Differences between competition kernels and traditional size-ratio based competition indices used in forest ecology

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A B S T R A C T
Both traditional competition indices and competition kernels are used in many studies to quantify competition between plants for resources. Yet it is not fully clear what the differences between these two concepts really are.

For characterising the two approaches we selected two fundamental types of competition indices based on distance weighted size ratios, an additional competition index without distance weighting and developed similar competition kernels. In contrast to the latter approach, competition indices require individual influence zones that for example can be derived from tree crown-radius measurements. We applied these competition measures to two spatio-temporal forest datasets in Europe and one in North America. Stem diameter increment served as observed response variable.

The results of both methods indicated similar performance, however, the use of competition kernels produced slightly better results with only one exception out of six computer experiments.

Although the performance of both competition measures is not too different, competition kernels are based on more solid mathematical and ecological grounds. Particularly the question of defining the local neighbourhood of a given tree seems to be better handled by competition kernels. Consequently, applications of this method are likely to increase. The trade-off of the use of competition kernels, however, is the need for more sophisticated spatial regression routines that researchers are required to program.

Finally, a tabulated summary of differences between competition indices and competition kernels is included.

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1. Introduction

Plant-to-plant competition is a fundamental notion in plant ecosystems and occurs when two or more individuals attempt to utilise the same resources that are limited in supply (Kimmins, 2004, p. 422). Competition sets in motion an interaction between individuals leading to a reduction of the performance (e.g. in terms of survival, growth and reproduction) of at least some of the competing individuals (Begon et al., 2006, p. 132).

In this context, symmetric competition is regarded as an equal sharing of resources among individuals whilst asymmetric competition is an unequal sharing of resources as a consequence of larger individuals having a competitive advantage over smaller ones (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001; Begon et al., 2006, p. 151f.). Symmetric and asymmetric competitions are collectively referred to as mode of competition (Bauer et al., 2004).

On a practical note, Freckleton and Watkinson (1999, p. 286) state that the interpretation of the outcome of competition can critically depend on the way competition is measured. In other words, the selection and use of competition measures by researchers has an important bearing on the way competition is assessed, which in turn may condition the inferences drawn from plant competition experiments (Weigelt and Jolliffe, 2003). Technically competition can be quantified by spatial and non-spatial measures. Spatial competition measures specifically take the locations of plants into account. As a spatial assessment of plant interactions has theoretical advantages and is often more effective particularly in ecosystems with complex structures (Berger and Hildenbrandt, 2000; Martin and Ek, 1984; Weigelt and Jolliffe, 2003), we focus on spatially explicit measures in this study. Spatial competition measures usually amalgamate several primary response variables along with spatial information (Weigelt and Jolliffe, 2003). Indices of spatial competition are based on the nearest-neighbour (NN)
concept of point-process statistics following the idea, that the
immediate neighbours surrounding a subject plant are likely to
have a competitive effect (Schneider et al., 2006). Using this
approach, a competition index is calculated for each plant as a
measure of the competition load exerted by neighbouring plants.
Competition index values typically are associated with the point
locations of the subject plants.

By contrast a different approach producing spatial competition
fields has been developed in the past thirty years. As a consequence
potential competition pressure is known for every point in a
research or monitoring plot. The concept has origins in different
fields of natural sciences including ecological field theory (Wu
et al., 1985; Walker et al., 1989; Li et al., 2000; Pukkala, 1989;
Miina and Pukkala, 2002), shot-noise fields in physics (Baccelli and
Blaszczyszyn, 2001; Baccelli et al., 1997), individual-based modelling
(Adler, 1996; Beazzi et al., 1999; Berger and Hildenbrandt, 2000;
Snyder and Chesson, 2004; Adams et al., 2011; Grabarnik and
Särkkä, 2011) and competition kernels (Snyder and Chesson, 2004;
Hernández-García et al., 2009; Baptestine et al., 2009; Vogt et al.,
2010). Competition kernels belong to a group of so-called interac-
tion kernels that are functions describing how biological processes
such as growth, survival and reproduction of an individual depend
on its own size and the size of and distance to other individu-
als (Snyder and Chesson, 2004; Vogt et al., 2010). Competition kernels
are therefore also related to the idea of dispersal kernels used in
modelling seed and plant dispersal (Bolker and Pacala, 1999;
Nanoo et al., 2010). For all of these approaches, every plant of a
given community emits a signal termed competition signal, impulse,
local competition effect or attenuation function, which is largest at
the location of a plant and decreases with increasing distance from
that plant. At any point in the community the plants’ competition sig-
als can be aggregated additively or multiplicatively to obtain the
total amount of competition pressure at that point. This aggregation
or superposition essentially results in a competition field. Competi-
tion signals are modelled by competition kernels and in the remain-
der of the text we will use this term to collectively refer to all
approaches that have the aforementioned definition in common.
For a good practical overview also refer to García (2014).

The practical use of competition kernels has recently been
much facilitated by the fast development of powerful computer
technology (Berger and Hildenbrandt, 2000). A historic shortcom-
ing of competition kernels has been the effort necessary for their
computation compared to the simpler competition indices. This,
however, is no longer a serious constraint and consequently as
shown above many applications of this modelling technique have
been published in recent years. However, to our knowledge there
has so far not been any study directly comparing both competition
measures and elaborating the merits of both concepts based on
comparable computational principles.

For this generic study, we have selected the most widespread
type of competition indices, i.e. that of size ratios. Size ratios are
very common expressions of competition. They have frequently
been used in modelling and usually involve stem diameters, total
heights and crown sizes (of trees for example) (Biging and
Dobbertin, 1992; Martin and Ek, 1984; Burkart and Tomé, 2012,
Chapter 9). The ratios typically include the size of a competitor
divided by the size of a subject plant. In our study, we used tree
stem diameter as the size variable, since it is the most common pri-
mary tree variable available whilst crown or height measures are
often estimated from stem diameter. However, any other size var-
iable including volume and biomass is possible.

For many competition indices, size ratios are often weighted by
subject-to-competitor distances to account for the decreasing
effects of competitors with increasing distances. There are two
basic strategies of expressing distance weights, as fractions and as
part of exponential functions. The well-known Hegyi competition
index (Hegyi, 1974) is an example of a size ratio weighted by the
reciprocal of the distance. It is a comparatively simple competition
index and has proved to be very effective and robust at the same
time (Daniels, 1976; Radtke et al., 2003; Sandoval and Cancino,
2008; Contreras et al., 2011). Exponentially weighted size ratios
are a little less common as competition indices and a good example
is the competition index by Martin and Ek (1984). By contrast,
exponential competition kernels are frequently used (Schneider
et al., 2006). Asymmetric competition emerges from both the com-
petition indices and the kernels.

A straightforward comparison between competition indices and
kernels is not easy. In this case study, we have compared the
indices to similar fractional and exponential competition kernels
and we devised the kernels for this study so that they share as
many similarities with the indices as possible. In addition we also
included a simple size ratio competition index without distance
weight to find out whether weighting matters at all.

The objective of this paper is therefore to establish and to
characterise the differences between competition indices and com-
petition kernels. Using trees as examples, we apply both concepts
to two different forest ecosystems in Europe and one in North
America.

2. Methods

2.1. Quantifying competition

In this study, we quantified plant-to-plant competition in two
alternative ways, (1) by using the aforementioned two basic types
of traditional competition indices and (2) based on corresponding
competition kernels.

The first method commonly involves (1a) the definition of a zone
of influence (ZOI) and (1b) the actual competition index sensu
stricto (Burkart and Tomé 2012, p. 204). A ZOI is an assumed cir-
cular area around a tree in which it predominantly draws on resources
like light, water and nutrients (Berger and Hildenbrandt, 2000;
Grimm and Railsback, 2005, p. 201). It is a common assumption in
plant ecology that all plants whose ZOIs overlap, interact via compe-
tition for resources (Grimm and Railsback, 2005, p. 201).

Whilst putting this definition into modelling practice, we found
that crown radius is a good proxy of ZOI radius, since this measure
is directly where photosynthetic processes take place. This is why
crown radius has been used before in many studies to define the
growing space of trees (see for example Gspaltl et al., 2012). This
modelling approach predominantly takes care of competition for
light and Genet et al. (2014) demonstrate how the ZOI approach
can be extended to other kinds of competition. To estimate crown
radius, ρ, we exploited the allometric relationship between dbh
crown radius. We collected crown radius and stem diameter data
from the same sites or regions as the main data of this study and
calculated the quadratic mean of four to sixteen measurements
(depending on the number of records available) following a recom-
mendation in Hasenauer (1997). Alternatives to this approach
include the use of crown data of open-grown trees, i.e. trees that
have grown in complete absence of tree competition (Hasenauer,
1997). As no data from open-grown trees were available to us,
we used data from dominant trees as a surrogate and identified
them by quantile regression (Cade and Noon, 2003). Assuming that
ZOIs increase with tree size and are restricted by environmental
resistance (Soares and Tomé, 1999; Burkart and Tomé, 2012, p.
205f.), we selected the Michaelis–Menten saturation curve (Eq.
(1), Michaelis and Menten, 1913; Bolker, 2008, p. 77ff.). The model
implies that ZOI size is different for every tree depending on stem
diameter, dbh, at 1.3 m above ground level. Model parameter a can
be interpreted as the asymptote of the saturation curve thus
defining the maximum possible ZOI size whilst \( b \) is the so-called half-maximum.

\[
r = \frac{a \cdot \text{dbh}}{b + \text{dbh}}
\]

When testing whether a neighbouring tree \( j \) is a competitor of subject tree \( i \), we calculated Eq. (1) twice, i.e. once for the subject tree \( i \) yielding \( r_i \) and once for the potential competitor \( j \) resulting in \( r_j \). Tree \( j \) is a competitor of tree \( i \), if \( r_i + r_j > \text{dist}_{ij} \), i.e. if the ZOIs of both trees overlap. The estimated model parameters that define the ZOIs are provided for the three tree species in Table 1. Fig. 1 illustrates the species-specific relationships between stem diameter (cm) and ZOI radius (m). The curves typically reflect the large demand on space of broadleaved trees compared to conifers, which is also expressed by the values of the asymptote parameter \( a \).

The competition index (denoted by “I” in the upper index) type based on a size ratio with fractional distance weight (denoted by “f” in the upper index) for tree \( i \) and its \( k \) competitors can be expressed by Eq. (2); Hegyi, 1974). The number of competitors, \( k \), is variable and depends on the local tree pattern with respect to tree size and tree locations.

\[
c_i^{f,k} = \frac{k \cdot \text{dbh}_i}{\text{dbh}_{n}^{f} \cdot \frac{1}{\text{dist}_{ij}} + \frac{1}{\text{dbh}_{n}^{f} \cdot \sum_{j=1}^{k} \text{dbh}_j}}
\]

In this context, inter-tree distances are used for two purposes, firstly for identifying competitors and secondly for deriving weights modelling their contribution to the overall competition load of a given subject tree. An important alternative competition index type is the exponentially weighted size ratio (denoted by “e” in the upper index). As a typical example we have used a generalised version of Martin and Ek's (1984) competition index (Eq. (3)).

\[
c_i^{e} = \frac{k \cdot \text{dbh}_i}{\text{dbh}_{n}^{e} \cdot \exp \left( -\frac{\text{dist}_{ij}}{\text{dbh}_i + \text{dbh}_j} \right)}
\]

\[
= \frac{1}{\text{dbh}_{n}^{e} \cdot \sum_{j=1}^{k} \text{dbh}_j} \cdot \exp \left( -\frac{\text{dist}_{ij}}{\text{dbh}_i + \text{dbh}_j} \right)
\]

Finally, to check up on the importance of the distance weight we also used an unweighted size ratio as in Eq. (4). In this case, competitors further away from the subject tree have the same influence as those of the same size nearby.

\[
c_i^{p,k} = \frac{k \cdot \text{dbh}_i}{\text{dbh}_{n}^{p} \cdot \sum_{j=1}^{k} \text{dbh}_j}
\]

As an alternative to the traditional concept of competition indices we applied equivalent competition kernels to the spatio-temporal datasets. There are many different competition kernels and Schneider et al. (2006) provide a good overview. To mimic the idea of fractionally and exponentially weighted size ratio we used a fractional or hyperbolic and an exponential competition kernel that we modified from Adler (1996), Schneider et al. (2006) and Pommerening et al. (2011). This resulted in the local competition effects or signals \( p_i^{f} (\xi) \) and \( p_i^{e} (\xi) \) of a competitor tree \( j \) at any location \( \xi \) in the forest given in Eqs. (5) and (6), respectively.

\[
p_i^{f} (\xi) = \frac{\text{dbh}_j^{\text{ex}}} {1 + (\text{dist}_{ij}(\xi)/\text{dbh}_j^{\text{ex}})^2}
\]

\[
p_i^{e} (\xi) = \text{dbh}_j^{\text{ex}} \times \exp \left( -\frac{\text{dist}_{ij}(\xi)}{\text{dbh}_j^{\text{ex}}} \right)
\]

These competition effects are defined continuously in space, whereas competition index values (Eqs. (2)–(4)) are only defined at tree locations.

To calculate the competition load of a given tree, \( i \), at its location, \( \xi \), following the shot-noise approach (Pommerening et al., 2011; Pommerening and Särkkä, 2013) we additively aggregate the competition effects of all other trees \( j \) according to Eqs. (7) and (8). “K” in the upper index denotes “competition kernel”.

\[
c_i^{f} (\xi) = \sum_{j=1}^{n} p_i^{f} (\xi) = \sum_{j=1}^{n} \frac{\text{dbh}_j^{\text{ex}}} {1 + (\text{dist}_{ij}(\xi)/\text{dbh}_j^{\text{ex}})^2}
\]

\[
c_i^{e} (\xi) = \sum_{j=1}^{n} p_i^{e} (\xi) = \sum_{j=1}^{n} \text{dbh}_j^{\text{ex}} \times \exp \left( -\frac{\text{dist}_{ij}(\xi)}{\text{dbh}_j^{\text{ex}}} \right)
\]

The aggregation, \( c_i^{f}(\xi) \) and \( c_i^{e}(\xi) \), of competition impulses at any point, \( \xi \), in a research plot is a pre-requisite for producing competition load maps as shown in Pommerening et al. (2011). Eq. (7) has similarities with the second term in Eq. (2) after the equal sign except for \( 1/\text{dbh}_j \). Likewise Eq. (8) is similar to the second term of Eq. (3).

Unlike traditional competition indices, competition kernels do not necessarily require ZOIs. As an approximation the competition signals of other trees are aggregated at the location of the subject tree rather than integrated over a larger area. The competition signal for example of a small tree \( j \) with large distance, \( \text{dist}_{ij}(\xi) \), is per definition near zero or zero at the location of tree \( i \) thus competition kernels are mathematically elegant as their ZOIs are automatically included or implicit.

In our study, we computed the \( c_i^{e} \) values with periodic boundary conditions (Illian et al., 2008, p. 184) to reduce edge effects. Note that the value of \( c_i^{e} \) is only dependent on the stem diameter

---

**Table 1**

<table>
<thead>
<tr>
<th>Species</th>
<th>ZOI definition</th>
<th>Eq. (1) with a and b</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech</td>
<td>14.73798</td>
<td>56.861277</td>
<td>0.99182</td>
</tr>
<tr>
<td>Interior Douglas fir</td>
<td>8.92849</td>
<td>20.84195</td>
<td>0.99077</td>
</tr>
<tr>
<td>Norway spruce</td>
<td>6.80408</td>
<td>23.54801</td>
<td>0.99631</td>
</tr>
</tbody>
</table>
of the trees influencing tree $i$ and the distance $\text{dist}_i(j)$ between tree $i$ and tree $j$.

However, the impact of competition load also depends on the size of the affected tree $i$. Therefore, for estimating the effect of the aggregated competition load $c^K_i$ on tree $i$ a transformation of $c^K_i$ is required, which was inspired by Adler (1996). This transformation applies to both kernel types used in this study and combines the size of the affected tree $i$ with its competition load $c^K_i$ and is given by:

$$c^{\text{trans}}_i = \frac{c^K_i \text{dbh}_i + c^K_i}{c^K_i}$$  \hspace{1cm} (9)

By construction, $c^{\text{trans}}_i$ is scaled between 0 and 1. Note that the exponent $z_K$ in Eq. (9) is the strength parameter in Eqs. (5)–(8). In contrast to $c^K_i$, $c^{\text{trans}}_i$ values are only defined at the location of trees $i$, as they require their size information. From Eqs. (5)–(9) it is clear that the effect of competitors is initially separated from that of the subject tree for retaining the option of a continuous random field, which is an important property of competition kernels and the shot-noise approach. Note that this transformation is not a “compulsory” modelling step. It just increases biological plausibility and improves model behaviour. Earlier approaches to modelling competition kernels have not included any transformation.

The parameters of the competition kernel can be easily interpreted: A large value of $z_K$ increases the strength of the competition signal, i.e. the magnitude of the peak. $b_K$, on the contrary, scales the decrease or attenuation of the competition signal with distance $\text{dist}_i(j)$: A large value of $b_K$ stretches the range of the competition impulse. $b_K$ is therefore a range parameter.

In modelling and applying the competition indices we have made an effort to give these traditional competition measures the best possible “starting conditions” for a meaningful characterisation of their performance. To this end, we also considered the same number of three model parameters for both competition models.

2.2 Stem diameter increment as response variable

In this study, we used stem diameter increment as a response and performance variable to assess the quality of competition modelling, i.e. the stem diameter increments estimated by the...
models were compared with the observed stem diameter increments. To link competition with diameter growth, we applied the potential-modifier approach (Newnham, 1964; Botkin et al., 1972). Potential diameter growth was estimated from dominant trees using quantile regression as specified in the section “Parameter estimation”. The competition load a subject tree is facing reduces the potential diameter increment.

Note that we have omitted indices relating to time throughout this paper to simplify the notation of the formulae used for ease of reading.

The potential diameter increment $\text{id}_{i}^{\text{pot}}$ was modelled for each tree $i$ according to the Chapman–Richards growth function (Pienaar and Turnbull, 1973; Zeide, 1993):

$$id_{i}^{\text{pot}} = Akp \times \exp(-k \cdot \text{dbh}) \times (1 - \exp(-k \cdot \text{dbh}))^{p-1} \quad (10)$$

where $A$, $k$, and $p$ are model parameters. In the corresponding Chapman–Richards growth function, parameter $A$ is the asymptote representing the maximum diameter for all trees of a given forest, parameter $k$ scales the growth rate and $p$ determines the location of the inflection point of the growth function, as explained in Pienaar and Turnbull (1973). Parameters $A$, $k$, $p$ and as a consequence $id_{i}^{\text{pot}}$ are the same regardless which of the two competition measures are used. Fig. 3 shows the potential annual diameter increment function according to Eq. (10) in relation to the observed periodic annual increments of the three species investigated.

Finally, both the competition indices and the kernels are separately used as growth modifiers with a view to reduce the potential diameter increment to match the real increment. Depending on whether we work with traditional competition indices or with the corresponding kernels, the modifying term is different. Traditional competition indices need to be wrapped in a modifier function (Pretzsch, 2009, p. 454f.). In preparatory calculations, we identified from several available modifier functions (Ek and Dudek, 1980; Vanclay, 1994; Pretzsch, 2009, p. 454f.) the bracket term of Eq. (11) as the best.

$$id_{i}^{k} = id_{i}^{\text{pot}} \times v_{i} \times \left( \alpha_{i} - \exp\left( -\frac{\beta_{i}}{c_{i}} \right) \right) \quad (11)$$

$\alpha_{i}$ and $\beta_{i}$ are less straightforward to interpret than their kernel counterparts. For the competition kernel Eq. (11) simplifies to Eq. (12).

$$id_{i}^{k} = id_{i}^{\text{pot}} \times v_{K} \times (1 - c_{i}^{\text{trans}}) \quad (12)$$

In Eqs. (11) and (12) $v_{i}$ and $v_{K}$ are further model parameters, which can be interpreted as additional modifiers. These parameters allow us to equate both sides of the equation. Without $v_{i}$ and $v_{K}$ both terms in Eqs. (11) and (12) would only be proportional (Pommerening et al., 2011). Table 2 gives the species-specific values of $A$, $k$, $p$ (Eq. (10)) and $v_{i}$ and $v_{K}$ of (Eqs. (11) and (12)).

2.3. Parameter estimation

For each forest all model parameters were estimated separately. The ZOI radius (Eq. (1)) required for the traditional indices was estimated from stem and crown diameter records by using quantile regression (Cade and Noon, 2003) with $\tau = 0.995$ for beech, $\tau = 0.985$ for interior Douglas fir and $\tau = 0.999$ for Norway spruce calculated with the R Quantreg package.

In contrast to traditional competition indices (Weigelt and Jolliffe, 2003; Biging and Dobbertin, 1992) the estimation of competition parameters $\alpha_{K}$ and $\beta_{K}$ (Eqs. (5)–(9)) must be processed simultaneously with parameter $v_{K}$ (Eq. (12)). This is the main computational difference to traditional competition indices and makes the estimation of competition kernel parameters more sophisticated: For the former it suffices to simply compute the competition indices and in a second step to estimate parameters $\alpha_{i}$ and $\beta_{i}$ of the modifier function in Eq. (11). This is computationally easier to accomplish. By contrast, competition kernels require a complex spatial regression routine that we programmed partly in R (R Development Core Team, 2013) and partly in C++ using the Rcpp package (Eddelbuettel and François, 2011; Eddelbuettel, 2013) to take advantage of a tremendous gain in computation time. For estimating parameters $\alpha_{K}$ and $\beta_{K}$ we used nonlinear regression based on maximum likelihood and the Nelder–Mead simplex algorithm Nelder and Mead (1965).

From periodic diameter growth records the mean annual diameter increments were derived. These were used to estimate the parameters $A$, $k$ and $p$ (Eq. (10); Table 2) through nonlinear quantile regression applying the R Quantreg package.

2.4. Study data

Three tree populations representing a wide range of growth conditions were selected to test the performance of the two alternative concepts of quantifying competition. To obtain clearer results the investigation was intentionally limited to mono-species woodlands to focus on intra-specific competition at this stage.

![Fig. 3. Annual periodic diameter increment, id, over stem diameter, dbh, of the three time series. The grey curves represent the potential annual diameter increment, id^{pot}, as defined in Eq. (10).](image-url)
Table 2
Parameters of $A$, $k$, and $p$ relating to the potential diameter increment model (Eq. (10)) and diameter increment parameters $\alpha_i$ (Eq. (11)) and $\nu_k$ (Eq. (12)) of the three spatial time series. “No distance” means that no distance weight was applied to the index term, see Eq. (4).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Type</th>
<th>Beech</th>
<th>Interior Douglas fir</th>
<th>Norway spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>Parameter in the potential diameter increment model (Eq. (10))</td>
<td>–</td>
<td>75.03706</td>
<td>53.87373</td>
<td>83.35942</td>
</tr>
<tr>
<td>$k$</td>
<td>Parameter in the potential diameter increment model (Eq. (10))</td>
<td>–</td>
<td>0.02700</td>
<td>0.03158</td>
<td>0.03590</td>
</tr>
<tr>
<td>$p$</td>
<td>Parameter in the potential diameter increment model (Eq. (10))</td>
<td>–</td>
<td>3.41053</td>
<td>1.18914</td>
<td>4.09376</td>
</tr>
<tr>
<td>$R^2$</td>
<td>Coefficient of determination of the potential diameter increment model</td>
<td>–</td>
<td>0.93632</td>
<td>0.75335</td>
<td>0.31827</td>
</tr>
<tr>
<td>$\alpha_i$</td>
<td>Parameter in the diameter increment estimation (Eq. (11))</td>
<td>Fractional</td>
<td>1.11986</td>
<td>0.59512</td>
<td>0.29867</td>
</tr>
<tr>
<td>$\nu_k$</td>
<td>Parameter in the diameter increment estimation (Eq. (12))</td>
<td>Exponential</td>
<td>2.12753</td>
<td>0.83389</td>
<td>0.87511</td>
</tr>
</tbody>
</table>

Table 3
Competition parameters $\alpha_i$, $\beta_i$, $\alpha_k$ and $\beta_k$ along with the evaluation criteria Bias, RMSE and AIC relating to estimated diameter increment. “No distance” means that no distance weight was applied to the index term, see Eq. (4).

<table>
<thead>
<tr>
<th>Species</th>
<th>Competition measure</th>
<th>Type</th>
<th>Parameters</th>
<th>Evaluation criteria</th>
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</thead>
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<tr>
<td></td>
<td></td>
<td></td>
<td>$\alpha_i$</td>
<td>$\beta_i$</td>
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<tr>
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<td>Index</td>
<td>Fractional</td>
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<td></td>
<td>Exponential</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>No distance</td>
<td>0.24145</td>
<td>39.52282</td>
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<tr>
<td></td>
<td></td>
<td>Kernel</td>
<td>3.24074</td>
<td>1.05879</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>1.45772</td>
<td>0.52339</td>
</tr>
<tr>
<td>Interior Douglas fir</td>
<td>Index</td>
<td>Fractional</td>
<td>0.95916</td>
<td>5.61447</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>0.93777</td>
<td>16.65314</td>
</tr>
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<td></td>
<td></td>
<td>No distance</td>
<td>0.94979</td>
<td>12.16664</td>
</tr>
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<td></td>
<td></td>
<td>Kernel</td>
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<td>0.55742</td>
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<td></td>
<td></td>
<td>Exponential</td>
<td>0.46267</td>
<td>0.27992</td>
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<td>Norway spruce</td>
<td>Index</td>
<td>Fractional</td>
<td>1.67389</td>
<td>6.73727</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>0.55300</td>
<td>61.43529</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No distance</td>
<td>0.53668</td>
<td>55.54871</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kernel</td>
<td>4.31822</td>
<td>0.20540</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>4.87799</td>
<td>-0.21178</td>
</tr>
</tbody>
</table>

Plots 41–193, 41–194 and 41–700 (0.22, 0.25, 0.25 ha in size) are part of a Swiss spatio-temporal dataset from an even-aged beech (Fagus sylvatica L.) forest at Embrach (longitude: 8°10.22.13', latitude: 47°22.18.32'). The plots were established between 1891 and 1905 and re-measured every 5–10 years until 1991. However, spatial information is available only since 1940. The site has a mean annual precipitation of 1030 mm, a mean annual temperature of 8.3 °C and is located at 590 m a.s.l. (Pommerening et al., 2011).

The multi-aged interior Douglas fir (Pseudotsuga menziesii var glauca (Mirb.) Franco) plots (6 plots with 0.05–0.10 ha in size) are part of a larger study in the Alex Fraser Research Forest in British Columbia (Canada, longitude: 52°3', latitude: 121°52'). The site has a mean annual precipitation of 450 mm, a mean annual temperature of 4.2 °C and is located at approximately 1000 m a.s.l. The plots were established in 1988 in an uneven-aged interior Douglas fir forest and re-measured three times until 2004. For at least 20 years there have been no cuttings in this forest and the site has been protected from large-scale fires which frequently happen in this forest type (LeMay et al., 2009).

16 plots with 0.12 ha in size are part of a replicated thinning experiment in predominantly even-aged Norway spruce (Picea abies (L.) Karst.) at Karlstift (Austria, longitude: 14°45.59.7', latitude: 48°34.50.8'). The site has a mean annual precipitation of 950 mm, a mean annual temperature of 4.5 °C and is located at 930 m a.s.l. (Pommerening et al., 2011). The plots were established in 1964 and re-measured every five years until 2004.

The interior Douglas fir forest can be considered as natural woodland with a complex forest structure while the beech and the Norway spruce woodlands are influenced by human disturbances and have a relatively uniform structure.

3. Results

Table 3 presents the values of the competition parameters $\alpha_k$ and $\beta_k$ which determine the competition signal curves visualised in Figs. 2a and 2b. Particularly Figs. 2a and 2b show that the scales of the signals are influenced by species, size and by the competition kernel type. The use of the exponential competition kernel for example seems to lead to a larger competition range in beech and interior Douglas fir and the values of the signal peaks also vary markedly between kernels. The signal peaks are highest for Norway spruce and smallest for interior Douglas fir and the differences between the species are considerable.

It is also interesting to note that the differences in signal strength between a 10-cm-diameter tree and a 20-cm-diameter tree vary as well. They are largest for Norway spruce followed by beech. In interior Douglas fir, the signal strength of small and large trees is much more similar than with the other two species. This pattern is the same for both kernel types.

The competition signal range is largest for beech whilst it is smallest for Norway spruce.

For beech and Norway spruce absolute Bias, RMSE and AIC relating to estimated diameter increment clearly demonstrate a moderate superiority of the kernel method (see Table 3). However, the differences are small. In interior Douglas fir, however, the evaluation criteria of the indices more or less break even with those of the two kernel methods, i.e. the application of the fractional
competition index leads to better results than that of the fractional kernel. However, in interior Douglas fir the exponential kernel performs slightly better than the exponential competition index. These results are particularly interesting, since the Canadian Douglas fir site is the most structurally diverse and also the most natural of all three study sites.

As far as the three competition indices are concerned, the fractional form of distance weighting always performs best. The opposite tendency is shown by the kernels, the exponential competition kernel always produces better results than the fractional form. Interestingly in interior Douglas fir and Norway spruce using no distance weight leads to a slightly better result than the exponential form of distance weighting.

4. Discussion

Despite more than 30 years of research in the areas of the ecological field theory, shot-noise fields, individual-based modelling and competition kernels and despite their theoretical importance Schneider et al. (2006) as well as Vogt et al. (2010) state that we still know comparatively little about kernel functions. Our study is a contribution towards a better understanding of the differences and similarities between traditional competition indices and competition kernels based on simulation experiments.

Pukkala (1989) and Miina and Pukkala (2002) made a first step in this direction, however, their competition indices and kernels differed markedly and they used multiplicative aggregation of competition signals instead of additive, which was common in early applications of the ecological field theory (Wu et al., 1985). In their study, Miina and Pukkala (2002) concluded that for Scots pine (Pinus sylvestris L.) and Norway spruce in Scandinavia competition kernels were better predictors of tree growth than competition indices and they attributed this to the multiplicative aggregation of competition signals. However, our study using additive aggregation reveals that other factors such as a better handling of neighbourhood effects must be responsible for the better performance of competition kernels in some forest ecosystems.

Our results clearly emphasise that any superiority of competition kernels cannot be justified by evaluation criteria relating to a response variable like plant growth alone. It is necessary to interpret the results in the context of the differences between the two concepts of quantifying plant-to-plant competition highlighted in this and in other papers. To this end we have compiled Table 4 as a summary. Going through these six most important differences it seems evident that the main advantages of competition kernels are in their theoretical foundation: Modifier functions and ZOIs that are not easy to define from a mathematical and ecological point of view. The competition parameters \( K_{\text{e}} \) and \( \mu_{\text{e}} \) are clearly interpretable and help to understand the ecological processes in an ecosystem. Revisiting Figs. 2a and 2b, for example, the wide range of the competition impulses in the beech forest can be explained by the high degree of shade tolerance and shade casting of this species. In a similar way on the dry interior Douglas fir site there is long-range competition for water (LeMay et al., 2009).

Kernel competition produces a field of competition load values that are useful for follow-on modelling like the modelling of offspring. Illian et al. (2008, p. 45, 423), for example, show the connection between competition kernels and spatial statistics. The potential benefits of competition kernels come, of course, at the expense of complex spatial regression routines that need to be programmed by the researcher or by a specialist and require advanced programming skills, because the competition parameters are included in the spatial algorithm.

One reason for the good performance of the competition index with fractional distance weights may be that the term 1/dist, the distance weight, – similar to the corresponding kernel – includes a robust mechanism by which the competition load is weighted depending on how close the competitor is located in relation to the subject tree. However, the exponential weights appear to be less effective than the fractional ones. One should expect that competition indices without such a term perform markedly worse than comparable competition kernels. The results in Table 3, however, show that the differences between the evaluation criteria of the unweighted and the weighted indices are not big at all and in two cases the unweighted competition index even produced better results than the exponentially weighted competition index. Obviously the contribution of the distance weights to the increment estimation should not be overestimated and in some situations they are not necessary.

---

### Table 4
Comparison of the two concepts of quantifying plant competition.

<table>
<thead>
<tr>
<th>Competition index</th>
<th>Competition kernel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Straightforward calculation and parameterisation</td>
<td>Complex parameterisation, requires special programming skills</td>
</tr>
<tr>
<td>Modifier function necessary</td>
<td>No modifier function required</td>
</tr>
<tr>
<td>Competition parameters (of modifier function) difficult to interpret</td>
<td>Competition parameters are easy to interpret and reveal much about plant interaction</td>
</tr>
<tr>
<td>Usually require a ZOI and as a consequence only considers nearest neighbours</td>
<td>Usually does not require a ZOI and as a consequence considers all plants in a given research plot</td>
</tr>
<tr>
<td>Only produces competition values at the location of a plant (variables of subject plant and competitor not separated)</td>
<td>Produces competition fields that can be used for other modelling purposes (variables of subject plant and competitor separated)</td>
</tr>
<tr>
<td>Models asymmetric competition</td>
<td>Models asymmetric competition</td>
</tr>
</tbody>
</table>

### Table 5
Model parameters and performance statistics relating to the simultaneous use of the fractional and exponential competition kernels in Eqs. (5) and (6) and of ZOIs as defined in Eq. (1) and in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Kernel type</th>
<th>Parameters</th>
<th>Evaluation criteria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech</td>
<td>Fractional</td>
<td>3.25341</td>
<td>1.39347</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>2.47535</td>
<td>0.27360</td>
</tr>
<tr>
<td>Interior Douglas fir</td>
<td>Fractional</td>
<td>0.93316</td>
<td>0.87405</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>0.65311</td>
<td>0.36695</td>
</tr>
<tr>
<td>Norway spruce</td>
<td>Fractional</td>
<td>4.06725</td>
<td>0.28802</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>4.87506</td>
<td>-0.21157</td>
</tr>
</tbody>
</table>
One could also argue that the inclusion of distance weights in both competition measures automatically defines an implicit ZOI so that no additional modelling of an explicit ZOI is required. This certainly also seems to be the understanding of competition kernels in Miina and Pukkala (2002), although other authors like Schneider et al. (2006) use additional explicit ZOIs and even found superior results. To check up on this we applied the same ZOI definition that we successfully used for identifying competitors in the case of traditional competition indices to the corresponding kernels as well (see Table 5). The results reveal only marginal improvements (if any). Minor improvements can be reported for two of the fractional kernels and for two of the exponential kernels. These results indicate that competition kernels in fact do not require ZOIs.

It is interesting to note that exponential kernels always performed better than fractional ones whilst fractionally weighted indices on the other hand were superior to exponentially weighted indices.

5. Conclusions

Competition kernels are an intriguing concept and we can expect more interesting findings connected to them in the future. The theoretical grounds – both in terms of ecology and mathematics – are well established and promising. Our results also imply that traditional size-ratio measures of competition can still be used with sufficient success if there are good reasons for not abandoning them. As expected, the local neighbourhood or zone of influence of a tree definitely is the area in a forest stand where most interactions with other trees take place. However, judging by the results of this study the more flexible kernel approach appears to handle these complex interactions better. Since we used generic competition concepts, the authors believe that the findings of this study are also relevant to a wide range of other plant science experiments that make use of competition kernels (e.g. Purves and Law, 2002; Snyder and Chesson, 2004; Vogt et al., 2010). Generic and freely available R packages such as the recently published siplab package (García, 2014) further reduce the computational effort and may contribute to continued systematic research in this area.

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References


