Demoecology the ecology of populations

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Demoecology: the link between autoecology and sinecology



Demoecology: the ecology of populations

Population is a group of individuals of the same species (conspecific) living in the same portion of habitat

Population is a reproductive (panmittic) and evolutionary (gene flow) unit

Members of the same population share the same environmental conditions (i.e. abiotic factors, climate etc.)

Members of a population share the same resources (food, refugia, water sources, reproductive partners etc.)

Members of the same population interact among themselves: competition, mutualism, cannibalism etc.

Main goals of Demoecology

a) To study demography of popolations

Population density, population structure (age classes)

Population dynamics:

How the population density and strucure vary in space and time

How the environment (conditions and resources) affect population dynamics

How intraspecific interactions (competition, mutualism) affect population dynamics

b) To predict (forecast) future population density and structure in a given environmental scenario

Applicative goals of Demoecology

To predict the effect of interactions given by other species, including humans, on the persistence of the population in a given habitat

Effect of human predation on natural populations (fishing, hunting, cropping etc.)

Design of exploitation policies (tradeoff between economy and conservation)

Effect of habitat modification (deforestation, habitat fragmentation, pollution, climate change)

Other applications:

Biological control of pests in agricolture

Optimization of farming and aquaculture

General methods of Demoecology

Descriptive tools

Counting techniques, statistical methods to obtain information on population density and structure, and spatial distribution

Experimental tools

Field or laboratory experiments to obtain information on resources' use and biotic interactions (predation, competition etc.)

Predictive tools

Forecasting techniques to predict future characteristics of the population (mathematical models)

Descriptive tools

To get quantitative information on the actual status of the population (density and structure)

a) Static techniques - instantaneous assessment

b) Dynamic techniques - long lasting assessment

Descriptive tools

To get quantitative information on the actual status of the population (density and structure)

Static techniques – instantaneous assessment

1) Census – total count of individuals in the whole area of interest

2) Sampling – extrapolation of population density in a given area, based on statistical elaboration of data obtained in some subunits of the whole area of interest

Sampling vs census



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Sampling

When it would be difficult or unpossible to performe the census:

- Population too large
- Unknown boundaries for the ditribution area
- Individuals not easy to count in a short time (e.g. too high mobility)

It is better to perform "sampling", i.e. to count individuals (or their traces) on single subunits of the distribution area and then extrapolate the density to the whole population

Sampling methods

Homogeneous habitat structure e.g. grassland



Random or uniform sampling

Heterogeneous habitat structure e.g. grassland-forest



Stratified sampling

Transect sampling

When individuals are sparsed over a large area Such as elephants, dolphins



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Transect sampling

When individuals are sparsed over a large area



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Indirect sampling (sampling of traces, scars, faeces, food remains)

When individuals are difficult to be counted directly

Pellet count along transects (Ungulates)



Faecal pellets specific shape/size Capture-recapture methods

When members of a population are highly mobile (e.g. fish, birds, mammals, reptiles, crabs etc.)

It is difficult to obtain precise counts (i.e. re-counting errors)

In this case it is better to perform a capture-recapture protocol with individual marking

Different trapping according to the species characteristics (nets, funnel traps, photographic traps etc.)

Different marking methods (tags, colours, radiotransmitters, transponders)



Capture-marking-recapture

How to obtain an estimate of population size (Petersen method)



Capture-marking-recapture

How to obtain an estimate of population size (Petersen method)

- M = number of individuals captured and marked on the first session
- C = total number captured on the second session
- R = number of individuals captured on the second session which are marked (already captured on the first session)

$$\hat{N} = \frac{C \cdot M}{R}$$

Capture-marking-recapture

How to obtain an estimate of population size (Petersen method)

$$\hat{N} = \frac{C \cdot M}{R}$$



M = 1000C = 1000R = 100 $\hat{N} = 10^{\circ}000$ $M = 1000 \\ C = 1000 \\ R = 10 \\ \hat{N} = 100^{\circ} 000$

Census or sampling count: the population size and structure French population censused on 1967



Pattern of population growth revealed by population structure



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Repeated static counts can release information on temporal variations in population size and structure

Nunivak Island 163° 1679 166 162910 A2520321 Cape Etolin, Nunivak Island 60°30' 60°30'N Etolin Alaska Strait Population (N) Nunivak Island 60°00 60°00' 800 Kuskokwim Bay 59°30'N - 59° 30' 600 167°W 166 ° 165° 164° 163° 162 400 Year counts 200 0000000000 0 1930 1940 1950 1960 1970 **Ovibos moschatus** Year

Repeated static counts can release information on trends



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Demographic forecasting

Extrapolation by repeated static counts alone do not always provide reliable information on future status of the population



Need for a "formal" hypothesis for population growth

Basic models of population growth (Demoecological Models)

Why to use DM ?

1) PREDICTIVE SCOPE (Demographic forecasting) To predict general trends of population dynamics or to predict theb effects of specific factors (climatic change, cropping, removal of preys etc.)

We can be confident with a forecasting based on DM which is able to generate some relevant property of actual population

2) EURISTIC SCOPE (to get better knowledge)To test hypotheses about general demographic processes(e.g. the importance of competition for demographic homeostasis)and about factors affecting population dynamics of single species

DM are formal expressions of ideas ("theories") which (should) release outcomes (predictions) to be "falsified" by empirical data A DM unable to do this a useless exercise Basic models of population growth (Demoecological Models)

A) Which "language" to formalyse our ideas in a DM ?

Any language, but maths is good because universal and non-semanthic

B) How "complex" should be a DM ? (a simple or very complex equation) ?

In general: good DM are a tradeoff between Completeness and Concision

Completeness is the capacity to reproduce the most relevat "traits" of Population dynamics

Concision is to be as simpler as possible to get a sufficient compmpleteness

No general rule abouth this C-C tradeoff, depends on the goal:

General DM should be very concise Spefic case DM (applicative) can be very complete (complex) Basic models of population growth (Demoecological Models)

Which "kind" of maths should be used ?

Demoecology handles variations (density, population structure)

A) Populations variyng in discrete steps (e.g. annual reproduction)

Discrete maths $N_{t+1} = N_t$ by "something"

B) Populations affected by continuous variations

Continuous maths i.e. variation in a time tending to zero dN/dt = N by "something"

Which are the general processes producing the modification of a population in time?

Mortality Reproduction Mobility (e.g. immigration to and emigration from a given area)

So the simplest (discrete) DM for a non structured pop is:

$$N_{t+1} = N_t + B - D + I - E$$

 N_t and N_{t+1} is population size now and after a unit of time

 $\begin{array}{l} B = number \ of \ individuals \ born \ between \ N_t \ and \ N_{t+1} \\ D = number \ of \ individuals \ died \ between \ N_t \ and \ N_{t+1} \\ I = number \ of \ individuals \ immgrated \ between \ N_t \ and \ N_{t+1} \\ E = number \ of \ individuals \ emigrated \ between \ N_t \ and \ N_{t+1} \end{array}$

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We can simplify by dropping I and E on the assumption that: a) the population is "closed" within rigid boundaries, so I=0, E=0 b) the population lives in an open habitat, so statistically I=E

$$N_{t+1} = N_t + B - D + I - E$$

Second, we normalize B and D to N_t because a) B is number of offsprings produced by members of the pop at N_t b) D is the fraction of N_t died between t and t+1

$$b = \frac{B}{N_t}$$

$$d = \frac{-D}{N_t}$$

Fertility coefficient per capita n. of offsprings

Mortality coefficient Pobability to die

The new simplified eqn is:

 $N_{t+1} = N_t + N_t \cdot b + N_t \cdot d$

hence

 $N_{t+1} = N_t$ (1+b+d) $\longrightarrow \lambda = 1+b+d$

 λ (lambda) is called "the finite rate of natural increase" of the population, i.e. the factor by which the population size grows in a (de)finite interval of time (e.g. one minute, one day, one year etc.)

1 interval
$$N_{_{t+1}} = N_{_t} \cdot \lambda$$

T intervals
$$N_{t+T} = N_t \cdot \lambda^T$$

The general prediction of this simple DM is that pop has a positive exponential growth if $\lambda > 1$, negative exponential if $\lambda < 1$ and is stationary ($N_{t+1} = N_t$) if λ is exactly equal to one.



How can lambda be empirically assessed

- a) By assessing fertility and mortality rate since $\lambda = 1-b+d$
- b) By repeated censuses or sampling since also $\lambda = Nt+1 / Nt$



Assessing lambda by repeated censuses or sampling reveals variability

- a) sampling errors
- b) demographic stochasticity due to internal, genetic variability
- c) environmental stochasticity due to variation of conditions & resources



Instead of
$$N_{t+1} = N_t \cdot \lambda$$
 \longrightarrow Deterministic, constant λ
We use $N_{t+1} = N_t \cdot P(\lambda)$ \longrightarrow Probability distribution of λ

We can obtain $P(\lambda)$ by "translating" observed frequencies to probabilities By dividing F / total

Ex. 1/17 = 0.059



Empirical values of lambda by annual counts (1945-1970)

Recursive (repetitive) computation using λ randomly extracted from a given probability distribution

$$N_1 = N_0 \cdot^r \lambda_0; N_2 = N_1 \cdot^r \lambda_1; \dots$$

Different computations (replicates) using the same N₀ and P(λ) generate different growth curves (demographic trajectories)



The PDM generates a distribution of probabilities reg the future status of the population

The precision of the outcome depends on the number of replicates



Population size after T intervals

Frequency

How many times the computation produced a given value

In probabilistic DM a population having average lambda >1 can undergo reduction with a given probability

R = 10.000



Probabilistic extinction

In probabilistic models also a population having an average lambda > 1 can undergo extinction in a given interval, with a probability p



Probabilistic extinction

Probabilistic models are used in Population Viability Analysis to assess the risk of extinction of natural populations or whole species



Population Viability Analysis using probabibilistic DM

The International Union for Conservation of Nature





The IUCN Species Survival Commission 2000 IUCN Red List of **Threatened Species**[™]

Class	EX	EW	Subt	CR	EN	VU	Subt	LR/cd	LR/nt	DD	Total
Vertebrates											
MAMMALIA	83	4	87	180	340	610	1130	74	602	240	2133
AVES	128	3	131	182	321	680	1183	3	727	79	2123
REPTILIA	21	1	22	56	79	161	296	3	74	59	454
AMPHIBIA	5	0	5	25	38	83	146	2	25	53	231
CEPHALASPIDOMORPHI	1	0	1	0	1	2	3	0	5	3	12
ELASMOBRANCHII	0	0	0	3	17	19	39	4	35	17	95
ACTINOPTERYGII	80	11	91	152	126	431	709	12	96	251	1159
SARCOPTERYGII	0	0	0	1	0	0	1	0	0	0	1
Subtotal	318	19	337	599	922	1986	3507	98	1564	702	6208
TOTAL ANIMALIA	693	33	726	925	1353	3157	5435	129	1885	1310	9485

Repeated census

When and how often ?

Depends on the life history of the population

What is life history?

Distribution in time, and duration, of the major biological events affecting individual life: birth, growth and development, reproduction, death



Life history

Life history traits are subject to darwinian selection, depending on habitat characteristics (e.g. stable vs fluctuating)



Almost continuous reproduction during a long segment of life

How life history affects population dynamics and structure

Synchronous semelparity: discrete generations



How life history affects population dynamics and structure



Dynamic vs static analysis

Static counts do not allow to compute two important characteristics of population dynamics: fertility (birth rate) and mortality (death rate)

To obtain such demographyc parameters it is necessary to perform a dynamic analysis

In the dynamic analysis a group of individual of the same age (cohort) is monitored during their life (from birth to death)



Dynamic (or cohort) analysis can be performed in the field (e.g. by radiotracking the single individuals) or by transferring the specimens into a controlled space (laboratory)

Dynamic analysis permits to obtain information on:

- 1) Age specific death rate
- 2) Age specific reproduction rate
- These data are organized in a table (life table)

	Number of individuals	Number of offsprings (eggs, embryos, seeds etc.)
	N0	FO
Age	N1	F1
class	N2	F2
771	Νω	Fω
771	Νω	Fω

Laboratory experiments on a grasshopper





Corthippus brunneus





 $I_{\rm a} = N_{\rm a} / N_{\rm 0}$

Survival probability Fraction of initial cohort Surviving to each subsequent stage

Ontogenetic stage (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙ m _a
0 (eggs)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I larval stage)	3513	0.080	0.022	0.28	0.15	0	0	0
2 (II larval stage)	2529	0.058	0.014	0.24	0.12	0	0	0
3 (III larval stage)	1922	0.044	0.011	0.25	0.12	0	0	0
4 (IV larval stage)	1461	0.033	0.003	0.11	0.05	0	0	0
5 (adults)	1300	0.030				22617	17	0.51

$$d_a = l_a - l_{a+1}$$

Probability to die during each stage

Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙m _a
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
2 (II stadio larvale)	2529	0.058	0.014	0.24	0.12	0	0	0
3 (III stadio larvale)	1922	0.044	0.011	0.25	0.12	0	0	0
4 (IV stadio larvale)	1461	0.033	0.003	0.11	0.05	0	0	0
5 (adulti)	1300	0.030				22617	17	0.51



$$p_a = 1 - q_a$$

Survival rate

Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙ m _a
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
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4 (IV stadio larvale)	1461	0.033	0.003	0.11	0.05	0	0	0
5 (adulti)	1300	0.030				22617	17	0.51

Absolute fertility Number of offsprings produced in total by specimens of each stage

Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙ m _a
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
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5 (adulti)	1300	0.030				22617	17	0.51



Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	$l_a \cdot m_a$
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
2 (II stadio larvale)	2529	0.058	0.014	0.24	0.12	0	0	0
3 (III stadio larvale)	1922	0.044	0.011	0.25	0.12	0	0	0
4 (IV stadio larvale)	1461	0.033	0.003	0.11	0.05	0	0	0
5 (adulti)	1300	0.030				22617	17	0.51

$$l_a \cdot m_a$$

Net reproduction of each class

Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙m _a
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
2 (II stadio larvale)	2529	0.058	0.014	0.24	0.12	0	0	0
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5 (adulti)	1300	0.030				22617	17	0.51

 $l_a \cdot m_a$ is the product of the survival probability to the class a, by the relative fertility of that class



Stadio ontogenetico (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	l _a ∙m _a
0 (uova)	44000	1.000	0.920	0.92	1.09	0	0	0
1 (I stadio larvale)	3513	0.080	0.022	0.28	0.15	0	0	0
2 (II stadio larvale)	2529	0.058	0.014	0.24	0.12	0	0	0
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4 (IV stadio larvale)	1461	0.033	0.003	0.11	0.05	0	0	0
5 (adulti)	1300	0.030				22617	17	0.51

Net reproduction rate

$$R_0 = \sum_{a=0}^{\infty} (l_a \cdot m_a) = 0.51$$

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$$R_0 = \sum_{a=0}^{\omega} \left(l_a \cdot m_a \right)$$

If $R_0 = 1$ each initial cohort has been replaced in the next generation by a cohort having exactly the same size (constant population density)

If $R_0 < 1$ each initial cohort has been replaced by a cohort smaller in size (decreasing population density)

Se $R_0 > 1$ each initial cohort has been replaced by a cohort larger in size (increasing population density)

Life table of the plant *Phlox drummondii* (Polemialceae) Each age interval corresponds to 63 days (arbitrarily)

	Età (a)	N _a	l _a	d _a	q _a	k _a	F _a	m _a	$l_a \cdot m_a$
	0	996	1.000	0.329	0.005	0.003	0	0	0
	1	668	0.671	0.375	0.009	0.006	0	0	0
	2	295	0.296	0.105	0.006	0.003	0	0	0
	3	190	0.191	0.014	0.002	0.001	0	0	0
	4	176	0.177	0.004	0.001	0.001	0	0	0
	5	172	0.173	0.005	0.002	0.001	0	0	0
yı _	6	167	0.168	0.008	0.003	0.002	0	0	0
	7	159	0.160	0.005	0.002	0.001	53	0.33	0.05
	8	154	0.155	0.007	0.003	0.001	485	3.13	0.49
	9	147	0.148	0.043	0.021	0.011	803	5.42	0.80
	10	105	0.105	0.083	0.057	0.049	973	9.26	0.97
	11	22	0.022	0.022	1.000		95	4.31	0.10
	12	0	0						





 $R_0 = \sum_{a=0}^{\omega} (l_a \cdot m_a)$

R₀=2.41

Age specific mortality rate: K and r strategies





Structured populations are composed of individuals having different characteristics (age, size, weight etc.) with class specific mortality and fertility



The dynamics of a structured population can be described by the variation in time of a "status vector" (an array of values expressing the number of individuals of each class present at time 0, 1, 2,)



Age specific mortality rate, growth rate and relative fertility determine the dynamics of single classes and of the whole population



Probabilities to enter into the following class, and to reproduce are organized in a "Transition Matrix" (also called Leslie Matrix)

The coefficients of the TM are obtained by conducting a cohort (dynamic) analysis (life table)

		seed	seedIn	Y pl	Old pl	
	seed	p1	0	f1	f2	
Time t+1	seedIn	p2	р3	0	0	Os are "impossible transitions
	Y pl	0	p4	p5	0	
	Old pl	0	0	р6	р7	

Time t

SDMs reveal that the population reaches a stable structure in time (if no perturbation occurs)

The equilibrium structure depends on the values of the transition matrix, and it is independent from the initial size of each class

