

eco-evolutionary models

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```
library(deSolve)
library(reshape2)
library(ggplot2)
theme_set(theme_bw())
```

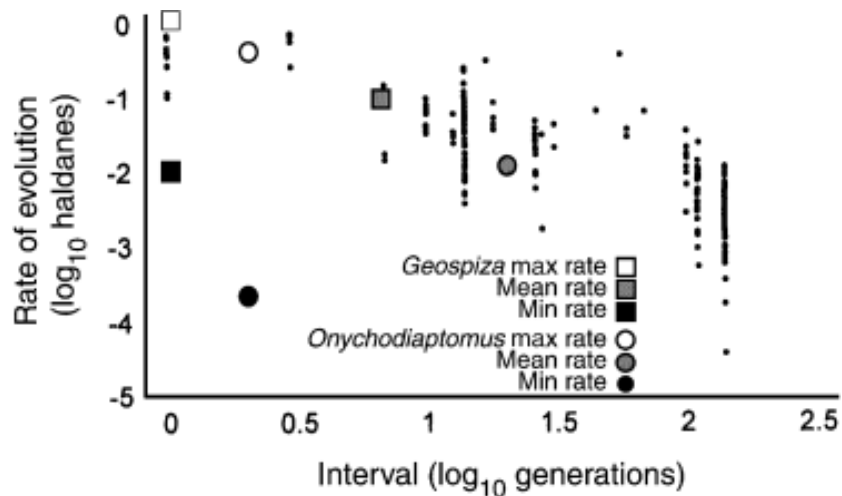
what are eco-evolutionary models?

- Slobodkin/Hutchinson: evolutionary theater, ecological play (i.e. ecological rates \gg evolutionary rates)
- what if the rates are similar?
 - ecological dynamics (e.g. logistic equation)
 - evolutionary dynamics (changes in traits)
- alternatively, population genetics plus population dynamics

why aren't all models like this?

- eco/evo time scales are often different
- it's hard!
 - most population genetic models assume constant population size
 - most ecological models assume constant traits

(Ellner, Geber, and Hairston 2011)



(1 Haldane = change by a factor of 1 standard deviation/generation)

endpoints

- ecology only: e.g. Lotka-Volterra predator-prey or competition; Rosenzweig-MacArthur model ...
- evolution (population genetics); e.g. see Lande, Lande and Arnold ... (discrete-time matrix models)

how do we do it?

- range of realism/complexity
- individual or agent-based models
 - each individual has a genotype and a phenotype
 - rules for life history and interactions
- models for the distribution of a continuous trait
 - partial differential equations
 - reaction-diffusion equations
 - includes demography, mutation
- moment equations
 - simplify PDEs to equations for the means and variances of traits, plus population densities
- Price equations:
 - further simplify to equations for the means of traits (assume constant variance)

individual-based models

- maximum detail, realism
- slow
- in R: try to be clever
- also: Python/Cython, C, NetLogo

distribution models

- write equations to follow the fractions of the population in each bin
- i.e. write out $dN(\alpha)/dt$ for $\alpha = 0.01, 0.02, \dots$
- move between bins via *mutation kernel*, e.g. $m(-1 + C \sum_{i \neq j} \exp(-((\alpha_i - \alpha_j)/\sigma^2)))$ where C is a *normalization constant*, i.e. make sure the sum is 1/ population is balanced
- boundary conditions!

PDEs

- advection (e.g. growth) $\partial N / \partial \alpha$
- diffusion (e.g. mutation): $\partial^2 N / \partial \alpha^2$

second partial derivatives by

moment equations

- figure out the dynamics of the mean *and* variance
- in general; mean follows
- Birch and Bolker (2015)

Price equations

- often used to decompose multi-level effects (Collins and Gardner 2009)
- simplest version reduces to $d\bar{T} = V_0 \partial(\text{fitness}) / \partial(T)$
- epidemic models: Troy Day and Proulx (2004); T. Day and Gandon (2006)

epidemic model

$$\begin{aligned}\frac{dS}{dt} &= m(N - S) - \beta(\bar{\alpha})SI \\ \frac{dI}{dt} &= \beta(\bar{\alpha})SI - (m + \alpha)I \\ \frac{d\bar{\alpha}}{dt} &= h \left(S \frac{\partial \beta}{\partial \bar{\alpha}} - 1 \right) \\ \beta(\bar{\alpha}) &= c\bar{\alpha}^{1/\text{gamma}}\end{aligned}$$

R implementation

```
## tradeoff curve
beta = function(alpha, c0, gamma = 2) {
  c0 * alpha^(1/gamma)
}
derivbeta = function(alpha, c0, gamma = 2) {
  c0/gamma * alpha^(1/gamma - 1)
}
derivfun1 = function(t, y, parms) {
  derivs = with(as.list(c(y, parms)), c(m *
    (N - S) - beta(alpha, c0, gamma) * S *
    I, (beta(alpha, c0, gamma) * S - (m +
    alpha)) * I, h * (S * derivbeta(alpha,
    c0, gamma) - 1)))
```

```
list(derivs)
}
```

Parameters

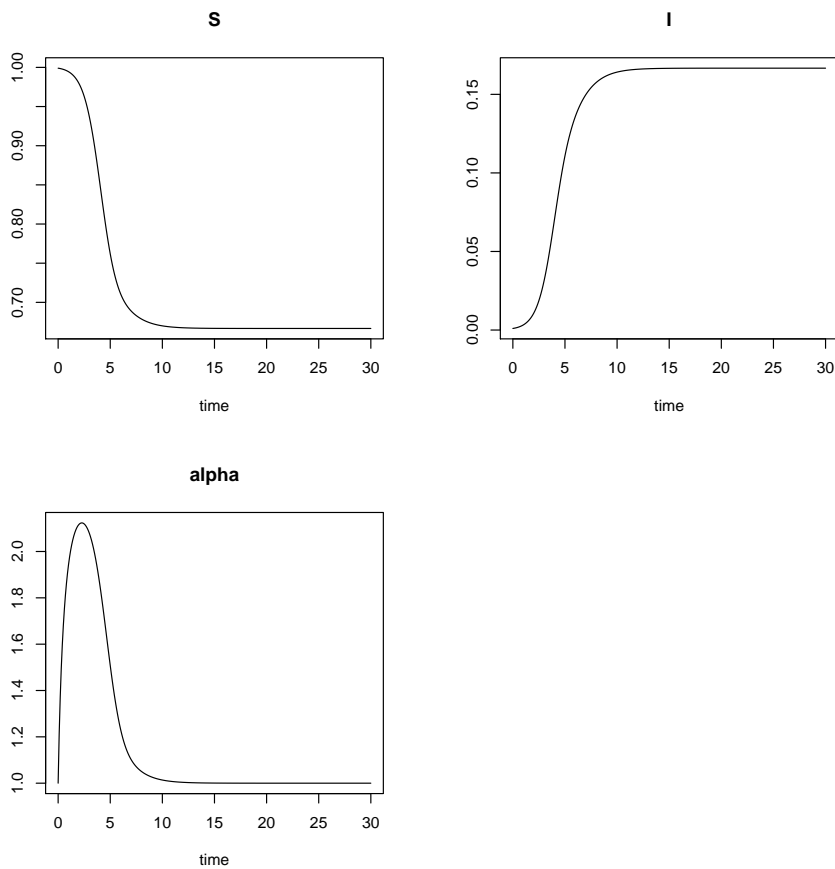
```
params3 = c(h = 5, c0 = 3, m = 1, N = 1, gamma = 2)
startvals = c(S = 0.999, I = 0.001, alpha = 1)
derivfun1(t = 0, y = startvals, parms = params3)

## [[1]]
## [1] -0.001997 0.000997 2.492500

L1 = ode(y = startvals, times = seq(0, 30, by = 0.1),
        parms = params3, func = derivfun1)
```

default plot (a bit ugly)

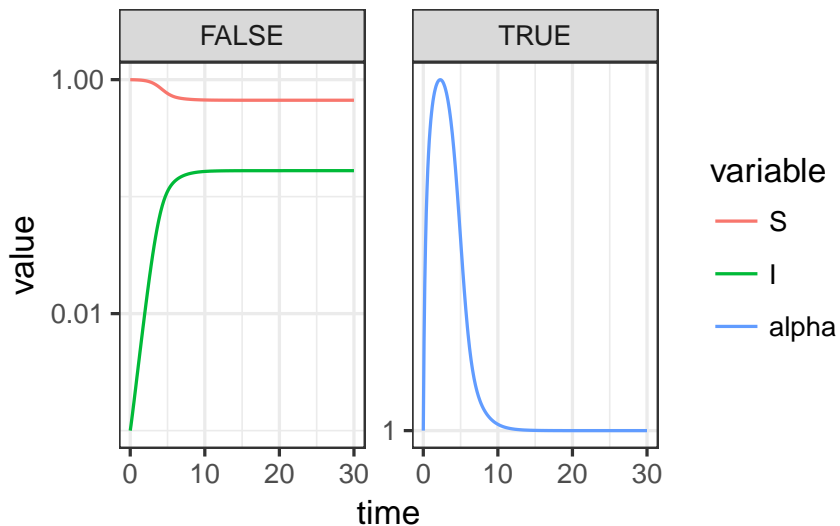
```
plot(L1)
```



nicer plot

```
Lm1 <- melt(as.data.frame(L1), id.vars = "time") ## convert to long format
Lm1 <- transform(Lm1, var = (variable == "alpha")) ## add var for faceting
```

```
gg1 <- ggplot(Lm1, aes(time, value, colour = variable)) +
  geom_line() + scale_y_log10()
print(gg1 + facet_wrap(~vir, nrow = 1, scale = "free"))
```

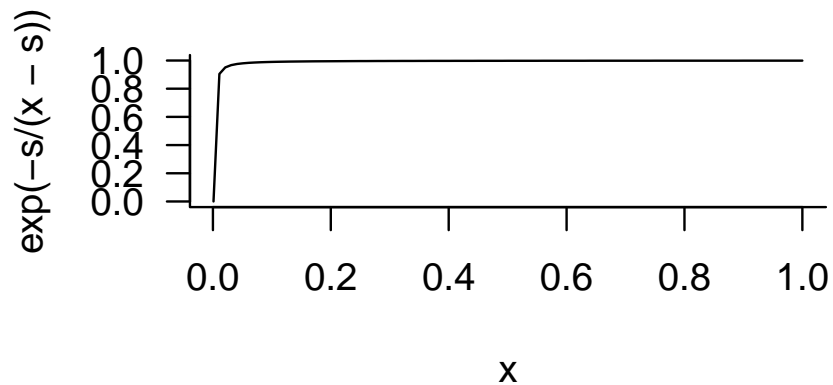


predator-prey system (Abrams and Matsuda 1997)

- MacArthur-Rosenzweig model: logistic growth + Holling type II predation
- trait C increases both growth rate and vulnerability of prey

$$\begin{aligned}\frac{dP}{dt} &= P \left(\frac{BCN}{1+hCN} - d \right) \\ \frac{dN}{dt} &= N \left(R + qC - kN - \frac{CP}{1+hCN} \right) \\ \frac{dC}{dt} &= V_0 \exp(-s/(C-s)) \left(q - \frac{P}{1+hCN} \right)\end{aligned}$$

what is the exponential term doing there?



predator-prey system

Depending on parameters, this system can show

- expanding cycles
- stable cycles
- chaos
- stable equilibrium

R implementation

```

parms1 <- c(h = 1, B = 1, q = 1.2, d = 0.5, V0 = 0.1,
           R = 0.5, k = 0.5, s = 0.001)
init <- c(P = 2, N = 2, C = 1)
AMgrad <- function(t, y, parms) {
  grad <- with(as.list(c(y, parms)), {
    c(P = P * (B * C * N / (1 + h * C * N) -
          d), N = N * (R + q * C - k * N - C *
          P / (1 + h * C * N)), C = V0 * exp(-s / (C -
          s)) * (q - P / (1 + h * C * N)))
  })
  return(list(grad))
}
## check that gradient function works
AMgrad(t = 0, y = init, parms = parms1)

## [[1]]
##           P           N           C
## 0.33333333 0.06666667 0.05327997

run the model

L2 = ode(t = 0:70, y = init, parms = parms1, func = AMgrad)
Lm2 <- melt(as.data.frame(L2), id.vars = "time")

plot

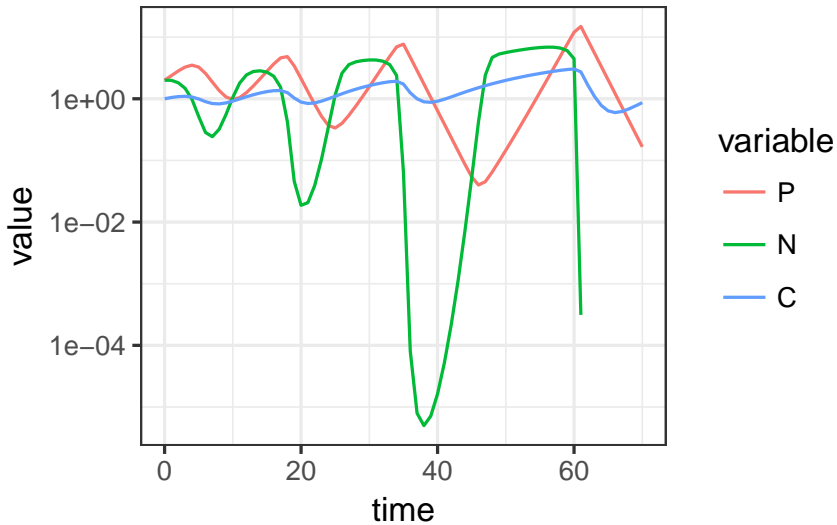
gg1 %>% Lm2

## Warning in self$trans$transform(x): NaNs
## produced

## Warning: Transformation introduced infinite
## values in continuous y-axis

## Warning: Removed 9 rows containing missing
## values (geom_path).

```



```
## limit cycles
parms2 <- c(h = 1, B = 1, q = 0.8, d = 0.5, V0 = 0.05,
           R = 0.5, k = 1, s = 0.001)
## same but higher V0: chaotic/long-period
## limit cycles?
parms3 <- c(h = 1, B = 1, q = 0.8, d = 0.5, V0 = 0.075,
           R = 0.5, k = 1, s = 0.001)
## expanding cycles for V0 larger (0.5) stable
## for V0 < 0.03148 ?
```

Full-distribution models

Now let's build a full model for the distribution.

```
## define vector of virulence values
alphavec <- seq(0.01, 10, by = 0.1)
## correspond vector of transmission rates
betavec <- beta(alphavec, c0 = 3, gamma = 2)
## mutation model
mut.sd <- 0.02 ## mutational std dev
## compute (alpha_i-alpha_j)^2 for all {i,j}
sqdist <- outer(alphavec, alphavec, "-")^2
## mutation distribution is Gaussian
M <- exp(-sqdist/(mut.sd)^2)
## make sure rows sum to 1 (conservation)
M <- sweep(M, MARGIN = 1, FUN = "/", STATS = rowSums(M))
all(abs(rowSums(M) - 1) < 1e-04) ## check

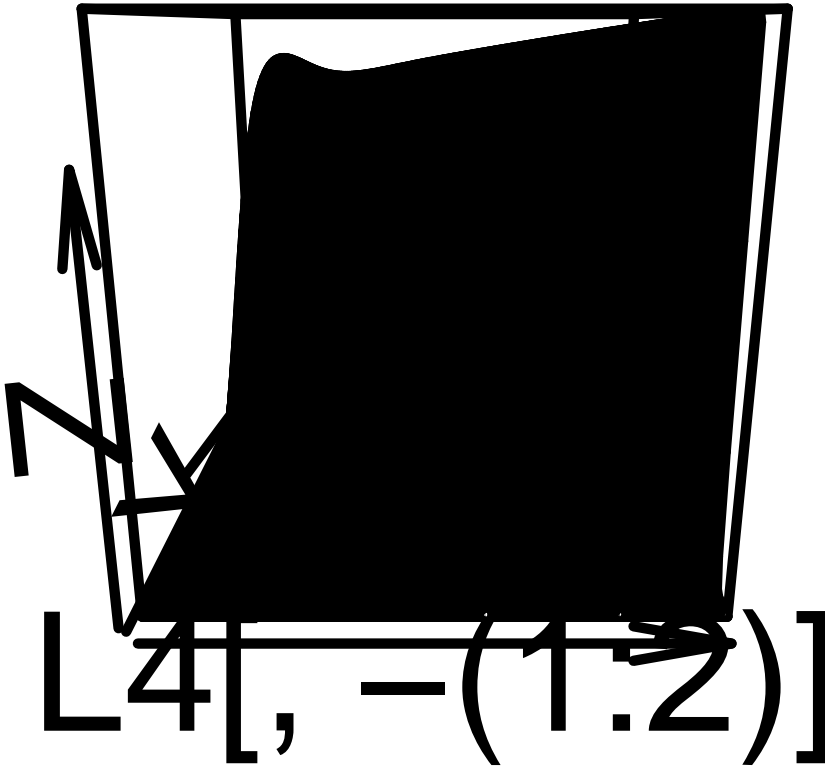
## [1] TRUE

## gradient function for distribution model
derivfun3 = function(t, y, parms) {
```

```

S <- y[1]
I <- y[-1]
derivs = with(as.list(parms), {
  inf <- M %**% (betavec * S * I) ## infection + mutation
  c(m * (N - S) - sum(inf), inf - (m + alphavec) *
    I)
})
list(derivs)
}
## initial values
init.I <- dnorm(alphavec, mean = 1, sd = 0.2)
init.I <- init.I/sum(init.I) * 0.001
startvals.d <- c(S = 0.999, init.I)
g1 <- derivfun3(t = 0, y = init, parms = params3)[[1]]
tvec = seq(0, 30, by = 0.1)
L4 = ode(y = startvals.d, times = tvec, parms = params3,
  func = derivfun3)
persp(L4[, -(1:2)])

```



```

Itot <- rowSums(L4[, -(1:2)])
## library(rgl)
## persp3d(tvec, alphavec, L4[, -(1:2)])

```


references

- Abrams, Peter A., and Hiroyuki Matsuda. 1997. "Prey Adaptation as a Cause of Predator-Prey Cycles." *Evolution* 51 (6): 1742–50. doi:10.1111/j.1558-5646.1997.tb05098.x.
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- Collins, Sinéad, and Andy Gardner. 2009. "Integrating Physiological, Ecological and Evolutionary Change: A Price Equation Approach." *Ecology Letters* 12 (8): 744–57. doi:10.1111/j.1461-0248.2009.01340.x.
- Day, T., and S. Gandon. 2006. "Insights from Price's Equation into Evolutionary Epidemiology." In *Disease Evolution: Models, Concepts, and Data Analyses*, edited by Zhilan Feng, Ulf Dieckmann, and Simon Levin.
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- Ellner, Stephen P., Monica A. Geber, and Nelson G. Hairston. 2011. "Does Rapid Evolution Matter? Measuring the Rate of Contemporary Evolution and Its Impacts on Ecological Dynamics." *Ecology Letters* 14 (6): 603–14. doi:10.1111/j.1461-0248.2011.01616.x.