Chapter 5: Density Dependence

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Overview

Because any demographic rate can be affected by competition, density dependence in an IPM can take many forms.

1. Examples 1 and 2: *Oenothera* and Platte thistle
    - Kachi (1983), Rose et. al. (2005)
2. Example 3: Idaho sagebrush steppe
    - Adler et. al. (2010)
3. General Theory
4. Case Study: Nonlinear dynamics in Soay sheep model

Oenothera and Platte thistle

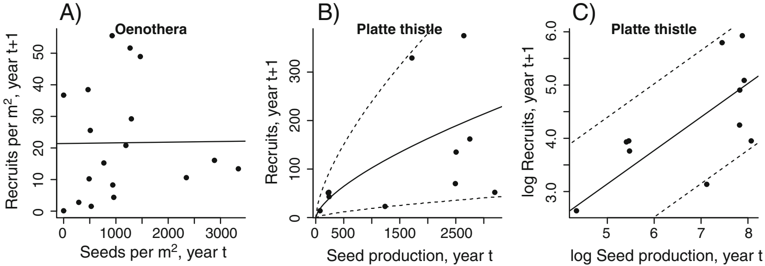
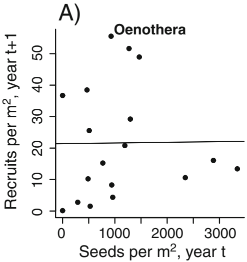


Fig. 5.1 Data on the relationship between total seed production and the number of new recruits the following year. (A) *Oenothera*, data from Kachi (1983). The solid line is the fitted linear regression; the slope is not significantly different from 0 ($P > 0.5$). (B) Platte thistle, data and fitted model from Rose et al. (2005). The solid line is Recruits=Seeds$^{0.67}$, fitted by negative binomial regression, and the dashed lines are the 10^{th} and 90^{th} percentiles of the fitted negative binomial distribution. (C) Fitted linear regression without intercept on log-log scale. Solid line is the fitted mean, and dashed lines are the 10^{th} and 90^{th} percentiles of the fitted Gaussian distribution. Data for this figure are in `OenotheraRecruit.csv` and `PlatteThistleFig4.csv`. Source file: `PlotRecruitmentData.R`

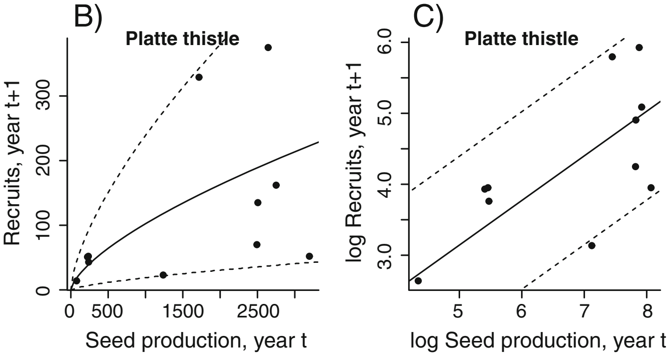
Oenothera IPM



$$n(z', t+1) = \mathcal{R} c_0(z') + \int_L^U P(z', z) n(z, t)\, dz,$$

- $\mathcal{R}$: Total number of new recruits
- $\mathcal{R} c_0(z')$: Seedling contribution to the subsequent year's population at size z'.
- $P(z', z) = (1 - p_b(z)) s(z) G(z', z)$: Density-independent survival kernel as in Chapter 2.

Platte Thistle



- Solid line represents Recruits $=$ Seeds$^{0.67}$, fitted by Rose et. al. (2005) using negative binomial regression.
- The dashed lines represent the 10th and 90th percentiles of the fitted negative binomial distribution

Platte Thistle Model Verification Using R

We linearize the Rose et. al. model using a log transformation,

$$\log(\text{Recruits}) = 0.67 \log(\text{Seeds})$$

and model it by fitting a negative binomial generalized linear model to the data under a log link function.

```
PlatteNB2 <- glm.nb(recruits ∼ log(seeds)-1,link="log",data=Platte)
```

The model was verified by fitting a linear regression model on a log-log scale.

```
PlatteLN1 <- lm(log(recruits) ∼ log(seeds)-1,data=Platte)
```

producing the equation, $\text{Recruits} = 1.35 \cdot \text{Seeds}^{0.62}$

Demographic Rate Functions for Platte Thistle IPM

Demographic rate	**Formula**
Flowering probability $p_b(z)$	$\text{logit } p_b = -10.22 + 4.25z$
Seed set $b(z)$	$b = \exp(-0.55 + 2.02z) \times (1 + \varepsilon(z)/16)^{-0.32}$
Mean weevil eggs per plant	$\varepsilon(z) = \exp(e_0 + 1.71z)$
Seedling size $c_0(z')$	$z' \sim \text{Normal}(\mu = 0.75, \sigma^2 = 0.17)$
Survival $s(z)$	$\text{logit } s = -0.62 + 0.85z$
Growth $G(z', z)$	$z' \sim \text{Normal}(\mu = 0.83 + 0.69z, \sigma^2 = 0.19)$

where

1. z: The measure of the log-transformed maximum root crown diameter,
2. ε: The mean number of weevil eggs oviposited on a plant of size z; the intercept ε_0 varied over time as the weevil infestation developed.

Platte Thistle IPM Construction

We again use a density-independent survival kernel P,

$$P(z',z) = (1 - p_b(z))s(z)G(z',z).$$

To compute the new recruits at time $t+1$, we first compute the total number of seeds produced at time t,

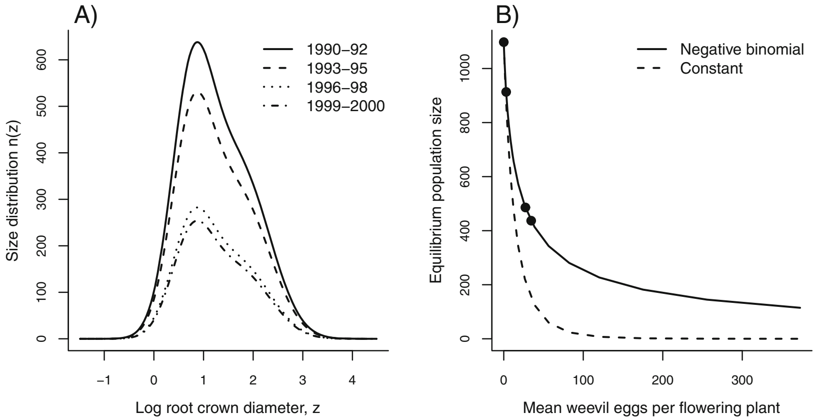
$$S(t) = \int_L^U p_b(z)b(z)n(z,t)\,dz,$$

producing $S(t)^{0.67}$ new recruits with size distribution $c_0(z')$.

A complete iteration yields the IPM,

$$n(z',t+1) = \underbrace{c_0(z')\left(\int_L^U p_b(z)b(z)n(z,t)\,dz\right)^{0.67}}_{\text{New Recruits}} + \underbrace{\int_L^U P(z',z)n(z,t)\,dz}_{\text{Survivors}}$$

Platte Thistle IPM Predictions



Idaho Sagebrush Steppe

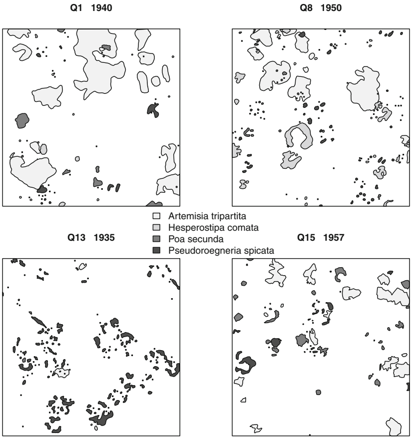
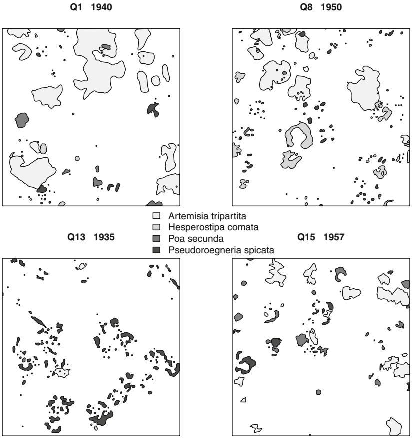


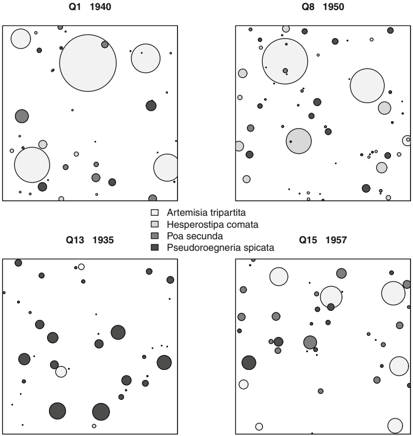
Fig. 5.3 Four examples of mapped quadrats from the Idaho sagebrush steppe data set (Zachmann et al. 2010). The heading on each panel gives the quadrat number and year.

IPM Goals:

- Compare the strengths of inter- and intra-specific competition among the dominant species.
- Remark on how the results of neighborhood competition may support the “neutral" or “niche" theories of community structure.
- Model density dependence of multiple vital rates spanning all stages of plant life: survival, growth, and recruitment.

Idaho Sagebrush Steppe





Left: Mapped quadrats from the Idaho sagebrush steppe data set (Zachmann et al. 2010).

Right: Genets in four quadrats from the Idaho sagebrush steppe data set (Adler et al. 2010).

Idaho Sagebrush: Vital Rates

The vital rates of interest in applying density-dependence to are

1. Survival,
2. Growth,
3. Recruitment.

For each of the four dominant species, each vital rate of interest will be modeled as a function of

1. The $\log$ genet area z,
2. Competitive pressure W,
3. Quadrat group (a categorical variable identifying a cluster of nearby quadrats).

Idaho Sagebrush: IPM Construction

Genet survival probability s in year t and quadrat g:

$$\text{logit}(s_{ij}) = \gamma_{jt} + \phi_{jg} + \beta_{j,t} z_{ij} + W_{ij}$$

Total competitive pressure (density-dependent) on genet ij is

$$W_{ij} = \sum_{m} \sum_{k} w_{ij,km},$$

where $w_{ij,km}$ is the competitive pressure on genet i in species j, from genet k of species m and has form,

$$w_{ij,km} = a_{jm} e^{-\alpha_{jm} d_{ij,km}^{2}} A_{km}$$

- $d_{ij,km}$: Distance between the centers of genets ij and km,
- A_{km}: Untransformed area of genet km,
- a_{jm}: Interspecific competition coefficient of species j and m.

Idaho Sagebrush: Parameter Estimation

α_{jj} values were fit by logistic regression, assuming only intraspecific competition.

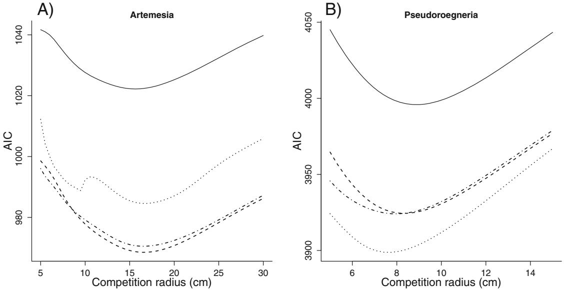


Fig. 5.5 Goodness of fit (AIC) for a set of logistic regression models of varying complexity for survival of (A) *Artemesia tripartita* and (B) *Pseudoroegneria spicata*, as a function of the intraspecific spatial scale parameter α_{jj}. The x-axis is $r_{jj} = 1/\sqrt{\alpha_{jj}}$, which we call the "competition radius" because the strength of competition between two genets depends on their distance d relative to r_{jj}. Source files: `PSSP_survival_Gaussian_alpha.R` and `ARTR_survival_Gaussian_alpha.R`

Idaho Sagebrush: Parameter Estimation

α_{jj} values were fit by logistic regression, assuming only intraspecific competition.

To estimate the remaining twelve α_{jm} values, we consider three possible reductions:

1. *Effects model:* $\alpha_{jm} \equiv \alpha_{mm}$ meaning each species has a characteristic zone of influence on other genets, regardless of their species.
2. *Response model:* $\alpha_{jm} \equiv \alpha_{jj}$ meaning each species has a characteristic zone within which it is affected by other genets, regardless of their species.
3. *Interaction model:* $\alpha_{jm} = (\alpha_{jj} + \alpha_{mm})/2$.

Idaho Sagebrush: Parameter Estimation

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Idaho Sagebrush Steppe IPM

The Model:

Genet Survival Probability: $\text{logit}(s_{ij}) = \gamma_{jt} + \phi_{jg} + \beta_{j,t} z_{ij} + W_{ij}$

Total competitive pressure on genet ij: $W_{ij} = \sum_m \sum_k a_{jm} e^{-\alpha_{jm} d^2_{ij,km}} A_{km}$.

Equations not listed explicitly in the chapter:

1. **Growth:** "A Gaussian distribution with size-dependent variance"
2. **Fecundity:** "A negative binomial distribution of offspring per quadrat"

Problem: Computationally expensive to compute the spatially explicit W_{ij}.

Idaho Sagebrush: Mean Field Approximation

Using a “mean field" approximation for genet location, the computation complexity is reduced:

$$\bar{W}_j = \pi \sum_m a_{jm} \Phi_m / \alpha_{jm},$$

where Φ_m is the fractional cover of species m.

Assumes plants are distributed at random, except circles that represent conspecific genets cannot overlap.

Community Structure Theoriess

- **Neutral theory:** Species similarities are more important than their differences. This implies:
    1. Species are so evenly balanced that random drift to extinction will be overcome by speciation.
    2. Nothing much would change if species were somehow less different than each other.
- **Niche theory:** Species differences are essential to coexistence, and if species were somehow made less different from each other it would change everything.

An Embarrassment of Niches

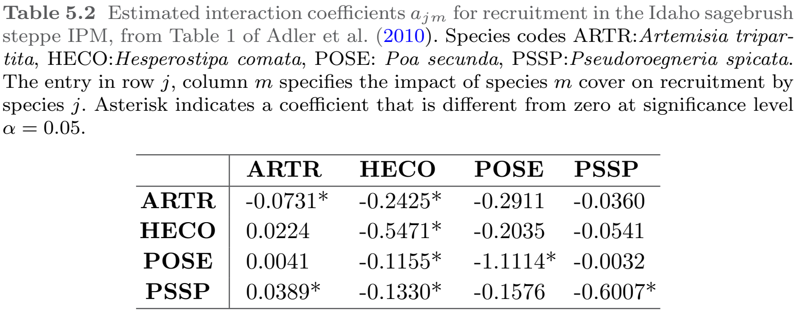


Table 5.2 Estimated interaction coefficients a_{jm} for recruitment in the Idaho sagebrush steppe IPM, from Table 1 of Adler et al. (2010). Species codes ARTR:*Artemisia tripartita*, HECO:*Hesperostipa comata*, POSE: *Poa secunda*, PSSP:*Pseudoroegneria spicata*. The entry in row j, column m specifies the impact of species m cover on recruitment by species j. Asterisk indicates a coefficient that is different from zero at significance level $\alpha = 0.05$.

	ARTR	**HECO**	**POSE**	**PSSP**
ARTR	-0.0731*	-0.2425*	-0.2911	-0.0360
HECO	0.0224	-0.5471*	-0.2035	-0.0541
POSE	0.0041	-0.1155*	-1.1114*	-0.0032
PSSP	0.0389*	-0.1330*	-0.1576	-0.6007*

- Columns represent coefficients for the impact of one species on itself and the others.
- Support of Niche theory: The diagonal elements are negative and larger in magnitude than other elements in the same column.

Theory of Density Dependent IPM

A generalization of the Platte thistle model yields:

$$n(z', t+1) = c_0(z')p_r(\boldsymbol{N}(t))\boldsymbol{N}(t) + \int_L^U P(z', z)n(z, t)\ dz$$

where $\boldsymbol{N}(t)$ represents total seed production,

$$\boldsymbol{N}(t) = \int_L^U p_b(z)b(z)n(z, t)\ dz$$

1. p_r: The density-dependent recruitment probability; assumed to be a decreasing function of $\boldsymbol{N}$.
2. P: The density-independent survival kernel.
3. $F(z', z, \boldsymbol{N}) = p_r(\boldsymbol{N})c_0(z')p_b(z)b(z)$: The density-dependent reproduction kernel.

Persistence or Extinction?

The expectation is the population will *persist* if a *small population increases.*

Population size only affects p_r, so if we let p_r be $p_r(0)$, we can approximate the dynamics of a very small population and we get a density-independent kernel, $K_0(z', z)$!

$$K_0(z', z) = P(z', z) + p_r(0)c_0(z')p_b(z)b(z)$$

By assuming K_0 satisfies the assumptions for stable population theory, then either,

1. A small population will increase if $R_0(0) > 1$.
2. A small population will decrease to extinction if $R_0(0) < 1$.

Persistence or Extinction: R_0

Let $R_0(x)$ denote the value of R_0 for the density-independent IPM when p_r is held constant at $p_r(x)$:

$$n(z', t+1; x) = c_0(z')p_r(x)\boldsymbol{N}(t) + \int_L^U P(z', z)n(z, t)\, dz$$

with kernel $K_x(z', z) = P(z', z) + p_r(x)c_0(z')p_b(z)b(z)$.

By Chapter 3: $R_0(x) = p_r(x)\langle p_b b, (I-P)^{-1}c_0\rangle$

- $(I-P)^{-1}c_0$: Distribution function for the expected total amount of time spent at each size during a lifetime.
- $\langle p_b b, (I-P)^{-1}c_0\rangle$: Adds up the total seed production at each size of the lifetime.
- $p_r(x)\langle p_b b, (I-P)^{-1}c_0\rangle$: The total number of recruits produced by an average individual.

Persistence or Extinction: Platte Thistle IPM

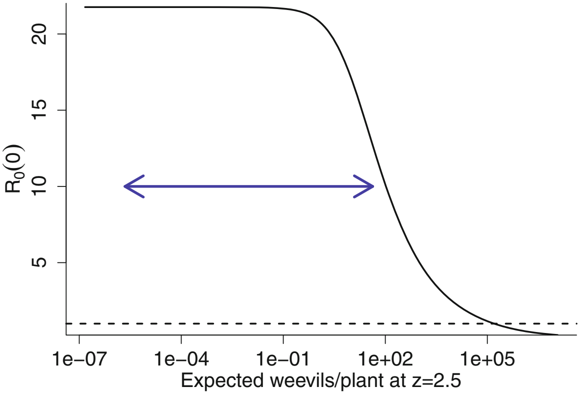


Fig. 5.6 $R_0(0)$ for the Platte thistle model as a function of the expected number of weevils on a typical-size flowering plant (log root crown diameter $z = 2.5$). The curve was computed by varying e_0 and computing $R_0(0)$ using equation 5.4.4. The arrow shows the range of e_0 values estimated for different years during the study period, with the largest values coming towards the end as the weevil infestation developed. Source file: `PlatteCalculations.R`

Local Stability of Equilibria

We limit our study for when near-equilibrium dynamics are linear IPMs and where we have a formula for the kernel, $K(z', z, \boldsymbol{N})$, for $\boldsymbol{N}$ is some measure of total population size (in which some individuals may count for more than others):

$$\boldsymbol{N}(t) = \langle W, n \rangle = \int_{\boldsymbol{Z}} W(z) n(z, t)\, dz$$

Assumptions:

- $K(z', z, \boldsymbol{N})$: Density-dependent kernel. The entire kernel can depend on $\boldsymbol{N}$.
- W: Any smooth nonnegative function.

Local Stability of Equilibria: Jacobian Kernel

For an $\boldsymbol{N}$-dependent kernel $K(z', z, \boldsymbol{N})$, the Jacobian kernel evaluated at equilibrium $\bar{n}$ with corresponding total population $\bar{\boldsymbol{N}} = \langle W, \bar{n} \rangle$ is, (Ellner and Rees 2006)

$$J(z', z, \bar{\boldsymbol{N}}) = K(z', z, \bar{\boldsymbol{N}}) + Q(z')W(z)$$

$$\text{where } Q(z') = \int_Z \frac{\partial K(z', z, \bar{\boldsymbol{N}})}{\partial \boldsymbol{N}} \bar{n}(z)\, dz$$

The near-equilibrium dynamics then are approximated by the linear system,

$$n(z', t+1) - \bar{n}(z') = \int_Z J(z', z, \bar{\boldsymbol{N}})(n(z,t) - \bar{n})\, dz$$

Conclusions: $\bar{n}$ is locally stable if the eigenvalues of the Jacobian kernel are all less than 1 in magnitude, and is unstable if any are greater than 1 in magnitude.

Equilibrium Perturbation Analysis

Question: How is the equilibrium affected by changes in the kernel entries, vital rate functions, or parameter values?

Sensitivity of $\bar{\boldsymbol{N}}$ to θ when θ is perturbed: $\boldsymbol{s}_{\bar{\boldsymbol{N}},\theta} = -\frac{\boldsymbol{s}_{\lambda,\theta}}{\boldsymbol{s}_{\lambda,\bar{\boldsymbol{N}}}}$

- λ: Population growth rate; dominant eigenvalues of the density-independent kernel $K(z', z; \bar{\boldsymbol{N}})$.
- $\boldsymbol{s}_{\lambda,\bar{\boldsymbol{N}}}$ is constant for all perturbations and can be computed by the general eigenvalues sensitivity formulas (Chapter 4). When crowding has only negative effects on vital rates, $\boldsymbol{s}_{\lambda,\bar{\boldsymbol{N}}} < 0$.
- In the case when crowding has only negative effects on vital rates, it is said that the sensitivity of $\bar{\boldsymbol{N}}$ to the perturbation is proportional to the sensitivity of λ evaluated at the equilibrium.

Sheep Soay Case Study

To focus our study on density-dependence, we model a "typical year" deterministic model by setting the time-varying parameters to their average values.

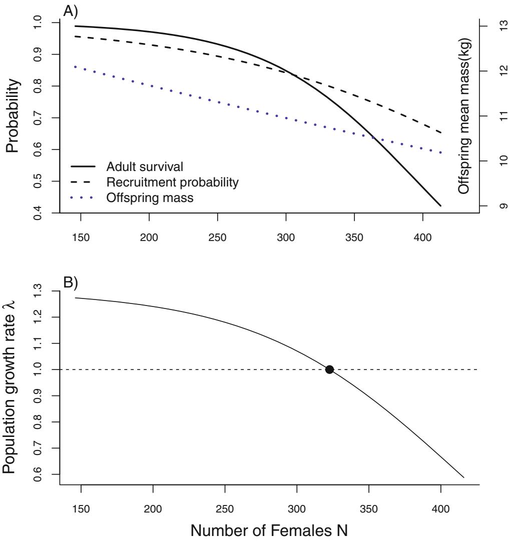
Density-dependence affects three processes in the kernel (Chapter 2),

$$k(z', z) = s(z)G(z', z) + s(z)p_b(z)p_r C_0(z', z)/2$$

1. The probability a newborn lamb successfully recruits into the population, p_r,
2. The size of the distribution of newborn recruits, C_0,
3. The survival of adults s.

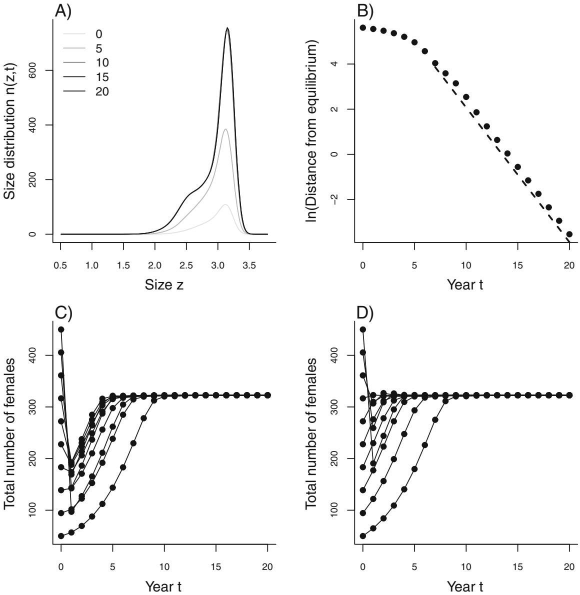
by adding the predictor $\boldsymbol{N}(t) = \int_{\mathbf{Z}} n(z, t)\, dz$ to each function.

Sheep Soay IPM Predictions

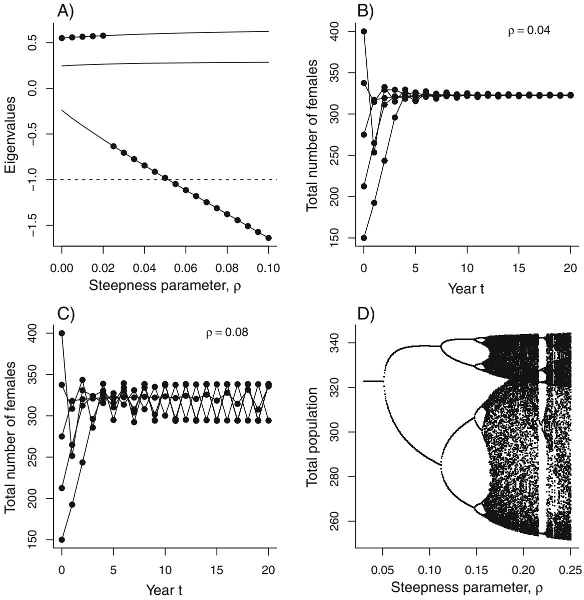


(A) The density-dependent rates are adult survival, recruitment probability, and mean offspring size, plotted over the observed range of female densities. Note that offspring size is not log-transformed; adult survival and offspring size are plotted for a typical-size adult female, $z = 2.9$. (B) Long-term population growth rate $\lambda(\boldsymbol{N})$; the dashed line at $\lambda = 1$ locates the equilibrium pop. size $\boldsymbol{N} \approx 323$.

Equilibrium stability, $\bar{N} = 323$



Non-Linear Dynamics & Chaos



1-Dimensional Dynamics

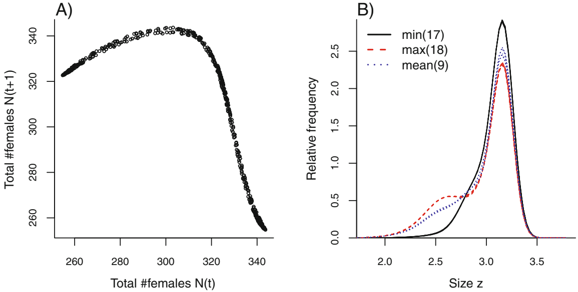


Fig. 5.10 (A) The dynamics of total female population $\mathbf{N}(t)$, for steepness parameter $\rho = 0.02$. The population was iterated for 1000 time steps, starting from 300 individuals. The graph shows $\mathbf{N}(t+1)$ as a function of $\mathbf{N}(t)$ for $t = 501$ to 1000. (B) Size distributions, normalized to total population $\mathbf{N} = 1$, at times when $\mathbf{N}(t)$ was within 1 of its minimum (black solid curve), maximum (red dashed curve), and mean (blue dotted curve) over $t = 501$ to 1000. Numbers in the figure legend are the number of overlaid curves in each case. Source file: `Soay Bifurcation Calcs.R`