3. Population Growth and Density Dependence

Jasper Slingsby, BIO2014F

2025-04-24

The Hutchinsonian Niche

G Evelyn Hutchinson proposed that *the niche is an n-dimensional hypervolume within which a species is* ***able to maintain a viable population*** - **Hutchinson 1957**

Does the occurrence of a species at a locality mean it is able to maintain a viable population there...?

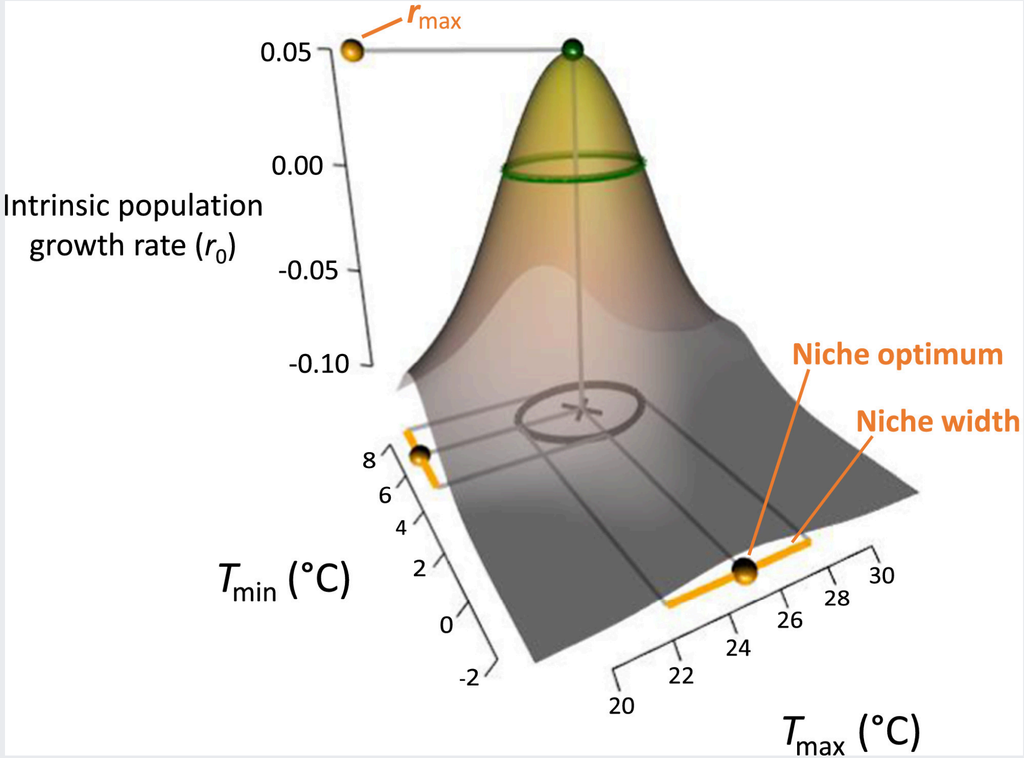


Figure from **Treurnicht et al. 2020**

What does maintaining a viable population even mean?

It means maintaining population growth...

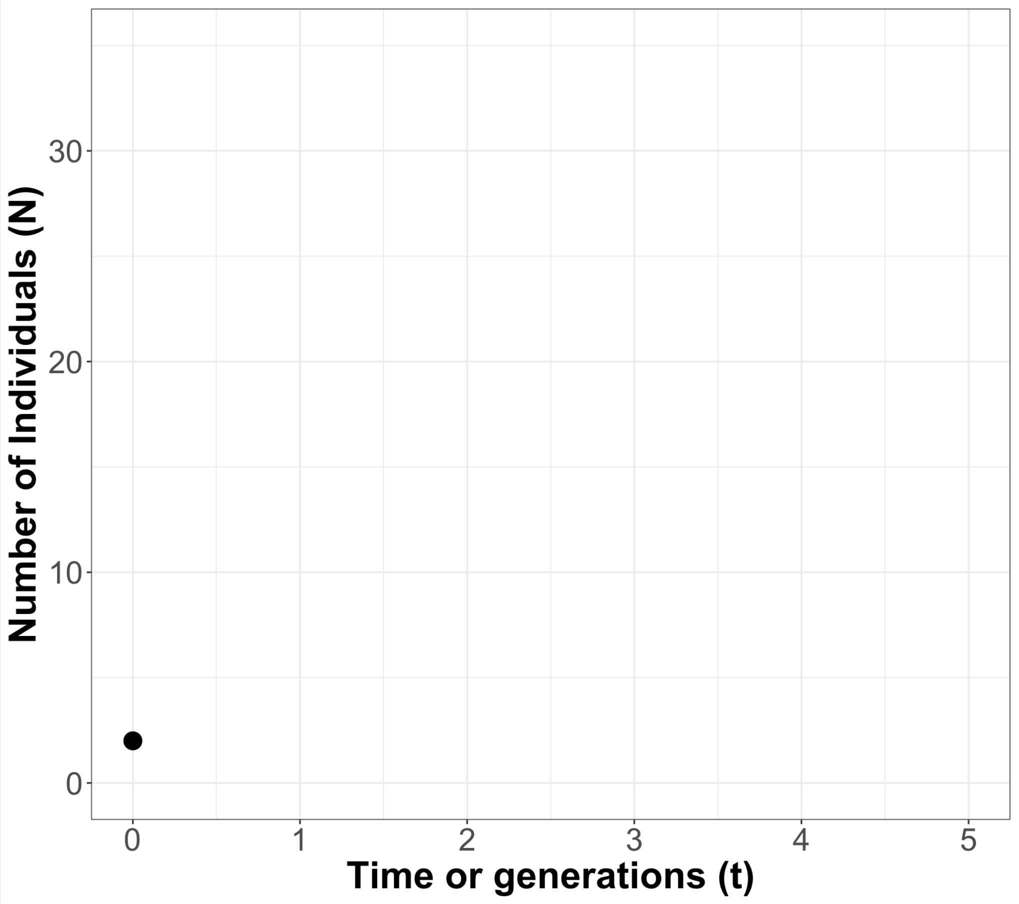
But that's not easy...

Especially where there is competition for resources...

Population growth curve

Consider growth of a population, starting with 2 individuals at t = 0.

- Assume a per-capita reproductive rate, r = 2



Population growth curve

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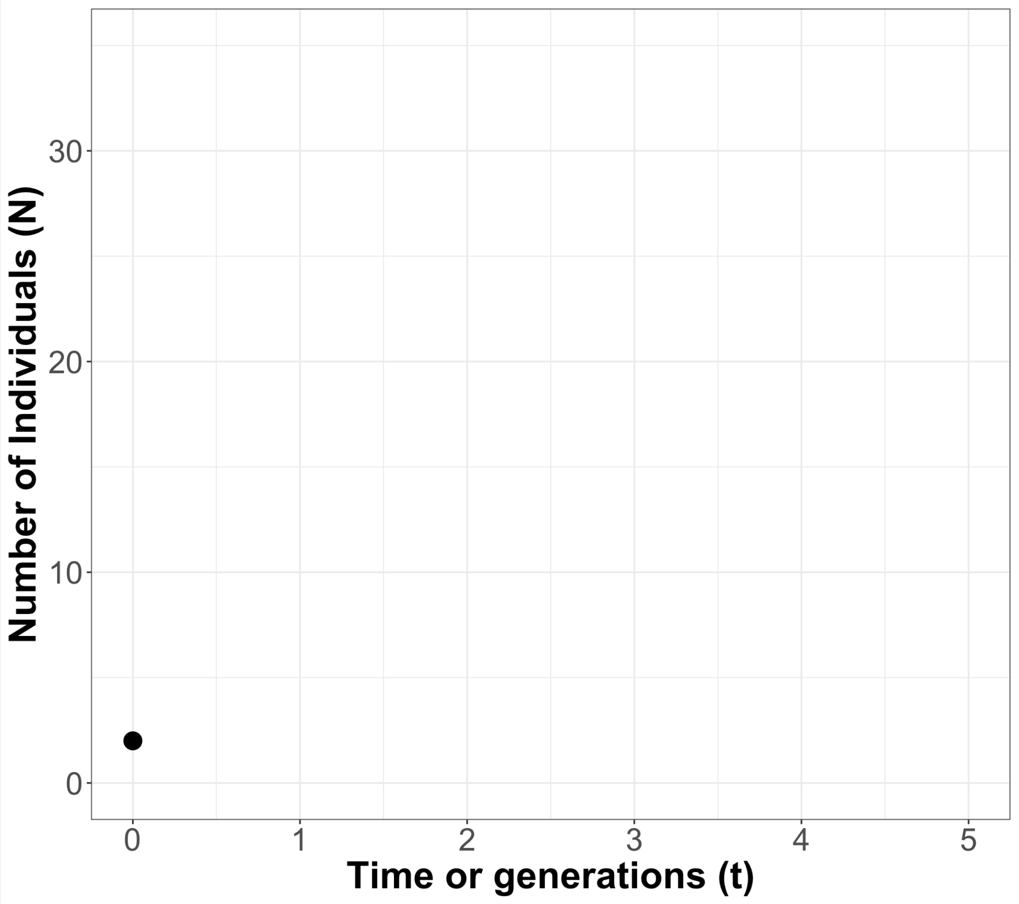
Note: *The per-capita reproductive rate (r) is the number of reproductively mature individuals contributed per individual from one generation to the next. Population growth is positive where $r > 0$.*

It is a fundamental biological parameter, determined by things like the number of eggs/seeds produced, the hatching/germination success of eggs/seeds, and the success with which hatchlings/germinants survive to reproductive maturity.

It is the birth rate minus the death rate.



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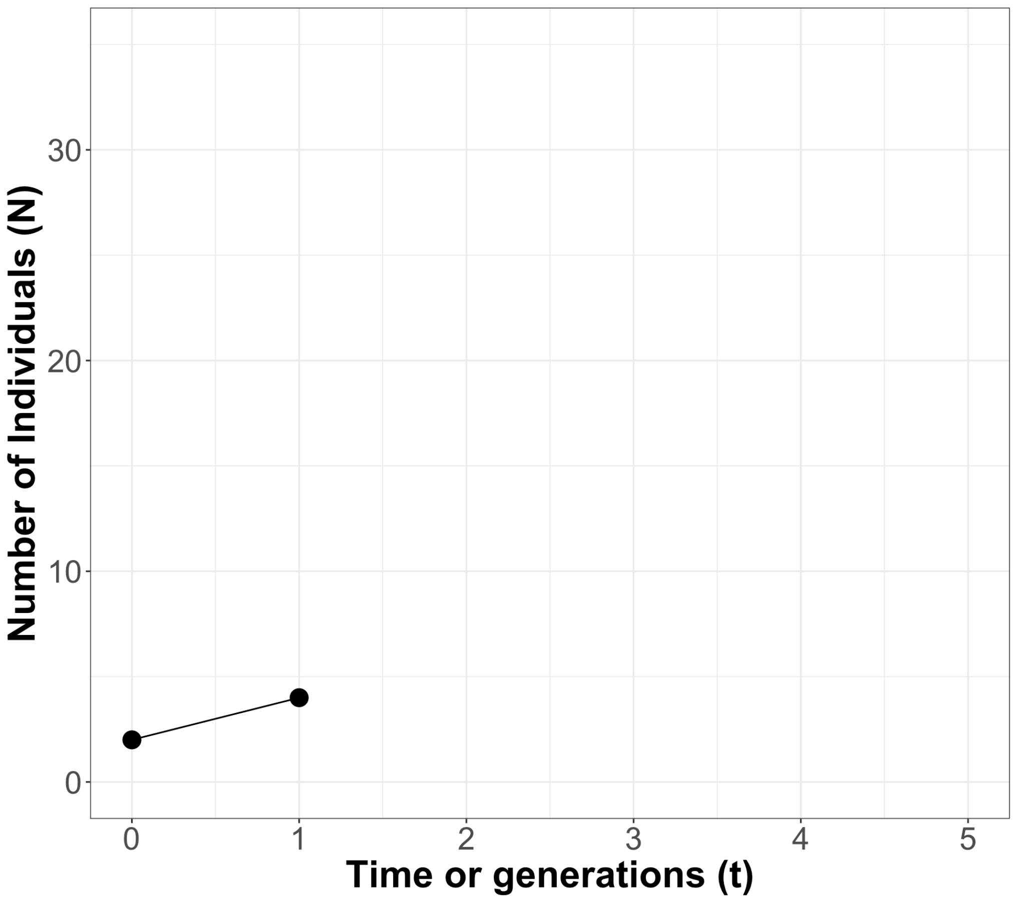

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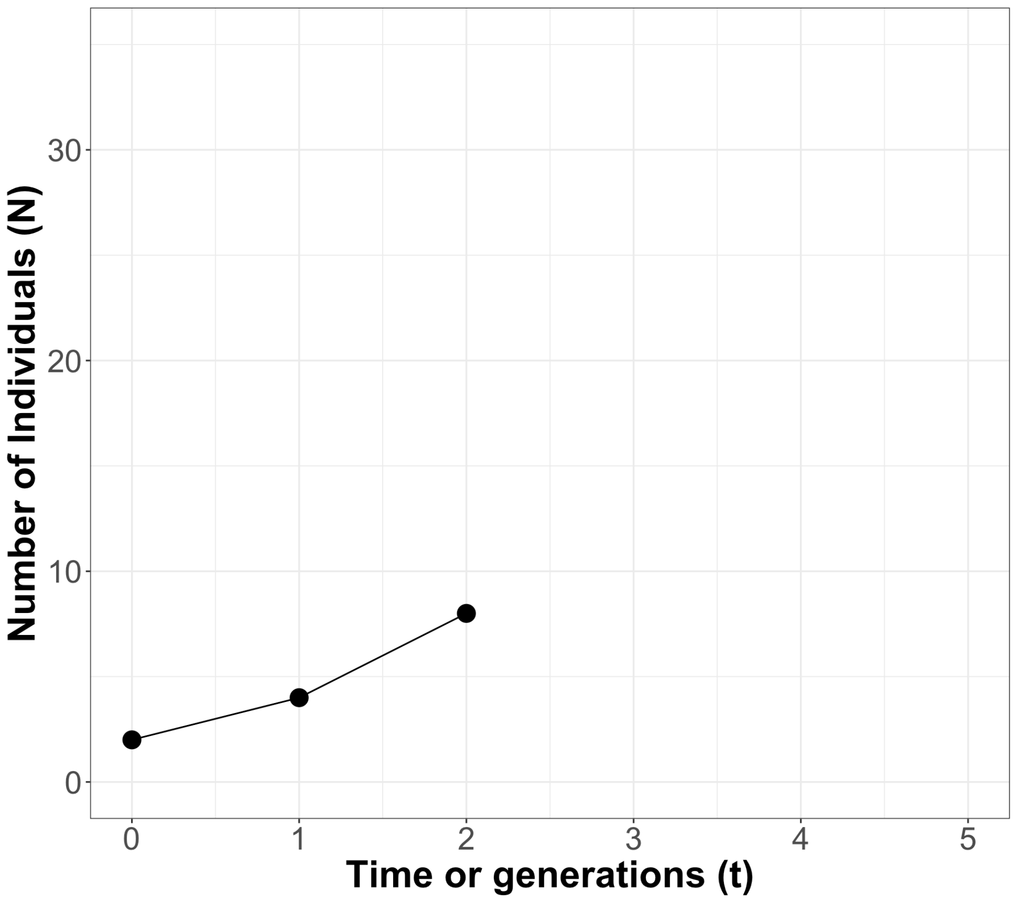

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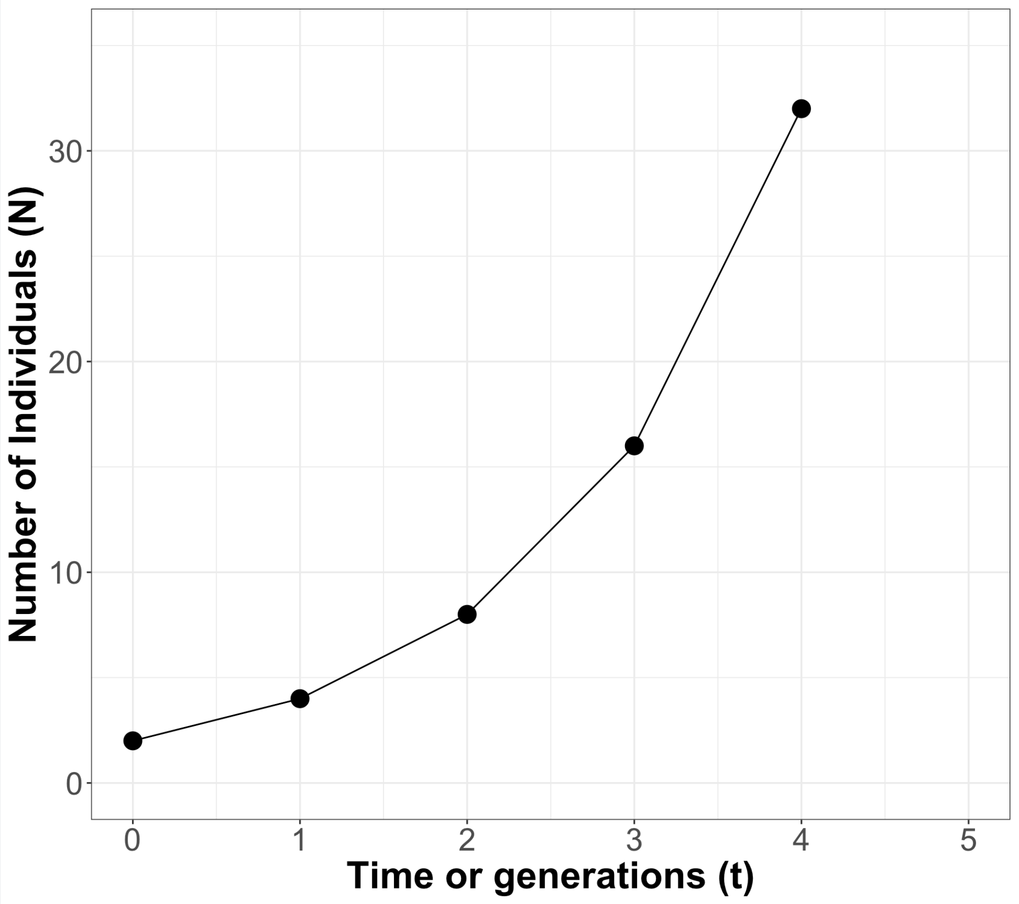
Growth is exponential!



Population growth curve

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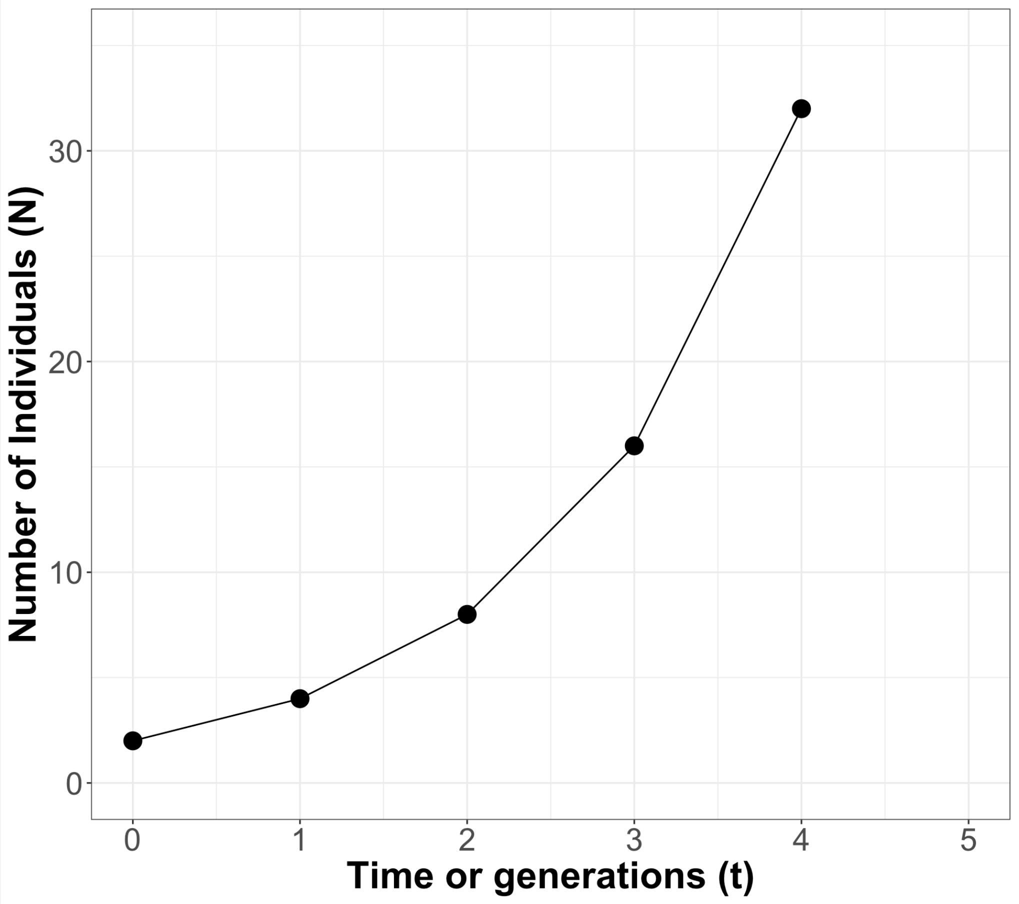
- Assume a per-capita reproductive rate, r = 2

Growth is exponential!

Using calculus, we can express growth as an instantaneous rate as dN/dt, the rate of change in number of organisms at a particular instant in time.

Since our example is an exponential function, the slope of this curve is given by $dN/dt = rN$



Is growth always exponential?

Resources available to individuals typically shrink as population size and density increase.

Competition between individuals limits growth and reproductive output.

A study of the Pear Limpet, *Scutellastra cochlear* (**Branch 1975**).

Photo: Allan Ellis, **iNaturalist**

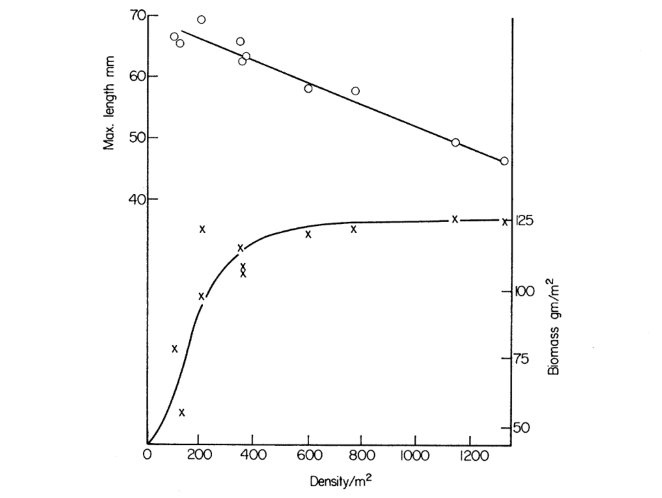


FIG. 3. Maximum length (○) and biomass (×) of *Patella cochlear* relative to density.

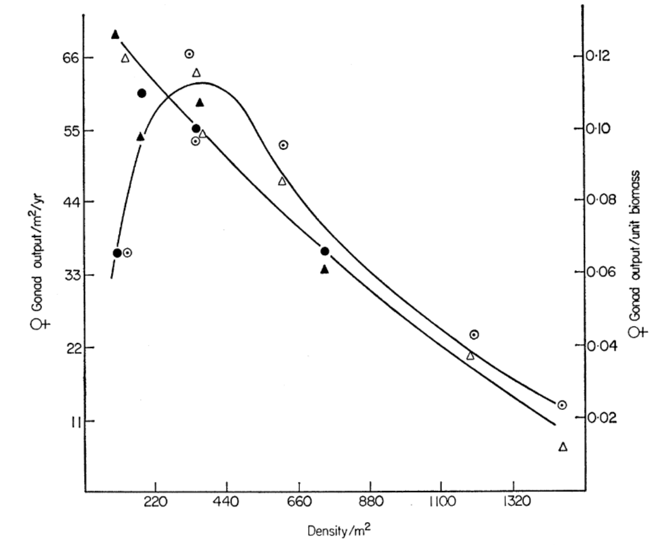
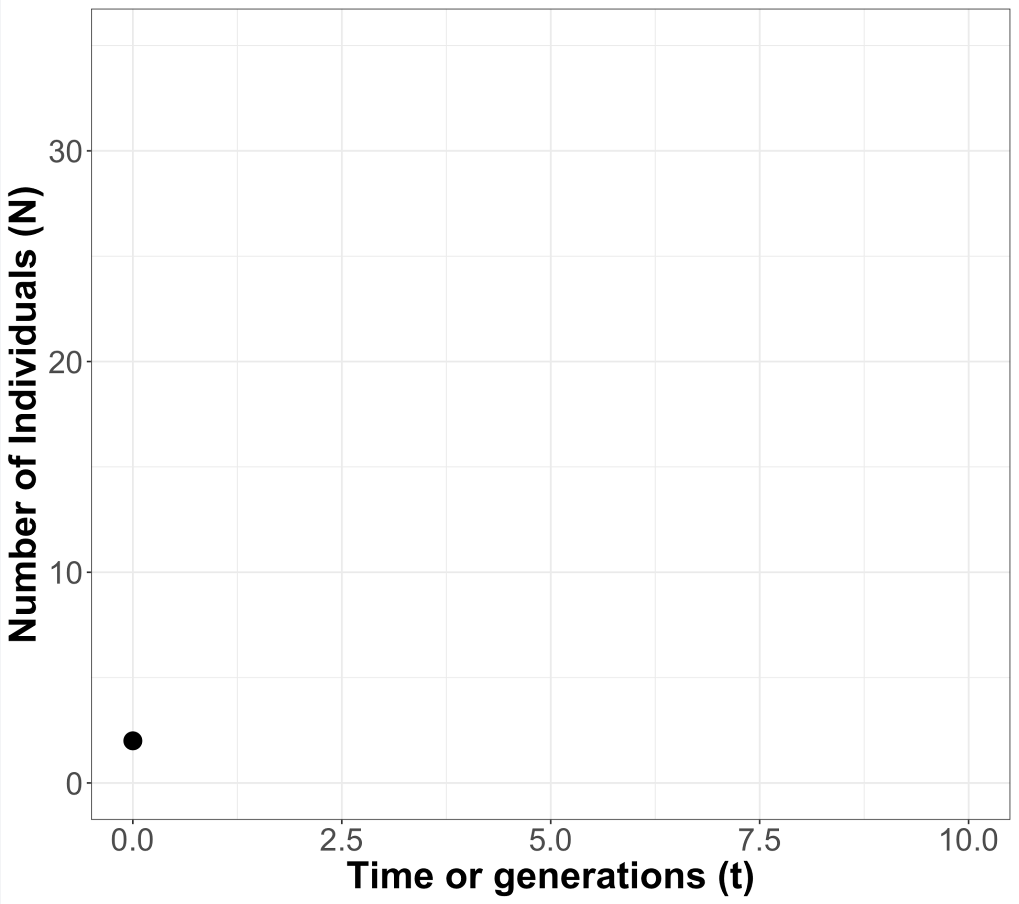


FIG. 6. Gonad output in *Patella cochlear*, relative to density. Gamete output per m²: ●, measured; ⊙, calculated. Gamete output per unit biomass; ▲, measured; △, calculated.

Population growth curve

What does our curve look like once we include **density-dependent** effects like int***ra***specific competition (competition among individuals of the same species)?



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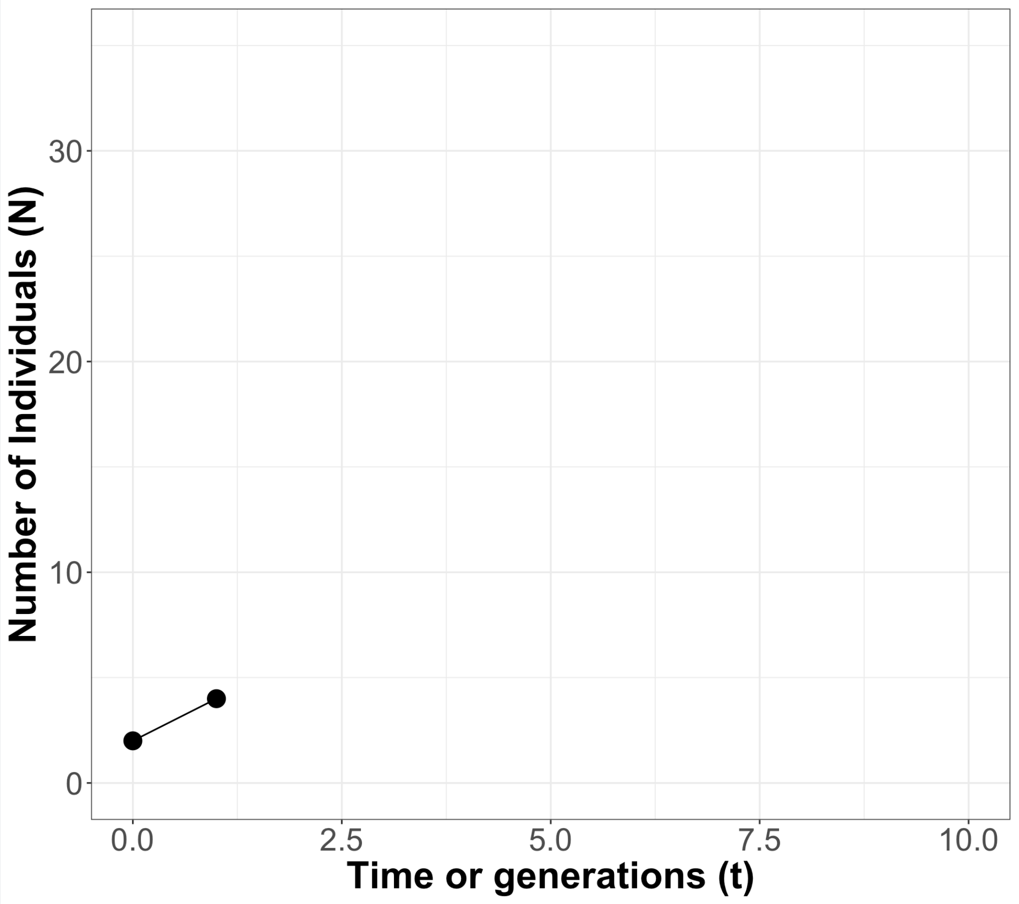

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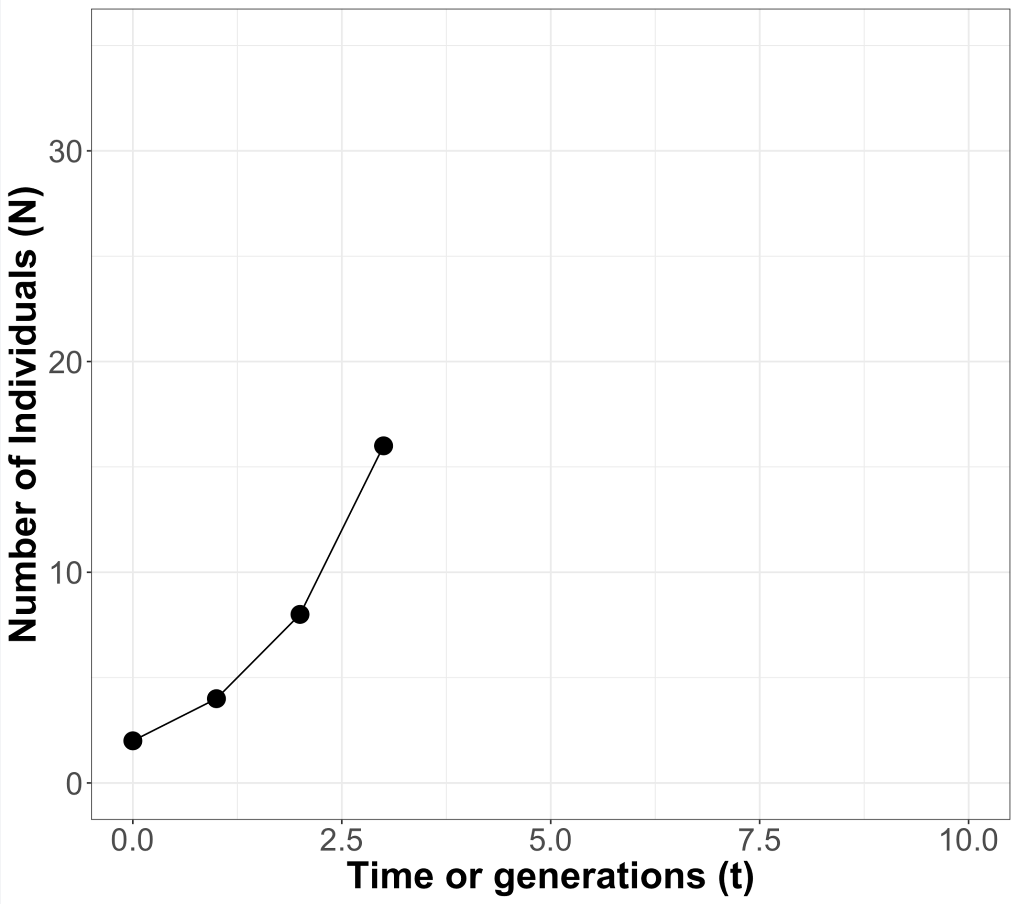

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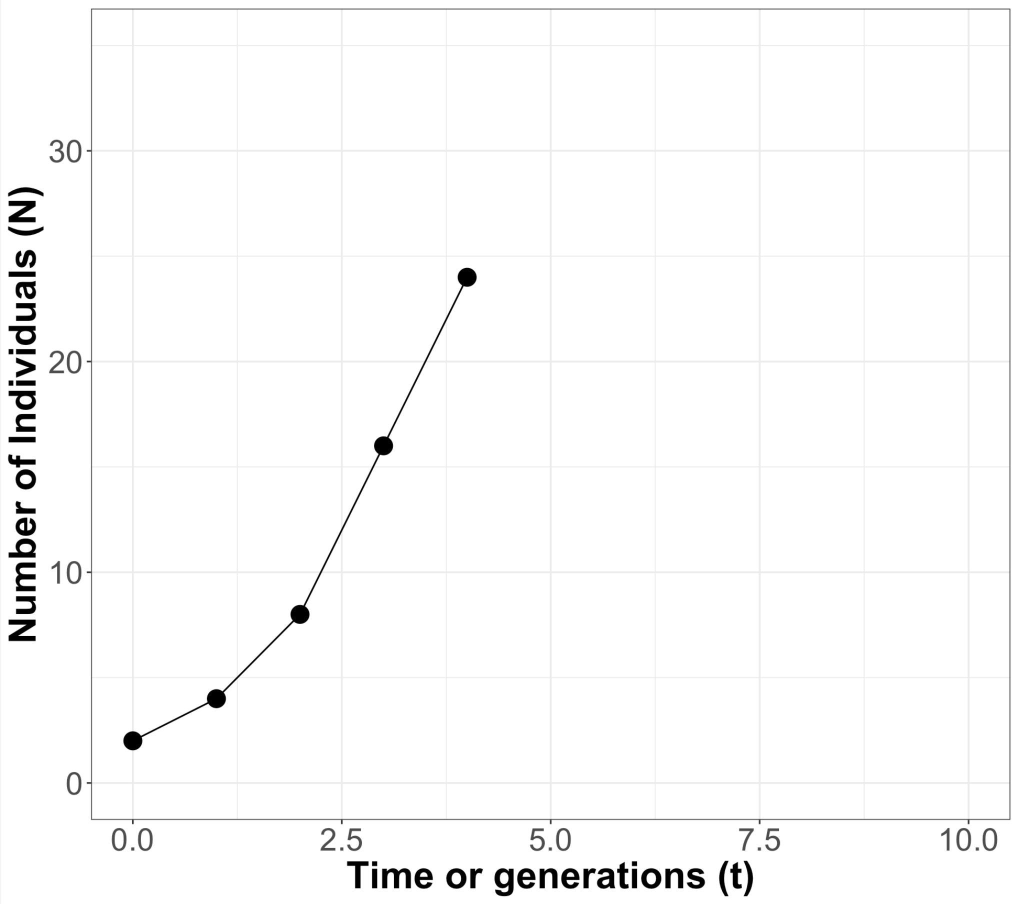
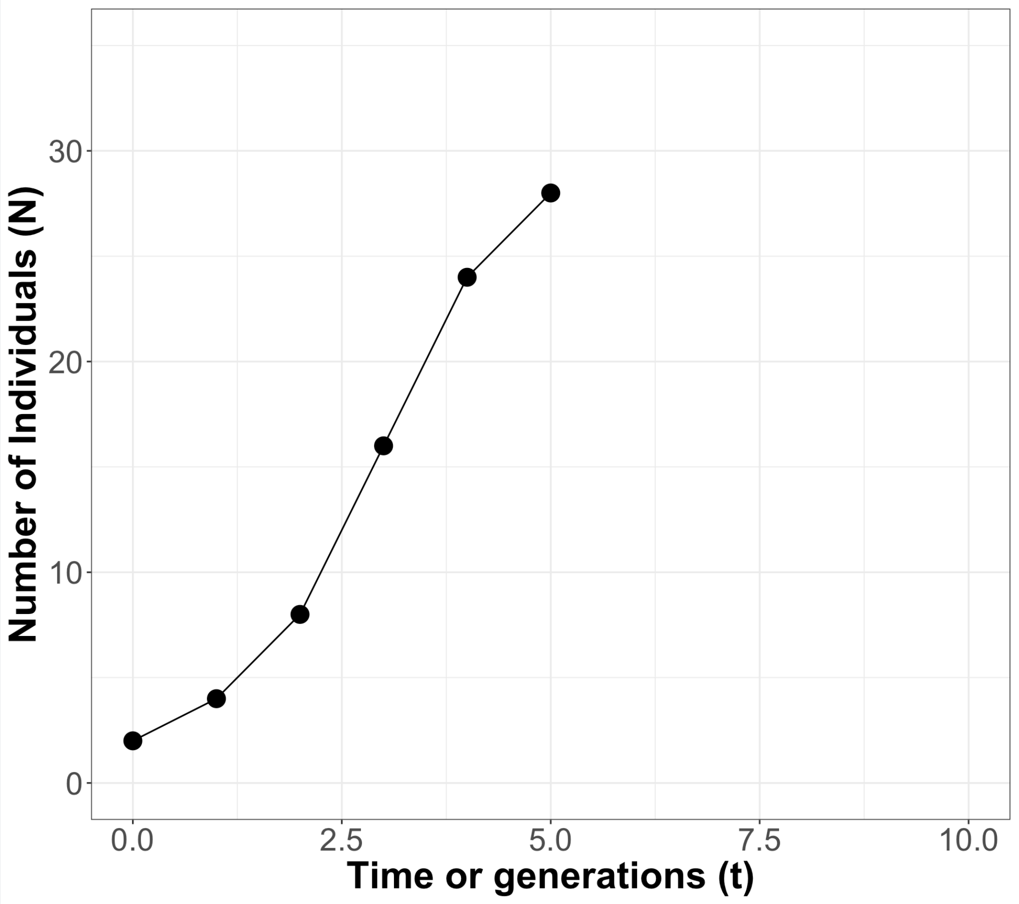


Population growth curve

What does our curve look like once we include **density-dependent** effects like int***ra***specific competition (competition among individuals of the same species)?

It starts out much the same while resources are abundant…

…but slows as resources become limiting…



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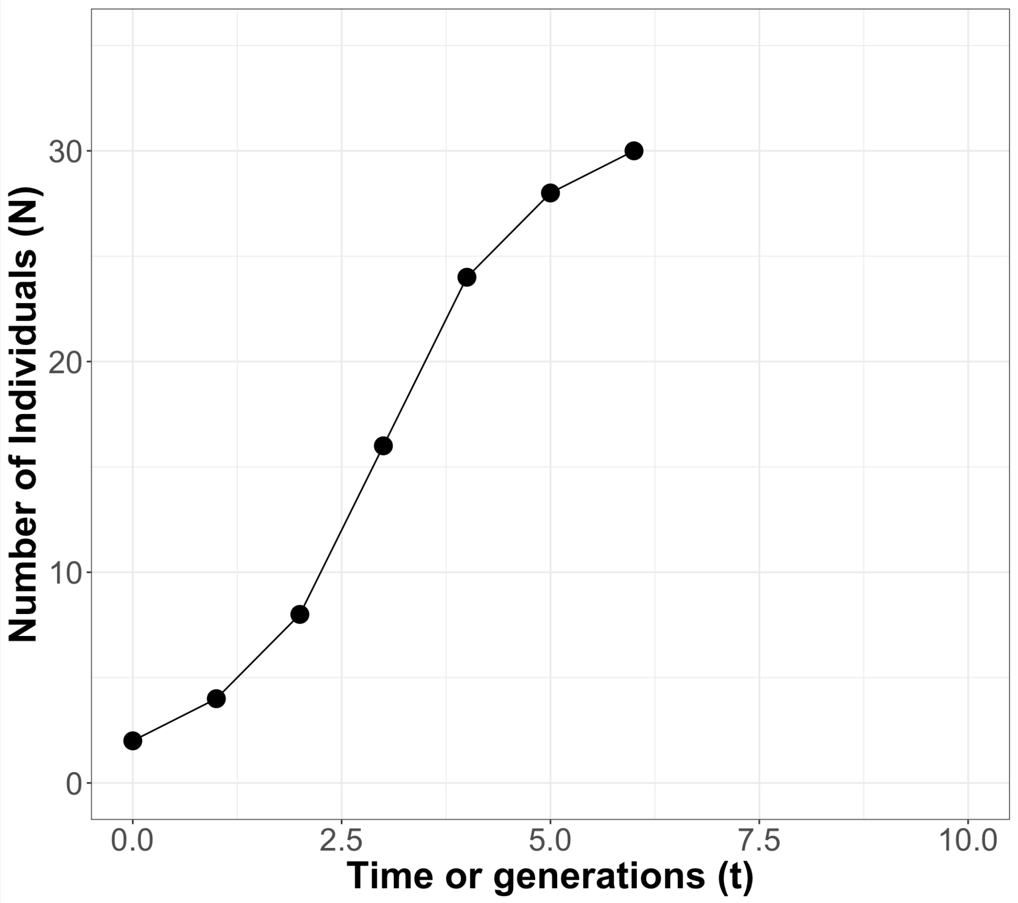

Population growth curve

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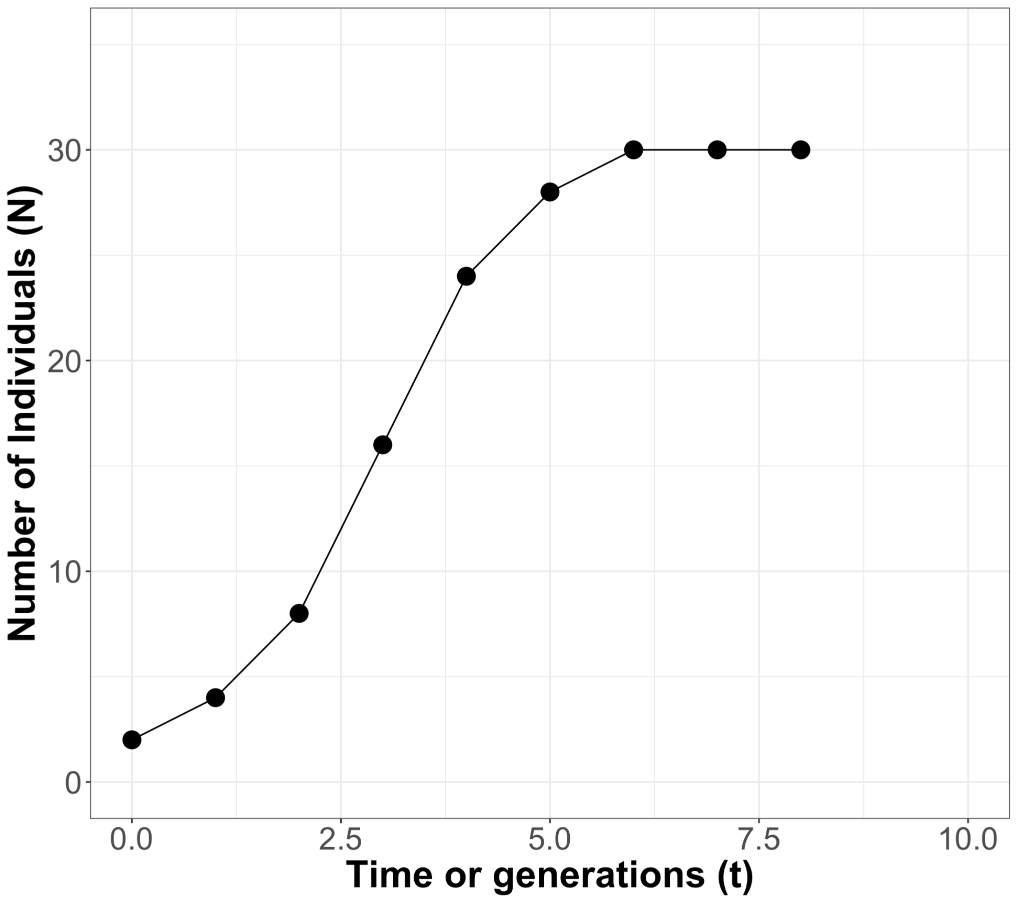
It starts out much the same while resources are abundant…

…but slows as resources become limiting…

…and eventually flattens out…



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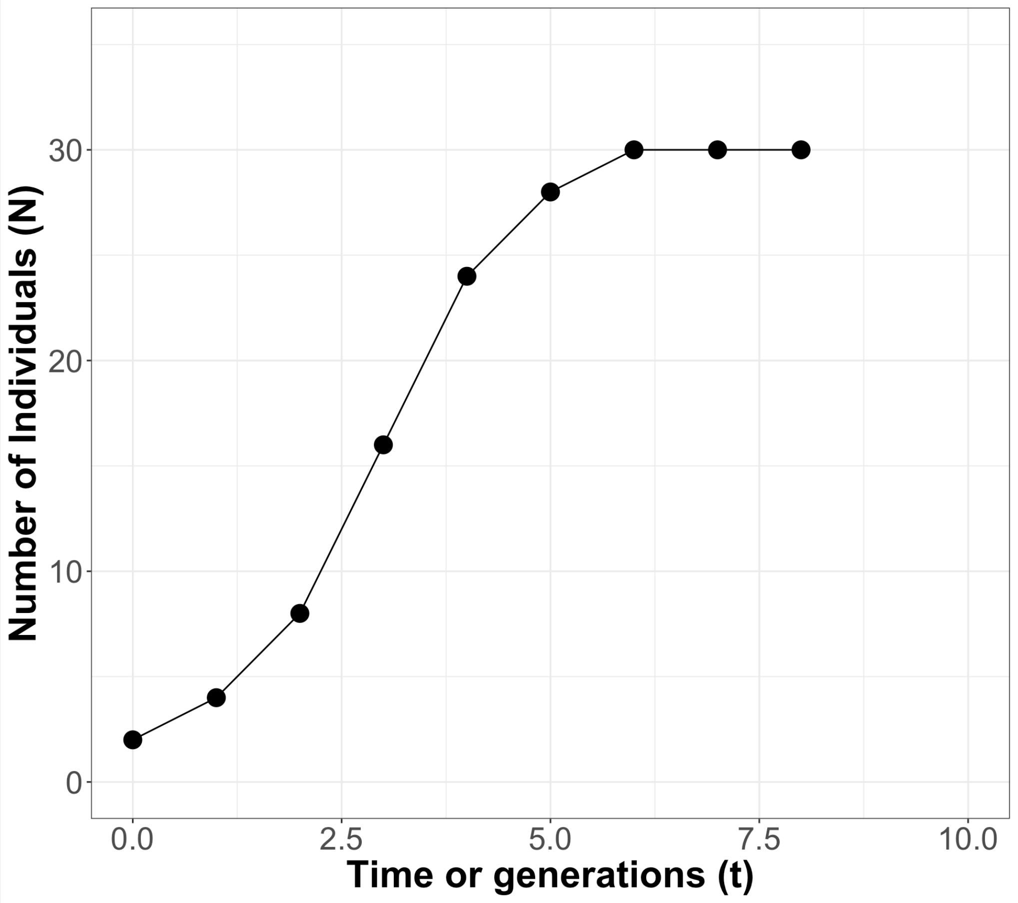
Any thoughts on the equation to fit this curve?

$dN/dt = ?$



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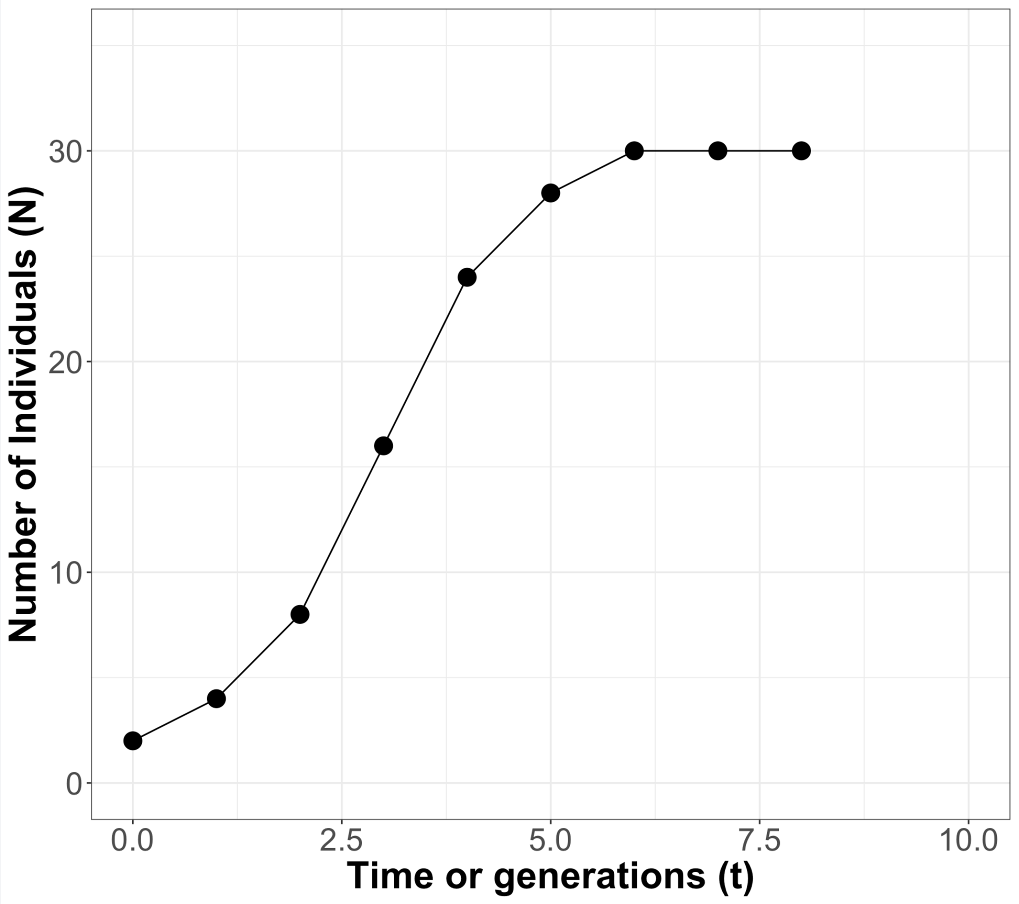
$$dN/dt = rN(K - N)/K$$

A logistic function, or what we call the logistic growth curve.

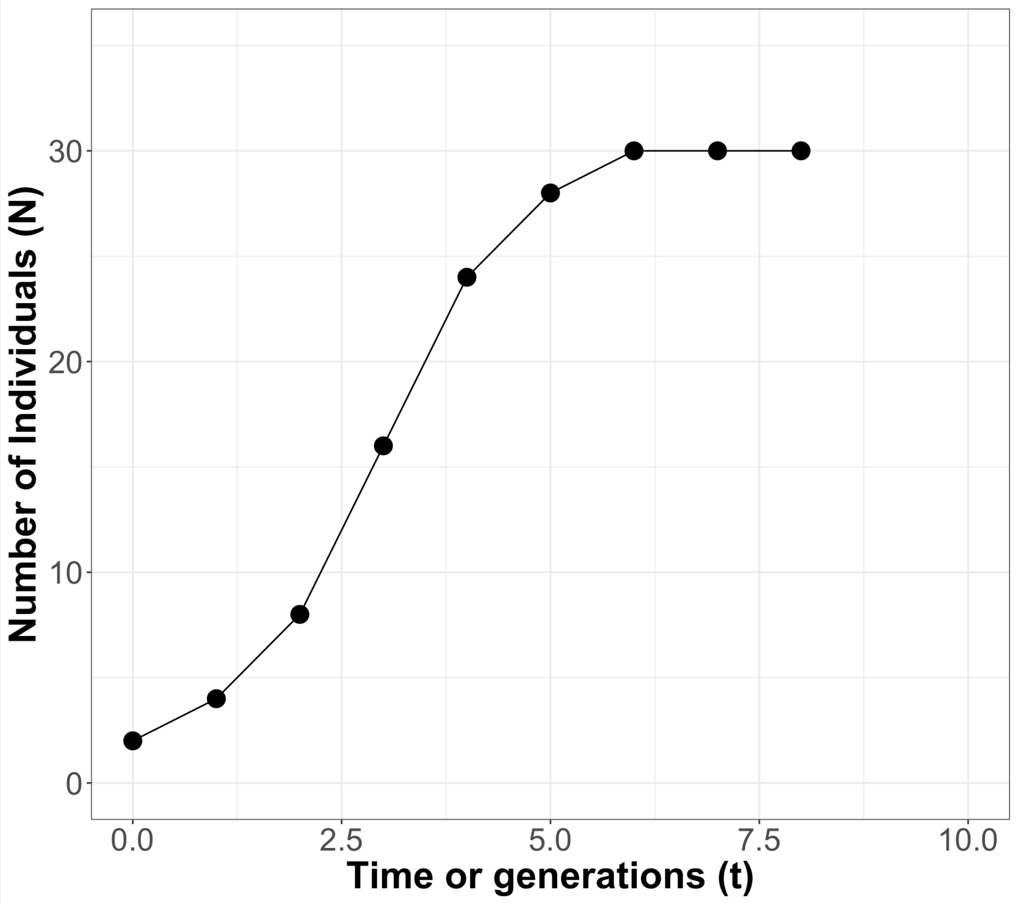


Population growth curve

The population growth curve including **density-dependent** effects like int***ra***specific competition (competition among individuals of the same species) is a logistic function, flattening out as resources become limiting.

$$dN/dt = rN(K - N)/K$$

We know N, t and r, but what is K?



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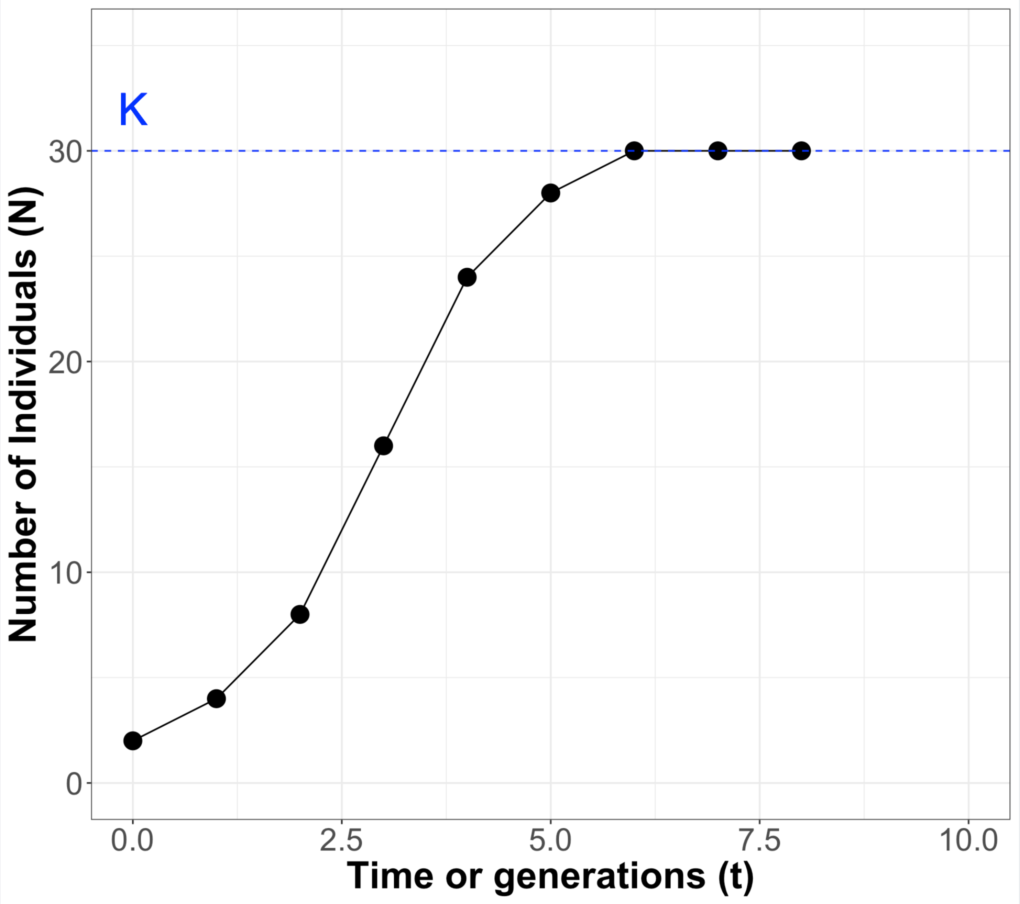
$dN/dt = rN(K - N)/K$

We know N, t and r, but what is K?

K = carrying capacity

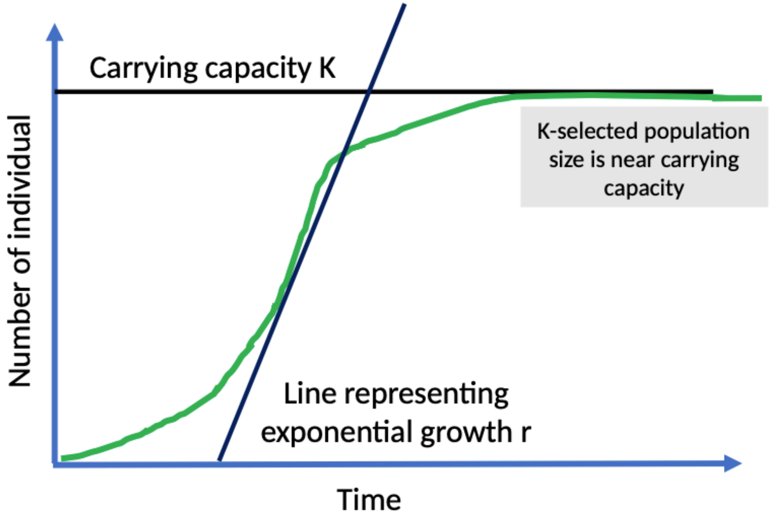
Familiar?



r and K selection

Mac Arthur & Wilson, 1967

- **r-selected**: (*r is for reproduction*). Favoured for the ability to reproduce rapidly (high r - values) in r-selecting habitats (more unstable).
- **K-selected**: Favoured for the ability to make a large proportional contribution to a population which remains at its *carrying capacity (K)* in K-selecting habitats (more stable).



2

Terry Hedderson's lecture on life history models

Population growth curve

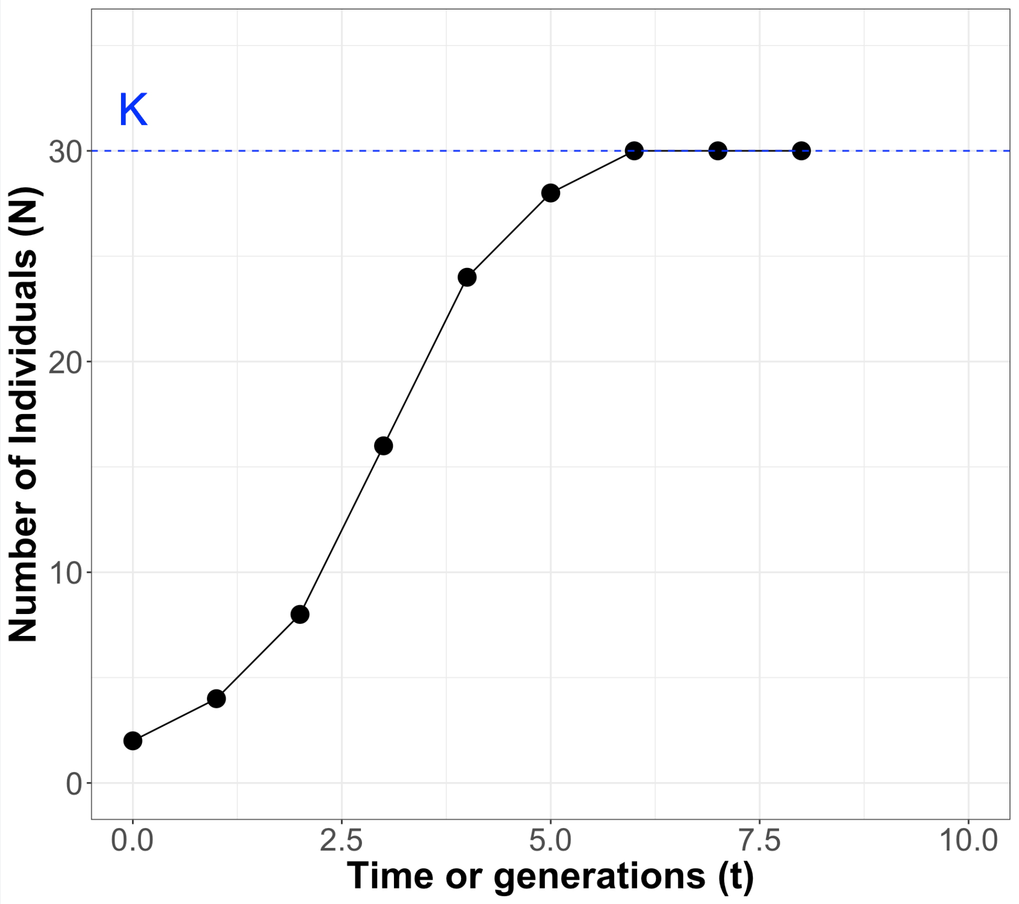
The population growth curve including **density-dependent** effects like int***ra***specific competition (competition among individuals of the same species) is a logistic function, flattening out as resources become limiting.

$$dN/dt = rN(K – N)/K$$

K = carrying capacity

Note: *Where N is small, the logistic growth curve approximates the exponential growth curve (rN), because $(K – N)/K$ is close to 1.*

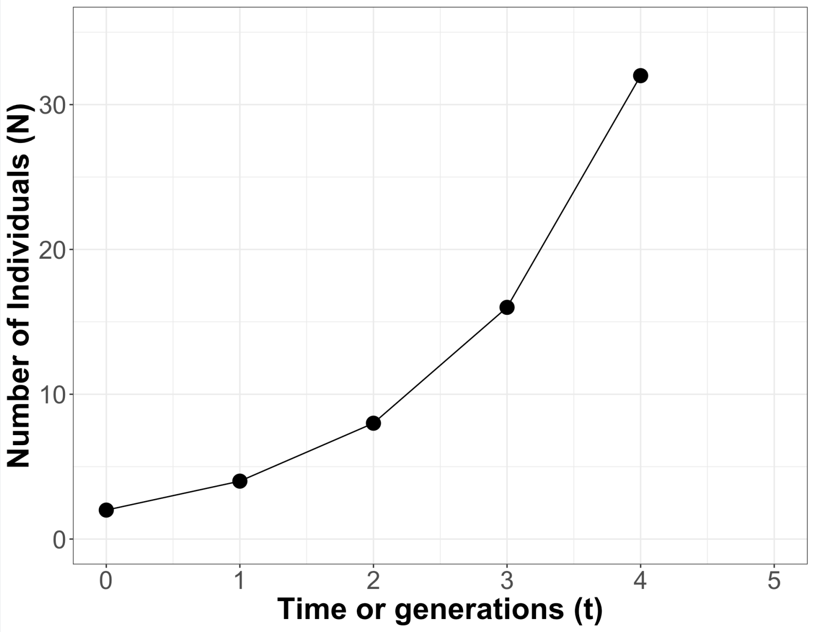
It begins to deviate as N increases.



Exponential growth

$dN/dt = rN$

Population growth rate, r, doesn't change with population size

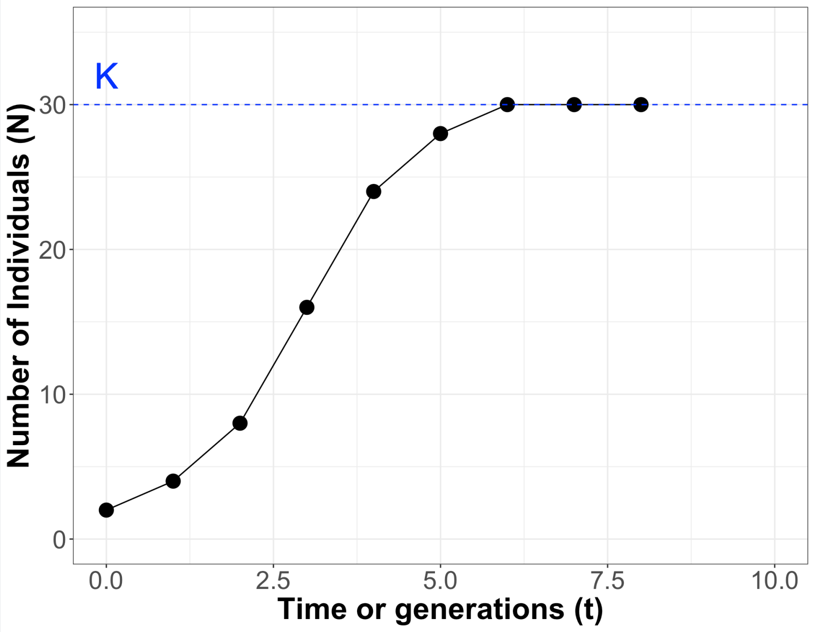


Density independent population growth

Logistic growth

$dN/dt = rN(K - N)/K$

Population growth rate, r, gets small as the population approaches carrying capacity, K



Density dependent population growth

What are the implications of density-dependent growth?

What are the implications of density-dependent growth?

Serotinous Proteaceae are well known for extreme population density fluctuations after fire.

image: Roets et al 2006

ECOSCIENCE

Fire life histories and the seeds of chaos[1]

William J. BOND, Kristal MAZE & Phillip DESMET, Botany Department, University of Cape Town, Private Bag, Rondebosch, 7700, South Africa, e-mail: bond@botzoo.uct.ac.za

While some of this may be exogenous, driven by external forces like climate fluctuations or variability in the fire regime, **Bond et al 1995** demonstrated that it could be endogenous, driven by internal population dynamics due to density-dependent effects.

Bond et al 1995

Density-dependence in serotinous Cape Proteaceae

Empirical datasets showed evidence for a negative impact of density-dependence on:

- recruitment (Figure 1)
- fecundity (Figure 4)

Notice the exogenous effect of aridity on *Protea repens* seedling establishment at the arid inland site (Figure 1, bottom).

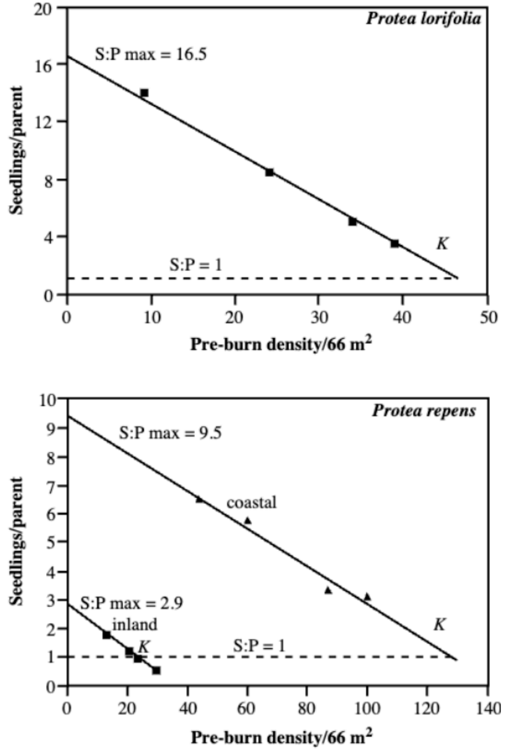


FIGURE 1. Density-dependent seedling recruitment in *Protea lorifolia* and *Protea repens* populations burnt in autumn fires. Values are derived from post-burn censuses of seedlings and skeletons of pre-burn individuals (Bond, Vlok & Viviers, 1984). The intercept of the regression equation gives λ_{max} (= S:P max) while *K*, the carrying capacity, is the pre-burn density at which seedlings reach replacement levels (λ = S:P = 1). Two populations of *P. repens* are shown, one from a mesic coastal site and one from a more arid inland mountain range.

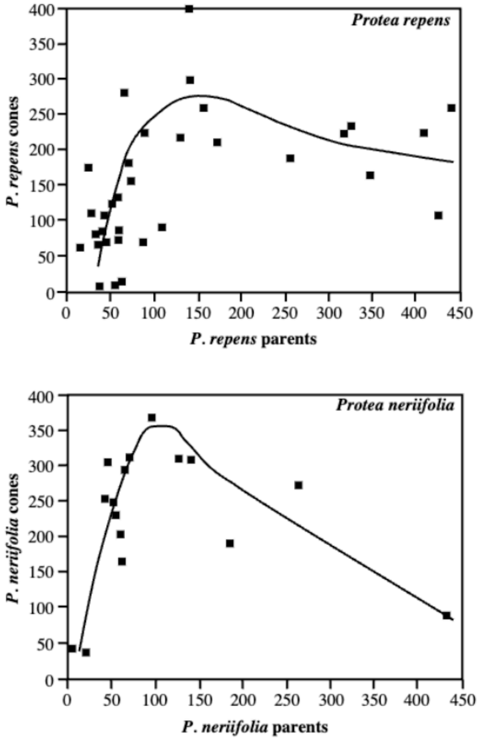


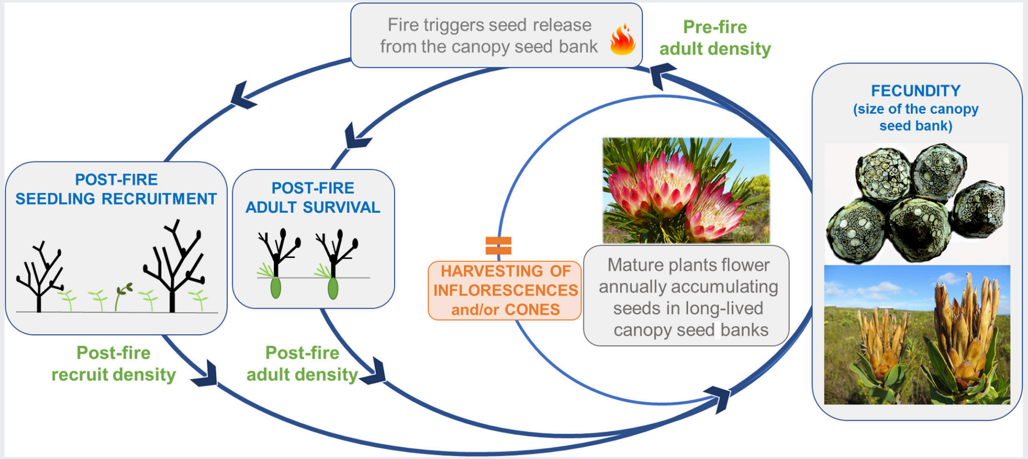
FIGURE 4. The relationship between number of cones per 10 m × 10 m plot and plant density for two proteoid shrubs, *Protea repens* and *P. neriifolia* (Maze & Bond, 1995). The curves are fitted by hand.

Bond et al 1995

Implications for populations?

They fed their empirical data into demographic models and projected population growth over multiple generations.

Note that generations and fires are synonymous, because serotinous Proteaceae mostly only recruit after fire.



Bond et al 1995

Figure from **Treurnicht et al 2021**. Ignore the harvesting…

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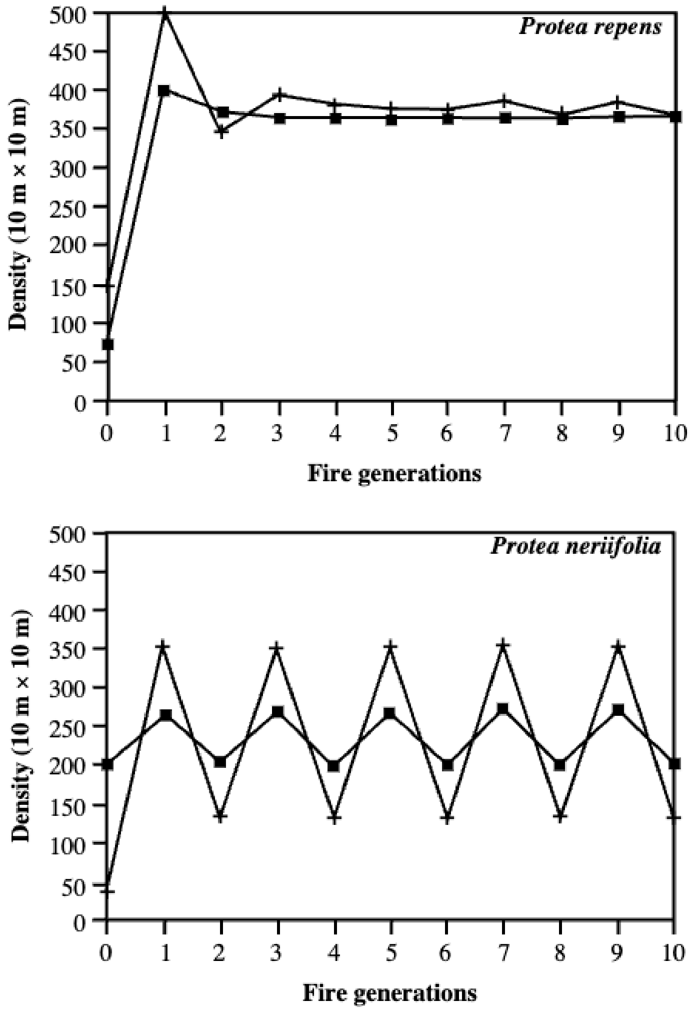


FIGURE 5. Graphic interpolation of population trajectories derived from the curves shown in Figure 4 (see Symonides, Silvertown & Andreasen, 1986 for the procedure used). The population trajectories were adjusted for seeds per cone, seed survival through fire and first dry season seedling mortality using data from Maze & Bond (1995) collected after an experimental burn. The different trajectories for each species indicate sensitivity to initial starting populations. N_o for *P. repens* = 75 (squares), 150 (crosses). N_o for *P. neriifolia* = 50 (crosses), 200 (squares).

Bond et al 1995

Implications for populations?

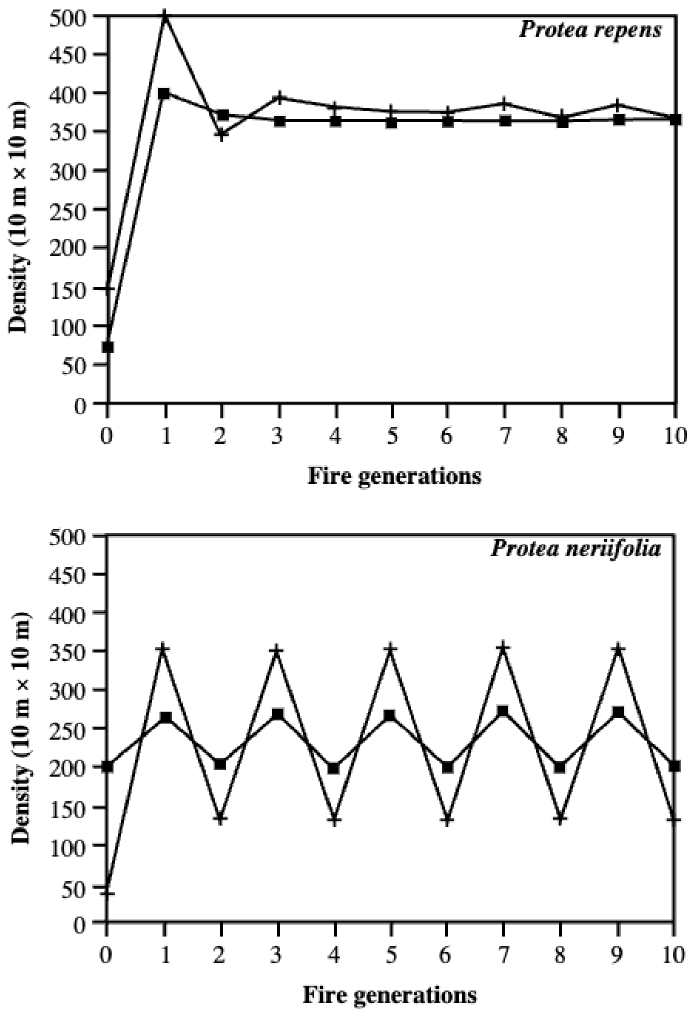
They fed their empirical data into demographic models and projected population growth over multiple generations.

Note that generations and fires are synonymous, because serotinous Proteaceae mostly only recruit after fire.

Decreasing the starting population size (N_0), which would reduce the initial effect of density on population growth, increased the amplitude of population fluctuations, creating risk of total population crashes.

This effect was stronger in *P. neriifolia*, because it had higher cone production (fecundity) and was more sensitive to population density.

Bond et al 1995



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What other factors could cause density-dependence?

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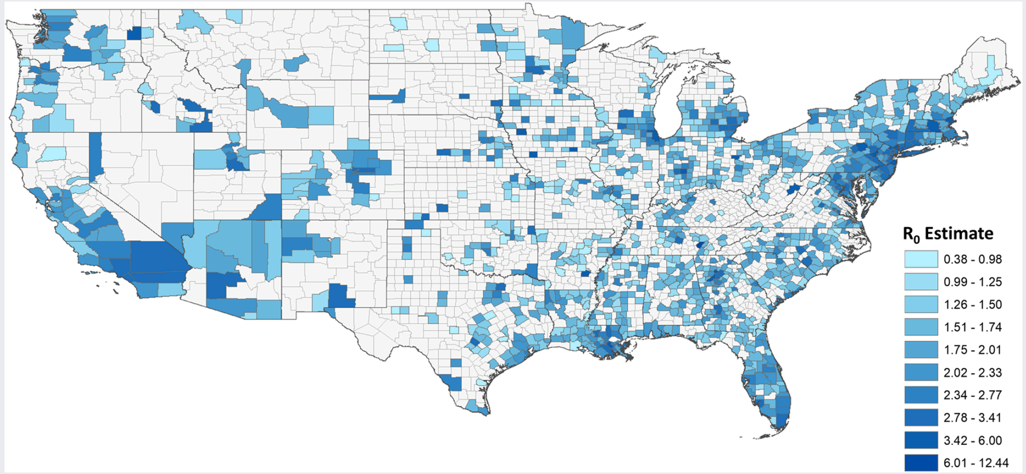
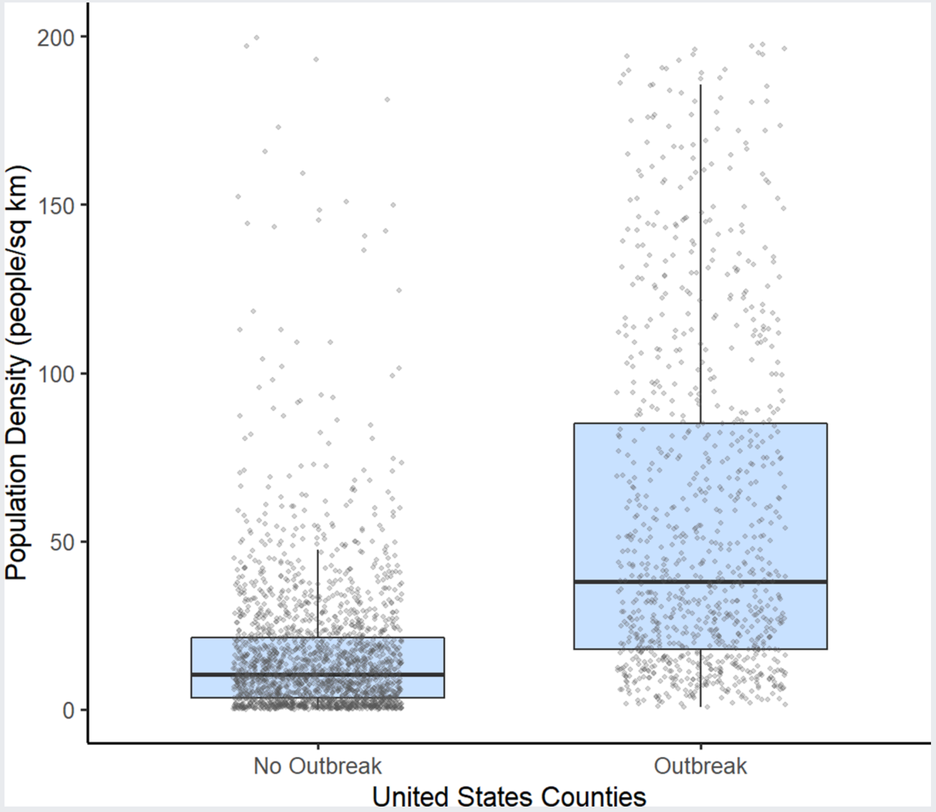
Disease or parasites

As population density increases, so does the probability of transmission, and thus mortality.





Covid transmission in the USA (**Sy et al. 2021**).

What other factors could cause density-dependence?

Predation

As the prey population density increases, so does the predator population. Eventually, the high number of predators causes the prey population to crash. This causes the predator population to crash, which allows the prey population to recover. This cycle continues, creating a predator-prey cycle.

There are many variations and elaborations of this theme that account for prey vigilance, predator aggression (e.g. territoriality), etc...

The same principle applies to **herbivory**, where the herbivore population increases with the plant population, but the plant population is reduced by the herbivores.

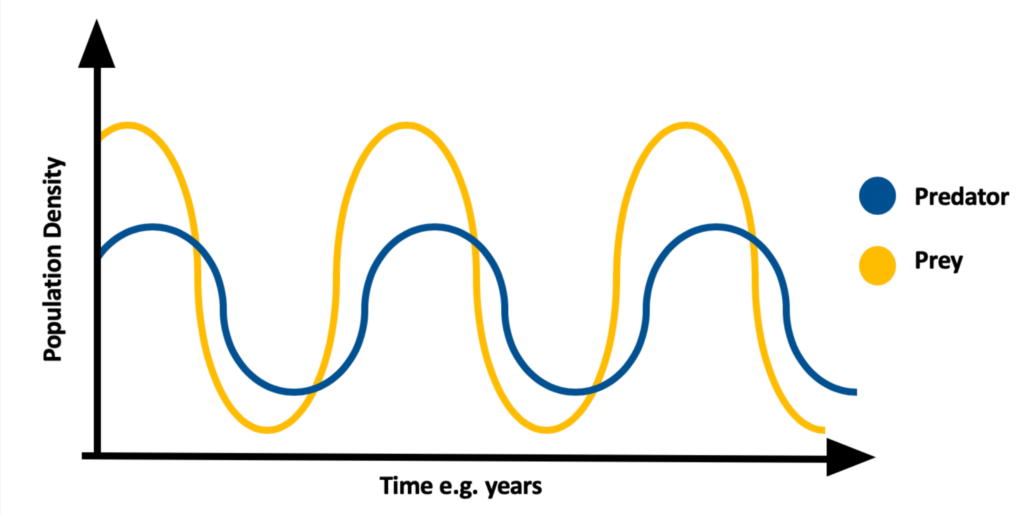


Image: Hczarn on **Wikimedia Commons**, CC-BY-SA 4.0

What other factors could cause density-dependence?

Accumulation of waste products

If the wastes can't be recycled fast enough, they can become toxic to the population. This is a common problem in aquaculture, where fish are kept in high densities and the water becomes polluted with their waste products.

Another example is fermentation in the making of wine. Alcohol is a waste product created by the yeast. As the yeast population grows, alcohol builds up, but it is toxic to the yeast. Above 13% alcohol content, the yeast population is doomed, which is why no naturally fermented wine contains more than 13% alcohol. To make stronger alcoholic beverages, they must be distilled out of wine or beer.

Image: **Pexels**, CC-0

What about positive density-dependence?

Often called Allee effects after ecologist W.C. Allee, who described the phenomenon in the context of cooperative feeding in social insects (**Allee 1931**).

What could cause positive density-dependence (Allee effects)?

Mate or pollination limitation

In some species, individuals need to be close together to find mates, creating a positive correlation between population growth rate and population density - at least initially. This is a huge problem for species of conservation concern, where populations have been thinned and/or become small and isolated, but now struggle to recover.

This may be a factor in the decline of species like the Clanwilliam cedar (*Widdingtonia cedarbergensis*), which is endemic to the Cederberg mountains of South Africa. The trees are wind-pollinated, and if the population density is too low, there may not be enough pollen available to fertilize the ovules.

What could cause positive density-dependence (Allee effects)?

Mate or pollination limitation

Another example are abalone (perlemoen), which are marine molluscs that are harvested for food. They are broadcast spawners, meaning that they release their eggs and sperm into the water column, where fertilization occurs. If the population density is too low, there may not be enough sperm available to fertilize the eggs.

Other examples include solitary species struggling to find a mate, or plants that need to be in high enough densities to attract their pollinators or seed dispersers.

Babcock and Keesing 1999

Image: **Peter Southwood on iNaturalist**, CC-BY-SA 4.0

What could cause positive density-dependence (Allee effects)?

Cooperative feeding

In some species, cooperation among individuals improves their ability to acquire food. This is common among most social animals where individuals work together to find and capture prey (e.g. insects, lions, wild dogs).

For example, orca (killer whales) hunt cooperatively, using sophisticated techniques to catch seals. Often, the more individuals there are in the pod, the more successful they are at hunting.

This is a classic example of a positive density-dependence effect, where the population growth rate increases with population density.

Images: **Pitman and Durban 2011**

What could cause positive density-dependence (Allee effects)?

Predator satiation

Periodical cicadas (genus *Magicicada*) are a classic example of predator satiation, where the adults all emerge synchronously every 13 or 17 years causing the population density to be so high that predators can't eat them all.

This is also a common strategy among many species of insects, which produce large numbers of offspring at once to overwhelm their predators.

Many plants employ the same strategy, producing large numbers of seeds at once to overwhelm seed predators. This is called masting, and is common among many species of trees, including oaks and pines.

Image: **jsatler on iNaturalist**, CC-BY-NC 4.0

What about positive *and* negative density-dependence?

Most populations are affected by multiple density-dependent factors at the same time, and the relative importance of each factor can change over time. For example, a population may be limited by mate or pollination limitation at low densities, but as the population grows, it may become limited by predation, disease or competition (or a combination thereof).

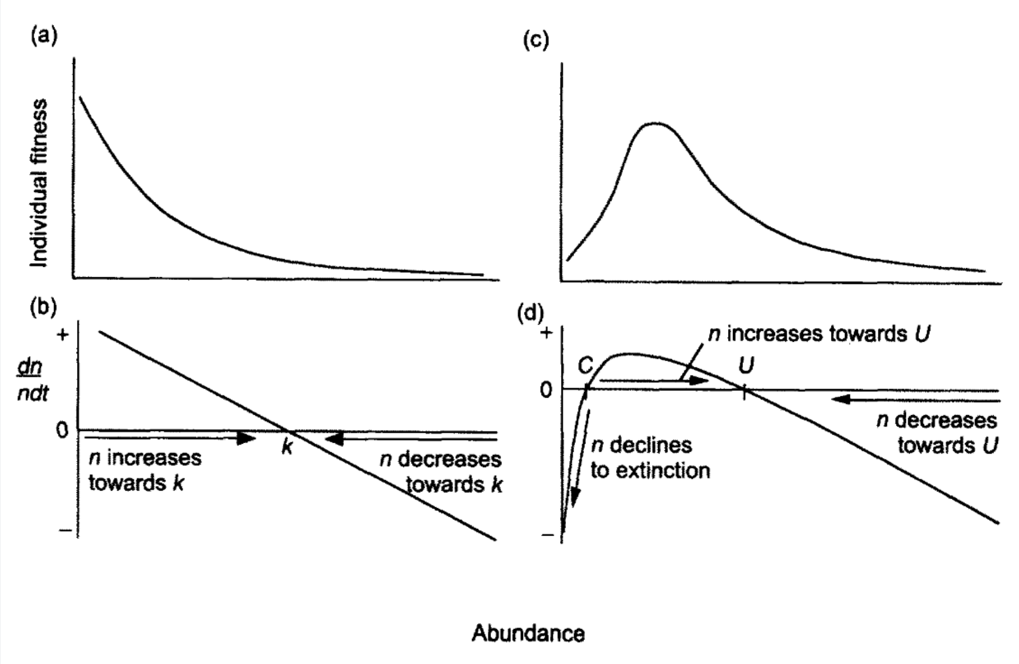
What about positive *and* negative density-dependence?

Fig. 1. Image and text from ***Stephens et al. 1999***

(a) As populations grow there will often be reductions in the fitness of individuals, for example from increasing competition and depletion of resources, resulting in decreased natality and survival.

(b) Population growth rate will decline linearly with increasing abundance, as illustrated by the logistic equation, giving a single, stable equilibrium (k).

(c) For many species however, there are benefits associated with the presence of conspecifics. At low numbers or densities, the benefits from the addition of each successive individual outweigh the costs, such that there is a net gain in individual fitness, and fitness is highest at intermediate numbers or densities.



(d) In this case, population growth rate may also be low at low levels of abundance, as shown by the adjusted logistic equation. If growth becomes negative at low numbers, two equilibria will result: a lower, unstable equilibrium (C) and an upper, stable equilibrium (U).

Take-home

> *If population growth were density-independent, it would be exponential...*
>
> *Most species exhibit density-dependent population growth due to intraspecific competition and other density-dependent factors (e.g. disease transmission), thus self-regulating their population size.*
>
> *Density-dependence creates an endogenous control on populations and has big implications for their size and stability.*
>
> *There are other factors that can cause negative density dependence (predation, disease, etc) and some that can cause positive density dependence (also known as Allee effects). Often they can act in unison.*
>
> *One needs estimates of population growth rates to know whether populations can be maintained and define the environmental conditions of the Hutchinsonian niche. This can be done if you can estimate birth, death and dispersal rates.*

Thanks!

Slides created via the R packages:

xaringan
gadenbuie/xaringanthemer

The chakra comes from remark.js, **knitr**, and R Markdown.