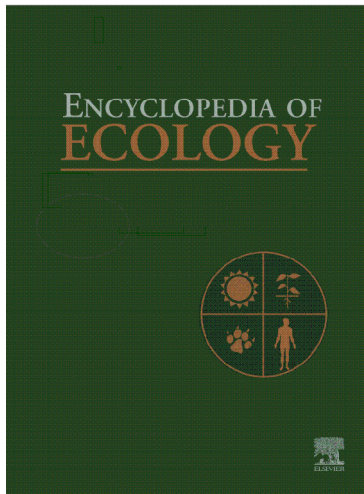


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Most existing contaminated sites are the result of historical rather than current emissions, arising from a time when there were fewer environmental controls.

Future work on dioxin ecotoxicology needs to take into account the effects of bioaccumulation of dioxins from the physical environment and from food. As with general toxicity, bioaccumulation appears to be low for congeners with fewer than four chlorine atoms or greater than six, because of rapid metabolism or elimination of sparingly chlorinated forms and poor bioavailability or cell membrane permeability of highly chlorinated forms. Similarly, only congeners with four to six chlorine atoms appear to biomagnify up the food chain.

See also: Trophic Structure.

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Dispersal-Migration

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Introduction

Dispersal, or the movement and subsequent breeding of individuals from one area to another, strongly influences the population dynamics of a species. Dispersal can help

regulate population size and density; many animals, such as aphids and female root voles, have increased dispersal rates under high density situations. Sometimes low density instead of high density is associated with greater dispersal rates. For example, during range expansions,

peripheral populations of some grasshoppers may experience higher dispersal rates though they are of lower density than central populations, probably because of fitness costs associated with morphologies specialized for dispersal.

Such dispersal events can have large effects on neighboring populations. Marginal populations that are subject to high rates of immigration may experience a rescue effect, where despite poor genetic or ecological conditions, populations are able to persist. On the other hand, high dispersal rates can inhibit adaptation to novel environments due to constant influx of nonadapted individuals. Small populations that experience high rates of emigration may have a higher probability of extinction under such situations.

Natural populations in highly fragmented areas, such as agricultural or urbanized settings, may not experience sufficient levels of dispersal. Lack of dispersal can lead to high rates of inbreeding, which can lead to decreased fitness in many species. Because dispersal can have such strong effects on populations, dispersal patterns and processes are important when considering the potential spread of a biocontrol agent, pathogen, or invasive species into a new range. Dispersal also has implications for species redistributions due to climate change, as the dispersal rates and distances of a species will affect its potential to shift its range in response to climate change.

Two types of dispersal are commonly distinguished: natal dispersal, which is movement and subsequent breeding away from the birth territory or area, and breeding dispersal, which is movement from one area to another after the first breeding season. Dispersal of spores, or haploid life stages (such as pollen), strongly affects patterns of gene flow in a species, but the process is not generally considered to be directly associated with population dynamics. Dispersal in plants is generally limited to natal dispersal, as little to no secondary movement is possible, while many animals disperse multiple times.

All species disperse to some extent, in part because resources become limited locally as populations grow. Seedlings of plants must grow at some distance from the parent plant in order to obtain enough water, nutrients, and light to survive. Similarly, animals must disperse to avoid competing for resources such as mates, food, and territory. Depending on intraspecific patterns of resource limitation, dispersal is often sex-biased. In mammals, females tend to disperse more often than males; the trend is reversed in birds.

In areas with high temporal environmental variation, or in areas prone to frequent disturbances, species with greater dispersal abilities are expected to have a greater likelihood of survival. When one population's habitat is rendered untenable, if the species has a high dispersal

rate, many individuals in that population will be able to move to a more suitable area. In the case of nonmotile organisms such as plants, high dispersal rates increase the likelihood that another population may be established even as the original population is rendered extinct. When studying populations that specialize in habitats with high temporal environmental variation, it is sometimes appropriate to distinguish between spatial and temporal dispersal. For example, many animals and plants that live in deserts with unpredictable rainfall will produce desiccation-resistant embryos that delay maturity until favorable environmental conditions cue further development. Instead of traveling long distances to reach suitable habitat, the individuals produce offspring that are able to lie dormant until the habitat is once again suitable for survival and reproduction. Because dispersal can enable escape from low-quality environments and access to higher-quality resources, many species that specialize in colonizing disturbed areas tend to have greater dispersal abilities than species that live in relatively stable habitats.

In some cases, dispersal can have a high cost associated with it, especially if individuals that disperse experience a higher mortality rate than those that do not disperse, or that disperse only a short distance. Because individuals are moving to an area that may not be as productive, and because they may have to travel through unsuitable habitats, mortality rates during the dispersal process may be high. The number of individuals that successfully establish in a new area may be far fewer than the number of individuals engaging in the dispersal process. In plants and other organisms with no choice involved in the dispersal process (passive dispersal), many propagules may never establish simply because they land in an unsuitable habitat. In animals where some choice may be involved in the final dispersal location (active dispersal), survival of dispersing individuals may be higher than individuals of species with passive dispersal, but there are still risks associated with dispersal, such as locating an appropriate territory, finding a mate, and successfully breeding in the new area. However, the benefits of dispersal can overcome the costs if mates and/or resources are limiting in the home range.

The process of dispersal is not necessarily as simple as suggested above, as it involves both emigration (leaving the original patch) and immigration (entering a new patch). The entire process of dispersal can be divided into approximately four different stages: (1) emigration, (2) exploring or traveling through the surrounding habitat, (3) immigrating to a different patch, and (4) successfully breeding in the new patch. Each of these stages has a cost involved. Leaving the original patch involves leaving an area where resources are known to exist, but may have become limiting. The exploratory phase of dispersal can

involve a high risk of mortality, as the individual may have to travel through territories with inadequate resources. In many plants and other passive dispersers, the exploratory phase entails a high rate of mortality, as seeds often land in areas unsuitable for growth. Even when a propagule successfully disperses to a hospitable environment, it may not be able to establish there, due to mortality rates associated with establishment. The risks involved with emigration, exploratory movement, and settling in a new patch can be outweighed by the potential benefits of dispersal if successful dispersal significantly increases the fitness of the individual.

There are varying degrees of active and passive dispersal, with many species exhibiting intermediate levels of participation in the dispersal process. In many animals, dispersal is active, involving a high level of choice during the dispersal process. In passive dispersal, there is little or no choice involved in selection of the final location. In many insects, many marine animals, and all plants, dispersal is largely passive, depending on air currents, water currents, or on the actions of vectors transporting the propagule. Larvae of many marine animals are often dispersed solely at the whims of the currents or in ship ballast. Insects are often at the mercy of the wind when entering a dispersal phase, especially if they cannot generate enough speed to overcome wind velocities. However, even dispersal of small insects need not be completely passive. Small insects, even if they are not large enough to overcome wind velocity, can have some level of choice as to where they land. They can begin exiting a wind stream when they decide to settle, then make short, self-powered trips to explore the surrounding area and find a suitable habitat.

Though considered passive dispersers, plants can regulate dispersal to some extent. Seed size, shape, and seed coat construction vary among species. Seed morphologies that aid dispersal include barbs (for attaching to animals), eliasomes (for attracting ants as dispersal vectors), or pappus scales (to assist in wind transport). However, because the seed itself is not actively involved in the decision process, it is still a passive process.

A species with little innate dispersal ability may be able to move greater distances and have higher survival than expected if it has the ability to be spread by a vector, such as ants, birds, or other animals. Plants commonly use vector-assisted dispersal, and there are many instances of adaptations by plants to use animals as dispersal agents. For example, mistletoe seeds are eaten by birds which then fly to another tree. The seeds are adapted to survive the digestive tract, and are subsequently deposited on the tree where the bird lands, which is usually a suitable tree for growth. Such assisted dispersal can lead to dispersal distances that would be impossible to achieve otherwise.

Most vector-associated dispersal regimes have evolved over hundreds of generations. Recently, however, many species of both plants and animals have serendipitously become associated with novel and extremely efficient dispersal vectors. Species associated with humans have always been dispersed in concert with human movements. However, the last few generations of humans have seen an exponential increase in the rates of movement around the globe. Many terrestrial and marine species have been spread at unprecedented rates through ship ballast and packing materials. In addition, ornamental plants and agriculturally associated species are deliberately transported from one location to another by humans, at distances and rates that would be impossible for each species to accomplish under its own power. Hundreds of species involved in these accidental experiments in dispersal and evolution have benefited tremendously, becoming the world's invasive species. Species such as cheatgrass in North America, *Caulerpa taxifolia* (an alga) in the Mediterranean, and the Nile Perch in Africa have successfully outcompeted hundreds of native species, often driving them to extinction.

Dispersal Patterns

There are several terms associated with dispersal patterns. Dispersal distributions, or dispersal curves, are frequency distributions of the proportion of individuals moving different distances; dispersal kernels are probability density functions used in modeling dispersal. Because a dispersal kernel describes the probability of a seed landing within a particular region, dispersal curves can be calculated from dispersal kernels. Dispersal modeled with a simple diffusion equation (a Gaussian kernel) generates a normal distribution curve, due to the random Brownian motion assumed in such simple diffusion models. Though accurate for some species, most species appear to have leptokurtic, or long-tailed dispersal curves.

The shape of a dispersal curve drastically affects estimated rates of population expansion, with normal curves having lower expansion rates than dispersal curves with longer tails. The fatter the tail of the distribution, the greater is the speed of the range expansion. Accurately estimating the shape of the curve is important, for example, in predicting spread rates of spread of the emerald ash borer. Rates and pattern of spread are often consistent with simple diffusion; however, some infestations in Michigan do not spread via simple diffusion, but have a higher frequency of long-distance dispersal events. If all control efforts and spread rate predictions are based on simple diffusion, management programs will be unprepared for long-distance dispersal events and the efficacy of management efforts will be greatly diminished.

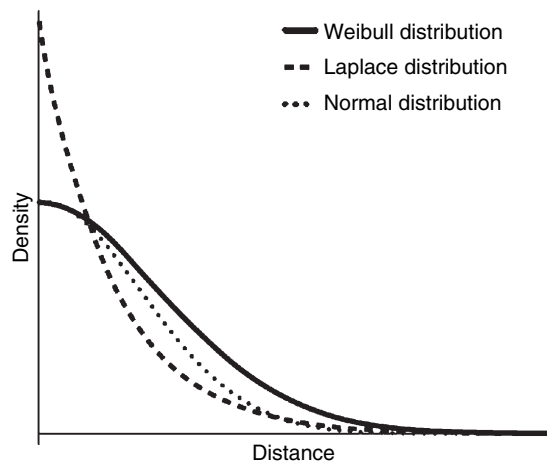


Figure 1 Normal curves are drawn in each graph for comparison. The Laplace distribution is more peaked than the normal curve, and leptokurtic. The Weibull distribution shown here has a fatter tail than both the normal and the Laplace distribution. Graphs by Hyrum Paulsen.

If the tail is exponentially bounded, as in curves with moderately fat tails (i.e., a Laplace distribution) (Figure 1), then models predict that the rate of expansion of a population will remain constant. However, in curves with unbounded tails (very fat tails, i.e., a Weibull distribution), the rate of expansion of a population can actually increase over time. Because different dispersal curves can drastically affect estimates of population expansion, it is important to choose appropriate dispersal curves when attempting to predict species' population dynamics.

Modeling Dispersal

A simple model of a species consists of one population, infinite in size, randomly mating, with no immigration or emigration. This idealized situation is never found in nature, though populations can approach this equilibrium. In real life, species are divided into populations that are subdivided to some extent, with dispersal occurring between the subdivisions at varying degrees. However, the idealized situation is often a good starting point for modeling species dispersal. Models investigating the effects of dispersal on population dynamics use several different approximations of natural situations. One of the simplest models of dispersal is a model proposed by Levins in 1969, one of the first metapopulation models (see Metapopulation Models). This model describes the colonization and extinction (see Colonization) dynamics of sites under different rates of colonization (dispersal) and mortality. An individual produces offspring which then disperse to other sites. When a propagule reaches an empty site, it occupies it completely, and any propagules reaching that same site are

subsequently eliminated. This model is termed a metapopulation model because it deals with colonization and extinction of sites. Though originally formulated as entire sites that are either colonized or not colonized, it can be viewed as a collection of sites where each site is the size of a single individual. In this way, a simple equation can be used to model the spread of a population through dispersal:

In this equation, the basis of the Levins model,

$$\frac{\partial s}{\partial t} = cs(1-s) - ms$$

s represents the proportion of sites colonized, c is the rate of propagule production, and m is the mortality rate. Though not spatially explicit, spatial relationships are implied in this model by having a proportion of sites either available or not available. Some of the assumptions this model makes are that propagules are distributed randomly, and that each propagule can occupy any space in the habitat. A proportion of sites will be filled until the population reaches an equilibrium, determined by the relationship between the rates of mortality and propagule production. The population will grow at a rate that increases with lower mortality rates and increased propagule production. As long as mortality rates are less than propagule production, the population can persist. Though extremely simplified, this model has led to some interesting predictions about population dynamics. Because the final density of individuals is dependent on mortality rate in addition to propagule production, it will be impossible for a species to occupy every suitable patch in the population's habitat. When one individual dies, the point it occupied is empty until recolonized by another propagule. Thus, the population reaches an equilibrium where a certain percentage of sites are empty, rather than completely filling the entire habitat.

Though this model yields some interesting predictions about the way population dynamics depend on propagule production and mortality rates, one of the drawbacks of this simple approximation of dispersal is that propagules in real life cannot occupy any unoccupied site in a habitat. Real dispersal is restricted in distance, with a large spatial component that is only implied in the basic Levins model. The spatial component of the model is unrealistic, being essentially infinitely large and infinitely accessible.

To observe the effects of dispersal on population dynamics in more realistic situations, greater spatial detail is required. Incorporating spatial information into a model of dispersal is relatively simple by using a cellular automaton or lattice model. This type of model does not have an explicit mathematical solution but can be evaluated through simulations that can lead to predictions about population dynamics based on certain assumptions (see Cellular Automata). In this type of model, individuals are placed on a grid of polygons. Each individual has a certain chance of mortality and of producing propagules.

A propagule can travel a certain distance away from its current position, and its direction can be determined by either having the propagule move through a side or corner of the parental polygon. The propagule can be restricted to land within a certain area or not restricted at all. Again, any propagule that lands in an occupied site is lost. Parameters in these models are relatively simple to modify, and any combination of requirements can be included. Different dispersal distribution curves, rates of long-distance dispersal, habitat extinction, propagule production rates, and mortality rates can all be included. However, more complex models will require more computational power, and they may not be as applicable to multiple species and/or situations as are more general models. One of the interesting predictions made by relatively simple cellular automaton models is that the distributions of individuals will be aggregated, even in a homogenous environment. The amount of aggregation of individuals depends on the average dispersal distance, the mortality rate, and fecundity. Some of these models have demonstrated that patchy spread is likely during population expansion simply through the stochastic nature of mortality and propagule dispersal distances. This is an important prediction, as patchiness need not be the direct result of unsuitable habitat, but instead can be merely the product of different dispersal patterns. Cellular automata models are often used in epidemiology, and have also been applied to species invasion dynamics.

Cellular automaton models are accurate if space, time, and population dynamics are best represented as discrete variables. In a species where many parameters are known, it is possible to reach a high degree of specificity in the simulations, which may be useful when trying to predict what may occur for a particular species under different scenarios. Less-specific models, though less applicable to a single species, can lead to more generalized predictions about the effects of dispersal on population dynamics.

Often, it is convenient to model a population or set of populations more generally, using mathematical equations. One such model involves a reaction-diffusion equation, describing the rate of change of the number of individuals in a population (N) over time (t):

$$\frac{\partial N}{\partial t} = rN \frac{(K-N)}{K} + D \frac{\partial^2 N}{\partial x^2}$$

This model consists of two parts: the reaction portion of the equation (which describes how the population acts in the absence of dispersal) and the diffusion portion (which is a partial differential equation that describes the movement of individuals in the population). The reaction portion can be as simple as the logistic equation for growth of a population, shown here immediately to the right of the equals sign, where r is the intrinsic rate of increase, and K is the carrying capacity. Other models of

population growth can be used as well, such as adding an Allee effect (see Allee Effects), where propagule production rate declines at a lower than expected rate at low densities (e.g., when a mate is difficult to find). The diffusion portion of the equation is usually the mathematical representation of simple passive diffusion

$$\frac{\partial}{\partial t} N(x,t) = D \frac{\partial^2 N}{\partial x^2}$$

where D is the diffusion coefficient, t is time, N is the number of individuals, and x represents space. The diffusion portion of the equation can be more complex, incorporating directional movement, changes in velocity, or interactions among individuals. Increasing complexity is not always necessary to make meaningful predictions, as the simplest version of this equation matches observations seen in mark-release-recapture studies in several animals. In models of invasion dynamics, a reaction-diffusion model produces waves of invaders that advance at a rate dependent in part on the rate of increase of the population. This type of equation is most appropriate when the environment is homogenous, all individuals have similar dispersal patterns, and reproduction/dispersal occurs constantly. Such models generally produce a smooth traveling wave front with a linear rate of spread.

To incorporate the discrete reproduction events (and hence dispersal events) frequently seen in plants and animals, it is appropriate to use an integrodifference equation. Integrals allow each moment in time to be dependent on the previous moment in time, thus incorporating discrete time intervals into the model, as opposed to differential equations, which assume that time is continuous. Integrodifference models consist of two main parts: a dispersal kernel (a function that describes the dispersal patterns of a population) and a density function.

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y)f[N_t(y)]dy$$

In this equation, $k(x-y)$ represents the dispersal kernel, or an equation that describes the movement of a propagule from the natal territory, x , to the final breeding place, y . The density function describes the density of individuals at the location y and time t . The various dispersal kernels used with these types of models are often derived from empirical data. There are many different dispersal kernels that can be incorporated into these models, including long-tailed (leptokurtic) kernels and other non-normal dispersal distributions. When production of propagules is not continuous, as is true in many animals and plants, this type of integrodifference model will better approximate reality than a reaction-diffusion model. In contrast to reaction-diffusion models, integrodifference models can show an accelerating rate of spread

over time if long-distance dispersal is relatively common. Integrodifference models are more consistent with observed patterns of range expansion than reaction-diffusion models because of the accelerating rate of spread often observed. The waves of invasions seen in these models have smooth fronts, similar to the reaction-diffusion models. Space is still represented as continuous in these models, and spatial relationships are implicit, not explicit as in cellular automata/lattice models.

There are many other models that can be used to investigate the effects of dispersal on population dynamics. Stratified diffusion is a variant of the reaction-diffusion equation, where a proportion of individuals are assumed to travel long distances. Stratified diffusion models have accelerating rates of spread, similar to the integrodifference models. Metapopulation models (see Metapopulation Models) are very applicable to modeling dispersal patterns and rates of spread, and are also applied to other problems in ecology such as persistence of groups of populations in specific spatial arrangements under various scenarios of habitat destruction. They are commonly associated with biogeographical studies. A variation on integrodifference equations that includes stochastic population dynamics (nonlinear integrodifference models) shows waves of invasion that are patchy, with variable spread.

Measuring Dispersal

Direct Measures

Generating an accurate picture of the entire process of dispersal in a species involves detailed demographic analyses in addition to tracking emigrating and immigrating individuals (see Spatial Distribution and Spatial Distribution Models). In order to know what demographic parameters drive effective dispersal, it is important to know how many individuals leave, survive the exploratory process, and breed successfully in the new area. Ideally, all parameters of dispersal should be quantified. However, because the dynamics of a population are directly driven by effective dispersal, it may be unnecessary to conduct detailed studies of each stage of dispersal, depending on the particular goals of the researcher.

Mark-recapture methods and demographic analyses can assist in the estimation of many dispersal-related parameters, and though the route traveled by the individual captured in a new patch is often unknown, it is still possible to gain an estimate of immigration and emigration rates. Many studies focus on relatively local effects of dispersal, studying population dynamics in a few interconnected populations that are spatially tractable. These studies involve either mark-recapture methods, genetic methods, seed traps (for plants), or radio- or satellite-tracking methods. Animals and seeds can both be marked using tags, paint, or dyes. Tracking methods, such as by

radio telemetry or satellite, show great promise for obtaining detailed information on dispersal patterns, especially on the tail of the dispersal curve. Genetic methods are becoming popular as well, because they can detect effects of very low rates of dispersal over long distances. Each method has advantages and disadvantages, and all these methods have assumptions and uncertainties associated with them, which must be taken into account when analyzing data and estimating dispersal curves.

Collecting data from the tail of the dispersal curve can be difficult, either hampered by the difficulty of maintaining sampling densities, or due simply to the rare and stochastic nature of long-distance dispersal events. The importance of long-distance dispersal in estimating the spread of populations was highlighted in scientific literature when the rate of post-Pleistocene expansion of trees in Europe estimated with models neglecting long-distance dispersal could not account for the rapid expansion rates observed as the glaciers receded. Incorporating long-distance dispersal by modeling spread with leptokurtic dispersal curves matched the estimated rates of spread more closely. Unfortunately long-distance dispersal events are extremely difficult to measure empirically, and hence estimating them has since received much attention.

For animals, one way of estimating dispersal patterns involves marking and releasing animals, then observing the animals when they are collected, usually during an annual harvest. In the case of mark-harvest methods, animals are only viewed twice, once during the marking

stochasticity associated with the occurrence and detection of such events.

Seed dispersal is often measured using seed traps to capture seeds at varying distances from the source. Seed traps usually involve pit traps or sticky traps placed in or near the ground. To identify seeds' origins, individual fruits can be marked, a chemical tagging method can be used, or a rare genetic variant can be used as a marker. The most common method is to measure the densities of seed deposited at various distances from a source. Because individual plants are not identified when only density of seeds can be recorded, likelihood methods are used to model dispersal curves. Seed traps work well for estimating dispersal curves near the source, but as distance from the source increases it becomes more and more difficult to detect dispersal events. If enough traps are used, long-distance dispersal events can be detected; however, such events will be rare, and their detection will be dependent on the resources available to the researcher.

Radio telemetry and satellite tracking provide excellent data, when practical. Such studies have documented that long-distance dispersal events are more common than estimates from mark–recapture methods suggest. Most studies involve large- to medium-sized animals, including marine mammals. Invaluable information about the long-distance travels of these animals has been collected, including information about movements of some seabirds. Ideally, a large proportion of a population could be followed individually, and detailed analyses made of their movements. In order to accomplish this, the radio or satellite transmission units should not inhibit movement or survival, and the batteries should be strong enough to allow signal detection at a distance for a long period of time. As technology advances, smaller tags can be used. For example, very small radar tags have lately been adapted for use on bumblebees, showing promise for generating detailed dispersal data for larger insects.

Indirect Methods

Genetic methods hold promise for estimating dispersal patterns, though it is important to remember that genetic methods only measure effective dispersal, and not dispersal of individuals that did not successfully breed in the new population. In addition, for organisms with motile gametes, genetic patterns will likely reflect the movement of gametes among populations as well as the movement of diploid individuals. Most genetic methods involve collecting DNA from immature or mature individuals, then analyzing the DNA to try and identify the origin of a particular individual. In addition, if a dispersed individual has the same genetic signature as the individuals in the new population, the dispersal event will be undetected; this becomes less likely when highly variable markers are used. Another possible drawback to genetic data is the

potential for unsampled source populations to contribute to apparent gene flow estimates between two sampled populations. Also, it is difficult to generate a detailed dispersal curve using solely genetic data, especially at local distances, due to the large amounts of data that would have to be collected and the heavy expense involved. Nevertheless, genetic data enable estimation of many parameters of interest, such as historical amounts of gene flow, effective dispersal rates among differentiated populations, and dispersal rates over long distances. Genetic data are also often (but not always) easier and faster to collect than detailed demographic data. These advantages can outweigh the potential difficulties with genetic data, depending on the parameters of interest.

The first genetic estimates of dispersal (see Evolutionary Algorithms were derived from Sewell–Wright's equation

$$N_e m = \frac{1}{4} \left(\frac{1}{F_{ST}} - 1 \right)$$

where N_e is effective population size (an estimate of the number of individuals in an idealized population that would show the same patterns of genetic diversity or levels of inbreeding), m is migration (dispersal) rate, and F_{ST} is a measure of population structure. This equation can be used to estimate dispersal among populations using DNA sequence data, DNA markers of variable length, or allozyme (protein) markers. However, more recently the use of this equation to estimate dispersal rates has come into question based both on unlikely assumptions made when calculating F_{ST} , and on the applicability of the above equation to natural populations as opposed to idealized populations. Some of the assumptions made include equal and constant population sizes, and equilibrium between gene flow and genetic drift (stochastic variation in genetic frequencies over time). In addition, F_{ST} -based methods do not distinguish between historical and contemporary gene flow. In some cases, however, as in well-established, large populations, F_{ST} -based methods may be sufficient for estimates of dispersal rates.

Parentage analyses and assignment methods are both techniques that use genetic marker data to estimate dispersal (see Behavioral and Ecological Genetics). They both assume that source populations are discrete and that there is no genetic linkage disequilibrium (nonrandom associations of genetic marker variants due to inbreeding or chromosomal proximity) among the different markers used. Parentage analyses are based on multilocus genotypes, and can generate data about local animal movement and both seed and pollen dispersal. However, parentage analyses require extensive sampling to ensure that all possible parents in the source area have been included in the study. If a parent present in source populations is not

sampled, dispersal from an unsampled (possibly quite far away) population may be inferred, potentially altering dispersal estimates. Depending on the situation, parentage analysis can be expensive enough to outweigh the potential advantages of genetic analyses over demographic studies.

Assignment methods, on the other hand, use allele frequencies, or frequencies of different variants of genetic markers, to predict from which source a particular individual came. This means that exhaustive sampling of source populations is unnecessary. It is still desirable to have representatives from all possible sources. In order to distinguish sex-biased dispersal, sex-specific markers must be used. Assignment methods assume discrete source populations and no linkage disequilibrium, and often assume equilibrium of populations. However, methods that enable dispersal estimates when populations are not in equilibrium are being developed.

A method that has come into use recently for many questions in genetics involves Bayesian analyses (see Bayesian Networks). Bayesian methods can be used in nonequilibrium situations, such as during range expansions, with high levels of inbreeding, or with unequal population sizes. Information known about the populations in question is entered in the analysis in the form of prior probability distributions. This information, commonly known as a prior, is basically a guess about how the populations might act based on data already available, such as experimental data. If no information is already known about the populations, an uninformative prior can be used. Then the genetic data is used, in conjunction with the prior, to calculate posterior probabilities of the data using a maximum likelihood algorithm, given the parameters currently in place in the maximum likelihood model. Markov chain Monte Carlo resampling is then used to explore parameter space and find values that optimize the fit of the parameters in the model to the data. The accuracy of detecting dispersal events with these methods is still being explored. Factors affecting accuracy of dispersal detection include the level of genetic diversity in the populations, amount of dispersal occurring among populations, how many genetic markers are used, and the level of variability in the markers themselves. Depending on the population structure in the system in question, these methods may be equally viable both for detection of local dispersal and long-distance dispersal events.

As mentioned in the beginning of this article, dispersal in the context of population dynamics usually refers to the dispersal of diploid individuals. However, especially when genetic methods are used, movement of haploid gametes can affect dispersal estimates. Male and female gametic dispersal patterns often differ, and if not accounted for, can skew dispersal estimates from genetic data. Nuclear genetic markers come from both paternal and maternal sources, due to the combination of

nuclear genetic material during fertilization. If gametic gene flow is significantly different than diploid dispersal patterns, such as with pollen in many plants, care must be taken not to confuse gametic patterns of gene flow with movements of diploid individuals. In plants, for example, the male pollen often travels farther than seeds, especially if the species in question is wind-pollinated. In order to distinguish the dispersal of diploid seeds from haploid pollen, sex-specific genetic markers must be used. In plants, the chloroplast genome is generally (but not always) maternally inherited, and comparing patterns of genetic differentiation between the chloroplast and the nucleus can be used to estimate pollen versus seed dispersal patterns. If only seed dispersal is of interest, it may be sufficient to focus on chloroplast genetic markers, if the chloroplast is indeed maternally inherited in the species in question. Similarly, markers based on mitochondrial DNA will only show dispersal patterns of the female in animals. If dispersal patterns of both males and females are desired, both nuclear and mitochondrial markers must be used.

Because different analysis techniques have different strengths, weaknesses, and assumptions, it is important to consider what the goals of a given study are, and what methods are best suited to the questions at hand. Genetic methods hold promise for dispersal estimations, as data can be gathered relatively quickly and with less cost than demographic data. However, depending on the species and/or populations under consideration, estimates may require more genetic data than are currently available to optimize the parameters of a genetic analysis technique. If this is the case, then the cost of genetic analyses could equal or exceed the costs of demographic data collection. In addition, some data must be gathered through observation, such as detailed movement patterns among sites or populations and breeding success rates. Other data can best be estimated using genetic data, such as historical patterns of gene flow or long-distance dispersal events, depending on the organism in question. As techniques for measuring dispersal and its consequences improve, we will be better able to predict the survival, extinction, range expansion, and range contraction of populations and species. These predictions will improve estimates of the effects of habitat destruction and fragmentation on populations, a growing concern at multiple scales worldwide. In addition, accurate predictions of range expansion and contraction rates based on models of global warming will enable us to prepare for the possible effects of a rapidly changing climate on both marine and terrestrial species.

See also: Spatial Models and Geographic Information Systems; Neutral Theory; Clines.

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Dominance

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Introduction

Patterns of Dominance

Mechanisms of Dominance

Consequences of Dominance

Further Reading

Introduction

The coexistence of species in ecological communities is almost always asymmetrical such that some species are dominant, but most are rare. This inequality of species contribution is reflected by the degree of dominance in species composition and the identity of the dominant species. The analysis of dominance has been a cornerstone in general ecology, tightly linked to questions of community structure and diversity. Understanding the degree of dominance and the identity of the dominant species is implicit in studies on community assembly and organization, on causes and consequences of diversity, and on evolutionary and macroecological constraints of regional species pools.

Dominance in a local community can be highly obvious as one species monopolizes the use of space and visually characterizes the structure of the assemblage (Figure 1). Such striking dominance of single or few species can be seen in many terrestrial and aquatic communities. However, even in communities with seemingly lower dominance, only a few species contribute the majority of the biomass or the count of individuals.

The degree of dominance can be characterized by the maximum proportion of individuals (or biomass)



Figure 1 Two adjacent rock pools at the Swedish west coast. The right rock pool is strongly dominated by ephemeral green algae (*Enteromorpha* sp.), the left rock pool is characterized by a large snail population (*Littorina* sp.) and crustose algae. Picture courtesy of Monika Feiling.

contributed by a single species in an assemblage (dominance ratio). The dominance ratio can fluctuate between 0 and 1, but values >0.5 are very common, both for individuals and for biomass (Figure 2). Another way of addressing dominance is represented by rank–abundance curves, where species are ordered in ranks according to