

*Article*

## **Measuring competition in plant communities where it is difficult to distinguish individual plants**

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### **Abstract**

A novel method for measuring plant-plant interactions in undisturbed semi-natural and natural plant communities where it is difficult to distinguish individual plants is discussed. It is assumed that the ecological success of the different plant species in the plant community may be adequately measured by plant cover and vertical density (a measure that is correlated to the 3-dimensional space occupancy and biomass). Both plant cover and vertical density are measured in a standard pin-point analysis in the beginning and at the end of the growing season. In the outlined competition model the vertical density at the end of the growing season is assumed to be a function of the cover of all species at the start of the growing season, and the cover at the start of the growing season is assumed to be a function of the vertical density of all species at the end of the previous growing season. The method allows direct measurements of the competitive effects of neighbouring plants on plant performance and the estimation of parameters that describe the ecological processes of plant-plant interactions during the growing season as well as the process of survival and recruitment between growing seasons. Additionally, the presented method is suited for testing different ecological hypothesis on competitive interactions along environmental gradients, investigating the importance of competition, as well as predicting the likelihood of different ecological scenarios.

**Keywords** plant-plant interaction; plant community dynamics; pin-point; state-space model; latent variables.

### **1 Introduction**

Competition among neighbouring plants arises because the resources needed for plant growth and reproduction are limited, and the plant that extracts or monopolises most of the limiting resources will grow faster and reproduce in greater numbers (e.g., Weiner, 1986; Goldberg et al., 1990). In principle, it is possible to examine competition at the level of the limiting resources if a detailed knowledge of the physiological processes of the competing plants is available (Tilman, 1982; Everard et al., 2010). However, in most terrestrial ecological studies, there is only little information on the uptake and dynamics of the resources that limit the growth of different plant species (Miller et al., 2005; Shipley, 2010), and, instead, competition is inferred from observed negative effects of neighbouring plants without knowing precisely which resources the plants were competing for. Consequently, in the following, the term “competition” will be used broadly as the negative effect of neighbouring plants on growth and reproduction (Damgaard, 2004).

The possibly important role of interspecific competitive interactions in regulating natural plant communities (e.g., Weiher et al., 1998; Silvertown et al., 1999; Gotelli and McCabe, 2002) has been investigated in a multitude of studies that have used different methods for attacking the question. The used methods may be categorised broadly into i) whether the study has been made in undisturbed plant communities or involved manipulative treatments; and ii) whether the process of competition was studied *directly* by measuring the effect of density on the performance of individual plants or *indirectly* by inferring interspecific competitive relationships as the causal mechanisms that underlie observed changes in species abundance or specific patterns in the distribution of species (Table 1).

**Table 1** Methods for studying interspecific competitive interactions in natural plant communities.

	<b>Undisturbed communities</b>	<b>Manipulative experiments</b>
<b>Direct</b>	Neighbourhood analysis Fixed-positioned pin-point frames	Competition experiments Removal and phytometer experiments
<b>Indirect</b>	Observed changes in species composition Non-random spatial distribution of species Niche separation Space for time substitution	Observed changes in synthetic or experimental plant communities

Most studies of plant competition are manipulated experiments where density and/or the proportion of different species are varied and the biomass or fecundity of the competing species are measured. Often, such competition experiments are made in rather artificial environmental conditions, e.g. with a limited number of individuals in small plots (e.g. Firbank and Watkinson, 1985; Law and Watkinson, 1987; Damgaard, 1998), but since there has been an increasing awareness that the interspecific interactions critically depend on the abiotic and biotic setting, it is now more common to conduct ecological manipulation experiments in natural plant communities, where the density of either the neighbours (removal experiments) or the target species (phytometer experiments) has been manipulated (Goldberg and Barton, 1992). Unfortunately, removal and phytometer experiments are mostly suited for qualitative demonstrations of possible competitive interactions, and the experiments do not enable the formulation of quantitative descriptions of the interspecific competitive interactions at variable local densities. Furthermore, there has been a rising awareness that the manipulations may have important local ecosystem effects, e.g. in the soil and on the behaviour of herbivores (Corcket et al., 2003), and other methods for measuring competition in undisturbed natural plant communities have been a topic of rising interest (Freckleton and Watkinson, 2001).

An increasingly popular method has been to infer interspecific competitive relationships indirectly as the causal mechanisms underlying observed changes in species abundance or specific patterns in the distribution of plant species in natural communities (Zhang, 2011). For example, Rees et al. (1996) analysed observed changes in the distribution of annual plants in thousands of small quadrates in a fixed dune plant community, and Law et al. (1997) estimated competition coefficients from spatial turnover data of four perennial grass species (see also Freckleton et al., 2000; Adler et al., 2006; Farrer et al., 2010). Other researchers have suggested that non-random spatial distribution of species is the fingerprint of competition that has taken place in the past (Conner and Simberloff, 1979; Wilson et al., 1996; Law et al., 1997; Gotelli and McCabe, 2002), and Silvertown et al. (1999) demonstrated niche separation along a hydrological gradient. Additionally,

competitive mechanisms in natural plant communities have been inferred from comparing plant communities at different successional stages, the so-called “space for time substitution” (Barclay-Estrup and Gimingham, 1969; Bakker et al., 1996). Finally, for testing specific ecological hypotheses, it may be difficult to find natural plant communities with the required variation in the initial conditions and it has, therefore, become increasingly popular to study the mechanism of competition indirectly by observing changes in synthetic or experimental plant communities (Fukami et al., 2005; Ejrnæs et al., 2006; Fridley et al., 2007).

The development of indirect methods for inferring interspecific competitive relationships has had a central role in the increasing awareness of the importance of linking ecological data with quantitative population models by means of advanced statistical approaches (Rees et al., 1996; Clark, 2007). However, in order to test specific hypotheses on the role of plant competition in determining plant community structures, it is necessary to make a direct link between the spatial arrangement of neighbouring plants and plant performance. Such direct studies of the importance of competition have been performed under the heading of neighbourhood analyses, where the effect of the distance between neighbouring plants on plant performance is quantified. Pacala and Silander (1990) described the community dynamics between two annual plant species in a neighbourhood analysis, and Turnbull et al. (2004) estimated the individual-level competition coefficients for seven annuals growing in limestone grassland over 2 years. However, the method of neighbourhood analysis is only feasible in plant communities that are dominated by plant species where it is easy to distinguish individual plants, and many open natural herbal and grassland communities are dominated by perennial species that form dense vegetation where it is difficult to distinguish individual plants and, consequently, to determine density. Furthermore, if individual plants may be distinguished, they almost always vary markedly in size, so that the number of neighbouring individuals within a certain distance is of limited value for describing the amount of competition experienced by the target plant. More generally, the degree of competition experienced by the target plant is expected to be species-specific spatial functions (competition kernels or field-of-neighbourhoods) that depend critically on the size and distances of the neighbouring plants (Berger and Hildenbrandt, 2000), and such field-of-neighbourhoods are not easily estimated in plant communities with several species.

In this paper a novel method for measuring competition in undisturbed natural plant communities is discussed. The method allows direct measurements of the competitive effects of neighbouring plants on plant performance and the estimation of parameters that describe the ecological processes of plant-plant interactions during the growing season as well as the process of survival and recruitment between growing seasons using data from a standard pin-point analysis (Damgaard et al., 2009). In a pin-point analysis, a frame with a fixed grid pattern is placed above the vegetation. At each grid point, a pin is inserted vertically into the vegetation and the number of times the pin touches different plant species is recorded (Levy and Madden, 1933; Kent and Coker, 1992). A pin-point measurement provides estimates of two important plant ecological variables: cover and vertical density. The species cover is the relative area that a species “covers” when projected onto the two-dimensional ground surface and, in a pin-point analysis, cover is estimated by the relative number of pins that touch the species. It is argued that cover in many open perennial plant communities will be a more suitable predictor of the competitive interactions than local plant density. The vertical density is defined as the number of times a single pin hits a specific species (for a discussion on terminology see Wilson, 2011), this measure is positively related to the 3-dimensional space occupancy (or volume) of the species and has been shown to be a non-linear function of plant biomass (Jonasson, 1983, 1988). For most plant species, both the cover and the vertical density will be relevant measures of the ecological success of the species (Damgaard et al., 2009).

The difference between a neighbourhood analysis and the presented pin-point method is that in a neighbourhood analysis, the performance of *individual* target plants is measured, whereas in the pin-point method, the performance of different *spatial entities* of a species is measured by a spatial sampling approach, without distinguishing individual plants. The pin-point method of measuring competition is, therefore, especially suited in plant communities that are dominated by perennial herbal and grass species, where it is difficult to distinguish individual plants.

The idea underlying the method of measuring competition is:

i) To express the vertical density at the end of the growing season as a function of the cover of all species at the start of the growing season, i.e. the vertical density of a species at the end of the growing season will reflect the growth of the species within the pin-point frame, which will depend on the cover of the species in the beginning of the season, availability of resources, and the cover of the other competing species in the beginning of the season.

ii) To express the cover at the start of the growing season as a function of the vertical density at the end of the previous growing season, i.e. plants are expected to allocate resources into occupying space the following year (on the Northern hemisphere), and a plant species that grows to a relatively high vertical density at the end of the growing season is expected to have a relatively high plant cover the following year.

In the following outline of the method it will be discussed how to i) sample cover and vertical density data in fixed-positioned pin-point frames; ii) model the observed competitive interactions; and iii) make predictions on the future states of the plant community.

For reasons of simplicity the effects of one or more abiotic environmental gradients on the plant-plant interactions have been ignored in the above introduction. However, in most current fundamental and applied plant ecological questions, e.g. the importance of competition in structuring plant communities, the possible evidence of niche separation, and prediction of the consequences of environmental changes on ecosystems, the preferred method of research is to study plant-plant interactions along one or more environmental gradients (e.g. Silvertown et al., 1999; Damgaard, 2003). Consequently, it will be assumed that the competition study will be performed along a single environmental gradient and that the research question will involve the possible effects of the environmental gradient on the plant community dynamics.

## 2 Data Collection

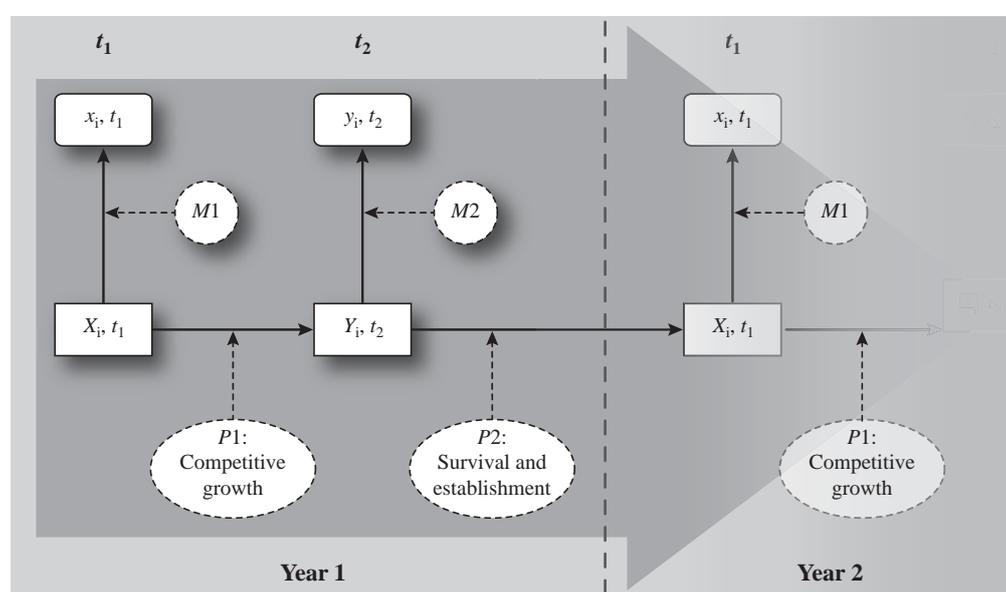
Depending on the number, size distribution and spatial arrangement of the plant species in the studied plant community a pin-point frame of a fixed size and a specific number of equidistant grid-points is chosen. Generally, the distance between the grid-points should increase with size and intraspecific aggregation of the plant species, but there are no fixed recommendations to the design of the pin-point frame, except that it is hard on the back if the size of the pin-point frame is too large. If the plant community has been digitized or the size distribution and intraspecific aggregation is known, then it is possible to simulate the statistical power of different designs of the pin-point frame.

In the field, a number of fixed markings are placed along the environmental gradient in such a way that the position of the frame and the pins are uniquely determined (the information on the pin-position within the frames is not used in the outlined model below, but this information may be used for other purposes as explained in the discussion). The fixed-positioned pin-point frames do not have to be randomly placed; if the research question is centred on a couple of key-ecological species then the statistical power of the competition

experiment is increased if the pin-point frames are placed in such a way that the species co-occur in variable abundances and proportion.

The cover of the different species is determined at the beginning of the growing season. The vertical density of the different species is determined and at the end of the growing season. When the data is collected, all species are recorded, but when the data are modelled, it will most likely be necessary to aggregate the species into different classes (Damgaard et al., 2009), or model the parameters as functions of species traits (Comita et al., 2010), e.g. by modelling the competition coefficients by the height and specific leaf area of the species.

The first data collection may be performed either at the beginning or at the end of the growing season, and the experiment may continue for as long as possible. If data are collected in atypical years, e.g. very wet years or very dry years, such data may be analysed separately and provide a unique opportunity for examining the effect of extreme climatic conditions on plant community dynamics.



**Fig. 1** Graphical model of the state-space model, the observations, and the studied competitive processes; the competitive growth during the growing season (from  $t_1$  to  $t_2$ ) is modelled by the process equation  $P1$  which expresses the vertical density of the different species at  $t_2$  as a function of the cover of all species at  $t_1$ , and survival and establishment between growing season (from  $t_2$  to  $t_1$  the following year) is modelled by the process equation  $P2$  which expresses the cover at  $t_1$  the following year as a function of the vertical density at  $t_2$  the previous year. The unknown states of cover and vertical density of the different species are modelled by latent variables (square boxes), and the latent variables are connected to measurements of the cover at  $t_1$  and the vertical density at  $t_2$  of the different species (rounded boxes) by the measurement equations  $M1$  and  $M2$ .

### 3 Competition Model

The competitive interactions along the environmental gradient are modelled by describing how cover and vertical density of the different species co-vary along the environmental gradient. The changes in the cover and vertical density of each species as affected by the competitive interaction and the environmental gradient is modelled in a state-space model (the model may also be called a structural equation model or a Bayesian network), which is a general tool for modelling repeated measurements where the variables may change dynamically. The advantage of using a state-space model for modelling longitudinal processes is that that the modelled processes are assumed to operate on the state of unbiased latent variables rather than observed values that may be biased, and that the observed variation is separated into measurement variation and process

variation (Clark, 2007). In the present state-space model (Fig. 1), the studied competitive processes are assumed to act on latent variables that model plant cover and vertical density by two process equations (or structural equations), and the latent variables are coupled to the observed plant cover and vertical density by two measuring equations.

### 3.1 State-space model

In order to simplify the description of the state-space model below, I will focus on the competitive effects experienced by species  $i$  when competing with two other species, but it is important to keep in mind that similar process and measurement equations may be fitted for all investigated plant species or aggregated taxa.

It is assumed that the vertical density of species  $i$  at the end of the growing season ( $t_2$ ) is an increasing function of the plant cover of species  $i$  at the beginning of the season ( $t_1$ ), a function of the plant cover of the other species  $j$  and  $k$  at the beginning of the season, and a function of environmental gradient and the competitive growth of plant species  $i$  is modelled as,

$$P1: Y_{i,t_2,y,r} = a_i(z_r) X_{i,t_1,y,r}^{b_i} \cdot \exp(-c_j(z_r) X_{j,t_1,y,r}^{d_j}) \cdot \exp(-c_k(z_r) X_{k,t_1,y,r}^{d_k}) + \varepsilon_{P1,i,y,r} \quad (1)$$

where the state of plant cover of species  $i$  at time  $t$  in year  $y$  and pin-point frame  $r$  is denoted by  $X_{i,t,y,r}$ , the state of the vertical density of species  $i$  at time  $t$  in year  $y$  and pin-point frame  $r$  is denoted by  $Y_{i,t,y,r}$ ,  $z_r$  is the level of the environmental gradient in pin-point frame  $r$ , and  $\varepsilon_{P1,i,y,r} \sim N(0, \sigma_{P1,i}^2)$  is the residual process variation during the growing season of species  $i$  across different years and pin-point frames. The environment is assumed to affect the vertical density of species  $i$  at the end of the season in two different ways: i) either by affecting growth directly by altering the relationship between the cover and vertical density of species  $i$ , i.e. the function  $a_i(z_r)$ ; or ii) by affecting the competitive effect of species  $j$  and  $k$ , i.e.,  $c_j(z_r)$  and  $c_k(z_r)$ . These functions may either be constant, i.e. the growth or the competitive effect are independent of the environmental gradient, linear functions, sigmoid functions with a parameterised threshold value, or functions with a maximal value at an intermediary value of the environmental gradient (Damgaard 2006), and depending on which functional relationship is best supported by the data, different ecological hypotheses concerning the effect of the environmental gradient on growth and competitive effects may be investigated, e.g. do different species have positive interaction effects on each other at stressful levels of the environmental gradient (facilitation hypothesis)? Or, is there a threshold level of the environmental gradient where the magnitude of the competitive effects suddenly shift (ecotone or niche separation hypothesis)?

It is assumed that perennial species with a relatively large vertical density have a relatively larger plant cover the following year, and the plant cover of species  $i$  in year  $y+1$  is, therefore, an increasing function of the vertical density of species  $i$  in year  $t$ , a function of the vertical density of other species  $j$  and  $k$  in year  $t$  and a function of the level of environmental gradient, and the survival and recruitment the following year of species  $i$  was modelled as,

$$P2: \text{logit}(X_{i,t_1,y+1,r}) = \text{logit}(a_i(z_r) Y_{i,t_2,y,r}^{b_i} \cdot \exp(-c_j(z_r) Y_{j,t_2,y,r}^{d_j}) \cdot \exp(-c_k(z_r) Y_{k,t_2,y,r}^{d_k})) + \varepsilon_{P2,i,y,r} \quad (2)$$

where  $\varepsilon_{P2,i,y,r} \sim N(0, \sigma_{P2,i}^2)$  is the residual process variation from one growing season to the next of species  $i$  across different years and pin-point frames. Correspondingly, as for (P1), different hypotheses on the effects of the environmental gradient on survival and establishment and the plant-plant interactions may be tested. Note that the parameters in both process equations, (P1) and (P2), have the same notation; this does not mean that the parameters of the two processes are identical, but only that the parameters with the same notation have an analogous interpretation.

The unknown states of the latent variables are connected to the observed cover and vertical density by the measurement equations in such a way that the latent cover variables are assumed to be the probability parameter in a binomial distribution,

$$M1: u_{i,t,y,r} \sim \text{Bin}(n, X_{i,t,y,r}) \quad (3)$$

where  $X_{i,t,y,r}$  is the latent variable for cover of species  $i$  at time  $t$  in year  $y$  at frame  $r$ , and  $u$  is the observed number of grid points where the species is hit by a pin in the same pin-point frame with  $n$  grid points.

The latent vertical density variables are assumed to be the mean vertical density in a generalised Poisson distribution,

$$M2: v_{i,t,y,r} \sim \text{gP}(Y_{i,t,y,r}, \delta_{M2,i}) \quad (4)$$

where  $Y_{i,t,y,r}$  is the latent variable for vertical density of species  $i$  at time  $t$  in year  $y$  at frame  $r$ ,  $v$  is as the observed number of times the species is hit in the same pin-point frame, and  $\delta_{M2,i}$  is the degree of under dispersion,  $(\text{variance} / \text{mean})^{-1}$ , compared to the Poisson distribution when measuring the number of times a pin hits a specific species in the pin-point frame.

The outlined state-space model is only one of many possible models from a large class of possible plant-plant interactions models, and the fitting properties of the model should be investigated and compared to other models. A simple model comparison approach is to fit each process equation (P1 and P2) independently using the observed values of cover and vertical density and check the fitting properties of the models using residual plots.

### 3.2 Estimation and statistical inferences

The state-space model may be parameterized using numerical Bayesian methods, where the joint posterior distribution of the model parameters and the latent variables are calculated using MCMC (Metropolis-Hastings) simulations (Carlin and Louis, 1996; Clark, 2007).

When using Bayesian methods, the prior distribution of the parameters and latent variables needs to be specified, and a simple but robust approach is to let all parameters and latent variables, except for the measurement error, arise from a uniform prior distribution within the domain of the parameter. For example, the latent cover variables,  $X$ , are assumed to arise from a uniform prior distribution between specified

minimum and maximum values of cover. The normal measurement error may be assumed to arise from an inverse gamma distribution (Carlin and Louis, 1996).

Using a first order Markov assumption, the likelihood function  $p(X_{i,t1,y1}, Y_{i,t2,y1}, X_{i,t1,y2}, \dots, Y_{i,t2,yn})$  may be described by  $p(Y_{i,t2,yn} | X_{i,t1,yn}) \cdot p(X_{i,t1,yn} | Y_{i,t2,yn-1}) \dots \cdot p(X_{i,t1,y1})$ , where  $p(X_{i,t1,y1})$  is a prior distribution of the latent variable, and since the likelihood function of the measurement equations may be formulated as  $p(u_{i,t,y,r} | X_{i,t,y,r})$  and  $p(v_{i,t,y,r} | Y_{i,t,y,r})$  and the likelihood function of the parameters and the latent variables as  $p(\theta | prior(\theta))$ , then the complete likelihood function of the full state-space model may be specified by multiplying a number of relatively simple conditional likelihood expressions (Clark, 2007).

Statistical inference may be based on the marginal posterior distribution of the parameters and different models may be compared using the deviance information criterion (Spiegelhalter et al., 2002).

#### 4 Intensity and Importance of Competition

The intensity and importance of competition (Welden and Slauson, 1986; Grace, 1991) along the environmental gradient may be calculated using the general method outlined in Damgaard and Fayolle (2010) using the fitted process equations. For example, the intensity of the competition of species  $j$  on species  $i$  during the growing season at a specific level of the environmental gradient may be calculated by

$$-\partial_{X_j} Y_i(X_j, z) \quad (5)$$

and the importance of competition of species  $j$  on species  $i$  during the growing season at a specific level of the environmental gradient may be calculated by

$$\frac{|\partial_{X_j} Y_i(X_j, z)|}{|\partial_{X_j} Y_i(X_j, z)| + |\partial_z Y_i(X_j, z)|} \quad (6)$$

#### 5 Prediction of Plant Community Dynamics

One of the advantages of using a state-space model for modelling the competitive effects is that the observed variation is separated into measurement variation and the two types of process variation. This feature allows quantitative predictions of different ecological scenarios where the uncertainty due to the process error may be included in the quantitative analysis (Clark, 2007). In the present case, the effects of the environmental gradient and intraspecific and interspecific competition on the growth, survival and establishment of the studied species are quantified in the estimated joint posterior distributions of the parameters of the process equations.

The cover of the studied species in year  $y+n$  may be predicted by the joint posterior distribution of the parameters in the process equations:

$$p(\mathbf{X}_{t_1, y+n}^{(p)} | \mathbf{X}_{t_1, y}^{(o)}, z(y), \boldsymbol{\theta}, \sigma_S^2) \quad (7)$$

where  $\mathbf{X}^{(p)}$  and  $\mathbf{X}^{(o)}$  are the predicted and observed covers of the investigated species, respectively,  $\boldsymbol{\theta}$  is location parameters in the two process equations for the investigated species, and  $\sigma_S^2$  is the estimated process variation in the two processes for the investigated species. Using the conditional relationship (9), the effects of different levels of the environmental gradient on the future cover of the studied species may be predicted and the uncertainty of the predictions may be quantified. For example, it may be predicted how the cover of different plant species changes over time as a function of a change in the environmental gradient  $z$ .

### 6 Accompanying Software: Pin-point-calc

In an accompanying *Mathematica* notebook (Wolfram, 2009) called “pin-point-calc”, which may be downloaded from the authors homepage, there is a simple example of simulated cover and vertical density data of two competing species along an environmental gradient. The competition data is both generated and analysed according to the above described state-space model.

The notebook is a demonstration of the application of the model, but it may also be used to: i) illustrate the functional relationships in the model, ii) generate new cover and vertical density data of two competing species along an environmental gradient, and iii) estimate model parameters of cover and vertical density data of two competing species along an environmental gradient using spreadsheet data. Thus, the notebook may be used as a help in the experimental dimensioning of ecological studies by generating data that mimic a specific ecological system, as well as in the analysis of observed competition data.

### 7 Discussion

The presented method for measuring competition in undisturbed natural plant communities allows direct measurements of the competitive effects of neighbouring plants on plant performance and the estimation of parameters that describe the ecological processes of plant-plant interactions during the growing season as well as the process of survival and recruitment between growing seasons. The advantage of partitioning observed changes in plant abundance into processes that take place during different times of the season has previously been discussed by Farrer et al. (2010), who found indications of time-lagged density dependencies and advocated the use of models that use two annual measurements of abundance for discovering facilitation among plants in a grassland community. Additionally, the presented method is suited for testing different ecological hypotheses on competitive interaction along environmental gradients, investigating the importance of competition, as well as predicting different ecological scenarios. Furthermore, the method allows a meaningful investigation of the plant-plant interactions in plant communities that are dominated by perennial species of variable size and where it is difficult to distinguish individual plants, e.g. most grassland ecosystems.

It is argued that the pin-point method is a valuable ecological field-method because it does not disturb the plant community, unlike the popular field-method of using removal or phytometer experiments (Corcket et al., 2003). However, there is a possible disadvantage of the pin-point method that needs to be discussed; i.e. the importance of the spatial arrangement of the plants within the pin-point frame. In the neighbourhood analysis and the phytometer method as well as in the theoretical “zone-of-influence” competition model (Gates and Westcott, 1978; Wyszomirski, 1983; Hara and Wyszomirski, 1994; Weiner et al., 2001; Weiner and Damgaard,

2006), the intuitive appealing notion of a central target plant is used to study competitive interaction between the central target plant and the neighbouring plants. However, the amount of competition “experienced” by the target plant depends on the competition kernel of the neighbouring plants (Berger and Hildenbrandt, 2000), and it is exceedingly difficult to estimate competition kernels of several perennial species of various age and sizes. Furthermore, the spatial position of many real perennial herbal and grass species may seldom be characterised by a single point and the interplant distances are not well defined. Consequently, I think that in most cases, it is more realistic to model the plant–plant interaction at the spatial level of e.g. a pin-point frame using the mean-field assumption, also because the mean-field approach has been demonstrated to give useful and credible results in many empirical competition studies (Bolker et al., 1997; Damgaard, 2004). In contrast, for some plant ecological questions, the information of the pin-position within the pin-point frame is essential; for example when estimating demographic parameters, such as mortality and recruitment rates (Damgaard et al., 2011).

The notion of replacing measurements of local density and biomass with plant cover and vertical density may be used in several other theoretical and empirical plant ecological studies of plant communities where the concept of equally-sized individual plants is inappropriate. However, a real draw-back of the pin-point method is that it is relatively labour intensive, and in order to deal with the important ecological questions that the world will face in the future, we need to be able to collect relevant ecological data more efficiently. Good estimates of the plant cover of different species will probably be standard in the near future using satellite- and other digitised images, but it is uncertain which measure may replace vertical density and be both easily-measurable and correlated to biomass. Never-the-less, for some species, e.g. woody plants, the notion that plant growth may be described as the growth from a two-dimensional surface (cover) to a measure of the three-dimensional structure (vertical density) during a growing season, gives little biological meaning, and in those cases it may be preferable to modify the  $P1$ ,  $P2$ , and  $M1$  equations and replace cover with vertical density.

As mentioned in the introduction, many ecological competition experiments have used either removal experiments or phytometer experiments (Goldberg and Barton, 1992) and, since it is valuable to be able to compare results using different methods, it should be noted that it is possible to compare the results of the presented method with the results of removal experiments by simulating the growth of isolated plants by setting the cover of the other species to zero, or more generally, to simulate the growth of a phytometer by setting the cover of the other species to the cover observed in the matrix population.

For a long time, it has long been argued that in order to advance the scientific field of plant ecology, there has to be more focus on producing ecological predictions rather than simply testing qualitative ecological hypotheses (Keddy, 1990; Cousens, 2001). This argumentation has not been contested, but the developments of the required new methods for making such ecological predictions have either been lacking or have been so technically demanding that they only slowly are being taken up by the scientific community. This paper is an attempt to facilitate the application of more quantitative and predictive methods in plant ecology.

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