

# Computer code for: A mathematical framework for evo-devo dynamics

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This file contains the computer code used to generate the figures of the Example given in the main text. This code was prepared in Mathematica 12.1.1.0 and it is made available under a Creative Commons Attribution licence (CC BY).

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## Non-social development

```
In[ ]:= Clear["Global`*"]
```

```
(*Choose parameters*)
NA = 4; (*number of ages*)
Pp = 0.7; (*survival probability*)
Finalτ = 200;

κ[Na_, p_] := Sum[pa-1, {a, 1, Na}]
T[Na_, p_] := Sum[a (1 - y[a]) x[a] × l[a, p], {a, 1, Na}]
partialwpartialx[Na_, p_] :=
  Table[ $\frac{1}{T[Na, p]} l[a, p] (1 - y[a])$ , {a, 1, Na}, {j, 1, 1}]
partialwpartialy[Na_, p_] := Table[- $\frac{1}{T[Na, p]} l[a, p] × x[a]$ , {a, 1, Na}, {j, 1, 1}]
partialxpartialy[Na_] := Table[Table[If[j == a + 1, x[a], 0], {j, 1, Na}], {a, 1, Na}]
partialxpartialx[Na_] :=
  Table[Table[If[j == a + 1, 1 + y[a], If[j == a, 1, 0]], {j, 1, Na}], {a, 1, Na}]
totalxtotalx[Na_] :=
  Table[Table[If[j > a, Product[partialxpartialx[Na][[k, k + 1]], {k, a, j - 1}],
    If[j == a, 1, 0]], {j, 1, Na}], {a, 1, Na}]
totalxtotaly[Na_] := partialxpartialy[Na].totalxtotalx[Na];
totalwttotalx[Na_, p_] := totalxtotalx[Na].partialwpartialx[Na, p]
totalwttotaly[Na_, p_] :=
  partialwpartialy[Na, p] + totalxtotaly[Na].partialwpartialx[Na, p]

l[a_, p_] := pa-1
Gy[Na_, τ_] := Table[
  If[a == j, (ysol[τ])[a, 1] (1 - (ysol[τ])[a, 1]), 0], {a, 1, Na}, {j, 1, Na}]

(*Substitute solutions in total selection gradient*)
```

```

Totalwtotalx[Na_, τ_, p_] :=
  totalwtotalx[Na, p] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Totalwtotaly[Na_, τ_, p_] :=
  totalwtotaly[Na, p] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]

(*Initial conditions*)
ysol[1] = Table[1/2, {a, 1, 4}, {j, 1, 1}];

Runs[Na_, T_, p_] := Table[{xsol[τ, 1, 1] = 1;
  Table[xsol[τ, a + 1, 1] = (1 + ysol[τ][[a, 1]]) xsol[τ, a, 1], {a, 1, Na - 1}];
  ysol[τ + 1] = ysol[τ] + κ[Na, p] × Gy[Na, τ].Totalwtotaly[Na, τ, p];}, {τ, 1, T}]

(*Plots of runs*)
PlotStyleFunction[τ_] := If[τ == Finalτ, {Black, Thickness[0.01]},
  If[τ == 1, {Black, Dashing[0.05], Thickness[0.01]}, {Gray}]]
PlotRuns[Na_, T_, p_] := {Runs[Na, T, p];,
  Export[StringJoin[ToString[NotebookDirectory[]],
    StringJoin["Fig.example.control.p=", ToString[p]], ".pdf"],
    Show[Table[ListLinePlot[Flatten[ysol[τ]], PlotRange → {-0.1, 1.1},
      PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
      PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],
  Export[StringJoin[ToString[NotebookDirectory[]],
    StringJoin["Fig.example.state.p=", ToString[p]], ".pdf"],
    Show[Table[ListLinePlot[Table[xsol[τ, a, 1], {a, 1, Na}],
      PlotRange → {0, 5}, PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
      PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]}

(*Do runs and plots*)
PlotRuns[NA, Finalτ, Pp];

(*Gz plots*)

(*To fix color scale in matrix plot*)
cf = Blend[{{0., RGBColor[0.260487, 0.356, 0.891569]},
  {0.166667, RGBColor[0.230198, 0.499962, 0.848188]},
  {0.333333, RGBColor[0.392401, 0.658762, 0.797589]},
  {0.499999, RGBColor[0.964837, 0.982332, 0.98988]},
  {0.5, RGBColor[1, 1, 1]}, {0.500001, RGBColor[0.95735, 0.957281, 0.896269]},
  {0.666667, RGBColor[0.913252, 0.790646, 0.462837]},
  {0.833333, RGBColor[0.860243, 0.558831, 0.00695811]},
  {1., RGBColor[1., 0.42, 0.]}, #1] &;
(*cfScaled=cf@Rescale[#, {-1,1}, {0,1}]&;*)
cfScaled = cf@Rescale[#, {-4, 4}, {0, 1}] &;

(*Compute Gx*)

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Totalxtotaly[Na_, τ_] :=
  totalxtotaly[Na] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Gx[Na_, τ_] := Transpose[Totalxtotaly[Na, τ]].Gy[Na, τ].Totalxtotaly[Na, τ]

(*Compute Gz*)
Totalztotaly[Na_, τ_] :=
  ArrayFlatten[{{Totalxtotaly[Na, τ], IdentityMatrix[Na]}}]
Gz[Na_, τ_] := Transpose[Totalztotaly[Na, τ]].Gy[Na, τ].Totalztotaly[Na, τ]

(*Plots of Gz*)
GzPlot[Na_, p_] := Table[Export[
  StringJoin[ToString[NotebookDirectory[]], StringJoin["Fig.example.Gz.p=",
    ToString[p], ".tau=", ToString[τ]], ".pdf"], MatrixPlot[Gz[Na, τ],
  FrameTicks → {{{{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}},
    {{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}}},
    {{{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}}},
    {{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}}}},
  FrameStyle → Large, PlotLegends → BarLegend[{Automatic, {-4, 4}},
  LabelStyle → Large], ColorFunction → cfScaled,
  ColorFunctionScaling → False]], {τ, {1, 2, 5, 10, 20, Finalτ}}]

(*Do plots of Gz*)

GzPlot[NA, Pp];

(*Plots of the total selection gradients*)

Totalwtotalz[Na_, τ_, p_] :=
  ArrayFlatten[{{Totalwtotalx[Na, τ, p]}, {Totalwtotaly[Na, τ, p]}}]
dwdyxPlot[Na_, p_] := {Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.dwdy.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Totalwtotaly[Na, τ, p]],
    PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
    PlotRange → {-0.4, 0.1}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],
  Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.dwdx.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Totalwtotalx[Na, τ, p]],
    PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
    PlotRange → {0, 0.5}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]}]
dwdyxPlot[NA, Pp];

(*Plots of the partial selection gradients*)

Partialwpartialx[Na_, τ_, p_] :=

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partialwpartialx[Na, p] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Partialwpartialy[Na_, τ_, p_] :=
  partialwpartialy[Na, p] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]

PartialwpartialyxPlot[Na_, p_] :=
  {Export[StringJoin[ToString[NotebookDirectory[]],
    StringJoin["Fig.example.partialwpartialy.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Partialwpartialy[Na, τ, p]],
    PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
    PlotRange → {-0.4, 0.1}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],
  Export[StringJoin[ToString[NotebookDirectory[]],
    StringJoin["Fig.example.partialwpartialx.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Partialwpartialx[Na, τ, p]],
    PlotStyle → PlotStyleFunction[τ], AxesStyle → Large,
    PlotRange → {0, 0.5}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]}

PartialwpartialyxPlot[NA, Pp];

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## Social development

```
In[ ]:= Clear["Global`*"]
```

```

(*Choose parameters*)
NA = 4; (*number of ages*)
Pp = 0.7; (*survival probability*)
Qp = 0.5; (*rate of social interaction*)
Finalτ = 200;

x[Na_, p_] := Sum[pa-1, {a, 1, Na}]
T[Na_, p_, q_] := Sum[a (1 - y[a]) x[a] × l[a, p]  $\frac{1+q}{1-qy[a]}$ , {a, 1, Na}]
partialwpartialx[Na_, p_, q_] :=
  Table[ $\frac{1}{T[Na, p, q]}$  l[a, p] (1 - y[a]), {a, 1, Na}, {j, 1, 1}]
partialwpartialy[Na_, p_, q_] :=
  Table[- $\frac{1}{T[Na, p, q]}$  l[a, p] × x[a]  $\frac{1+q}{1-qy[a]}$ , {a, 1, Na}, {j, 1, 1}]
partialxpartialy[Na_, q_] :=
  Table[Table[If[j == a + 1, x[a]  $\frac{1+q}{1-qy[a]}$ , 0], {j, 1, Na}], {a, 1, Na}]
partialxpartialx[Na_] :=
  Table[Table[If[j == a + 1, 1 + y[a], If[j == a, 1, 0]], {j, 1, Na}], {a, 1, Na}]
totalxtotalx[Na_] :=

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Table[Table[If[j > a, Product[partialpartialx[Na][[k, k + 1]], {k, a, j - 1}],
  If[j == a, 1, 0]], {j, 1, Na}], {a, 1, Na}
totalxtotaly[Na_, q_] := partialpartialy[Na, q].totalxttotalx[Na];
totalwtotalx[Na_, p_, q_] := totalxttotalx[Na].partialwpartialx[Na, p, q]
totalwtotaly[Na_, p_, q_] :=
  partialwpartialy[Na, p, q] + totalxttotaly[Na, q].partialwpartialx[Na, p, q]

l[a_, p_] := pa-1
Gy[Na_, τ_] := Table[
  If[a == j, (ysol[τ])[a, 1] (1 - (ysol[τ])[a, 1]), 0], {a, 1, Na}, {j, 1, Na}]

(*Substitute solutions in total selection gradient*)
Totalwtotalx[Na_, τ_, p_, q_] :=
  totalwtotalx[Na, p, q] /. Table[y[a] → ysol[τ][a, 1], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Totalwtotaly[Na_, τ_, p_, q_] :=
  totalwtotaly[Na, p, q] /. Table[y[a] → ysol[τ][a, 1], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]

(*Initial conditions*)
ysol[1] = Table[1/2, {a, 1, 4}, {j, 1, 1}];

Runs[Na_, T_, p_, q_] := Table[{xsol[τ, 1, 1] = 1;
  Table[xsol[τ, a + 1, 1] =  $\frac{1 + \text{ysol}[\tau][a, 1]}{1 - q \text{ysol}[\tau][a, 1]} \text{xsol}[\tau, a, 1]$ , {a, 1, Na - 1}];
  ysol[τ + 1] = ysol[τ] + κ[Na, p] × Gy[Na, τ].Totalwtotaly[Na, τ, p, q];},
{τ, 1, T}]

(*Plots of runs*)
PlotStyleFunction[τ_, T_] := If[τ == T, {Black, Thickness[0.01]},
  If[τ == 1, {Black, Dashing[0.05], Thickness[0.01]}, {Gray}]]
PlotRuns[Na_, T_, p_, q_] := {Runs[Na, T, p, q];,
  Export[StringJoin[ToString[NotebookDirectory[]], StringJoin[
    "Fig.example.social.control.p=", ToString[p], ".q=", ToString[q]],
    ".pdf"], Show[Table[ListLinePlot[Flatten[ysol[τ]], PlotRange → {-0.1, 1.1},
    PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],
  Export[StringJoin[ToString[NotebookDirectory[]], StringJoin[
    "Fig.example.social.state.p=", ToString[p], ".q=", ToString[q]], ".pdf"],
    Show[Table[ListLinePlot[Table[xsol[τ, a, 1], {a, 1, Na}], PlotRange → {0, 20},
    PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]}

(*Do runs and plots*)
PlotRuns[NA, Finalτ, Pp, Qp];

(*Hz plots*)

```

```

(*To fix color scale in matrix plot*)
cf = Blend[{{0., RGBColor[0.260487, 0.356, 0.891569]},
  {0.166667, RGBColor[0.230198, 0.499962, 0.848188]},
  {0.333333, RGBColor[0.392401, 0.658762, 0.797589]},
  {0.499999, RGBColor[0.964837, 0.982332, 0.98988]},
  {0.5, RGBColor[1, 1, 1]}, {0.500001, RGBColor[0.95735, 0.957281, 0.896269]},
  {0.666667, RGBColor[0.913252, 0.790646, 0.462837]},
  {0.833333, RGBColor[0.860243, 0.558831, 0.00695811]},
  {1., RGBColor[1., 0.42, 0.]}}, #1] &;
(*cfScaled=cf@Rescale[#, {-1,1}, {0,1}]&;*)
cfScaled = cf@Rescale[#, {-50, 50}, {0, 1}] &;

(*Compute Gx*)
Totalxtotaly[Na_, τ_, q_] :=
  totalxtotaly[Na, q] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Gx[Na_, τ_, q_] := Transpose[Totalxtotaly[Na, τ, q]].
  Gy[Na, τ].Totalxtotaly[Na, τ, q]

(*Compute Gz*)
Totalztotaly[Na_, τ_, q_] :=
  ArrayFlatten[{{Totalxtotaly[Na, τ, q], IdentityMatrix[Na]}]}]
Gz[Na_, τ_, q_] := Transpose[Totalztotaly[Na, τ, q]].
  Gy[Na, τ].Totalztotaly[Na, τ, q]

(*Compute Hz*)
partialxpartialxbar[Na_, q_] :=
  Table[Table[If[j == a, y[a] q, 0], {j, 1, Na}], {a, 1, Na}]
Partialxpartialxbar[Na_, τ_, q_] :=
  partialxpartialxbar[Na, q] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
totalxtotalxbar[Na_, q_] := partialxpartialxbar[Na, q].totalxtotalx[Na]
Totalxtotalxbar[Na_, τ_, q_] :=
  totalxtotalxbar[Na, q] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
sxsxbarTranspose[Na_, τ_, q_] :=
  Inverse[IdentityMatrix[Na] - Transpose[Totalxtotalxbar[Na, τ, q]]]
sxsyTranspose[Na_, τ_, q_] :=
  sxsxbarTranspose[Na, τ, q].Transpose[Totalxtotaly[Na, τ, q]]
szsyTranspose[Na_, τ_, q_] :=
  ArrayFlatten[{{sxsyTranspose[Na, τ, q]}, {IdentityMatrix[Na]}]}]

Hz[Na_, τ_, q_] := szsyTranspose[Na, τ, q].Gy[Na, τ].Totalztotaly[Na, τ, q]

(*Plots of Hz*)

```

```

HzPlot[Na_, p_, q_] := Table[Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.social.Hz.p=", ToString[p], ".tau=", ToString[τ]],
  ".pdf"], MatrixPlot[Hz[Na, τ, q],
  FrameTicks → {{{{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}},
    {{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}}},
    {{{{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}},
    {{1, 1}, {2, 2}, {3, 3}, {4, 4}, {5, 1}, {6, 2}, {7, 3}, {8, 4}}}}},
  FrameStyle → Large, PlotLegends → BarLegend[{Automatic, {-50, 50}},
  LabelStyle → Large], ColorFunction → cfScaled,
  ColorFunctionScaling → False]], {τ, {1, 2, 5, 10, 20, Finalτ}}]

```

(\*Do plots of Hz\*)

```
HzPlot[NA, Pp, Qp];
```

(\*Plots of the total selection gradients\*)

```

Totalwtotalz[Na_, τ_, p_, q_] :=
  ArrayFlatten[{{Totalwtotalx[Na, τ, p, q]}, {Totalwtotaly[Na, τ, p, q]}}]
dwdyxPlot[Na_, T_, p_, q_] := {Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.social.dwdy.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Totalwtotaly[Na, τ, p, q]],
    PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,
    PlotRange → {-0.4, 0.1}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],
  Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.social.dwdx.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Totalwtotalx[Na, τ, p, q]],
    PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,
    PlotRange → {0, 0.5}, PlotStyle → {Black, Thickness[0.01]},
    PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]}
dwdyxPlot[NA, Finalτ, Pp, Qp];

```

(\*Plots of the partial selection gradients\*)

```

Partialwpartialx[Na_, τ_, p_, q_] :=
  partialwpartialx[Na, p, q] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]
Partialwpartialy[Na_, τ_, p_, q_] :=
  partialwpartialy[Na, p, q] /. Table[y[a] → ysol[τ][[a, 1]], {a, 1, Na}] /.
  Table[x[a] → xsol[τ, a, 1], {a, 1, Na}]

```

```

PartialwpartialyxPlot[Na_, T_, p_, q_] :=
  {Export[StringJoin[ToString[NotebookDirectory[]],
  StringJoin["Fig.example.social.partialwpartialy.p=", ToString[p]], ".pdf"],
  Show[Table[ListLinePlot[Flatten[Partialwpartialy[Na, τ, p, q]],
    PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,
    PlotRange → {-0.4, 0.1}, PlotStyle → {Black, Thickness[0.01]},

```

```
PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]],  
Export[StringJoin[ToString[NotebookDirectory[]],  
StringJoin["Fig.example.social.partialwpartialx.p=", ToString[p]], ".pdf"],  
Show[Table[ListLinePlot[Flatten[Partialwpartialx[Na, τ, p, q]],  
PlotStyle → PlotStyleFunction[τ, T], AxesStyle → Large,  
PlotRange → {0, 0.5}, PlotStyle → {Black, Thickness[0.01]},  
PlotMarkers → {"●", Large}], {τ, {1, 2, 5, 10, 20, Finalτ}}]]]  
  
PartialwpartialyxPlot[NA, Finalτ, Pp, Qp];
```