Landsepi: List of assumptions and parameters

Stochastic, spatially-explicit, demo-genetic model simulating the spread and evolution of a plant pathogen in a heterogeneous landscape to assess resistance deployment strategies.

Assumptions:

In orange assumptions that can be relaxed with appropriate parameterization.

1. The spatial unit is a polygon, i.e. a piece of land delimited by boundaries and possibly cultivated with a crop. Such crop may be host or non-host, and the polygon is considered a homogeneous mixture of host individuals (i.e. there is no intra-polygon structuration). A field may be composed of a single or several polygons.
2. Host individuals are in one of these four categories: H (healthy), E (exposed and latent, i.e. infected but not infectious nor symptomatic), I (infectious and symptomatic), or R (removed, i.e. epidemiologically inactive).
3. A host 'individual' is an infection unit and may correspond to a given amount of plant tissue (where a local infection may develop, e.g. fungal lesion) or a whole plant (e.g. systemic viral infection). In the first case, plant growth increases the amount of available plant tissue (hence the number of individuals) during the cropping season. Plant growth is deterministic (logistic growth) and only healthy individuals (state H) contribute to plant growth (castrating pathogen).
4. The decreasing availability of healthy host tissues (as epidemics spread) makes pathogen infection less likely (i.e. density-dependence due to plant architecture).
5. Host are cultivated (i.e. sown/planted and harvested), thus there is no host reproduction, dispersal and natural death.
6. Environmental and climate conditions are constant, and host individuals of a given genotype are equally susceptible to disease from the first to the last day of every cropping season.
7. Crop yield depends on the average amount of producing host individuals during the cropping season and does not depend on the time of epidemic peak. Only healthy individuals (state H) contribute to crop yield.
8. Components of a mixture are independent each other (i.e. there is neither plant-plant interaction nor competition for space, and harvests are segregated).
9. Crops may be treated with chemicals which reduce the pathogen infection rate (contact treatment). Treatment efficiency decreases with host growth (i.e. new biomass is not protected by treatments) and time (i.e. pesticide degradation). Crops to be treated and dates of chemical applications are fixed prior to simulations (thus they are independent from the epidemic dynamics) and are the same for all polygons cultivated with the crops to be treated.
10. The pathogen is haploid.
11. Initially, the pathogen is not adapted to any source of resistance, and is only present on susceptible hosts (at state I).
12. Pathogen dispersal is isotropic (i.e. equally probable in every direction).
13. Pathogen reproduction can be purely clonal, purely sexual, or mixed (alternation of clonal and sexual reproduction).
14. If there is sexual reproduction (or gene recombination), it occurs only between parental infections located in the same polygon and the same host genotype. At that scale, the pathogen population is panmictic (i.e. all pairs of parents have the same probability to occur). The propagule production rate of

a parental pair is the sum of the propagule production rates of the parents. For a given parental pair, the genotype of each propagule is issued from random loci segregation of parental qualitative resistance genes. For each quantitative resistance gene, the value of each propagule trait is issued from a normal distribution around the average of the parental traits, following the infinitesimal model (Fisher 1919).

15. Each type of propagule (i.e. either clonal or sexual) has its own dispersal ability.
16. At the end of each cropping season, pathogens experience a bottleneck representing the off-season and then propagules are produced (either via clonal or sexual reproduction). Clonal propagules are released during the following season only, either altogether at the first day of the season, or progressively (in that case the day of release of each propagule is sampled from a uniform distribution). Sexual propagules are gradually released during several of the following seasons (between-season release). The season of release of each propagule is sampled from an exponential distribution, truncated by a maximum viability limit. Then, the day of release in a given season is sampled from a uniform distribution (within-season release).
17. Pathogenicity genes mutate independently from each other.
18. Pathogen adaptation to a given resistance gene consists in restoring the same aggressiveness component as the one targeted by the resistance gene.
19. If a fitness cost penalises pathogen adaptation to a given resistance gene, this cost is paid on hosts that do not carry this gene, and consists in a reduction in the same aggressiveness component as the one targeted by the resistance gene.
20. When there is a delay for activation of a given resistance gene (APR), the time to activation is the same for all hosts carrying this gene and located in the same polygon.
21. Variances of the durations of the latent and the infectious periods of the pathogen are not affected by plant resistance.

Parameter	Notation in article	Possible values	Default value		Meaning	Remarks
			Rust	Mildew		
SIMULATION PARAMETERS						
Nyears	Y	$\mathbb{N}^*$	20	20	Number of cropping seasons (e.g. years)	
nTSpY	T	$\mathbb{N}^*$	120	120	Number of time steps per cropping season (e.g. days)	Duration of the epidemic season
seed		$\mathbb{N}$	12345	12345	Seed for random number generator	
writeTXT		{TRUE ; FALSE}	TRUE	TRUE	Whether or not outputs must be written in text files	
graphic		{TRUE ; FALSE}	TRUE	TRUE	Whether or not graphics must be generated	
videoMP4		{TRUE ; FALSE}	FALSE	FALSE	Whether or not a video must be generated	Works only if graphic=TRUE and epid_outputs="audpc" (or epid_outputs="all"). Requires ffmpeg library. Up to 9 different croptypes can be properly represented.
keepRawResults		{TRUE ; FALSE}	FALSE	FALSE	Whether or not raw outputs (binary files) must be kept	Keeps 6 binary files (H, Hjuv, L, I, R, P) per simulated year
PATHOGEN PARAMETERS					Basic pathogen aggressiveness components on a susceptible host for a pathogen genotype not adapted to resistance	Parameters of random draws, thus every infection has its own values (stochastic variability)
infection_rate	e_{max}	[0 ; 1]	0.40	0.90	Maximal expected infection rate of a propagule on a healthy individual	Given that the propagule landed on the host individual
propagule_prod_rate	r_{max}	$\mathbb{R}^+$	3.125	2.0	Maximal expected effective propagule production rate per time step and per infectious individual	Number of viable propagules that disperse and land on another host individual
latent_period_mean	γ_{min}	$\mathbb{R}^+$	10	7	Minimal expected latent period duration	Parameter of the gamma distribution of the latent period (in time steps)
latent_period_var	γ_{var}	$\mathbb{R}^+$	9	8	Variance of the latent period duration	Parameter of the gamma distribution of the latent period (in time steps)
infectious_period_mean	Υ_{max}	$\mathbb{R}^+$	24	14	Maximal expected infectious period duration	Parameter of the gamma distribution of the infectious period (in time steps)
infectious_period_var	Υ_{var}	$\mathbb{R}^+$	105	22	Variance of the infectious period duration	Parameter of the gamma distribution of the infectious period (in time steps)
survival_prob	λ	[0 ; 1]	10^{-4}	10^{-4}	Off-season survival probability of a propagule	Determine the size of the bottleneck at the end of the cropping season
repro_sex_prob		[0 ; 1]	0	0	Probability for an infectious individual to reproduce via sex (same value for every time step)	=0 for purely clonal reproduction =1 for purely sexual reproduction

						between 0 and 1 for both reproduction modes at the same time
repro_sex_probs		$[0 ; 1]^{nTSpY+1}$			Vector of probabilities for an infectious individual to reproduce via sex for each time step	Vector size is (nTSpY+1) Useful to simulate alternation between clonal and sexual reproduction
sex_propagule_release_mean		$\mathbb{R}^{+*}$	1	1	Average number of cropping seasons (e.g. years) after which a sexual propagule is released	Parameter of the exponential distribution of the season of release.
sex_propagule_viability_limit		$\mathbb{N}^*$	1	5	Maximum number of cropping seasons (e.g. years) up to which a sexual propagule is viable	All sexual propagules are released before the viability limit (i.e. no simulated mortality).
sigmoid_kappa	κ	$\mathbb{R}^+$	5.33	5.33	Kappa parameter of the sigmoid contamination function	$\kappa=0$ and $\sigma=1$ for linear relationship
sigmoid_sigma	σ	$\mathbb{R}^+$	3	3	Sigma parameter of the sigmoid contamination function	$\sigma=0$ to relax density-dependence assumption
sigmoid_plateau		[0 ; 1]	1	1	Plateau parameter of the sigmoid contamination function	
clonal_propagule_gradual_release		{TRUE ; FALSE}	FALSE	TRUE	Whether or not clonal propagules surviving the bottleneck are gradually released along the following cropping season.	if FALSE, propagules are released at the first time step of the following season. if TRUE, the day of release is sampled from a uniform distribution, with parameters [0, nTSpY].
CROPTYPE PARAMETERS					Characteristics of the landscape and of each cultivated croptype	
GPKGLandscape					Landscape in shapefile format, containing spatial coordinates of every polygon	Buit-in simulated landscapes are available. Areas must be expressed in square meters.
aggreg		$\mathbb{R}^+$			Level of spatial aggregation of the landscape	Units relative to the maximal distance between two polygons of the landscape: between 0 and 0.1 for fragmented landscape, 0.1 and 0.5 for balanced landscape, 0.5 and 3 for aggregated landscape, and above 3 for bloc planting
algo		{“exp”; “periodic”; “random”}			Algorithm used to control spatial aggregation in croptype allocation	Parameter “aggreg” is ignored for random allocation. Algorithm “exp” is preferable for big landscapes.
croptypeName					Name of the croptype	
prop		[0 ; 1]			Proportion of the landscape surface cultivated with the croptype (cropping ratio)	A minimum of 1 polygon is allocated to each croptype
rotation_period		$\mathbb{N}$			Number of years before rotation of the landscape	There is no rotation if rotation_period=0 or rotation_period=Nyears

rotation_sequence		$\mathbb{N}$			Indices of cultivated croptypes for each period of the rotation sequence	There is no rotation if the list contains only one element
rotation_realloc		{TRUE ; FALSE}	FALSE	FALSE	Whether or not a new random allocation of croptypes is performed when the landscape is rotated.	rotation_realloc=FALSE for static allocation ; rotation_realloc=TRUE for dynamic allocation
DISPERSAL PARAMETERS					Probability of dispersal from any polygon to any other polygon of the landscape (total number of polygons in the landscape is N_{poly})	
disp_patho_clonal	μ	$[0 ; 1]^{Npoly \text{ X } Npoly}$			Pathogen dispersal matrix for propagules produced by clonal reproduction.	To compute from dispersal kernel via RCALI package Dispersal matrices for rust pathogens are available for each built-in landscape. Identity matrix = no dispersal
disp_patho_sex		$[0 ; 1]^{Npoly \text{ X } Npoly}$			Pathogen dispersal matrix for propagules produced by sexual reproduction	To compute from dispersal kernel via RCALI package Identity matrix = no dispersal
CULTIVAR PARAMETERS					Characteristics of each host genotype as if cultivated in pure crop	
cultivarName					Name of the cultivar	Avoid using spaces in cultivar names A “cultivar index” is assigned to each cultivarName (starting from 0)
initial_density	C^0	$\mathbb{R}^+$	0.1	1	Host individuals density (in pure crop) per surface unit at the beginning of the cropping season	$C^0=0$ if the crop is not cultivated. $C^0 \leq C^{max}$
max_density	C^{max}	$\mathbb{R}^{+*}$	2	20	Maximum host individuals density (in pure crop) per surface unit at the end of the cropping season	$C^0=C^{max}$ if individual hosts are whole plants or do not grow
growth_rate	δ	[0 ; 1]	0.10	0.10	Host growth rate	$\delta=0$ if individual hosts are whole plants or do not grow
yield_H		$\mathbb{R}^+$	2.5		Theoretical yield in pure crop (in weight or volume unit / ha / cropping season) associated with the sanitary status ‘H’	yield_H=0 if the crop is not a cash crop
yield_L		$\mathbb{R}^+$	0		Theoretical yield in pure crop (in weight or volume unit / ha / cropping season) associated with the sanitary status ‘L’	yield_L>0 for non-castrating pathogen
yield_I		$\mathbb{R}^+$	0		Theoretical yield in pure crop (in weight or volume unit / ha / cropping season) associated with the sanitary status ‘I’	yield_I>0 for tolerant cultivar
yield_R		$\mathbb{R}^+$	0		Theoretical yield in pure crop (in weight or volume unit / ha / cropping season) associated with the sanitary status ‘R’	yield_R>0 for tolerant cultivar

planting_cost		$\mathbb{R}^+$	225		Planting costs in pure crop (in monetary units / ha / cropping season)	
market_value		$\mathbb{R}^+$	200		Market value of the product (in monetary units / weight or volume unit)	
GENE PARAMETERS					Characteristics of each plant resistance gene and of each corresponding pathogen pathogenicity gene	
geneName					Name of the resistance gene	
target_trait	w	{"IR" ; "LAT" ; "IP" ; "PR"}	"IR"	"IR"	Aggressiveness component targeted by the resistance gene	IR=e_{max} ; LAT=γ_{min} ; IP=Υ_{max} ; PR=r_{max}
efficiency	ρ	[0 ; 1]	1.00	1.00	Efficiency of the resistance gene (percentage of reduction of the targeted aggressiveness component: IR, 1/LAT, IP or PR)	$\rho=1$ for complete resistance, $\rho<1$ for partial resistance, $\rho=0$ for no resistance
time_to_activ_mean		$\mathbb{R}^+$	0	0	Expected delay to resistance activation (for APRs)	time_to_activ_exp>0 for APRs
time_to_activ_var		$\mathbb{R}^+$	0	0	Variance of the delay to resistance activation (for APRs)	time_to_activ_var=0 for deterministic activation at time_to_activ_exp
mutation_prob	τ	[0 ; 1]	10^{-7}	10^{-7}	Probability for a pathogenicity gene to mutate	$\tau=0$ for no evolution
Nlevels_aggressiveness	Q	$\mathbb{N}^*$	2	2	Number of adaptation levels related to each resistance gene (i.e. 1 + number of required mutations for a pathogenicity gene to fully adapt to the corresponding resistance gene)	$Q=1$ for no adaptation; $Q=2$ for adaptation via a single mutation; $Q>2$ for gradual adaptation to resistance. Careful, value of Q severely impacts computational time.
fitness_cost	θ	[0 ; 1]	0.50	0.50	maximal fitness penalty paid by a pathogen genotype fully adapted to the resistance gene on hosts that do not carry this gene	$\theta=0$ for no fitness cost ; $\theta=1$ for matching allele model
tradeoff_strength	β	$\mathbb{R}^{+*}$	1.0	1.0	Strength of the trade-off relationship between the level of aggressiveness hosts that do and do not carry the resistance gene	$\beta=1$ for linear trade-off ; $\beta>1$ for strong trade-off (cost higher than gain) ; $\beta<1$ for weak trade-off
recombination_sd		$\mathbb{R}^{+*}$	0.27	0.27	Standard deviation of the normal distribution used for recombination of quantitative traits during sexual reproduction (infinitesimal model)	Standard deviation is the product of recombination_sd and the value of traits on susceptible hosts.
INOCULUM PARAMETER					Initial conditions	
pI0	ϕ	[0 ; 1]	5.10^{-4}	5.10^{-4}	Initial probability for the first host (usually parameterised as a susceptible cultivar) to be infectious (state I) at the beginning of the simulation	$\phi=0$ for absence of disease Note: if ϕ is too high the epidemic collapses before the end of the first season due to lack of healthy hosts to infect
TREATMENT PARAMETERS						

treatment_cultivars		$\mathbb{N}^{t\_cultivar}$			Vector of cultivar indices that receive treatments	All polygons cultivated with the selected cultivars are treated at the same time. Vector size is t_cultivar, i.e. the number of cultivars receiving treatments
treatment_timesteps		$\mathbb{N}^{t\_timesteps}$			Vector of time-steps corresponding to treatment application dates	Application dates are fixed prior to simulation (and thus independently from the epidemic dynamics). Vector size is t_timestep, i.e. the number of treatments within a cropping season (year)
treatment_efficiency		[0 ; 1]	0	0	Maximal efficiency of chemical treatments (i.e. fractional reduction of pathogen infection rate at the application date)	
treatment_reduction_rate		$\mathbb{R}^+$	0.10	0.10	Reduction per time step of treatment concentration	0.10 for protectant fungicides, 0.07 for locally systemic fungicides, 0.06 to 0.05 for systemic fungicides, and 0 for no pesticide degradation.
treatment_cost		$\mathbb{R}^+$	0	0	Cost of a single treatment application (monetary units/ha)	multiplied by the number of applications and equivalent surface (i.e. weighted by the relative proportion of the cultivar in mixtures) to obtain the total cost of treatment for a given cultivar.
OUTPUT PARAMETERS						
epid_outputs			"all"	"all"	Epidemiological and economic outputs to generate: ▪ "audpc" : Area Under Disease Progress Curve ▪ "audpc_rel" : relative Area Under Disease Progress Curve ▪ "gla" : Green Leaf Area ▪ "gla_rel" : relative Green Leaf Area ▪ "eco_cost" : operational crop costs ▪ "eco_yield" : total crop yield ▪ "eco_product" : total crop products ▪ "eco_margin" : margin (products – operational costs) ▪ "contrib" : contribution of pathogen genotypes to LIR dynamics ▪ "HLIR_dynamics", "H_dynamics", "IR_dynamics", etc. : epidemic dynamics related to the specified sanitary status ▪ "all" : compute all these outputs ▪ "" : none of these outputs will be generated.	▪ AUDPC: average number of diseased hosts (status I + R) per time step and per square meter. ▪ AUDPC_{rel}: average proportion of diseased hosts (status I + R) relative to the total number of existing hosts (H+L+I+R). ▪ GLA: average number of healthy hosts (status H) per time step and per square meter. ▪ GLA_{rel}: average proportion of healthy hosts (status H) relative to the total number of existing hosts (H+L+I+R). ▪ Economic outputs in monetary units per hectare. ▪ Margin = market_value * (yield – loss) – operationalCost ▪ Contribution = for every year and every host, fraction of cumulative LIR infections attributed to each pathogen genotype. ▪ HLIR_dynamics: graphic only

evol_outputs			“all”	“all”	Evolutionary outputs to generate : ▪ "evol_patho" : dynamics of pathogen genotype frequencies ▪ “evol_patho_bi”: pathogen genotype frequencies after the off-season (after bottleneck) ▪ "evol_aggr" : evolution of pathogen aggressiveness ▪ "durability" : durability of resistance genes ▪ "all" : compute all these outputs ▪ "" : none of these outputs will be generated.	For durability, several computations are performed for each pathogen genotype: - time to first appearance (as propagules); - time to first true infection of a resistant host; - time when the number of infections of resistant hosts reaches thres_breakdown.
audpc100S		$\mathbb{R}^{+*}$	0.76	8.48	AUDPC in a fully susceptible landscape	(used as reference value for graphics and video)
thres_breakdown		$\mathbb{N}^{*}$	50,000	50,000	Threshold (i.e. number of infections) above which a pathogen genotype is unlikely to go extinct and resistance is considered broken down	Used to characterise the time to invasion of resistant hosts (several values are computed if several thresholds are given in a vector)