



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



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ARTICLE INFO

Article history:

Received 10 June 2014

Received in revised form 28 July 2014

Accepted 28 July 2014

Available online 29 August 2014

Keywords:

Spatial plant interaction

Ecological field theory

Individual-based modelling

Zone of influence (ZOI)

Potential-modifier approach

Stem diameter increment

ABSTRACT

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)

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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 (Bacelli and Blaszczyzyn, 2001; Bacelli et al., 1997), *individual-based modelling* (Adler, 1996; Bezzi 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 *interaction 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 individuals (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; Nanos 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 signals 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. Competition signals are modelled by competition kernels and in the remainder 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 shortcoming 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; Burkhart 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 primary tree variable available whilst crown or height measures are often estimated from stem diameter. However, any other size variable 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 competition 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 competition 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* (Burkhart and Tomé 2012, p. 204). A ZOI is an assumed circular 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 competition 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, r , we exploited the allometric relationship between dbh and 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 recommendation 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 predominant 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; Burkhart 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

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