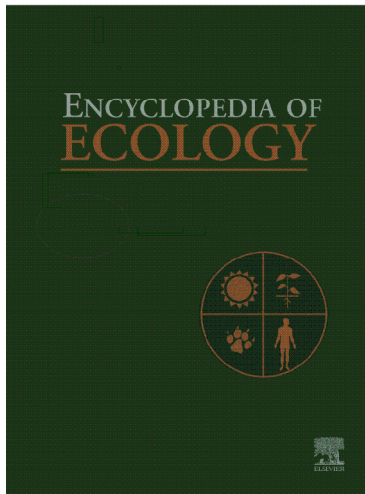


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incubation of a series of parallel cores. The porewater from sediment slices can be retrieved by pressure, suction, or centrifugation. By correction for porosity and differences in ion size between the tracer and an element, an apparent diffusion coefficient can be estimated. The importance of bioturbation can be estimated by introducing known numbers of organisms in undisturbed sediment cores.

By comparing process rates in the water body and in the sediments, guidelines can be set up for the selection of complexity of sediment models. Diffusional fluxes across the sediment-water interface in lakes vary from 0 to  $0.1 \text{ yr}^{-1}$ , sedimentation and growth of porewater volume vary from 0 to  $0.05 \text{ yr}^{-1}$ , water exchange through outflow varies from  $0.1$  to  $1 \text{ yr}^{-1}$ , and first-order decay rates vary from 0 to  $35 \text{ yr}^{-1}$ . In general, dilution and decay rates are faster than sediment dilution and diffusional fluxes. This means that decomposition at the sediment surface is more important than transport-limited decay in the deeper parts of the sediment. If the range of diffusion is increased by moving deeper in the sediment or if the gradients are becoming weaker, the influence of sediment pools is reduced. Consequently, in lakes with short hydraulic residence time the sediment fluxes are not important, if both water renewal and sediment fluxes are evenly distributed over the year. But if exchange rates both to and from the sediment are fast in the summer and water renewal is low at that time, the sediment can cause a significant delay in response to reduced loading. In such cases high resolutions in time and space are necessary, for

the understanding of lake ecosystem's responses to reduced loading. In lakes with residence times of several years, the sediment will not be the reason for a delay in the response, since the hydraulic residence time and the sediment dilution effects will be the most important.

See also: Empirical Models.

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## Seed Dispersal

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## Background

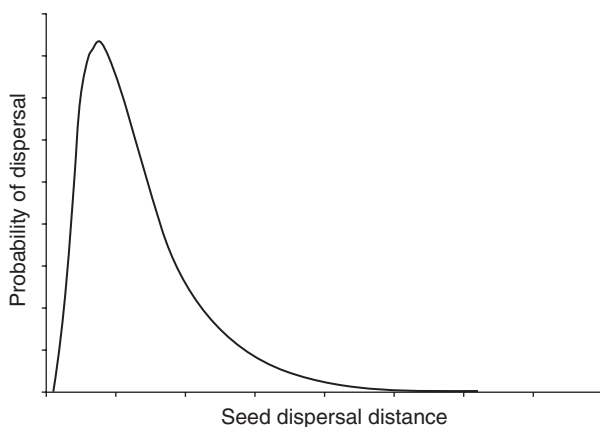
The ecology of seed dispersal is a topic of much interest to naturalists, although it has not been until the last three decades that it has received considerable attention by

scientists. Seed dispersal is one of the key phases in the process of plant regeneration, as it determines the potential area of recruitment at the same time that acts as a template for the rest of stages in such process. Dispersal can be defined as the process by which individuals move

from the immediate environment of their parents to establish in an area more or less distant from them. In contrast to animal dispersal, plant dispersal is always passive in the sense that seeds have no control of where they will end up; moreover, seed dispersal is more determined by the traits of the maternal parent than by the traits of the seeds themselves. Two widely used terms in the study of seed dispersal are 'seed shadow' and 'seed rain', both referring to the spatial distribution of dispersed seeds either around a parent plant (shadow) or around multiple parents, within a population perspective (rain). The seed shadow is usually used to assess evolutionary aspects of seed dispersal whereas seed rain is more employed in the demographical perspective of seed dispersal. Both perspectives, the individual and the population, are needed if we are to understand the shaping of the spatial seed distribution and, ultimately, the spatial dynamics of recruitment.

### Advantages of Dispersal

The two major benefits of seed dispersal are: (1) departure from the parent plant, which usually avoids sibling competition and reduces seed/seedling mortality by predators or pathogens; and (2) colonization of new sites. Seed density usually decreases with distance from the parent plant, following a unimodal leptokurtic distribution (with a peak at or close to the source, followed by rapid decline and a long, more or less fat, tail; **Figure 1**). Deviations from this conventional seed shadow shape can result from patchiness of habitat structure or from other ecological factors such as the behavior of frugivores, which can promote nucleation process due to preference for certain sites (for instance, by depositing seeds under particular trees used for resting). The tail of the distribution can be, in fact, as important as the modal portion of the curve, as



**Figure 1** Relationship between dispersal distance and probability of seed dispersal.

seeds in such tail have the potential to spread the parental genes to long distances as well as to maintain genetic connectivity among distant populations (see below).

Frequently, the benefits of leaving the immediate vicinity of the mother plant depend upon the advantages obtained by (1) increasing the distance to it and (2) avoiding a highly intense sibling competition. Therefore, the effects of both factors (seed density and distance from the parent plant) are not easy discernible without field experimentation.

Regarding the advantage of colonizing new sites, seeds that leave the mother plant have the capacity of occupying vacant habitats and suitable microhabitats for germination and growth. This allows, for instance, the latitudinal or altitudinal migration of many plants in front of climate changes, the recolonization of a land after a volcanic eruption, the colonization by many herbs and shrubs of an abandoned field, enhancing thus the ecological succession. There are also species that have 'directed seed dispersal', benefiting from it as seeds are deposited in sites or microsites that are especially suitable for germination and seedling establishment. Seed of mistletoes, for instance, are usually defecated by birds on host twigs, which are required for the successful germination and seedling recruitment.

### Mechanisms of Dispersal

Seeds are dispersed in a great variety of ways. The morphological devices that enhance dispersal are usually quite evident and interpretable. Thus, for instance, we find wind-borne diaspores bearing wings, hairs, or plumes that increase air resistance and slow the rate of fall (a dispersal syndrome named anemochory), seeds that float in the water by means of a buoy (hydrochory), seeds with hooks or barbs that adhere to the exteriors of animal vectors (exozoochory), seeds with elaiosomes for ant dispersal (myrmechory), or diaspores with flesh appendages or coverings that are consumed by animals which later eject the seeds (endozoochory, within which we distinguish ornithochory, saurochory, etc., depending upon the taxonomical order of the frugivore in question). Some plants disperse their offspring ballistically, by the explosive opening of the fruits or the springing of a trip lever. It is also not uncommon that plants combine two or three modes of dispersal; we thus find plants that are dispersed ballistically and by ants (e.g., *Viola*), others dispersed by ants, birds, and mammals (e.g., *Myrtus*), etc. Other species lack any evident dispersal device, which makes us wonder whether dispersal is less advantageous in these species or how they achieve effective dispersal.

The dispersal mode of seeds has commonly been associated with seed size; thus, for instance, species with mammal-dispersal syndrome have significantly larger

seeds than those with bird-dispersal syndrome. This occurs even within a genus, such as in *Pinus*, in which seeds weighing less than *c.* 100 mg are wind dispersed whereas heavier seeds tend to have adaptations for bird dispersal. However, the usefulness of dispersal syndromes has often been questioned, especially for vertebrate seed-dispersal syndromes, which have been found to be only minimally attributable to plant adaptations to dispersers and, on the contrary, appear to reflect more the influence of plant phylogeny on fruit traits. In fact, after accounting for phylogeny, fruit size has been found to be the only trait out of a large number of fruit traits considered in a review, significantly associated to dispersal.

### Secondary Dispersal

Seeds may have more than one opportunity of being dispersed. After a first phase consisting of the initial movement of seeds away from mother plant (primary dispersal), there may be a second phase (secondary dispersal) in which seeds are further dispersed, usually by another mechanism or agent. This is common in plants which are first dispersed by endozoochory or ballistically and are subsequently moved by ants, dung beetles, rodents, birds, or even predators of such frugivores that carry seeds in their digestive tracts (the latter has been reported, for instance, for several species in the Canary Islands that are primarily dispersed by reptiles and secondarily dispersed by shrikes and

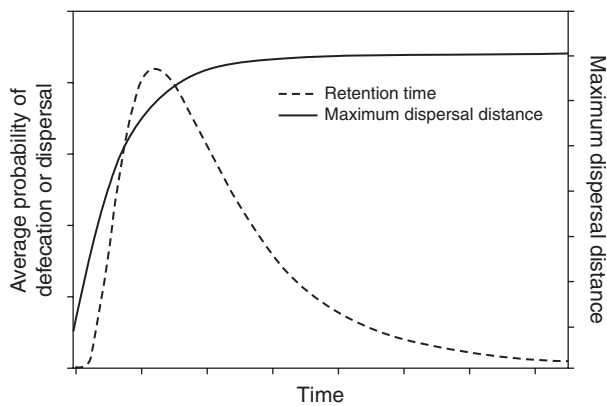
raptors; **Figure 2**). There are cases where seeds have reward structures to attract ants, such as elaiosomes or flesh appendages, which are removed once the seeds are dispersed (in *Rhamnus*, *Euphorbia*, etc.). In other species, however, primarily dispersed seeds are removed by seed predators (rodents, granivorous ants, etc.) that store a fraction of them in sites like holes in trees or in soil, ant nests, etc., and later 'forget' to collect them; in some cases, these sites are especially suitable for further seedling emergence and establishment.

### Long-Distance Seed Dispersal

Recent population and community models show that the entire distribution of dispersal distances, and not only mean dispersal distances, is critical for rates of range expansion, recruitment patterns, genetic structure, metapopulation dynamics, and ultimately for community diversity at different scales. The use of dispersal mechanistic models, and especially those that are spatially explicit, is a promising tool because it provides reliable predictions of standard (local dispersal) as well as non-standard (long-distance dispersal, LDD) events of seed dispersal, which are especially difficult to capture in nature. For wind-dispersed species, for example, the processes that affect seed dispersal distance are either atmospheric (the spatial and temporal statistics of the wind velocity field (vertical, longitudinal, and



**Figure 2** Fruits of *Lycium intricatum* (Solanaceae) that are secondarily dispersed by the predators (*Falco tinnunculus*) of the primary seed disperser, the lizard endemic to the Canary Islands, *Gallotia atlantica*. Photos courtesy of Manuel Nogales.



**Figure 3** An example of a mechanistic biotic model combining the data on retention time (left axis) with the net displacement movement considered as maximum dispersal distance from the origin (right axis). For a territorial disperser as in the given case, the maximum seed dispersal distance strongly depends on its home range or territoriality, but not on the retention time. From Santamaría L, Rodríguez-Pérez J, Larrinaga AR, and Pias B (2007) Predicting spatial patterns of plant recruitment using animal-displacement kernels. *PLOS ONE* 2(10): e1008 doi:10.1371/journal.pone.0001008.

latitudinal), their covariance structure, and their integral timescale properties) or biological (terminal velocity of the dispersal unit, release height, and timing of release) factors. The scale at which the dispersal model makes predictions will influence which factors are included in the model. Knowledge of the average wind velocities appears to be sufficient to predict local dispersal. However, in order to predict LDD, additional information on updrafts and strong gusts is needed. By contrast, seed dispersal distance in endozoochorous species is mostly a function of seed retention time in the frugivore's digestive tract and of frugivore's movement patterns (home range, habitat use; **Figure 3**). These mechanistic models are predicting that dispersal could be up to 2 orders of magnitude higher than those previously obtained by empirical methods.

### Plant and Animal Adaptations

The dispersal mode of any plant species is probably the result of many different pressures and constraints. Phylogenetic constraints are responsible for the fact that entire families or genera usually exhibit only slight variations on a single mode of dispersal. Nonetheless, large variation in some families or genera (e.g., *Acacia*) is evidence that these constraints are not universal. Other limits to the evolution of fruits and seeds also emerge from the many, sometimes conflicting, selection pressures impinging on different traits (size, shape, pulp chemical composition, seed coat thickness, etc.). Fruit consumption



**Figure 4** Bicolored fruits of *Rhamnus alaternus*; red fruits are unripe and turn black when mature. Photo by Anna Traveset.

by vertebrate dispersers, in particular, has selected for fruit traits that enhance their detectability; these fruits, thus, tend to have a conspicuous coloration, distinctive odor, or a combination of both. A common pattern found both in the tropics and in the temperate zones is that bird-dispersed plants usually have red- or black-colored fruits. In some species, a bicolored fruit advertisement, contrasting the ripe fruits with the surrounding foliage, is what presumably gives visual conspicuousness (what has been termed the 'foliar flag' hypothesis) (**Figure 4**). Also, some ripe fruits reflect ultraviolet (UV) light which enhances the detectability by birds, as their color vision extends to the near-UV. The fruits dispersed by vertebrates also tend to have a pulp rich in water and carbohydrates while being poor in protein and lipids; however, there is much interspecific variability in nutrient composition, and fruit pulp quality does not show to be a trait reflecting plants' adaptations to dispersers. Fruit pulp also usually contains secondary metabolites (phenolics, alkaloids, etc.), sometimes to the point of being lethal to animals, which require an adaptive explanation not yet found. One possibility is that such compounds serve as defense against microbial pathogens and invertebrate pests that preclude the consumption of the fruits by legitimate dispersers.

Regarding animal adaptations, frugivores do not require important morphological and physiological adaptations, especially those that are only occasional frugivores, although the 'strict frugivores' can have the following distinctive traits: such birds tend to have shorter, broader, and flatter bills, and wider gapes than those not consuming fruits; some birds also have smaller and less muscular gizzards, larger livers, and shorter intestines; frugivorous bats have shorter canines and broader palates than insectivorous ones; frugivorous lizards have longer intestines than those consuming mostly animal material. Besides coping with the nutritional imbalance and the secondary compounds of the pulp, these frugivores need to cope with the spatial and

temporal unpredictability of fruits. This is probably the reason why there are not frugivores specializing on only one or a few plant species.

### Fruiting Phenology

A few general patterns in dispersal phenology have been described. Wind-dispersed neotropical trees, for instance, mature their fruits during the dry season, when trade winds are strong and trees are leafless, contrasting with the more or less constant throughout-the-year production of fleshy or dry fruits. By contrast, in the north temperate zones, mature fruits are produced in late summer and autumn, when avian frugivores are usually abundant, whereas further south, ripe fruits are also found through the winter, when flocks of wintering migrant birds are foraging. Nevertheless, such fruiting patterns do not need to be interpreted as adaptations to dispersal, as constraints to such timing may derive from selection to avoid pathogens or predators, to shift the flowering time, or to modify the length required for fruit maturation. It is widely accepted that seasonality in temperature and water availability set limits on the time of fruit and seed development and maturation.

### Quantitative and Qualitative Components of Seed Dispersal Effectiveness

The effectiveness of a disperser is defined as the contribution that it makes to plant fitness, or in other words, the number of new adult plants produced by the activities of a disperser relative to the number produced by other dispersers. This term has both quantitative and qualitative components, and both need to be considered to assess how effective a disperser is for a given plant; it can be considered at a variety of scales from individuals to communities. The quantity component is dependent upon the number of visits made to the plant by the disperser, upon the number of seeds dispersed in each visit, and is influenced by factors that are either intrinsic to the plant (e.g., size, fruit crop size, pulp/seed ratio) or extrinsic to it (e.g., neighborhood of conspecifics, surrounding vegetation, fruit crops of neighbors) and also by the biology of the dispersers (fruit-handling methods, degree of generalism in feeding, etc.). By contrast, the quality of seed dispersal, usually more difficult to evaluate, is a function of (1) the quality of the dispersed seed (often associated with fruit and/or seed size and rather variable within an individual plant, and influenced by factors such as number of seeds/fruit); (2) the quality of seed treatment in the digestive tract of the disperser, in turn dependent upon traits like seed coat thickness, chemical composition of pulp, gut passage time, morphology

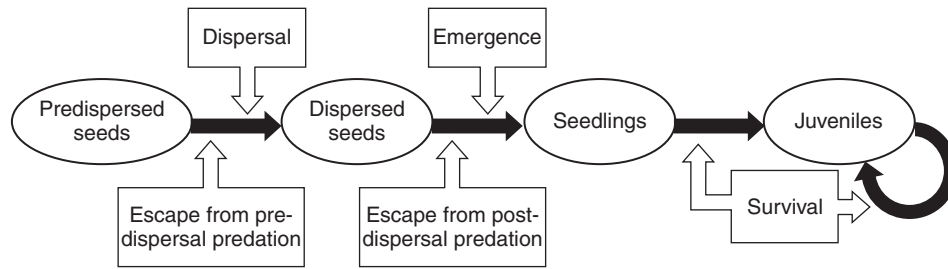
and physiology of the digestive tract, type of food ingested along with seeds, etc.; and (3) the quality of the microhabitat where the seed is deposited, which will ultimately determine the probability of germination and establishment; the sites where the seeds are deposited will be determined by factors such as frugivore movements after fruit removal, frugivore habitat preferences, etc., while the quality of the microsite will depend on abiotic (light levels, soil texture and humidity, etc.) and biotic conditions (levels of predation, competition, herbivory, etc.).

The successfulness of recruitment resulting from frugivore activity, thus, depends on what type of fruit is selected, how it is processed, and the movements of the dispersers, and is further determined by the biotic and abiotic factors prevailing in the recipient microhabitat where the seed is dropped. Considering all this is crucial if we are to assess the demographic and evolutionary consequences of frugivore activity. With the available information, we know that the effects of the qualitative components of dispersal may erase the initial differences among dispersers in their quantity component, but more studies are needed to know which is more important determining the final pattern of plant recruitment.

### Linking Seed Dispersal Patterns with Seedling Establishment

Dispersal is the first of a series of stages that affects the subsequent plant regeneration process (Figure 5), determining the spatial arrangement and, consequently, the population dynamics of most plant species. In the case of fleshy-fruited plants, the facilitation effect of nurse or shelter plants is in turn enhanced by the fact that most seeds are deposited under shrubs that act as feeding source and shelter for frugivores (the so-called perching effect). The effect of nurse plants seems to be crucial in many ecosystems because they ameliorate the negative effect of summer drought in seedling survival, at least when resources are limiting, as it occurs in arid ecosystems.

However, in most cases, the recruitment dynamics is usually very complex, being the seed template produced by seed dispersal subsequently modified by other regeneration stages (from seed dispersal to seedling establishment). This is because processes acting at different stages are usually independent and 'uncoupled', and promote subsequently seed-seedling conflicts. For example, the deposition of large amounts of seeds by frugivores in a given microhabitat may be subjected to intense post-dispersal seed predation and/or be unsuitable for emergence or recruitment of seedlings. Moreover, such uncoupling among regeneration stages may be also variable across spatial and temporal scales and an increase of



**Figure 5** Diagram representing the different stages (in circles) and processes (in squares) affecting them along the plant regeneration cycle. The overall probability of recruitment is obtained from the product of the partial probabilities of recruitment of each stage.

variability in a given stage may produce spatiotemporal mosaics through the plant regeneration process. Still, another possible source of conflict in the plant regeneration process is seed size. In general, larger seeds tend to have a higher chance of seedling emergence or establishment but may also have a lower probability of being ingested by frugivores or escaping from postdispersal seed predators. These conflictive pressures will consequently affect the optimal value of seed size in many species to maximize the fitness through the overall regeneration process.

### Consequences of Seed Dispersal for Population Genetic Structure

In contrast to the great effort dedicated to figuring out the demographic consequences of dispersal, the effects of seed dispersal on the genetic structure of populations have received far less attention. Plant genes are dispersed either through haploid pollen or diploid seeds, and inheritance may be maternal (chloroplast DNA in angiosperms), paternal (chloroplast DNA in conifers), or biparental (nuclear DNA). Recent studies have revealed that zoochorous plant species have characteristically high levels of within-population genetic variation compared to other seed dispersal syndromes, and that such variation is associated with extensive gene flow via seed dispersal in addition to outbreeding via pollen flow. Moreover, when zoochorous populations are structured in space (e.g., fragmented populations, metapopulations), frugivores have shown to strongly influence the among-population gene flow via seeds. The tools provided by microsatellites have also provided unequivocal genetic fingerprints of source mother plants in the population, revealing a marked heterogeneity in the genetic composition of the seed rain in different microhabitats, and also making it possible to know the fraction of seeds that come from other populations. Therefore, despite their low occurrence in nature, LDD events can now be tracked at different scales (i.e., landscape, regional, or continental) by these genetic markers.

### Plant–Frugivore Networks: Interpreting the Biodiversity of Interactions

In many ecological communities, plant–frugivore interactions are a key process in the maintenance of diversity. At the community level, the interactions between plants and frugivores are integrated in complex webs of species interactions. The analytical methodology developed in the ecology of food webs has offered an ideal conceptual framework for the study of such mutualistic networks. This approach allows the description of the macroscopic structure of the entire web at the time that allows determining how fragile such interactions are in front of different types of disturbances (e.g., introduction of an alien species, changes in the abundance of particular species, extinctions, etc.). Common patterns emerging from these studies are: (1) a low number of strong dependences; (2) a high level of asymmetry in the interactions (thus if a plant depends strongly on a frugivore species, the animal depends weakly on the plant); and (3) a great heterogeneity in the strength of interactions among species. The three characteristics contribute to the maintenance of species coexistence in the community. A recent study performed in the Mata Atlantica of Brazil with this network approach has revealed strong levels of unpredictability in the final number of disturbed species as well as the seed dispersal collapse of a number of plants after the extinction of endangered vertebrate seed dispersers.

### Implications of Seed Dispersal for Conservation

Seed dispersal is universally considered important for biodiversity conservation. The structure of the landscape has strong effects on the distances traveled by seeds, regardless of whether they are dispersed by abiotic factors (wind) or by animals. Therefore, any type of disturbance, such as habitat fragmentation or habitat modification by an invasive plant species for instance, is likely to change the patterns of seed movement, the



**Figure 6** *Daphne rodriguezii* is a fleshy-fruited shrub endemic to the Balearic Islands that is in regression in those populations where the only disperser of the plant, the endemic lizard *Podarcis lilfordi*, has become extinct. Photos by Javier Rodríguez-Pérez.

patterns of seed recruitment, as well as the genetic structure of the plant populations. For wind-dispersed species, it is known that seeds travel much further distances in open landscapes than in dense forest, due to differences in the shape of the wind profile. On the other hand, plants depending on animals for seed movement are susceptible to dispersal failure when their seed vectors become rare or extinct. Disruption of the seed dispersal mutualism can have serious consequences for the maintenance of the plant populations. An increasing number of studies are showing how the populations of seed dispersers are being decimated, both in the tropics and in the temperate zones, and how this translates into a lower dispersal success of the plants depending upon them (Figure 6). In tropical areas in particular, the widespread decimation of dispersers by overhunting and habitat loss are expected to have devastating long-term consequences for the maintenance of tree species diversity. An excessive LDD of elements alien to ecosystems also represents a threat to biodiversity, especially if it goes along an insufficient dispersal of native species.

See also: Life Forms, Plants; Plant Ecology; Pollination.

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