

Population Ecology

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Population ecology is the discipline in ecology that deals with the structure and dynamics (e.g. growth and decline) of biological populations. The focus may be on a single population in isolation, or one of a few interacting populations. Population ecology is closely related to other ecological disciplines, e.g., physiology and community ecology, but separate from them. A physiologist might study the mechanisms that enable a plant species to tolerate a temporarily stressful environment; a population ecologist might estimate the fecundity and survival rates in that environment, then use those rates to estimate the probability that the population goes extinct if the stressful conditions continue. A community ecologist might describe the abundance of all the mammal species in an area and describe the changes in relative abundance over time; a population ecologist might seek to explain the temporal changes in a few important species by estimating the interactions between those species. Introductory treatments of population ecology include [2, 23, 51]. More detailed accounts of specific ecological issues include [7, 27, 53]. The history of population ecology is summarized in [23] and [30, esp. pp 146-192].

A biological population is a collection of individuals of the same species, usually associated with a specific geographic area [2]. Examples of populations include the mallard ducks in the Central flyway of the United States, the *Daphnia laevis*, a zooplankton, in a specific lake, the white footed mice in a specific 0.1 ha patch of grassland, and the Northern Monkshood, a rare plant, found along a specific 10m long stretch of river bank. The choice of geographic area is arbitrary, so long as the choice is appropriate for the ecological context. For example, Northern Monkshood occurs in distinct patches along stream banks. The population can be defined at a small spatial scale, e.g., the plants in a specific patch, at a larger scale, e.g., all plants along a single stream, or at a very large spatial scale, e.g., all plants of the species. Small scales definitions of populations are appropriate for site specific issues, e.g., describing relationships between local population dynamics and environmental conditions or estimating a site-specific probability of extinction. Larger scale definitions are needed to estimate extinction probability for a species or when individuals range over large areas.

Population ecology has a long history of using quantitative models to connect theory and data [26]. Some of

these models are mathematical; they are often used to explore the behavior of populations that follow simplified mathematical rules. Others are statistical; they are often used to estimate population quantities, e.g. survival rate, or compare different models. Because the topic is vast, this article only summarizes major uses of statistical models in population ecology. Details and examples can be found in [31, 59], in cited books and papers, or in other articles in this encyclopedia. Details on mathematical models can be found in [23, 26, 45].

Many of the major issues in statistical population ecology relate to estimation or model selection of the quantities in a fundamental equation of population dynamics (1) or (2). In discrete time, this equation is:

$$N_{t+\Delta t} - N_t = B_t - D_t + I_t - E_t, \quad (1)$$

where N_t is the population size at time t , B_t is the number of births in the interval between t and $t + \Delta t$, D_t is the number of deaths in that interval, I_t is the number of immigrants added to the population during that interval, and E_t is the number of emigrants leaving during that interval [1]. The continuous time equivalent is

$$\frac{dN}{dt} = b(t) - d(t) + i(t) - e(t), \quad (2)$$

where $b(t)$, $d(t)$, $i(t)$, and $e(t)$ are the instantaneous rates of birth, death, immigration, and emigration. The quantities on the right hand side of equations 1 and 2 are usually functions of N_t , but they may also be functions of numbers of individuals in other patches, population sizes of other species, or environmental conditions. They may also be constants.

ESTIMATING ABUNDANCE AND RELATED QUANTITIES FOR A SINGLE POPULATION

One of the first questions about a population is “how many individuals are there?”. This requires estimating the population size, N_t , which almost always involves sampling. The most appropriate methods depend on certain aspects of the species biology. For example, if it is possible to observe all individuals in the population, N_t can be enumerated. Usually, the population is too large or too widespread to count all individuals, so N_t is estimated by sampling areas (e.g., quadrats for plants or plankton tows for small aquatic species). It is reasonable for these species to assume that all individuals in the sampled areas are observed. However, in studies of larger animals (e.g. mammals, birds, or fish), an individual might be present in the sampled area, but not observed (i.e. seen or trapped). Estimating the number of individuals that are present, but not observed, can be done using mark-recapture methods [40, 49, 43], removal sampling [49], distance sampling [5], or a variety of other

methods that simultaneously estimate the population size and the probability of observing an individual. Closed population methods [40, 49] assume no births, deaths, immigration or emigration during the study interval. Open population methods [43, 49] allow turnover of individuals and provide estimates of the population size, survival rates, and recruitment (birth + immigration) rates.

Estimation of the survival rate, $\phi_t = 1 - D_t/N_t$, and number of births, B_t , is relatively straightforward when all individuals in the sampled areas are observed. All that is required is some way of distinguishing, at time $t + \Delta_t$, the individuals that were alive in the population at time t from those that were born into the population. This might be done from biological knowledge (e.g. the relative size of newborn individuals) or by marking individuals at time t . Then, births, B_t , during the interval $(t, t + \Delta_t)$ can be enumerated and survival can be estimated as $\hat{\phi}_t = (N_{t+\Delta_t} - B_t)/N_t$. When $P[\text{observe}] < 1$, the Jolly-Seber model, or some other open population model, can be used to estimate ϕ_t and B_t from mark-recapture data [49, 43]. Jolly-Seber estimates of population size and recruitment are sensitive to the assumption of equal capture probability. More robust estimates can be obtained from the Pollock's robust design [42], which combines features of open and closed populations.

Survival and per capita fecundity rates (B_t/N_t) may differ between groups of individuals. For example, in many bird species, survival of juveniles is less than that of adults [23]. In many mammal species, survival and fecundity differ among age groups (e.g., 0-1, 1-2, 2-3 year old individuals). In many plant species, survival and fecundity rates are more influenced by the size of the plant than by its calendar age [51]. Models for structured populations include this variation in vital rates between groups of individuals.

Age- or size-specific survival and fecundity can be estimated in a variety of ways, depending on what sorts of data are available [8, pp. 133-175]. Two common approaches include repeated observation of the size (or age) and fate of marked individuals and using separate open-population models for each age- or size- group of individuals [49]. Survival and fecundity rates can also be estimated from a time series of population counts using regression or other methods [8, pp 142-154]. These methods are collectively called inverse methods, because they are the inverse of projecting population size given survival and fecundity rates. They require data on the number of individuals in each age or size group at each time and require some variability in survival or fecundity rates among age or size groups.

Age- or size- specific estimates are less precise than total population estimates because the sample size is smaller. If fecundity and survival rates vary smoothly with age or size, models can be used to increase the precision of age- or size-specific estimates. Models may be parametric (e.g. a linear logistic regression on age) or non-parametric (e.g. a smoothing spline); the appropriate choice depends on biological knowledge about the

age- or size-related change in rates. When prior information is available, a Bayesian approach can be used [44].

MODELS FOR POPULATION GROWTH

Various well-known models for population growth can be derived from (1) and (2) by specifying the relationship between births, deaths, and the current population size.

Continuous time models

The simplest population models ignore any differences between individuals and consider only instantaneous birth and death rates in continuous time. The two most common and simple models are the exponential and logistic. If per capita instantaneous birth rate, $b = b(t)/N(t)$, and per capita instantaneous death rate, $m = d(t)/N(t)$ are constant, the population size grows or declines exponentially, $N(t) = N(0) \exp(t * r)$, where $r = b - m$. If the per capita instantaneous birth rate is constant but the per capita instantaneous death rate is proportional to the population size, $m(t) = (r/K)N(t)$, the population size follows a logistic growth curve, $N(t) = N(0) K / (1 + (K - N(0)) \exp(-tr))$ to reach an asymptote at $N(\infty) = K$. K is often called the carrying capacity of the population. [23].

The difference between the exponential and logistic models is important biologically. If the parameters are constant over time, there are two possible outcomes from the exponential model: either the population goes extinct when $r < 0$ or the population size increases without bound when $r > 0$. The outcome from the logistic model is more biologically appealing: the population size approaches the equilibrium population size, K . Because population sizes rarely appear to go to extreme values (0 or ∞), it would seem that the population dynamics of most species include some form of negative feedback or density dependence [3]. However, clearly demonstrating density dependence in a natural population has been difficult.

A variety of statistical tests of density dependence have been proposed [6, 10, 41, 14]. None appears to be completely satisfactory. Two major problems are lack of power and adequate treatment of measurement error. Time series of population counts are often short (e.g. less than 15 observations), so the data may be insufficient to provide a powerful test [52]. Also, density dependence is a general concept; most procedures test a specific null hypothesis (e.g. lag 1 autocorrelation, $\rho(N(t), N(t-1)), = 0$), so a test may lack power to detect other forms of density dependence. Measurement error complicates the analysis and interpretation of density

dependence. In natural populations, $N(t)$ is rarely estimated precisely; often the measurement error is quite large [17]. One realization of a random walk (no density dependence) observed with a large measurement error may be indistinguishable from a realization of a density-dependent time series. The interpretation of tests of density dependence has been hotly debated (see [57] for references to one debate); one position is that there is little justification for using any statistical test because either the type I error is incorrect or the test lacks power [50].

There are continuous time models for structured populations, using delay-differential equations [38] or partial differential equations [13]. However, it is easier to construct flexible models for structured populations using discrete time models, especially matrix population models.

Discrete time models

Matrix population models [8] are a popular discrete time model for structured populations, because of their ease of construction and analysis and their ability to describe biologically important variability. The population is subdivided into components, e.g. age groups or size groups, that may have different per capita survival rates or per capita fecundity. The population size, N_t , is a vector of the number of individuals in each age or size group. The most commonly used models do not include density dependence, so $N_{t+\Delta_t} = AN_t$, where A is the matrix of age- or size-specific survival or fecundity rates [8]. The long-term growth rate, λ , the age (or size) distribution, and the reproductive values are given by the dominant eigenvalue and associated eigenvectors of A and A_T [8]. The sensitivity of λ to changes in any vital rate can be estimated using these eigenvalues [8, pp. 206-257].

The statistical issues associated with matrix population models include selecting boundaries between age or size groups [56, 34, 16], estimating the uncertainty in λ or the associated eigenvectors [8, pp. 299-345], and relating changes in λ to experimental treatments or changes in environmental conditions (Life Table Response Experiments) [8, pp. 248-278].

The dynamics of the discrete time equivalent of logistic growth, $N_{t+\Delta_t} = rN_t(K - N_t)/K$ are more complicated than those of the continuous time logistic equation. If r is small, i.e. $r < 3$, the discrete time and continuous models have similar dynamics; over time, the population size converges to the carrying capacity, K . If r is larger, $3 < r < 3.57$, the population size in the discrete time model jumps between two values. As r increases further, the population size jumps among an increasingly large number of possible values, until at $r > 3.57$, the population size is chaotic [32]. The time series of population sizes appears to be random, even

though $N_{t+\Delta_t}$ is a deterministic function of N_t [32].

When the dynamics are chaotic, N_t is very sensitive to the initial conditions. Consider two time series that start at almost identical initial values (e.g. one at $N_0^a = x$ and the other at $N_0^b = x + \delta$, where δ is close to 0). Over time, the difference between the time series, $N_t^a - N_t^b$, may decrease to 0 if both series are converging to a stable point (e.g. the carrying capacity, K), remain constant, or increase exponentially if the system is chaotic [46]. Exponential divergence, or sensitive dependence to initial conditions, means that small differences in N_0 lead to increasingly large change in N_t . The rate of divergence or convergence can be quantified by the Lyapunov exponents [46]. A positive exponent indicates chaotic dynamics. If the deterministic model for the dynamics is known, the Lyapunov exponents can be calculated analytically. It is more difficult to identify chaotic dynamics when the true dynamic model is unknown.

Statistical methods that have been used to identify chaotic dynamics from a time series of population sizes include fitting linear or non-linear regression models [21, 55], graphical analysis [47], and estimating Lyapunov exponents [39]. The general idea behind the regression methods is to fit a model of the form $N_t = f(N_{t-1}) + \varepsilon_t$ and use the estimated parameters to determine if the series is chaotic. For example, if $f(N_{t-1})$ is the discrete logistic growth function, the dynamics are chaotic if $\hat{r} > 3.57$. Although simple to use, the approach is not robust. Conclusions are sensitive to the choice of model and estimator [35]. Currently, the best approach appears to be to fit a non-parametric model to the time series, then estimate the largest Lyapunov exponent using that model [39].

Stochastic growth models and variable environments

All the models in the previous sections are deterministic: two populations with exactly the same vital rates and initial conditions will have exactly the same $N(t)$ at any time, t . A deterministic model assumes no random variability in the population growth. This assumption may be violated in three different ways: uncertainty, demographic stochasticity, and environmental stochasticity. Uncertainty is the sampling variation arising from parameter estimation. Demographic stochasticity [48] is the variation arising because birth and death are discrete random events that happen to individuals. A small population (e.g. $N=10$) with a growth rate, $\lambda, > 1$ may still go extinct if it experiences by chance a few years of lower than expected births or higher than expected deaths. Demographic stochasticity can be modelled by a stochastic process (e.g. a stochastic birth-death process) or by including discrete event distributions in a model.

Environmental stochasticity is the variation arising because demographic parameters are not constant. This variation can be included in a model either as an extra random component to the change in population size (e.g. a stochastic differential equation [12]) or as random changes to the vital rates (e.g. a stochastic matrix model). The most commonly used approach is some form of stochastic matrix model for a structured population. These models can be setup as a random coefficient model, a mega-matrix model, or a random sequence of matrices [36]. In the random coefficient approach, each coefficient in the transition matrix, A , is considered a random variable and given a distribution [11]. Pairs of coefficients are usually considered to be independent because of insufficient data to estimate all the correlations. In the mega-matrix approach, the transition matrix is expanded to describe transitions between each combination of age- or size-stage and environment [22]. Because this approach includes different environments in the transition matrix, it models population dynamics in an ensemble of patches with different environments.

In the random sequence of matrices approach, the environment is assumed to vary between a fixed number of unique states, each with a population transition matrix [54]. For example, random year-year variation can be modelled by considering each year-to-year transition as one environmental state and transition matrix [15]. A random sequence of environments (and corresponding sequence of transition matrices) is modelled by a Markov chain. One important consequence of environmental variation is that stochasticity reduces the average population growth rate [54].

One application of stochastic population models is to estimate extinction probabilities, i.e., under a specific set of conditions, what is the probability that $N(t) = 0$ at any time in the future. Such information can aid the evaluation of conservation priorities and management decisions. Conditional on estimates of the vital rates, the extinction probability and expected time to extinction can be calculated analytically for stochastic birth-death processes [25] and estimated by simulation for the other stochastic models. Estimates of extinction probability are often sensitive to the choice of the vital rates, which are uncertain. Uncertainty in the vital rates can be incorporated using Bayesian methods [29].

OTHER MODELS

The models discussed up to now describe the dynamics of a single species in an isolated population. Real populations exist in an environment that includes other species and other populations of the target species.

Multispecies models

Models for multiple species are usually constructed from pairwise interactions between species. These interactions are one of three general types: competition (both species negatively affected), predation (one species, the prey, negatively affected, but the other, the predator, positively affected), and mutualism (both species positively affected). Each type of interaction has different consequences for the population dynamics. At equilibrium, multiple species may coexist, one species may drive all or most of the others extinct, or abundances may oscillate in stable limit cycles [23]. In particular, the abundances of boreal mammals (e.g., lemmings, snowshoe hares, lynx, and foxes) have fluctuated in semi-regular cycles for many generations. Predator-prey dynamics are suspected of contributing to these cycles, although their ecological causes remain contentious. Mathematical analysis of multi-species models focuses on estimating the equilibrium dynamics for a species model and parameters.

Estimating the parameters that describe competitive or predator-prey effects is the major statistical issue in multi-species models. Sometimes, coefficients describing interactions between species are estimated from experimental manipulations of density. More commonly, they are estimated from time series of observed abundance of each species. Some form of regression (linear or non-linear, depending on the mathematical model) [18, 24] or time series model (multivariate or non-linear) [20] is used, but the details vary for each study.

Spatial models

The models in the previous sections generally assume that populations are isolated (no immigration and emigration) and considered in isolation (the dynamics of a population can be understood without knowledge of the dynamics in nearby populations). Most biological populations do not exist in isolation; instead they occur as patches in a spatial landscape. The spatial structure can be described with a variety of statistics (e.g. the variogram, nearest neighbor methods, or Ripley's K statistic).

The consequences of spatial dependence between local populations includes three related, but different, sorts of biological questions and models. One set of questions concern the synchrony of local population dynamics across large areas. A second set concern the dynamics in a metapopulation (a collection of local populations connected by dispersal). The last set concern the dynamics of a single spatially distributed population.

When abundances in a local population fluctuate in semi-regular cycles, it is natural to ask whether or not nearby populations fluctuate in synchrony [4]. Synchrony can arise by dispersal of individuals between local populations or from spatially correlated environmental change (the Moran effect). The magnitude and spatial

scale of spatial synchrony can be estimated using spatial cross-correlation functions [4].

A metapopulation is a collection of local populations connected by dispersal [19]. The dynamics and persistence of a metapopulation can be quite different from those of any local population because a local population that goes extinct can be reestablished by dispersal. Metapopulation models are commonly used when the occupiable habitat occurs in discrete patches surrounded by unusable habitat (e.g., a collection of islands). Since immigration and extinction rates are usually small, direct estimation of them is difficult. They can be estimated indirectly, if it is possible to enumerate presence or absence of the species on a network of patches [19, 33].

When the occupiable habitat is continuous, the population may be considered as a single spatially distribution population. The dynamics that are observed at any arbitrarily chosen spot depend on both local conditions and the dynamics at nearby locations [28]. Although mathematically more complicated than single population models, space-time models can be used to model the spread of invading species into new habitat or to combine information from spatial replicates to better estimate demographic parameters [28].

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