Control of Competitive Bioinvasion

Horst Malchow, Alex James, and Richard Brown

Abstract The invasion of alien and displacement of indigenous species is a crucial ecological and economical problem of even increasing significance. Measures to control and perhaps to stop and reverse such invasive processes are urgently needed. Mathematical models are a suitable tool to preview the impact of control measures before utilizing them in nature. Here, a reaction-diffusion model is used to describe the competition and dispersal of invasive and native species. Not only the environment is changing but also growth, harvesting and dispersal of the two competitors vary in space and time. Extreme events such as fires or landslides or any other processes yielding bare re-invadable ground lead to temporary extinction of both species at a randomly chosen time and spatial range. The spatiotemporal dimension of these extreme fragmentation events, the ratio of the dispersal rates of the competing species as well as the selective removal of the invader turn out to be the crucial driving forces of the system dynamics. Finally, the controlling effect of a targeted infection of the invasive species with a specific pathogen is studied in an eco-epidemiological competition-diffusion model.

H. Malchow (✉)
Institute of Environmental Systems Research, University of Osnabrück
Barbarastr. 12, 49076 Osnabrück, Germany
e-mail: horst.malchow@uni-osnabrueck.de

A. James · R. Brown
Department of Mathematics and Statistics, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
e-mail: a.james@math.canterbury.ac.nz; r.brown@math.canterbury.ac.nz

M.A. Lewis et al. (eds.), *Dispersal, Individual Movement and Spatial Ecology*,
Lecture Notes in Mathematics 2071, DOI 10.1007/978-3-642-35497-7_10,

1 Introduction

The negative econo-ecological effects of bioinvasions including the spread of infectious diseases [8,36] have led to a remarkable push of bioinvasion science. Not only an increasing number of laboratory and field studies but also the rapid development of theoretical methods to describe bioinvasions and their control could be noticed during recent years, cf. [17,31,39,50]. Mathematical and computational methods are meanwhile recognized tools to investigate the dynamics of invasions, both supplementary to and initiating field studies as well as control measures. Related summaries and overview publications are for instance [7,18,26,32,35,38,41] as well as [43].

Here, to model the invasion of alien species such as weeds and their competition with indigenous plants, the textbook model of Lotka–Volterra type with diffusion is used. Carrying capacities are not explicitly defined. Growth, selective harvesting of the invading weed as well as spatial spread undergo seasonal cycles. Furthermore, extreme events such as fires or landslides or any other processes yielding bare re-invadable ground lead to temporary extinction of both species at a randomly chosen time and spatial range. In a previous paper [27], it has been shown that, without seasonal cycles of the mentioned parameters, the frequency and spatial dimension of these extreme fragmentation events, the ratio of the dispersal rates of the competing species as well as the efficiency of selective removal of the invader turn out to be the crucial driving forces of the system dynamics. In the first part of the present paper, the robustness of these results against those seasonal cycles is studied.

Furthermore, in the second part, the targeted infection of the invader with a specific pathogen is considered as biological control measure. There are applications of biological methods of bioinvasion control for more than half a century and it has been a changeful history of magnificent successes and risky failures [1,11,16,20,30,51]. Ecological and epidemiological models are known since more than 200 years. But it is only about 25 years ago that first attempts to merge these models have been published, cf. [2,12,14,15] as well as [47]. In this paper, the invading model weed will be controlled by a frequency-dependently transmitted fungus infection.

2 A Competition-Diffusion Model with Annual Cycles and Random Extreme Events

For the description of the spatiotemporal invasion of a resident population by a competing alien, the Lotka–Volterra competition-diffusion model is used, i.e.,

$$\frac{\partial N_i(\mathbf{x},t)}{\partial t} = r_i N_i - N_i \sum_{j=1}^{2} c_{ij} N_j + D_i \Delta N_i \,; i = 1,2\,, \tag{1}$$

where N_1 and N_2 are resident and invader densities at position $\mathbf{x} = \{x_1, x_2\}$ and time t respectively. Carrying capacities will not explicitly be introduced because they can suppress a higher variety of solutions and rather appear as emergent property of the system [13, 22, 23]. The r's stand for the growth rates that can be thought as superposition of biomass generation and loss rates b_1, b_2 and m_1, m_2 respectively as well as density-dependent harvesting h_1, h_2, i.e.,

$$r_i = b_i - m_i - h_i = r_i^* - h_i \; ; \; i = 1, 2 \, . \tag{2}$$

The c's are the inter- and intraspecific competition coefficients and the D's the diffusivities. $\Delta = \partial^2/\partial x_1^2 + \partial^2/\partial x_2^2$ is the Laplacian for the considered horizontal processes.

2.1 Existence and Stability Ranges of Spatially Uniform Stationary Solutions

There are the four stationary solutions with their stability ranges:

1.	$(0, 0)$	always unstable ,	
2.	$\left(\frac{r_1}{c_{11}}, 0\right)$	stable for	$\frac{r_2}{r_1} < \frac{c_{22}}{c_{12}}; \frac{r_2}{r_1} < \frac{c_{21}}{c_{11}}$,
3.	$\left(0, \frac{r_2}{c_{22}}\right)$	stable for	$\frac{r_2}{r_1} > \frac{c_{22}}{c_{12}}; \frac{r_2}{r_1} > \frac{c_{21}}{c_{11}}$,
4.	$\left(\frac{r_1 c_{22} - r_2 c_{12}}{c_{11} c_{22} - c_{12} c_{21}}, \frac{r_2 c_{11} - r_1 c_{21}}{c_{11} c_{22} - c_{12} c_{21}}\right)$	stable for	$\frac{c_{22}}{c_{12}} > \frac{r_2}{r_1} > \frac{c_{21}}{c_{11}}$,
2./3.	Bistability of extinction states (2,3)	for	$\frac{c_{22}}{c_{12}} < \frac{r_2}{r_1} < \frac{c_{21}}{c_{11}}$.

In the extinction states (2.,3.), the surviving population k is at its emergent carrying capacity r_k/c_{kk}. Later on, the bistability range of both extinction states from the last row is used for modelling strong competition in time and space.

2.2 Annual Cycles of Growth, Harvesting and Diffusion

The growth processes undergo an annual cycle approximated by a cosine

$$r_i^*(t) = r_{i,min}^* + \frac{1}{2}\left(r_{i,max}^* - r_{i,min}^*\right)\left[1 + cos\left(\frac{2\pi}{a}t\right)\right] \; ; \; i = 1, 2. \tag{3}$$

where $r_{i,max}^*$ and $r_{i,min}^*$ are the corresponding summer and winter extrema.

Only the invading species is harvested from spring to autumn, usually through manual removal, i.e., $h_1 = 0$ and $h_2 \geq 0$. Harvesting is not possible instantaneously on the whole managed field of size $L \times L$. The search for the weed starts at one of the field boundaries, say at $\{x_1 \in [0, L], x_2 = 0\}$. Once a weed patch is found, harvesting begins in x_2 direction on a stripe of size $w \times L$ where w is the width of the patch that is removed within time δt. Then, the search continues and after arriving at the other side of the field, $\{x_1 \in [0, L], x_2 = L\}$, it perhaps restarts at the initially chosen boundary. If the search is assumed always in direction of x_2, this procedure is modelled through

$$h_2^*(x_2, t) = h_2\; g(x_2, t)\; \Theta\left[\epsilon + cos\left(\frac{2\pi}{a}t\right)\right], \tag{4}$$

where $\Theta[.]$ is the Heaviside function and for $g(x_2, t)$ applies

$$\begin{aligned} &\text{if} \quad \int_0^L N_2(x_1, x_{20}, t_0) dx_1 > 0 \\ &\text{then} \quad g(x_2, t) = 1 \text{ for } x_2 \in [x_{20}, x_{20} + w] \text{ and } t \in [t_0, t_0 + \delta t] \\ &\text{else} \quad g(x_2, t) = 0\,. \end{aligned} \tag{5}$$

The reduced mobility from late autumn to early spring is considered by a corresponding seasonality of the diffusivities

$$D_i^*(t) = D_i\; \Theta\left[\epsilon + cos\left(\frac{2\pi}{a}t\right)\right]\; ; \; i = 1, 2. \tag{6}$$

2.3 Random Extreme Events and Assisted Long-Distance Transport

As in the previous paper [27], extreme events such as fires or landslides or any other occurrence yielding bare re-invadable ground lead to temporary extinction of both species. It is assumed that these events may randomly take place within certain time intervals and spatial ranges throughout the year.

Furthermore, wind-born or however assisted long-distance transport of seeds is considered in the spring-summer season, cf. (6). At random times raised and transported seeds settle down at a randomly chosen location and form small population patches of random size having in mind typical dispersal distance kernels [6, 33]. If the location falls into a hostile zone the patches have to fight the surrounding enemies. This type of transport has also been called stratified diffusion [42].

The modelling and simulation of the above mentioned random processes is not equation- but rather rule-based similar to formerly developed models of rule-based fish school motion coupled to equation-based resource dynamics [25].

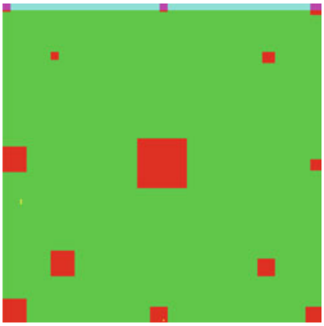

Fig. 1 Initial condition, cf. text

2.4 Numerical Simulations I

As in the previous work [27], the initial conditions have been arbitrarily chosen and are the same for all runs in this section. Because weed patchiness is rather generic e.g. in crops [5,49,54,55], a number of (red) initial invader patches at their emerging carrying capacities of different size has been distributed in a certain artificial way on the habitat of the (green) native species, cf. Fig. 1. At the top, the (teal) initial harvested stripe can be identified. Zero-flux boundary conditions have been applied.

One expected result is that initial invader patches smaller than a certain critical size will be immediately recaptured by the native species. This spatial critical size problem in spatially two- and three-dimensional systems with multiple steady states is known from nucleation theory [9,10,24,34]. Though it is necessary to be stronger or fitter, it is not sufficient to win the competition. One must also have occupied a sufficiently large spatial range.

It is assumed that landslips may randomly take place within intervals of 20 time units and clear areas of up to 50 × 50 spatial units of a total of 200 × 200. The time-lag and the size of the landslips are control parameters of the system, the shorter the interval and the greater the spatial dimension the stronger the landslide's impact on the spatiotemporal competition of natives and invaders.

Time is measured in days, space in meters. Hence, denoting the plant's dry weight by dw, the N's are given in $\mathrm{kg\,dw\,m^{-2}}$, the r's and h's in d^{-1}, the c's in $\mathrm{kg\,dw^{-1}\,m^2\,d^{-1}}$ and the D's in $\mathrm{m^2\,d^{-1}}$. ϵ is a dimensionless quantity. The following parameter values have been used:

$$\begin{aligned} r^*_{1,max} &= 1.0\,,\ r^*_{1,min} = 0.3\,,\ r^*_{2,max} = 1.0\,,\ r^*_{2,min} = 0.35\,,\\ c_{11} &= 1.0\,,\ c_{12} = 1.3\,,\ c_{21} = 1.2\,,\ c_{22} = 1.0\,,\\ \epsilon &= 0.2\,,\ h_1 = 0.0\,,\ h_2 = 0.35\,,\ D_2 = 22.5\,,\ L = 3000.0\,,\ w = 60.0\,. \end{aligned} \tag{7}$$

The competition coefficients of both species have been raised away from the critical value of unity. The invader is assumed to be the stronger competitor, following the enemy release hypothesis [21].

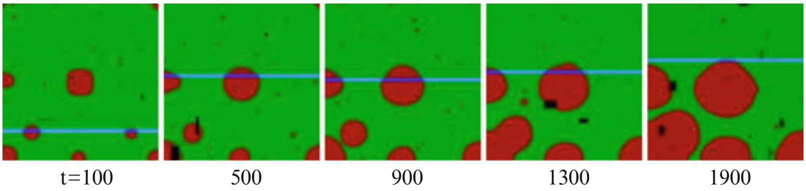

Fig. 2 Sample simulation 1: Parameters as given in (7), $D_1 = D_2$. Black spots have been cleared due to eradicating extreme event

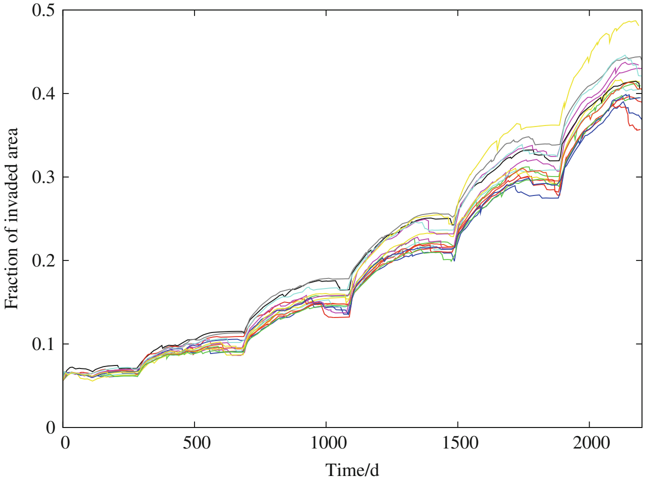

Fig. 3 Results of 15 simulation runs: slow but continuous invasion of the resident's area

At first, it is assumed that both species have the same diffusivities. It is seen that the competitive advantage of the alien leads to a slow but continuous displacement of the resident, cf. Fig. 2. As to be expected, the long-distance transport does not help either of the species because landing in the hostile environment inevitably leads to extinction because the formed patches are not larger than the required critical size.

The results of 15 simulations with different seeds of the random number generator [28] are collected in Fig. 3. Compared to the results for a constant environment, the periodicities in the selected parameters slow down the invasion. However, finally the invading weed wins.

The outcome immediately changes when the resident is twice as fast as the alien. The disadvantage in direct contact competition still exists, however, the higher mobility becomes the essential advantage over the intruder. An illustration is presented in Figs. 4 and 5. In a constant environment the resident needed a four times higher mobility to overcome the invader.

It can be preliminary summarized that the more realistic periodically changing environment stabilizes the resident's living conditions and reduces the invasibility. However, from qualitative point of view, a higher mobility remains a crucial competitive edge.

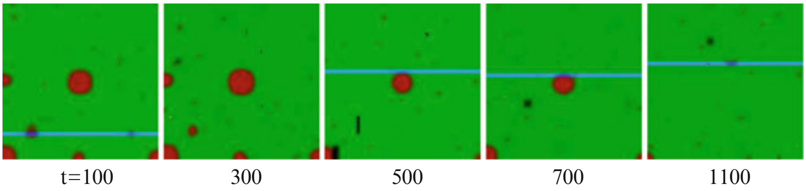

Fig. 4 Sample simulation 2: Parameters as given in (7), $D_1 = 2D_2$. Black spots have been cleared due to eradicating extreme event

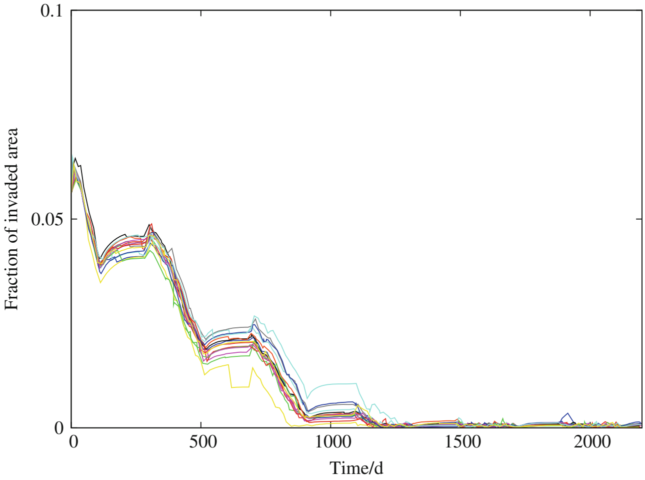

Fig. 5 Results of 15 simulation runs: rapid reversal and extinction of invasion

3 A Competition-Diffusion Model with Infected Invader

A specific infection of the invading population can be used as biocontrol measure to stop and reverse the invasion, cf. [16, 20, 30, 37]. To model this, the invader population is split into susceptibles S and infecteds I,

$$N_2 = S + I.$$

The model of the local dynamics then reads

$$\frac{dN_1}{dt} = r_1 N_1 - c_{11} N_1^2 - c_{12} N_1 (S + I), \tag{8}$$

$$\frac{dS}{dt} = r_S S - c_{22} S(S + I) - c_{21} N_1 S - \lambda \frac{SI}{(S + I)^k}, \tag{9}$$

$$\frac{dI}{dt} = r_I I - c_{22} I(S + I) - c_{21} N_1 I + \lambda \frac{SI}{(S + I)^k} - \mu I\ , \tag{10}$$

where λ is the transmission coefficient of the disease and μ the disease-induced higher mortality rate of the infecteds. The exponent k allows to describe mass-action type ($k = 0$) and frequency-dependent transmission ($k = 1$) of the disease respectively [2, 29]. For $k = 0$, disease-induced oscillations have been found [45, 48]. A difference in the growth rates of susceptibles r_S and infecteds r_I with $0 \leq r_I < r_S$ has been taken into account. In general, one should also not expect that the competition intensities of susceptibles and infecteds are the same. However, for demonstrating the effect of the invader infection this rough model structure is sufficient.

3.1 Local Dynamics with Infection

For convenience, the model of the local dynamics is not analysed in terms of N_1, S and I but rather in N_1, i and N_2 where i is the prevalence, i.e., the infected fraction of the total invader population N_2 [19],

$$i = \frac{I}{S+I} = \frac{I}{N_2} \text{ with } 0 \leq i \leq 1 \,.$$

Having in mind that

$$\frac{di}{dt} = \frac{1}{N_2}\left(\frac{dI}{dt} - i\frac{dN_2}{dt}\right) , \tag{11}$$

it follows

$$\frac{dN_1}{dt} = r_1 N_1 - c_{11} N_1^2 - c_{12} N_1 N_2 \,, \tag{12}$$

$$\frac{di}{dt} = \left(r_I - r_S + \lambda N_2^{1-k} - \mu\right)(1-i)i \,, \tag{13}$$

$$\frac{dN_2}{dt} = \left[r_S(1-i) + r_I i\right] N_2 - c_{21} N_1 N_2 - c_{22} N_2^2 - \mu i N_2 \,. \tag{14}$$

A prominent example of the control of a weed by a fungal disease is the fight against the yellow starthistle in the United States [44, 52, 53]. In phytopathology, the transmission of especially fungal diseases is described with standard incidence [46]. A corresponding model of the invasion of a fungal disease over a vineyard has been investigated by [4]. Further on, only the standard incidence is considered, i.e., $k = 1$. More details of the fungus disease cycle like latent and infectious periods and corresponding compartments [40] are neglected because this is out of scope of the present work. The reduction to the above formulated $S - I$ model (9,10) is sufficient to find the effect of the infection on the invasion.

It is readily seen that the sign of the first factor in (13) determines the dynamics of the system, it reads for $k = 1$

$$r_I - r_S + \lambda - \mu \lesseqgtr 0 \,. \tag{15}$$

- If it is less than zero, the prevalence approaches zero, i.e., the infecteds go extinct and one obtains a standard Lotka–Volterra system with $r_2 = r_S$.
- If the factor is greater than zero, the prevalence approaches unity, i.e, the susceptibles go extinct and one obtains a standard Lotka–Volterra system with $r_2 = r_I - \mu$.
- Finally, if it is equal to zero, the prevalence will remain at its initial value $i = i_0$, and one finds a standard Lotka–Volterra system with $r_2 = r_S - \lambda i_0$.

Hence, any of the cases results in a standard Lotka–Volterra system and the table of the stability properties of Sect. 2.1 can be simply adopted.

3.2 Spatiotemporal Dynamics with Infection

For modelling the dynamics in time and space, one has to come back to (8)–(10) and to add the diffusion terms, i.e.,

$$\frac{\partial N_1}{\partial t} = r_1 N_1 - c_{11} N_1^2 - c_{12} N_1 (S + I) + D_1 \Delta N_1 , \tag{16}$$

$$\frac{\partial S}{\partial t} = r_S S - c_{22} S (S + I) - c_{21} N_1 S - \lambda \frac{SI}{S + I} + D_S \Delta S \,, \tag{17}$$

$$\frac{\partial I}{\partial t} = (r_I - \mu) I - c_{22} I (S + I) - c_{21} N_1 I + \lambda \frac{SI}{S + I} + D_I \Delta I \,. \tag{18}$$

The mechanisms of diffusion of infected and healthy plants are quite different because the spread of spores also has to be taken into account. However, the most simple Fickian formulation has been chosen for simplicity. The differences have been considered by different numerical values. The seasonality of system parameters is omitted here because the role of the infection should not be masked.

3.3 Numerical Simulations II

For the numerical simulations of system (16)–(18) a slightly different initial condition is used without qualitatively changing the outcomes. Again, Neumann zero-flux boundary conditions are applied. Initially, the infection is absent. It is

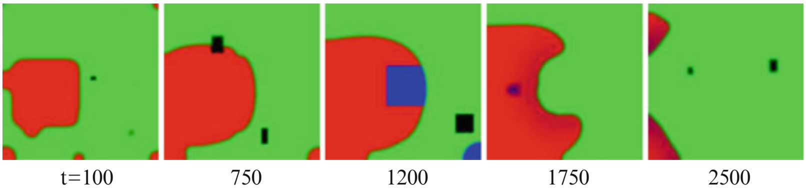

Fig. 6 Sample simulation 3: Parameters as given in (19). Black spots have been cleared due to eradicating extreme event. The repelling of the invasion after introducing the infection at $t = 1,200$ is obvious

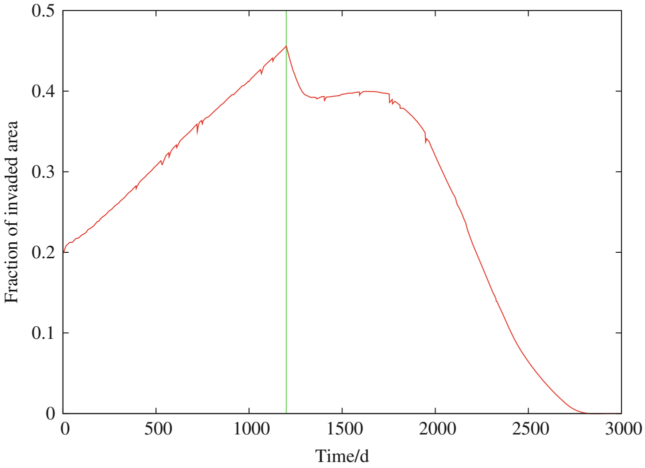

Fig. 7 Presentation of one sample run, also showing the sharp decline of invasion after infecting the invader at $t = 1200$

rather selectively introduced after the invading weed has overtaken a significant portion of the model area, cf. Fig. 6 below.

The following parameter values have been used:

$$\begin{aligned} &r_1 = 1.0\,,\ r_S = 1.0\,,\ r_I = 0.8\,,\ \lambda = 0.405\,,\ \mu = 0.2\,,\\ &c_{11} = 1.0\,,\ c_{12} = 1.3\,,\ c_{21} = 1.2\,,\ c_{22} = 1.0\,,\\ &D_1 = 45.0\,,\ D_S = 22.5\,,\ D_I = 45.0\,,\ L = 3000.0\,. \end{aligned} \tag{19}$$

The clear model result is that a targeted infection of the invading weed is a reliable strategy to win the fight against the bioinvasion. It is robust against different ratios of diffusivities as well as periodicities of growth and dispersal such as described in Sect. 2 if the random perturbations are alike (Fig. 7).

4 Concluding Remarks

As in constant environments, in the bistable parameter range, population patches of subcritical size disappear as expected from nucleation theory. The driving force of the competition process remains the temporary erosion in combination with a sufficiently effective harvesting of the invader and different mobilities of the species. However, the latter effect of different mobilities is tempered in the periodically changing environment. But still, even a strongly competitive alien has no chance to invade if the mobility of the indigenous species is sufficiently high.

It has turned out that the most efficient biological control measure is the specific partial infection of the invading population. In laboratory and field studies, however, it has been found that it can be hard to find such a specific agent, cf. [3]. Forthcoming work has to clear the role of non-symmetric competition of susceptible and infected alien species among themselves as well as with the native species. Also the impact of seasonality of system parameters including the infection rate has to be studied.

Acknowledgements H.M. would like to dedicate this paper to his academic teacher and friend Werner Ebeling (Berlin) on occasion of his 75th birthday on 15 September 2011. Furthermore, he is thankful to the Erskine Foundation at the University of Canterbury at Christchurch, New Zealand, for a Visiting Erskine Fellowship.

References

1. H.M. Alexander, R.D. Holt, The interaction between plant competition and disease. Perspect. Plant Ecol. Evol. Syst. **1/2**, 206–220 (1998)
2. R.M. Anderson, R.M. May, The invasion, persistence and spread of infectious diseases within animal and plant communities. Phil. Trans. R. Soc. Lond. B **314**, 533–570 (1986)
3. W. Bruckart, C. Cavin, L. Vajna, I. Schwarczinger, F.J. Ryan, Differential susceptibility of Russian thistle accessions to *Colletotrichum gloeosporioides*. Biol. Contr. **30**, 306–311 (2004)
4. J.B. Burie, A. Calonnec, M. Langlais, Modeling of the invasion of a fungal disease over a vineyard, in *Mathematical Modeling of Biological Systems*, vol. II, ed. by A. Deutsch, R.B. de la Parra, R.J. de Boer, O. Diekmann, P. Jagers, E. Kisdi, M. Kretzschmar, P. Lansky, H. Metz. Epidemiology, Evolution and Ecology, Immunology, Neural Systems and the Brain, and Innovative Mathematical Methods, Modeling and Simulation in Science, Engineering and Technology (Birkhäuser, Boston, 2008), pp. 11–21
5. J. Cardina, G.A. Johnson, D.H. Sparrow, The nature and consequence of weed spatial distribution. Weed Sci. **45**, 364–373 (1997)
6. R. Cousens, C. Dytham, R. Law, Dispersal in plants. A population perspective, in *Oxford Biology* (Oxford University Press, Oxford, 2008)
7. O. Diekmann, J.A.P. Heesterbeck (eds.), Mathematical epidemiology of infectious diseases. Model building, analysis and interpretation, in *Wiley Series in Mathematical and Computational Biology* (Wiley, Chichester, 2000)
8. J.A. Drake, H.A. Mooney (eds.), Biological invasions: a global perspective, in *SCOPE*, vol. 27 (Wiley, Chichester, 1989)
9. W. Ebeling, L. Schimansky-Geier, Stochastic dynamics of a bistable reaction system. Phys. A **98**, 587–600 (1979)

10. W. Ebeling, C. Ivanov, L. Schimansky-Geier, Stochastic theory of nucleation in bistable reaction systems. Rostocker Phys. Manuskripte **2**, 93–103 (1977)
11. J. Frantzen, Disease epidemics and plant competition: control of *Senecio vulgaris* with *Puccinia lagenophorae*. Basic Appl. Ecol. **1**, 141–148 (2000)
12. H.I. Freedman, A model of predator-prey dynamics as modified by the action of a parasite. Math. Biosci. **99**, 143–155 (1990)
13. J.S. Fulda, The logistic equation and population decline. J. Theor. Biol. **91**, 255–259 (1981)
14. L.Q. Gao, H.W. Hethcote, Disease transmission models with density dependent demographics. J. Math. Biol. **30**, 717–731 (1992)
15. K.P. Hadeler, H.I. Freedman, Predator-prey populations with parasitic infection. J. Math. Biol. **27**, 609–631 (1989)
16. K. Harley, I.W. Forno, *Biological Control of Weeds: A Handbook for Practitioners and Students* (Inkata Press, Melbourne, 1992)
17. R. Hengeveld (ed.), *Dynamics of Biological Invasions* (Chapman and Hall, London, 1989)
18. F.M. Hilker, *Spatiotemporal Patterns in Models of Biological Invasion and Epidemic Spread* (Logos, Berlin, 2005)
19. F.M. Hilker, H. Malchow, Strange periodic attractors in a prey-predator system with infected prey. Math. Popul. Stud. **13**(3), 119–134 (2006)
20. M. Julien, G. White, Biological control of weeds: theory and practical application, in *ACIAR Monograph Series*, vol. 49 (Australian Centre for International Agricultural Research, Bruce ACT, 1997)
21. R.M. Keane, M.J. Crawley, Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. **17**(4), 164–170 (2002)
22. B.W. Kooi, M.P. Boer, S.A.L.M. Kooijman, On the use of the logistic equation in models of food chains. Bull. Math. Biol. **60**, 231–246 (1998)
23. E. Kuno, Some strange properties of the logistic equation defined with r and K: inherent effects or artefacts? Res. Popul. Ecol. **33**, 33–39 (1991)
24. H. Malchow, L. Schimansky-Geier, Noise and diffusion in bistable nonequilibrium systems, in *Teubner-Texte zur Physik*, vol. 5 (Teubner, Leipzig, 1985)
25. H. Malchow, B. Radtke, M. Kallache, A.B. Medvinsky, D.A. Tikhonov, S.V. Petrovskii, Spatio-temporal pattern formation in coupled models of plankton dynamics and fish school motion. Nonlinear Anal. Real World Appl. **1**, 53–67 (2000)
26. H. Malchow, S.V. Petrovskii, E. Venturino, Spatiotemporal patterns in ecology and epidemiology: theory, models, simulations, in *CRC Mathematical and Computational Biology Series* (CRC Press, Boca Raton, 2008)
27. H. Malchow, A. James, R. Brown, Competitive and diffusive invasion in a noisy environment. Math. Med. Biol. **28**, 153–163 (2011)
28. M. Matsumoto, T. Nishimura, Mersenne Twister: a 623-dimensionally equidistributed uniform pseudorandom number generator. ACM Trans. Model. Comput. Simul. **8**(1), 3–30 (1998)
29. H. McCallum, N. Barlow, J. Hone, How should pathogen transmission be modelled? Trends Ecol. Evol. **16**(6), 295–300 (2001)
30. P.B. McEvoy, E.M. Coombs, Biological control of plant invaders: regional patterns, field experiments, and structured population models. Ecol. Appl. **9**(2), 387–401 (1999)
31. D. Mollison, Modelling biological invasions: chance, explanation, prediction. Phil. Trans. R. Soc. Lond. B **314**, 675–693 (1986)
32. D. Mollison (ed.), Epidemic models. Their structure and relation to data, in *Publications of the Newton Institute*, vol. 5 (Cambridge University Press, Cambridge, 1995)
33. R. Nathan, F.M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, A. Tsoar, Mechanisms of long-distance seed dispersal. Trends Ecol. Evol. **23**, 638–647 (2008)
34. A. Nitzan, P. Ortoleva, J. Ross, Nucleation in systems with multiple stationary states. Faraday Symp. Chem. Soc. **9**, 241–253 (1974)
35. S.V. Petrovskii, B.L. Li, Exactly solvable models of biological invasion, in *CRC Mathematical Biology and Medicine Series* (CRC Press, Boca Raton, 2006)

36. D. Pimentel (ed.), Biological invasions, in *Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species* (CRC Press, Boca Raton, 2002)
37. E.N. Rosskopf, R. Charudattan, J.B. Kadir, Use of plant pathogens in weed control, in *Handbook of Biological Control. Principles and Applications of Biological Control*, ed. by T.S. Bellows, T.W. Fisher, L.E. Caltagirone, D.L. Dahlsten, G. Gordh, C.B. Huffaker (Academic, San Diego, 1999), pp. 891–918
38. L. Sattenspiel, The geographic spread of infectious diseases, in *Princeton Series in Theoretical and Computational Biology* (Princeton University Press, Princeton, 2009)
39. D.F. Sax, J.J. Stachowicz, S.D. Gaines (eds.), Species invasions, in *Insights into Ecology, Evolution, and Biogeography* (Sinauer, Sunderland, 2005)
40. J. Segarra, M.J. Jeger, F. van den Bosch, Epidemic dynamics and patterns of plant diseases. Phytopathology **91**(10), 1001–1010 (2001)
41. N. Shigesada, K. Kawasaki, *Biological Invasions: Theory and Practice* (Oxford University Press, Oxford, 1997)
42. N. Shigesada, K. Kawasaki, Y. Takeda, Modeling stratified diffusion in biological invasions. Am. Nat. **146**(2), 229–251 (1995)
43. I. Siekmann, *Mathematical Modelling of Pathogen-Prey-Predator Interactions* (Verlag Dr. Hut, München, 2009)
44. J. Suszkiw, Fungus unleashed to combat yellow starthistle. Agric. Res. Mag. **52**(8), 20–22 (2004)
45. P. van den Driessche, M.L. Zeeman, Disease induced sscillations between two competing species. SIAM J. Appl. Dynam. Syst. **3**(4), 601–619 (2004)
46. J.E. van der Plank, Host-pathogen interactions in plant disease (Academic, New York, 1982)
47. E. Venturino, The influence of diseases on Lotka-Volterra systems. Rocky Mt. J. Math. **24**, 381–402 (1994)
48. E. Venturino, The effect of diseases on competing species. Math. Biosci. **174**, 111–131 (2001)
49. L.J. Wiles, G.W. Oliver, A.C. York, H.C. Gold, G.G. Wilkerson, Spatial distribution of broadleaf weeds in North Carolina soybean (*Glycine max*) field. Weed Sci. **40**, 554–557 (1992)
50. M. Williamson, Biological invasions, in *Population and Community Biology Series*, vol. 15 (Chapman & Hall, London, 1996)
51. C.L. Wilson, Use of plant pathogens in weed control. Annu. Rev. Phytopathol. **7**(1), 411–434 (1969)
52. L.M. Wilson, C. Jette, J. Connett, J.P. McCaffrey, Biology and biological control of yellow starthistle, in *FHTET Technology Transfer Series 17-1998* (Forest Health Technology Enterprise Team, Morgantown WV, 2003)
53. D.M. Woods, W.L. Bruckart III, M. Pitcairn, V. Popescu, J. O'Brien, Susceptibility of yellow starthistle to *Puccinia jaceae* var. *solstitialis* and greenhouse production of inoculum for classical biological control programs. Biol. Contr. **50**, 275–280 (2009)
54. M. Yokozawa, Y. Kubota, T. Hara, Effects of competition mode on spatial pattern dynamics in plant communities. Ecol. Model. **106**, 1–16 (1998)
55. R.L. Zimdahl, *Weed-Crop Competition. A review* (Blackwell Publishing, Oxford, 2004)