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The effects of neighbours in plant communities: mathematical and experimental approaches

Ph.D. Thesis

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Annotation The effect of plant neighbourhood was investigating for hemiparasitic plants, productivity and diversity effects, constant final yield and recruits establishment. The research was based on a wide range of methods including the system of differential equations for population dynamic, individual based model with field of neighbourhood approach, glasshouse experiment and field experiment with gaps in the wet meadow.

Declartion [in Czech] Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované.

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List of papers and manuscripts with author's contribution

(Paper 1) **Fibich, P., Berc, L. & Lepš, J. (2010).** Modelling the population dynamics of root hemiparasitic plants along a productivity gradient. *Folia Geobotanica*, **45**, 425-442.

PF, JL and LB designed the system of differential equations for the host-hemiparasite interaction. PF and LB analyzed it. PF wrote the major part of paper.

(Paper 2) **Fibich, P. & Lepš, J. (2011).** Do biodiversity indices behave as expected from traits of constituent species in simulated scenarios? *Ecological Modelling*, **222**, 2049-2058.

PF and JL designed the individual based model (IBM) and prepared scenarios. PF implemented IBM in C++ and wrote the major part of paper.

(Manuscript 1) **Fibich, P., Lepš, J. & Weiner, J.** Individual variability and mortality required for constant final yield in a Field of Neighbourhood model of plant competition. *Manuscript*.

PF and JL designed the individual based model (IBM). PF, JW and JL prepared and discussed scenarios. PF wrote the major part of paper.

(Paper 3) **Stachová, T., Fibich, P. & Lepš, J. (2012).** Plant density affects measures of biodiversity effects. *Journal of Plant Ecology*, doi [10.1093/jpe/rts015](https://doi.org/10.1093/jpe/rts015). *TS, PF and JL designed the experiment. TS and PF together established the experiment, analysed the data and wrote the major part of paper.*

(Manuscript 2) **Fibich, P., Stachová, T. & Lepš, J.** Analysis of biodiversity experiments: a comparison of traditional and linear-model-based methods. *Submitted*.

PF and TS together analyzed the data and wrote the major part of paper.

(Manuscript 3) **Fibich, P., Vítová, A., Macek, P. & Lepš, J.** Establishment and spatial associations of recruits in meadow gaps. *After revision in Journal of Vegetation Science*.

AV and PM designed and established the experiment. PF and AV digitalized positions of recruits. PF analyzed the data and wrote the major part of paper.

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General introduction

To see a world in a grain of sand,
And a heaven in a wild flower,
Hold infinity in the palm of your hand,
And eternity in an hour.

William Blake

Plants are sedentary organisms rooted in one place. Their ability to change the position – e.g. if their imminent neighborhood influences them much – is limited to growth and dispersal. The effects of the neighborhood differ by intensity, resistance of plant, timing and frequency, by the driver of the effect (e.g. biotic or abiotic) and by the impact on the plant which is either positive or negative. In addition, the location where these effects occur (e.g. above or below the ground), spatial scale and distance of neighborhood effects is important too (Vogt *et al.*, 2010; Tilman & Kareiva, 1997). For example, the annual temperature affects all plants in a large area similarly, but when watering the plant, one must make sure that the water comes close to the plant. Similarly, plant–plant interactions are essentially local in nature and the plant is affected only by neighbors in the imminent distance. For example, an individual plant in the grassland can be shaded by neighboring plants up to a meter distance, but not further. Thus, while plants are not able to move (except dispersal), local conditions are crucial for them (Stoll & Weiner, 2000; Pacala, 1997).

As plants grow, they occupy more space and if they are in a community, sooner or later they will interfere with neighbors. Interactions between plants occur on basis of resources that are necessary for their growth. These are mostly light, nutrients, water. All of these resources require space where they are acquired. Many of the interactions with the neighborhood are negative (or can be defined as interference *sensu* Harper (1977)), some are positive (they are also called facilitation). In the plant–plant interactions, positiveness or negativeness of the effect of interaction can differ for each plant and mechanism. For example root hemiparasitic plants get nutrients from the host plants (the +− effect, + for hemiparasite and − host plant), they compete for light with hosts (the − effect), but they have nutrient rich litter (the ++ effect). Negative effects can be divided depending on mediator of the effects (Stoll & Weiner, 2000), into resource driven (e.g. competition for light) and other mechanisms or organisms driven (e.g. allelopathy). Competition with neighboring

plants is the most important process and selective force driving plant community dynamics. Above ground competition is often assumed as asymmetric (one-sided or non-proportional) and below ground competition as symmetric (two-sided or proportional; Weiner (1990)). Positive interactions where a nurse plant improves local micro-habitat conditions (e.g. increases soil moisture or protects from wind or herbivore) or provide mechanical support are more common in harsh environments (Pakeman *et al.*, 2009; Bertness & Shumway, 1993).

1.1 Spatial patterns and density

The past processes (e.g. competition between neighbors) in an individual interaction are projected into spatial patterns (Perry *et al.*, 2002). Analysis of spatial patterns classified them as a regular, clumped (aggregated) and random pattern, nowadays mostly by the methods based on the well-known Ripley's K-function (Law *et al.*, 2009; Diggle, 2003; Ripley, 1976). A regular pattern is often found for relatively short distances and old or large individuals as a result of competition in the close neighborhood or competition over a long time (Stoll & Bergius, 2005; Stoll & Prati, 2001). On the other hand, a clumped pattern is the most common for younger or smaller individuals (Lepš & Kindlmann, 1987; Wiegand *et al.*, 2006). Although various causes of clumping can be statistically indistinguishable (Ripley (1987), they can often be explained by environmental heterogeneity (e.g. temperature patchiness, micro-scale heterogeneity of moisture), type of dispersal or by positive interactions among individuals (Brooker *et al.*, 2008). Several experiments with artificial sowings have shown that competitive interactions are changed according to the spatial pattern of individual species (Wassmuth *et al.*, 2009; Monzeglio & Stoll, 2008; Turnbull *et al.*, 2007; Stoll & Prati, 2001); in particular the competitively superior species had lower biomass in an aggregated pattern than in a random pattern at high density. Further, weaker species have increased fitness when they are intraspecifically aggregated but segregated interspecifically.

Moreover, sown or observed density of plants affects the plant interactions, too. Extremely high seedling densities in even-aged populations in empty space were reported for example, Prach (1982) observed density of seedlings of several species more than 10^3 per 0.01 m^2 in nature. In such populations, there is a strong intraspecific competition, and the process called "self-thinning" (density-dependent mortality) reduces the number of individuals (Silvertown & Charlesworth, 2001). The self-thinning is closely related to the "constant final yield" (CFY) concept, a positive saturated relationship between total biomass of plant population and sown density (Yahuza, 2011; Weiner & Freckleton, 2010; Willey & Heath, 1969). There is no competition at low densities which results in a linear increase of biomass with density: biomass is proportional to density. At higher densities, the rate of increase of yield with density decreases as the mean plant mass declines and mortality increases which causes the increase in total biomass to be less than proportionate to the increase in density (Weiner & Freckleton, 2010).

1.2 Biodiversity experiments and effects

Loss of global biodiversity during the past few decades has stimulated numerous scientific studies about the importance of species richness for ecosystem functioning (Hooper *et al.*, 2005; Loreau & Hector, 2001). Ecosystem functioning is an umbrella term for various processes operating in an ecosystem, mainly flow of energy and matter within and between ecosystems (e.g. primary productivity, nutrient cycling, etc.). Recent meta-analyses have shown that, on average, species-rich communities 'function' better than poor ones (Balvanera *et al.*, 2006; Cardinale *et al.*, 2006).

In biodiversity experiments, performance of differently species-rich communities and the mechanisms that are behind the interacting species are evaluated by measures of biodiversity (biodiversity effects), statistical methods based on yield (Schmid *et al.*, 2008; Fargione *et al.*, 2007). These methods often compare observed yield of mixtures with expected yield (typically based on monocultures) under a null model (Fox, 2005; Loreau & Hector, 2001). The processes in species interactions are described by indices (or effects). The most widespread measures for evaluating the diversity effects are overyielding (OI) and net effect (NE) – (Cardinale *et al.*, 2007; Naeem *et al.*, 2009). Transgressive OI compares the species mixture with the best monoculture. Positive net effect values are usually interpreted as complementarity (CE; or facilitation) and the selection (SE) effect. To quantify these effects, Loreau & Hector (2001) introduced additive partitioning of the NE to CE and SE. Positive SE values indicate that mixtures are dominated by species with the highest yield in monoculture. CE should reflect niche differentiation of individual species and facilitation.

Previous, traditional, methods for biodiversity experiments firstly evaluate values of indices or effects and analyzed them later (so called "semi-mechanistic" *sensu* Hector *et al.* (2009). Beside them, linear-model-based methods (Bell *et al.*, 2009; Kirwan *et al.*, 2009); so called "mechanistic" *sensu* Hector *et al.* (2009) apply classical statistical fitting and later interpret fitted terms (i.e. identity effects of species, diversity effects of species mixtures, treatment's effects). Outcomes of the different methods range from one overall effect (e.g. overyielding), several overall effects (e.g. selection effect, complementarity and net effects in additive partitioning (Loreau & Hector, 2001) and its extensions (Fox, 2005)) or many individual species and their interactions effects (e.g. in the linear-model-based methods). Although we considered neighborhood effects as important, they are not discussed in the context of biodiversity experiments, because of a coarse-grained scale of such experiments.

1.3 Mathematical methods

Evaluation and presentation of the results of experiments are now impossible without proper mathematical or statistical methods. Also in the phase of the experiment design one must consider methods for future analyses. Besides the results based on experimental approaches, the mathematical and modeling methods (also called models) are successfully applied in many areas of biology (Adam, 2003; Ellner & Guckenheimer, 2006; Spiegel, 1981). Working with models can generate hypotheses

or save money for expensive or infeasible experiments. First of all, models provide a formal representation of some system which is often a goal itself. Each model has some simplifications or conditions restricting truthfulness of its results, however, it is a similar problem as in biological field experiments, which are also – often crude – simplifications of real ecosystems which they should represent. Simplifications are made because of complexity of ecological systems or to make the model easily solvable which leads to straightforward biological interpretations.

One of the basic divisions of mathematical or modeling approaches is into mean-field and individual-based models (Kot, 2001). During the past decades, focus has been shifted from the mean-field approach toward the level of the individuals (Berger *et al.*, 2008). Although the progress of modeled system (e.g. competition of two plants) can be visualized along time steps for both approaches (Fig. 1.1), they are quite different.

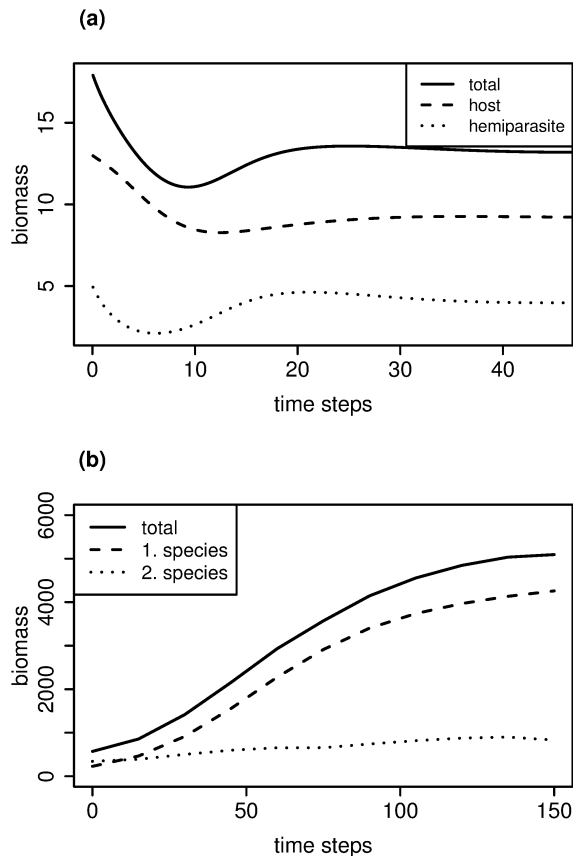


Figure 1.1: The biomass of individuals in the mean-field host-hemiparasite model from (*Paper 1*) (a) and individual-based model with two species from (*Paper 2*) (b) along time steps.

The first group, the mean-field models (or often called "unstructured population models"), mostly assume that all individuals are on average the same and interact

in the same way. Therefore neighborhood is mostly averaged and is considered to be the same for each plant (Murrell *et al.*, 2002). These models often consist of one or set of differential or difference equation with state variable or variables that reflect number of individuals or sum of their mass (e.g. biomass). Their advantages are straightforward description of processes and mathematical tractability of stable and unstable states (also called equilibria). Even they are mostly simple, they can capture many real life problems from biology like predation, competition, mutualism (Hastings, 1997) and Allee effect (Boukal *et al.*, 2007).

The second group, the individual-based models (IBMs), are bottom-up approaches where the modeler starts from individuals and tries to capture the functioning of the community emerging from interactions between individuals (Grimm, 1999; Grimm & Railsback, 2005). Individual plants have their own set of parameters (e.g. position in space, growth rate, maximum biomass, etc.) that make them unique (see Fig. 1.2,1.3 for virtual population of plants), not the same or transformed to the mean individual as it is in state variable or top-down approaches like in the mean-field models.

IBMs have many different approaches to define the growth of individuals (Damgaard & Weiner, 2008), time step and spatial location (Berec, 2002), as well as definitions of individuals and views of what is a close neighborhood where plant interact (Law *et al.*, 2003; Lepš, 1988). As a matter of fact, a simpler group of individual based models, those that are not spatially explicit, takes individuals as independent entities with their own state variables, but the neighborhood is averaged for all the individuals (as in the JABOWA type models); these models were developed in early seventies (Botkin *et al.*, 1972), i.e. in the time when similar spatially explicit model exceeded the computational ability even of the best computers of that time.

We proposed the mean-field model for the root hemiparasite–host plant interactions to show the importance of productivity gradient and above ground competition for light in this relationship (*Paper 1*). We developed spatially explicit IBM using a Field of neighborhood approach (Berger and Hildenbrandt, 2000) to investigate (1) the role of spatial pattern, density, CFY and species traits for the results of biodiversity indices (*Paper 2*), (2) the role of spatial pattern, variability and mortality for CFY and to ask under what conditions the model results violate the CFY (*Manuscript 1*). In the glasshouse experiment with four grassland species and five sown densities, we (1) studied the density–biomass relationship of monoculture and species mixtures, and the effect of sown density on the results of biodiversity indices (*Paper 3*), (2) compared the methods for analysis of biodiversity experiments and discussed their results, advantages and drawbacks (*Manuscript 2*). We studied spatio-temporal dynamics in pattern of recruits (seedlings and vegetative sprouts) of common meadow species to characterize development and underlying ecological processes during gap colonization (*Manuscript 3*).

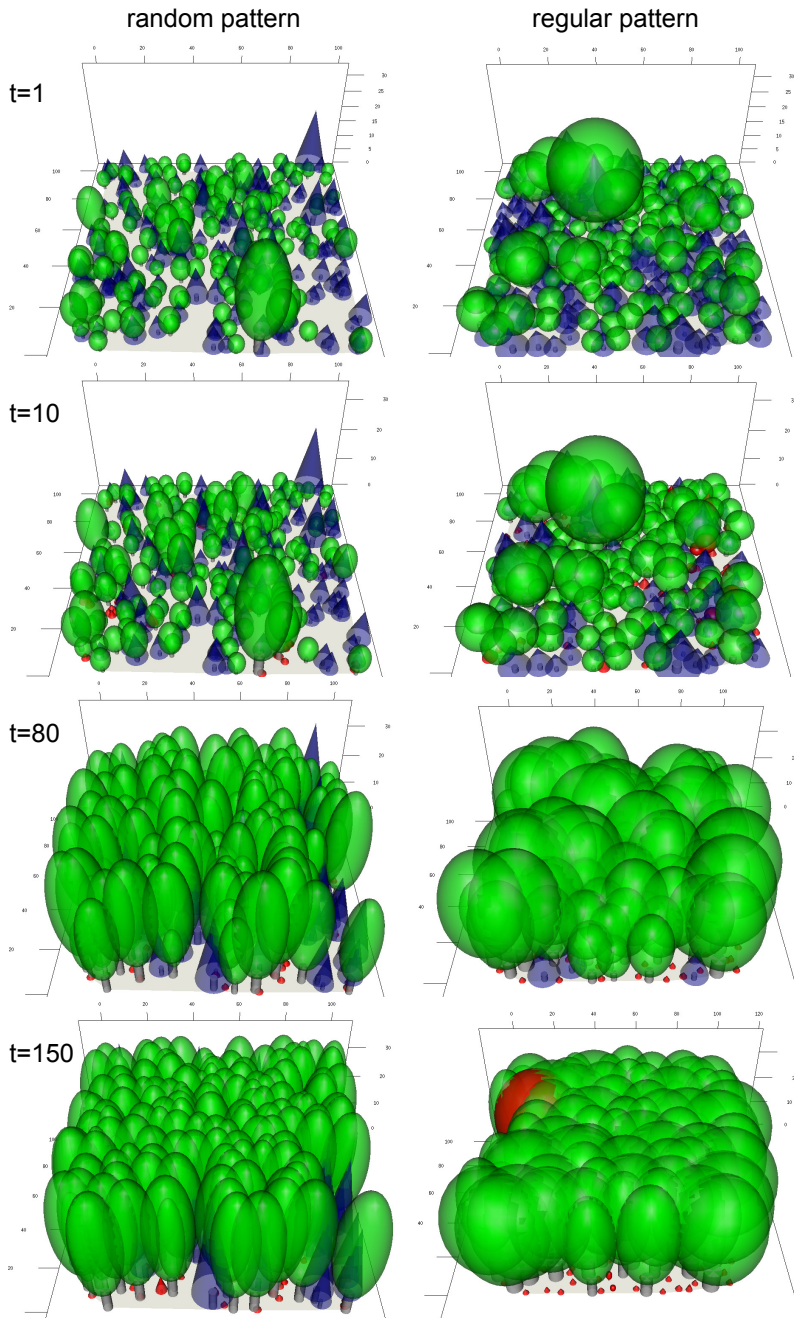


Figure 1.2: Two species (green and blue) IBM from (*Paper 2*) for the random and regular spatial patterns along time steps (t). Red individuals are dead and their biomass decreases in time.

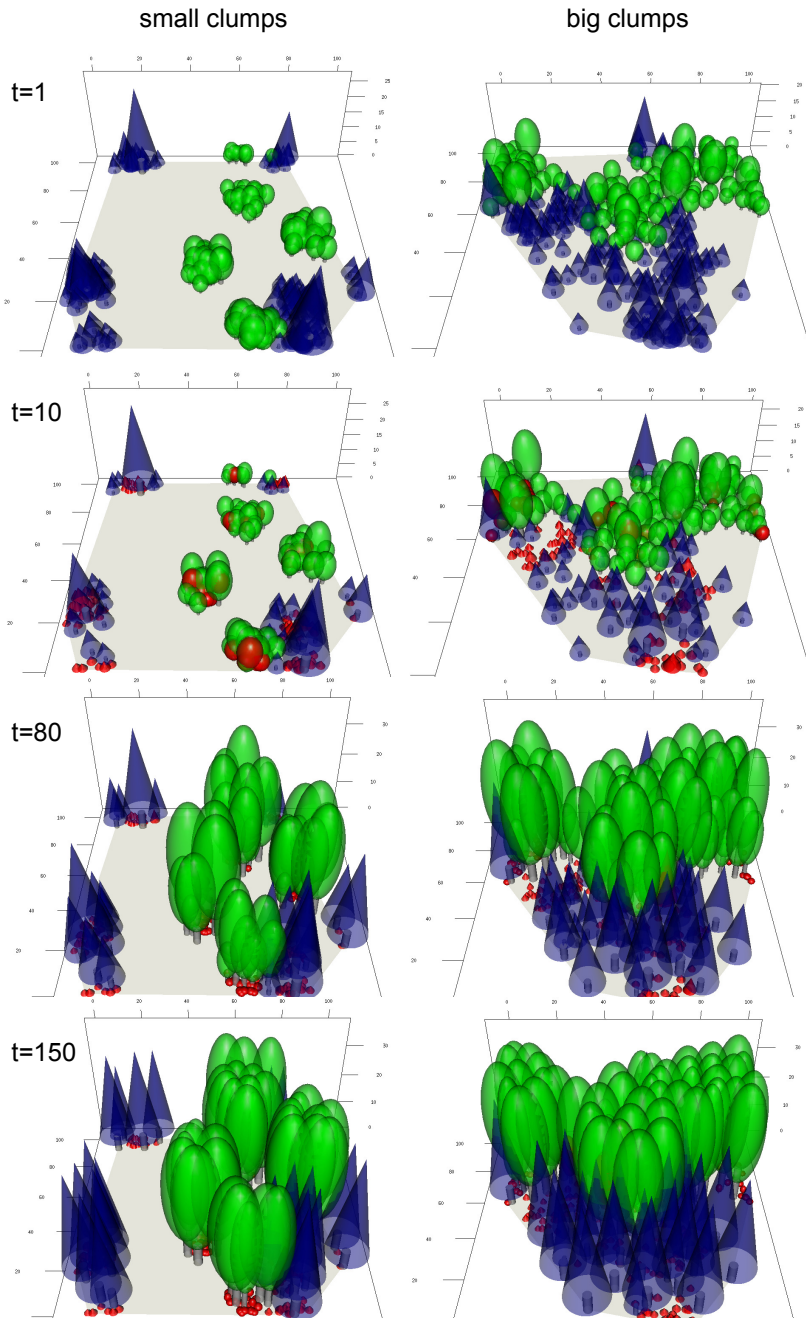


Figure 1.3: Two species (green and blue) IBM from (*Paper 2*) for two clumped spatial patterns along time steps (t). Red individuals are dead and their biomass decrease in time.

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Modelling the population dynamics of root hemiparasitic plants along a productivity gradient

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ABSTRACT Root hemiparasitic plants interact with their host plants through parasitism and competition. The interactions can be divided into aboveground and belowground interactions. Because both groups of plants are autotrophic, they compete for light aboveground. Belowground interactions are more complex. The host plants compete for resources in the soil and the hemiparasitic plants prey on the host plants through haustoria, using the hosts as the main source of water and nutrients. In this paper, we modeled the relationship between these two plant types, extending the well-known Rosenzweig-MacArthur predator-prey model to cover both light competition and intra-specific parasitism among hemiparasites. We included a realistic relationship of carrying capacity to environmental productivity and followed model behavior on a productivity gradient. The model shows that, at very low productivities, there are only a few poor hosts and hemiparasites have no chance to persist. As productivity increases, there is a range of productivity where both plant types coexist. A further increase in productivity gets the system out of the coexistence range, and only host plants survive. This final prediction successfully explains patterns observed in empirical data, contrary to the results of an earlier, oversimplified model of the explored interaction. Comparison of various models demonstrates that the model is able to reproduce the decline of hemiparasites with increasing productivity only when competition for light is included.

KEYWORDS Hemiparasites, Light competition, Productivity gradient, Rosenzweig-MacArthur model

Do biodiversity indices behave as expected from traits of constituent species in simulated scenarios?

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ABSTRACT It is believed that diversity of plant communities has a positive effect on their productivity. The benefits of diversity are described by "biodiversity indices", comparing yield of mixtures with yields of monocultures of constituent species. These indices are supposed to capture also the main mechanisms leading to increased yield. We have constructed a spatially explicit individual based model, simulating even-aged stand development, and compared the behaviour of selected biodiversity indices (overyielding, selectivity and complementarity) with expectations based on life history traits of constituent species. The results are based on comparisons of two species mixtures with corresponding monocultures. We designed three scenarios of changes in the two species life history differentiation, and compared the behaviour of the indices with expectation based on it. In the first scenario, selectivity was driven by increasing size inequality of the two species, mostly in accordance with expectations. The second scenario presents increasing shade tolerance of the smaller species that increased complementarity, again mostly as expected. In the last scenario, shortening of length of stress tolerance of the weaker species surprisingly increased values of the biodiversity indices. For each setting, we varied sowing density and spatial pattern of the constituent species. The behaviour of the indices was influenced by both factors, but the effect of density was more pronounced. In particular, at high sowing densities, the most important interactions happened in the very early stages of mixture development, and the behaviour of the indices was often counter-intuitive.

KEYWORDS Individual based model, Productivity, Density, Spatial pattern, Biodiversity index

Individual variability and mortality required for constant final yield in a Field of Neighbourhood model of plant competition

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ABSTRACT Constant Final Yield (CFY) describes the relationship between total biomass yield and plant density for populations grown over a wide range of densities for a given period of time. Biomass increases in proportion to density at low densities and then levels off, reaching an upper asymptote at high densities. This relationship is very general, but a few exceptions, in which biomass yield decreased at high densities, have been documented. We have used an individual-based "Field of Neighborhood" model of plant competition to investigate the potential role of spatial pattern, individual variability and mortality for CFY and to explore the theoretical conditions under which CFY is violated. CFY was observed whenever the initial variability in the size of individuals was high. A clumped (aggregated) pattern produced CFY because variation in local crowding generated variability in size. In the random pattern, faster mortality (or self-thinning) led to CFY, because of faster differentiation among individuals. A regular (uniform) pattern did not produce CFY because the forces leading to mortality operate with the same intensity on all individual. CFY was observed at intermediate rates of mortality: lower mortality resulted in inhibition of growth of most individuals, while fast mortality caused quick decline in population density, producing decreased biomass production at high densities in both cases. Our results emphasize the importance of individual variation for population processes and suggest that CFY is most likely to be violated in homogeneous, uniformly sown populations such as plantations.

KEYWORDS constant final yield, variability, mortality, field of neighborhood, simulation model

Plant density affects measures of biodiversity effects

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ABSTRACT Aims: We tested for the effect of final sowing plant density (i.e. density of established seedlings) on the values of biodiversity effects [transgressive overyielding, net effect, complementarity effect (CE) and selection effect (SE), trait-dependent complementarity and dominance effect] in a glasshouse pot experiment.

Methods: We conducted a single-season (4 months) glasshouse experiment. Species monocultures and mixtures containing up to four common meadow species from different functional groups were sown and subsequently thinned to five density levels (8-128 individuals per pot, i.e. 200-3200 individuals m²). Community functioning was characterized by yield (both living and dead biomass) of all constituent species.

Important Findings: Our results show that plant density (final sowing density in our case, but this finding can be generalized) affects the yields of both monocultures and mixtures. As these and their relationships are the basis for calculation of biodiversity effects, these effects also varied along the density gradient. Net biodiversity effect, CE and SE all increased with density. The net biodiversity effect and the CE switched from negative to quite positive in the four-species mixture. Using Foxs tripartite partitioning, trait-dependent complementarity was minor in comparison to the dominance effect. One of our experimental species did not follow the densityproductivity relationship, called constant final yield (CFY), which was reflected in the biodiversity measures. The shape of the densityproductivity relationship for experimental species affects also the values of biodiversity indices, particularly when species do not follow the CFY relationship. According to our data and recent simulation experiments, the values of commonly used biodiversity effects can be rather misleading if a species has, e.g. a unimodal dependence of yield for the density gradient and the density level used in the experiment is higher than the peak density.

KEYWORDS Biodiversity effects, Plant density, Constant final yield

Analysis of biodiversity experiments: a comparison of traditional and linear-model-based methods

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ABSTRACT The relationship between diversity and ecosystem functioning is often studied by biodiversity experiments: species mixtures differing in their species richness are sown and their performance (usually productivity) is measured. In analyses, the species richness is taken as a predictor, and the performance of a mixture as a response. The most often traditionally used method is the additive partitioning of net biodiversity effect by Loreau and Hector, and newly also the methods of Kirwan et al. and Bell et al., based on application of general linear models. We compared requirements and results given by these methods of analysis using data from our pot biodiversity experiment. Additive partitioning has much higher requirements for data collection: the monoculture performances of all species must be present and contributions of all species to all the mixtures must be known. This logistically limits the size of an experiment: species pool and plot size as well as the number of replications. Also, with further statistical analysis of the dependence of biodiversity effects on richness measures, the problem of inflated significance arises. The results of individual methods are difficult to compare directly, because each of them measures different features. Nevertheless, the ecological interpretations were similar in many respects, and in some respects provided complementary information. In our view, additive partitioning, together with Relative Yield of individual species (which is part of the additive partitioning calculation), provided better insights into mechanisms affecting the final outcome than the linear-model-based methods. In linear-model-based methods, a distinction should be made between interactions among species in the community and statistical interactions among the effects of the presence of individual species in statistical models.

KEYWORDS biodiversity effects, diversityinteraction models, species identity, species interactions, sown density

Establishment and spatial associations of recruits in meadow gaps

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ABSTRACT Questions: What is the spatio-temporal dynamics of recruit (seedlings and vegetative sprouts) establishment in meadow gaps? What processes prevail during recruit establishment? At what spatio-temporal scales do they operate?

Location: A wet meadow in South Bohemia, a region of the Czech Republic.

Material and Methods: We studied spatio-temporal dynamics in pattern of recruits (seedlings and vegetative sprouts) to characterize development and underlying ecological processes during gap colonization. We established four types of artificial gaps laid out in 10 replicated blocks. To distinguish the effects of generative versus vegetative reproduction we used gaps with sterilized and non-sterilized soil (manipulating the seed bank) and manipulated the possibility of clonal spreading by inserting mesh or felting along the borders of the gaps.

Results: The majority of recruits appeared during July and August. Recruits were surrounded by empty spaces of 5-9 mm, and formed clumps 20mm or larger. Clumping of even aged seedlings and a lower number of vegetative recruits was observed in the gaps with non-sterilized soil. Overall, clonal spreading was limited to the gap borders, being far less common than recruit establishment from seeds. The recruits emerged preferentially close to the gap center where the temperature was highest as well as red to far-red ratio (R/FR). However, during the season, the majority of late recruits were observed in the southern, coolest parts of the gaps, reflecting the increasing importance of the facilitative effect of the surrounding vegetation.

Conclusions: Gaps were colonized predominantly from seeds, vegetative propagation was very slow and appeared at the end of the season. The presence of a seed bank enabled earlier gap colonization; the effect of seed rain became increasingly important during the season.

The recruits were clumped, which further supports environmentally driven establishment, although other factors (e.g. facilitation) cannot be excluded. For the shortest distances, recruits were lacking close neighbors due to the strongest competition. We hence suggest there was a spatial continuum between competition and facilitative effects among individual recruits.

KEYWORDS meadow gap, recruitment, spatial pattern, seed bank, seedlings, vegetative propagation

General discussion

Plant–plant interactions are local and spatially dependent (Stoll & Weiner, 2000). Spatial structure (e.g. spatial pattern, plant density) changes the interactions of plants. For example, clumped pattern with interspecific segregation is more suitable for weak competitors, and in this way can promote the species co-existence (Stoll & Prati, 2001; Tilman, 1994). Moreover, spatial pattern also provides information about past processes in plant interactions (Perry *et al.*, 2002; Pacala & Levin, 1997). For example, regular spatial pattern is driven by competition between individuals (Stoll & Bergius, 2005; Perry *et al.*, 2002). Despite this fact, the evidence obtained from manipulative experiments is usually stronger than that deduced from observed patterns (Lepš, 1990). In fact, the mean-field models average the neighbourhood and in this way ignore the spatial structure, some of the ecological phenomena can be modeled in this way. For example, we managed to demonstrate that high productivity of the environment leads to high host biomass which can finally lead to extinction of the hemiparasite species (*Paper 1*). Although this effect is undoubtedly based on neighbourhood interactions, the phenomenon is so pronounced that it is not suppressed by spatial averaging in the mean-field model.

8.1 Hemiparasite-host interactions

It is crucial for the root hemiparasitic plants (e.g., Rhinanthoidae in Orobanchaceae) not to be far from the host plant. They are parasitic belowground, obtaining most of their water and nutrients from their hosts, and simultaneously autotrophic, producing carbohydrates by photosynthesis (Press, 1989; Cameron *et al.*, 2005; Press & Phoenix, 2005). Resource parasitism allows root hemiparasites to overcome deficits in their competitive abilities (Smith, 2000). We proposed a new mean-field model of the root hemiparasite-host plant interaction that include below ground parasitism and above ground competition (*Paper 1*). Results from our model confirmed the conjecture of Matthies (1995) suggesting that hemiparasites are restricted to nutrient-poor habitats because of the balance between the effects of parasitism and light competition. Our predictions are also in agreement with the field data (Hadač, 1969; Hejčman *et al.*, 2011), showing that increasing the total biomass of plants leads to a decrease in the percentage of hemiparasitic plants. Similarly, fertilizing and higher

host community biomass lead to decreased seedling survival (Mudrak & Lepš, 2010), decreased fruiting (Vanhulst *et al.*, 1987) and density of hemiparasites (Westbury & Dunnett, 2007). In high-productivity environments, increased shading may reduce competitiveness of these autotrophic plants with respect to their host plants which usually score better in the competition for light (Press & Phoenix, 2005). The importance of aboveground competition grows with increasing productivity of the environment (Grime, 1979; Tilman, 1988; Wilson & Tilman, 1993; Lepš, 1999).

8.2 Sown density and spatial patterns

To study plant interactions, the simplest populations are monocultures, where differences between individuals are given by phenotypic plasticity of one species (Silvertown & Charlesworth, 2001). According to the law of constant final yield, total biomass of a monoculture will increase, level off and then remain constant with increasing density (Weiner & Freckleton, 2010). However, published experimental data show that in some cases, total biomass may also have a unimodal shape, decreasing at high densities (Chu *et al.*, 2008; Kristensen *et al.*, 2008; Stoll *et al.*, 2002; Willey & Heath, 1969); this phenomenon is also simulated by our individual based model (*Paper 2*) and confirmed by our glasshouse experiment with common meadow species (*Paper 3*) for rather large range of sowing densities.

Low variability among plants is reflected by low asymmetry of competition even though size-asymmetric competition increases variability (Weiner *et al.*, 2001). Increased plant density strengthens this trend even though it also increases self-thinning (Yoda *et al.*, 1963). In our IBM (*Manuscript 1*), we introduced variability also by using a clumped pattern. There is a higher variability because plants at the centers of the clumps will experience stronger competition than plants at the borders having fewer neighbours. Even under the conditions when the regular and random populations do not show CFY, the spatial variability in the clumped pattern with the same parameters as in other two spatial patterns produced CFY. This is consistent with the observation that a non-uniform pattern of individuals can mimic the effect of asymmetric competition (Schwinning & Weiner, 1998; Weiner *et al.*, 2001). The coefficient of variation of individual biomass was the highest in the clumped pattern, consistent with previous results (Hara & Wyszomirski, 1994; Weiner *et al.*, 2001). In the random pattern, faster self-thinning led to CFY, because of faster differentiation among individuals (*Manuscript 1*). The regular pattern mostly did not follow CFY because the competition leading to self-thinning operates in all individuals at the same time. Promoting of CFY had unimodal shape based on the speed of self-thinning; it should be neither too slow (stuck of population) nor too fast (sudden decline of the population) for CFY. For all spatial patterns, CFY were observed when there is a high variability in the initial biomass.

8.3 Biodiversity experiments

Our glass house experiment showed that all results of the traditional and linear-model-based-methods, including the values of the biodiversity effects, changed with sowing densities (*Paper 3, Manuscript 2*), in concordance with our modeling study (*Paper 2*). Sowing densities were very important because they determine at which stage strong competition among individuals starts, and this might also determine the relative success of individual species in the competition. The importance of carefully selected densities in a biodiversity experiment was shown also by He *et al.* (2005) who concluded that high density in multispecies communities reduced species evenness and altered functional group abundances, similarly to Flynn *et al.* (2008) who found decreased variability with increasing density.

If population of plants do not follow CFY (*Paper 2*), both spatial pattern and plant density affect values of biodiversity effects too and therefore are important factors in biodiversity experiments. As expected, selectivity effect was driven mainly by differences in the maximum biomass between species, while an increase in shade tolerance of weaker species could increase the complementarity effect. In accordance with the experimental data (Wassmuth *et al.*, 2009; Monzeglio & Stoll, 2008; Stoll & Prati, 2001), we showed that competitively weaker species benefits from clumped (aggregated) pattern. Also, we showed that biodiversity effects do not work well for all densities if the total biomass of monocultures has a unimodal shape, both using a model (*Paper 2*) and our experimental data (*Paper 3, Manuscript 2*).

Our experiment (*Paper 3, Manuscript 2*) and results of IBM (*Paper 2*) suggested that the belief that the results of biodiversity experiments are rather insensitive to sowing density need not be fully warranted, and so confirmed the caveat of Garnier *et al.* (1997) that density is not a negligible factor in biodiversity experiments. Therefore, as recommended elsewhere (Weiner & Freckleton, 2010), we similarly suggest to use sowing densities for ecological experiments where plants obtain the maximum biomass. We advise to test the shape of total biomass dependence on density. Nevertheless, extremely high densities are considered or known a priori as non-economical and so are not used in experiments (Berger *et al.*, 2004), but they undoubtedly appear in natural populations (Prach, 1982).

8.4 Spatial patterns in gaps

Disturbed sites or gaps in vegetation provide suitable conditions for regeneration of many species thanks to usually more abundant nutrients and light, while competition is lower and litter often does not limit establishment of recruits (seedlings and sprouts) there. In our experimental gaps in wet meadow (*Paper 6*), we observed growth of recruits in a regular pattern for the shortest distances (no other recruits of any age grew within a distance of ca. 5-9 mm) and in a clumped (aggregated) spatial pattern at larger distances (ca. from 2 cm). Empty space around recruits suggests stronger competitive interactions at a certain small distance around them (Stoll & Prati, 2001). Although this distance was rather small (but considering

seedling size it may have been large enough), it was significant and consistent across the treatments, indicating a dog eats dog world is governing the surroundings of the first coming species. The regularity (empty space around recruits) was stronger for early than for late recruits (appear at the end of the season), likely because they were under competition for a longer time and the closest neighbouring recruits were already outcompeted, which is concordant with other studies (Wiegand *et al.*, 2006). On the contrary, the clumped pattern indicates the prevalence of other processes at larger distances (i.e. environmental heterogeneity, type of dispersal or by positive interactions among plants).

However, it may also indicate a switch from more competitive interactions toward more facilitative interactions during the season as a response to changing environmental conditions. We therefore focused on interactions between early (appear at the beginning of the season) and late recruits and asked whether facilitation may explain such clumping. We showed that late recruits grew apart from early recruits at the smaller scale (ca. up to 7 mm no recruits were around), and we again attributed such regularity to be the result of negative interactions between late and early recruits. Beside , the mark correlation function showed that there were clumps of recruits of even age at the small scales in the gaps without soil sterilization (ca from 4 to 14 mm). This implies that spatially close recruits (mainly originating from the seed bank) appeared at the same time during the season.

8.5 Final remark

While the research of plant ecology has a long standing history in scientific research, the spatial aspect, density and structure neighbourhood in plant interactions are often neglected or hard to capture. This thesis provides a novel insight into the role of the neighbourhood using theoretical and experimental studies. Namely, the importance of spatial structure and sown density as drivers and results of interactions between plants was clearly demonstrated.

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