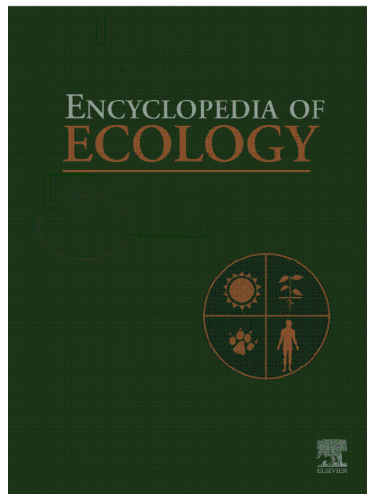


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Terrestrial Arthropods

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Introduction

Density-Independent Effects

Density-Dependent Effects

Cyclic Population Dynamics

Anthropogenic Effects on Arthropod Population Dynamics

Models of Arthropod Population Dynamics

Local Extinction and Metapopulation Dynamics

Summary

Further Reading

Introduction

The term population dynamics refers to the variation in time and space in the size and density of populations. The dynamics of any population are driven by a combination of density-dependent and density-independent processes. Density-dependent processes are those that intensify or decrease with increasing population size, such as competition for food or space. Density-independent processes are those that occur at the same intensity regardless of population size, such as with weather conditions. In this article, we will discuss how terrestrial arthropod populations vary in response to density-dependent and -independent processes. Special cases of distinct arthropod dynamics are given, such as with periodic cicadas, and Lepidoptera populations that show distinct cyclic dynamics. We will give examples of how humans have modified arthropod population dynamics, through the use of pesticides or biological control agents. Finally, we will describe several models that predict arthropod population dynamics.

Density-Independent Effects

Climate is a key density-independent process for most arthropod populations. All species have specific environmental requirements and reach greater population sizes when these conditions are met. For example, annual variation in climate explained 78% of variation in the densities of apple blossom thrips (*Thrips imagines*) feeding on rose blossoms. Thrip densities were highest in summer, but the size of summer peaks differs from year to year (Figure 1a). Differences between summer peaks were correlated with annual changes in temperature and precipitation. Years with greater winter temperatures and higher spring precipitation produce greater numbers of thrips, perhaps because these climatic conditions favor the growth of roses. Disturbances, such as landslides, tsunamis, and fire can also have density-independent effects on arthropod numbers. Most disturbances cause sharp declines in arthropod densities, though some have positive effects on population dynamics. For example, the larvae of buprestid beetles in the genus *Melanophila* forage

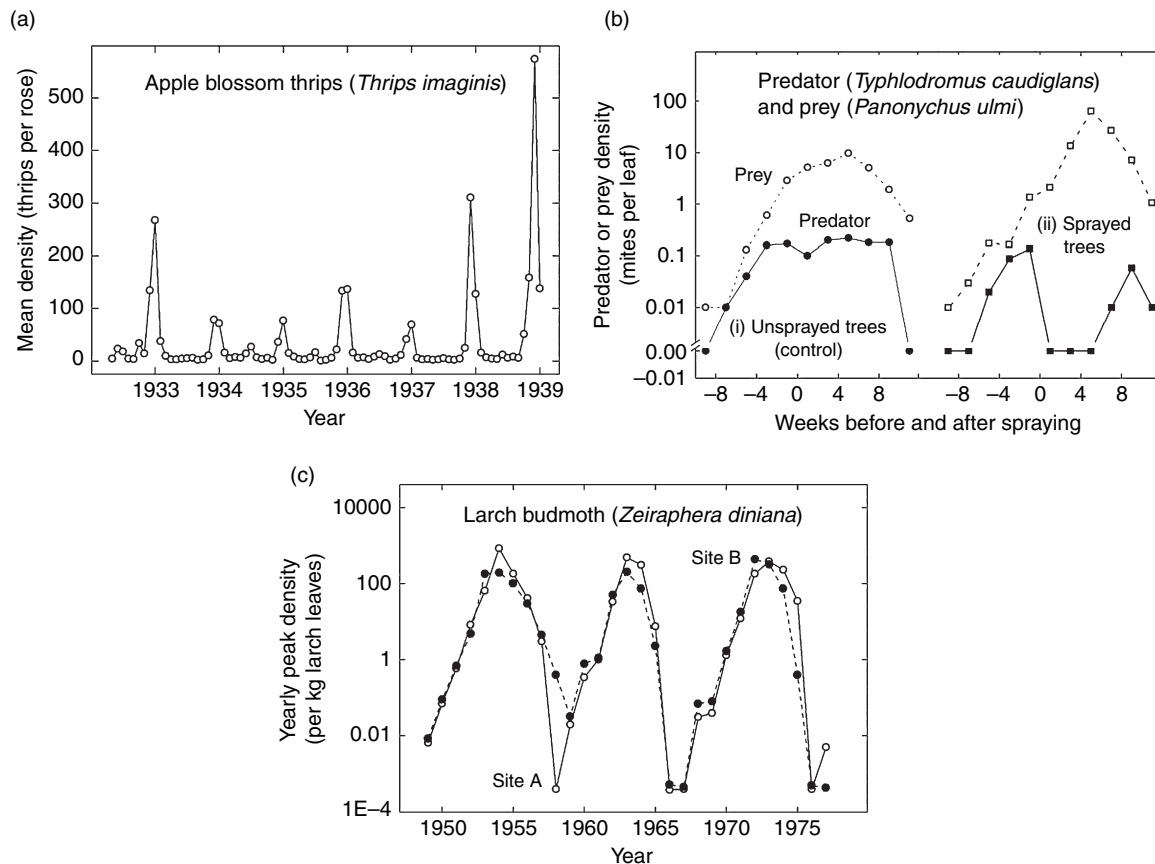


Figure 1 Examples of arthropod population dynamics. (a) Average monthly densities of apple bloom thrips (*Thrips imaginis*) on roses in Adelaide, Australia. The size of the peak densities in November or December each year appear to be driven by climatic conditions. (b) An example of pesticide-disrupted biological control. On unsprayed or control trees, predators limit prey to under 10 mites per leaf. The application of a broad-spectrum pesticide reduces predator densities to undetectable levels and results in prey densities that are of an order of magnitude higher than controls. (c) Yearly peak densities of the larch budmoth in the Engadine Valley of Switzerland. Data are shown for two sites (solid or open symbols). Population densities cycle by 6 orders of magnitude every 9 or 10 years. (a) Data adapted from Davidson J and Andrewartha HG (1948) Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). *The Journal of Animal Ecology* 17(2): 193–199, with permission from Blackwell. (b) Data from Lester PJ, Thistlewood HMA, Harmsen R (1998) The effects of refuge size and number on acarine predator–prey dynamics in a pesticide-disturbed apple orchard. *The Journal of Applied Ecology* 35(2): 323–331, with permission from Wiley-Blackwell. (c) Data adapted from Myers JH (1988) Can a general hypothesis explain population cycles of forest Lepidoptera? *Advances in Ecological Research* 18: 179–242, with permission from Elsevier.

on burnt trees and adult beetles may travel as far as 100 km to find smoldering trees for oviposition. Therefore, the occurrence of forest fires, or lack thereof, can substantially influence the size of *Melanophila* populations.

Environmental variability often results in chaotic population dynamics, or spatially and temporally irregular population fluctuations. Periods of cold weather retard population growth and may cause high mortality rates, and long periods of optimal weather can promote sustained periods of population growth and outbreaks. Under these conditions populations may still fluctuate around some equilibrium density, but often in an unpredictable fashion. Stochastic weather events that create variation in densities across landscapes are likely to enable weaker competitors to coexist. Some ecologists suggest that stochasticity plays an essential role in the dynamics

of all species and we cannot hope to understand population dynamics without explicit consideration of random fluctuations.

Density-Dependent Effects

Density-dependent processes are those that intensify with total population size. For example, death rates are density-dependent if the probability an individual will die increases with the number of co-occurring individuals. Death rates can also be inversely density dependent, if they decrease with population size. For example, animals that live in groups for protection against predators often have inversely density-dependent mortality rates. Examples include species of tent caterpillars

(e.g., *Malacosoma americanum*) that live socially and build silken enclosures that offers some degree of protection from natural enemies.

Predation and parasitism often limit arthropod populations in a density-dependent fashion, and this form of density dependence forms the basis of most biological control programs. The efficacy of biological control is most clearly observed when predators disappear from the environment, such as in situations where prey evolve resistance to the pesticides but predators remain susceptible (Figure 1b). Competition, both within species (intraspecific) and between species (interspecific), can limit food availability and regulate populations in a density-dependent fashion. For example, many ants in North American deserts compete with mice for seeds. When mice are experimentally removed from an area, ant numbers boom, presumably because seed resources normally consumed by mice become available. In addition to food quantity, food quality can also be important, such as with chemical defenses of plants which can adversely affect herbivorous arthropods. This type of effect can also be density dependent, as the actions of herbivores can induce the production of defensive chemicals.

Unlike mammals, some insects are capable of producing different types of dispersal morphologies to increase their capability to colonize new locales. These dispersal polymorphisms can have huge implications to population dynamics. For example, aphids develop alate (winged forms) when high densities of conspecifics lower food concentrations.

Processes limiting arthropod numbers can also decrease with population size, or be inversely density dependent. Bark beetle mortality rates are a good example of inverse density dependence. The natural defenses of trees such as the lodgepole pine (*Pinus contorta*) can eat, repel, and kill one, ten, or even hundreds of the mountain pine beetle (*Dendroctonus ponderosae*). However, thousands of beetles can overwhelm the tree's defenses, resulting in a much lower per capita mortality rate.

For many species, both density-dependent and density-independent factors simultaneously influence population dynamics. Damage to lodgepole pine trees in Canada by the mountain pine beetle is a good example; while their ability to overwhelm trees is density dependent, mild winters result in large outbreaks of beetles and widespread tree mortality. Tree mortality in turn results in density-dependent beetle mortality as the availability of suitable trees declines. To estimate the relative contribution of such factors to the overall population dynamics, key factor analysis is often used. Key factor analysis utilizes life tables, which are produced to identify life-history stages that are most limiting to population growth. To construct a life table, a cohort of individuals are followed through time and gains and losses of individuals at different life-history stages are quantified. After

Table 1 Factors involved with the population regulation and population dynamics of arthropods

Exogenous (extrinsic)

1. Density-independent factors
 - (a) Weather
 - (b) Random changes
2. Density-dependent factors
 - (a) Predation/ parasitism
 - (b) Food
 - (c) Combination of predators and food
 - (d) Space or favorable habitats
3. Intermediate between 1 and 2
 - (a) Imperfect density dependence

Endogenous (intrinsic; all probably density dependent)

1. Pathological effects due to crowding
 - (a) Shock disease
 - (b) Adrenopituitary exhaustion
2. Processes with a genetic component
 - (a) Aggressive behavior or increase in congenitally less-viable individuals
 - (b) Genetic breakdown of populations during a flush phase
 - (c) Polymorphic behavior in dispersal
 - (d) Changes in developmental times
 - (e) Genetic feedback
3. Social interaction
 - (a) Evolution of social checks on populations
 - (b) Intraspecific competition
 - (c) Aggressive behavior
4. Dispersal
 - (a) The adaptive nature of dispersal
 - (b) Density-regulated dispersal

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summarizing this information in a life table, it is possible to determine the primary or 'key' factors limiting population densities. For example, success in adult dispersal has been noted as a key factor limiting populations of the Colorado potato beetle, as all other life-history stages have a low impact of survivorship. However, key factor analysis is likely to be spatially and temporally specific. Adult dispersion may limit the abundance of Colorado potato beetles (*Leptinotarsa decemlineata*) in one area and time, but not at other times and places. The factors limiting arthropod populations are by no means restricted to those listed above. Climate, disturbances, predators, parasitoids, pathogens, food availability, and dispersal polymorphisms frequently limit population sizes. However, other processes can be equally important. Table 1 provides a more comprehensive list of these processes, although further research will undoubtedly uncover new processes.

Cyclic Population Dynamics

Cyclic population dynamics resulting from delayed density dependence occur when there is a delay between a change in population density and the effects of a

density-dependent process. For example, many North American moth species exhibit population cycles with an average periodicity of between 8 and 11 years (Figure 1c). Cyclic population dynamics have been documented in 18 moth species, but it is likely that more exhibit such cycles, perhaps 1–2% of forest Lepidoptera species. Several hypotheses have been proposed to explain these cycles, including (1) variation in insect quality hypothesis, which includes ideas about genetic and behavioral variation; (2) the climatic release hypothesis; (3) the food quality deterioration hypothesis, which involves induced plant defenses; (4) the food quality improvement hypothesis or plant stress hypothesis; and (5) the disease susceptibility hypothesis. The commonality of these hypotheses is delayed density dependence, resulting from annual variation in food supply or disease susceptibility. A key aspect of delayed density dependence is overcompensation, which occurs when a population grows larger than its carrying capacity. If overcompensation does not occur, population densities will reach equilibrium without oscillating. If density dependence is overcompensating, population cycles will develop because the processes limiting population growth have a delayed effect on population size. Populations that exhibit overcompensation often undergo stable limit cycles, with a fixed interval and amplitude, such as the larch budmoth which has a population cycle of approximately 9 or 10 years between peak densities (Figure 1c). Higher levels of overcompensation can lead to chaotic fluctuations in densities without fixed interval or amplitude.

Predators or other natural enemies can also generate cyclic population dynamics through evolutionary means. One of the most striking life-history patterns that appears to have evolved to limit the impact of predators is with the 'periodic cicadas'. In North America, there are seven species of periodic cicadas that belong to the genus *Magicicada*. Four of these species have 13-year life cycles, while three have 17-year cycles. Nearly all of the periodical cicadas in a specific location will emerge in mass in the same year, resulting in densities as high as 1.5 million per acre. Such a massive adult density ensures that any predators present will quickly become satiated, but as the cicadas are only present every 13 or 17 years, predators cannot build up sufficient numbers to have any major effect on population dynamics of adult cicadas (Figure 2).

Anthropogenic Effects on Arthropod Population Dynamics

Much of our knowledge on arthropod population dynamics has its roots in agricultural entomology and specifically the need to control insect pests. Large numbers of specialist herbivore species may congregate in cropping systems because they represent a large concentration of

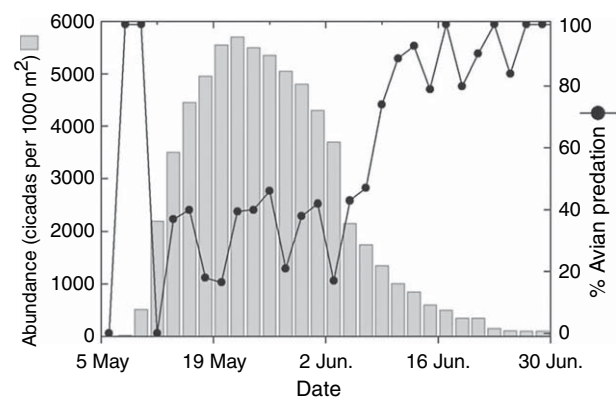


Figure 2 Relative magnitude of avian predation as a source of mortality of adult periodical cicadas in White River, Arkansas, during 1985. Data adapted from Williams KS, Smith KG, and Stephen FM (1993) Emergence of 13-year periodical cicadas (*Cicadidae: Magicicada*): Phenology, mortality, and predator satiation. *Ecology* 74: 1143–1152, with permission from Ecological society of America.

resources (~Root's resource concentration hypothesis). Such monocultures may also have a reduced insect diversity compared to native plant communities, leading to a relative reduction in the number of generalist predators attacking herbivores in monocultures (~Root's natural enemies hypothesis). Human selection of varieties with fewer toxic defense chemicals, such as glucosinolates, can also result in higher arthropod survival and reproductive rates. Consequently, over the last century we have heavily relied on chemicals for the control of insect pests. However, the use of pesticides and in particular broad-spectrum chemicals have also resulted in insect outbreaks.

Many insect pests quickly develop resistance to pesticides, though such resistance development in natural enemies is much rarer and develops more slowly. For example, resistance to new pesticides may take as little as four generations to develop in the Colorado potato beetle. Broad-spectrum pesticides may have little direct effect on pests after they develop resistance, but may have a large indirect effect as the pests' natural enemies are killed by the pesticide. A 'pest resurgence' can then occur, to much higher densities than were observed prior to the pesticide application. Due to broad-spectrum pesticides killing the natural enemies of a variety of arthropod pests, 'secondary pest outbreaks' can also occur after pesticide application. The population dynamics represented on Figure 1b are a good example of a secondary pest outbreak, where a pyrethroid pesticide was applied for the control of oriental fruit moth (*Grapholita molesta*). The pesticide also killed populations of a phytoseiid predatory mite (*Typhlodromus caudiglans*), releasing a phytophagous mite (*Panonychus ulmi*) from biological control.

Models of Arthropod Population Dynamics

Models are defined as 'an imitation and representation of the real world'. Early models of predator–prey dynamics include the Lotka–Volterra model and the Nicholson–Bailey model of predator–prey interactions. (see Prey–Predator Models). These models deal specifically with biotic interactions. Because insect populations are heavily influenced by abiotic factors such as temperature, 'degree–day models' are often used to predict arthropod population dynamics. Within suitable limits, higher temperatures generally result in more rapid development. In many cases, the tradeoff between temperature and duration of development can be modeled by a cumulative degree–day model, also known as the law of total effective temperature. In these models a threshold temperature and a thermal constant are defined so as to portray the metabolic and developmental equivalence of a long time spent a few degrees above the threshold, compared to a much shorter time at considerably higher temperatures. The range of temperatures over which this 'law' holds true generally encompasses typical field conditions; therefore the relationship can be a useful component of models used to predict the timing of pest outbreaks or the geographical limits of an insect's distribution. Such a model

predicting the spatial distribution of Argentine ants (*Linepithema humile*) in New Zealand is shown in **Figure 3**.

Key factor analyses are another class of models incorporating biotic and abiotic factors. Such analyses have been discussed above, but essentially are a statistical analysis of population demographics designed to identify factors responsible for a change in population size. Another similar approach is via *k*-factor analysis. *k*-factor analysis relates age-specific mortalities (*k*-values) with total mortality (*K*) for a number of generations in order to identify, by correlation analysis or inspection, which factor is most closely similar in temporal pattern to that of total mortality. These analyses are restricted by the limited power of regression analyses, and do not necessarily indicate the underlying mechanisms and factors governing the control of population dynamics. However, such models can be enlightening. For example, key factor analysis has been used to accurately predict the population dynamics of the winter moth (*Operophtera brumata*).

Several models of arthropod population dynamics have been developed to incorporate steady states or equilibrium densities, as well as outbreak dynamics as described above. An important step towards a general model of population dynamics is Southwood, and Southwood & Commins synoptic population model.

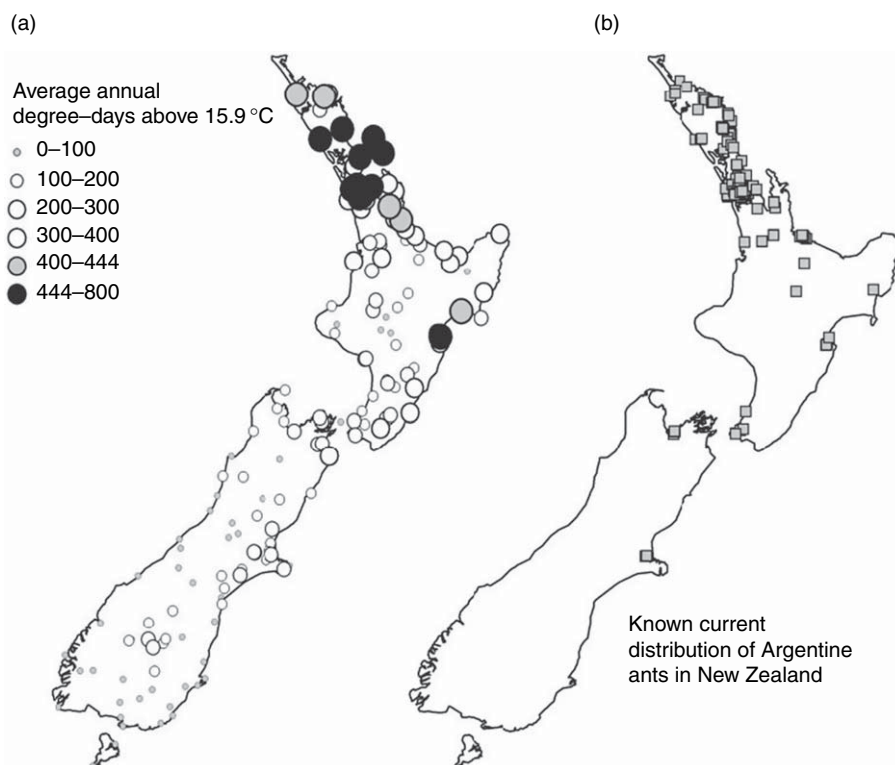


Figure 3 A degree–day model predicting the distribution of Argentine ants (*Linepithema humile*) in New Zealand, which suggested that complete development, from egg to worker, requires approximately 445 degree–days above a threshold of 15.9°C. In sites with < 445 degree–days, these ants are not predicted to persist. (a) Sites in New Zealand specific numbers of degree–days. (b) The current distribution of Argentine ants in New Zealand. Adapted from Hartley S and Lester PJ (2003) Temperature-dependent development of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): A degree–day model with implications for range limits in New Zealand. *New Zealand Entomologist* 26: 91–100, with permission from New Zealand Entomologist.

Three key aspects of life history are considered. First, natality, which is limited at low densities because mates are hard to find, then increases with increasing densities until intraspecific competition causes the population to decline. Second, the impact of natural enemies is assumed to increase with increasing prey density but then declines as populations escape from this limiting factor. Finally, intraspecific competition, disease, and emigration all increase with increasing herbivore density producing additional mortality to the above effects of natality. When combined, these factors interact to produce dramatic

changes in population dynamics at different densities (Figure 4). Extinction is predicted to be likely when populations are at low densities when population growth is low. Populations then increase until natural enemies become effective and a stable equilibria is reached. Upon extremely favorable climatic conditions or the disruption of natural enemies, the population is 'released' until an upper equilibrium point is reached due to the stabilizing effect of factors such as intraspecific competition. However, disease and a shortage of food may result in massive mortality and a much reduced natality, causing the population to crash to

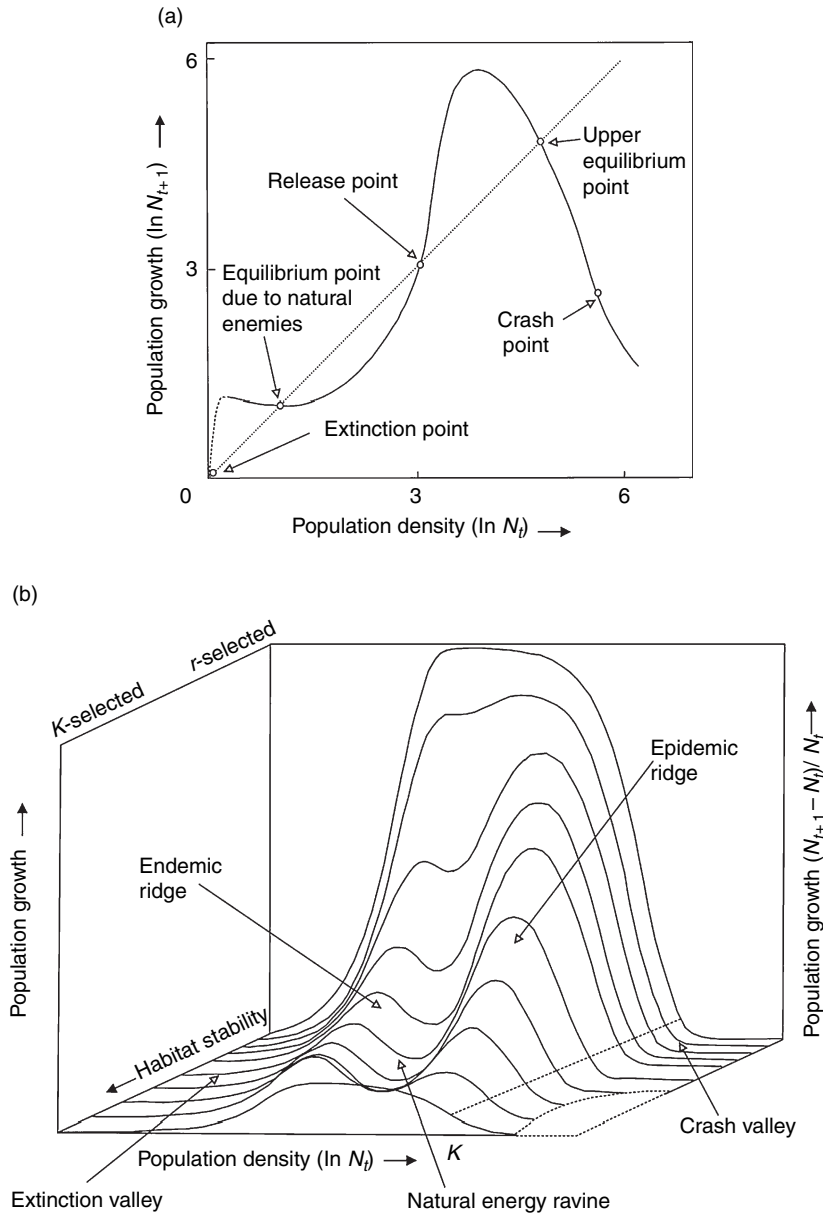


Figure 4 The synoptic population model. (a) Population growth ('Ricker-type') curves representing the synoptic population model applied to the eucalyptus psyllid *Cardiaspina albitextura*. The 45° represents no change between the two generations. In this system, natural enemies were important at endemic levels, while intraspecific competition (destruction of host-tree foliage and reduction of fecundity) acted at epidemic levels. (b) This model incorporates the population dynamics as a landscape along the axes of population growth, population density, and habitat stability. Reproduced from Southwood TRE and Comins HN (1976) A synoptic population model. *Journal of Animal Ecology* 45: 949–965, with permission from Wiley-Blackwell.

a density below the release point. Such a scenario is represented for the eucalyptus psyllid (*Cardiaspina albiflora*) (Figure 4a). The synoptic model incorporates the range of life-history types from r - to K -selected species. The r -selected species quickly colonize new resources and have a fast reproductive rate, often escaping the limiting effects of natural enemies. In contrast, K -selected species have slow reproductive and colonization rates. These K -selected species less frequently escape natural enemies, which increase to outbreak population dynamics much less frequently (Figure 4b).

Catastrophe theory has also been used to model outbreak dynamics of terrestrial arthropod populations. A catastrophe can be defined as the loss of stability in a dynamic system. Specifically, catastrophe theory examines the specific conditions in which discontinuous behavior can arise from underlying smooth potential, or in this case, population dynamics. There are several types of catastrophe models, depending on the number of 'control' (e.g., age of host trees, temperature, or rainfall) and behavior (e.g., the densities of an insect) dimensions. The three-dimensional (3D) 'cusp' catastrophe model with two control and one behavior variables is the most widely used in biology. The simplest being the 2D 'fold' catastrophe, which deals with one control and one behavior variable. A 2D representation of a catastrophe model is represented in Figure 5, specifically in regard to spruce budworm (*Choristoneura fumiferana*) densities. In these models, the single control variable is the average age of the host trees. As the average age of the trees increases, so does the abundance of budworm. However, there is a critical point at which an unstable equilibrium is reached. This unstable equilibria may encompass a range of densities: for example, in the spruce budworm, the unstable equilibria range between average tree ages ~ 38 to 75 years

old. Within that range, an outbreak may or may not occur. An ensured dramatic return to endemic population is only observed if there is a decrease of average tree age (<38), through host tree death or other means. Similarly, an outbreak to high densities is only predicted with any degree of certainty for trees >75 years of age.

Although catastrophe models have been used to model the dynamics of other arthropod populations including rangeland grasshoppers, authors have considered such modeling approaches too simplistic. More specific and complex modeling approaches have been developed, including models incorporating a spatial component. These spatial population models can be classified into three categories: diffusion models, cellular automata, and metapopulation models. All of these will be dealt with in another article (see Spatial Distribution Models), although aspects of metapopulation dynamics are worthy of mention here.

Local Extinction and Metapopulation Dynamics

Population dynamics are often visualized by assuming that individuals live in a single locale isolated from other populations. However, this is rarely the case and individuals of many arthropod species migrate between spatially isolated patches of suitable habitat. Populations inhabiting spatially segregated habitat patches can also go locally extinct, and these patches are subsequently colonized by future immigrants. This way of conceptualizing population dynamics is known as metapopulation dynamics. The key concept here is that different populations within the metapopulation are connected by dispersal but are undergoing different dynamics, but are connected by dispersal. Nevertheless, the density-independent and

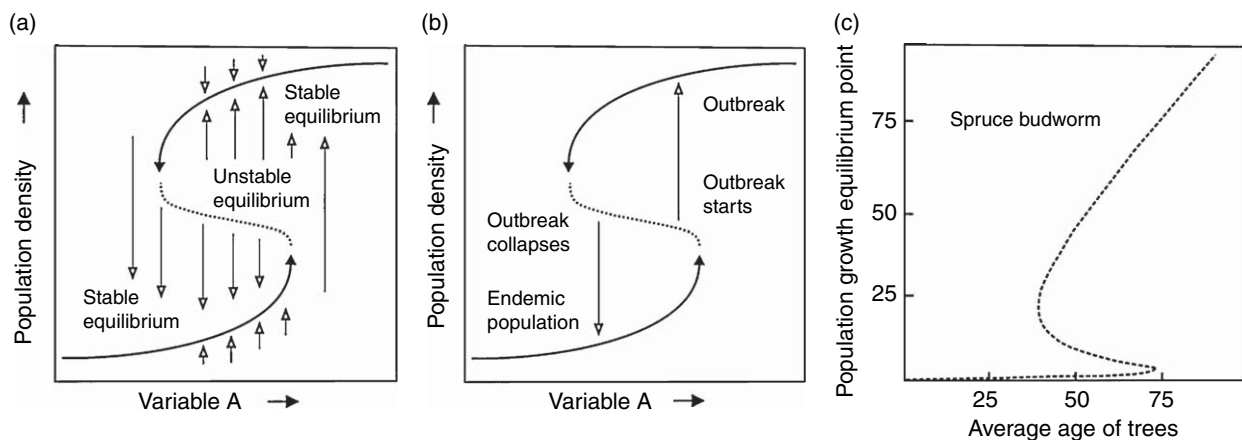


Figure 5 Catastrophe theory as applied to insect population dynamics. (a and b) Population dynamics are described as a limit cycle that includes two periods of slow change and two periods of fast change. Transition to a fast process, or an outbreak, is a catastrophe. (c) Catastrophe theory applied to the population dynamics of spruce budworm (*Choristoneura fumiferana*) with parameters for the model described within the text. Data adapted from Casti J (1982) Catastrophes, control and the inevitability of spruce budworm outbreaks. *Ecological Modelling* 14: 293–300, with permission from Elsevier.

density-dependent dichotomy described earlier may still be important and play a major role in the fluctuations and persistence of the metapopulation. The full role of metapopulation dynamics is discussed in another article (see Metapopulation Models).

Summary

Probably all terrestrial arthropod populations are influenced by a combination of both density-dependent (e.g., death rates) and density-independent (e.g., climatic factors) processes. However, the relative role of each process type in influencing population dynamics will vary both spatially and temporally over the life history of the arthropod. Models such as the synoptic population model, catastrophe theory, or degree-day models may enable the broad prediction of arthropod population dynamics and are especially useful with arthropods as their ectothermic life-history patterns often reflect environmental conditions. However, it is becoming increasingly recognized that while population models may enable us to predict much of the variation in population dynamics, stochastic influences or random variation in aspects such as natural enemy abundance also play a role. These processes are likely to be contributing factors to both population outbreaks and the persistence, or even extinction, of small populations.

See also: Cycling and Cycling Indices; Death; Metapopulation Models; Parasites; Predation; Recruitment; Resilience; Stability; Temperature Regulation.

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The Significance of O₂ for Biology

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History of O₂ on Earth
 PSII and the Generation of O₂
 The Reactive Properties of Oxygen
 Cytochrome c Oxidase
 Alternative Oxidase

Plastid Terminal Oxidase
 RuBisCO
 Metabolic Consumption of O₂
 Final Comments
 Further Reading

History of O₂ on Earth

The early life on Earth was initially populated by archaean microorganisms that lived in the absence of significant amounts of O₂. These organisms survived

during a period of anaerobiosis that lasted for ~1 billion years during which much of the fundamental metabolic biochemical pathways were established. About 2.2–2.5 billion years ago, the Earth entered a transition period where O₂ began to accumulate. Initially the majority of