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Appendix 1

This Appendix complements the model description in the main text and contains the second and third part – Design concepts and details – of Grimm et al. 's (2006) ODD-protocol for the description of individual-based models. The first part of the protocol, the Overview, is part of the Methods section in the main text. The names of the model parameters appearing in Table A1 are given in italics in the text.

Model description – design concepts

Emergence

Shoot and root biomass and quality dynamics over time emerge from the model, as well as the population dynamics of aboveground herbivores, parasitoids, and hyperparasitoids and belowground herbivores and antagonists. Plant and above- and belowground herbivore mortality over one growing season also emerge from the model.

Sensing

Aboveground herbivores have information on their own body size, sex, the shoot biomass they need for survival, shoot quality on which their body size depends and whether they are parasitized and adult. Aboveground parasitoids have information on their own body size, number of remaining eggs, and whether they are hyperparasitized and adult. Aboveground hyperparasitoids have information on their own body size and whether they are adult. Parasitoids and hyperparasitoids have information on the body size of the host they emerged from because their own body size depends on their host's body size.

Interactions

Aboveground herbivore larvae interact with the plant through feeding leading to increased shoot quality, reduced shoot biomass and induced plant volatile presence. The plant interacts with parasitoid adults by increasing their efficiency through the production of volatiles. Parasitoid adults kill herbivore larvae before reproduction, because their offspring destroy the host larva from inside, and modify the shoot biomass consumption of their host larvae. Hyperparasitoid adults kill parasitoid prematures after parasitism of herbivores but before parasitoid reproduction. Root herbivores reduce root biomass and root and shoot quality. Belowground antagonists kill root herbivores before reproduction and before they can affect the plant.

Stochasticity

All demographic processes (mortalities, reproduction probabilities, sex ratios) and parasitism processes incorporate stochasticity. Body sizes are initially drawn from normal distributions. Environmental stochasticity is incorporated by drawing the proportion of nutrients that can be extracted by the plant from a normal distribution.

Observation

We record population sizes of aboveground herbivores, parasitoids, and hyperparasitoids, as well as belowground herbivores and antagonists; root and shoot biomass; root and shoot quality; individual body sizes and number of eggs produced for the aboveground trophic levels.

Model description – details

Initialization

Individuals are created according to initial values of population sizes in field experiments (see *Initialisation parameters* in Table A1). Aboveground herbivore, parasitoid, and hyperparasitoid individuals are assigned to one list each to facilitate their handling during the simulations. Body sizes are drawn from normal distributions with mean *Average initial body mass of aboveground herbivores* and corresponding *standard deviation* (Table A1). The sex of an individual is determined by drawing a random number and making the individual a female if the random number is smaller than the *Proportion of females* of the respective trophic level and a male otherwise (Table A1). All aboveground individuals initially are in the active trophic stage, i.e. hyperparasitoids and parasitoids are adult wasps while herbivores start as caterpillars. Parasitoid eggload is determined from individual body size:

$$r = \frac{c_{p,1} \cdot \left(\frac{s_p \cdot 1000}{c_{ls,1}}\right)^{c_{ls,2}}}{c_{hl}} - c_{p,2} \qquad \text{(A1)}$$

where r is the number of eggs, $c_{p,1}$ and $c_{p,2}$ are the slope and the intercept of the relationship between *Number of eggs and own head width* (Lemasurier 1991), s_p is the body size of the parasitoid individual, $c_{ls,1}$ and $c_{ls,2}$ are a *Factor* and an *Exponent converting body length into body mass* (Honek 1993), and c_{hl} is the *Factor converting head width into body length* (Table A1). All input parameters are scaled to the specified number of generations per season (particularly: maximum number of root herbivore eggs killed per antagonist couple lifetime, maximum number of eggs produced per female antagonist lifetime, proportional bioturbator effect on shoot quality and shoot and root biomass, initial numbers of antagonists and root herbivores). Predation mortality of belowground herbivore eggs is recalculated to represent mortality per antagonist couple:

$$m_{pred,new} = 1 - (1 - m_{pred,old})^{\frac{1}{(1-m_{anta})\cdot c\cdot anta_{ini}\cdot\frac{1}{g}}} \quad \text{(A2)}$$

where $m_{pred,new}$ is the predation mortality of belowground herbivore eggs per antagonist couple, $m_{pred,old}$ is the specified predation mortality of belowground herbivore eggs, m_{anta} is the natural mortality of antagonists, c is the proportion of antagonist couples equal to the proportion of female antagonists or to one minus the proportion of female antagonists (whichever is smaller), $anta_{ini}$ is the initial number of antagonists and, g is the number of antagonist generations per year.

Input

The nutrient pool is raised by a constant amount each time step (*Nutrient supply* in Table A1) and subsequently depleted by plant growth (see submodel plant growth below).

Submodels

The scheduling of the processes tracks the natural sequence of events wherever possible (Fig. A1). The order of the individuals on the aboveground herbivore, parasitoid and hyperparasitoid lists is randomized before demographic and trophic processes are applied to them. In the following, the submodels of ABBE are described in detail following the sequence of processes in Fig. A1.

Plant growth

Each time step, root and shoot biomass are updated separately by adding the extractable proportion of the nutrient pool (*Nutrient uptake efficiency of root* in Table A1) multiplied with a factor converting nutrients into biomass. This converting factor can differ for root and shoot biomass (*Conversion efficiency root* and *shoot* in Table A1). The extractable proportion is drawn from a normal distribution with mean equal to the specified extractable proportion and standard deviation equal to 10% of the mean to introduce environmental stochasticity. Roots and shoots are independently modelled and do not shift with respect to external factors such as nutrients or herbivory in the model. This is due to the lack of specific data quantifying the interaction between nutrient availability and herbivory on root-shoot ratio shifts for the set of species our parameterization was based on. Our validation shows that such extra complexity is not needed in the model, because the current version can already explain the observed shoot and root biomass values (Fig. 2). For explicit tests of the implications of root-shoot ratio shifts for model results, future model versions may incorporate and contrast alternative hypotheses and expert guesses on the interactive effect of herbivory and nutrient availability on root-shoot ratio shifts.

Bioturbator effect

Bioturbator presence leads to a proportional increase of shoot quality, root biomass and shoot biomass of the plant depending on the parameters *Proportional bioturbator effect on shoot quality*, *root biomass*, and *shoot biomass*, respectively (Table A1). If shoot quality is increased to a value greater than 1, it is set to 1.

Shoot herbivore mortality

For each herbivore individual, a random number is drawn from a uniform distribution between 0 and 1. If this random number is smaller than the *Natural mortality of aboveground herbivores* (Table A1) then the individual is removed from the simulation.

Shoot herbivore size update

If shoot quality is 1, individual shoot herbivore body size is drawn from a normal distribution with mean *Average initial body mass of aboveground herbivores* and the respective *standard deviation* (Table A1). If shoot quality is smaller than 1, mean and standard deviation are first multiplied with the *Body mass proportion on low quality plants* (*average* and *SD*, Table A1) to represent the negative effect of lower shoot quality on herbivore body size.

Volatile induction

If at least one aboveground herbivore individual is present, plant volatiles are induced resulting in an increase of the *Parasitism success probability* of the aboveground parasitoid (*Volatile-induced parasitism success probability increase* in Table A1).

Shoot quality update

If at least one herbivore individual is present, shoot quality is increased by *Shoot quality increase due to aboveground herbivores* (Table A1). If shoot quality is increased to a value greater than 1, it is set to 1.

Parasitoid mortality

For each parasitoid individual, a random number is drawn from a uniform distribution between 0 and 1. If this random number is smaller than the *Natural mortality of aboveground parasitoids* (Table A1) then the individual is removed from the simulation.

Parasitoid reproduction and body size update

Aboveground parasitoids reproduce if they can successfully parasitise a herbivore individual. Every herbivore can potentially be parasitized by every parasitoid. Parasitoids and herbivores meet in randomized order. Parasitism is successful if the parasitoid is an adult female that still has at least one egg remaining and that is assigned a random number smaller than the *Parasitism success probability* (Table A1). The successful parasitoid will lay *Number of eggs per host* eggs or all its remaining eggs, whichever is the smaller value. Every egg gives rise to a juvenile parasitoid whose body mass depends on the body mass of its host including stochastic variation:

$$s_p = (rnd \cdot 2 \cdot c_{s,CI} + (c_s - c_{s,CI})) \cdot s_h$$

where rnd is a random number from a uniform distribution between 0 and 1, c_s is the slope of parasitoid *Body mass per host body mass* (R. Soler unpubl.), $c_{s,CI}$ is the 95% confidence interval of this slope (R. Soler unpubl.), and s_h is the body mass of the aboveground herbivore serving as host. Once a parasitism attempt was successful, the herbivore cannot be parasitised anymore, but the parasitoid can parasitise other herbivores if it still possesses eggs.

Shoot herbivore consumption of shoot biomass

Before shoot herbivores affect shoot quality (see submodel *Shoot quality update* above), the amount of shoot biomass that one aboveground herbivore is removing in its lifetime (shoot portion) is determined as *Maximum amount shoot biomass eaten per shoot quality unit* divided by shoot quality. If shoot quality is 0, the shoot portion is equal to the whole shoot biomass. Parasitised herbivores remove a shoot portion reduced by the *Proportional consumption reduction due to parasitism* (Table A1), non-parasitized herbivores remove the shoot portion. If the shoot biomass is smaller than the shoot portion, shoot biomass is set to 0 and the current herbivore dies as well as those herbivores that did not have their shoot portion yet.

Shoot herbivore mortality through parasitism
Parasitised herbivores die after consumption (but before reproduction). After consumption, the status of the surviving herbivores (that were neither parasitised nor suffered from food shortage) changed from caterpillar to adult.

Hyperparasitoid mortality
For each hyperparasitoid individual, a random number is drawn from a uniform distribution between 0 and 1. If this random number is smaller than the *Natural mortality of aboveground hyperparasitoids* (Table A1), then the individual is removed from the simulation.

Hyperparasitoid reproduction incl. body size update
For every hyperparasitoid adult female, the individual number of eggs is determined as *Number of eggs per adult body mass* times individual body mass (J. A. Harvey unpubl., Table A1). As long as a hyperparasitoid has remaining eggs, it gets the chance to lay an egg into each juvenile parasitoid, meeting the parasitoids in randomized order. Hyperparasitism is successful if a random number from a uniform distribution between 0 and 1 is smaller than the *Hyperparasitism success probability* (Table A1) and the parasitoid is not yet hyperparasitised. If hyperparasitism is successful, a juvenile hyperparasitoid is created with body mass

$$s_h = c_{ph,1} \cdot s_p + c_{ph,2}$$

where $c_{ph,1}$ and $c_{ph,2}$ are the slope and the intercept of the relationship of hyperparasitoid *Body mass per host body mass* (Table A1), and s_p is the body mass of the parasitoids.

Parasitoid mortality through hyperparasitism
Hyperparasitised parasitoids die through parasitism before they can reproduce but after they affected herbivores.

Hyperparasitoid adult mortality
Hyperparasitoid adults die after the hyperparasitism process regardless of whether the hyperparasitism was successful or not. Hyperparasitoid juveniles become adults.

Parasitoid adult mortality
Parasitoid adults die at the end of each time step regardless of whether parasitism was successful or not. Parasitoid juveniles become adults and obtain an individual number of eggs depending on their body size based on Eq. A1.

Plant mortality due to shoot herbivory
If shoot biomass is smaller than *Minimum proportion of initial shoot biomass for plant survival* (Table A1) multiplied with initial shoot biomass, the plant dies regardless of root biomass.

Antagonist mortality
The population size of belowground antagonists is reduced according to the *Natural mortality* of belowground antagonists (Table A1) including demographic stochasticity. Antagonists have only two generations per year instead of 4 generations of all other trophic levels. Therefore, mortality is applied only every second model time step for antagonists while it is applied at every time step for all other trophic levels.

Antagonist reproduction
Antagonist reproduction depends on the number of eggs of the root herbivore that are successfully acquired. Every antagonist couple attempts to kill root herbivore eggs until either the root herbivore eggs are all dead or the *Maximum number of belowground herbivore eggs killed per antagonist couple lifetime* (Table A1) is reached (whichever happens first). The killing is successful if a random number drawn from a uniform distribution between 0 and 1 is smaller than the per couple predation mortality of root herbivore eggs. This mortality is derived from the *Predation mortality of root herbivore eggs* (Table A1) by applying Eq. A2. The number of antagonist couples is calculated as the product of the current number of antagonists and the *Proportion of female antagonists* or one minus this proportion (whichever is smaller; Table A1). The antagonists produce one new offspring if a random number drawn from a uniform distribution between 0 and 1 is smaller than the ratio of the *Maximum number of eggs per female lifetime* and the *Maximum number of belowground herbivore eggs killed per antagonist couple lifetime* (Table A1). Since one antagonist generation corresponds to two root herbivore generations, antagonists can attack root herbivores twice during one generation, but their offspring is collected until the end of one antagonist generation. Then, all old antagonists die, and the new offspring represents the new adult population.

Root herbivore predation mortality
If the killing attempt of the antagonists as described in the previous section is successful, the population size of the root herbivores is reduced by one.

Root herbivore mortality
Since the literature estimates of the *Natural mortality of the root herbivores* includes egg predation (Table A1)(Hughes and Mitchell 1960), natural mortality has to be recalculated excluding egg predation mortality:

$$m_{r,new} = \frac{m_{r,old} - m_{anta}}{1 - m_{pred,old}}$$

where $m_{r,new}$ is the natural mortality of root herbivores excluding egg predation, $m_{r,old}$ is the *Natural mortality of root herbivores including egg predation*, and $m_{pred,old}$ is the *Predation mortality of eggs* (Table A1). The population size of root herbivores is reduced according to this new root herbivore mortality including demographic stochasticity.

Root herbivore consumption of root and effect on root and shoot quality
The remaining root herbivores decrease the root biomas according to the *Proportional root biomass decrease per individual* (Table A1):

$$b_{ro,new} = b_{ro,old} - n_r \cdot c_{rro} \cdot b_{ro,old}$$

where $b_{ro,new}$ and $b_{ro,old}$ are the root biomass after and before root herbivory, N_r is the population size of root herbivores, and c_{rro} is the *Proportional root biomass decrease per individual*. When at least one root herbivore is present, root and shoot quality are decreased by the *Proportional root and shoot quality decrease* (Table A1).

Plant root-herbivory mortality
If root biomass is smaller than *Minimum proportion of initial root biomass for plant survival* (Table A1) multiplied with initial root biomass, the plant dies regardless of shoot biomass.

Shoot herbivore reproduction
For each adult female shoot herbivore, a random number is drawn from a uniform distribution between 0 and 1. If this random number is smaller than the *Reproduction probability of an adult* (Table A1), the herbivore produces offspring. The number of offspring depends on its own body mass:

$$r_h = c_{sr,1} \cdot s_h + c_{sr,2}$$

where r_h is the number of offspring of the herbivore, $c_{sr,1}$ and $c_{sr,2}$ are the slope and the intercept of the relationship between *Number of eggs and own body mass* (Table A1)(Gilbert 1984), and s_h is the body mass of the herbivore. For each offspring, the sex is determined by drawing a random number from a uniform distribution between 0 and 1. If this number is smaller than the *Proportion of female shoot herbivores*, the offspring is female. Every offspring obtains the *Average initial shoot herbivore body mass* as body mass. The parents die after having produced the offspring.

Root enemy reproduction
The number of root herbivore couples is determined as the product of the number of root herbivores and the *Proportion of females* or one minus the *Proportion of females* (whichever is smaller; Table A1). Each root herbivore couple can potentially produce *Number of eggs per female lifetime* (Table A1) number of eggs. If a random number drawn for every egg from a uniform distribution between 0 and 1 is smaller than the *Egg viability* (Table A1), one offspring is produced. The adults die after reproduction and offspring become adults.

References

Alleyne, M. and Beckage, N. E. 1997. Parasitism-induced effects on host growth and metabolic efficiency in tobacco hornworm larvae parasitized by *Cotesia congregata*. – J. Insect Physiol. 43: 407–424.

Brodeur, J. et al. 1998. Effects of *Pieris* host species on life history parameters in a solitary specialist and gregarious generalist parasitoid (*Cotesia* species). – Entomol. Exp. Appl. 86: 145–152.

Felkl, G. et al. 2005. Tolerance and antibiosis resistance to cabbage root fly in vegetable *Brassica* species. – Entomol. Exp. Appl. 116: 65–71.

Feltwell, J. 1982. Large white butterfly: the biology, biochemistry and physiology of *Pieris brassicae* (Linnaeus). – Dr W. Junk Publishers.

Fournet, S. et al. 2000. Life history comparison between two competitive *Aleochara* species in the cabbage root fly, *Delia radicum*: implications for their use in biological control. – Entomol. Exp. Appl. 96: 205–211.

Fournet, S. et al. 2004. Influence of a bimodal emergence strategy of a Dipteran host on life-history traits of its main parasitoids. – Ecol. Entomol. 29: 685–691.

Gilbert, N. 1984. Control of fecundity in *Pieris rapae* .1. The problem. – J. Anim. Ecol. 53: 581–588.

Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based models. – Ecol. Modell. 198: 115–126.

Harvey, J. A. and Witjes, L. M. A. 2005. Comparing and contrasting life history and development strategies in the pupal hyperparasitoids *Lysibia nana* and *Gelis agilis* (Hymenoptera : Ichneumonidae). – Appl. Entomol. Zool. 40: 309–316.

Harvey, J. A. et al. 2003. Interactions over four trophic levels: foodplant quality affects development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid. – J. Anim. Ecol. 72: 520–531.

Harvey, J. A. et al. 2004. Development of hyperparasitoid wasp *Lysibia nana* (Hymenoptera : Ichneumonidae) in a multitrophic framework. – Environ. Entomol. 33: 1488–1496.

Honek, A. 1993. Intraspecific variation in body size and fecundity in insects – a general relationship. – Oikos 66: 483–492.

Hughes, R. D. and Mitchell, B. 1960. The natural mortality of *Erioischia brassicae* (Bouche) (Dipt, Anthomyiidae) – life-tables and their interpretation. – J. Anim. Ecol. 29: 359–374.

Ibrahim, M. A. et al. 2005. Response of *Plutella xylostella* and its parasitoid *Cotesia plutellae* to volatile compounds. – J. Chem. Ecol. 31: 1969–1984.

Kostal, V. 1993. Oogenesis and oviposition in the cabbage root fly, *Delia radicum* (Diptera, Anthomyiidae), influenced by food quality, mating and host-plant availability. – Eur. J. Entomol. 90: 137–147.

Kristensen, C. O. 1994. Investigations on the natural mortality of eggs and larvae of the large white *Pieris brassicae* (L) (Lep-Pieridae). – J. Appl. Entomol. – Z. Angew. Entomol. 117: 92–98.

Lemasurier, A. D. 1991. Effect of host size on clutch size in *Cotesia glomerata*. – J. Anim. Ecol. 60: 107–118.

Meyer, G. A. 2000. Interactive effects of soil fertility and herbivory on *Brassica nigra*. – Oikos 88: 433–441.

Neveu, N. et al. 2000. Host-stage selection by *Trybliographa rapae*, a parasitoid of the cabbage root fly *Delia radicum*. – Entomol. Exp. Appl. 96: 231–237.

Schopf, A. and Steinberger, P. 1996. The influence of the endoparasitic wasp *Glyptapanteles liparidis* (Hymenoptera: Braconidae) on the growth, food consumption, and food utilization of its host larva, *Lymantria dispar* (Lepidoptera: Lymantriidae). – Eur. J. Entomol. 93: 555–568.

Soler, R. et al. 2005. Root herbivore effects on above-ground herbivore, parasitoid and hyperparasitoid performance via changes in plant quality. – J. Anim. Ecol. 74: 1121–1130.

van Dam, N. M. and Raaijmakers, C. E. 2006. Local and systemic induced responses to cabbage root fly larvae (*Delia radicum*) in *Brassica nigra* and *B. oleracea*. – Chemoecology 16: 17–24.

Wurst, S. and Jones, T. H. 2003. Indirect effects of earthworms (*Aporrectodea caliginosa*) on an above-ground tritrophic interaction. – Pedobiologia 47: 91–97.

Wurst, S. et al. 2004. Combined effects of earthworms and vesicular-arbuscular mycorrhizas on plant and aphid performance. – New Phytol. 163: 169–176.

Wurst, S. et al. 2006. Effects of belowground biota on primary and secondary metabolites in *Brassica oleracea*. – Chemoecology 16: 69–73.

Table A1. ABBE model parameters.

Parameter	Acc	Default	Source	Specifications for sensitivity analysis		
				Range	Distr	Source
Initialisation parameters						
Nutrient pool size (g N)	0	0	MCE	0–0.96	u	Meyer 2000
Root biomass (g)	1	0.839	Meyer 2000	0–1.5	e	Soler et al. 2005
Root quality	0	1	MCE	0–1	u	EG
Shoot biomass (g)	1	1.349	Meyer 2000	0–3	e	Soler et al. 2005
Shoot quality	0	1	MCE	0–1	u	EG
Presence of plant volatiles	0	0	MCE	0–1	u	EG
BG herbivore number	2	944	Hughes and Mitchell 1960	0–2000	u	Hughes and Mitchell 1960
BG antagonist number	1	1136	Fournet et al. 2000	600–1600	n	± SD, Fournet et al. 2000
AG herbivore number	2	1935	EG	0–3870	n	+ 2*Def
AG parasitoid number	3	6	EG	0–60	u	+ 10*Def
AG hyperparasitoid number	3	2	EG	0–20	u	+ 10*Def
Average initial body mass of AG herbivores (g)	1	0.377	DT R. Soler	0.364–0.390	n	± SD
SD of initial body mass of AG herbivores (g)	2	0.01284	DT R. Soler	0.0116–0.0141	u	± 10%
Average initial body mass of AG parasitoids (g)	2	0.00166	DT R. Soler	0.0015–0.00182	n	± SD
SD of initial body mass of AG parasitoids (g)	2	0.00016	DT R. Soler	0.000144–0.000176	u	± 10%
Average initial body mass of AG hyperparasitoids (g)	2	0.001247	DT J. A. Harvey	0.001058–0.001436	n	± SD
SD of initial body mass of AG hyperparasitoids (g)	2	0.000189	DT J. A. Harvey	0.00017–0.000208	u	± 10%
Nutrient and plant parameters						
Nutrient supply [g N]	1	0.32	Meyer 2000	0–0.96	u	Meyer 2000
Nutrient uptake efficiency of root [g^{-1}]	2	0.5	Meyer 2000	0–10	u	+ Def*20
Conversion efficiency root [g $(gN)^{-1}$]	2	3.5	Meyer 2000	2.854–11.415	e	*/ 2
Conversion efficiency shoot [g $(gN)^{-1}$]	2	10.5	Meyer 2000	4.145–16.579	e	*/ 2
Minimum proportion of initial shoot mass for plant survival	4	0.3125	EG	0.001–0.999	u	EG
Minimum proportion of initial root mass for plant survival	4	0.417	EG	0.001–0.999	u	EG
Shoot quality increase due to AG herbivores	2	0.55	Soler et al. 2005	0.1–0.9	u	EG
AG herbivore parameters						
Maximum amount shoot biomass eaten per shoot quality unit [g]	4	0.03	EG	0.001–2	e	EG
Natural mortality	1	0.969	Kristensen 1994	0.5–0.99	u	EG

Body mass proportion on low quality plants (average)	3	0.8	EG	0–0.99	u	EG
Proportion of reduced body mass on low quality plants (yielding SD)	4	0.1	EG	0–1	u	EG
Proportional consumption reduction due to parasitism	1	0.5	Alleyne and Beckage 1997, EG J. A. Harvey	0.3–3	e	Schopf and Steinberger 1996, EG J. A. Harvey
Reproduction probability of an adult	2	0.6	EG	0.3–0.9	n	EG
Number of eggs per own body mass [g^{-1}] (slope)	2	3670	Gilbert 1984	4500–2500	u	Kristensen 1994
Number of eggs per own body mass [g^{-1}] (intercept)	2	–215	Gilbert 1984	–	–	–
Minimum number of parasitoid eggs for AG herbivore weight reduction	3	50	EG	5–500	e	EG
Proportional weight reduction due to parasitoid eggs	3	0.75	EG	0–2	u	EG
Proportion of females	2	0.56	Feltwell 1982	0.506–0.616	n	± 20%
AG parasitoid parameters						
Natural mortality	1	0.38	Brodeur et al. 1998	0.08–0.68	n	± 0.3
Parasitism success probability	1	0.662	Brodeur et al. 1998	0.01–0.99	u	EG
Volatile-induced parasitism success probability increase	2	1.2	Ibrahim et al. 2005	1.0–2.0	u	EG
Body mass per host body mass (slope) [$g\ g^{-1}$]	1	0.004441	DT R. Soler	0.003–0.006	u	± 6 * [95% CI]
Body mass per host body mass (intercept) [g]	1	0	DT R. Soler	–	–	–
Body mass per host body mass (95% CI of slope) [$g\ g^{-1}$]	1	0.00025	DT R. Soler	0.000025–0.0025	e	*/ 10
Number of eggs per own head width (slope) [mm^{-1}]	1	4337	Lemasurier 1991	4000–5000	u	Lemasurier 1991
Number of eggs per own head width (intercept)	1	2225	Lemasurier 1991	–	–	–
Factor converting body length into body mass [$g\ mm^{-1}$]	2	0.0305	Honek 1993	0.00305–0.305	e	*/ 10
Exponent converting body length into body mass	2	0.381679	Honek 1993	0.01–1	u	EG
Factor converting head width into body length [$mm\ mm^{-1}$]	2	6.5	Honek 1993	4.0–9.0	n	± 2.5
Number of parasitoid eggs per parasitized host	2	25	EG J. A. Harvey	12.0–50.0	e	*/ 2
Proportion of females	1	0.72	Harvey et al. 2004	0.1–0.9	u	EG
AG hyperparasitoid parameters						
Natural mortality	1	0.2	Harvey et al. 2004, Harvey et al. 2003	0.01–0.99	u	EG
Hyperparasitism success probability	1	0.82	Harvey and Witjes 2005	0.01–0.99	u	EG
Body mass per host body mass (slope) [$g\ g^{-1}$]	1	0.3738	Soler et al. 2005	0.2–0.55	u	Soler et al. 2005
Body mass per host body mass (intercept) [g]	1	0	Soler et al. 2005	–	–	–
Number of eggs per adult body mass [g^{-1}]	1	28865	DT J. A. Harvey	20 000–40 000	u	DT
Number of eggs per host	1	25	Harvey and Witjes 2005	12.0–50.0	u	*/ 2
Proportion of females	2	0.6	EG	0.4–0.8	n	± 0.2

BG herbivore parameters						
Natural mortality	1	0.9712	Hughes and Mitchell 1960	0.5–0.999	u	Neveu et al. 2000, EG
Predation mortality of eggs	2	0.9	Hughes and Mitchell 1960	0.01–0.99	u	EG
Proportional root quality decrease	2	0.3	van Dam and Raaijmakers 2006	0.01–0.99	u	EG
Proportional shoot quality decrease	2	0.9	van Dam and Raaijmakers 2006, Soler et al. 2005	0.01–0.99	u	EG
Proportional root biomass decrease per individual	2	0.023	Soler et al. 2005	0.01–0.99	u	EG
Proportional shoot biomass decrease per individual	2	0	Soler et al. 2005	0.01–0.99	u	EG
Number of eggs per female lifetime	1	426	Kostal 1993	0–800	u	Kostal 1993
Proportion of females	1	0.61	Felkl et al. 2005	0.51–0.71	n	SD, Felkl et al. 2005
Egg viability	1	0.56	Kostal 1993	0.08–0.86	u	Kostal 1993
BG antagonist parameters						
Natural mortality	1	0.6	Fournet et al. 2000	0.27–0.8	u	Fournet et al. 2004, EG
Maximum number of BG herbivore eggs killed per antagonist couple lifetime	1	1210	Fournet et al. 2000	605–1420	e	*/ 2
Maximum number of eggs per female lifetime	2	1160	Fournet et al. 2000	580–2320	e	*/ 2
Proportion of females	1	0.53	Fournet et al. 2000	0.4–0.66	n	± 4SD, Fournet et al. 2000
BG bioturbator parameters						
Proportional bioturbator effect on shoot quality	2	0.5	Wurst et al. 2004	0.4–0.6	u	SD, Wurst et al. 2004
Proportional bioturbator effect on root biomass	2	0.27	Wurst and Jones 2003	0.22–0.3	u	SD, Wurst and Jones 2003
Proportional bioturbator effect on shoot biomass	2	0.48	Wurst et al. 2006	0.03–1.16	n	SD, Wurst et al. 2006
Technical parameters						
Number of runs	0	1000	MCE	–	–	–
Duration of one growing season [months]	2	6	EG	–	–	–
Number of generations per year for all except plant and BG antagonists	3	4	EG	–	–	–
Number of generations per year for BG antagonist	2	2	Fournet et al. 2000	–	–	–

Parameter: AG – aboveground, BG – belowground, SD – standard deviation; Accuracy (Acc): 0 – null hypothesis, 1 – very well known, 2 – well known, 3 – approximately known, 4 – not well known; Source: CI – confidence interval, MCE – most conservative estimate, EG – educated guess, DT – unpublished data; Sensitivity analysis/ Range: minimum and maximum value of the parameter range explored in the sensitivity analysis; Sensitivity analysis/ Distribution (Distr): u – uniform distribution, e – exponential distribution, n – normal distribution; Sensitivity analysis/ Source: EG – educated guess, ±SD – range refers to default ± 1 standard deviation, +*x**Def – range refers to default and default + *x**default, ±*x*% – range refers to default ± *x*%, */*x* – range refers to default * 10 and default/ 10, DT – unpublished data.

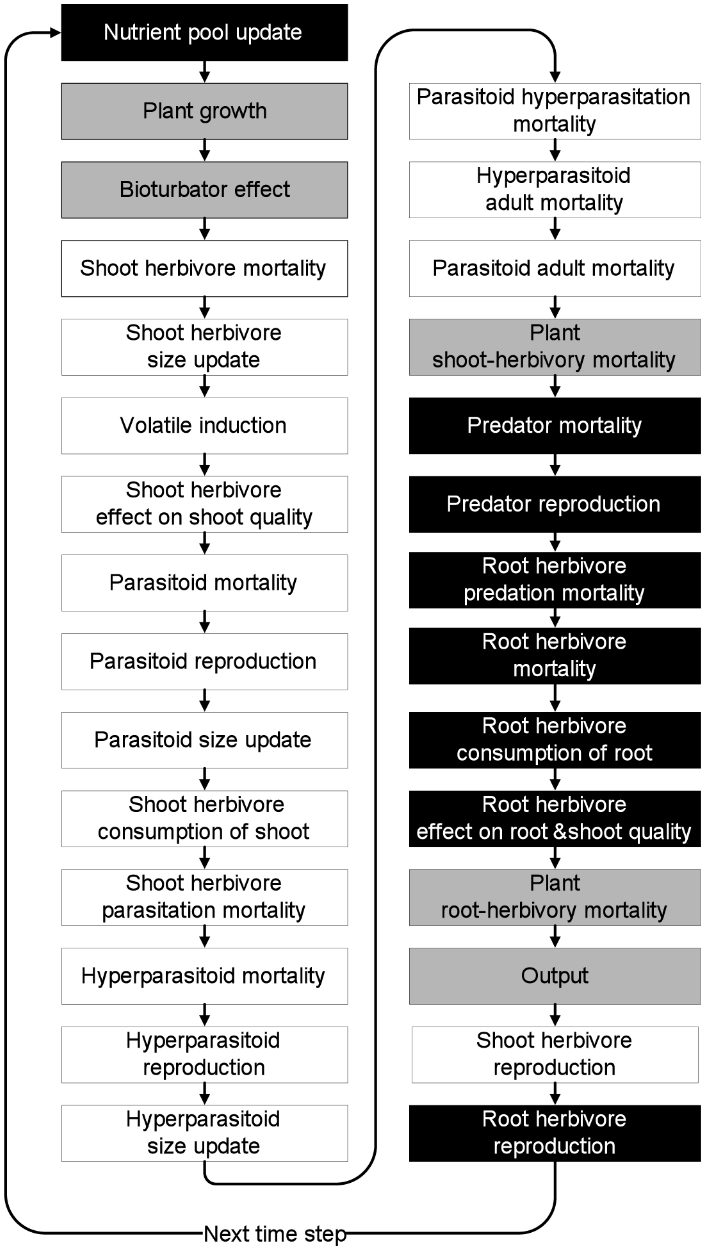

Figure A1. Scheduling of the main processes in the simulation model ABBE. Processes occur aboveground (white boxes), belowground (black boxes), or both above- and belowground (grey boxes).

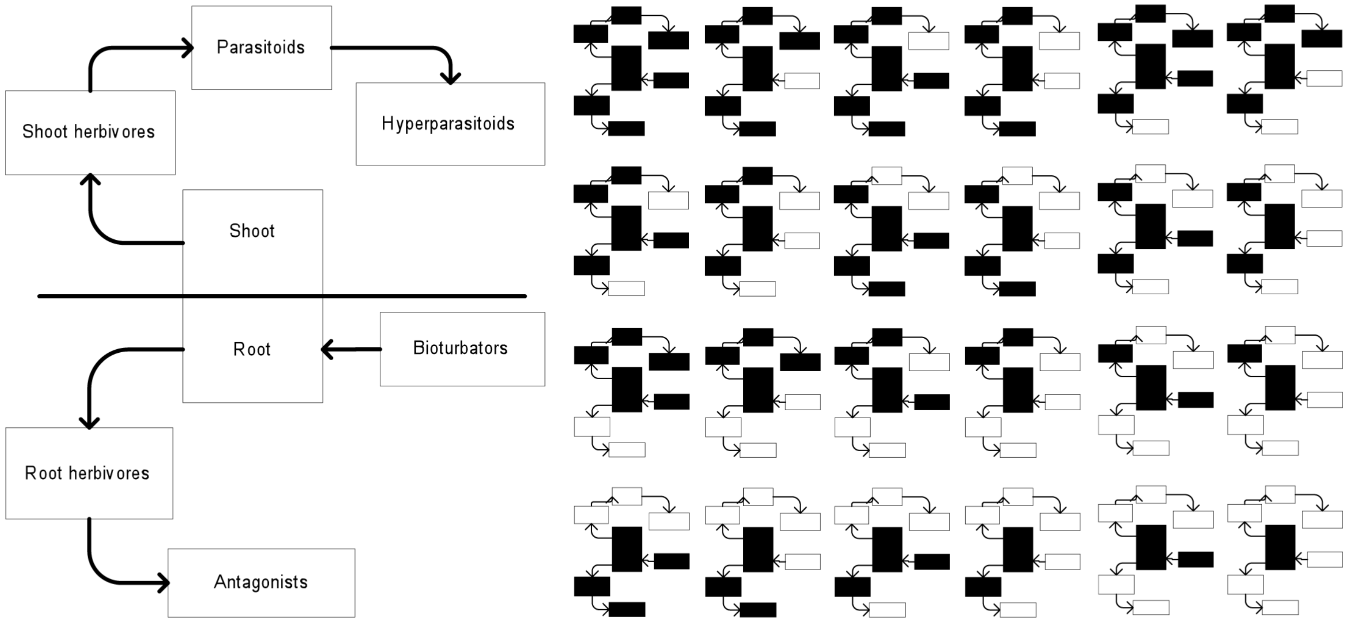

Figure A2. Overview of the treatment combinations tested in the simulation experiments. Treatments were presence (black boxes) and absence (white boxes) of the trophic levels named in the flow diagram on the left. Arrows indicate interactions.