Chapter 3
Modeling Aboveground–Belowground Interactions

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3.1 Introduction

Aboveground–belowground interactions are complex (Wardle 2002), because they include nonlinear relationships, interconnected feedbacks, scale-dependent dynamics, and an intermediate number of constituents. Large numbers of constituents can be averaged, small numbers can be addressed individually, but the study of intermediate numbers can be very challenging in practice (Schaffer 1981). Models can help to capture the complexity of aboveground–belowground interactions (van der Putten et al. 2009). They offer a systematic approach to explore consequences of assumptions where data are scarce, they provide mechanistic, bottom-up system information that might not be apparent from empirical top-down system samples, and they can be used to identify knowledge gaps and generate testable hypotheses. Nevertheless, models are purposeful simplifications of reality and thus always simplify and always need a specific purpose or question to guide the simplification. This means that models are not a universal remedy for aboveground–belowground complexity and need to be applied wisely and where possible in conjunction with empirical approaches to shed light on aboveground–belowground interactions.

Questions are thus at the heart of all modeling endeavors. Many of the questions addressed by aboveground–belowground models are not exclusive to modeling, but models can often include more factors, more interactions, more perspectives, and more types of data (e.g., qualitative data) than many empirical approaches (Meyer et al. 2009a). Hence, questions of aboveground–belowground models are typically

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derived from the more complex realms of aboveground–belowground community ecology, for instance:

- How do all aboveground and belowground functional groups interact to influence plant performance (Schröter et al. 2004)?
- What is the relative importance of the different relationships in an aboveground–belowground community (Eisenhauer et al. 2012; Meyer et al. 2012)?
- Which aboveground–belowground effects are direct and which are indirect (Veen et al. 2010)?
- What are important thresholds in community dynamics given certain aboveground–belowground interactions (Fibich et al. 2010)?
- What are the underlying (physiological) mechanisms of aboveground–belowground interactions (Biondini 2001)?
- How does global change influence the interactions and feedbacks in aboveground–belowground communities (Sistla et al. 2014)?
- How are trophic interactions related to competitive interactions (Körner et al. 2014)?
- How do spatial relationships influence aboveground–belowground interactions (Levine et al. 2006)?
- How do individual properties of aboveground organisms affect plant and herbivore performance belowground and vice versa (Meyer et al. 2009b)?

These questions are reflected in the aims of the models.

Aims of models can generally be description, explanation, or prediction (Grimm and Railsback 2005, p. 36). Descriptive models identify and represent the characteristic properties of the system at hand. They can be used to demonstrate principles for the purposes of clarifying the corresponding relationships. In aboveground–belowground community ecology, descriptive models may, for instance, aim to identify and visualize aboveground and belowground functional types and their interactions (Schröter et al. 2004). Models that aim at explanation often implement hypotheses about a system to test them by model analysis. This can involve several model scenarios representing alternative hypotheses which are then compared by means of the respective model outputs. For example, such a model could be used to implement and test the hypothesis that aboveground trophic levels are more important than belowground trophic levels for plant performance (Meyer et al. 2009b). Models that aim to make predictions usually require the greatest level of detail and thus large amounts of data. Validation of model results against independent data is very important for predictive models, because only successfully validated models generate credible predictions. Predictive aboveground–belowground models are, for instance, common in crop sciences, where yields are predicted depending on pest species dynamics (Tixier et al. 2013).

Many model types are available to pursue the different questions and aims of community ecology studies (Fig. 3.1). Here, the typology of van der Putten et al. (2009) is used as a starting point and extended by two model types: statistical models and functional–structural models (Table 3.1). Conceptual models and graphical models describe and visualize relevant components of a system and their

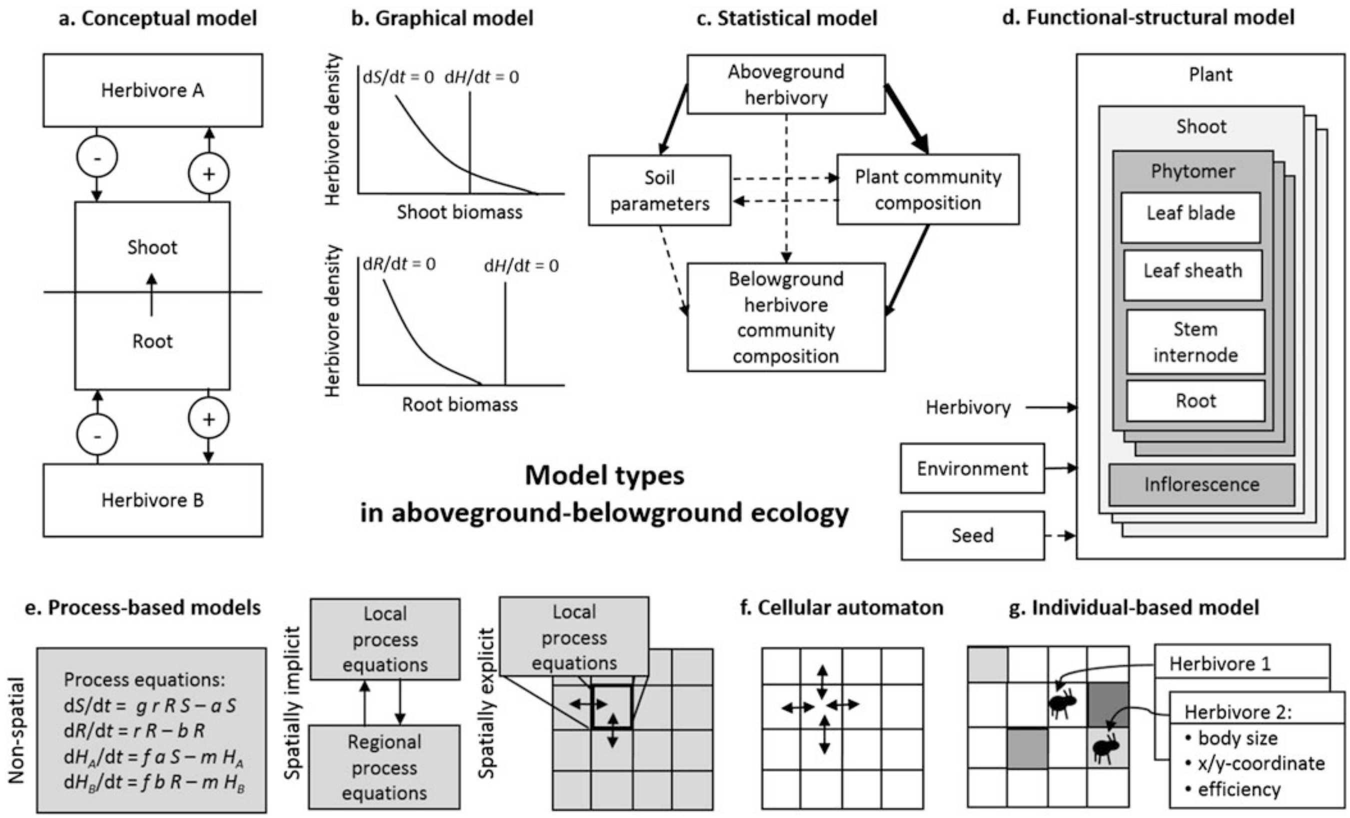

Fig. 3.1 Examples visualizing the different model types in aboveground–belowground ecology. (**a**) Conceptual model consisting of boxes for factors or actors or state variables and arrows for processes. Plus signs indicate positive effects and minus signs indicate negative effects. (**b**) Graphical model with zero-net-growth

relationships. Graphical models additionally rely on mathematical models and often take the form of isocline graphs. Statistical models describe relationships and can be used to test hypotheses and make predictions within the limits of the specific statistical method. This chapter only considers statistical models that go beyond simple tests such as structural equation models (Eisenhauer et al. 2015). Functional–structural models are also called plant growth models and simulate plant architecture arising from physical and/or physiological processes (Guo et al. 2011). They often take an object-oriented approach to simulate plant modules. Process-based models capture relevant processes in equations that can be solved analytically or numerically. Due to their mechanistic nature, they are often applied for explanation and prediction. Spatially implicit models only address rough spatial differentiations, such as local versus regional processes. Spatially explicit models consider spatial relationships at much greater detail. For instance, in cellular automata, neighboring cells influence the state of a cell. In other grid-based approaches, all cells can influence any one cell depending on distance and location (Meyer et al. 2010). Individual-based models or agent-based models simulate interactions between individual organisms giving rise to population and community dynamics (Grimm and Railsback 2005). This bottom-up approach is opposite to the top-down approach of most process-based models that impose population and community dynamics and

Fig. 3.1 (continued) isoclines that show combinations of x- and y-values for which the model produces zero net growth of root biomass R, shoot biomass S, or herbivore densities H. (**c**) Statistical structural equation model inspired by Veen et al. (2010). Bold arrows correspond to significant effects, dashed arrows to hypothesized but non-significant effects, and arrow width reflects effect size. (**d**) Functional–structural model inspired by Groot and Lantinga (2004). Boxes represent objects in the model, solid arrows indicate effects, dashed arrows indicate transformations. Each object can perform actions. (**e**) Process-based models formalize processes with process equations (grey boxes) corresponding to the arrows in conceptual models (see **a**). Process-based models can be nonspatial (left grey box), spatially implicit (centre grey boxes), and spatially explicit (right grey boxes). The nonspatial model consists of a possible set of equations for the processes in the conceptual model in panel (**a**); S: shoot biomass, R: root biomass, H_A: density of herbivore A, H_B: density of herbivore B, t: time, g: conversion rate of root growth into shoot growth, r: root growth rate, a: proportion of shoot biomass eaten by herbivore A, b: proportion of root biomass eaten by herbivore B, f: conversion efficiency of shoot or root biomass eaten into herbivore individuals, m: mortality rate of herbivore A and B. Spatially implicit process-based models couple a set of process-based equations for local dynamics with a set of equations for regional dynamics. Spatially explicit process-based models (including reaction–diffusion models) are usually based on a grid whose cells contain local process equations and equations on interactions with neighboring cells. The grid represents the regional dynamics. (**f**) Cellular automata are based on grids whose cells have states such as presence/absence of species or amounts of biomass. The cells interact with their direct neighbors according to predefined transition rules. These rules can (but do not have to) be formalized as equations. Thus, cellular automata include spatially explicit process-based models if these are based on a grid (see **e**). (**g**) Individual-based models or agent-based models simulate individual organisms as objects (Herbivores 1 and 2). Objects have properties whose values change from individual to individual. Individuals interact with each other and with their environment. The environment is often implemented as spatial grid cells that can have different properties, e.g., amount of vegetation (grey shades). In contrast to cellular automata, interactions can stretch beyond the direct neighbors and organisms are not only represented as states, but as objects with properties in individual-based models

Table 3.1 Overview of model types, basic model aims (description, explanation or prediction), selected examples from aboveground–belowground community ecology, and the modeled interactions in these examples[a]

Model types[b]	Model aims[c]	Examples	Modeled interactions[d]
Conceptual models	Description (explanation)	Cahill (1999)	PC
		Schröter et al. (2004)	PT_2^2M
Graphical models	Description (explanation)	Fibich et al. (2010)	PT_1C
Statistical models	Description (explanation) (prediction)	Lamb (2008), Lamb and Cahill Jr. (2008), Lamb et al. (2009)	PC PCF
		Eisenhauer et al. (2012)	PT_1CF
		Veen et al. (2010)	PT_1^1
Functional–structural models	Description (explanation) (prediction)	Drouet and Pagès (2003, 2007), Postma and Lynch (2011)	P
		Groot and Lantinga (2004)	PT^1
Process-based models	(Description) explanation prediction	Cheeseman (1993), van Wijk (2011), Feller et al. (2015), Eid et al. (2016)	P
		Asaeda et al. (2000, 2001), Lazzarotto et al. (2009)	PC
		Sistla et al. (2014), Biondini (2001), Ruget et al. (2002), Brisson et al. (2003), Scheiter and Higgins (2013)	PT_1
		Van Noordwijk and Lusiana (1998)	PT^1CF
		Bever (2003)	PT_1C
		Tixier et al. (2013)	PT^2C
		Goudard and Loreau (2008)	PT^2
		Jia et al. (2009)	PT_1^1
		Willocquet et al. (2008)	PT_1^1C
Spatially implicit process-based models	(Description) explanation prediction	Huston and DeAngelis (1994)	P
Spatially explicit reaction–diffusion models	(Description) explanation prediction	Barbier et al. (2008)	PCF
Spatially explicit cellular automaton models	(Description) explanation (prediction)	Levine et al. (2006)	PT_1
Individual-based models	Description explanation (prediction)	Zhang et al. (2013)	PCF
		Bonanomi et al. (2005)	PT_1
		May et al. (2009)	PT^1C
		Körner et al. (2014), Pfestorf et al. (2016)	PT_1^1C
		Meyer et al. (2009b, 2012)	PT_2^2M

[a] Only those examples are included that explicitly consider root–shoot interactions (and not only plant–resource interactions)

[b] Based on van der Putten et al. (2009) except for statistical models and functional–structural models

[c] Parentheses indicate less importance

[d] *P*—pure root–shoot interactions inside the plant, T_x^y—trophic interactions between plant and *x* belowground trophic levels and *y* aboveground trophic levels, *C*—competitive interactions among plants, *F*—facilitative interactions among plants, *M*—mutualistic interactions between plants and mutualists such as earthworms

simulate matter or energy fluxes instead of individual organisms (Schröter et al. 2004). Individual-based models are most often used for explanation, i.e., to demonstrate principles and analyze scenarios.

The origins of aboveground–belowground models are very diverse. Whereas many empirical aboveground–belowground studies have arisen from pure aboveground studies (Chap. 2), aboveground–belowground models are not necessarily extensions of aboveground approaches. Rather, it is the model type that influences the genesis of an aboveground–belowground model. For instance, functional–structural aboveground–belowground models have more commonly arisen from pure root architecture models than from pure aboveground models (Guo et al. 2011; e.g., Postma and Lynch 2011). Process-based aboveground–belowground models often originate from classical physiological models that early on have considered interactions between roots and shoots (e.g., Cheeseman 1993). In cases where aboveground–belowground process-based models arose from food-web models, it is more common that these food-web models capture only belowground interactions and no aboveground interactions (e.g., de Ruiter et al. 1995). Some process-based models (e.g., Bever 2003) and all graphical aboveground–belowground models (e.g., Fibich et al. 2010) are based on classic models from ecological theory such as the Lotka–Volterra model or the Rosenzweig–MacArthur model. These models are not specific to aboveground or belowground communities and neither are conceptual or statistical models. Individual-based aboveground–belowground models are an exception to this rule, because they more commonly originate from models that focus on aboveground interactions (e.g., May et al. 2009; as basis of Körner et al. 2014).

In the following, first, a review of model applications that link aboveground and belowground interactions will show that there are only relatively few approaches thus far. Then, promising avenues for future application of models in aboveground–belowground community ecology will be delineated. A practical guide on how to model aboveground–belowground interactions will conclude this chapter.

3.2 Models of Aboveground–Belowground Interactions

Application examples of models of aboveground–belowground interactions are not as manifold as the diversity of available model types might suggest. The examples compiled here (Table 3.1) are representative of all the available models, with a bias towards studies that involve trophic rather than non-trophic interactions with many rather than few trophic levels. This focus on trophic interactions reflects the aboveground–belowground perspective adopted in this book. In the following, first, simple shoot–root interaction models will be explained, because they are the core of all models compiled in this chapter. Then, models involving trophic interactions aboveground or belowground will be introduced. Finally, it will be explained how non-trophic interactions such as plant–plant and plant–mutualist interactions are integrated into aboveground–belowground models, either alone or in combination with trophic interactions.

3.2.1 Shoot–Root Interactions

Shoot–root interactions are the simplest form of aboveground–belowground interactions and are thus the target of most aboveground–belowground models ("P" in Table 3.1). These models simulate allocation of plant biomass to shoot and root at various levels of resolution. Most functional–structural models are restricted to pure shoot–root interactions. Accurate simulation of plant structure already requires great levels of detail, so computational capacities for additional trophic or non-trophic interactions are limited. Functional–structural models are often more highly resolved belowground than aboveground (e.g., Postma and Lynch 2011). However, most shoot–root allocation models are mechanistic process-based models. One of the classic shoot–root allocation models is SIMPLE (Cheeseman 1993), which simulates carbon and nitrogen fluxes between shoot and root compartments and can be used to test physiological hypotheses. Eid et al. (2016) modeled shoot and root growth as a function of photosynthesis, respiration, mortality, and translocation from shoots to roots. With his ecohydrological shoot–root-allocation model, van Wijk (2011) explains plant rooting strategies in dry ecosystems with the maximization of transpiration. Taking a systems biology approach, Feller et al. (2015) simulate aboveground–belowground interactions as exchange of sugars and phosphate between shoot and root compartments to explain the dynamic adaptation of shoot–root ratios in response to environmental conditions.

3.2.2 Trophic Interactions

Trophic interactions have been considered as implicit effects and as explicit interactions belowground and aboveground ("T_x^y" in Table 3.1). Trophic interactions are much more commonly addressed in the form of implicit effects than as explicit dynamic interactions in aboveground–belowground models. Implicit effects are given when, for instance, grazing or cutting aboveground biomass is simulated as biomass reduction without feedbacks to the herbivore organisms. Taking an object-oriented functional–structural modeling approach, Groot and Lantinga (2004) explored the effect of cutting on plant growth and digestibility. They simulated plant morphology as aggregation of objects such as leaf blade, leaf sheath, stem internode, and root and found good agreement between field experimental data and model outputs. Implicit belowground effects have been modeled in the form of plant–soil feedback effects (Bonanomi et al. 2005; Levine et al. 2006). Implicit aboveground and belowground effects have been taken into account in a process-based model of mowing and root fragmentation effects on an invasive weed species that aimed at identifying the management interval that maintains shoot biomass at a constant level (Jia et al. 2009). Explicit belowground interactions are part of the biogeochemical ecosystem model SCAMPS that simulates interactions between plant and microbial pools via soil organic matter (Sistla et al. 2014). When the study systems become more complex, direct and indirect trophic effects can be revealed with statistical structural equation models. For instance, Veen et al. (2010) differentiate between alternative hypotheses on direct and indirect effects of aboveground vertebrate herbivory on belowground nematode herbivores. This study also exemplifies how effects (here of aboveground herbivores) and responses (here of belowground herbivores) can be studied, linking aboveground and belowground interactions.

3.2.3 Plant–Plant Interactions

Non-trophic interactions between neighboring plants can have negative (competition) or positive (facilitation) effects on the interacting plants. In their simplest form, plant–plant interactions have been combined with shoot–root interactions without considering any trophic interactions (“C” for competitive interactions, “F” for facilitative interactions, and “CF” for both in Table 3.1). Conceptual models on competitive asymmetry (Cahill 1999) have inspired a statistical structural equation model that shows that root competition—even when it is very intense—is unimportant for plant community structure (Lamb and Cahill 2008). Rather, aboveground competition affects plant diversity (Lamb et al. 2009). A more mechanistic approach has been adopted in the process-based model PROGRASS (Lazzarotto et al. 2009). It simulates belowground competition of grass and clover for nitrogen and can be used to study effects of management such as fertilization and harvesting schemes. One of the rare aquatic examples in aboveground–belowground modeling captures the competition between macrophytes and different functional types of phytoplankton (Asaeda et al. 2001). The spatial nature of competitive and facilitative interactions is reflected in the zone-of-influence approach adopted to simulate facilitation and size-symmetric and size-asymmetric competition aboveground and belowground (e.g., Zhang et al. 2013). Another spatially explicit aboveground–belowground model (Barbier et al. 2008) uses kernels to reflect the variation in the decrease in competition strength around plant individuals of different plant species. Where zones-of-influence or kernels of different individuals overlap, the resources in the overlapping areas or volumes must be shared between individuals. The large number of available models involving plant–plant interactions may be due to three reasons. First, there might be more questions that require the consideration of plant–plant interactions than questions requiring trophic interactions. Second, trophic interactions may only recently have come into the focus of research. Finally, it might simply be easier to incorporate interactions among plants than interactions between plants and other trophic levels.

3.2.4 Plant–Plant and Trophic Interactions

Non-trophic interactions between plants have in some cases been combined with trophic interactions in aboveground–belowground models ("T_x^y" in combination with "C" or "F" or both in Table 3.1). Interactions between plants are usually competitive or facilitative, but can also be trophic when (hemi-) parasitic plants are involved. Along these lines, Fibich et al. (2010) implemented a classic Rosenzweig–MacArthur predator–prey model for the relationship between a plant and its root hemiparasite. The model was extended by including aboveground competition for light between the plant and its hemiparasite. This model was the first to successfully reproduce the reduction in hemiparasite numbers seen empirically at high environmental productivity. The statistical structural equation model by Eisenhauer et al. (2012) connects plant communities and decomposer communities, which can be thought of as implicit competitive, facilitative, and trophic interactions. Based on their model analysis, Eisenhauer et al. (2012) claim that the role of decomposers in the relationship between plant diversity and ecosystem functioning has been underappreciated. The WaNuLCAS model on tree–soil–crop interactions in agroforests treats aboveground trophic interactions implicitly (as harvest), but considers competition between plants explicitly. This model allows the inclusion and analysis of complex management scenarios such as alley cropping, contour hedgerows, parkland systems, and fallow–crop mosaics. Similarly, a series of individual-based models (May et al. 2009; Körner et al. 2014; Pfestorf et al. 2016) simulates herbivory implicitly, but competition explicitly via aboveground and belowground zones-of-influence. Whether or not an individual plant is affected by grazing depends on a weighted lottery based on the overall grazing probability, whereas belowground herbivory is modeled as percentage effect on the total available belowground biomass.

Competitive and trophic interactions have been considered more explicitly in the soil feedback model by Bever (2003). This model links two plants by competition and includes the effects of their soil communities on themselves and on each other as well as the effects of the plants on the soil communities. The difference between explicit and implicit inclusion lies in these two-way trophic interactions. By linking a crop model and a food web model, the banana growth model (Tixier et al. 2013) benefits from both (usually separate) worlds: explicit population dynamics of three trophic levels beyond the plant and explicit output of harvestable biomass of the banana crop and of a cover crop, including explicit competition for nitrogen between the two crops. Another example of an agrophysiological model that explicitly includes competitive and trophic interactions is the WHEATPEST model (Willocquet et al. 2008). Moreover, this model is very flexible in that it has been parameterized for an exceptionally broad range of aboveground and belowground pest species.

3.2.5 Mutualistic and Trophic Interactions

Non-trophic mutualistic interactions between plants and mutualists (often earthworms) have been combined with trophic interactions in a few aboveground–belowground models ("$T_x^y M$" in Table 3.1). Mutualistic interactions are difficult to include in classic equation-based models without generating positive feedback loops. However, mutualistic interactions and also other non-trophic interactions can be modeled as modifiers of trophic interactions in process-based food web models (Goudard and Loreau 2008). This means that trophic interactions would have a less detrimental effect on a plant when a mutualist is present. Mutualistic interactions have also been considered in the conceptual model for enhancing the biological realism of dynamic global vegetation models by Schröter et al. (2004). This conceptual model asks for several trophic levels aboveground and belowground on top of the mutualistic interactions. However, it might be difficult to implement all these demands in dynamic global vegetation models due to their already complex nature and large-scale applications.

If aboveground–belowground interactions of several trophic and non-trophic levels are to be implemented at a smaller scale such as food chains linked to one plant individual, individual-based models are very suitable for the task. An aboveground–belowground interactions model (Meyer et al. 2009b, 2012) involved three trophic levels aboveground, two trophic levels belowground, a plant with shoot and root compartments, and a mutualist. This model showed that belowground interactions can be more important for plant performance than aboveground interactions. Mutualistic interactions between earthworms and the plant had especially substantial effects on plant biomass (Meyer et al. 2009b). This model was also used to demonstrate that the paradox of enrichment can also apply in communities with multiple aboveground and belowground trophic and non-trophic levels. At high levels of enrichment at one end of a land-use gradient, there were abrupt destabilizations of the multitrophic aboveground–belowground system in the form of high plant mortalities (Meyer et al. 2012). Moreover, the effects of aboveground trophic levels on plant performance were more important under enriched conditions, whereas belowground effects were more important under more natural conditions.

3.2.6 Community Complexity

The complexity of a community is a real challenge for aboveground–belowground models (as it is for empirical approaches). Only very few of the existing aboveground–belowground models are community models in the sense that they incorporate more than three species and more than one type of interaction (e.g., Willocquet et al. 2008; Meyer et al. 2009b; Tixier et al. 2013; Körner et al. 2014; Pfestorf et al. 2016). Of course, complexity should not be pursued for complexity's sake. But modelers should take advantage of the added value that modeling approaches offer, especially in complex cases such as aboveground–belowground interactions in communities. For instance, where empirical data are scarce and the true value of a parameter is unknown, models can be used to explore the consequences of many different parameter values for community dynamics. Moreover, the relative importance of different interactions for community dynamics can be evaluated with a sensitivity analysis.

Different aspects of complexity pose different kinds of challenges to modeling. None of the models with more than one trophic level aboveground and belowground explicitly includes the spatial dimension of the community. Hence, addressing spatial relationships in aboveground–belowground interaction models seems to be a greater challenge than including more species or more interactions. However, spatial relationships are important for population and community dynamics (Durrett and Levin 1994). They determine whether a theoretically possible interaction really takes place or is absent or restricted due to spatial vegetation patterns, limited home ranges, differential movement speeds aboveground versus belowground, or the existence of refuges. However, explicitly including space (and time) in a model also raises questions of scaling.

Scaling in space and time poses a serious challenge to complex aboveground–belowground models. Sooner or later in the model development process, the question arises at which scale or scales the aboveground–belowground model should operate. For instance, accounting for different spatio-temporal scales has been pointed out as a problem of models that aim at optimizing ecosystem services (Tixier et al. 2013). Models that cover multiple spatial or temporal scales have been developed (e.g., Fig. 3.2), but they are rare. This is because the transfer of information between scales is technically challenging and virtually always involves loss of information. The technical challenge of scaling is due to the heterogeneities, nonlinearities, and feedbacks of the interactions to be modeled and scaled. More commonly, the modeled processes are integrated at one specific scale. This may also involve loss of information, but is technically easier once the specific scale has been identified. Mismatches in the spatial and temporal scales of the real processes underlying the model (Sayre and Vittorio 2009) aggravate the scaling problems in aboveground–belowground models, because spatial and temporal scales then have to be treated separately.

Another dimension of complexity is the fact that models always must be linked to empirical data for validation. This has been considered a serious bottleneck for crop models (Meine van Noordwijk 1996). Coupling a model to empirical data does not necessarily increase the complexity of the modeled system, but it does enhance the complexity of model analysis. This is especially true when empirical data are scarce and inverse modeling techniques (Grimm et al. 2005) have to be applied to determine parameter values. Inverse parameterization compares available empirical data to the outputs of several model versions that differ in the value of the parameter to be determined. The parameter value that produces the best match is then chosen. In spite of these difficulties, aboveground–belowground models and empirical data from greenhouse experiments or field studies have successfully been coupled in some cases (e.g., Cheeseman 1993; Meyer et al. 2009b; van der Putten et al. 2009; Jeltsch et al. 2013; Hol et al. 2016; Pfestorf et al. 2016).

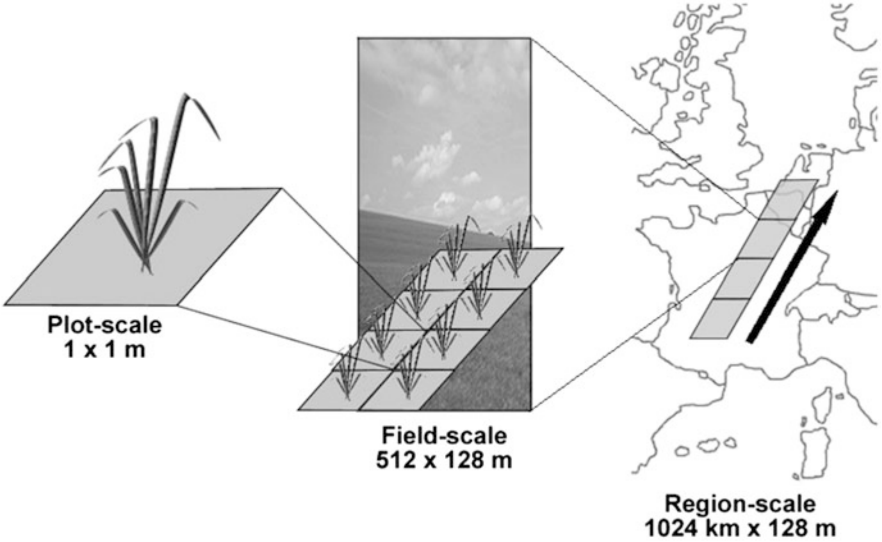

Fig. 3.2 Multi-scale concept of a model simulating northwards range expansion of Mediterranean plants that captures abiotic and biotic interactions with aboveground and belowground enemies. One plot accommodates one plant individual. Biotic interactions occur at the plot and field scale. The population-level output of the individual-based field-scale simulations is used as input to the regional-scale model. Based on the probability of a population to reach the northern end of a field, populations of plants and their aboveground and belowground enemies move northwards in the region-scale model. The field-scale submodel is run for several scenarios differing, for instance, in enemy identity or in temperature to provide the required input to the regional-scale model. Such a multi-scale model can be used to assess intracontinental range expansion speed or the enemy release hypothesis (Figure design by M. van Oorschot)

3.3 The Future of Aboveground–Belowground Models

Future modeling endeavors can advance aboveground–belowground community ecology threefold: first by providing more complete analyses, second by filling gaps in knowledge, and third by inspiring new perspectives. Examples of gaps in knowledge that models can help filling are:

- How do competitive, facilitative, trophic, and mutualistic interactions influence and modify each other in their effect on the involved organisms?
- Which roles do positive and negative feedbacks play for aboveground–belowground interactions?
- How important are interactions between plants and microorganisms relative to other aboveground–belowground interactions in a community?
- How do different types of aboveground–belowground interactions affect the invasibility of a community?
- What is the role of intraspecific interactions and intraspecific variability in the context of aboveground–belowground interactions?

- How do interactions of plants with the environment influence community dynamics relative to interactions with other organisms?

Technically, these advancements correspond to three main avenues for future aboveground–belowground modeling: first to improve and simplify current models, second to develop more complex models, and third to adopt entirely new modeling approaches. The following sections explore how these avenues look like and how we can advance aboveground–belowground community ecology when going along these avenues.

3.3.1 The First Avenue: Model Simplification

The first avenue is to improve current models by updating their data basis, implementing more efficient algorithms, and simplifying model structure where possible. This may involve reformulating the original research question and adapting model structure accordingly. Such continuous model updating is also known as the modeling cycle (Grimm and Railsback 2005) (Fig. 3.3), but is not very often put into practice because it requires extra investment in an apparently completed model project. However, the investment is worthwhile because newly available data may open up new topics for investigation with the model and more efficient model structure may make more complete analyses or other types of analyses possible. In the most extreme case, the original model and its outputs turn out to be wrong, which makes updates mandatory. This first avenue of improving current models also encourages further data collection targeted at filling gaps in the input parameters and reference data for the validation of aboveground–belowground models.

3.3.2 The Second Avenue: Model Expansion

The second avenue for future aboveground–belowground modeling is to take advantage of increasing computing power to expand research questions and models to include more factors. Model expansion can help to fill current gaps in knowledge. However, caution should be taken to not make a model unnecessarily complex with respect to the research question and the available empirical data for parameterization and validation. Unnecessary model complexity can be avoided by starting with the simplest possible model with the fewest variables, parameters, and processes, iterating through the modeling cycle (Fig. 3.3) and always considering to further simplify rather than adding model structure. Where question and data allow for model expansion, there are several factors that can be included in future aboveground–belowground models to fill knowledge gaps. These factors can be grouped into three directions of interaction: interactions between species,

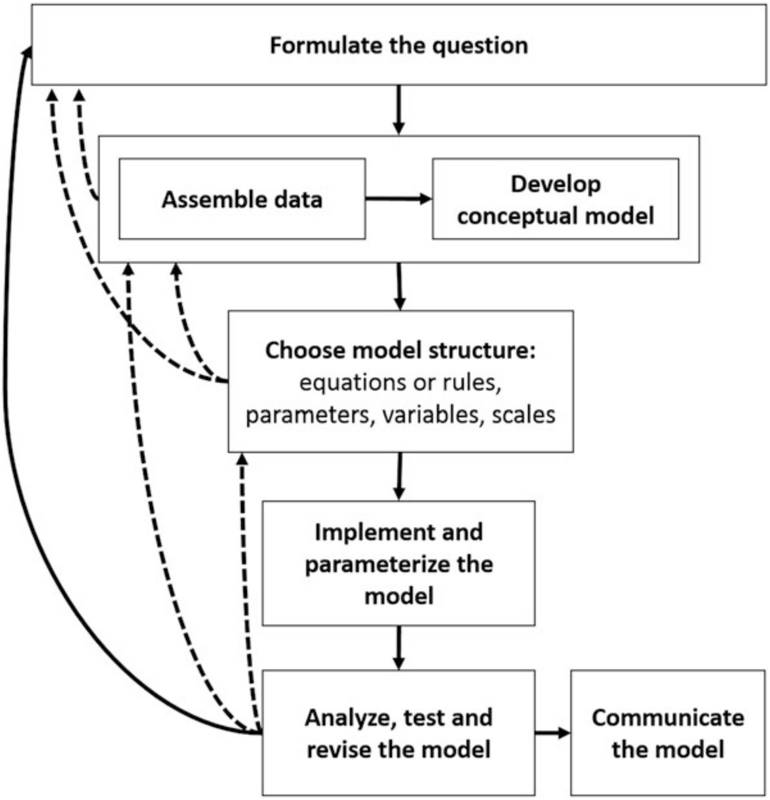

Fig. 3.3 The modeling cycle detailing the steps from question to model and back (modified based on Grimm and Railsback 2005)

intraspecific interactions and variability, and interactions between species and the environment.

In the first interaction direction, more different types of interactions such as trophic, competitive, facilitative, mutualistic, or other interspecific interactions could be combined to provide a more complete picture of a community. To this end, Tixier et al. (2013) suggested linking soil–plant models that stress plant–plant interactions with food web models that focus on trophic interactions. Moreover, negative and positive feedbacks should be considered explicitly (van der Putten et al. 2009), because they can enhance mechanistic understanding of aboveground–belowground interactions. It should also be explored under which conditions negative feedbacks become positive feedbacks and positive feedbacks become negative ones. Where applicable, special roles of selected functional groups in an interaction network should be implemented, as in the case of ecosystem engineers (Schröter et al. 2004). Some groups of organisms are underrepresented in aboveground–belowground models, among them microorganisms that colonize plant leaf and root surfaces (Meyer and Leveau 2012; Esser et al. 2015). Considering interactions with microorganisms may fill gaps in the understanding of the mechanisms of aboveground–belowground interactions. When these interactions are more fully reflected in future aboveground–belowground models, these models can also be used to investigate the invasibility of communities and to test interaction-related hypotheses such as the enemy release hypothesis (see also Fig. 3.2). Here, models have the great advantage over experimental approaches that they allow for countless manipulations and scenarios that can be run with very high replication (Meyer et al. 2009a).

In the second interaction direction, intraspecific interactions and variability may also be benefits of future aboveground–belowground models (Pfestorf et al. 2016). Intraspecific interactions mainly refer to intraspecific competition, i.e., density-dependent reproduction or mortality that give rise to positively or negatively density-dependent population growth. This is particularly important where coexistence of species is investigated, because classical ecological theory in the form of the Lotka–Volterra model predicts that intraspecific competition needs to be stronger than interspecific competition to promote stable coexistence of two species (see also Gause 1934). In terms of intraspecific variability, it is especially important that greater resolution of root traits is included in future approaches (May et al. 2009). Along similar lines, physiological and ecological aspects should be linked more tightly and different pathways of information flow should be considered, for instance in the form of volatiles (Meyer et al. 2012).

In the third interaction direction, interactions with the environment could be included more explicitly in future aboveground–belowground models. Such models with more detailed representations of the relevant environmental conditions such as temperature, pH, soil moisture, or nutrient availability could be used to study how context-dependent the outcomes of aboveground–belowground interactions are (Meyer et al. 2009b). These models will also allow agronomists to address the full complexity of agricultural questions, which requires models with great environmental detail (Tixier et al. 2013). One of these questions is, for instance, how large are the trade-offs between pesticide use and environmental risks (Tixier et al. 2006). Fortunately, there are also some types of models that require only a coarse spatial resolution and thus less detail, such as decision models in agricultural applications (Tixier et al. 2013). When environmental conditions are more explicitly covered, their changes can also be explicitly simulated to investigate the responses of aboveground–belowground interactions to, for instance, global climate change or to the abiotic components of land-use change. Of course, biotic components of land-use change should also be considered when land-use change is modeled. This involves replacing plant species identities by those of the species planted in the new land use and adapting the whole network of associated species aboveground and belowground. This will provide a more complete perspective on the relative importance of abiotic and biotic interactions for the implications of land-use change. Changes in environmental conditions also have consequences for ecosystem services. Hence, more aboveground–belowground model applications that produce output on ecosystem services are called for (Schröter et al. 2004; Tixier et al. 2013).

3.3.3 The Third Avenue: New Modeling Techniques

The third avenue towards future aboveground–belowground models is to explore entirely new technical approaches as bases for the modeling endeavors. These approaches also encompass empirical approaches that help to provide more complete or more finely resolved data on which to base parameterization or validation of the models. For example, molecular tools such as stable isotope analysis should be used more frequently in order to obtain full food web data for complex aboveground–belowground models (Tixier et al. 2013). For aboveground–belowground models that focus on plant morphogenesis and the genetic regulation of plant development, cell-based simulation approaches have been advocated to capture different types of plant cells (Dupuy et al. 2007). Game theory offers new techniques that have not yet been applied in aboveground–belowground modeling. These techniques can be used to model plant defense strategies or plant allocation responses to global change (McNickle and Dybzinski 2013). Similarly, static or dynamic Bayesian network models have not yet been frequently applied in aboveground–belowground modeling. However, they can be very useful where food web modelers want to include stochasticity (Tixier et al. 2013). Adopting new modeling techniques can thus also open up new ecological perspectives on aboveground–belowground community ecology.

3.4 Practical Guide to Modeling Aboveground–Belowground Interactions

How can you now make your own model of aboveground–belowground interactions? Whether you are an experienced modeler or a modeling novice, all your modeling endeavors (not only the ones related to aboveground–belowground interactions) will usually follow the same general principles that make up the modeling cycle (Fig. 3.3) (Grimm and Railsback 2005). These principles are derived from the definition of a model as a purposeful simplification of reality. Thus, the first step of the modeling cycle is to define the purpose of a model in form of the model question. This question needs to be as specific as possible to be useful as a decision tool for simplification (see the examples of model questions in the introduction to this chapter). Often, model questions arise either explicitly or implicitly from the exploration of empirical data. This is an explicit process when data give rise to questions on the underlying mechanisms, and these mechanisms are more amenable to modeling than empirical approaches. This can for instance be due to logistic constraints. Implicitly, the data that we process influence our preconceptions about the mechanisms that shape and drive community dynamics and thus also influence the questions that we ask about them.

The second step is to develop a conceptual model based on data assembly. The conceptual model is a collection of hypotheses about the factors, influences, and interactions that may be relevant for answering the model question. These hypotheses might only be mental hypotheses, but they are in fact often expressed in the form of graphics with factors in boxes and arrows representing influences or interactions. A conceptual model is a crucial milestone for a successful model of a system, because it makes explicit the knowledge, assumptions, and intuition about the system. Note that conceptual models can be a step in the modeling cycle or a self-contained model type (Fig. 3.1). The quality of the conceptual model strongly depends on the available data. Data are explicitly required for parameterization and validation of a model, but also more implicitly as a guideline during the definition of model structure. Data quality obviously varies, but any type and quality of data related to the model question is welcome at the conceptual modeling stage. This includes quantitative data obtained from literature sources or from experiments and observations carried out by the modelers themselves, as well as qualitative data in the form of expert knowledge or "guesstimates." If the model concept is transparent about the nature of the data and the estimated uncertainty in the data, even the most uncertain data can be useful in the modeling process if it is related to the model question. It is good practice go back and forth between question formation and data assembly/model conceptualization in several iterations to sharpen and synchronize question and concept until the next step can be taken.

In the third step, the model structure is fixed, i.e., concrete model equations, rules, and algorithms are devised, the set of parameters and variables is defined, and the temporal and spatial scales are determined. Parameters are the input values of a model that stay constant in any one model run, whereas variables express different states of the modeled system and vary accordingly. Scale is composed of grain and extent, i.e., the smallest and the largest spatial or temporal unit to be distinguished in the model. A careful definition of the model scales is especially important in aboveground–belowground interaction models, because the dynamics of aboveground–belowground interactions is often scale-dependent. Deciding to choose a particular model structure may have as a consequence that the conceptual model and sometimes even the model question have to be modified.

The fourth step is to implement and parameterize the model. This means that the model structure is turned into a set of spelled-out equations in the case of equation-based models such as process-based and reaction–diffusion models and into programming code in the case of rule-based models such as most cellular automata and individual-based models (Table 3.1). Additionally, standard parameter values and the initial values of the variables need to be defined based on data from the second step. This requires a certain degree of technical knowledge in mathematics or software design, which can of course also be outsourced to mathematicians or software experts. Literature on equation-based modeling in biology abounds; classic references are Adler (2005) and Edelstein-Keshet (2005). For rule-based models, the free software NetLogo (Wilensky 1999) is highly suitable for programming novices, because it offers ample self-learning material and an extensive library with ready-made models as starting points. This software is specialized on agent- or individual-based models, but can also be applied to implement any other rule-based model structure. Grimm and Railsback (2005) line out the theoretical basis of agent- and individual-based modeling in ecology, and Railsback and Grimm (2012) provide a practical introduction to agent-based modeling for beginners. Once all obvious mistakes have been eliminated from the set of equations or from the code and the model is running smoothly, the next step can be taken.

The fifth step involves model analysis, testing, and revision. For model analysis, scenarios need to be defined in the form of sets of parameter values that reflect different aspects of the model question. Parameter values can also be defined beyond the scope of the model question to test how the model responds to more extreme parameterizations. Testing should also include checking the plausibility of all model results and explicit model validation against reference data that were not used during parameterization. Once the model is successfully validated, model analysis can also include a sensitivity analysis to determine the relative importance of the input parameters with respect to model output (Cariboni et al. 2007). A sound model analysis usually takes ten times as much time as all previous steps taken together (Grimm and Railsback 2005). A particularly efficient and systematic way to test a rule-based model is pattern-oriented modeling (Grimm et al. 2005), which can also be used for inverse parametrization. Patterns for which reference data exist need to be discerned in the model output. These patterns can be spatial patterns, but can also be nonspatial patterns, e.g., size-frequency distributions or number and identity of species in an aboveground–belowground food web. The model is then run with several different model structures and sets of parameter values, and the resulting patterns are compared with the reference patterns from reality. The model version that produces the best fit between modeled and real patterns can then be considered as most realistic model structure and parameterization. Thereby, pattern-oriented modeling can also be used to identify unknown parameter values in an inverse parameterization where data for the unknown parameters are scarce, but data for reference patterns abound. During the process of model analysis, there is often cause for model revision, sometimes back to the modification of the original model question. This can either be because errors or uncertainty in important model parts have emerged and force the discarding of the current model and starting anew or because the results of the model analysis have inspired entirely new questions.

As the last step after successful model analysis, the model can be communicated in presentations and publications. This requires precise documentation of the model (e.g., Grimm et al. 2010, 2014). Ideally, documentation accompanies the whole model building process right from the start at the model question. Finally, spin-offs of the model can be considered, so that the modeling cycle starts again.

3.5 Conclusions

Models can capture parts of the complexity of aboveground–belowground interactions with the aim to describe, explain, and predict aboveground–belowground community patterns. Models come with the advantage of broad independence of logistic constraints, except, of course, for computing power limitations. Many of the existing aboveground–belowground models have been developed in applied fields such as the agricultural sciences, but classic community ecology and theory is underrepresented. Similarly, community models that address the full range of possible interactions are rare in aboveground–belowground ecology. One reason for this might be that in aboveground–belowground community ecology expertise from many different disciplines is required. Another reason is that models must simplify, by definition, so that at least initially not all factors or interactions should be included in a model. Once the simple initial models are understood, more factors and interactions can be added by iterating the modeling cycle. A broad range of model types is available to implement these models, but their full potential is yet to be exploited. This is particularly true for game theoretical approaches and Bayesian network models. One of the challenges that future modeling endeavors face is the appropriate representation of spatial and temporal scales including methods for scaling up and down between different scales. All these challenges require concerted efforts of modelers and empiricists in the future. Ideally, modelers and empiricists should work closely together right from the start of a project, defining question, data requirements, and methods together (Jeltsch et al. 2013). Along the same lines, greater emphasis should be put on targeted data collections to fill gaps in parameterization and validation of models. With these efforts, more facets of the complexity of aboveground–belowground interactions will be elucidated in future aboveground–belowground models.

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