



ODD Protocol for IPS-SPREADS modified after Pietzsch et al. (2021)

Bruno Walter Pietzsch, Chris Wudel & Uta Berger

December 16, 2021

1 Preamble

This is the modified ODD protocol for IPS-SPREADS which was modified after its original from Pietzsch et al. (2021). The main changes lie within the removal of random placement of spruce trees during model setup. Now the random placement of spruce trees is done beforehand during the data processing with R and incorporated into the imported raster file *PAS.asc.* Further modifications include the introduction of a new global result in the form of amount of trees cut after each generation: *ncut1*, *ncut2* and *ncut3*.

2 Purpose and patterns

IPS-SPREADS (Infestation Pattern Simulation Supporting PREdisposition Assessment DetailS) is an advanced version of, IPS (Kautz et al., 2014, 2016) (Infestation Pattern Simulation). In addition to the purposes of the original IPS model this new version allows the following three main objectives:

- 1. Dispersion and infestation of spruce trees (*Picea abies* (L.) H. Karst 1881) of an European spruce bark beetle (*Ips typographus* L. 1758) population in real landscapes through import capabilities of geographical data such as tree height or spruce proportions,
- 2. test of different management strategies (e.g. sanitation felling), and
- 3. account for different climate scenarios and their impact on the beetle population as well as the spruce vitality through adjustments in the imported geographical data as well as beetle population features (e.g. beetle generations per year).

These objectives enable IPS-SPREADS to simulate risk and predisposition assessments for current and future forest protection scenarios in managed as well as in unmanaged spruce forests.

The patterns used for assessing the usefulness of IPS-SPREADS are infestation patterns observed 2015 to 2017 in the Saxon Switzerland national park (Germany). For this, simulated spatio-temporal distributions of both infested trees and whole infestation cohorts were compared with the observational data.

3 Entities, state variables, and scales

The following three entities are simulated within the model:

- 1. patches representing the abiotic (for example streets) or biotic (for example spruce trees) environment,
- 2. beetles which represent *lps typographus* individuals, and
- 3. volatiles which represent kairomones emitted from infested spruce trees as well as pheromones produced by infesting bark beetles.

The state variables of these entities as well as their ranges, standard values and sources for their settings are listed in Table 1. Unless otherwise stated, the corresponding variable was taken directly from the IPS model (Kautz et al., 2014, 2016), or with some adjustments. Otherwise, the variable was added for the enhancement of IPS to IPS-SPREADS.

Grid size is 5 m x 5 m for each patch (Kautz et al., 2014, 2016). The total world size depends on the extent of the underlying GIS data imported into the model. Reasonable sizes are 1 km^2 (ca. 450 x 450 patches) due to huge computational cost if a mass outbreak with large beetle numbers has to be simulated in that area.

Time is measured in ticks, where one tick represents the time a bark beetle needs to fly from one patch to another. Using 1.667 $\frac{m}{s}$ as mean flight speed for the bark beetles (Byers, 1996a,b), one tick simulates three seconds in reality. To shorten the simulation time, 200 ticks represent one day, as after that time more than 90 - 95 % individuals of one flight wave have reached one of the possible destinations (e.g. successful infestation of a spruce tree).

4 Process overview and scheduling

4.1 Processes

The model is developed to cover the whole dispersal and infestation cycle of up to three bark beetle generations in one year. It is structured into thirteen processes: four related to the environment (import of GIS data, application of those data to patch variables, placement of beetle source trees and updating state variables), three concerning beetles (creation, movement and infestation attempt), two performed by volatiles (creation, movement), one concerning management (removal of infested trees) and three related to the model results (calculating those results, updating all plots and exporting the infestation pattern as a raster file). The patches update their state variables during the import and application of GIS data as well as every time step. Bark beetles perform each of their processes every time step of the simulation, but for spawning which only happens at the beginning of each day (every 200 time steps). Volatile spawning and subsequent movement occurs on a time-step basis. The removal of infested trees occurs only once each beetle generation (after all beetles have finished their dispersal flight). Processes concerning the calculation of model results happen at three different times throughout the simulation: at the beginning of each day (updating the plots), at the end of each beetle generation (calculating the results) and at the end of the whole simulation (exporting the infestation pattern as a raster file).

Table 1: State variables of the entities present in IPS-SPREADS with their minimum and maximum values.

entity	variable	description	min	max
patch	infestlev	infestation level: 0 - non-infested, 1 - infested, 2 - fully occupied, 3 - not susceptible, 4 - pheromone trap	0	4
	primattract	kairomone-induced attractiveness [n] (0 - not infestable, 9 - very vulnerable); calculated with predisposition assessment systems (Netherer and Nopp-Mayr, 2005)	0.0	9.0
	secattract	pheromone-induced attractiveness [n] produced by infesting beetles or emitted by pheromone dispensers	0.0	8,913.0
	totalattract	sum [n] of <i>prim-</i> and <i>secattract</i>	0.0	8,922.0
	n _{min}	minimum number of attacking beetles for a successful infestation: $n_{min} = 221.25 - 21.25 * primattract$	30	200
	n _{max}	capacity [n] for infesting beetles depending on tree size	0	8,913
	height	tree height [m] derived from digital difference model	0.0	50.0
	n _{start}	capacity [n] for emerging beetles depending on tree size	0	21,958
	n _{stay}	number [n] of currently attacking beetles	0	n_{min}
	n _{inf}	number [n] of currently infesting beetles	n_{min}	n_{max}
	n_{lock}	number [n] of currently locked or trapped beetles	0	∞
	tree _{infestdist}	distance [m] to the nearest beetle source	5.0	∞
	delay	starting day [n] of beetle swarming (counted from the 1st of April)	0	274
	wave-count	number [n] of emerged beetle flight waves from this patch	0	56
	inf	moment of real world infestation: 0 - no data available, 1 - infested during the previous year, 2 - infested during the simulated year, 3 - infested more than one year before	0	3
	infestday	day [n] of simulated infestation (counted from the 1st of April)	0	274
	local-speed	global wind speed $\left[\frac{m}{5}\right]$ reduced by <i>roughness</i>	0	5.5
	roughness	canopy flow index (attenuation coefficient)	1.45	4.03
	neighbour-height	mean height [m] of surrounding patches	0.0	50.0
beetles	status	life status: dispersing or staying	-	_
	energy	energy level	3.0	30.0
	t_dispers	time steps [n] since start of dispersal flight	0	∞
	staytime	time steps [n] since attacking a tree	0	200
	efficiency	energy efficiency	1.0	100.0
	flightdist	distance flown [m] from start to final destination	0.0	∞
	starttime	time step [n] the dispersal flight started	0.0	∞
	driftdist	distance drifted [m] by wind	0.0	∞
	traveldist	sum [m] of <i>drift-</i> & <i>flightdist</i>	0.0	∞
	airline origin	linear distance [m] between starting point and final destination patch that sprouted the beetle	0 -	∞ -
volatiles	flightdist	distance [m] moved due to diffusion	0.0	∞
	driftdist	distance [m] drifted by wind	0.0	∞
	traveldist	sum [m] of <i>drift-</i> & <i>flightdist</i>	0.0	∞
	voattract	totalattract [n] of volatiles' source patch	0.0	8,922.0
	origin	volatiles' source patch	-	-

4.2 Schedule

The simulation starts with the first day of beetle flight, which is set by the minimum delay of all patches capable of producing beetles (beetle sources). The start of beetle flight is scheduled first because subsequent beetle actions as well as volatile interactions are based on the existence of beetles. Volatiles are produced and moved before beetle movement because beetles cannot sense patches other than their current one without volatiles. Movement is the first beetle action because subsequent actions depend on a reduced energy level (timing and target of infestation attempt) and it can be assumed that beetles looking for a susceptible host tree begin their day with flying. The decision for an infestation attempt is scheduled after the beetle movement as their decision for such an attempt is based on their current energy level and the surrounding volatiles. Tree defenses are performed after the actions performed by beetles because their defense is directly influenced by the amount of beetles attacking them. Plots are updated at the beginning of each day to depict the daily baseline of all units and properties (Figure 1). Removal of infested trees only happens after all beetles ended their dispersal flight (end of one beetle generation) because it should represent the management attempt of killing the next beetle generation which is produced in all trees infested by the previous generation. Results are calculated for each beetle generation separately, therefore the corresponding process is scheduled after each beetle generation and after the removal of infested trees. The infestation pattern is exported at the end of the whole simulation because it contains the infestations of all beetle generations.

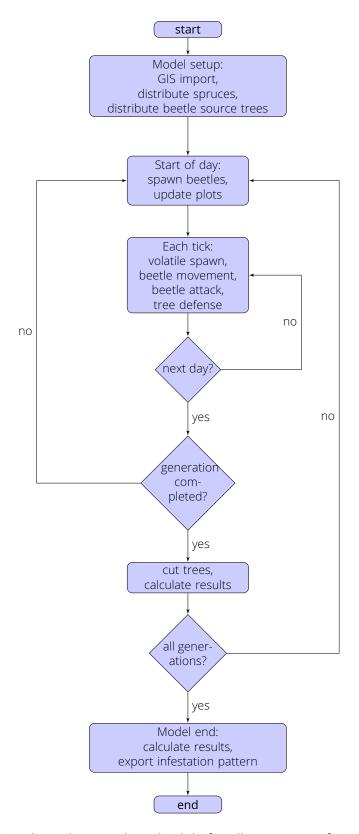


Figure 1: Flow chart showing the schedule for all processes of IPS-SPREADS.

5 Design concepts

5.1 Basic principles

5.1.1 Overview

The basic principles used in IPS-SPREADS are as follows:

- 1. correlated random walk(Renshaw and Henderson, 1981) for beetle dispersal
- 2. carrying capacity(Begon et al., 2007) for tree capacities for infesting and emerging beetles
- 3. canopy flow index(Mursch-Radlgruber and Kovacic, 1990) for wind reduction

Furthermore, two well accepted models for the European Spruce Bark Beetle (*Ips typogra-phus*) are used:

- 1. predisposition assessment systems (PAS)(Netherer and Nopp-Mayr, 2005) for spruce tree primary attractiveness
- 2. phenology model (PHENIPS)(Baier et al., 2007) for calculating the begin of beetle swarming

In the following sections, the basic ideas of these principles and models as well as their usage in IPS-SPREADS are described.

5.1.2 Correlated random walk

The correlated random walk (Renshaw and Henderson, 1981) was used to simulate the beetle movement during undirected dispersal flight (Kautz et al., 2014, 2016; Byers, 1996a, 2000): Each beetle randomly picks a new moving direction depending on its directional angle from the time step before as well as the predefined angle sector (*moveangle*). The new heading is randomly drawn from a normal distribution with the old heading as mean and a standard deviation of approximately 0.408*moveangle. Minimum and maximum are defined by the old heading and plus or minus *moveangle*.

5.1.3 Carrying capacity

The carrying capacity "[...] represents the population size that the resources of the environment can just maintain ('carry') without the tendency to either increase or decrease." (Begon et al., 2007) As such, the possible number of beetles breeding on as well as emerging from a spruce tree is limited and depends on the tree size and on the density of breeding beetles. The latter was derived from several publications (Weslien and Regnander, 1990; Botterweg, 2009; Komonen et al., 2011) measuring these densities on different occasions as well as research sites (Table 2).

The surface area of the tree had to be calculated from tree height (the digital difference model nDOM) as well as forest yield tables (Wenk et al., 1984) taking the site's productivity into account. For this, the measured tree height (nDOM) was converted into tree age and BHD using forest yield classes (Wenk et al., 1984). Using the dependency between infestable tree surface area and BHD(Weslien and Regnander, 1990), this diameter was converted into an habitable surface area as well as into the corresponding capacities for beetles (Table 3) using the overall means of Table 2.

Table 2: Mean densities and standard deviations of parental and juvenile beetles used for calculating the tree capacities for IPS-SPREADS.

Source	Year	Egg galleries	σ	Eggs	σ
		$\left[\frac{n}{m^2}\right]$	$\left[\frac{n}{m^2}\right]$	$\left[\frac{n}{m^2}\right]$	$\left[\frac{n}{m^2}\right]$
(Weslien and Regnander, 1990)	1979	467	81	1,635	722
	1981	485	121	581	425
(Botterweg, 2009)	1983	-	-	990	629
(Komonen et al., 2011)	2006	446	207	1,385	875
μ	-	466	84	1,148	341

5.1.4 Canopy flow index

To calculate the reduced wind speed within the forest, the canopy flow index (Mursch-Radlgruber and Kovacic, 1990) is applied for each 5×5 m raster cell of IPS-SPREADS. To achieve this, 6.3 m as the mean beetle flight height (Duelli et al., 1986), the tree height on the given raster cell, the global windspeed and, canopy indexes for spruces as well as gum oaks (Cionco, 1978) is used.

5.1.5 Predisposition assessment systems (PAS)

The predisposition assessment systems (PAS) for the European Spruce Bark Beetle (*Ips ty-pographus*) were first published by (Netherer and Nopp-Mayr, 2005) and later updated by (Schopf et al., 2009, 2013). They consist of knowledge-based additive expert models which assess the predisposition of forest stands and sites for biotic (bark beetle infestation) and abiotic damages (wind and snow breakage). For different indicators (e.g., slope position, tree age or canopy closure) predisposition values are calculated and summed for each forest stand. These sums are related to the maximum value achievable within the system and the resulting percentage correspond to the relative predisposition level of the respective assessment unit. In IPS-SPREADS, these predisposition assessment systems are used to calculate the primary attractiveness (*primattract*) of each 5 x 5 m raster cell inside the model.

5.1.6 Phenology model (PHENIPS)

The phenology model PHENIPS was developed by (Baier et al., 2007) "[...] for spatial and temporal simulation of the seasonal development of *Ips typographus* at the Kalkalpen National Park in Austria." The model uses the digital elevation model (DEM) to interpolate measurements of temperature and solar radiation and to calculate the micro-climatic conditions for beetle development. Using PHENIPS, it is possible to calculate the day of onset of beetle swarming for which it was used in IPS-SPREADS.

5.2 Emergence

The emergent key outputs of IPS-SPREADS are the dispersion pattern of *Ips typographus* as well as the amount and spatial pattern of infested spruce trees in the research are. If management strategies such as the usage of pheromone traps are tested, then the number of trapped beetles and the change in infested trees are further emergent key results of the model.

Table 3: Results of calculating tree capacities for infesting (n_{start}) and emerging (n_{max}) beetles.

productivity	max height	BHD	Ao	n	n
chr	_		m^2	n _{max}	n _{start}
	m	cm	[11]	n	n
rich	4.20	5.65	0.0	0	0
	9.60	9.35	1.1	532	1,312
	15.25	13.05	3.2	1,481	3,648
	19.85	17.80	5.8	2,698	6,647
	23.65	23.30	8.8	4,108	10,120
	26.85	27.85	11.3	5,274	12,992
	31.75	35.75	15.7	7,299	17,981
	35.00	42.05	19.1	8,913	21,958
strong	3.10	4.00	0.0	0	0
	7.00	7.50	0.1	58	144
	11.90	11.00	2.1	955	2,353
	16.20	14.90	4.2	1,955	4,816
	19.80	19.40	6.7	3,108	7,657
	23.00	23.60	9.0	4,185	10,309
	28.20	31.40	13.3	6,184	15,234
	32.00	38.20	17.0	7,927	19,527
medium	2.00	2.55	0.0	0	0
	5.00	5.70	0.0	0	0
	9.20	8.85	0.9	404	996
	13.00	12.15	2.7	1,250	3,080
	16.45	15.85	4.7	2,198	5,416
	19.50	19.60	6.8	3,159	7,783
	24.85	27.15	10.9	5,095	12,551
	29.00	34.10	14.8	6,876	16,939
rather poor	1.50	1.60	0.0	0	0
	3.30	4.30	0.0	0	0
	6.70	7.00	0.0	0	0
	10.20	9.70	1.3	622	1,533
	13.40	12.80	3.0	1,417	3,490
	16.30	16.10	4.9	2,262	5,574
	21.60	23.20	8.8	4,082	10,056
	26.00	30.10	12.6	5,851	14,413
poor	1.00	0.85	0.0	0	0
	2.50	2.80	0.0	0	0
	4.90	5.25	0.0	0	0
	7.85	7.70	0.2	110	270
	10.75	10.35	1.7	789	1,943
	13.40	13.20	3.3	1,519	3,742
	18.50	19.60	6.8	3,159	7,783
NIA	23.00	26.40	10.5	4,902	12,077
NA	1.80	2.00	0.0	0	0
	4.20	5.10	0.0	0	0 E0E
	8.40	8.20	0.5	238	585
	12.00	11.30	2.2	1,032	2,543
	15.40	14.80	4.1 6.1	1,929	4,753
	18.40	18.40	6.1	2,852	7,026
	23.70	25.80	10.2	4,749 6 5 4 2	11,698
	28.00	32.80	14.0	6,543	16,118

5.3 Adaptation

Beetles' adaptive traits are the decision for an infestation attempt in dependence of their current energy level and the total attractiveness of the most attractive volatile in their perception distance or the patch they are currently passing. With this, the beetles try to maximize the overall number of successfully infesting individuals. The tree's secondary attractiveness (which is always zero at the beginning of the simulation) adapts to the amount of beetles waiting on (marginal increase) or infesting (strong increase) the tree. After the capacity of infesting beetles is reached the total attractiveness of the tree is set to zero (due to the beetles anti-aggregation pheromones).

5.4 Objectives

The beetles' objective is to successfully infest a spruce tree. This can be measured by the proportion of infesting beetles of the overall population at the end of each simulation run. If management strategies are implemented, the objective of the management is to reduce the number of infested trees in a specific part of the given landscape by reducing the number of susceptible trees or to reduce the beetle population density with pheromone traps there. The effectiveness of these strategies can be measured by repeating the exact same simulations with and without the chosen management actions and calculation of the difference between the different management actions in infested trees in the chosen area.

5.5 Learning

Learning is not included in the IPS-SPREADS model.

5.6 Prediction

Prediction is not included in the IPS-SPREADS model.

5.7 Sensing

Beetles sense their energy level, movement direction, wind speed and direction, the attractiveness of all volatiles inside their perception distance as well as of the tree they are currently passing. Volatiles sense their traveled distance (sum of flight and drift distance), wind speed and direction as well as their own attractiveness. Spruce trees sense the number of beetles staying on or infesting them.

5.8 Interaction

The interactions in the IPS-SPREADS model are fully based on the intra-specific volatiles (pheromones) of the bark beetles. At first, beetles are attracted to spruce trees by kairomones (represented by the primary attractiveness of the trees). Later, after a successful infestation, the infesting beetles produce pheromones to attract more beetles (aggregation pheromones; depicted by the turtle breed *volatiles*) as well as to repel any further beetles after the tree capacity is reached (anti-aggregation pheromones). Traps supplied with a pheromone dispenser also attract beetles imitating a successfully infested host tree by emitting turtles of the breed volatiles depicting aggregation pheromones.

5.9 Stochasticity

Stochasticity plays a major role in the IPS-SPREADS model as many parts of the model are different every simulation run due to stochastic code implementation (Table 4).

Table 4: Overview of model parts with implemented stochasticity. For more details on the implementation see sections *Initialization* (p. 10) and *Sub-models* (p. 16).

model part	moment of stochasticity	further information
beetle energy	during creation	follows a Gaussian distribution for the whole population
beetle energy efficiency	during creation	follows a negative exponential distribution for the whole population
beetle starting direction	during creation	equally distributed (0.0 - 360.0°)
moving direction	every tick during flight	follows a Gaussian distribution inside the defined angle
chance of directed beetle flight	every tick during flight	10 % probability to fly directly to the volatiles' source patch; also depends on the beetle energy
sanitation felling	after each generation	the infested trees to be cut are randomly cho- sen according to the defined sanitation proportion and the total number of host trees of the given beetle generation

5.10 Collectives

Collectives are not included in the IPS-SPREADS model.

5.11 Observation

At the end of each simulation run, the number of successfully infesting beetles and their proportion of the total population is calculated. Furthermore, the amount of infested trees as well as the number of beetles caught in pheromone traps, starved to death, left the world, killed by the tree defense or by sanitation felling are calculated. Also, the mean and maximum distance of infested trees to the nearest beetle source, the mean and maximum flight distance, drift distance and travel distance of all successful beetles are measured. Last but not least, IPS-SPREADS provides the opportunity to export the infestation pattern all beetle generations at the end of the simulation.

6 Initialization

6.1 General information

The initial state of IPS-SPREADS heavenly depends on the imported data. See section *Input data* on page 14 for detailed information on this data and its corresponding parameters inside IPS-SPREADS.

6.2 World size

The size of the model world is depending on the extent of the imported data. For example, if the raster layer containing information on the vitality of spruce trees (PAS.asc is 500 x 500 meters, the initial world size of IPS-SPREADS would be 100 x 100 patches as each patch resembles one tree and its stand size of five meters.

6.3 Patches

Staying with the above example of a world with 500×500 meters, this would result in 1000 patches. Each patch can be a spruce, a pheromone trap, a beetle source, a cut tree or empty (which simply means that on this patch is neither a spruce tree, nor a beetle source nor a pheromone trap nor a cut tree). The state variables and their values for initialization for each type of patch can be found in Table 5.

6.4 Entity beetles

This entity resemble the European Spruce Bark Beetle (*Ips typographus* L.), which are sprouted by beetle sources. At the beginning of the simulation (step 0), no beetles are present. They are first sprouted during the first tick (step 1) of the model. Nevertheless, Table 6 gives an overview on their state variables and values.

Table 5: State variables and their possible values for all patch types (spruce trees, pheromone traps, beetle sources and other) at the beginning of a simulation and an example world of 500×500 patches.

stato		nato	h typo		short
state variable	spruce	trap	h type source	other	description
pxcor		0 < x	≤ 100		The x-coordinate.
pycor		$0 \le x$	≤ 100		The y-coordinate.
pcolor	72 - 78	5	35	0	Higher primattract values result in a
					darker green for spruces: $78 - \frac{primattract}{1.5}$.
					Traps are grey, sources are brown and
					emtpy patches are black.
infestlev	0	4	3	3	0 - susceptible, 1 - infested, 2 - fully occu-
n ring attract	0 0	0			pied, 3 - not susceptible, 4 - trap.
primattract	0 - 9	0	-	-	Precalculated primary attractiveness based on the predisposition assessment
					systems (Section 5.1.5).
secattract	0	15	_	_	The secondary attractiveness resembling
Security det	O	13			pheromones emitted by infesting beetles
					or by a pheromone dispenser.
totalattract	0 - 9	15	_	_	The sum of primary and secondary at-
					tractiveness.
n _{min}	30 - 200	-	-	-	The minimum threshold for a successful
					infestation is calculated on the primary
					attractiveness (Kautz et al., 2014, 2016):
					221.25 – 21.25 * primattract
n _{max}	0 - 8,913	∞	-	-	The precalculated capacity for infesting
	0 50		0 50	0 50	beetles (Section 5.1.3).
height	0 - 50	0	0 - 50	0 - 50	The tree height from the digital difference
n	0 21 050		0 21 050		model (nDOM).
n _{start}	0 - 21,958	-	0 - 21,958	-	The precalculated capacity for starting beetles (Section 5.1.3).
n -+	0	_	_	_	Amount of beetles currently attacking the
n _{stay}	O				patch.
n _{inf}	0	_	_	-	Amount of beetles currently infesting the
···					patch.
n _{lock}	-	0	-	-	Amount of beetles trapped by the patch.
tree_infestdist	0	-	-	-	Distance of infested patch to nearest
					beetle source.
spruceprop	0 - 100	-	-	-	Probability to be a spruce.
delay	0 - 274	-	0 - 274	-	Precalculated day of first beetle flight
			0		(Section 5.1.6).
wave-count	-	-	0	-	Counter for released beetle flight waves.
inf	0 or 2	-	1	0 or 3	0 - no data on real world infestation available 1 patch was infested in provious
					able, 1 - patch was infested in previous year, 2 - patch was infested in current
					year, 3 - patch was infested two or more
					years before.
infestday	0	_	-	_	Day number on which the infestation
,					takes place during the simulation.
local-speed		0 -	5.5		Global wind speed is reduced by the
,					canopy roughness (Section 5.1.4).
roughness		1.45	- 4.03 12		Canopy roughness based on spruce pro-
					portion and tree height (Section 5.1.4).
neighbor-height		0	- 50		The mean height of all neighboring
					patches.

Table 6: State variables and their possible values for the entity beetle for the given example of a world with 100×100 patches.

state variable	value	description
who	0 - max	The ID of the turtle. The maximum number of beetles depends on
		the amount of beetles sources as well as the starting capacity of those
		sources.
color	15	All beetles are colored red.
heading	0 - 360	The beetles' heading is chosen randomly via an equal distribution.
xcor	0 - 100	The same as the beetles' source pxcor.
ycor	0 - 100	The same as the beetles' source <i>pycor</i> .
shape	default	There are no adjustments to the basic NetLogo settings here.
label	NULL	There is no labeling in IPS-SPREADS.
label-color	9.9	There is no labeling in IPS-SPREADS.
breed	beetles	All beetles belong to the breed beetles.
hidden?	false	All beetles are visible.
size	0.5	Beetles are small.
pen-size	1	There are no adjustments to the basic NetLogo settings here.
pen-mode	up	There are no adjustments to the basic NetLogo settings here.
status	dispersing	All beetles start their life with the dispersal flight.
energy	1 - 30	The energy level of each beetle is drawn from a normal distribution
	_	with $\mu = meanenergy$, $\sigma = 2$, min = 1 and max = 30.
t_dispers	0	Measures how long each beetle is flying in ticks.
staytime	0	Tick counter for how long the beetle is trying to attack a tree.
efficiency	1 - 100	The energy consumption $(\frac{1}{efficiency})$ of each beetle during dispersal flight.
		It is drawn from a negative exponential distribution with λ = 10, min =
		1 and max = 100.
flightdist_all	0	Measures the distance each beetle flew during its dispersal flight.
starttime	1	Saves the tick number on which the beetle started its dispersal flight.
driftdist	0	Measures how far a beetle is drifted by wind.
traveldist	0	Measures how far a beetle traveled (<i>driftdist</i> + <i>flightdist_all</i>) during its dispersal flight.
airline	0	Measures the distance between the beetles' source patch and its final destination.
origin	patch x y	Stores the identity of the patch that sprouted the beetle.

6.5 Entity volatiles

This entity depicts the pheromones emitted by infesting beetles as well as pheromone dispenser from traps. At the beginning of the simulation (step 0), no volatiles are present. They are first sprouted during the first tick (step 1) of the model. Nevertheless, Table 7 gives an overview on their state variables and values.

Table 7: State variables and their possible values for the entity volatile for the given example of a world with 100×100 patches.

state variable	value	description
who	0 - ∞	The ID of the turtle breed volatile. The maximum number depends on the amount of deployed pheromone traps and infested trees as well as the time of infestation of those trees as each time step each pheromone trap and each infested tree sprouts one turtle of the breed volatile.
color	45	All volatiles are colored yellow.
heading	0 - 360	The volatiles' heading is drawn from an equal distribution.
xcor	0 - 100	At the time of sprouting this is identical with the <i>pxcor</i> of the patch emitting the volatile.
ycor	0 - 100	At the time of sprouting this is identical with the <i>pycor</i> of the patch emitting the volatile.
shape	dot	Volatiles are depicted as dots.
Iabel	NULL	There is no labeling in IPS-SPREADS.
label-color	9.9	No adjustments to the basic NetLogo setting was done here.
breed	volatiles	Each volatile belongs to the breed <i>volatiles</i> .
hidden?	false	All volatiles are visible.
size	0.3	Volatiles are even smaller than beetles.
pen-size	1	No adjustments to the basic NetLogo settings were done here.
pen-mode	ир	No adjustments to the basic NetLogo settings were done here.
flightdist	0	Measures the volatiles flight distance.
driftdist	0	Measures the volatiles distance drifted by wind.
traveldist	0	Measures the volatiles travel distance (flightdist + driftdist).
voattract	0 - 8,922	Saves the attractiveness (<i>totalattract</i>) of its source patch as its own attractiveness.
origin	patch x y	Saves the identity of the patch that sprouted the corresponding volatile.

7 Input data

Input data for IPS-SPREADS is used for the generation of the biotic and abiotic environment as well as the simulation of long term changes in climate, in population dynamics as well as in management strategies. For that, GIS data of the chosen research area is imported as raster (.asc) file. Table 8 gives an overview on the data IPS-SPREADS is capable of importing.

Table 8: Overview on data imported in IPS-SPREADS

input	description	data source
firstwave.asc	calculated begin of beetle swarming (Baier et al., 2007)	weather stations & digital elevation model (DEM)
hostcapacity.asc	tree capacities for infesting beetles	tree height, site productivity & breeding densities (Botterweg, 2009; Wenk et al., 1984; Weslien and Lindelow, 1990; Komonen et al., 2011)
inf.asc	localization of real world infesta- tions	remote sensing data
PAS.asc	location and primary attractiveness of spruces (Netherer and Nopp- Mayr, 2005; Schopf et al., 2009, 2013)	forestry inventory data & forest site data
sourcecapacity.asc	tree capacity for emerging beetles	tree height, site productivity & breeding densities (Botterweg, 2009; Wenk et al., 1984; Weslien and Lindelow, 1990; Komonen et al., 2011)
tree-height.asc	used for wind speed reduction	digital difference model (nDEM)

8 Sub-models

8.1 Overview

In IPS-SPREADS three main model parts are calling sub-models: the setup, the graphical user interface and the go function. While the first and second one are only run once each simulation, the latter is performed after the other two until the stop condition is met. These main model parts call various sub-models (Table 9), which are explained in detail within each main model parts section in the following.

Table 9: Sub-models called during the two main procedures of IPS-SPREADS in their exact order during a simulation.

#	procedure setup	procedure interface	procedure go
1	import-GIS-data	deploy-beetle-source	spawn-beetles
2	create-environment	deploy-detention-device	draw-plots
3	distribute-source-trees		spawn-volatiles
4	draw-plots		move-volatiles
5			move-beetles
6			try-to-infest
7			tree-defense
8			cut-infested-trees
9			calculate-results
10			export-infestation-pattern

8.2 Setup

8.2.1 Overview

Detailed information on the sub-models called during the setup procedure (*import-GIS-data, create-environment, distribute-source-trees, draw-plots*) is given in the following sections. Despite calling the aforementioned sub-routines the setup procedure does the following things in that exact order:

- 1. clears everything using clear-all,
- 2. resets the models ticks using reset-ticks,
- 3. clears all agent-sets:
 - a) host
 - b) waiting-tree
 - c) source
 - d) spruce
 - e) device
- 4. clears all lists:
 - a) *b_airline*

- b) b_traveldist
- c) b_flightdist_all
- 5. sets the day counter to zero
- 6. sets the generation counter (ngeneration) to one
- 7. calls sub-model import-GIS-data
- 8. sets random-seed to seed (if seed \neq 0)
- 9. calls sub-model create-environment
- 10. adds all patches with primattract above zero to agent-set spruce
- 11. calls sub-model *draw-plots*
- 12. sets random-seed to new-seed (if seed \neq 0)

8.2.2 import-GIS-data

With this procedure the GIS data is imported into IPS-SPREADS and is assigned to the corresponding model parts. Table 10 gives an overview on all the data parts and their model representation. The *PAS.asc* file is imported using *gis:load-dataset* and used to resize the Net-Logo world to its extent using *resize-world*, *gis:width-of* and *gis:height-of* functions as well as the *gis:set-world-envelope-ds* and *gis:envelope-of* functions. After this the data is applied with *gis:apply-raster* and the displayed world size is adjusted using *set-patch-size* $\frac{702.5}{max-pxcor}$ to get nearly the same displayed world size for each scenario inside the model interface. All files are imported using the *gis:load-dataset* function and applied to the corresponding model parts without any adjustments.

8.2.3 create-environment

With this procedure the placement of the spruce trees inside the NetLogo world is done as well as calculations on total attractiveness and infestation thresholds of each spruce tree. For this, each patch is asked if it got a primary attractiveness (accounting for missing values in the imported data, see last paragraph of this procedure for details). If this is the case, the patch creates an empty list *infest-dist* for the infestation distance of successfully infesting beetles and calculates the infestation threshold is calculated using equation 1 (Kautz et al., 2014, 2016). If *primattract* is zero, *infestlev* is set to three (no infestation possible).

$$n_{min} = 221.25 - 21.25 * primattract$$
 (1)

After this, *secattract* is set to zero and *totalattract* of each patch is calculated by adding *primattract* and *secattract*. If *primattract* is higher than zero, the patches are colored using equation 2 below. All other patches are colored black.

$$pcolor = 78 - \frac{primattract}{1.5} \tag{2}$$

If no *primattract* is available (missing data), *primattract*, *secattract* and *totalattract* are set to zero, the patch is colored black and *infestlev* is set to three (not susceptible).

Despite all this, the *create-environment* sub-model calculates *neighbor-height*, *roughness* and *local-speed* of each patch in the following way:

· calculates *neighbor-height* of all patches using the mean height of its neighbors

Table 10: Overview on all data imported by the import-GIS-data procedure with a short description and its corresponding model parts.

file	description	parameter
PAS.asc	spruce attractiveness to beetles as calculated by the adjusted predisposition assessment systems (Netherer and Nopp-Mayr, 2005; Schopf et al., 2009, 2013)	primattract
firstwave.asc	begin of beetle swarming as calculated with PHENIPS (Baier et al., 2007)	delay
inf.asc	location, size and year of real world infestations	inf
hostcapacity.asc	capacity for infesting beetles derived from tree height, site productivity and breeding densities (Bot- terweg, 2009; Wenk et al., 1984; Weslien and Regnan- der, 1990; Komonen et al., 2011)	n _{max}
sourcecapacity.asc	capacity for emerging beetles derived from tree height, site productivity and breeding densities (Botterweg, 2009; Wenk et al., 1984; Weslien and Regnander, 1990; Komonen et al., 2011)	n _{start}
tree-height.asc	tree height derived from the digital difference model (nDSM)	height

- sets *roughness* of all patches using the following distributions:
 - μ = 2.74, σ = 1.29, if mean *spruceprop* of its neighbors ≥ 50 %
 - $-\mu = 2.68$, $\sigma = 0.66$, if mean spruceprop of its neighbors < 50 %
- calculate local-speed of all patches
 - if neighbor-height ≤ 6.3: local-speed = windspeed
 - if neighbor-height > 6.3: $local-speed = windspeed * exp^{-roughness*(1-\frac{6.3}{neighbor-height})}$

8.2.4 distribute-source-trees

This procedure is run only if *source-data* is set to *true*. During this sub-model, all patches with an *inf* of one and a *primattract* above zero (infestable spruces) get a *primattract* and *totalattract* of zero and are added to the agent-set *source*. Furthermore, their color is set to brown and their *infestlev* is set to three (not susceptible).

All patches with an *inf* of two (infestation of the following year) and a *primattract* above zero (spruce tree) change their color to white.

All patches with *inf* = three (infestation of a previous period) are set to not susceptible by setting *infestlev* to three, *primattract*, *secattract* and *totalattract* to zero. Their color is changed to black.

8.2.5 draw-plots

During this procedure all plots of the interface are updated. This is done in the following order:

1. histogram of beetle energy (*meanenergy*)

- 2. histogram of patch primary attractiveness (primattract)
- 3. line plot of beetle status
 - a) number of all killed beetles (beetle_killed)
 - b) number of all staying beetles (beetle_staying)
 - c) number of all infesting beetles (beetle_infesting)
 - d) number of all dispersing beetles (beetle_dispersing)
 - e) number of all emerged beetles (beetle_emerged)
 - f) number of all starved beetles (beetle_starved)
- 4. line plot of beetle survival ((1 beetle_infesting) * 100)

8.3 Interface

8.3.1 Overview

Detailed information on the sub-models callable from the interface can be found in the following sections. It has to be emphasized, that both of these sub-models (*deploy-beetle-source* and *deploy-detention-devices*) can only be called and applied after *setup* was run and the *go* procedure has not started. The reason for this is, that both of these sub-models add abiotic environment (change status and content of one or more patches, therefor they need an already existing model world) that affect the whole simulation from the very beginning. Further necessities that have to be met for those two sub-models are described in their respective subsections below.

8.3.2 deploy-beetle-source

This sub-model is run if the user wishes to deploy beetles sources manually and independently from real world data (e.g. observed infestation patterns) and can only be used after *setup* and before the *go* function. As long as *deploy-beetle-source* is running, the model checks if the user is left clicking inside the model world. If this is happening, the patch where the mouse cursor was at the time of clicking becomes a beetle source:

- set primary attractiveness to 0
- set secondary attractiveness to 0
- set total attractiveness to 0
- · add itself to the agent-set source
- set its color to brown
- set its infestation level to three (not susceptible)

As soon as the procedure is stopped and the go function is running, beetles will be spawned from each of the so defined beetle source patches.

8.3.3 deploy-detention-devices

This sub-model is run if the user wishes to deploy pheromone traps (detention devices) inside the simulated world. As long as *deploy-detention-devices* is running, the model checks if the user is left clicking inside the model world. If this is happening, the patch where the mouse cursor was at the time of clicking becomes a pheromone trap:

- set infestation level to four (pheromone trap)
- set its color to gray
- set primary attractiveness to 0
- set secondary attractiveness to the predefined value of dispattract
- set total attractiveness to the sum of primary and secondary attractiveness
- set infestation threshold (n_{min}) to 0
- set infestation capacity (n_{max}) to 1,000,000,000 (mimicking no capacity)

- set juvenile capacity (n_{start}) to 0
- add itself to the agent-set device

As soon as the procedure is stopped and the *go* function is running, pheromone traps start producing volatiles (pheromones from a dispenser) and trap all beetles that try to infest them.

8.4 Go

8.4.1 Overview

Detailed information on the sub-models called during the go procedure (*spawn-beetles*, *draw-plots*, *calculate-results*, *spawn-volatiles*, *move-volatiles*, *move-beetles*, *try-to-infest*, *tree-defense*, *cut-infested-trees* and *export-infestation-pattern*) can be found within the following subsections. In addition, the go procedure is executing the following things in that exact order:

- 1. if day = 0:
 - a) sets day to the minimum of delay
 - b) repeats procedure draw-plots as often as current day number
 - c) all sources with $day \ge delay$ call spawn-beetles
- 2. tick
- 3. if *ticks* mod 200 = 0:
 - a) increase day by one
 - b) all sources with $day \ge delay$ call spawn-beetles
 - c) draw-plots
- 4. if all *sources* have sprouted the predefined *swarming* and there are no dispersing or attacking beetles anymore:
 - a) call *cut-infested-trees*
 - b) call calculate-results
 - c) if all generations have been simulated or no trees have been infested *stop* the simulation
 - d) if not all generations have been simulated:
 - i. increase day by one
 - ii. perform draw-plots
 - iii. increase ngeneration by 1
 - iv. remove all source patches from agent-set source
 - v. host patches:
 - A. color them blue if inf = 2 (infestation in real world)
 - B. color them red if *inf* != 2 (no infestation in real world)
 - C. set their wave-count to 0
 - D. calculate their delay with: day + infestday (ngeneration 2) * swarming
 - E. set their *primattract* to 0
 - F. add them to agent-set source
 - G. remove them from agent-set host
- 5. creates volatiles by calling spawn-volatiles
- 6. moves volatiles by calling move-volatiles
- 7. ask all dispersing beetle:
 - a) call move-beetles

- b) call sub-model try-to-infest if energy < totalattract of patch-here
- 8. ask all staying beetles:
 - a) increase staytime by 1
 - b) if staytime exceeds 200:
 - i. increase beetle_killed counter by 1
 - ii. decrease beetle_staying counter by 1
 - iii. decrease n_{stay} of patch-here by 1
 - iv. store *airline*, *traveldist* and *flightdist_all* in the corresponding result lists and *kill* the beetle
- 9. ask agent-set host:
 - a) calculate $secattract = 0.1 * n_{stay} + n_{inf}$
 - b) calculate *totalattract* = *primattract* + *secattract*
 - c) if $n_{inf} > n_{max}$:
 - i. set totalattract 0
 - ii. set infestlev 2
- 10. asks agent-set waiting-tree to call tree-defense

8.4.2 spawn-beetles

As long as the *wave-count* of the patch calling this procedure does not reach the predefined *swarming* this sub-model sprouts $\frac{n_{start}}{swarming}$ turtles of the breed beetle and increases the *wave-count* of the respective patch each time it is run by 1. The sprouted turtles get the following properties:

- color red
- · status dispersing
- size 0.5
- starttime = ticks
- energy = random-normal with μ = meanenergy, σ = 2, min = 3 and max = 30
- efficiency = random-exponential with μ = 20, min = 1 and max = 100
- t_dispers 0
- origin patch-here
- increase counters beetle_dispersing and beetle_emerged by 1

8.4.3 draw-plots

For information see section *draw-plots* on page 18, where this sub-model was already described for the setup procedure.

8.4.4 spawn-volatiles

During this procedure, volatiles are produced by infested trees (infestlev = 1) and pheromone traps (if present). Each infested tree and each pheromone trap sprout one volatile per time step. The sprouted turtles get the following properties:

- voattract = totalattract of patch-here
- origin = patch-here
- size 0.3
- color = yellow
- shape = dot

8.4.5 move-volatiles

During this procedure, volatiles drift with the wind and perform a small diffusion movement (Figure 2). The wind drift is achieved by using equations 3 and 4 below while checking if the volatile is leaving the world. In latter case the turtle is killed. Otherwise, the *driftdist* is updated and the diffusion movement is performed by changing the volatile heading with *random-float* 360 and forwarding 0.3 (15 cm in the real world). After this, *flightdist_all* and *traveldist* are updated.

$$xcor + sin winddirection * 0.6 * windspeed$$
 (3)

$$ycor + cos winddirection * 0.6 * windspeed$$
 (4)

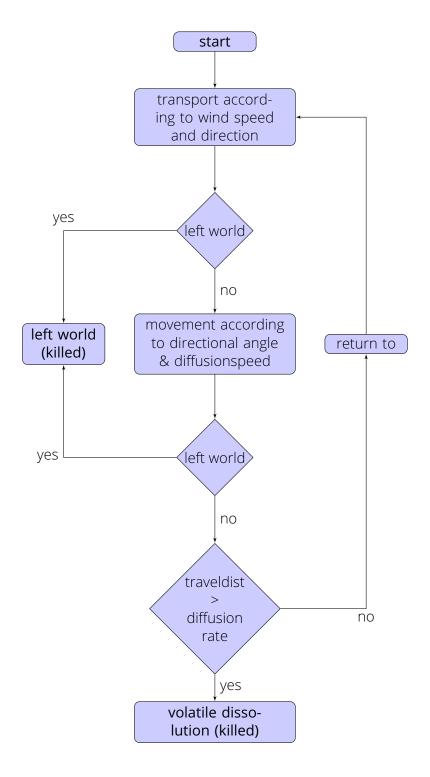


Figure 2: Flow chart showing the schedule for volatiles.

8.4.6 move-beetles

The movement of each beetle starts with its drift by wind (Figure 3) in the exact same manner as described for the volatiles (Equation 3 and 4). If the beetle is leaving the world the following things happen in that exact order:

- 1. set status lost
- 2. increase beetle_lost counter by 1
- 3. decrease beetle_dispersing counter by 1
- 4. store its airline, flightdist all and traveldist in the corresponding result lists
- 5. kill the beetle

After the drift by wind is performed and the *driftdist* is updated, the beetle flight is simulated with the following steps (in that exact order):

- 1. if percept dist = 0:
 - a) change heading with rt random moveangle and lt random moveangle
 - b) if can-move = false
 - i. set status lost
 - ii. increase beetle_lost counter by 1
 - iii. decrease beetle_dispersing counter by 1
 - iv. store its airline, flightdist all and traveldist in the corresponding result lists
 - v. kill the beetle
 - c) if can-move = true
 - i. forward 1
 - ii. increase *t_dispers* by 1
 - iii. reduce energy by $\frac{1}{efficiency}$
 - iv. increase flightdist_all by 1
 - v. update traveldist
 - vi. update airline
- 2. if perceptdist \neq 0:
 - a) if random-float 1 < 0.1, there is at least one volatile inside perceptdist and the difference in attractiveness of the most attractive volatile and the beetles current patch is > 2:
 - i. move beetle to the origin of the most attractive volatile
 - ii. decrease beetle energy by $\frac{\textit{distance_to_origin_of_volatile}}{\textit{efficiency}}$
 - iii. update t_dispers, flightdist_all, traveldist and airline accordingly
 - b) otherwise:
 - i. change heading with rt random moveangle and lt random moveangle
 - ii. if patch-ahead ≠ no-one
 - A. move 1 forward

- B. increase *t_dispers* by 1
- C. decrease energy by $\frac{1}{efficiency}$
- D. update flightdist_all, traveldist and airline accordingly
- iii. otherwise:
 - A. set status lost
 - B. increase beetle_lost counter by 1
 - C. decrease beetle_dispersing counter by 1
 - D. store flightdist_all, traveldist, and airline in the corresponding result lists
 - E. kill the beetle

If the beetle depleted its energy during its movement procedure above, it will be killed and the respective counters are being updated:

- 1. add one to the beetle starved counter
- 2. reduce the beetle_dispersing counter by one
- 3. store airline, traveldist and flightdist_all in the respective result lists
- 4. kill the beetle

8.4.7 try-to-infest

This procedure describes what happens to the beetles once they try to infest a susceptible patch. For this, the procedure first checks if the number of already infesting beetles (n_{inf}) exceeds the maximum capacity (n_{max}) and stops if this is the case. Otherwise, there are three possible scenarios that are handled in the following way:

- 1. the attacked patch is a spruce and not yet infested
 - a) set status staying
 - b) decrease beetle_dispersing counter by 1
 - c) increase beetle_staying counter by 1
 - d) change the beetle color to orange
 - e) set staytime to 0
 - f) add the attacked patch to the agent-set waiting-tree
 - g) increase n_{stay} of the attacked patch by 1
- 2. the attacked patch is a spruce and already infested
 - a) set status infesting
 - b) increase beetle_infesting counter by 1
 - c) decrease beetle_dispersing counter by 1
 - d) increase n_{inf} of the attacked patch by 1
 - e) store the beetles *flightdist_all* in *infest-dist* list of the attacked patch
 - f) store the beetles flightdist_all, traveldist and airline in the corresponding result lists
 - g) kill the beetle

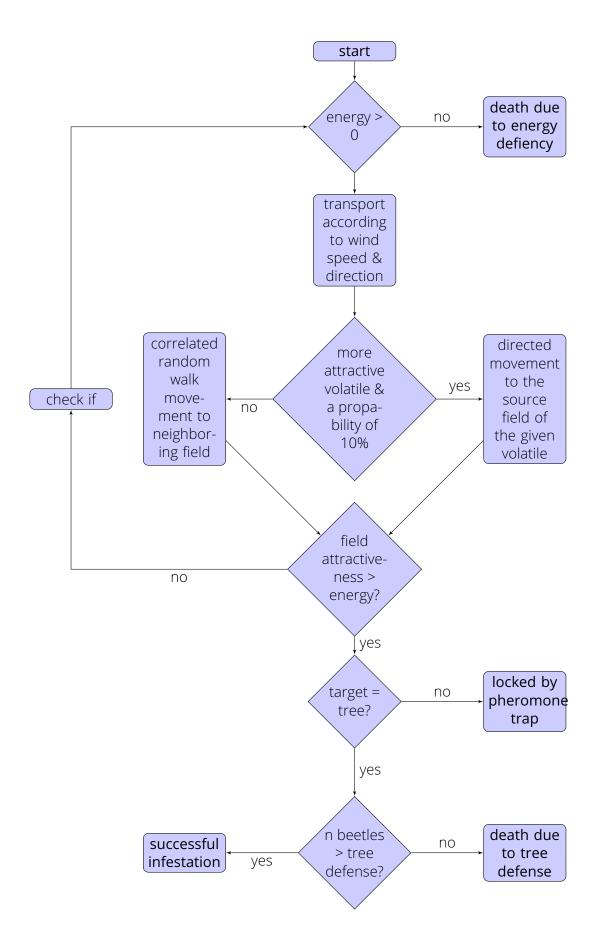


Figure 3: Flow chart showing the schedule for beetles; edited from (Kautz et al., 2014, 2016)

- 3. the attacked patch is a pheromone trap
 - a) increase beetle locked counter by 1
 - b) decrease beetle_dispersing counter by 1
 - c) store the beetles *flightdist_all*, *traveldist* and *airline* in the corresponding result lists
 - d) increase n_{lock} of the attacked patch by 1
 - e) kill the beetle

8.4.8 tree-defense

Within this procedure all susceptible patches check if the number of beetles attacking them exceeds the minimum threshold for a successful infestation. If this is the case the following things happen in that exact order:

- 1. set *infestlev* to 1
- 2. add patch to agent-set host
- 3. remove patch from agent-set waiting-tree
- 4. color patch red
- 5. update n_{inf} and n_{stay} accordingly
- 6. set infestday to current day
- 7. ask all beetles on this patch with status staying to:
 - a) increase beetle_infesting counter by 1
 - b) decrease beetle_staying counter by 1
 - c) store flightdist_all in patch' infest-dist list
 - d) store the beetles *flightdist_all*, *traveldist* and *airline* in the corresponding result lists
 - e) kill the beetle
- 8. calculate secattract = $0.1 * n_{stay} + n_{inf}$
- 9. calculate totalattract = primattract + secattract
- 10. if $n_{stay} = 0$: remove patch from agent-set waiting-tree

8.4.9 cut-infested-trees

Within this procedure the sanitation felling of infested host trees is taking place:

- 1. calculates the amount of trees to be cut (local variable sfn) = number of infested trees * sanitation-felling / 100
- 2. rounds sfn using build-in function round
- 3. asks *sfn* randomly chosen host trees:
 - a) remove itself from the agent-set *host*
 - b) decrease counter beetle infesting by ninf of the respective patch
 - c) increase counter beetle killed by ninf of the respective patch
 - d) set *pcolor* yellow
 - e) set primattract, secattract and totalattract to 0
 - f) set infestlev to 3

8.4.10 calculate-results

This procedure calculates for every beetle generation following results separately (each result gets a number at the end corresponding to the beetle generation, for example n_{host} 1, n_{host} 2 and n_{host} 3):

- 1. $beetle_percentsucc = \frac{beetle_infesting}{beetle_emerged} * 100$
- 2. nright = number of trees infested in reality and in the model (host trees with <math>inf = 2)
- 3. max_flightdist_inf = maximum flight distance of all infesting beetles
- 4. *mean_flightdist_inf* = mean flight distance of all infesting beetles
- 5. max_distance_host = maximum distance of infested trees to the nearest beetle source
- 6. *mean_distance_host* = mean distance of infested trees to the nearest beetle source
- 7. *nhost* = number of infested trees
- 8. max_traveldist = maximum travel distance (flight distance + drift distance) of all beetles
- 9. mean_traveldist = mean travel distance (flight distance + drift distance) of all beetles
- 10. max_airline = maximum distance between start location and final destination of all beetles
- 11. mean_airline = mean distance between start location and final destination of all beetles
- 12. max_flightdist_all = maximum flight distance of all beetles
- 13. mean_flightdist_all = mean flight distance of all beetles
- 14. *ncut* = number of host trees that were cut during sanitation felling (*pcolor* = yellow)
- 15. nshould = number of trees infested in reality (inf = 2 and pcolor = black)

If anything was entered in *path-to-output* in the interface of IPS-SPREADS, procedure *export-infestation-pattern* is called.

8.4.11 export-infestation-pattern

Within this procedure the day of infestation of all patches is exported as ESRI asc grid file (.asc) giving it the name of the current behaviorspace run number (which is zero if no behaviorspace experiment is running):

- 1. set export-raster to infestday using the GIS-extension function gis:patch-dataset
- 2. store export-raster with: gis:store-dataset and word path-to-output behaviorspace-run-number ".asc"

References

- Baier, P., Pennerstorfer, J., and Schopf, A. (2007). PHENIPS—A comprehensive phenology model of lps typographus (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology and Management*, 249(3):171–186.
- Begon, M., Townsend, C. R., and Harper, J. (2007). *Ecology from individuals to ecosystems*. Blackwell, Malden, Massachusetts, 4. ed. edition.
- Botterweg, P. (2009). The effect of attack density on size, fat content and emergence of the spruce bark beetle lps typographus L.1. *Zeitschrift für Angewandte Entomologie*, 96(1-5):47–55.
- Byers, J. A. (1996a). An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, 91(1-3):57–66.
- Byers, J. A. (1996b). Temporal clumping of bark beetle arrival at pheromone traps: Modeling anemotaxis in chaotic plumes. *Journal of Chemical Ecology*, 22(11):2133–2155.
- Byers, J. A. (2000). Wind-aided dispersal of simulated bark beetles flying through forests. *Ecological Modelling*, 125(2-3):231–243.
- Cionco, R. M. (1978). Analysis of canopy index values for various canopy densities. *Boundary-Layer Meteorology*, 15(1):81–93.
- Duelli, P., Studer, M., and Näf, W. (1986). Der Borkenkäferflug außerhalb des Waldes. *Journal of Applied Entomology*, 102(1-5):139–148.
- Kautz, M., Imron, M. A., Dworschak, K., and Schopf, R. (2016). Dispersal variability and associated population-level consequences in tree-killing bark beetles. *Movement Ecology*, 4(1):9.
- Kautz, M., Schopf, R., and Imron, M. A. (2014). Individual traits as drivers of spatial dispersal and infestation patterns in a host–bark beetle system. *Ecological Modelling*, 273:264–276.
- Komonen, A., Schroeder, L. M., and Weslien, J. (2011). Ips typographus population development after a severe storm in a nature reserve in southern Sweden. *Journal of Applied Entomology*, 135(1-2):132–141.
- Mursch-Radlgruber, E. and Kovacic, T. (1990). Mean canopy flow in an oak forest and estimation of the foliage profile by a numerical model. *Theoretical and Applied Climatology*, 41(3):129–136.
- Netherer, S. and Nopp-Mayr, U. (2005). Predisposition assessment systems (PAS) as supportive tools in forest management Rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *Forest Ecology and Management*, 207(1-2 SPEC. ISS.):99–107.

- Pietzsch, B. W., Peter, F. J., and Berger, U. (2021). The Effect of Sanitation Felling on the Spread of the European Spruce Bark Beetle—An Individual-Based Modeling Approach. *Frontiers in Forests and Global Change*, 4(July):1–15.
- Renshaw, E. and Henderson, R. (1981). The correlated random walk. *Journal of Applied Probability*, 18(2):403–414.
- Schopf, A., Baier, P., and Pennerstorfer, J. (2009). *Entwicklung eines Systems zur örtlich und zeitlich differenzierten Abschätzung des Gefährdungspotenzials durch den Buchdrucker (Ips typographus L.) in Sachsen auf Basis des Modells PHENIPS*. Bericht, Universität für Bodenkultur Wien, Wien.
- Schopf, A., Baier, P., and Pennerstorfer, J. (2013). *Modellbasierte Abschätzung der Prädisposition fichtenreicher Waldbestände gegen biotische Kalamitäten insbesondere durch rindenbrütende Borkenkäfer*. Bericht, Universität für Bodenkultur Wien, Wien.
- Wenk, G., Römisch, K., and Gerold, D. (1984). DDR-Fichtenertragstafel. TU Dresden, Tharandt.
- Weslien, J. and Lindelow, A. (1990). Recapture of marked spruce bark beetles (Ips typographus) in pheromone traps using area-wide mass trapping. *Canadian Journal of Forest Research*, 20(11):1786–1790.
- Weslien, J. and Regnander, J. (1990). Colonization densities and offspring production in the bark beetle lps typographus (L.) in standing spruce trees. *Journal of Applied Entomology*, 109(1-5):358–366.