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TOWARDS A STANDARD FOR THE INDIVIDUAL-BASED MODELING OF PLANT POPULATIONS: SELF-THINNING AND THE FIELD-OF-NEIGHBORHOOD APPROACH

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ABSTRACT. In classical theoretical ecology there are numerous standard models which are simple, generally applicable, and have well-known properties. These standard models are widely used as building blocks for all kinds of theoretical and applied models. In contrast, there is a total lack of standard individual-based models (IBM's), even though they are badly needed if the advantages of the individual-based approach are to be exploited more efficiently. We discuss the recently developed 'field-of-neighborhood' approach as a possible standard for modeling plant populations. In this approach, a plant is characterized by a circular zone of influence that grows with the plant, and a field of neighborhood that for each point within the zone of influence describes the strength of competition, i.e., growth reduction, on neighboring plants. Local competition is thus described phenomenologically. We show that a model of mangrove forest dynamics, KiWi, which is based on the FON approach, is capable of reproducing self-thinning trajectories in an almost textbook-like manner. In addition, we show that the entire biomass-density trajectory (*bdt*) can be divided into four sections which are related to the skewness of the stem diameter distributions of the cohort. The skewness shows two zero crossings during the complete development of the population. These zero crossings indicate the beginning and the end of the self-thinning process. A characteristic decay of the positive skewness accompanies the occurrence of a linear *bdt* section, the well-known self-thinning line. Although the slope of this line is not fixed, it is confined in two directions, with morphological constraints determining the lower limit and the strength of neighborhood competition exerted by the individuals marking the upper limit.

KEY WORDS: Individual-based model, standard model, phenomenological description, plant population, field of neighborhood, self-thinning, skewed size distribution, mangrove forest.

Introduction. During the last decade, individual-based modeling (Huston et al. [1988], DeAngelis and Gross [1992], Grimm [1999]) has become established in ecology. Due to the enormous increase and general availability of computing power, it became possible to model aspects of populations which had previously to be ignored in population level models because of the constraints of mathematical methodology, the main ones being individual heterogeneity, random variation, space, and local interactions. However, the 'unification' of ecological theory, which Huston et al. [1988] predicted would emerge from the individual-based approach, failed to materialize. In a review of individual-based models (IBM's) of animal populations, Grimm [1999] discusses possible reasons for this situation. He concludes that a lack of appropriate modeling strategies and strategies for analyzing individual-based simulation models is the main reason why more theories have not yet emerged.

We would like to emphasize an additional problem of the individual-based approach: in contrast to classical theoretical population ecology, there are to date no simple, generally applicable *standard* IBM's. In classical theory, there are many standard models which are widely used, e.g., the logistic equation, the Ricker model, the Lotka-Volterra models of competition and predator-prey interactions, and the Holling types of functional response. Even though after closer examination many of these classical standard models may be criticized or even rejected, they are still widely used because they are simple, generally applicable, and have well-known properties. They are generally accepted as building blocks for all sorts of models and thus provide a common framework for many different investigations.

By contrast, most IBM's are more or less developed from scratch. Time and again, modelers re-invent the wheel; they spend huge amounts of time and resources on developing, documenting, explaining and justifying their models. The major obstacle to unification is that the resulting models are hard to compare because of major differences between even the most basic model structures. We are not sure whether this unfortunate situation can in principle be overcome in animal population ecology because it seems hard to find a unified, general description of animals at the individual level (but see Lomnicki [1978], Grimm and Uchmanski [1994], Uchmanski [1999, 2000]). With plants, however, the prospect of a standard IBM seems more promising, because all plant species are sessile, and therefore the interactions between established plants are local and they basically require the same resources (Stoll and Weiner [2000]). A standard IBM of plant populations would have to describe interactions between neighboring plants in a sufficiently detailed but still general way.

In a recent review, Stoll and Weiner [2000] discuss key elements of modeling neighborhood interactions in plants: they should have an explicit location, a basal extension where no other plant can exist (i.e., stem, tussock, rosette), and a zone of influence on which interactions with other plants occur; moreover, the size and distance of neighboring plants should be taken into consideration. The two approaches taking account of these key elements are the 'zone of influence' (ZOI; Gates and Westcott [1978], Gates [1982], Wyszomirski [1983], Czárán and Bartha [1992], Czárán [1998]) and the 'ecological field' (EF; Wu et al. [1985], Walker et al. [1989]) approach. In ZOI models, individuals have a circular zone of influence whose resources they use. This zone grows as the plant grows. Competition between plants occurs when their zones of influence overlap. Although this approach is conceptually very simple, it has a number of snags: the division of resources on the overlapping area, i.e. the mode of interaction, has to be specified by the modeler (e.g., symmetric or asymmetric division of resources (Weiner [1990])), and thus does not emerge from the interaction (Railsback [2000]). And, for small plants, e.g., seedlings, which are completely inside the ZOI of another, adult plant, its position within the zone makes no differences with regard to its performance. Moreover, the resources for which plants compete are often not obvious, and in most cases competition will be for more than just one resource. Regarding this, ecological field models can be seen as improvements of ZOI models. They define a spatially explicit field within the zone of influence which indicates how strongly the plant modifies its environment, e.g. by resource use. This is more realistic than the ZOI approach that implicitly assumes a constant field, but the details of the EF approach are rather complicated, which may be why it has not yet been widely used.

To summarize, there seems to be no standard IBM approach in modeling plant populations. Yet such a standard is urgently needed, not only because of the theoretical unification which might emerge from such an approach, but also because many applied problems of natural resource modeling would benefit from an easy-to-use but still powerful approach. Berger and Hildenbrandt [2000] noticed the lack of such an approach when they started modeling mangrove forest dynamics within the Brazilian-German co-operation project MADAM (Berger et al. [1999], Lara et al. [1999], Thüllen and Berger [2000]). They could not use the grid-based (or cellular automaton) approach (Czárán [1998]), because this would have required more empirical knowledge about local interactions than is available for mangroves. Therefore, they developed a new approach from scratch, the 'field of neighborhood' (FON) approach, which combines the advantages of ZOI, EF and grid-based models while trying to avoid their drawbacks.

Although the FON approach was not designed to be a standard IBM approach for plants, it now seems as if it does indeed have some properties of such an approach: it is conceptually and computationally simple, it is realistic but still general, and, most importantly, it is phenomenological with regard to competition and thus very similar in philosophy to classical standard models which are also phenomenological with regard to the processes they describe.

The purpose of this article is to put forward evidence that, despite its phenomenological design, the FON approach is capable of reproducing realistic phenomena at the population level. To this end, one of the very few general patterns of ecology, the self-thinning line of plant monocultures, is analyzed with KiWi, a mangrove model using the FON approach (Berger and Hildenbrandt [2000]).

2. Self-Thinning. Yoda et al. [1963] have shown that during the so-called self-thinning stage of higher plant cohorts, the logarithms of the averaged biomass are linearly related to the logarithms of the stand density (Harper [1977], Westoby [1984], Silvertown [1992]). The proportionality factor between these two values, the 'self-thinning exponent,' was found to be $-3/2$. This finding was explained geometrically, i.e., by packing evenly sized plants with circular crowns in a plane, and its generality was postulated. Since then, numerous empirical and theoretical investigations have been presented which demonstrate that there are in fact other plant species for which the '$-3/2$ self-thinning rule' applies. However, many examples deviating from this rule have also been found (Weller [1987]). The current consensus is that a fixed value of the self-thinning exponent cannot be specified. However, whether there is a fixed boundary value that cannot generally be exceeded by the slopes of the self-thinning lines is still under discussion, with values of $-3/2$ or $-4/3$ being debated. An allometric explanation is provided for the latter, see, e.g., (White [1981], Enquist et al. [1998]).

The debate about self-thinning is controversial. The value of the thinning exponent is mainly questioned, but also whether the rule really merits this name or does not actually exist (Lonsdale [1990], Weller [1991]), whether the explanation of the linear section of the *bdt* is basically geometric or allometric (Westoby [1984]), and whether the 'line' really is a straight line or a concave curve (Zeide [1987]). Instead of taking up this debate here, we will focus on the following questions: Does the FON approach lead to self-thinning trajectories which can be observed in nature? And, can different parts of the *bdt* be attributed to different stages of development in the plant cohort, i.e., size hierarchies?

3. Methods.

We use the KiWi simulation model (Berger and Hildenbrandt [2000]) which is an application of the FON approach. Since both KiWi and FON are described in detail in Berger and Hildenbrandt [2000], we confine our explanation in the following to the essentials.

3.1 The FON modeling approach.

FON is the abbreviation for 'field of neighborhood.' This particular approach is based on the description of a 'zone of influence' (ZOI) according to which an individual is firstly characterized in terms of its (stem-) position. A circular zone whose diameter increases with the size of the individual surrounds this position. This zone defines the area within which the individual interacts with its environment and with potential neighbors. The extension of the FON approach as compared to the ZOI approach consists in a competition function of field that is defined within the ZOI. This field describes the location-dependent competition strength exerted by the individual on its neighbors and its environment. Assuming that the neighborhood fields of all individuals superimpose, two quantities are important (Figure 1): $F(x,y)$ quantifies the competition strength exerted by the established individuals at position (x,y), whereas F_A is a measure of the competition which an individual encounters from its neighbors. It is summarized from the overlapping parts of the neighborhood fields of all competitors and is related to the ZOI of the individual in focus, i.e., is normalized by the ZOI area A of the target plant. $F(x,y)$ and F_A thus indicate the neighborhood situation for a point and/or an individual defined in terms of the number of neighbors, their size and their spatial configuration.

3.2 The KiWi simulation model. KiWi applies the FON approach to the description of mangroves. The radius of the zone of influence is described by the expression:

$$a \cdot rbh^b \tag{1}$$

where rbh stands for the stem radius in breast height. The parameters a and b were first chosen arbitrarily. The neighborhood field within the stem is by definition equal to 1. Outside the stem, it decreases exponentially to the minimum value $FON_{\min}$, which is reached at the edge of the ZOI (Figure 1). KiWi uses only one level of description for all trees, regardless of size (Berger and Hildenbrandt [2000]). This compact handling is possible since the fields of neighborhood completely describe the competition effect on all demographic processes. Environmental factors such as pore water salinity or soil moisture are each described in separate description levels.

The growth of the trees is described according to Chen and Twilley [1998]: the annual increment in stem diameter is calculated using a sigmoid function which is valid for optimal environmental conditions. Damaging environmental factors are taken into account using correction factors. In addition to the salinity factor introduced by Chen and Twilley [1998], KiWi uses a correction factor for neighborhood competition (Berger and Hildenbrandt [2000]). It is equal to 1 if the tree has no competing neighbors. Otherwise, it decreases with increasing competition strength F_A. If $F_A \geq 0.5$, the correction factor is zero, which means the tree cannot grow. Obviously, growth is also influenced by

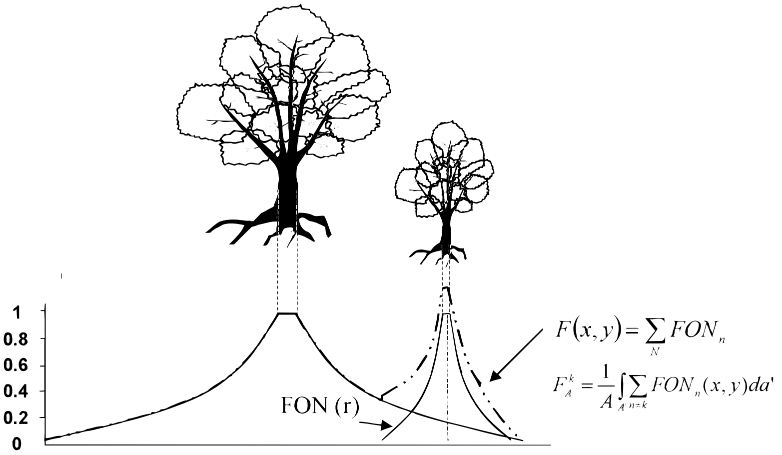

FIGURE 1. The *Field of Neighborhood* describes the competition strength that an individual exerts on its neighbors or on its environment. $F(x,y)$ indicates the competition strength of all established trees at the location (x,y). F_A records the competition that an individual encounters from its neighbors. A is the area of the zone of influence of the target plant.

other ecological factors such as salinity, nutrients and inundation. However, in this work we wish to concentrate on the effects of intra-specific competition. We therefore assume the dominant nutrients and moisture content of the sediment to be optimal. The pore water salinity may be benign, at ≤ 40 PSU.

Virtually nothing is known about the mean age of mangrove trees. References vary between 70 and 350 years for different species (Burns and Ogden [1985], Chen and Twilley [1998]). Therefore, mortality is not linked directly to the tree age in KiWi. Instead, we assume that the probability of dying will increase with reduced growth. In order to enable a tree to recover after a period of bad growth years, this relation is represented in a “memory function” (Berger and Hildenbrandt [2000]). According to this function, a tree dies if its mean stem diameter increase within 5 years is less than half the average increase it would have achieved under optimal conditions.

3.3 Simulations. Using the growth parameters of *Rhizophora mangle* (Chen and Twilley [1998]), the development of a mangrove cohort was simulated. The initial stem diameter of all trees was

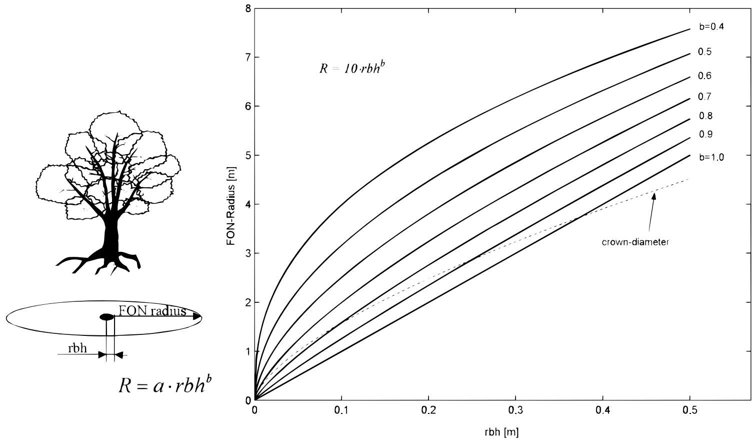

FIGURE 2. The FON radius (R) depends on the stem diameter of the tree. The curve of the crown diameter was calculated after Fromard et al. [1998].

1 cm. They were randomly distributed at a plot 1 ha in size. The initial density was 2,000 individuals per hectare. The influence of individual competition strength on the dynamics of the population was investigated. The competition strength was varied by the form and extension of the neighborhood field. For this, the parameter b of equation (1) was varied between 0.4 and 1.0, whereas $a = 10$ was held constant. Figure 2 shows that the FON radius increases if b decreases. Moreover, at a specific distance from the stem, the competition strength will be stronger the lower b is. For each b value, 50 simulations were carried out. The number of individuals and their stem diameter were registered in each simulation year. The biomass distribution of the trees was calculated on the basis of these data according to Fromard [1998]; Berger and Hildenbrandt [2000].

4. Results. As a result of the competition between the growing trees, the distribution of the stem diameters in breast height (*dbh*) widens in the course of development. Depending on their local neighborhood situations, some trees will be unobstructed at least for a while, and others will be slowed down. It was expected that a size hierarchy would develop, in which a few large trees would dominate many smaller ones as a result of this process. This characteristic of asymmetric com-

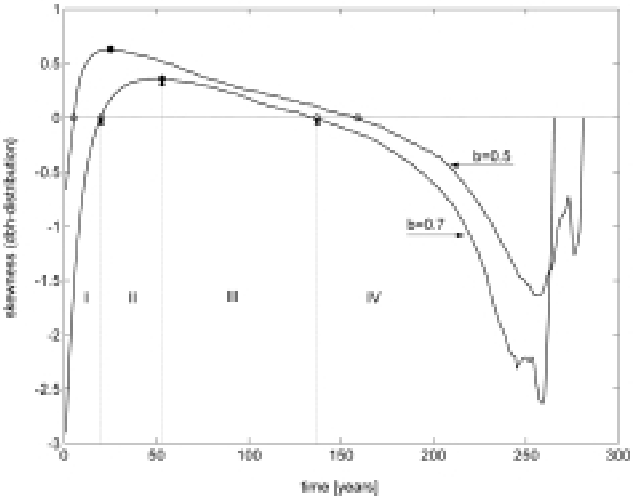

FIGURE 3. The skewness of the *dbh*, distribution over time. The curves for $b=0.5$ and $b=0.7$ were drawn as examples. The qualitative shape of the curves is the same for other values of b.

petition is regarded as typical of self-thinning populations, e.g., Adler [1996], Davie [1999]. It can be tracked by means of the skewness (third moment) of the stem diameter distribution. If skewness is negative there is a minority of small trees in the stand compared to a majority of larger ones. Positive skewness indicates that the cohort consists of a few large trees and many smaller ones.

Figure 3 shows the dynamics of the skewness for $b = 0.5$ and 0.7. The shape of these dynamics is identical for the entire range of b examined here. The first values were computed after one year of growth. They show that, at the beginning of the growth period, only a few trees are more strongly hindered in their growth than their neighbors. However, this negative skewness is quickly reduced during the growth process. A period follows in which the *dbh* distribution is positively skewed, as initially expected. The duration of this stage and the maximum skewness achieved increase with decreasing b which corresponds to, as explained above, increasing competition strength. An interpretation of the dynamics after 250 years is not feasible. The densities are so small here that any death of an individual can lead to a change of the skewness sign.

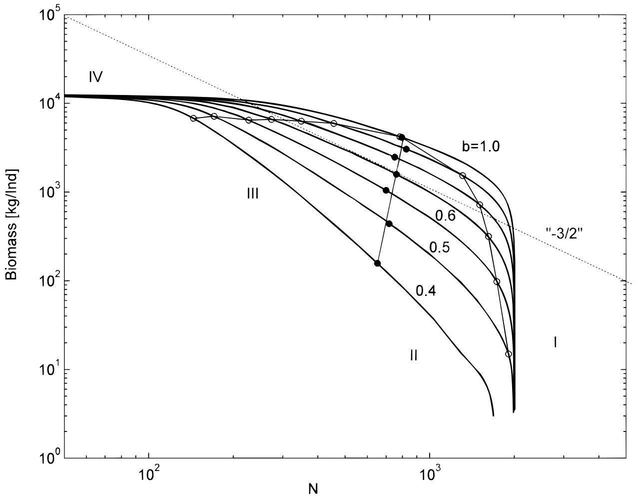

FIGURE 4. The biomass-density trajectories for different b values. The dots mark the crossover and the maximum skewness of the *dbh* distribution. They indicate different stages of the simulated development of the population, see Figure 3.

To relate the modification of the population structure presented in Figure 3 to the self-thinning of the cohort, the self-thinning trajectories for different competition strengths are plotted in Figure 4. The trajectories show the number of surviving individuals and their mean biomass during the development of the cohort. Since the first results were registered after one year, the *bdt* resulting from $b = 0.4$ does not originate from the same point as all others. Although all simulations were initialized with the same number of individuals, the high competition strength of the individuals realized in this case reduces the number of trees established compared to the scenarios with higher b values. In turn, the qualitative shape of the curves is similar for all b values examined and describes the stages of development of a cohort as they are described in textbooks, e.g., Begon et al. [1991], Silvertown [1992]. The direction of the trajectories, i.e., the course of time, is from bottom right to top left.

The first section is marked by a rapid increase in the biomass of the individuals. Mortality is not significant in the initial years because most plants do not experience any neighborhood at all. The onset of mortality due to the onset of local competition is indicated in the trajectory by the 'left turn,' and occurs more pronouncedly the greater the competition strength as specified by smaller b-values. The linear section of the trajectory that follows is the classical self-thinning line. For $b = 0.7$, a line with the 'classical' slope of $-3/2$ is attached to the trajectory. This line shows that stronger competition strength results in steeper slopes.

The trajectory bends away from the linear section as soon as the overall potential growth rate decreases to zero. Thus, the natural limitation of growth of the individuals becomes visible. The last curve section, parallel to the x-axis, indicates the maximum mean biomass that is attainable. Since the latter is determined by the growth parameters and not by the competition strength, it is identical for all b-values. However, the density at which the individuals can achieve this biomass increases with b. For this reason, the maximum absolute biomass increases if the individual competition strength becomes smaller. Assuming that there is no other resource limitation, the maximum absolute biomass consequently defines the optimal stand density of the area.

5. Discussion. We presented an analysis of self-thinning in a mangrove model, KiWi, which is based on a new approach to individual-based modeling of plant population dynamics, the FON ('field of neighborhood') approach. Since FON is a phenomenological approach, it was not clear whether it would produce realistic dynamics and structures at the population level. The results show that FON is indeed capable of reproducing such emergent properties. The self-thinning trajectory of growing plant monocultures was reproduced in an almost textbook-like manner.

To discuss the relationship between population structure and the development of the cohort, the crossover points (I and IV in Figure 3) and the maximum skewness of the *dbh* distribution (III) are marked in the *bdt* (Figure 4). They subdivide the trajectories into four characteristic sections. Section I contains the 'pure growth stage' of the cohort. Only a few trees are hindered in their growth such that they die by the end of this section. Sections II and III are defined by the crossover points and the maximum of the skewness dynamics. They mark the stage of 'asymmetric competition' and hence the process of self-thinning in the classical sense. However, whereas in Section II the logarithmic relation between the biomass increase and the density loss is not linear, Section III corresponds to the 'self-thinning line.' It is delineated by the maximum and the second crossover point of the skewness. The fourth section of the *bdt* is characterized by only little growth because the plants achieved almost maximum size.

Gates [1982] performs modeling experiments similar to those presented here, but uses the ZOI approach and does not consider mortality, i.e., self-thinning. Like us, he first finds negative skewness which then changes to zero and positive values. Weiner and Thomas [1986] review experiments on growth and self-thinning in plant monocultures and conclude that "during the development of an even-aged monospecific stand, size inequality increases over time until the onset of self-thinning, then inequality decreases as self-thinning progresses."

The results hitherto discussed can be summarized as follows:

1. The occurrence of self-induced mortality is not completely bound to a positive skewness of the stem diameter distribution.

2. In the first stage of asymmetric competition (Section II), the skewness of the size distribution increases despite the high mortality rate of the smallest trees. This explains the substantial differences in the growth rates of the residual trees.

3. The classical self-thinning line (Section III) is characterized by a decrease in the skewness of size distribution. Consequently, its occurrence is linked to the homogenization of the stem diameters of the surviving individuals.

4. The slope of the thinning line is determined by the individual competition strength. The greater the maximum (positive) skewness of the diameter distribution, the steeper the slope of the thinning line.

Since these results are of a qualitative nature, they are valid for all trajectories generated by the model. Now, by varying the FON parameter b, almost any slope of the self-thinning line could be achieved. At first, we chose its value arbitrarily but looked for a limitation of the range that could be adequate for the description of the development of *R. mangle* cohorts under optimal conditions. Since for this purpose no survey data are available, a direct parameter estimation is not possible. However, the field of the potentially possible curves is indirectly limitable. For this purpose, the crown diameter was drawn in Figure 2 depending on the stem radius (Fromard et al. [1998]). If we assume that this diameter determines the minimum space a tree requires, then b parameters which result in very small FON diameters are unrealistic, as they lead to tree densities per area which cannot naturally occur. For the biomass-density trajectories in Figure 4, this means that no curves are allowed for $b > 0.7$. For this reason, the following general hypothesis is produced with regard to the slope of the self-thinning line for cohorts that develop under natural, optimal conditions: the slope of the self-thinning line is downwardly limited by the physical extension of the individuals (and, therefore, morphological constraints of the species) and upwardly by the individual competition strength. In this case, the morphological boundaries need not always be directly perceptible. A limitation is possible over the entire root area, for example. The curves in Figure 4 refute the thesis of a universal, fixed self-thinning factor. Depending on competition strength and the minimum area claim of the individuals, different self-thinning lines must be expected.

Although FON and KiWi were not at all designed to perform theoretical studies like that of self-thinning presented here, we were surprised by how well essential features of self-thinning were reproduced and how easy it was to examine features of the self-thinning trajectories with regard to individual characteristics, e.g., competition strength. This 'natural' performance of our model led us to wonder whether FON could possibly be a candidate for a standard in the individual-based modeling of plant populations. It seems as if realism and the phenomenological description of local interactions are combined in just the right balance needed for a standard model. Of course, a model can never be declared a standard model by its constructors but has to be pronounced a standard by the scientific community. Therefore, our goal here was not to immodestly declare the FON approach as a standard model, but to pinpoint two essentials of individual-based modeling which have not previously been considered explicitly: First, individual-based modeling needs, besides models which are tailored to specific situations, standards. This is not only important for theoretical unification, but also for applied issues, such as modeling natural resources. Applied models could be constructed much more effectively if standard approaches with known properties existed. A model similar to KiWi could, for example, easily be constructed for grassland dynamics. And second, a standard model would, at least partly, have to rely on a phenomenological description of key processes in order to be generally applicable. What we tried to show is that such a description is possible not only in classical population level models, but also in individual-based models.

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