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DISPERSAL, PLANT

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Plant dispersal is the movement in space of a seed or other unit of plant tissue that is capable of giving rise to one or more reproductive adults. Plant dispersal patterns are highly variable and can be studied and modeled in a variety of ways. Dispersal contributes to plant population and community structure and dynamics, including species coexistence and rates of spread. Human activities are altering plant dispersal patterns and the consequences of dispersal, with important implications for conservation and management.

PLANT DISPERSAL STRATEGIES

The Unit of Dispersal

The unit of dispersal in a plant is referred to as the diaspore. This may be the seed, the fruit, the spore (in lower plants such as ferns), a vegetative part of the plant that is capable of growing into an adult plant, or even the whole plant. Most plants are sessile as adults and disperse exclusively at the seed or spore stage. However, dispersal of whole plants or viable fragments is the dominant mode of dispersal in aquatic plants. Further, quite a number of herbaceous plant species have special vegetative dispersal organs, termed bulbils. While seeds are the result of sexual reproduction, bulbils and viable fragments result in asexual or clonal propagation. A single plant species may have more than one type of diaspore; for example, an aquatic species may disperse both viable vegetative fragments and seeds.

Modes of Dispersal

Plants can be dispersed by wind, water, and animals, including humans and their conveyances. Diaspores of the

same species may be dispersed in multiple ways, either alternatively or in succession. Modes of rare long-distance dispersal may be different from modes of more frequent short-distance dispersal; for example, seeds that are usually dispersed short distances by wind may occasionally be transported long distances by water. Where the same diaspores are often moved two or more ways in succession, the initial movement away from the mother plant to the ground or other substrate is termed primary dispersal, while subsequent movement over the ground or substrate is termed secondary dispersal. Thus, for example, a seed may first experience primary dispersal by wind, and later secondary dispersal by ants.

Many plant species use animals for dispersal. Animals may consume fruits and subsequently defecate or spit out viable seeds; they may move seeds to caches with the intention of consuming them later, yet leave some untouched; and they may unintentionally transport seeds attached to their bodies by, for example, burs. A wide range of animal groups are involved—mammals, birds, reptiles, fish, ants, beetles, snails, earthworms, and more. In many cases, the relationship is a mutualism in which the animal species benefit by consuming plant tissue; in others, the animals receive no benefit and may even incur a cost. Tight dispersal mutualisms between single plant and animal species are the exception: typically, any given plant species will have its diaspores moved by multiple animal species, and any given animal species will be involved in moving diaspores of multiple plant species. However, though many animal species may be involved in dispersing diaspores of a particular plant species, there may be one species that is disproportionately important for the plant, because it moves more diaspores and/or places diaspores in particularly favorable conditions and is thus a more effective disperser, from the plant's perspective. This is reflected in plant traits: the coloration, mode of display, and chemical composition of fruits and seeds may enhance their attractiveness to some animals, and reduce attractiveness to others. For example, the capsaicin in chile peppers deters consumption by mammals, a phenomenon known as directed deterrence, while the red color of the ripe fruits increases visibility to birds.

Plants may instead (or in addition) rely on wind or water for dispersal, or may disperse without any external aid. Many species have seeds, spores, fruits, or even bulbils that are dust-like particles, balloons, plumed, or winged, and thereby adapted for dispersal by wind. Other plants are regularly dispersed by water: this includes aquatic plants and plants of seasonally flooded habitats whose diaspores may float or be transported submerged,

as well as terrestrial plants whose seeds are moved by rain wash. Some plant species explosively disperse their diaspores; wind, water, or a passing animal may or may not be needed to provide energy or the trigger for such ballistic dispersal. Finally, there are plant species in which diaspores spread by growth alone (e.g., stalked infructescences curving toward the ground), and those in which the diaspores seem to have no adaptation for dispersal and are said to disperse by gravity or weight alone.

Human activities have provided novel modes of dispersal, and especially long-distance dispersal for many plants. Seeds, viable plant fragments, and whole plants may be moved from place to place deliberately for agriculture, horticulture, or silviculture, or accidentally as hitchhikers on such shipments, on clothing, on vehicle treads, in ballast water, and so on.

MEASURING PLANT DISPERSAL

Two qualitatively different approaches can be used to measure plant dispersal. The Lagrangian approach quantifies the trajectories of individual diaspores by, for example, following marked seeds. The Eulerian approach quantifies the spatial pattern of diaspores after dispersal by, for example, measuring seed arrival in seed traps. Genetic techniques can be applied to either approach and offer the promise of combining the best of both approaches.

The Lagrangian Approach: Tracking Diaspore Movement

Plant dispersal distances and patterns can be evaluated by following the trajectories of individual diaspores. In some cases, the diaspore can be directly observed during dispersal. In other cases, it may be possible to label seeds before dispersal and relocate them afterward. Such labeling can be accomplished with dyes, radioisotopes, metal inserts (permitting relocation with a metal detector), or even radio transmitters. Diaspores may be followed or relocated after natural dispersal from their mother plant or after experimental release or deployment (e.g., previously collected wind-dispersed seeds are dropped by hand, or marked seeds are placed on the ground beneath a fruiting tree).

The advantage of this method is that the source of the seed is known and often also its mode of transport. The key disadvantage is that the observed trajectories are unlikely to be representative of the population of diaspores as a whole. First, some fraction of target diaspores invariably cannot be followed or relocated, and it is likely that these escapees have a different distribution of fates than diaspores that are successfully tracked (long-distance

seed dispersal is disproportionately likely to be missed). Second, tracking methods may capture only one mode of dispersal, missing others, especially those associated with secondary dispersal, and thus measurements may fall short of the complete trajectories of the diaspores. Third, experimental releases of diaspores tend to be concentrated in time and space, for logistic reasons, and the dispersal trajectories thus sampled may not be representative of the trajectories in the population as a whole because of temporal and spatial variation in dispersal conditions (e.g., windspeed) as well as failure to correctly mimic the distribution of conditions under which diaspores are naturally dispersed (e.g., seeds naturally released disproportionately when windspeeds are high).

The Eulerian Approach: Quantifying Post-Dispersal Diaspore Distributions

Alternatively, the spatial distribution of diaspores can be mapped following dispersal, and combined with information on the distribution of sources to infer dispersal patterns. This is most commonly done through the use of appropriate seed traps—for example, sticky traps, netting on a frame, or soil in seed trays. Juvenile plants are sometimes mapped instead of diaspores, as they are generally easier to find; however, spatial patterns of juveniles are influenced not only by dispersal but also by spatial variation in establishment success, complicating analyses, and inferences.

The major disadvantage with the Eulerian approach is that the sources of individual diaspores are usually uncertain—except in the extreme case where there is only one source—which introduces corresponding uncertainty into estimates of dispersal patterns. In principle, the key advantage is that the observed patterns usually integrate over complete seasons and include dispersal via all modes. However, many seed traps prevent or restrict secondary dispersal, so that in practice this method often provides information only about primary dispersal. Further, for practical reasons, sampling is unlikely to capture long-distance dispersal to locations far from source plants, and thus, as with the Lagrangian approach, long-distance seed movement is disproportionately likely to be missed.

Genetic Tools

Genetic markers offer additional direct and indirect methods for gaining insight into plant dispersal. The classical indirect method uses measures of spatial genetic structure to estimate long-term effective seed dispersal distances. A key point is that these estimates reflect *effective* dispersal, that is, dispersal that leads to reproductive adults, and thus incorporate the

influences of post-dispersal processes, which are likely to vary systematically with dispersal distance. Biparentally inherited markers also reflect the influence of pollen dispersal.

The newer direct genetic method uses high-resolution molecular markers to match seeds (or seedlings) with parents (or specifically mothers). In principle, this could capture the key advantages of the Lagrangian and Eulerian approaches, making it possible to sample representatively from the whole post-dispersal distribution and simultaneously obtain certainty about sources and thus trajectories. In practice, however, the direct method has thus far fallen well short of this promise, and not only because its application continues to be exceptionally time-consuming and expensive. Genotyping errors bias toward overestimation of the number of immigrant diaspores outside the genotyped source pool, while inability to uniquely identify all source trees and inability to distinguish mothers from fathers bias toward underestimation of dispersal distances and immigration. Further, it has only belatedly been recognized that the distribution of dispersal distance estimates obtained with direct genetic methods is not in and of itself an unbiased sample of dispersal distances in the whole population but is contingent upon the distribution of sampling points relative to sources. Appropriate statistical analyses need to be applied to correct for these influences. Direct genetic methods, like all other tools, are imperfect windows on plant dispersal.

MODELING PLANT DISPERSAL

Decomposing Dispersal Patterns

A key concept in analyzing and modeling plant dispersal is the seed shadow, or diaspore shadow—the spatial distribution of diaspores that originated from a single plant (usually in a single season or year). The overall spatial distribution of diaspores in a plant population is the sum of diaspore shadows produced by individual plants. The diaspore shadow of a plant can itself be thought of as the product of its fecundity (number of diaspores produced) and the probability density function for the locations of these diaspores relative to the source plant, termed the dispersal kernel.

The focus of the vast majority of plant dispersal models is the dispersal kernel for a plant species or population, averaged over all individuals. Dispersal kernels are typically defined as functions of distance from the source alone, ignoring other systematic sources of variation in diaspore arrival probability, but this need not be the case. Dispersal by wind is generally anisotropic, reflecting prevailing wind directions, and this pattern can be

captured in dispersal kernels that incorporate direction as well as distance. Diaspore arrival often varies systematically with substrate; for example, wind-dispersed seeds are more likely to come to rest in tall grass than on sand, and animal-dispersed seeds are more likely to be deposited in habitats preferred by the disperser. Such substrate-specific deposition generally defies inclusion in simple dispersal kernels that apply for all sources in a population, but can be incorporated into more complex models. It can be particularly important where seeds are disproportionately deposited in favorable habitats, so-called directed dispersal. Finally, focus on the dispersal kernel alone ignores the influences of clumping of diaspore arrival, such as that which results when multiple seeds are dispersed in a group (e.g., an animal disperser defecates multiple seeds in one place). Characterization of the magnitude and scale of this clumping can be important to accurately model the distribution of dispersed diaspores and consequences for recruitment. Clumping can in the simplest case be modeled with a negative binomial distribution around the expectation derived from a dispersal kernel.

Phenomenological Models

Plant dispersal is most often analyzed by fitting purely phenomenological models for dispersal kernels to empirical data. In most cases, the dispersal kernel is a function only of distance from the source. Commonly used empirical models for the dependence upon distance include the exponential, Gaussian, inverse power, lognormal, Student's, Weibull, and the exponential power (exponential function of distance raised to a power). These may be used to describe the dispersal kernel in two dimensions, or the radial integration of this dispersal kernel, i.e., the probability distribution of dispersal distances; this is unfortunately a frequent point of confusion. Many of these functional forms can be motivated in general terms. For example, a Gaussian distribution is expected if diaspores move by Brownian motion for a fixed period of time. More complex phenomenological models may be constructed as mixtures of two distributions, motivated as the sum of two different dispersal processes (e.g., two exponential distributions reflecting frequent short-distance and rare long-distance dispersal).

Empirically, dispersal distance distributions are generally strongly leptokurtic. Thus, among one-parameter models, the (relatively fat-tailed) inverse power generally fits better than the exponential, which generally fits better than the (thin-tailed) Gaussian. Unsurprisingly, models with more parameters tend to more closely fit the

data, but they are also more vulnerable to overfitting and have wider confidence intervals on parameter estimates. Thus, two-parameter Student's t , lognormal, Weibull, and exponential power models generally outperform the one-parameter exponential, inverse power, and Gaussian models, and may themselves be outperformed by four-parameter mixed models. The lognormal is the only widely used phenomenological model in which the highest expected seed density is not (necessarily) at the source, and thus it generally provides the best fit to datasets exhibiting this pattern. Overall, no one phenomenological model outperforms the rest for all datasets; different dispersal datasets are best fit by different models.

Mechanistic Models

An alternative approach is to develop mechanistic models based on an understanding of the underlying dispersal process. Truly mechanistic models can predict diaspore distributions from independently measured characteristics of the dispersal process.

The mechanistic approach is best developed for dispersal by wind. The simplest model of dispersal by wind is the ballistic model, in which dispersal distance is the product of horizontal wind velocity and release height, divided by the fall velocity of the diaspore. This can be used to generate dispersal kernels from empirical measurements of the three parameters and their probability distributions. More complex and realistic mechanistic models can incorporate nonzero vertical wind speeds, systematic variation in windspeed with height above the ground, autocorrelated random variation in wind velocity during flight, differential diaspore release as a function of wind conditions, and more. Most of the resulting models cannot be expressed analytically but must instead be evaluated numerically (with simulations). An exception is the WALD, or inverse Gaussian, derived from simplification of a stochastic model of turbulent transport. The two parameters of this model can be estimated directly from wind statistics, release height, and fall velocity and/or fit based on dispersal data.

Some of the same general approaches used for dispersal by wind have also been applied to dispersal by water. However, overall, there has been little research specifically on plant dispersal by water. It is likely that models of plant diaspore transport in water could usefully borrow from models of the transport in water of flotsam, of animals that possess limited independent movement capacity, and even of certain pollutants.

The biggest challenge in mechanistic models of plant dispersal by animals is the heterogeneity in behavior within and among individuals and species that serve as

dispersers of a given plant species. The simplest models compound distributions of the time a diaspore is retained by an animal (e.g., in the gut or on the coat) with distributions of displacement distances as a function of time. Where multiple animal species are involved, and differ in their retention or displacement distributions, a combined kernel can be constructed as the appropriate weighted sum of kernels due to the activities of each species. More realistic models have further incorporated clumped diaspore deposition by animals, differential movement through and deposition in different habitats or substrates, diurnal variation in disperser behavior, spatial variation in disperser behavior depending on resource plant density, and more. Aided by the increasing availability of high-resolution animal movement data and ever-better computing resources, models of animal movement and behavior continue to improve rapidly, promising further improvements in mechanistic models of seed dispersal by animals. At present, however, the utility of these complex models is limited by their requirements for extensive data on the relevant disperser species.

CONSEQUENCES OF DISPERSAL

Dispersal patterns have direct consequences for the fitness of individual plants, as plants whose diaspores are dispersed into relatively more favorable locations will be better represented in subsequent generations. This leads to natural selection on dispersal-related traits. Dispersal also affects population and community patterns, as described below.

Population and Community Structure and Dynamics

Seed dispersal determines the spatial pattern of potential recruitment and thereby can contribute greatly to spatial structure of populations and communities. The probability of successful establishment of a juvenile and successful maturation to adulthood typically varies extensively in space within a plant population. This variation may be related to environmental factors such as temperature and water availability, as well as to purely biotic factors such as proximity to competitors or natural enemies. In many plant species, per-diaspore recruitment probabilities are depressed close to conspecific adults, because of intensified resource competition and/or natural enemy attack in these areas. Spatial patterns among juveniles and adults reflect the combined influences of seed dispersal and post-dispersal processes. The same patterns can arise in multiple ways; for example, clumped distributions of adults may arise from a predominance of short dispersal distributions or from the combination of widespread dispersal

and patchy distributions of sites favorable for recruitment, among other possibilities. In general, shorter dispersal distances are expected to increase clustering of individuals, decrease local diversity (of both genes and species), and increase turnover in space (of both genes and species).

Seed dispersal can be critical to understanding the dynamics and structure of populations and communities. For example, in metapopulations (collections of island populations bound loosely together by occasional migration between the islands), the rate of dispersal among island populations is critical to determining patch occupancy, overall species abundance, and persistence in the face of disturbance. Dispersal from favorable to unfavorable habitats may also result in source–sink dynamics, in which species persist in areas in which their per capita population growth rates are negative.

Seed dispersal may also contribute to plant species coexistence. Competition–colonization tradeoffs between the ability to reach potential recruitment sites with diaspores and the ability to succeed following arrival can enable stable species coexistence. Tradeoffs between dispersal and fecundity can contribute to stable coexistence given spatial variation in the density of favorable sites. More generally, variation in dispersal strategies can also contribute to coexistence insofar as it gives each species an advantage in a different set of circumstances. Finally, limited dispersal overall within a community reduces interspecific interactions and thereby slows competitive exclusion and increases opportunities for nonequilibrium coexistence.

Rates of Spread

Plant dispersal patterns are critical to determining the rate of advance of a species in favorable habitats. This is of practical interest for the spread of invasive species and in determining the maximum rate of advance as species respond to changing climates. Where the dispersal of a species is well approximated by random walk and thus by diffusion, the population advances continuously from its periphery, and the asymptotic rate of spread is approximately $2\sqrt{Dr}$, where D is the diffusion coefficient and r is the rate of per capita population growth when rare. This approximation works well for species with Gaussian dispersal. However, many species have dispersal kernels whose tails are fatter than those of the Gaussian, and these can lead to more complicated dynamics of expansion and accelerating rates of spread. Long-distance dispersal events from the tails of these distributions may form satellite patches in advance of the main front that themselves become foci for population expansion. Rates of spread in these cases can be estimated by integrodifference equations, or by simulation.

APPLICATIONS TO CONSERVATION AND MANAGEMENT

Anthropogenic alteration of dispersal patterns

Human activities are changing plant dispersal opportunities, frequencies, and patterns. Intentional and unintentional plant dispersal by humans has increased as diaspores travel in cars, boats, planes, clothing and more. Hunting and habitat fragmentation have reduced abundances of many animal species even in relatively pristine areas. Densities of some species of animal seed dispersers have thus declined; densities of others may increase in response to the loss or decline of their predators and/or competitors. A number of studies have documented associations of such changes in animal disperser abundance with a decrease in the frequency of fruit and seed removal, changes in seed dispersal distances, and decreases in seedling recruitment. Even where animal dispersers are still present in historic densities, their behavior may be altered in such a way that dispersal services change if, for example, they tend not to cross roads.

Windspeeds, and thus the patterns of seed dispersal by wind, are also affected by human activities. The higher temperatures associated with global warming are expected to increase atmospheric instability and thus the frequency of long distance dispersal by wind. Landscape alteration also affects wind regimes; for example, forest fragments are generally exposed to higher wind speeds than are intact forests. Construction of canals, damming of rivers, constriction of floodplains, and other alterations of water bodies have similarly altered water flows and thus plant dispersal by water.

Anthropogenic Alteration of the Consequences of Dispersal

Human activities are also fundamentally altering the payoffs to dispersal on different scales, and arguably the necessity of dispersal. Habitat fragmentation means that dispersal that takes diaspores outside natural remnants yields nothing for many plant species, whereas historically dispersal to this distance might have been beneficial. At the same time, dispersal that goes far enough to reach another remnant may result in enhanced opportunities relative to the historical norm. Case studies of the evolution of dispersal on islands illuminate the potential consequences—selection for reduced dispersal within remnants, which in the long-term reduces the possibility of colonizing or recolonizing other remnants. Such landscape structure also disproportionately rewards directed dispersal, for example, by birds that fly between remnants.

Global climate change is increasingly making migration a necessity for long-term persistence of many species. Increasing temperatures and shifting rainfall regimes are leading to a growing mismatch between species' current distributions and the climates to which they are best suited. This places a premium on plant dispersal into the newly suitable areas and, indeed, threatens extinction for many species if they fail to disperse. In practice, this often requires dispersing over or around large areas of anthropogenically modified landscapes or through narrow corridors crossing such landscapes. The paleorecord shows that past climate shifts have been accompanied by associated shifts in plant species' ranges, although these have often lagged considerably. Historic climate shifts were accompanied by more extinctions on continents in which east–west mountain ranges barred the way. Unfortunately, anthropogenically modified habitats may for many species prove as much a barrier to dispersal as mountain ranges.

Manipulating Dispersal Opportunities to Promote Conservation

Deliberate measures to preserve, enhance, or inhibit plant dispersal opportunities can constitute valuable tools for conservation and management. Restoration and maintenance of natural densities of animal seed dispersers is an integral part of the conservation of any plant population, community, or ecosystem. Construction of corridors that connect habitat remnants can enable dispersal that enhances short-term population persistence and long-term viability in the face of global change. Habitat restoration and reestablishment of native vegetation can often be speeded through the provision of perches for birds that bring in seeds. Deliberate assisted migration of plant propagules to track climate change should be considered, especially where anthropogenic barriers restrict the possibility for unassisted migration. Finally, the introduction and spread of invasive species can be reduced by measures that restrict the transport of propagules by humans.

SEE ALSO THE FOLLOWING ARTICLES

Dispersal, Animal / Dispersal, Evolution of / Integrodifference Equations / Metapopulations / Restoration Ecology / Spatial Ecology

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DIVERSITY MEASURES

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Diversity is a measure of the compositional complexity of an assemblage. One of the fundamental parameters describing ecosystems, it plays a central role in community ecology and conservation biology. Widespread concern about the impact of human activities on ecosystems has made the measurement of diversity an increasingly important topic in recent years.

TRADITIONAL DIVERSITY MEASURES

The simplest and still most popular measure of diversity is just the number of species present in the assemblage. However, this is a very hard number to estimate reliably from small samples, especially in assemblages with many rare species. It also ignores an ecologically important aspect of diversity, the evenness of an assemblage's abundance distribution. If the distribution is dominated by a few species, an organism in the assemblage will seldom interact with the rare species. Therefore, these rare species should not count as much as the dominant species when calculating diversity for ecological comparisons. This observation has led ecologists (and also economists and other scientists studying complex systems of any kind) to develop diversity measures which take species frequencies into account.