The role of biotic factors during plant establishment in novel communities assessed with an agent-based simulation model

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Abstract

Background. Establishment success of non-native species can be influenced by interactions with native competitors and novel enemies. Magnitude of interactions between species is mediated by traits, e.g. reflecting competitive strength or defence mechanisms. We combine the concepts to investigate the importance of species traits for successful establishment in a novel community exhibiting biotic resistance in the form of competition and herbivory.

Methods. We developed an individual-based simulation model that tracks survival rate of non-native plants in a native community. Non-native plants are characterized by high or low values of traits relevant for interaction with competitors and herbivores.

Results. Traits related to competition had a much greater impact on survival of non-native species than traits related to defence. Survival rates of strong competitors never fell below 50% while survival of weak competitors averaged about 10%. Weak competitors were also much more sensible to competitive pressures including community density, composition and asymmetry while strong competitors responded negatively to changes in competition intensity but hardly to composition or density of native community. High initial numbers of non-native individuals did decrease survival rate of strong competitors but slightly increased survival rate of weak competitors. In the current model configuration we detected only minor advantages in terms of higher survival from high defensive ability as compared to low defensive ability under enemy attack. Surprisingly, herbivory increased survival rate of species classified as weak competitors.
Discussion. High survival rates of strong competitors relate to a higher chance of establishment as compared to weak competitors. However, the negative effect of high initial numbers for strong competitive non-natives indicates a self-thinning effect, probably through creation of a highly competitive milieu. For weak competitors, our model predicted increasing survival rates at high initial densities. Positive effects of high propagule pressure have been proposed in field studies and are underlined with this model. However, our model largely overestimated mortality as compared to the preceding experiment. This could be improved by implementing more sophisticated competition modes and traits reflecting tolerance and avoidance of competition by non-native plants. This would, however, be very costly in terms of parameterization. Herbivory had a very low negative effect on survival in general and an advantage of high defence was almost untraceable. However, the positive effect of herbivory on survival of weak competitors indicated that herbivory should not be neglected in estimation of establishment success of species. Although the immediate and expected effect of herbivory might be small, side effects as weakening of resident competitors might play an important role for establishment in a new community.

Introduction

In response to current climate change, range borders and distribution patterns of many species have shifted along with changes in environmental conditions (Chen et al., 2011; Maggini et al., 2011; Parmesan and Yohe, 2003; Walther et al., 2002). For capturing and eventually predicting range shift dynamics of single species, they cannot be regarded detached from their biotic and abiotic environment (Berg et al., 2010). While on a large scale range shifts are correlated with bioclimatic and environmental factors and the ability of a given plant species to reach a novel habitat, local establishment of viable populations determines whether border shift can be realized (Bakkenes et al., 2002). Local establishment success strongly depends on biotic interactions with the resident community. Such interactions are for example competition with resident plants or herbivore attack (Levine et al., 2004). In fact, diverging trends in speed, extent and directions of species range shifts may be not only an expression of their ability to reach a novel habitat, but also to persist in novel communities (Lenoir et al., 2010; Maggini et al., 2011). These local processes can add up and might eventually prevent further range shifts. Thus, although a species range is typically described on large, often continental scales it is limited by small-scale processes on the leading edges of the range. This is in line with the claim to consider dispersal and local establishment success of species and individuals in order to gain insights on range dynamics (Guisan and Thuiller, 2005; Pearson and Dawson, 2003; Wisz et al., 2013). The magnitude of the effect of biotic pressures exerted by the resident community on the non-native species is partially determined by the its’ ability to respond to
these interactions (Kempel et al., 2013; Roux et al., 2012; Wisz et al., 2013). This ability is mediated by plant traits. Despite the general acknowledgement of the importance of both traits and biotic pressures for establishment success, the interaction of these factors is not well studied in the context of range expansion.

We constructed an agent-based simulation model to scrutinize the combined effects of these factors in affecting success or failure of plant establishment in a novel community. We have chosen a modelling approach for capturing local establishment during range expansion rather than a field survey, because in most settings only successful expansions can be tracked in the field, but not those which failed (Zenni and Nunez, 2013). Additionally, modelling allows for comprehensive systematic modifications of the setup that are often not feasible under field conditions. Data from a preceding greenhouse experiment were used to link the model to reality during model construction and basic parametrization (see 2.2. parametrization).

In this model, we examined early establishment of populations in novel habitats in a local context as an essential first step in range shift dynamics of a species. Therefore, we focus on such biotic interactions that operate on local scales and with immediate contact between the interacting entities, i.e. competition for resources between neighbouring plants and enemy attack. From a modeller’s point of view, continuous range expansion of a species can be described as a series of successful local establishment events of individuals in discrete spatial units embedded in a large-scale landscape (Figure 1). Local models thus can serve as a basis for capturing the large-scale picture of range expansion.

Biotic pressures such as competition and enemy attack may hamper establishment success of a non-native species in a community by decreasing individual fitness. The causes are obvious: when mutually contested resources are captured by competing species, the inferior competitor can use less of the contested resource for its own growth and reproduction and may even die when resource uptake falls below a metabolic threshold (Lin et al., 2012; Schmitz, 2000). Enemy attack can strongly weaken a plant through damage of plant tissue or organs and even result in lethal consumption. Loss of tissue may pose an additive negative effect on plants under competition (Heard and Sax, 2013; Kim et al., 2013; Kuijper et al., 2004). In fact, invasion biology studies have often pointed out that very effectively expanding, i.e. invasive, non-native species suffer less than native or non-invasive non-native species from enemy attack (Cappuccino and Carpenter, 2005; Engelkes et al., 2008; Matter et al., 2012; but see Heard and Sax, 2013). This effect, referred to as enemy release, is one line of argument to explain invasiveness of non-native plant species in intercontinental invasions (Joshi and Vrieling, 2005; Keane and Crawley, 2002) and since lately is also studied in intracontinental
Traits of species mediate interactions and are often used to describe community composition in classical community ecology (McGill et al., 2006). Intercontinental invasion biology relies on certain traits that are shared by successful invaders to inform risk assessments, although the trait set of the “perfect invader” yet remains to be found (Speek et al., 2011). For our model, we use the framework of biotic resistance composed of resource competition and herbivore attack (Levine et al., 2004), and describe non-native species by a set of traits to respond to these components of biotic resistance. Our central model aim is to assess how non-native species with different trait profiles can establish in a novel community during climate change-induced range expansion. Following the parsimony principle we have not yet considered facilitative interactions in this model.

The traits used in the model reflect the ability of a plant to a) compete with neighbours and b) defend against enemies. Based on size-symmetric competition models (Connolly and Wayne, 1996; Damgaard and Weiner, 2008), we use seed mass as a measure of plant size and as a proxy trait for competitive ability (Metz et al., 1992). Other traits have also been associated with competitive strength (Goldberg, 1996), but plant size is a straightforward measure (Domingos, 1999) which is well supported (Aikio, 2004; Weiner and Damgaard, 2006). Mechanical barriers and toxins are the most obvious traits a plant can use to prevent herbivore attack, and often plants build up a complex defence syndrome of multiple traits (Agrawal and Fishbein, 2006). For our purpose, the form of defence mechanism is not of interest. Thus, we implemented the defence mechanism as the stochastic ability of enemy repulsion. Dispersal ability was included as a trait in the model in spite of the small spatial extent of the model as the local simulation is intended to be embedded into future large-scale simulations that will reflect regional and supra-regional movement. Since dispersal is not relevant for the local dynamics simulated here, we will discuss it only briefly in the following.

In summary, the model presented here is designed to address how the local establishment success of non-native species under special considerations of trait combinations, biotic resistance of the resident native community, and the interactions of traits and biotic resistance.

2. Methods

2.1. Model description

Our model description follows the ODD protocol (Grimm et al., 2006, 2010). Model structure is partly based on (Lin et al., 2012).
2.1.1. Purpose

The model compares first generation establishment success of generic range expanding species in a novel community, based on a hypothetical ecological profile. The ecological profile is expressed in a trait vector and built through combinations of high or low ability to compete with neighbouring plants and defend against insect herbivores. We assign seed size to competitive ability and repulse of herbivores to defence ability (see table 1). Additionally, plants have different values of mean dispersal distance, so that the full profile is described in a three-dimensional vector (Figure 2). As dispersal happens only in the very last step of the model routine (Figure 3), different dispersal abilities do not result in differences in the simulations presented here, but are recorded for future spatial upscaling purposes. Further details on dispersal will therefore not be discussed within this paper. In the following, generic species are called “species” for better readability.

2.1.2. Entities, state variables, and scales

We implement two general types of agents, plants and herbivores. Plants are non-mobile agents, characterized by their x-y-position and values of growth, reproduction, defence and dispersal values (see Table 1 and 2). Plants are hatching from seeds. We distinguish two general types of plants, native and non-native, and twelve species, of which four are native and eight are non-native. Parameters have been retrieved from a preceding experiment and literature values (see 2.2 parametrization).

The simulated world comprises a homogenous 100 x 100 cell grid. Each grid cell represents 1 cm², thus we model a 1 x 1 m plot. To avoid edge effects, the world is a torus, i.e. opposing edges are connected (Grimm and Railsback, 2005).

Each time step is representing one day. A simulation comprises 76 days, i.e. the average lifespan of a non-native species in the preceding experiment (Radny et al., unpublished). The simulation was aborted earlier when no non-native individuals were left on the grid.

2.1.3. Process overview and scheduling

During each time step, the simulation routine is exerted in the following order: herbivore appearance and herbivory on random plants, calculation of competition intensity for each plant individual,
growth according to this competitive intensity and ageing of the plants. After 76 days, the plants produce and disperse seeds and die. Dead plants are removed from the grid. The process schedule is visualized in figure 1.

2.1.4. Basic principles

We follow the assumption that community composition can at least partly be explained by biotic interactions and that biotic interactions are closely connected to functional traits of species (McGill et al., 2006). We apply a basic profile of functional traits, relevant for species’ ability to a) compete with neighbours and b) defend against enemies. Biotic resistance, i.e. negative impacts of the resident community of herbivores and competitors on novel plants, is often influencing local establishment success (Kempel et al., 2013).

2.1.5. Emergence

Several patterns related to individual plant development and population dynamics, including reproductive output emerge from the model. Examples include spatial patterns of plant individuals, population dynamics of non-native and native plants, or plant size distributions. For the purpose of this paper, we focus on initial and final number of individuals of non-native species per time step as a basis for deriving survival rate in the establishment phase (see 2.2 data analysis).

2.1.6. Interactions

We explicitly model competitive interactions between neighbouring plants via the Zone-Of-Influence (ZOI) approach (Lin et al., 2012; Weiner and Damgaard, 2006). Furthermore, herbivores are interacting with plants by consuming proportions of aboveground biomass of plants on the same patch.

2.1.7. Stochasticity

Plant individuals are initialized with random xy-coordinates. To reflect individual deviance from population mean values, initial biomass of plants is calculated as seed mass multiplied by a random number, drawn from a normal distribution with a mean of 1 and a standard deviation of 0.1. As plants determine their own growth rate by \( \ln(\text{maximum biomass}) - \ln(\text{initial biomass}) / \text{maximum age} \) (Hunt, 1982), this approach propagates the stochasticity involved in initial biomasses to the distribution of relative growth rates. Dispersal distance of individual seeds as well as direction of dispersal is randomized (see submodels: dispersal). Daily density of herbivores is stochastic, as grasshopper density is multiplied with a stochastic number of meals per herbivore (see submodels: dispersal).
Success of each foraging attempt of herbivores on a given plant is stochastic, based on the repulse value of the plant.

2.1.8. Initialization

Each simulation run starts with placement of seeds on the grid at random xy positions. Initial native community population size is based on plant densities in the greenhouse experiment (Radny et al., unpublished). In that experiment, planting pots of 18x18 cm carried either 12 or 44 native individuals, i.e. 300 or 1100 individuals per m². Composition of the native community based on either the experiment or approximated literature values (see Table 2) depending on the simulation scenario. For experiment-based composition, each native species is represented with the same number of individuals, called “even composition” hereafter. For literature values, we use the reported seed bank size of the respective species as initial numbers (see Table 2). Per simulation scenario, there is one non-native species mixed into the native community. Different simulation scenarios were run with initially 8, 16, 32, 64, 128 and 256 seeds of non-native species. These scenarios reflect different levels of introduction efforts or proximity to core range with higher population densities (Kolar and Lodge, 2001).

2.1.9. Input data

The model does not require any input data beyond the model parameters.

2.1.10. Submodels

2.1.10.1. Herbivory

Herbivore agents are created at the beginning of each time step (see Figure 3). The grasshopper Locusta migratoria is used as herbivore model species due to its wide distribution (CABI, 2013) and generalist feeding behaviour (Macel et al., 2005; Schmitz and Booth, 1997). We had also chosen this species as herbivore in the preceding experiment. Herbivore density is varied based on literature values and density in the experiment, ranging from 3.2 grasshoppers per m² (literature value Ledergerber et al., 1997) to 18.75 grasshoppers per m² (experimental value, based on Morriën et al., 2011). One scenario is implemented without herbivores. Here, neither native nor non-native species experience herbivory.

L. migratoria is consuming 50-70 mg of plant material per day (Simpson and Abisgold, 1985). Consumption does not happen all at once, but in 7 to 10 meals of about 7.5 mg each. In a natural setting, it is not likely that a highly mobile insect is feeding on the same plant individual all day. Thus, we implemented in-between meal movement by multiplying each herbivore by a random number drawn from the interval [7, 10]. This effectively generates one new herbivore individual per meal, so
that movement of the new herbivore individuals reflects in-between meal movement of the one original herbivore. This simplification is justified, because we are not interested in the fate of individual herbivores, but just their effect on plant biomass. This multiplication allows us to model a process which is operating at a finer temporal scale than the global time step (one day).

Each new herbivore is initialized at random xy-coordinates and approaches a random plant in a radius of 50 patches. To consume the approached plant, a random number drawn from the interval $[0, 1]$ must be greater than the repulse value of the respective plant. A high repulse value thus represents high defence of a plant, e.g. through physical barriers or toxins. Herbivores have a once-in-a-lifetime chance to feed, so if they are not successful on foraging on that plant, the agent is removed from the grid without foraging. Again, this is justified, because we are not interested in the fate of individual herbivores and this procedure still adequately represents the overall effect of herbivory on plants. All other herbivores are removed directly after foraging. Thereby, herbivore density fluctuates daily. Under herbivore attack, the biomass of the attacked plant is reduced by the number of successfully feeding herbivores on that plant multiplied with 7.5 mg consumption per herbivore. As we observed in our greenhouse experiment, a plant dies if more than 90% of its current biomass is consumed by herbivores, and it is removed from the grid.

2.1.10.2 Plant competition and growth

Plants interact competitively with their neighbours. To model competition, we follow the Zone-Of-Influence (ZOI) approach (Berger et al., 2008; Lin et al., 2012; Weiner et al., 2001; Weiner and Damgaard, 2006). The ZOI of a plant is represented by a circular area $A_{ZOI}$ with radius $r$. Based on Lin et al. (2012), radius $r_i$ is allometrically related to biomass $B$ of plant $i$ at time $t$:

$$r_i = B(i, t)^{3/8} \sqrt{\frac{1}{\pi}}$$

(Eq 1)

Note that $B(t)$ is determined after herbivore attack. The area of the ZOI determines plant growth in the next time step:

$$\frac{dB}{dt} = r_{gr} * A_{ZOI} * \left(1 - \left(\frac{B}{B_{max}}\right)^{1/4}\right)$$

(Eq 2)

In most cases, the ZOI of a plant covers several grid cells. Thus, $A_{ZOI}$ consists of the sum of the area of the single grid cells $c$ that are occupied. Eq. 2 applies when a plant is growing without neighbours, i.e.
none of the cells within $A_{20}$ is occupied by another but the focal plant. When two or more plants are neighbours, i.e. their ZOIs are overlapping in at least one cell, they calculate their effective area $A_{\text{eff}}$ as:

$$A_{\text{eff},i}(t) = \sum_{c_j} \frac{B_i(t)^\theta}{\sum_j B_j(t)^\theta} dc$$

(Eq 3)

In Eq. 3, $\Theta$ indicates the degree of asymmetry of competition and is located between 0 and $\infty$ (Schwinning and Weiner, 1998). We use the degree of asymmetry as a measure of competition intensity. Intensity of competition determines how the contested resources at any patch are shared among the competing plants, depending on their biomass relative to the other competitors. With $\Theta = 0$, resources are shared equally among plants regardless of their biomass. Increasing $\Theta$ leads to an increasing weight of biomass for capturing contested resources in a shared cell. With $\Theta = 1$, a larger plant receives a larger share of the contested resources than a smaller plant, proportional to its biomass (perfect size-symmetry).

To assess the importance of size-symmetry of competition for species of different relative sizes, we are using $\Theta = 0, 0.5$ and 1 in different model runs.

Plant growth under competition is implemented as:

$$\frac{dB}{dt} = rgr * A_{\text{eff}} * \left(1 - \left(\frac{B}{B_{\text{max}}}\right)^{1/4}\right)$$

(Eq 4)

The difference between Eq. 2 and Eq. 4 is that either all resources within the zones of influence are considered to calculate growth, regardless of neighbouring competitors ($A_{\text{zoi}}$), or that only the resources captured after competition with neighbours are considered to calculate growth ($A_{\text{eff}}$).

If growth and resource uptake falls below the threshold of 0.05 of biomass $B^{3/4}$, the plant cannot serve its metabolic costs and dies (Lin et al., 2012; Schmitz, 2000).

When plants reach maturity, i.e. maximum age, they produce seeds as a function of their final biomass. Note that under strong competition, final biomass does not necessarily match maximum
biomass. In our greenhouse experiment, we obtained a positive correlation between aboveground
biomass and seed mass, i.e. total mass of all seeds produced per plant. Based on this empirical
correlation, in this model, we use the ratio of 0.41 mg seed mass per mg shoot biomass for strong
competitors and 0.65 mg seed mass per shoot biomass for weak competitors. The number of seeds
per plant is implemented in the model as seed mass produced by the respective plant divided by
average weight of a single seed. In order to include stochasticity, we allowed a stochastic variation
rate of +/- 10%. To reduce computational ballast, the number of seeds produced is reduced by winter
mortality, including seed predation, and germination probability is applied. Thus, only seeds that
survive winter and germinate in the next year are explicitly created. Seeds are then dispersed in a
random angle with dispersal distance following a Weibull distribution to allow for long-distance
dispersal (Colbach and Sache, 2001; Paradis et al., 2002). Number of seeds remaining on or being
dispersed beyond the parental patch is recorded for upscaling approaches.

2.2. Model parametrization

Model parameters were partly derived from literature and partly from a preceding greenhouse
experiment (Radny et al. unpublished) (Tables 1, 2). The greenhouse experiment consisted of
microcosms with a native community of four plant species mixed with one non-native species per
microcosm. The non-native species in the experiment differed in life-history traits related to
competitive and defensive strength. In the experiment, non-native species were exposed to two
densities of natives to create different intensities of competitive pressures. Half of the microcosms
were exposed to herbivory by two generalist herbivore species, *Locusta migratoria* (L.) and
*Mamestra brassicae* (L.).

For parameterization of non-native species in the model, we used data on the Mediterranean grass
species *Stipa capensis* (Thunb.) and *Bromus fasciculatus* (C.Presl.) from our experiment and from the
literature (Table 1). The model differentiates between four trait profiles for non-native species:
strong versus weak competitors combined with strong versus weak defenders.

Competitive strength is represented by average seed weight of *S. capensis* for strong competitors
and *B. fasciculatus* for weak competitors (Table 1). Maximum biomass was assigned as a value
relative to the native community. Additionally, we derived the fitness measure biomass-seed mass
ratio from the experiment by dividing total seed mass by total aboveground biomass of a species.
This ratio was different for strong and weak competitors in the experiment and thus serves as
another distinctive index for competitive strength (Table 1).
Defensive strength was modelled as repulse of herbivores reflecting the chance of a plant to avoid herbivore attack. Repulse values were derived from the percentage of individuals without or less (>5%) clearly visible leaf damage of all individuals of a species that were exposed to herbivory during the experiment. Values for strong defenders were obtained from B. fasciculatus, whereas values for weak defenders were obtained from S. capensis.

The parameterization of the native community in the model is based on the species in the experimental native community, i.e. Agrostis capillaris (L.), Festuca rubra (L.), Hypericum perforatum (L.) and Plantago lanceolata (L.). These four species are fairly widespread over Europe (Roscher et al., 2004) and thus range-expanding plants from southern latitudes are likely to encounter these species as interaction partners. With the exception of repulse of herbivores which was based on the overall observations of high and low attack rates, parameters used in the model for native species were based on literature data (Table 2).

### 2.2 Data analysis

The major goal of our simulation model was to investigate the local establishment of non-native species in a novel community, based on different trait configurations. To assess local establishment, we determined final population size, i.e. number of reproducing adults at the end of a simulation run. To account for scenario-based differences in initial population sizes, we calculated survival rate as the ratio of final and initial numbers of non-native species. To reach our overall goal, we applied a binomial generalized linear model of the form

\[
\text{Survival rate of non-natives} \sim \text{competitive strength of non-natives} + \text{defensive strength of non-natives} + \text{initial population size of non-natives} + \text{herbivore density} + \text{competition index } \Theta + \text{community density} + \text{composition of native community} \text{ and all two-way interactions.}
\]

Competition index \( \Theta \) describes the degree of asymmetry in competition and takes in our model the values 0, 0.5 and 1. Composition of native community is a two-level factor, where native individuals are either mixed evenly or percentage of native individuals of a species is derived from literature values about seedbank sizes.

We used the software R version 3.2.4 (R Development Core Team, 2016) and the package “nlme” (Pinheiro et al., 2011) for data analysis.

### 3. Results
The importance of competitive strength was very dominant in the current model setting and was a much stronger source of variation than defensive ability for survival rate of non-natives (Table 3, Figure 5). Overall, weak competitors had a much lower survival rate than strong competitors. Although the populations of weak competitors had an increased chance of persistence with an increasing initial population size (invasion level) they were not able to not catch up with survival rates of strong competitors (Figure 6).

Intensity of competition $\Theta$ had a marked negative effect on survival rates of plants, especially on weak competitors. For weak competitors, average survival dropped by 80% when comparing equal share ($\Theta = 0$) and perfect size-symmetry ($\Theta=1$). Decrease in survival rate was more severe in the even community composition, as well as under high community density (Figure 7). Strong competitors were neither visibly affected by community composition nor by increased population densities (Figure 7).

In our model runs, we found that herbivores were only able to kill a plant in very early stages when they were very small. Herbivore damage was increasing survival of smaller plants by up to factor 1.5 (Figure 8). For larger plants, this effect was the other way round, i.e. presence of herbivores was on average lowering the mean survival rate. However, for larger plants the decrease in survival rate was almost intractable, lowering survival by only 4% under complete size symmetry. Strongly defended species (70% chance of repulse) did only have a minor advantage over weakly defended species (40% repulse).

**Discussion**

With our model, we investigated the establishment success of different types of generic non-native plant species in a resident native community. We targeted three aspects that could influence establishment success: trait profile of the non-native species, biotic pressures of the resident community, and the interactions between traits and pressures.

Competitive pressures and competitive traits exerted a much stronger influence on establishment success than pressures and traits related to herbivory.

Surprisingly, strong competitive traits were negatively correlated with initial density of non-natives in their effect on survival rates. High survival in scenarios with a low initial number of non-natives was not so surprising due to a potential release effect from competition through their dominance over the native species. These scenarios may reflect a distant satellite population or the very edge of the expansion front, because there is evidence that population density on the range borders can be
lower than in the core range (Brown, 1984; Maggini et al., 2011). High survival in these conditions may translate to an effective range border shift, and the more likely so if long distance dispersal is included. However, a higher initial number led to a decrease of survival rate for strong competitors. An explanation may be that the high density of individuals with strong competitive traits led to a milieu of competitive stress, provoking intra-specific self-thinning effects (Morris, 2003). In our model setting, there was no evidence of complete extinction of non-native species due to competitive stress. Thus, the high intra-specific competition decreased individual survival, but did not decrease establishment success of the populations and thus would probably not strongly impede range expansion of non-native species, but probably lead to a self-balancing of the magnitude of the expansion.

Populations of weak competitive plants showed much lower survival at lower densities than strong competitors, implying a much lower chance of long-term establishment. Only with very high initial numbers survival of weak competitors increased compared to scenarios with few initial individuals in the population. This might be due to the sheer mass of non-native individuals that competed with the native community. In the most extreme setting 256 non-native individuals faced 300 native competitors. Thus, even if native species were the stronger competitors, a high number of weak non-native competitors might be able to overcome the biotic resistance, a trend that has already been observed in studies of intercontinental invasions (Lockwood et al., 2005; Simberloff, 2009).

The advantage of strong competitors compared to weak competitors persisted in community settings with more intense community-borne competitive stress, i.e. at higher community density and community composition with higher proportion of strong competitors. Higher community density results obviously in a higher number of competitors for each individual plant and thus in most cases a lower amount of resources that can be captured by any plant. For the community composition, an even number of individuals of all species led to a community with a much larger proportion of strong competitors, i.e. *P. lanceolata*, the largest native species in our setting, than in the seed bank-based composition. However, since strong non-native competitors were characterized by twice the seed weight as compared to *P. lanceolata* they were probably not massively impacted by numbers of competitors or community composition. We observed this effect in the preceding empirical experiment as well, where strong non-native competitors were massively dominating the native community (Radny et al, unpublished).

These results indicate that a range border shift should be more effective for such plants that are strong competitors relative to species of the receiving community, provided that their seeds can reach a novel habitat. For intercontinental invasions competitive strength is among the major lines of explanation of invasive success (Vilà and Weiner, 2004). In the context of climate-change induced...
range expansion this might become just as important or even more important as changes in the
microclimatic regime of habitats beyond current range borders may weaken the currently strong
resident competitors and thus increase invasibility of communities (Alexander et al., 2016; Bauer,
2012; Stanton-Geddes et al., 2012).

However, the very low survival rates of weak competitors in our model may overestimate the
negative impact of community competition on weak competitors in reality. For instance, in our
preceding experiment, drop-out rate of weak competitors was almost zero while in the model weak
competitors responded very drastically to increased competitive pressure from the community in
form of increased density, composition and intensity of competitive asymmetry ($\Theta$).

Probably, in our model, we underestimated the abilities of weak competitors to avoid or tolerate
competitive pressure from other species. This might be partly due to the implementation of
competition with the Zone-of-influence approach. For theoretical models of competition between
plant individuals, the Zone-of-Influence approach has been used many times at different degrees of
complexity (e.g. Berger et al., 2008; Lin et al., 2012; Weiner and Damgaard, 2006). Despite several
simplifications, it is a straightforward and comparatively easy method to investigate competition
(Berger et al., 2008). However, most of these models address monocultures of species and thus
implement the same type of interaction, i.e. degree of asymmetry $\Theta$, for all individuals. However,
interspecific interactions may be different from intraspecific interactions due to many different
mechanisms. This does not only imply for example a different $\Theta$ between species A and B as
compared to the intraspecific $\Theta$, but also a different $\Theta$-values depending on the identity of the focal
species (Connolly and Wayne, 1996). Such mechanisms include for example allelopathy (Bais et al.,
2003) or adaption to the competitive disadvantage, e.g. development of shade tolerance in trees
(Dislich et al, 2010). Of course, parameterizing different competition types for all interactions in our
five-species system would require a lot of data, which were not available in our case, and has also
been attempted in only very few comparable cases thus far.

We strongly advocate for the extension of multispecies models to incorporate different forms of
neighbourhood interactions not only as negative (competition) or positive (facilitation), but also
accounting for different intensities of inter- and intraspecific interactions. This approach will require
enhanced efforts in the collection of adequate data for parametrization, but we expect a much
better understanding of multispecies systems from such approaches (Svenning et al 2014).

The effect of herbivory was comparatively small in our model. Herbivory has been reported to
influence range expansion and invasions, i.e. in spatial pattern and speed (Fagan et al., 2005;
Herrero et al., 2016), yet it is unlikely that herbivory may entirely block establishment of non-native
species (Jeschke et al., 2012; Levine et al., 2004). However, although herbivory as single factor may not pose a hard barrier to establishment, studies found herbivory to be an important interacting effect under competition through altering the competitive impact of individuals (Huang et al., 2012; Kim et al., 2013; Kuijper et al., 2004). Our model results support such an interaction between herbivory and competition, where weak competitors showed increased survival under herbivory, especially with higher densities of herbivores. We suspect that weak competitors benefited from being small relative to their neighbours – either due to initial small size or due to cumulated negative effects on biomass gain from competition. In this model, the ability to capture resources from competing neighbours depends on the current biomass of any focal plant relative to its direct competitors. The degree of asymmetry thereby is varied through the scenarios and is regulated by the index \( \Theta \). Thus, loss of biomass due to herbivory hindered the larger competitors in the neighbourhood of the weak competitors to capture the full amount of resources and leave more than without herbivory to the weak competitors. The minimum amount of resource uptake for maintenance of metabolism and thus survival is in our model directly related to current biomass of the individual (Brown et al., 2004). Thus, even a relatively small increase in resources capture can increase survival of smaller plants.

Of course, our model did not capture the full complexity of possible herbivore impacts on plant distribution and range expansion. Body size of herbivores and timing of herbivory have been shown to differentially affect plant biodiversity (Kim et al., 2013; Olff and Ritchie, 1998), as well as presence or absence of specialist herbivores (Joshi and Vrieling, 2005; Lakeman-Fraser and Ewers, 2013). Future model extensions could reflect these factors as well as plant internal mechanisms such as compensatory growth (Lu and Ding, 2012) and increase of defence mechanisms (Strauss and Agrawal, 1999). However, even with our simple model design, we found a significant effect of herbivory – although not the expected global decrease of survival, but an indirect effect through harming the competitors. This indicates that herbivory effects may sometimes be overseen when they are not turning out as expected and that this might be also a reason for the sometimes contradicting results of different studies (Jeschke et al., 2012; Levine et al., 2004).

**Conclusion**

We conclude that traits related to competitive strength of species can change the effectiveness of biotic resistance from resident competitors and should be taken into account when attempting to predict establishment success of range expanding species. Where the impact of herbivores is of minor importance, strong defence traits do not result in an apparent advantage as compared to weak
defence. However, herbivory might have a stabilizing effect on competition and thus should not be neglected when analysing range expansion dynamics. For further developments of local competition models in a community context, we advocate to develop approaches that include tolerance strategies.

Acknowledgements

This work was supported by the Deutsche Forschungsgemeinschaft DFG (ME_3575/2-1).

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Table 1: Parameter values for traits of non-native plants. Seed weight was directly measured and averaged from plant material used in the preceding experiment (Radny et al. unpublished) and based on the species S. capensis and B. fasciculatus. We chose maximum biomass relative to the native community. Repulse of herbivores was averaged from all strongly and weakly defended species in the preceding experiment.

| Parameter                | Unit | Value | Source                      |
|--------------------------|------|-------|-----------------------------|
| Competitive strength values |      |       |                             |
| Strong competitors       |      |       |                             |
| Seed weight              | mg   | 3     | 1                           |
|                         |      |       | Radny et al. (unpublished)  |
| Maximum biomass          | mg   | 15000 | 4000                        |
| Weak competitors         |      | 4000  |                             |
| Defensive strength values |      |       |                             |
| Strong defenders         |      |       |                             |
| Repulse of herbivores    | %    | 70    | 30                          |
|                         |      |       | Radny et al. (unpublished)  |

Table 2: Parameter values and sources for the native species in the model. Note that maximum age is aligned for all species. Reproduction and dispersal values are not considered for native species as we were not interested in the fate of native species in this approach. Parameter values were either directly retrieved or approximated (*) from the available literature. The composition of the native community in uneven community composition is based on seed bank values. Initial seed density for F. rubra has been approximated from vegetation cover (30%) as retrieved from Edwards and Crawley (1999), assuming that all seeds germinate and build the entire native community.

| Species         | Parameter    | Unit | Value | Source                      |
|-----------------|--------------|------|-------|-----------------------------|
| Plantago lanceolata | Seed weight  | mg   | 1.4   | Schmitt et al. (1992)*      |
|                 | Maximum biomass | mg | 8000 | Janeček et al. (2014)      |
|                 | Repulse of herbivores | []  | 0.4   | Radny et al. (unpublished)  |
|                 | Initial seeds | $\frac{1}{m^2}$ | 85 | Edwards and Crawley (1999)* |
| Hypericum perforatum | Seed weight  | mg   | 0.09  | Fox et al. (1999)           |
|                 | Maximum biomass | mg | 5800 | Vilà et al. (2003)          |
| Species/Crop          | Trait                  | Value | Source                          |
|-----------------------|------------------------|-------|---------------------------------|
| *Agrostis capillaris* | Seed weight (mg)       | 0.06  | Stukonis and Slepety (2013)     |
|                       | Maximum biomass (mg)   | 4000  | Ehlers (2011)                   |
|                       | Repulse of herbivores  | 0.3   | Radny et al. (unpublished)      |
|                       | Initial seeds ($\frac{1}{m^2}$) | 1343  | Edwards and Crawley (1999)**    |
| *Festuca rubra*       | Seed weight (mg)       | 0.77  | Larson et al. (2001)            |
|                       | Maximum biomass (mg)   | 12000 | Corbin and D’Antonio (2004)*    |
|                       | Repulse of herbivores  | 0.3   | Radny et al. (unpublished)      |
|                       | Initial seeds ($\frac{1}{m^2}$) | 654   | Edwards and Crawley (1999)**    |

Table 3: Effects of trait values (competitive and defensive ability) and community configuration (herbivore density, community density and composition, intensity of competition and initial number of non-natives) on survival rate of non-native species presented as estimates of the effects and their corresponding standard errors, z-values and p-values. The intercept corresponds to low competitive ability, low defensive ability, high community density and even community composition. Asterisks indicate p-values smaller than 0.05 (*), 0.005 (**), or 0.001 (***).
| Interaction                     | Coefficient | Standard Error | t-statistic | p-value |
|--------------------------------|-------------|----------------|-------------|---------|
| InitNN:DensHerb                | 0.00        | 0.00           | -2.11       | 0.035 * |
| InitNN:Theta                   | 0.00        | 0.00           | -6.02       | 0.000 ***|
| InitNN:DensComm                | 0.00        | 0.00           | 4.32        | 0.000 ***|
| InitNN:Mix                     | 0.00        | 0.00           | 1.99        | 0.047 * |
| DensHerb:Theta                 | -0.17       | 0.06           | -2.97       | 0.003 **|
| DensHerb:DensComm              | -0.20       | 0.04           | -5.74       | 0.000 ***|
| DensHerb:Mix                   | -0.02       | 0.03           | -0.69       | 0.491   |
| Theta:DensComm                 | 0.53        | 0.10           | 5.26        | 0.000 ***|
| Theta:Mix                      | 0.64        | 0.10           | 6.67        | 0.000 ***|
| DensComm:Mix                   | 0.05        | 0.06           | 0.93        | 0.352   |
Figure 1: Range border shift occurs on a large scale and at species level (a). This movement can be disaggregated into successful establishment events of local satellite populations beyond the native range border (red dots, b). Local persistence depends on individual fitness of individuals in this local population. This is influenced by direct interactions, e.g. with neighbouring competitors (plant symbols) or resident herbivores, on this local scale (c).

Figure 2: Three-dimensional trait vector. Plants can be characterized by high or low trait values for dispersal, defense and competition ability. Exemplarily, species X in the figure is characterized by high competitive values, low defense values and high dispersal values. Species Y is characterized by low competitive values, high defensive values and high dispersal values.
Figure 3 Order of executed routines during each simulation. Green-coloured routines are executed only once, orange-coloured routines are executed on a "daily" basis, i.e. each time step. Herbivory and Competition can lead to individual death of plants.
Figure 4: Model community after 14 days with varying initial community density (low: 308 plants, high: 1108 plants) and varying mixtures of the native community (even: same initial density of all species; literature based: species initial densities differ based on reported seed bank sizes and germination rates). Species are color-coded: Red = non-native species, all other colours: native species, i.e. yellow = A. capilaris, green = F. rubra, purple = H. perforatum, blue = P. lanceolata.
Figure 5: Survival rates of non-natives with the following trait profiles: high competitive and high defensive (HiAll), high competitive and low defensive (HiComp), low competitive and high defensive (HiDef), and low competitive and low defensive (LowAll). Values were averaged over all scenarios.
Figure 6: Survival rates of non-native plants under different invasion levels in high (left panel) and low (right panel) density native communities. Invasion level corresponds to initial population sizes of 8, 16, 32, 64, 128 and 256 individuals of the non-native species. Non-natives are split into the following trait profiles: high competitive and high defensive (HiAll, orange), high competitive and low defensive (HiComp, green), low competitive and high defensive (HiDef, blue), and low competitive and low defensive (LowAll, purple).
Figure 7: Effect of the intensity of competition $\Theta$ in different configurations of the resident community. Left panels show high density of natives, right panels show low density of natives. Note that different initial numbers of non-natives are not separated in this figure. Upper panels show an even mixture of natives in the initial community, the lower panels show a mixture based on literature values of seed bank sizes. With $\Theta = 0$, resources are shared among competitors regardless of their biomass, with $\Theta = 1$, resources are shared proportionally to the biomass of the individual competitors. $\Theta = 0.5$ reflects an intermediate stage. Non-natives are split into the following trait profiles: high competitive and high defensive (HiAll, orange), high competitive and low defensive (HiComp, green), low competitive and high defensive (HiDef, blue), and low competitive and low defensive (LowAll, purple).
Figure 8: Survival rate of non-native species at three densities of herbivores per m$^2$ (0 (control scenario) – red, 3.2 – green, 18.75 – blue). Non-natives are split into the following trait profiles: high competitive and high defensive (HiAll, orange), high competitive and low defensive (HiComp, green), low competitive and high defensive (HiDef, blue), and low competitive and low defensive (LowAll, purple).