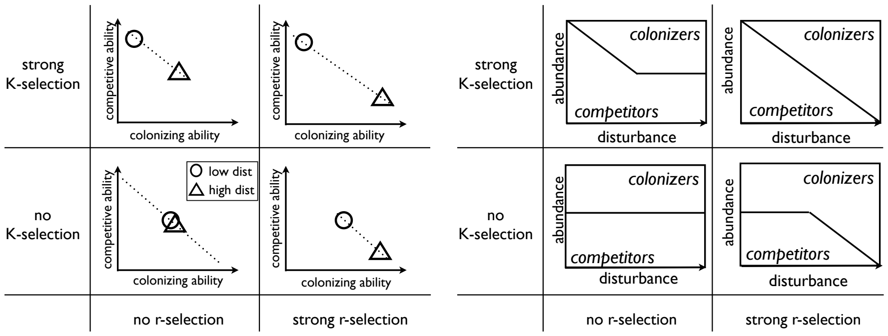
Disturbance is a key factor that shapes species abundance and diversity in plant communities. Here, we use a mechanistic model of vegetation diversity to show that different strengths of selection result in different disturbance-diversity relationships (DDRs). Selection constrains the range of viable species through the colonization-competition tradeoff, with strong r-selection favoring colonizers and strong K-selection favoring competitors, but the level of disturbance also affects the success of species. This interplay among selection and disturbance results in different shapes of DDRs, with little variation of diversity with no selection, a decrease in diversity with r-selection with disturbance rate, an increase in diversity with K-selection, and a peak at intermediate values with strong r- and K-selection. We conclude that different DDRs found in observations may reflect different intensities of selection within communities, which should be inferable from broader observations of community composition and their ecophysiological trait ranges.

1 Introduction

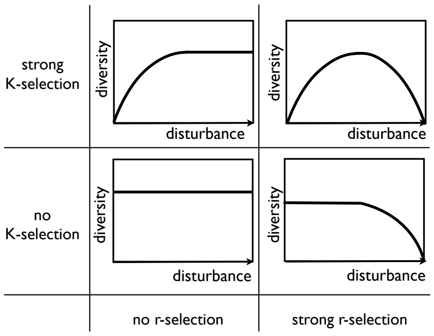
The level of disturbance is one of many factors that shape patterns of plant species diversity (Chesson, 2000). The Intermediate Disturbance Hypothesis (IDH) (Grime, 1973; Connell and Fox, 1979) states, that the diversity of a community is greatest at intermediate levels of disturbances. This peak in diversity should result from the contrasting effects of disturbance on the ability of species to persist in a community. Greater rates of disturbance require more rapid recolonization of sites, which should exclude species that are slow in reproduction, thus decreasing the diversity in a community. However, with decreasing rates of disturbance, strong competitors increasingly outcompete weaker competitors, resulting in increased levels of competitive exclusion and lower levels of diversity. Thus, the combination of the two effects suggest a peak in diversity at intermediate levels of disturbance, resulting in a unimodal disturbance-diversity relation (e.g. Roxburgh et al., 2004; Shea et al., 2004).

The IDH and, more generally, disturbance-diversity relationships (DDRs) can thus be interpreted as the outcome of how well species are able to compete and colonize. This ability is not arbitrary, but constrained by the colonization-competition tradeoff to which the different plant species in a community are subjected to. Plant strategies differ in their traits, thus affect their competitive and colonizing ability. A plant strategy that produces high biomass has a greater ability to harvest light and reach other resources and thus has a good competitive ability. Such a strategy is favored by K-selection (MacArthur and Wilson, 1967). In contrast, a plant strategy that allocates to reproduction instead of biomass can rapidly establish on free sites, thus having a greater colonizing ability. Such a strategy is favored by r-selection (MacArthur and Wilson, 1967). Since plants cannot be both, good competitors and good colonizers, they are subjected to the fundamental tradeoff between allocation to biomass and reproduction. Hence, the colonization-competition tradeoff is seen as the main mechanism that results in the IDH (e.g. Sousa, 1984).

The universality of the IDH has been tested for a wide range of empirical systems (e.g. Folder and Sommer, 1999; Molino and Sabatier, 2001) and with theoretical studies (e.g. Roxburgh et al., 2004; Johst and Huth, 2005). The unimodal DDR associated with the IDH has not been consistently observed (summary in Mackey and Currie, 2001). The relationship of diversity with disturbance rate can also be U-shaped, increasing or decreasing, or even no variation has been found (e.g. Cadotte, 2007; Mackey and Currie, 2001). Several alternative explanations have been proposed to explain these different shapes. Huston (1994); Proulx and Mazumder (1998); Kadmon and Benjamini (2006) explained different DDRs with an interdependence of productivity between different species. Following this idea, a unimodal relationship between diversity and disturbances can be realized only under intermediate levels of productivity (e.g. Kondoh, 2001; Kadmon and Benjamini, 2006). They suggest that with high productivity, diversity increases with disturbances, while under low productivity, diversity decreases with disturbances. However, productivity and diversity are not independent variables, but reflect different aspects of the



(a) Colonization-competition tradeoff (b) Frequencies of competitors versus colonizers



(c) Disturbance-diversity relationships (DDR)

Figure 1: Different strength of selection lead to exclusion of different species and thereby result in different DDRs. In the absence of selection, no species are excluded, and the colonization-competition tradeoff should have the widest range. K-selection shifts this tradeoff towards competitive species, while r-selection shifts this tradeoff towards colonizers. Under both, r- and K-selection, the tradeoff (a) should have a wider range, because it shifts from competitors towards colonizers under increasing disturbances. The abundances of colonizers versus competitors (b) reflect these relationships and lead to different shapes of DDRs (c): flat, increasing, decreasing and unimodal.

environment, the disturbance regimes as well as the level of competition within communities. Hence, a general theory to explain different shapes of DDRs is still missing (White and Jentsch, 2012).

Here, we hypothesize that different shapes of DDRs result from different strengths by which r- and K-selection exclude species from plant communities. With no competitive exclusion, the neutral theory of biodiversity (Hubbell, 2001) assumes that differences among species are irrelevant to their success, so that neither r- nor K- selection exclude species from a community. At this extreme, we should find the widest range of the competition-colonization tradeoff being realized in the community (Fig. 1(a)), because selection does not exclude sections of this tradeoff. Since the success of species is independent of their differences, colonizers and competitors should be present at a similar abundance (Fig. 1(b)), thus resulting in a flat DDR (Fig. 1(c)). K-selection should result in a reduction of the range of the competition-colonization tradeoff due to competitive exclusion. Colonizers should be absent at low disturbances and become increasingly present at higher disturbance rates. This isolated effect of K-selection should result in a increase in diversity to a saturating value with increasing rates of disturbance. With r-selection, we should find the competition-colonization tradeoff to be reduced towards the other end, favoring colonizers at the expense of strong competitors. This should result in a greater abundance of colonizers towards higher disturbance rates, but also reducing the diversity at this end because competitors are increasingly excluded. This should result in a decline of diversity with greater disturbance rates. When both forms of selection are considered, we should tend to find a less reduced range of the competition-colonization tradeoff, a continuous shift in the abundance from competitors to colonizers, resulting in the unimodal DDR that is associated with the IDH.

To evaluate this hypothesis, we use a plant physiology-based numerical model of plant diversity (JeDi-DGVM, Kleidon and Mooney (2000); Pavlick et al. (2012)) in combination with a model of population dynamics (DIVE, Bohn et al. (2011)). The JeDi-DGVM tests a wide range of plant growth strategies for their reproductive success under different climatic conditions and thereby represents a mechanistic climate filter (Woodward, 1987). It has been used successfully in previous studies to understand biogeographical patterns of plant species richness (Reu et al., 2011), relative abundance distributions (Kleidon et al., 2009), as well as vegetation productivity (Pavlick et al., 2012). The model is used here as a mechanistic way to obtain the range of the colonization-competition tradeoff for a given climatic setting. The DIVE model (Bohn et al., 2011) represents a competitive filter, in which we can vary the strength of r- and K-selection as well as disturbance rate and evaluate their effects on the resulting simulated diversity of the community. With this we estimate the effects of selection on the resulting DDRs.

In the following, we first provide a brief description of the two models in the methods section, describe the setup of the sensitivity simulations as well as the analysis of the simulations. The simulation results are presented in a similar way as the line of reasoning was presented in Fig. 1. We then describe potential limitations and interpret the results in terms of our hypothesis and close with a brief summary and conclusion.

2 Methods

We use two simulation models to test our hypotheses in an approach that is summarized in Fig. 2.

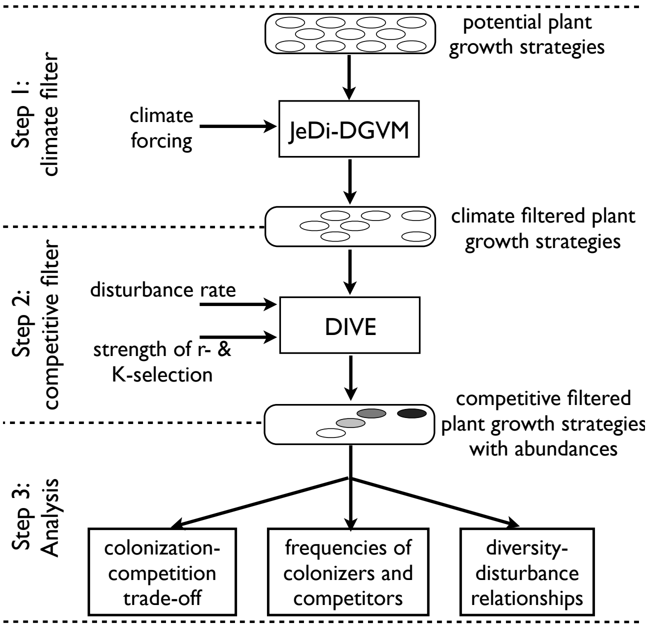


Figure 2: Schematic diagram of our approach, in which we use two simulation models. The first model, the JeDi-DGVM, represents the climatic filter that estimates the plant growth strategies that are potentially able to be reproductively successful in a given climatic environment. The second model, the DIVE model, simulates the population dynamics of these plant growth strategies and represents a competitive filter. The strength of r- and K-selection and the rate of disturbance are external model parameters. DIVE calculates the abundance of the plant growth strategies, from which the colonization-competition trade-off, the abundance of colonizers and competitors and the diversity-disturbance relationships are being derived.

2.1 Step 1: The climate filter

The first step represents the climate filtering of a wide variety of potential plant growth strategies for their reproductive success. This filter is implemented by the Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM, Kleidon and Mooney (2000); Pavlick et al. (2012)). JeDi-DGVM simulates plants in terms of several carbon pools associated with leaves, stem, roots, and reproduction and in terms of their physiological processes of photosynthesis, respiration, resource allocation to different biomass pools as well as reproduction, and phenology. The simulated processes are affected by the climatic conditions, particularly solar radiation, temperature and soil moisture, and by a set of functional traits. These functional traits include, for instance, the relative allocation to different carbon pools, ecophysiological tradeoffs, and phenological responses and thereby control plant growth and life history. Competition, however, is not simulated by the model.

We simulated a large number of trait combinations of randomly chosen values using a realistic climatic forcing and evaluated these combinations for their reproductive success. These successful strategies were then used in step 2.

2.2 Step 2: The competition filter

The second step represents the explicit simulation of population dynamics using the successful plant growth strategies from step 1. This step uses the DIVE model (Bohn et al., 2011), which is a simple representation of population dynamics. The DIVE model simulates the abundances of the different plant growth strategies resulting from the dynamics of establishment, competition, and mortality. It has been previously be shown to adequately reproduce successional patterns (Bohn et al., 2011).

The simulated population dynamics are affected by the performance of the different plant growth strategies. For instance, the simulated biomass of a particular strategy determines its competitive ability, the simulated allocation to reproduction and growth rate determine its colonizing ability, and the biomass turnover relates to the mortality of a strategy. We used several performance traits (Violle et al., 2007), such as biomass, seed flux, productivity, and biomass turnover, to derive demographic parameters, such as growth and mortality rates for the population dynamics (see Bohn et al., 2011, for details).

In addition, the dynamics of establishment, competition, and mortality are affected by externally prescribed parameters relating to the strengths of r- and K-selection as well as the disturbance rate. The strength of r-selection is a parameter that mediates the importance of the seed flux in the rate of establishment of a particular plant growth strategy. In the absence of r-selection, the magnitude of the seed flux of a particular strategy does not influence the rate of its establishment. Under strong r-selection, the strategy with the highest seed flux has the highest potential to establish. The realized establishment rate is also dependent on the growth rate, so that a colonizer, or r-strategist, is characterized by a high seed flux and a high growth rate. The strength of K-selection is a parameter that determines the importance of the biomass of a strategy for competitive exclusion. In the absence of K-selection, differences in biomass among strategies do not result in competitive exclusion. With strong K-selection, exclusion is proportional to the difference in biomass among different strategies (with the assumption that strategies with higher biomass are more dominant). Hence, a good competitor, or K-strategist, is characterized by a high biomass. The disturbance rate is a parameter that acts to uniformly increase the mortality and thereby reduces the abundance of all simulated strategies. The higher the disturbance rate, the higher is the reduction in abundance.

2.3 Step 3: Analysis

The simulated abundances from step 2 are analyzed to infer the colonization-competition tradeoff, the relative abundance of competitors and colonizers, and the diversity of the simulated community to reproduce the sensitivities shown in Fig. 1.

The colonization-competition tradeoff is derived directly from the different, successful plant growth strategies. We use the simulated biomass as an indicator for the competitive ability of a strategy, and the simulated growth rate as an indicator for its colonizing ability.

To classify the simulated strategies in terms of good competitors or colonizers, we use the distribution of simulated growth rates of the different strategies as a basis (see Fig. 3). We define colonizers to be strategies that are in the top 1/3 quantile of the distribution, while competitors are taken to be those strategies that are in the bottom 1/3 quantile. We refer to the middle quantile as intermediate strategies.

To infer DDRs, we measured the diversity of the resulting steady state community in terms of the Shannon information entropy of the relative abundances. We normalized the diversity by the maximum, resulting in the so called evenness.

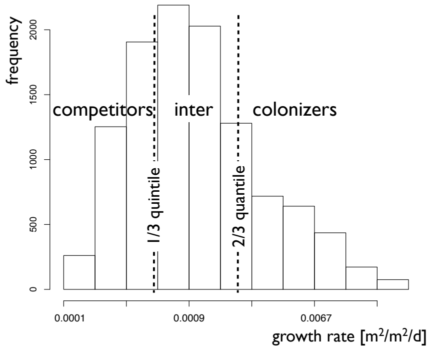


Figure 3: The successful plant growth strategies simulated by the model are characterizes as competitors, colonizers and intermediates dependent on their growth rate. We use three quantiles of the distribution of growth rates from all simulations, as shown by the dashed lines, for the partitioning.

2.4 Simulation setup

We used a climatic forcing representative of a moist tropical climate with a mean daily precipitation of 9 mm/day and a mean temperature of 26.3 °C. We tested a set of 500 initial plant growth strategies. The JeDi-DGVM was run for 70 years, so that the characteristics of each strategy represent the mean properties of an adult population. The simulated properties were used to run the DIVE model. The simulated abundances from the DIVE model were returned to the JeDi-DGVM at a monthly time step to establish a feedback between population dynamics and the computation of seed production in the JeDi-DGVM. This setup was run for a total of 100.000 years to ensure a steady state composition of the community.

We conducted a number of sensitivities with this model setup to different strengths of r- and K-selection as well as the disturbance rate. Three levels of r- and K- selection were used, representing none, moderate, and strong selection ($c_{R1} = [10000, 50, 1]$ and $c_{R2} = [10000, 1.5, 1]$ respectively, Bohn et al. (see 2011, for details)). We used five disturbance rates from low to high ($c_{MORT} = [0.001, 0.01, 0.1, 1, 10]$ respectively). In total, this resulted in 45 model simulations.

3 Results

In the presentation of the results, we follow the sequence shown in Fig. 1. We first show the simulated colonization-competition tradeoff for different strengths of selection, the abundance of colonizers and competitors, and finally the simulated diversity-disturbance relationships (DDRs).

3.1 The colonization-competition tradeoff

The simulated colonization-competition tradeoff for different strengths of r- and K-selection for low and high disturbance rates is shown in Fig 4. In the absence of selection, the colonization-competition tradeoff spans the widest range (Fig 4a and e). Since neither competitive nor colonizing ability can increase the abundance of a particular growth strategy due to the lack of selection in the model, the simulated abundances are entirely determined by the growth and mortality of the different growth strategies. The colonization-competition tradeoff is very similar in terms of range and abundances under low and high disturbances. The most abundant strategy in both cases is classified as a colonizer.

When r-selection is included in the simulations, the tradeoff is strongly constrained to a narrow range (see Fig 4b and f). Both, strong competitors as well as colonizers are excluded in the simulations, and the resulting strategies are mostly classified as intermediates. In the model, this results from the combined need of high seed production as well as high growth rate to be an effective colonizer.

With strong K-selection, the range of the tradeoff is hardly different compared to the case of no selection (Fig 4c and g). In contrast to the case of no selection, the strategies of highest abundance is clearly different in the cases of low and high disturbance. In the case of low disturbance, the most abundant strategy is a strong competitor with high biomass and low growth rate. In the case of high disturbance, the most abundant strategy is a colonizer with a relatively high growth rate.

With both, strong r- and K-selection, the range of the tradeoff is reduced compared to the case of no selection (Fig 4d and h), but wider compared to the case of only r-selection. The most abundant strategy in the case of low disturbance rate is a strong competitor as in the case of only K-selection, while in the case of high disturbance, the most abundant strategy is shifted along the tradeoff towards a stronger colonizing ability.

Overall, we find that the model simulates the colonization-competition tradeoff very well. The model results broadly support the expected differences in the tradeoff under different settings

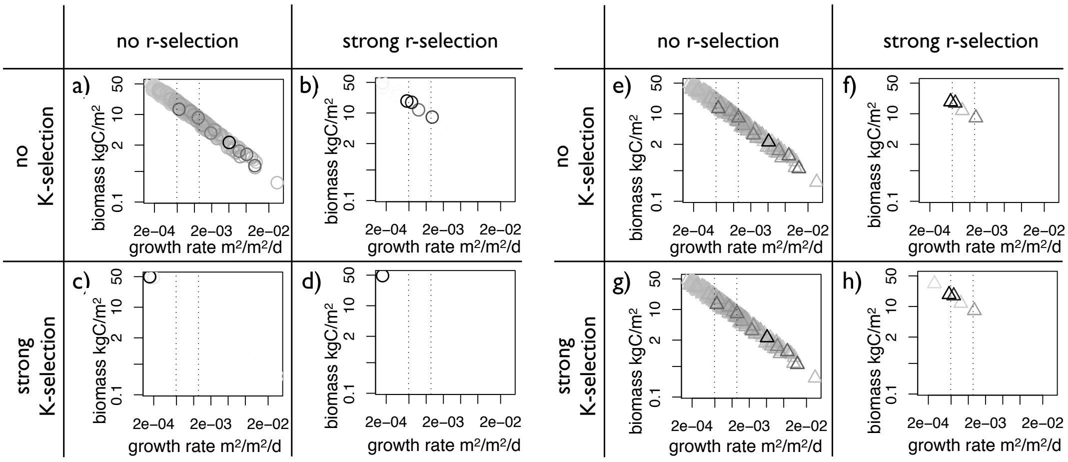


Figure 4: Sensitivity of the simulated colonization-competition tradeoff to r- and K-selection. Every symbol in the figure reflects a successful plant growth strategy. The grey scale indicates the normalized abundance of these strategies from low abundance (white) to high abundance (black). Circles represent the simulations of low disturbance rates (a-d), while triangles represent the simulations with high disturbance rates (e-h). The dotted lines show the breaks for colonizers, intermediates and competitors.

of selection and disturbance. K-selection shifts the most abundant strategy towards a strong competitor with a low disturbance rate, and towards a better colonizer with a high disturbance rate. With respect to r-selection, we find a somewhat different behavior, because the tradeoff is shifted less towards colonizing ability as hypothesized. This can be attributed to the way that the model describes establishment. The highest rate of establishment is achieved in the model by strategies that have high seed production in addition to a relatively high growth rate, whereas the number of produced seeds is not explicitly treated in the model. Nevertheless, the range of the tradeoff is reduced with r-selection as hypothesized.

3.2 Abundances of colonizers, intermediates, and competitors

The differences in composition in terms of colonizers, intermediates, and competitors for the different scenarios of selection and the sensitivity to disturbance rates are shown in Fig. 5. We find that with no selection, neither colonizers nor competitors are favored under different disturbance

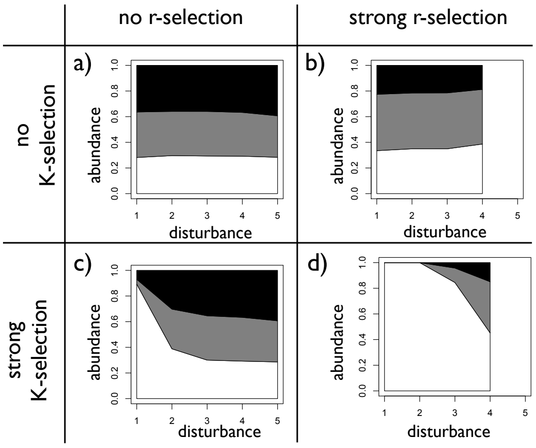


Figure 5: Abundances of competitors (white), intermediates (grey), and colonizers (black) for the different scenarios of r- and K-selection and disturbance rate. In the case of strong r-selection and high disturbance rate (level 5), no strategies survive so that no relative abundances are shown for this disturbance rate.

rates, because of the lack of selection in the model. This lack of sensitivity is consistent with the tradeoff being essentially identical under the different disturbance regimes shown in Fig. 4. With strong r-selection, the abundance of competitors is increased. This somewhat surprising result is nevertheless consistent with the reduction and shift of the tradeoff shown in Fig. 4. With strong K-selection, competitors have a higher abundance under low disturbance rates than the case of no selection, and their abundance is reduced with increasing disturbance rates. Consequently, the abundance of colonizers is enhanced with higher disturbance rates. This is, again, consistent with the shift in abundance that was seen in the tradeoff in Fig. 4. When both forms of selection are included, competitors have the highest abundance at low disturbance rates, which successively decrease with greater disturbance rates. This sensitivity is again consistent with the tradeoff characteristics shown in Fig. 4.

In summary, we find that the simulated sensitivities of the abundances of competitors and colonizers are consistent with the hypothesized trends shown in Fig. 1 for the cases of no selection and K-selection. The results for r-selection deviate somewhat from the hypothesized trend, because the most favored strategies under r-selection are not the strategies with the highest growth rates. In the case of both, r- and K-selection, we nevertheless find a trend that is somewhat consistent to our hypothesis.

3.3 Diversity-disturbance relationships

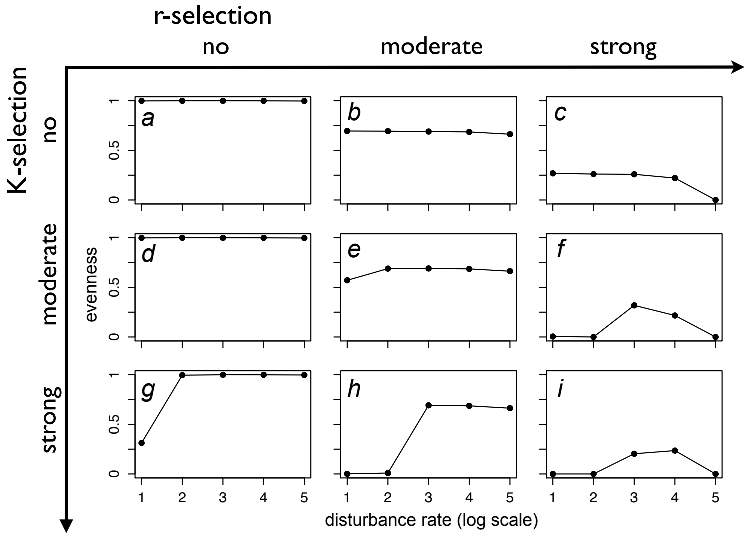


Figure 6: Simulated DDRs for different strengths of r- and K-selection.

The resulting shapes of the DDRs for the different scenarios are shown in Fig. 6. With no selection, the simulated diversity of the community is insensitive to disturbance rate and remains at the maximum level of diversity. With increasing r-selection (Fig. 6a-c), we find a successive decrease in the diversity, and an increased sensitivity of the diversity at high disturbance rates. In the case of strong r-selection, diversity is reduced at high disturbance rates, resulting in a decreasing DDR. This is consistent with the reduced range of the colonization-competition tradeoff shown in Fig. 4. With increasing strength of K-selection (Fig. 6a,d,g), we find that the diversity is first relatively unaffected, but then is reduced at low disturbance rates in the case of strong K-selection. Hence, this results in an increasing DDR at strong K-selection. The relative insensitivity of diversity to K-selection is consistent with the insensitivity of the range of the tradeoff axis shown in Fig. 4, while the reduction of diversity at low disturbance rates is consistent with the reduction of the tradeoff axis at strong K-selection at low disturbance rates. When both, r- and K-selection, are considered, we note an increasing combination of the two effects. The maximum diversity reached in the different scenarios of selection strength successively is reduced with increasing r-selection as is the diversity at high disturbance rates.

Hence, the combination of r- and K-selection results in an unimodal DDR. This relationship is consistent with the differences in the tradeoff shown in Fig. 4. The range of the tradeoff with strong r- and K-selection is reduced at low disturbance rates, and is broadened in the case of high disturbance rates.

In total, we find that different shapes of the DDRs can be reproduced with different strengths of r- and K-selection. These different shapes can clearly be attributed to the effects that selection has on the range of the colonization-competition tradeoff as represented in the model. This, in turn, is consistent with the hypotheses that we formulated in the introduction.

4 Discussion

Limitations

We used two different models, JeDi and DIVE, in our study. Each model by itself has, obviously, limitations that affect the results to some extent. A general discussion of the limitations of the models can be found in their respective publications (Bohn et al., 2011; Kleidon and Mooney, 2000; Pavlick et al., 2012). Here, we focus on those aspects that directly relate to the testing of our hypotheses regarding the different shapes of the diversity-disturbance relationships (DDRs).

The JeDi-DGVM is the basis for our study, as it yields the potential range of the colonization-competition tradeoff that is compatible with the prescribed climatic conditions. The tradeoff is simulated via describing the competitive ability by the biomass, and the colonizing ability by the growth rate, which is proportional to biomass, and does not include seed production. This tradeoff is therefore simulated to be a relatively narrow line (see Fig. 4), which means that the assimilated carbon is either used for growth or colonization. However, real plants also use carbon for other processes than just growth, for instance defense and nutrient acquisition. These processes represent carbon allocation to different uses than the tradeoff, so that this could result in a tradeoff that is more spread out than what is being simulated by the JeDi-DGVM. Given that the JeDi-DGVM can reproduce a range of observations very well (Kleidon and Mooney, 2000; Kleidon et al., 2009; Reu et al., 2011; Pavlick et al., 2012), it is reasonable to assume that this tradeoff, despite probably being too constrained to a line, is nevertheless reasonably simulated.

This tradeoff represents the key input for the DIVE model, which, based on the representation of r- and K-selection, simulates the actual abundances of competitors and colonizers. The DIVE model was shown to reasonably represent successional dynamics in ecosystems (Bohn et al., 2011), so that in principle, the effect of r- and K-selection should be adequately represented. We notice, however, that the abundances of competitors and colonizers with increasing disturbance rates (Fig. 5) did not fully follow the trends that we expected (as shown in Fig. 1). We attribute this to the way that colonization is represented in the DIVE model as a combination of seed production and growth rate. In this representation, the tradeoff between seed size and seed numbers is not considered. However, this tradeoff was found to be important (Moles and Westoby, 2006), because it partly modulates the colonization-competition tradeoff and leads to species coexistence (e.g. Muller-Landau, 2010; Coomes and Grubb, 2003). In our model, plants with a higher biomass may have a higher seed production than plants with a smaller biomass, so that the plants with the highest seed production may not be the ones with the smallest biomass. An explicit representation of this tradeoff could therefore result in a sensitivity to the strength of r-selection that would be more consistent with our hypotheses.

To obtain DDRs, a range of prescribed disturbance rates were simulated. Disturbances are modeled in a relatively simple way by a single parameter that influences the mortality equally across all plant growth strategies (Bohn et al., 2011). In the real world, disturbances represent a range of singular events, such as droughts, fire, herbivory, and wind throw. Furthermore, several disturbance types interact (summary in Seifan et al., 2012), as well as the intensity and the frequency of disturbances (Hall et al., 2012; Miller et al., 2011). Despite the simplicity of our representation, the simulated sensitivities to disturbance rates are nevertheless plausible and consistent with our hypotheses, indicating that our representation captures the overall role of disturbances on the simulated abundances.

Interpretation

Our results mostly support our hypothesis that different types of DDRs can be attributed to different strengths of selection. We confirm our hypothesis that a flat relationship is obtained in the absence of selection, because the abundances are then shaped entirely by the growth and mortality of the different plant strategies. Diversity decreases with disturbance with strong r-selection in our results mostly due to a decrease in overall diversity of the community. With strong K-selection, colonizers are less excluded at stronger disturbance rates, thus resulting in an increase of diversity with disturbance. With strong r- and K-selection, both effects are combined and yield an unimodal DDR.

Our interpretation of the role of r- and K-selection for DDRs is a straightforward and simple extension of the original work on the IDH (Grime, 1973; Connell and Fox, 1979), in which the different strengths by which selection acts to exclude species from the composition of a community is being varied. By doing so, different strengths of the mechanism that results in the IDH is implemented, yielding different shapes of the DDR.

However, we do not explicitly state the mechanism by which such a difference in selection could take place. One plausible explanation may be the spatial scale that is being considered. Tilman (1994) showed that greater coexistence and diversity in communities is possible with the explicit consideration of space. Consistent with this interpretation, the neutral model of Hubbell (2001) shows that increasing space leads to greater diversity. Combined, it would appear that a greater consideration of space makes the overall composition more neutral, corresponding to a lower strength of selection acting on the composition. In addition, climate may also alter the strengths of selection as well. These aspects would need to be further evaluated in future work.

Our results are largely consistent with Johst and Huth (2005). They used a patch model of successional dynamics and found a unimodal DDR for most forest ecosystems under discrete disturbances. The unimodal DDR was generated through the successional order from early towards late successional species, where at intermediate disturbances a mixture of all successional stage species coexisted. Their results correspond to our scenario where r- and K-selection are present. Under such conditions we also observe an unimodal DDR but considering continuos disturbances. Under some circumstances Johst and Huth (2005) also found a bimodal DDR. In their study, the occurrence of a species rich intermediate successional group led to a local minimum between the maxima of mixtures of successional groups. We did not find such a bimodal relationship, likely because we do not consider the diversity of successional groups and do not represent discrete disturbance events.

The results of dos Santos et al. (2011) are only in part consistent with ours. They used a spatially explicit individual-based model and showed that tradeoff mechanisms usually led to unimodal DDRs, while neutrality led to decreasing DDRs. Tradeoff mechanisms support the transition from pioneers towards late successional species, while neutral communities do not support this transition. The tradeoff mechanism supports succession only under selection, which is consistent with our results. The neutral community in our study would be reflected in the absence of selection, which led to a flat DDR. However, dos Santos et al. (2011) also found a flat DDR for a neutral community of long dispersers with a negative density dependent recruitment. This negative density dependent mechanism of long dispersers corresponds to the absence of r-selection, thus being consistent with our results.

The study of Seifan et al. (2012) provided an alternative mechanism for unimodal DDRs compared to ours. They used a demographic temperate grassland model and found an unimodal DDR but this was not generated by the colonization-competition tradeoff. In their study, tradeoffs between species-specific responses to disturbances (Seifan et al., 2012) maintained diversity. However, in grasslands most species are colonizers, so that the whole range of the colonization-competition tradeoff was likely not considered in their study.

5 Conclusion

We presented a hypothesis that explains different shapes of diversity-disturbance relationships (DDRs) by different strengths of competition. The colonization-competition tradeoff plays a key role in this hypothesis. A plant needs to trade, whether it invests into its competitive ability and grows tall but slowly (competitor) or whether it can establish rapidly but grows only small (colonizer). While r-selection favors colonizers, K-selection favors competitors. This results in four types of DDRs. A flat DDR is achieved in the absence of selection. Diversity increases with disturbance under K-selection, and decreases under r-selection. An unimodal DDR is achieved under both, r- and K-selection. We successfully tested our predictions with a process-based simulation model of tropical plant communities. Our results are consistent with other modeling studies on the effects of disturbances for diversity.

Our results show that different intensities of selection have different effects on the range of the colonization-competition tradeoff, therefore affecting the abundances of colonizers versus competitors and thus influence community structure and the shape of the DDR. The strength of selection in a community should thus be reflected in the combined information of abundances of colonizers versus competitors, the range of the colonization-competition tradeoff, the diversity, and possibly the spatial scale of observation as this may affect the strength of selection. What this implies is that a broader range of field observations should help us to better identify the underlying mechanisms that result in observed diversity patterns.

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Contrasting the effects of climate versus competition on diversity-disturbance relationships

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Abstract

Climate, disturbances, and plant interactions are key factors shaping diversity patterns and community composition. Recently we have shown that different strengths of r- and K-selection can lead to four forms of diversity-disturbance relationships (DDRs): flat, increasing, decreasing and unimodal. However, the influence of climate on these relationships was not evaluated. Here we use a mechanistic model of vegetation diversity (JeDi-DGVM) coupled to a community model (DIVE) to analyze the role of climate for DDRs that are shaped by r- and K-selection. Thereby, climate first filters viable plant strategies through constraints on growth. Second, r- and K-selection further filter viable plant strategies to select those that cope with competition. We analyze the effects of the two filters on the resulting DDRs through their constraints on the colonization-competition trade-off. We find that r- and K- selection have similar effects in different climates on the shape of DDRs. In less favorable climates, diversity decreases more strongly with high disturbances. R-selection has strongest effects in the tropics, and leads there to the highest diversity reduction. Under strong r- and K-selection, the warm temperate climate has highest diversity. We conclude that climate does not have a strong effect on the shape of DDRs, but rather modulates the strength of selection that affects diversity and the trade-off axis. Favorable climates allow for higher diversity and are less affected by K-selection than less favorable climates. Nevertheless, strong r- or both r- and K-selection can lead to diversity in favorable climates that is lower than in less favorable climates. We conclude, that vegetation in the temperate climates is at first restricted to climatic condition, while the tropical climates allow for a wide variety of vegetation. In the following, selection has limits diversity more in the tropical climates then in the temperate ones.

1 Introduction

Disturbances are a key factor that control and maintain diversity (e.g. White & Jentsch, 2012). Grime (1973) and Connell & Fox (1979) hypothesized that diversity has a maximum at intermediate levels of disturbances, which is known as the Intermediate Disturbance Hypothesis (IDH). Under low rates of disturbance, competitive exclusion drives the best competitor to dominate the community. Higher rates of disturbance make it increasingly harder for plant species to persist, and the ability to rapidly colonize gains importance. Thus, the combination of both effects should lead to a maximum in diversity at intermediate rates of disturbances (Sousa, 1984).

However, besides the proposed unimodal diversity-disturbance relationship (DDR), other types of relationships, such as an increase or decrease of diversity with disturbance rate, have been found (see summary by Mackey & Currie, 2001). We have recently hypothesized that different types of relationships reflect different intensities of selection and demonstrated with a process-based model, how strength of competition in terms of r and K-selection (MacArthur & Wilson, 1967; Pianka, 1970) shape DDR in a tropical climate (Bohn *et al.*, 2013). Bohn *et al.* (2013) showed the differing effects of r- and K-selection under increasing levels of disturbances. In case of no selection, it does not matter if a plant species has a higher competitive or colonizing ability, their chances to persist are equal, resulting in a flat DDR. Strong K-selection favors competitive species, and therefore leads to competitive exclusion under low disturbances. This results in a DDR in which diversity increases with disturbance rate. Strong r-selection favors colonizers, so that the ability to colonize is increasingly important for the abundance with higher disturbance rates. This leads to less species surviving under high disturbances, and therefore to a decreasing DDR. Thus, a combination of strong r- and K-selection lead to the unimodal DDR as proposed by the IDH.

However, Bohn *et al.* (2013) did not look into the role of climate, which acts as a first filter for plant species (Woodward, 1987). Climate constrains plant species through the availability of resources, particularly light and water, and the length of the growing period, with which plants need to cope with. Fewer plant species persist in more restricted climates, such as temperate or semiarid regions, compared to the tropical humid climates, in which the highest plant species richness is observed (Barthlott *et al.*, 1999). The large scale distribution of plant species richness can thus be related to the extent to which climate restricts the various ways by which plants cope with their climatic restrictions (Kleidon & Mooney, 2000).

The climatic restrictions also shape the abilities of species to compete and colonize, hence

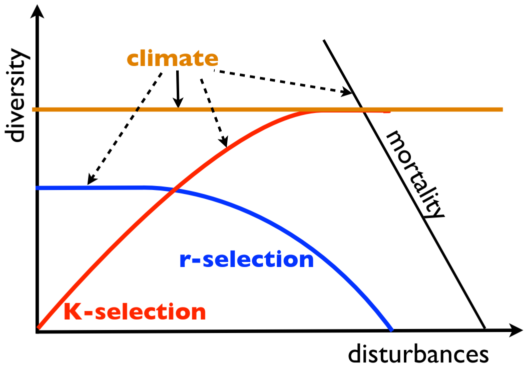

Figure 1: Conceptual diagram of the effects of climate, r- and K-selection on diversity-disturbance relationships. Climate sets up the upper limit of diversity (orange). Strong r- (blue) and strong K-selection (red) further limit diversity under high and low disturbances, leading to four possible shapes: flat, increasing, decreasing or hump-shaped. Different strength of r- and K-selection are for simplicity not shown, but as strength of selection decrease, the curves saturate towards the climate limit. Climate may not only affect the upper limit of diversity, but also the influence of r/K-selection on diversity, and how strongly increasing disturbances limit diversity because of increasing mortality.

resulting in the colonization-competition trade-off. This trade-off has been shown to modulate DDRs under strength of r- and K-selection (Bohn *et al.*, 2013). This suggests that in different climates the quantitative and qualitative effects of selection strength might differ. For example, some savannas are dominated by colonizing grasses, while the temperate regions are naturally mostly dominated by trees, which exclude grasses by competition. Hence, the colonization-competition trade-off might be realized differently in different climates. Further, the number of plant species that form this trade-off may be different in different climates. The main question we investigate here is if competition has the same effects in different climates and how important biotic versus abiotic factors are in shaping community composition. Dobzhansky (1950) reasoned that competition is more intense in tropical climates than in temperate ones. He argued that selection of species in the temperate zones is mainly controlled by the environment, whereas in the tropics, competition is more important due to the more favorable conditions. This, he argued, should lead to a greater restriction of resources and food types in the tropics, and more species can co-exist in smaller niches Pianka (1966).

This study aims to separate the effects of climate and competition on community composition, extending the work of Bohn *et al.* (2013). We hypothesize that r- and K-selection have qualitatively similar effects in different climates because the colonization-competition trade-off applies to all climates. This should, in principle, result in similar forms of DDRs, including flat, increasing, decreasing or unimodal relationships (Fig. 1). Climate plays an important role here because it first sets to upper bound on these curves (solid arrow in Fig. 1) and because it modulates the strength by which selection reduces diversity (dashed arrows in Fig. 1). Considering only the effect of climate without competition, we would expect to see a diversity decrease from the tropical climates towards the temperate climates, as shown by previous, related modelling work (Kleidon & Mooney, 2000; Reu *et al.*, 2011; Pavlick *et al.*, 2012). However, following the reasoning of Dobzhansky (1950), we would expect that stronger selection and competition will have stronger effects on diversity in the tropics than in the temperates.

To understand the role of species interactions versus climate, we use the mechanistic simulation model JeDi-DGVM coupled to the population dynamics model DIVE. Thereby the JeDi-DIVE model considers climate as constraint of many different random plant strategies and simulates the effect of r/K-selection and disturbances on the resulting community composition. We ran our model in four different climates that span a wide range of climates that differ in the length of their growing season. Further, we apply different rates of disturbances and different strength of r- and K-selection to test our hypothesis. In the following section, we explain our model in more detail. We then first show the effects of climate per se on diversity. Second, we investigate how climate and selection modulate the colonization-competition trade-off and diversity. This then allows us to compare the effect of climate versus the effect of r- and K-selection on diversity. Finally, we show the sensitivities of the diversity-disturbance relationships to the strength of r- and K-selection in the four chosen climates. We close with a discussion of our results with regard to model limitations and relate it to previous research.

2 Methods

For our study we use two models: a plant physiology-based numerical simulation model of plant diversity (JeDi-DGVM, Kleidon & Mooney (2000); Pavlick *et al.* (2012)) in combination with a model of population dynamics (DIVE, Bohn *et al.* (2011)) (Fig. 2). The JeDi-DGVM model simulates many functional plant strategies constrained by climatic conditions. The model includes mechanistic processes such as photosynthesis, respiration and carbon allocation into different pools. The model reproduces observed diversity pattern (Kleidon & Mooney, 2000;

Reu *et al.*, 2011). The JeDi-DGVM model includes the dynamic calculation of abundances via biomass dominance of the surviving species and models realistic biogeochemical fluxes such as productivity (Pavlick *et al.*, 2012).

The DIVE model (Bohn *et al.*, 2011) has been developed in order to calculate plant strategies abundances and community composition mechanistically. Abundances are simulated from the explicit simulation of rates of establishment, competition and mortality. All these processes depend on species specific parameters that are gained from species performance such as biomass, productivity and seed production. Mortality is influenced by disturbances, establishment depends on strength of r-selection and competition on strength of K-selection.

In our study, we dynamically couple the two models. The JeDi-DGVM yields simulated values of productivity, respiration, litter flux, seed production and biomass. These simulated properties are used in DIVE to calculate growth rates, mortality rates, dominance and germination rates of the plant strategies, which express the abilities of plant strategies to colonize and to compete. Additionally, DIVE needs three parameters as input: strength of r-selection, strength of K-selection, and level of disturbance. These modulate the importance of competitive and colonizing abilities for success of individual strategies. Out of all these parameters, DIVE calculates the abundances of the plant strategies. These abundances are returned to the JeDi-DGVM model at a monthly time step. Details of the models can be found in Bohn *et al.* (2011) and Pavlick *et al.* (2012).

Simulation setup

We set up the model using four different climates (Fig. 3). We label these climates as moist tropical (MT), dry tropical (DT), warm temperate (WT) and a cold temperate climate (CT). The MT climate is characterized by warm temperatures and precipitation during the whole year. The growing season spans over the whole year, and this climate represents the most favorable growing conditions. The DT climate shows a strong seasonality with a pronounced dry period that reduces the length of the growing season. The WT climate is moist throughout the year, but has periods of low temperatures and frost. The CT climate is characterized by extended periods of frost, leading to the shortest growing season. The climate data at a daily time step including downward shortwave and longwave radiation, precipitation, and near-surface air temperature is gained from an improved NCEP/NCAR atmospheric reanalysis dataset (Qian *et al.*, 2006). Each model run starts with the same 500 plant strategies, where each is defined by 15 trait

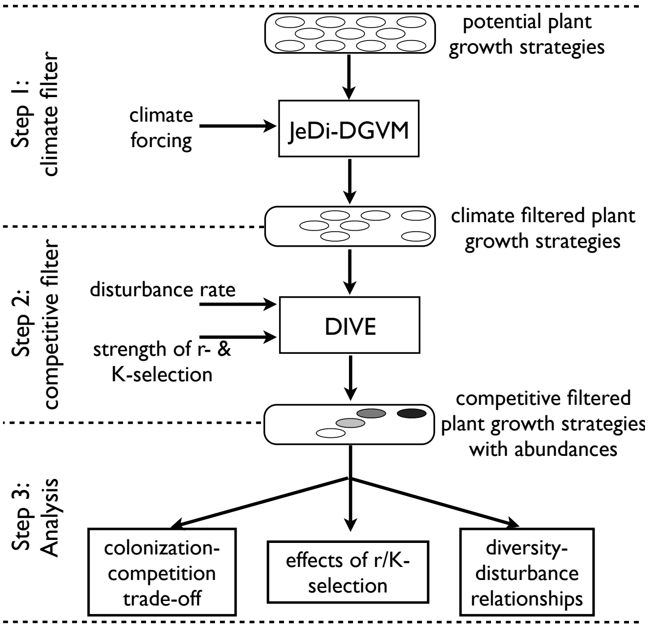

Figure 2: Overview of the methodology. In a first step, many randomly generated plant species are subjected to a climatic filter using the JeDi-DGVM that sorts out those strategies that are unable to reproduce in a given climate. In the second step, the DIVE model acts as the competitive filter that calculates the abundances for different strengths of r- and K-selection and disturbance rate (indicates as grey-scale colors). In the third step, the simulated abundances are analyzed regarding the colonization-competition trade-off and the diversity-disturbance relationships. (Graphic adopted from Bohn *et al.*, 2013, .)

parameters that are randomly sampled. The simulations were run for 100000 years to reach a steady state in the species composition.

We performed a set of sensitivity simulations with respect to the three DIVE model parameters that describe the rate of disturbance and the strengths of r- and K-selection. We use five disturbance levels, equally distributed over a logarithmic range. For strength of selection we use three different settings of no, intermediate and strong competition. This results in a total number of 180 model runs (= 4 climates * 5 disturbance levels * 3 strengths of r-selection * 3 strength of K-selection).

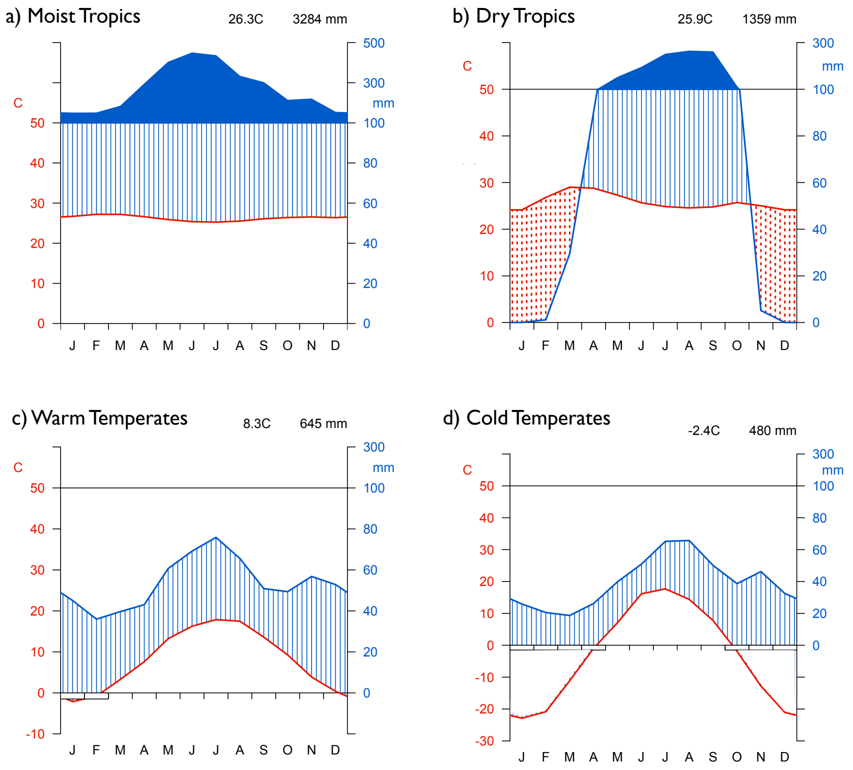

Figure 3: Climate diagrams of the four climates used in this study using the representation by Walter (Walter & Lieth, 1967). The blue and red lines show precipitation and temperature respectively. The striped areas indicate humid periods, the dotted areas represent dry periods. The mean temperature and the yearly precipitation is given at the top of each diagram.

Analysis

From the simulated abundances, we calculated the trade-off axis of the colonization-competition trade-off directly from the model output. The length of the axis is calculated as the maximal distance between the best competitive plant strategy and the best colonizing plant strategy. This axis is calculated for four scenarios: no r- and no K-selection, strong r and no K-selection, no r- and strong K-selection and strong r- and K-selection.

We measured diversity as the Shannon Information Entropy H that is based on the abundances of the plant strategies, p_i, by $H = -\sum_i (p_i \ln p_i)$ where i runs over all plant strategies. A low diversity is reached when only one plant strategy dominates the community. Diversity increases the more plant strategies are present with high abundances. Diversity reaches a maximum, if all plant strategies have equal abundances and the number of plant strategies is high. For instance, if 500 plant strategies have equal abundances, diversity reaches its maximum with a value of 6.2.

3 Results

3.1 Biomass and reproduction in different climates

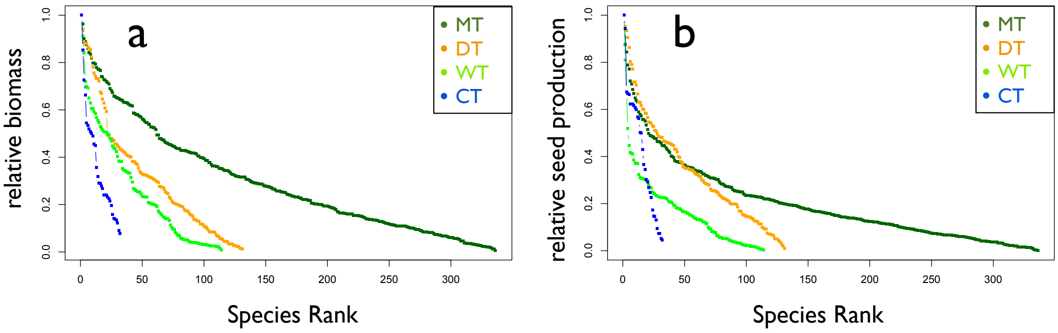

Figure 4: Rank plots of simulated (a) biomass and (b) seed production for communities only constraint by climate for the four different climates. In all climates, the same number of 500 random plant strategies was tested. For comparison, the simulated properties were normalized by the highest simulated value in each of the climates.

To illustrate the effect of climate on the key parameters that shape r- and K- selection, we first show the simulated values of biomass and seed production for the four different climates, ranked by their value (Fig. 4). The moist tropical climate (MT) with the longest growing season allows for the highest number of plant strategies, which is reflected by the widest span on the rank axis. At the other extreme, the cold temperate climate (CT) shows the lowest species richness. This difference in range demonstrates the effect of climate on the richness of viable plant strategies and follows the expected diversity gradient from the tropics towards the poles. Further, the MT climate allows for a high number of species with high biomass (Fig. 4 a), while the number of high seed producing species is more similar in the 4 climates (Fig. 4 b). The MT climate allows also for many strategies with low seed production, relative to the other climates, while in the CT climate, there are only a few strategies.

3.2 The colonization-competition trade-off affected by climate and r- and K-selection

We next evaluated the effect of the different climates on the colonization-competition trade-off. This trade-off is shown in Fig. 5 for the different climates and for the different competition scenarios. The trade-off is characterized by the position of the trade-off axis and by its length from the best competitor to the best colonizer. Under no selection, the favorable tropical climates allow for the longest trade-off axis. As shown in Tab. 1, the length of the trade-off axis is successively reduced in the WT climate, the DT climate, and the CT climate. This reduction in trade-off length broadly follows the observed trend of lower richness (Barthlott *et al.*, 1999).

K-selection hardly changes the length of the trade-off. Still, K-selection affects the abundances of plant strategies through competition, which cannot be seen in this analysis, because we include strategies in the trade-off merely by their presence, but not by their abundance. The effect of r-selection is to shorten the trade-off at the end of higher colonizing abilities. This effect is most strongly seen for the MT and DT climates, is less strong for the WT climate, and is weakest for the CT climate. This effect is contrary to what we have expected as we would expect that r-selection favors colonizers, hence shift the trade-off axis towards higher colonizing ability. The reason for this effect is that the model does not simulate seed number and seed size, but only total seed mass. Therefore, a strategy with a high biomass is likely to produce more seed mass than a strategy with low biomass. Under both, r-and K-selection, the trade-off axis is reduced only slightly compared to r-selection only. This reduction is mostly seen in the MT and CT climates. In summary, we find that the most favorable MT climate has the highest potential for diversity, but r-selection restricts the trade-off length strongly. In comparison, the temperate climates seem to be least affected by r/K-selection.

3.3 Diversity affected by climate and r- and K-selection

The effects of climate and selection on the colonization-competition trade-off are closely mirrored in the simulated diversity in the different climates, although differences in the relative abundances

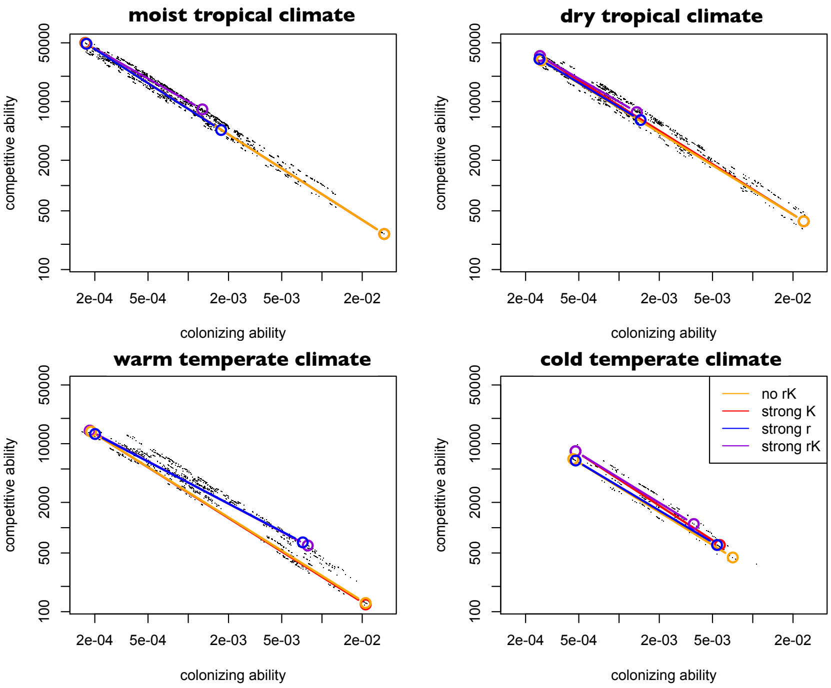

Figure 5: The simulated colonization-competition trade-off in four different climates. The colored lines indicate the length of the trade-off axis under no rK- (yellow), only r- (blue), only K- (red) and rK-selection (violet). Competitive ability is measured as biomass in gC/m2, colonizing ability is measured as growth rate in m2/m2/d.

are also reflected in diversity. The close correspondence in the effects is shown in Fig. 6 and in Tab. 1. The reduction in the trade-off axis with increased selection strength we observed above is closely mirrored in the diversity of the communities in the four climates, although the decrease in diversity is generally stronger than the reduction in trade-off length. This stronger effect of selection strength on diversity is plausible because strong selection does not only result in competitive exclusion, but also affects the relative abundances of the non-excluded strategies.

In all four climates, the diversity is highest under no selection, and is reduced to lowest values for r- and K- selection. Under no selection, the highest values of richness and diversity are found in the MT climate, while the lowest values are found in the CT climate. K-selection has little effects on these measures, and the same sequence of decreasing values from the MT climate to the DT climate, WT climate and CT climate is found. This sequence is different in the cases of only r- and both, r- and K-selection. Here, the WT and CT climates loose the fewest richness and diversity, while the tropical climates (MT and DT climates) loose the most. In the extreme case, the diversity is lowered to only 2% of the plant strategies in the MT climate with strong r- and K- selection (Tab. 1).

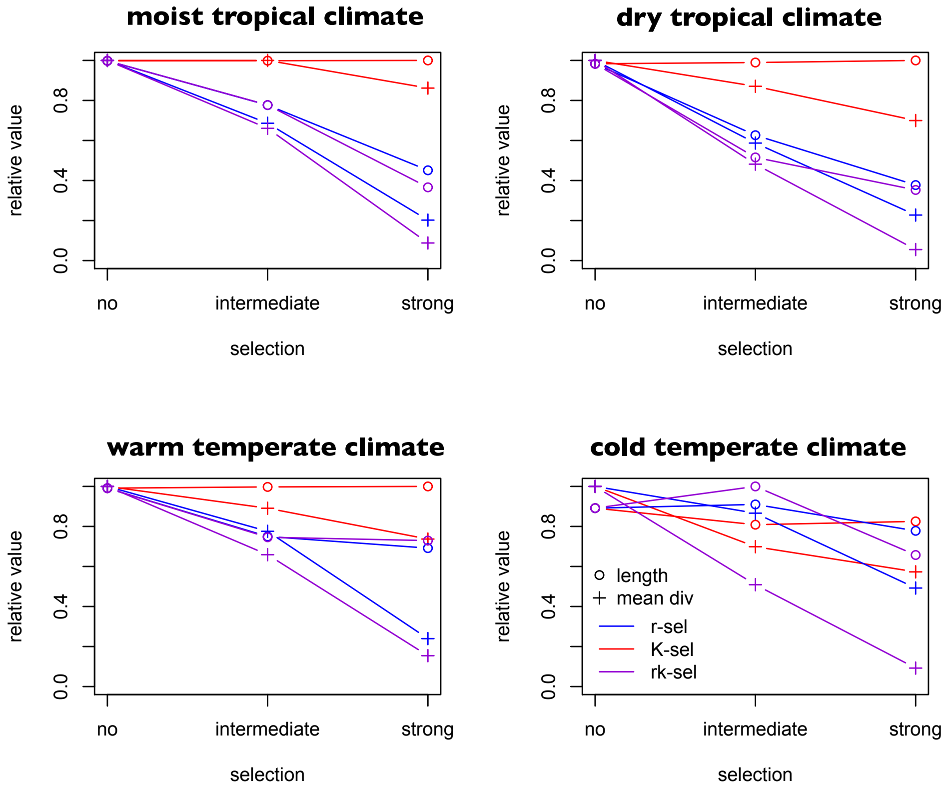

Figure 6: The simulated effects of different strengths of r- (blue), K- (red) and rK-selection (violet) for the length of the colonization-competition trade-off axis (circles) and diversity (crosses, averaged over disturbance levels) for the four climate.

Table 1: Comparison of the simulated length of the colonization-competition trade-off axis, richness and diversity for strong r-, K- and both r/K-selection with values under no selection in the four climates. Highest values are colored in blue, lowest values in red.

	MT	DT	WT	CT
No rK-selection, absolute max values				
Length	7.3	6.3	6.7	3.9
Richness	366	131	114	32
Diversity	5.8	4.8	4.3	3.0
Percentage of max values under K-selection				
Length	100%	100%	100%	93%
Richness	100%	100%	100%	100%
Diversity	86%	70%	73%	57%
Percentage of max values under r-selection				
Length	45%	38%	70%	87%
Richness	13%	18%	44%	60%
Diversity	20%	23%	24%	50%
Percentage of max values under rK-selection				
Length	37%	36%	74%	74%
Richness	2%	5%	20%	19%
Diversity	9%	5%	15%	9%

3.4 Diversity-Disturbance Relationships

These effects of climate and selection strengths are reflected in the diversity-disturbance relationships (DDR) for the different climates. The DDRs for the four different climates for the different selection setups are shown in Fig. 7. In the absence of selection, the DDR is flat in the tropical climates (MT and DT climate), and declines slightly under high disturbances in the temperate climates (WT and CT climate). In the less favorable climates, we do not observe a flat DDR, because high disturbance rates in these climates reduce diversity by an increase in mortality. However, we might observe the same diversity decline in the MT and DT climate if we would further increase the disturbance rate. Strong K-selection decreases diversity under low disturbances, resulting in an increasing DDR with disturbance. In the MT climate, a lower disturbance level (level 2) already leads to the reached maximum diversity compared to the other climates, in which the maximum is reached at level 3. At higher disturbance rates, the curves follow the ones under no selection. Therefore, the temperates already have a slight hump-shaped DDR.

When r-selection is considered, diversity decreases to zero for high disturbances, leading to a

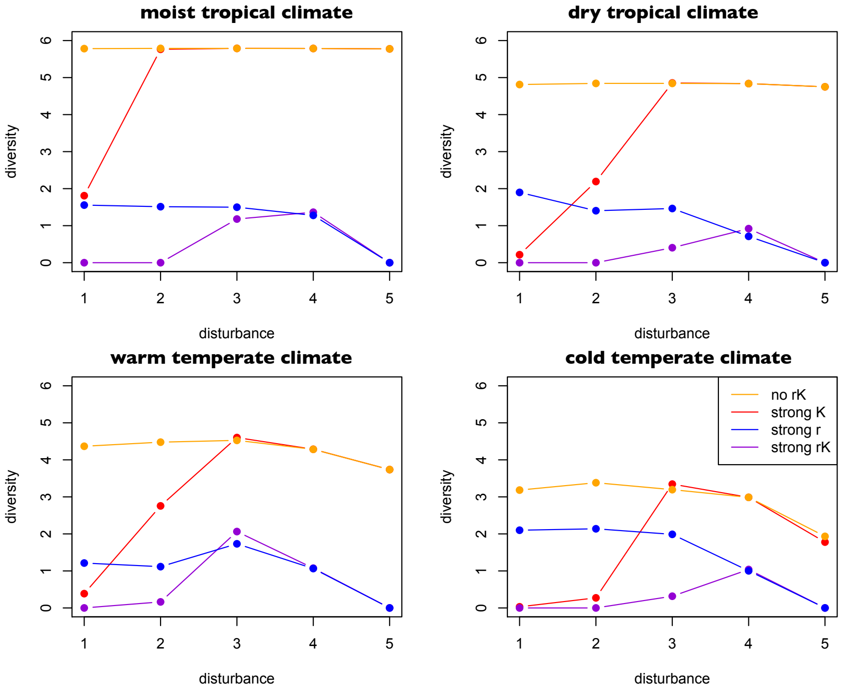

Figure 7: Simulated DDRs in four different climates under no selection (yellow), strong K- (red), strong r- (blue) and strong r- and K-selection (violet).

decreasing DDR. This effect is found in all climates, although in the WT climate, there is a slight peak under intermediate levels of disturbance. This decrease of disturbance under r-selection can be attributed to the effect of seed mass, which is very important for colonizing open areas that result from the disturbances. In the absence of r-selection, a minimal seed mass is sufficient to colonize the open areas while additional seed mass does not provide an advantage. Therefore, under strong r-selection, many plant strategies that do not produce much seed biomass are excluded.

Under both strong r- and K-selection, the DDRs in all climates are hump-shaped. The peak occurs at the intermediate disturbance levels (level 4 in the DT and CT climates, level 3 in the MT and WT climates). The peak in the DT and WT climate is slightly higher than the reached maximum under strong r-selection.

In summary, we find climatic effects in the different DDRs. In less favorable climates, diversity is more strongly reduced in the case of high levels of disturbance so that a hump-shaped DDR can already result merely by considering strong r-selection (as in the case of the WT climate). On the other hand, we also find that the effect of K-selection is less strong in the MT climate than in the other climates.

4 Discussion

4.1 Limitations

We used two models in our study, the JeDi-DGVM and DIVE. Each model by itself has certain limitations that have been discussed previously (Kleidon & Mooney, 2000; Bohn *et al.*, 2011; Pavlick *et al.*, 2012; Bohn *et al.*, 2013). In the following, we discuss the most important limitations that specifically apply to this study.

Speciation and migration might be important processes that shape community structure. It has been shown, that speciation might be higher in the tropics than in other climate zones (Mittelbach *et al.*, 2007). Newly evolved species can then disperse or migrate into neighborhoods. The inclusion of speciation therefore might lead to different diversity-disturbance relationships. Especially under r-selection, speciation could reduce the powerful effects in reducing tropical diversity and may thus lead to higher diversity than simulated. Nevertheless, here we look on the effects of r- and K-selection. R-selection might still be stronger in the tropical climates than in others.

A strange effect of r-selection is the cutoff of the colonization-competition trade-off towards colonizers (Fig. 5), while we would expect the opposite. The reason is the simulation of seeds in JeDi-DGVM, and already discussed (Bohn *et al.*, 2013). JeDi-DGVM simulates only total seed mass, so that in our model competitive strategies with high biomass can produce high seed mass, while small colonizers may only produce low seed mass. Still, seed number and seed size, which are not modeled in JeDi-DGVM, modulate the colonization-competition trade-off (e.g. Muller-Landau, 2010; Coomes & Grubb, 2003). Therefore, r-selection excludes colonizers. Still, the growth rate is higher for colonizers, and leads to higher abundances of strategies that are intermediate colonizers (Bohn *et al.*, 2013).

4.2 Interpretation

Our results capture the overall effect of climate in selecting viable plant species. Diversity has shown to be highest in the moist tropics (MT), then dry tropics (DT), warm temperate (WT) and finally lowest in a cold temperate climate (CT). One reason is that the climatic constraints are stronger in the higher than in the lower latitudes (Kleidon & Mooney, 2000). For example, the length of the growing periods in the four chosen climates correspond to the diversity gradient (Fig. 3). Furthermore, interactions between plants and disturbances influence community composition. High disturbances generally limit growth due to less favorable conditions, as Reineking *et al.* (2006) has shown for desert regions. The same applies for the temperate regions, as there is a cold season. In these climates, diversity decreases under increasing disturbances. Further we found, that r- and K-selection change diversity and especially r-selection can change the expected diversity gradient from the tropics to the poles. We find the expected diversity gradient only under no r/K-selection or K-selection, while under r-selection the cold temperates and under r/K-selection the warm temperates are most diverse.

High r-selection changes the expected diversity gradient. Comparing the maximal reachable diversity under strong r-selection, the CT climate is most diverse, followed by the DT, WT and MT climate. Further, the WT and CT climates loose fewest richness, diversity and axis length, while the MT and DT climates loose the most. This on the one hand suggests that global rates of r/K-selection are in general low, or differentially distributed on the globe.

Our results tell us how powerful r/K-selection acts in different regions. K-selection has the smallest effects in the moist tropics, as there diversity is hardly reduced compared to the other climates. Kleidon *et al.* (2009) had shown, that in the tropics we find more species with equal biomass, compared to the other regions. We see the same effect in our results where we explicitly account for selection (see Fig. 4). This might result in less effective K-selection, because species with equal biomass express equal dominance. Thus it is harder to competitively exclude other species. If there are many species with different biomass, it is easier to competitively exclude less dominant species, as it happens in the other climates. The trade-off axis is not affected by K-selection, because under K-selection seeds are not important for survival. Therefore, the abundances of the less successional species go to almost zero and diversity decreases, but the species still persist, so the trade-off axis does not change.

However, r-selection strongly reduces diversity in all four climate, but fewest in the cold temperates. Here diversity is in total highest, and also the difference to its reachable maximum is lowest. Under r-selection seeds are important. In the CT climate, seed production decreases first slowly but then very fast (Fig. 4). In general the difference in high seed production between the climates is small. Therefore, seed production does not explain why the CT climate has more species under r-selection, but the length of the growing period can give an insight. If the growing period is shorter, time is shorter to compete for open areas. With more open areas more species can coexist.

Under strong r- and K-selection all climates express a peak in diversity as the Intermediate-Disturbance-Hypothesis proposes. The highest diversity peak occurs in the warm temperates. This result is surprising, as the warm temperate climate is neither under K- nor r-selection the most diverse climate. Also, this peak is higher than the reached maxima under r-selection, and also the trade-off axis is longer as in the case of only r-selection. The effect of r- and K-selection is thus not simply the sum from r- and K-selection, but rather the interplay between them.

Further, the trade-off axis is most reduced in the tropical climates under r- and r/K-selection. We hypothesized this reduction to be low in the temperate climates, because the existing species are already strongly selected from environmental constraints. In comparison, in the tropical climates there are many species that could be ineffective. Selection sorts these out and the trade-off axis shortens drastically.

Many studies have shown a diversity gradient from the poles towards the tropics (e.g. Willig *et al.*, 2003). Our simulation results reproduce the gradient under no selection or only K-selection under certain rates of disturbances. However, Willig *et al.* (2003) also identified studies that did not show the diversity gradient. The explanation is, that such studies often used only narrow latitudinal extents for their analysis. This can be understood as an effect of scale. Scale could be reflected in our approach by different scenarios of r- and K-selection. Thereby scale can modulate the strength of selection to be important on the local scale, as niche theory suggest, or to be unimportant for the global scale, as the neutral theory of biodiversity suggests Hubbell (2001).

Interspecific interactions have been identified as one factor that control the gradient in biodiversity (Dobzhansky, 1950). Following this hypothesis, increased competition facilitates greater species richness in the tropics, mainly due to predator-prey dynamics (Pianka, 1966). Further the assumption exists, that interspecific effects are greater at low latitudes, while abiotic control is greater at high latitudes (e.g. Willig *et al.*, 2003). This would tell us, that realistic tropical scenarios should consist of higher strength of selection than in the temperate zone. Such scenarios would lead in our simulations to decreased diversity in the tropics, and less decreased diversity in the temperate zone, contradicting diversity gradients. However, we simulate strength of selection as continuos parameters, and show only results of no, intermediate and strong selection. Still, there should be scenarios of strength of r- and K-selection in which selection in the tropics is stronger than in the temperates, that lead to the expected diversity gradient.

Our results are largely consistent with Johst & Huth (2005). They used a patch model of successional dynamics and found a hump-shaped DDR for most tropical and temperate forest ecosystems under discrete disturbances. The unimodal DDR was generated through the successional order from early towards late successional species, where at intermediate disturbances a mixture of all successional stage species coexisted. Their results correspond to our scenario where r- and K-selection are present. Under such conditions we also observe a unimodal DDR but we considered continuos disturbances. Interestingly, the tropical forests expressed lowest diversity, which can be due to the fact that they calculated diversity from successional groups but not on the species level as we do.

The study of Piou *et al.* (2008) shows consistency with our results. They tested the IDH in a species-poor tropical mangrove forest using an individual-based model. The IDH was found only when plants interact, which lead to successional patterns. Still, they also found other DDRs than the IDH, dependent on the competitive scenario and the disturbance regimes. Such scenarios are possible in nature and can particularly occur in mangrove forests (Piou *et al.*, 2008). This shows, that by modulating different strengths of r- and K-selection, we can replicate specific ecosystems, such as mangrove forest.

Miller *et al.* (2011) and Hall *et al.* (2012) give a possible extension to our study. They investigates how disturbance frequency and intensity interact to shape DDRs by using a simple 2-species model. They identified the conditions under a specific DDRs is produced. Thereby they found a U-shaped DDR, which we could not find in our scenarios. In future work, a refined formulation of disturbances in our approach could be implemented to evaluate other forms of DDRs as well.

4.3 Conclusion

In this work we evaluated, how strength of r- and K- selection shape diversity-disturbance relationships (DDRs) in different climates. We confirmed our hypothesis, that r- and K-selection have the same effects on diversity in different climates. However, the realized DRRs differ, because less favorable climates such as the temperate climates are stronger limited by high disturbances. Therefore in the temperate climates, diversity always decreases to some extend under high disturbances. However, under further increasing disturbances, we would expect also a diversity decrease in the favorable tropical climates.

Interestingly, strength of r- and K-selection have quantitatively differing effects on diversity in different climates. Strong r-selection has greatest influence on diversity in the tropical climates, while diversity in the temperate climates is only little effected. This leads to the warm temperate climate showing the highest diversity peak under both strong r- and K-selection. This is to some extent consistent with the competition theory of Dobzhansky (1950). We conclude, that vegetation in the temperate climates is at first restricted to climatic condition, while the tropical climates allow for a wide variety of vegetation. In the following, selection or competition has more effects on diversity in the tropical climates then in the temperate ones.

Our study shows, that to reproduce global diversity pattern, a low r-selection should be expected in the tropics, and rates of selection might in general be different in different climates. However, it still remains challenging to know, how strength of selection should be chosen in order to reproduce global diversity patterns. Thereby, the scale might play an important role and might relate to strength of selection.

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Meine Arbeit hat sich ja u.a. mit Diversität beschäftigt. Und so wie viele Wissenschaftler zu zeigen versuchen, dass Diversität wichtig ist, so ist Diversität auch im Leben eines jeden wichtig. Eine Balance zwischen Arbeit und Freizeit zu finden, und dann dazu noch eine Familie gründen... Vielleicht eine Herausforderung, aber eine, die mir gezeigt hat, was wirklich wichtig ist im Leben und das Diversität nicht nur die pflanzliche Produktivität steigern kann!

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Erklärung

Ich erkläre hiermit, dass ich diese Arbeit selbst angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Ferner erkläre ich, dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

Bayreuth, den ... .
(Kristin Bohn)