

Numerical continuation for the spatial model of vegetation-water-herbivore system

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Abstract

We describes the codes for the manuscript "*Traveling vegetation-herbivore waves may sustain ecosystems threatened by droughts and population growth*" by Singha et al. The methods include numerical continuation using `pde2path`.

1 Brief description of the model

In [SUM24] we consider a spatially explicit model that describes the coupled dynamics of vegetation, soil water, and herbivores in dryland ecosystems. The model captures two critical stressors—limited water availability and herbivory—and incorporates feedback mechanisms that can give rise to spatial self-organization. In particular, the model accounts for a behavioral component of herbivore movement, referred to as “vegetaxis,” in which herbivores are attracted to denser vegetation patches. This feature plays a crucial role in shaping vegetation-herbivore patterns.

Let $B(x, t)$, $W(x, t)$, and $H(x, t)$ represent the vegetation biomass density, soil water content, and herbivore biomass density, respectively, at spatial location x and time t . The governing equations are:

$$\begin{aligned}\partial_t B &= \Lambda BW(1 + EB)^2 \left(1 - \frac{B}{K_B}\right) - M_B B + D_B \nabla^2 B - G(B)H, \\ \partial_t W &= P - \frac{NW}{1 + RB/K_B} - \Gamma BW(1 + EB)^2 + D_W \nabla^2 W, \\ \partial_t H &= -M_H H + AG(B)H \left(1 - \frac{H}{K_H}\right) - \nabla \cdot \mathbf{J}_H.\end{aligned}$$

Vegetation growth depends on local water availability and is enhanced by root development, modeled through the nonlinear term $\Lambda BW(1 + EB)^2$. Growth is also limited by saturation effects and competition, captured by the factor $1 - B/K_B$. Vegetation biomass decreases due to natural mortality at rate M_B and through consumption by herbivores, where the consumption rate $G(B)$ follows a saturating function:

$$G(B) = \frac{\alpha B}{\beta + B},$$

with α representing the maximum per capita consumption rate and β the biomass at which half-maximum consumption occurs.

The soil water balance includes a constant precipitation input P , reduced by evaporation, which is itself mitigated by shading from vegetation ($NW/(1 + RB/K_B)$). Plants extract water from the

soil via a nonlinear uptake term proportional to $BW(1 + EB)^2$, while water diffuses laterally at a rate D_W .

Herbivores grow by consuming vegetation, reproducing at a rate proportional to the product $G(B)H$, moderated by density dependence via the factor $1 - H/K_H$. Herbivore losses are due to natural mortality at rate M_H and spatial redistribution. Movement is governed by the flux term:

$$\mathbf{J}_H = -D_R(B)\nabla H + HD_V(B)\nabla B,$$

where $D_R(B)$ describes biomass-dependent random movement:

$$D_R(B) = D_{HH} \frac{H\xi^2}{\xi^2 + B^2},$$

and $D_V(B)$ describes biased movement up vegetation gradients (vegetaxis):

$$D_V(B) = D_{HB} \frac{B}{\kappa + B}.$$

In this framework, herbivores tend to move more rapidly in bare-soil regions and slow down as they approach vegetation, while also being drawn toward denser patches. This behavior mimics an exploitation strategy, allowing herbivores to efficiently locate and graze on vegetation.

This system of equations can give rise to a rich variety of spatial and temporal patterns, including stationary vegetation stripes, localized herbivore aggregations, and traveling vegetation–herbivore waves. These emergent behaviors are critical for understanding the resilience of dryland ecosystems under increasing stress due to climate change and population-driven grazing pressure.

All scripts can simply be run by calling them from the **Matlab** command line; however, we strongly recommend running them in cell-mode from the **Matlab** editor, to see the results of individual cells and commands. For easy online use, the folder **bwhcont** contain cmds.m with cell blocks beginning with a brief description in each block.

The folder **bwhcont** contains all the necessary files to reproduce the bifurcation diagrams presented in the manuscript (see Table 1 for an overview). Before making any modifications, we recommend consulting the relevant documentation or references [Uec21], [Uec25] to become familiar with the **pde2path** command structure and workflow.

The function **bwhinit.m** initialises the problem, with the inputs the domain size **lx**, the number of discretization points **nx**, the model parameter **par**, an initial homogeneous solution **[B, W, H]**, and the output folder name **'bwh'**. The basic procedure is to use **p = stanparam** to general a problem structure with standard values of numerical parameters and control switches to obtain the bifurcation branch. The default value of are often overwritten to make it suitable for the problem description, for example we have modified **hobra.m** to **hobrax.m** as function handler for output. The function **oosetfemops.m** creates the necessary finite element matrices such as stiffness matrix in **p.mat.K** and the mass matrix **p.mat.M** appropriate for periodic boundary condition (see Listing 1).

```

1 function p=bwinit(lx,nx,par,varargin)
2 p=stanparam; % initialize fields with defaults, then overwrite some:
3 p.nc.neq=3; p.sw.sfem=-1;
4 p.fuha.outfu=@hobrax; % mod of llibrary function hobra
5 p.pdeo=stanpdeo1D(lx,2*lx/nx); p.vol=2*lx; % standard 1D PDE object
6 p.np=p.pdeo.grid.nPoints; p.nu=p.np*p.nc.neq; % # PDE unknowns
7 p.sol.xi=1/p.nu; p.file.smod=1; p.sw.para=2; p.sw.foldcheck=1;
8 p.nc.ilam=6; % use par(6) (P) for continuation
9 p.sol.ds=0.1; p.nc.dsmax=10.0; % initial and maximal stepsize
10 p.nc.lammin=0.0001; p.nc.lammax=500; % min and max values for cont parameter
11 p.nc.dlammax=10; %max step size in lam (bifurcation param)
12 p.file.smod=20; % save each smod'th cont.step, increase saves less data points
13 p.sw.bifcheck=2; %
14 p.nc.tol=1e-6; % tolerance
15 p.sw.jac=0; % switch for jacobian, zero as we use numerical jacobian (no sGjac)

```

Table 1: Scripts and functions in **bwhcont/**

file	purpose, remarks
cmds1	continuation of homogeneous branches and branch switching to and continuation of Turing branches and travelling wave branches; to cont. speed
cmds2	branch, fold and hopf point continuation
cmdsplot	plot commands for the bifurcation diagrams
cmdsdatext	to extract data to text files
bwhinit	Initialisation of problem struct p with the required parameter values; generates the FEM matrices by calling oosetfemops ; sets the pde2path parameters according the requirement of the problem
oosetfemops	creates the mass matrix M and the laplacian K for periodic boundary condition
nodalf	kinetic terms without the spatial derivatives
sG	right hand side of the PDE with the spatial terms in the moving co-ordinate system
hobrax	mod of library function hobra
twswibrax	mod of library function twswibra
qf, qf1, qf1der, qjac	standard phase condition for translational invariance in 'x'

```

16 p.nc.mu1=1; % tolerance for entering BP localization by bisection
17 %default initial condition
18 p.sw.verb=2;
19 p.nc.neig=30; % #eigenvalues to compute, and reference point for this
20 p.nc.eigref=-4;
21 np=p.np; B=zeros(np,1); W=(par(6)/par(7))*ones(np,1); H=zeros(np,1);
22 p.u=[B; W; H; par']; % initial solution (bare soil) and parameters
23 p=box2per(p,1); % switch on periodic BCs, this also calls oosetfemops
24 p.plot.pcmp=[1 2 3]; p.plot.cl={'k','b','r'}; % plotting settings
25 screenlayout(p); p.sw.verb=2; % place windows; choose verbosity of output

```

Listing 1: **bwhcont/bwhinit.m**,

```

1 function p=oosetfemops(p)
2 gr=p.pdeo.grid; fem=p.pdeo.fem;
3 [K,M,~]=fem.assema(gr,1,1,1); % FEM/mass matrices
4 M=kron([1,0,0];[0,1,0];[0,0,1],M);
5 p.mat.M0=p.mat.fill'*M;
6 p.mat.M=filltrafo(p, M);
7 p.mat.K=filltrafo(p, K);
8 Kx=fem.convection(gr,1); Kx=kron([1,0,0];[0,1,0];[0,0,1],Kx);
9 p.mat.Kx=filltrafo(p,Kx);

```

Listing 2: **bwhcont/oosetfemops.m**, precompute the FEM matrices.

```

1 %% Please each section of this code to get the branches of
2 close all; keep pphome;rng(42);
3 %% specification of the system, parameter values, domain size, grid size
4 Lambda=0.5; % rate of vegetation growth per unit soil water
5 E=10; % root to shoot ratio
6 K=0.9; % maximal standing biomass per unit area
7 M=11.4; % plant mortality rate
8 DB=1.2; % seed dispersal rate
9 P=0.0; % precipitation
10 N=20.0; % evaporation rate
11 R=0.01; % Reduction in evaporation due to shading (dimensionless)
12 GamW=10.0; % water uptake rate

```

```

13 DW=150; % lateral soil water diffusion
14 mH=0.06; % herbivore mortality rate
15 GamH=0.3; % fraction of consumed biomass used in herbivore production
16 AlphaH=0.603; % maximum rate of plant consumption per unit herbivore
17 BetaH=0.82; % satiation biomass
18 DHH=400; % maximal random motility
19 Zeta=0.001; % reference biomass at which the motility drops to 50%
20 DHB=700; % maximal vegetaxis motility
21 k=0.0001; % reference biomass at which the motility drops to 50%
22 K_H=175; % maximum herbivore capacity per unit area
23 s=0; % speed
24 % parameters are refered to by their number in p.nc.ilam; note numbers here!
25 par=[Lambda, E, K, M, DB, P, N, R, GamW, DW, mH, GamH, AlphaH, BetaH, DHH, Zeta, DHB, k,
      K_H, s];
26 % 1 6 12 17
27 nx=256; lx=pi/2;
28 p=bwinit(lx,nx,par); p=setfn(p,'bwh3/BS'); % init and initial folder-name
29 % Bare soil solution branch (BS)
30 p=cont(p,1000); %continuation with number of steps

```

Listing 3: /Users/joydeepsingha/Documents/Matlab/bwhcont/cmds1.m, init and cont of bare soil.

From the first branch point of the BS branch, we continue the UV branch (see Listing 4).

```

31 %% branch switching to uniform vegetation solution branch without herbivore (UV)
32 % arguments: input dir, branch point no, output dir, initial stepsize
33 p=swibra('bwh3/BS','bpt1','bwh3/UV',-0.05); pause; % pause to inspect kernel in Fig.6
34 p.nc.dsmax=1.0; p=cont(p,100000);

```

Listing 4: /bwhcont/cmds1.m continued; swibra to UV; use firstnumber and label, see source

From the UV we then continue to the UH branch (see listing 5).

```

35 %% Uniform solution branch with vegetation and herbivore (UH) using swibra command
36 p=swibra('bwh3/UV','bpt3','bwh3/UH',-0.01); p.nc.dsmax=5.0;
37 p.file.smod=20; p=cont(p,10000);

```

Listing 5: /bwhcont/cmds1.m continued; swibra to UH;

Here if **swibra** does not work, we can manually switch to the UH branch by using **loadp** jump from the branch point to UH (see listing 6).

```

38 %% Uniform solution branch with vegetation and herbivore (UH) through manual
   initialisation if swibra does not work
39 p=loadp('bwh2/UV','bpt3','bwh2/UH'); %load from a pt in the in dir to an out dir
40 p.u(p.nu+6)=p.u(p.nu+6)+1.0; %manually increasing the lam
41 n=p.nu/3; p.u(2*n+1:3*n)=2.0;p=resetc(p); %changing H and resetting struc count
42 p.sw.bifcheck=2;
43 p.sol.ds=1.0; p.nc.dsmax=2;
44 p=cont(p,200);

```

Listing 6: /bwhcont/cmds1.m continued; manuall switching to UH;

At low precipitation, UV has a turing bifurcation point. Using **swibra** the SP_0 branch is obtained. Here also use the phase condition (see listing 7).

```

45 %% stationary periodic solution branch of vegetation without herbivore (SP0)
46 p=swibra('bwh3/UV','bpt2','bwh3/SP0',0.01); pause;
47 p.sw.bifcheck=0; p.nc.dsmax=0.1; p=cont(p,20); pause;
48 p.nc.nq=1; p.nc.ilam=[6,20]; %phase condition on and adding speed as another bifurcation
   parameter
49 p.fuha.qf=@qf1; p.fuha.qfder=@qf1der; %standard phase condition and derivative
50 p.sw.qjac=1; %phase condition jacobian
51 p.sw.bifcheck=2; p.nc.dsmax=5.0;p=cont(p,168);

```

Listing 7: /bwhcont/cmds1.m continued; swibra to SP_0 ;

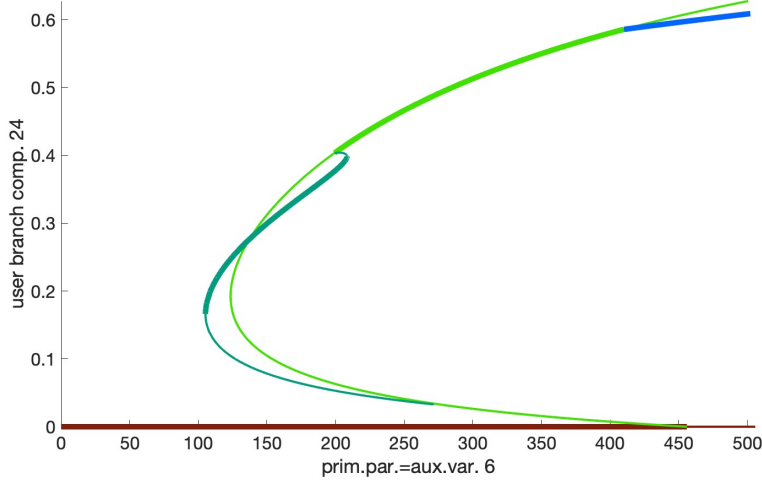


Figure 1: Bifurcation diagram obtained at $\alpha = 0.48$ using `plotbra` for parameters in set A . This is Fig. 3a of [SUM24].

Using the above settings for $\alpha = 0.48$ and setting the other parameters in set A, we obtain the complete bifurcation diagram (See Fig 1).

For $\alpha = 0.57$, we get the 4 solution branches as before but SP_0 loses stability at low P . From here we access the SP_H solution branch using `swibra` from the corresponding branch point on SP_0 (see listing 8).

```
52 %% stationary periodic solution branch vegetation and herbivore (SPH)
53 p=swibra('bwh3/SP0','bpt1','bwh3/SPH',0.1); pause;
54 p.nc.tol=1e-8; p.nc.dsmat=1.0; p=cont(p,100);
```

Listing 8: `/bwhcont/cmds1.m` continued; `swibra` to SP_H ;

This SP_H branch quickly loses stability and from there, the TW branch can be continued using `swibra` (see listing 9). In this way we can obtain the bifurcation diagram in Fig. 3b of [SUM24] (see figure 2).

```
55 %% travelling solution branch of both vegetation and herbivore (TW at low P)
56 % DRIFT bif., hence swibra, not twswibra
57 p=swibra('bwh3/SPH','bpt1','bwh3/TW_W',0.01); pause;
58 p.nc.tol=1e-5; p.nc.dsmat=1.0;
59 p.sw.bifcheck=2; p=cont(p,150);
```

Listing 9: `/bwhcont/cmds1.m` continued; `swibra` to TW at low P ;

Setting, $\alpha = 0.603$, we again get all of the 6 solutions branches as before. However in this case UH solution loses stability to a Hopf bifurcation. Using `twswibrax` we switch to the travelling wave branch here (see listing 10). In this way we can generate Fig. 5.

```
60 %% travelling solution branch from UH branch (TW at high P)
61 kwnr=1.0; %guess for spatial wave number
62 aux.z=[1 -1i]; %auxiliary arg for twswibrax, this comb of guesses of z1 and z2 works well
    for hp point on UH
63 hp='hpt1'; outb='bwh3/TW_H'; %hopf point number;output directory
64 p=twswibrax('bwh3/UH',hp,20,kwnr,outb,aux); %branch switching from hopf point to
    travelling wave branch
65 p.sol.ds=0.1; p.nc.dsmat=0.1;
66 p.u0(1:p.nu)=p.tau(1:p.nu); %reference profile
67 p.u0=p.u0'; p.u0x=p.mat.Kx*p.u0; % setting PC
68 plotsolu(p,p.u0x,1,3,1);
69 p.u(1:p.nu)=p.u(1:p.nu)+0.01*p.tau(1:p.nu);
70 p.nc.tol=1e-6; p.nc.nq=1;
71 p.nc.ilam=[6;20]; p.fuha.qf=@qf; p.sw.qjac=1; p.fuha.qfder=@qjac;
72 p.sw.bifcheck=2; pause;
```

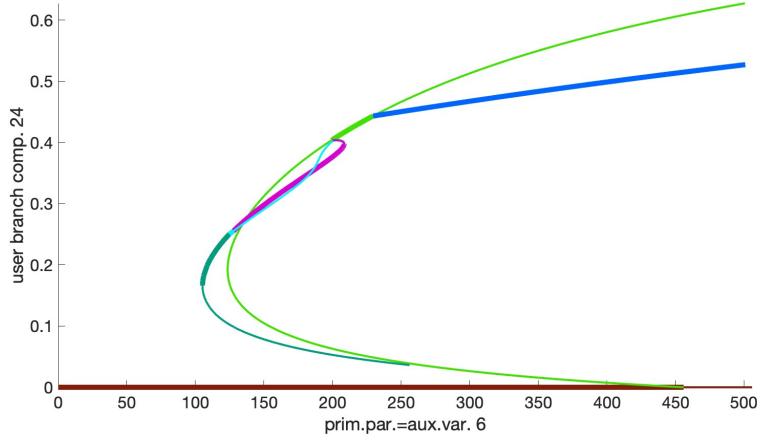


Figure 2: Bifurcation diagram obtained at $\alpha = 0.57$ for set A. (Fig. 3b of [SUM24]).

```
73 p.nc.dsmax=0.2; p=cont(p,570);
74 par=getaux(p); par(20) %to check speed
```

Listing 10: /bwhcont/cmds1.m continued; twswibrax to the *TW* branch at high P ;

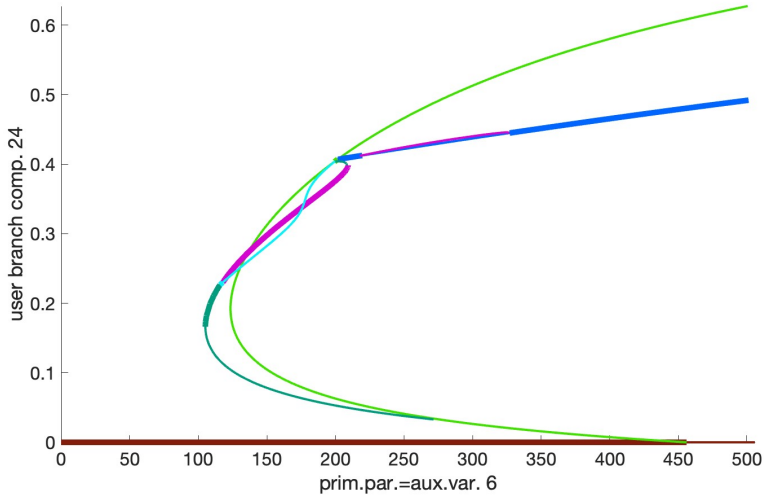


Figure 3: Bifurcation diagram obtained at $\alpha = 0.603$ for set A. (Fig. 3c of [SUM24]).

All of the bifurcation diagrams in [SUM24] (Figs. 3, 5, 6, 7, 14, 16) were obtained using the above for different values of parameters. To generate Fig. 16, low values of $\mathbf{p.sol.ds}$ and $\mathbf{p.nc.dsmin}$ on the order of 10^{-4} were used, as they were necessary to zoom in on a narrow range of P . For a few customisation advantage we use pyplot (script not provided but available upon request) after extracting the data in a text file (see listing 11).

```
1 %% solution branches
2 P=zeros(110,3); %array size depends on the number of points in the dir
3 for i=1:110;
4     pt=['bwh/BS/pt' mat2str(0+i*1)]; tmp=load(pt);tmpp=tmp.p; %change input
5     directory accordingly
6     P(i,1)=tmpp.u(tmpp.nu + 6);
7
8     np=p.nu/p.nc.neq;n=p.nu;
9
```

```

10 P(i,2)=(tmpp.u(1:np)')*(p.mat.M(1:np,1:np)*(tmpp.u(1:np)))/tmpp.vol;
11 p(i,2)=sqrt(P(i,2));
12
13 P(i,3)=tmpp.sol.ineg;
14 end
15 ptr=fopen('BS.txt','w'); %change output directory accordingly
16 fprintf(ptr,'%e\t%e\t%e\n',P');
17 fclose(ptr);

```

Listing 11: /bwhcont/cmdsdatext.m continued; bifurcation diagram data extraction;

Similarly the the solution profiles in Fig. 3, 5, 6, 7 are also obtained (see listing 12).

```

32 %% solution profile data
33 n = p.nu/3;
34 p=loadp('bwhcont/BS','pt198');
35 B = p.u(1:n);
36 W = p.u(n+1:2*n);
37 H = p.u(2*n+1:3*n);
38 ptr=fopen('bwhcont/pt198.txt','w');
39 fprintf(ptr,'%f\t%f\t%f\n',[B W H]');
40 fclose(ptr);

```

Listing 12: /bwhcont/cmdsdatext.m continued; solution profile data extraction;

Figures 10.b, c were obtained by changing **p.nc.ilam** corresponding to the number of position of D_{HB} with other corresponding parameters and changing the output component in **p.plot.bpcmp** to observe speed (see listing 13). Figure 15 is also obtained simply by changing **p.plot.bpcmp** for the TW branches for the corresponding value of the parameters.

```

76 %% continuation wrt DHB
77 p=loadp('bwh/TW','pt137','bwh/speed_DHB');
78 p.sol.ds=10.0;p.nc.ilam=[17,20];
79 p=resetc(p);p.nc.lammax=6000;pause;
80 p.nc.tol=1e-4;
81 p.sw.bifcheck=0; p.nc.dsmax=10.0;
82 p.plot.bpcmp=23;p=cont(p,3); pause;
83 p.nc.nq=1; p.fuha.qf=@qf1;
84 p.fuha.qfder=@qf1der; p.sw.qjac=1; % switch on PC
85 p.sw.bifcheck=2;p=cont(p,1000);

```

Listing 13: /bwhcont/cmds1.m continued; speed vs D_{HB} diagrams;

As before, their data were extracted and plotted in pyplot (see listing 14).

```

18 %% branch, fold, hopf points
19 P=zeros(27,3); %array size depends on the number of points in the dir
20 for i=1:27;
21 pt=['bwh/BS' ...
22 '/pt' mat2str(0+i*1)]; tmp=load(pt);tmpp=tmp.p; %change input directory
    accordingly
23 P(i,1)=tmpp.u(tmpp.nu + 6);
24
25 P(i,2) = tmpp.u(tmpp.nu + 13);
26 P(i,3)=tmpp.sol.ineg;
27
28 end
29 ptr=fopen('bwh/UV2bpcont.txt','w'); %change output directory accordingly
30 fprintf(ptr,'%e\t%e\t%e\n',P');
31 fclose(ptr);

```

Listing 14: /bwhcont/cmdsdatext.m continued; speed vs D_{HB} plot data extraction;

The phase diagrams in Figs. 9.a and 10.a in [SUM24] were mostly obtained using branch point continuation method in **pde2path** (see listings 15, 16, 17 for branch, fold and hopf point continuation respectively.). We advise caution for these continuations whenever H is non-zero or branch points are

nearby as the `p.nc.ntol` needs to be adjusted during continuation. Whenever there are convergence errors the boundaries between these stable solutions are completed manually from the bifurcation diagram. We also advise that the boundary of the phase diagram should be checked always using direct numerical simulation whether above and below the boundary the desired solutions are obtained.

The listing 15 shows that `pde2path` commands for branch point continuation for branch point on UV which generates UH that runs for few continuation steps (see figure ??).

```

9 %% For branch point continuation to find variation in the position of the turing
  bifurcation point on UV
10 p=bpcontini('bwh1/UV','bpt3',13,'bwh1/Turing_UV'); %branch point continuation w.r.t
  parameter 13
11 plotsol(p); mclf(2); pause %solution profile; to clear fig 2;
12 p.nc.dlamax=0.0001; p.nc.lammax=1.0; p.sw.bifcheck=0;
13 p.sw.foldcheck=0; %switch of fold
14 p.sol.ds=-0.01;
15 p.nc.tol=1e-7; p.nc.del=0.001; p.nc.njthreshsp=1e3;
16 p.sw.spjac=0; %for fuha.spjac
17 p.nc.dsmax=0.01; p.nc.dsmin=0.00001;
18 p.file.smod=1; p=cont(p,10);

```

Listing 15: `/bwhcont/cmds2.m` continued; branch point continuation;

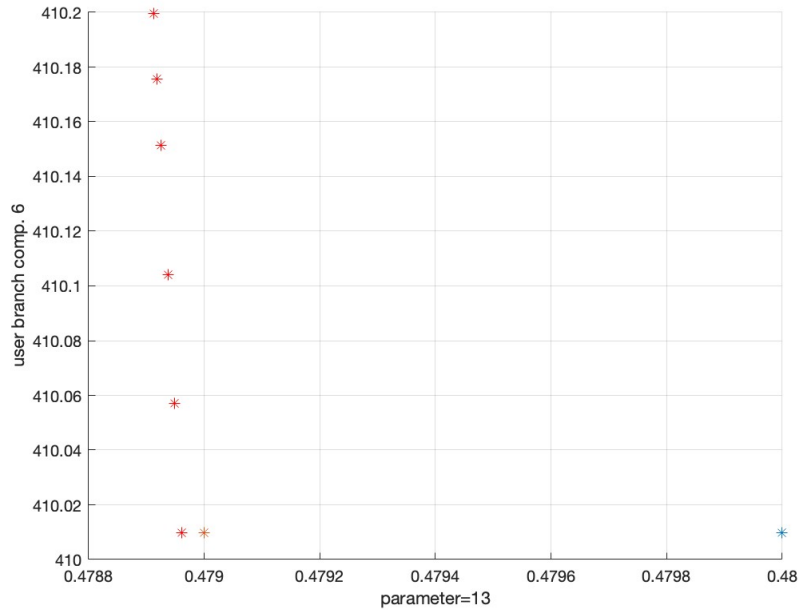


Figure 4: Branch point continuation.

Both the fold point continuation and hopf continuations (see listings 16, 17) runs for few steps initially however we get convergence errors so therefore we mostly use manual evaluation of the bifurcation diagrams and obtain the phase boundaries.

```

30 %% for fold point continuation
31 p=spcontini('bwh3/SP0','fpt2',13,'bwh3/SP0_fold_point'); %fold point cont.
32 huclean(p);
33 plotsol(p); pause
34 p.nc.dlamax=10; p.nc.lammax=1.5;
35 p.nc.del=1e-2; p.nc.njthresh=1e-2; p.nc.njthreshsp=1e5;
36 p.sol.ds=0.0001; p.plot.bpcmp=p.nc.ilam(2);
37 p.nc.tol=1e-5; p.sw.spjac=0; %for fuha.spjac
38 p.file.smod=1; p.sw.bifcheck=0; p.sw.foldcheck=0;

```



```
39 p.sw.verb=2; p.nc.dsmax=0.001; p=cont(p,50);
```

Listing 16: /bwhcont/cmds2.m continued; fold point continuation;

```
41 %% Hopf point continuation
42 p=hpcontini('bwh3/UH','hpt1',13,'bwh3/UH_hopf_point'); %hopf point cont
43 huclean(p); plotsol(p); p.nc.dlammax=0.0001;
44 p.nc.lammax=0.608; pause
45 p.plot.bpcmp=p.nc.ilam(2);
```

Listing 17: /bwhcont/cmds2.m continued; hopf point continuation;

References

- [SUM24] J. Singha, H. Uecker, and E. Meron. Traveling vegetation–herbivore waves may sustain ecosystems threatened by droughts and population growth, 2024. Preprint.
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- [Uec25] Hannes Uecker. pde2path - a matlab package for continuation and bifurcation in system of pdes, v3.1. 2025.