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The efficacy of dispersal in relation to safe site area and seed production

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Summary. A model is developed to define the efficacy of dispersal in relation to safe site area and seed production. Efficacy is measured as the expected number of progeny from one parent. It is shown that maximization of efficacy does not depend on the density of safe sites. When safe sites are confined to a restricted area around the parent, and safe sites are small or few propagules are produced, dispersal curves with short tails are most efficacious; when safe sites are larger or when more propagules are produced, distributions with longer tails become more advantageous.

Introduction

Green (1983) developed a graphical model to describe the efficacy of dispersal in relation to safe site density. Efficacy was measured as the maximum number of safe sites that can be occupied by propagules. This is given by the shaded area in Fig. 1, and is equal to the number of propagules or safe sites, whichever is less, integrated over all distances from the parent. Maximization of this area by varying the shape of the dispersal curve, a process that may reflect the evolution of dispersal curves, gives the largest offspring under a specified safe site density. Green argues that "Dispersal curves with long tails are most advantageous for species with rare safe sites. For species with more abundant safe sites, a broad peak in propagule density and gentle decline with distance are more important features than maximum dispersal distance".

Although intuitively appealing, this conclusion can be shown to be incorrect. In the following, a model is developed using the expectation of the number of offspring from one parent as a measure of efficacy. This measure has a clearer biological interpretation than the one used by Green, because not all seeds actually land in safe sites and some land in sites that have already been occupied. The term "safe site" is used to denote locations that support the germination of a species' seeds and where only one plant eventually will become established. Therefore, the number of progeny is always less than the maximum number of safe sites that can be occupied (Fig. 2.I). The measure used by Green may be insusceptible to variation in the shape of the dispersal curve when safe sites are confined to a restricted area around the parent (Fig. 2.II), whilst the number of offspring still reflects these variations. The model calculates the expected number of progeny from one parent as a function of the dispersal curve. The total seed production by the parent, the safe-site density and the area of safe sites are the parameters involved.

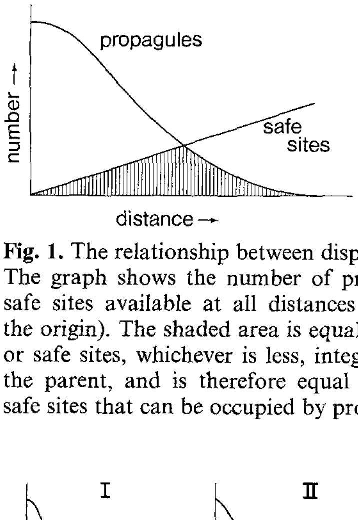

Fig. 1. The relationship between dispersal and safe site abundance. The graph shows the number of propagules and the number of safe sites available at all distances from the parent (located at the origin). The shaded area is equal to the number of propagules or safe sites, whichever is less, integrated over all distances from the parent, and is therefore equal to the maximum number of safe sites that can be occupied by propagules (Green 1983)

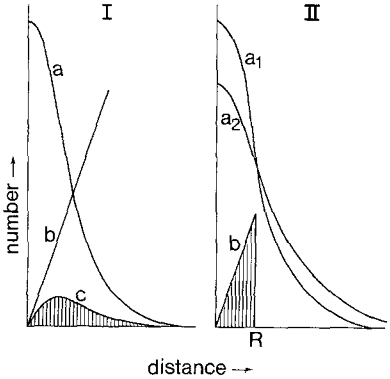

Fig. 2I, II. Measures of efficacy. The curves labeled *a*, *b* and *c* represent the dispersal curve, the distribution of safe sites and the distribution of the expected number of offspring respectively. **I** The shaded area gives the expected number of offspring from one parent. **II** The shaded area gives the maximum number of safe sites that can be occupied by propagules within a distance *R* from the parent. The distribution of safe sites has been cut down at a distance *R*. Variation of the shape of the dispersal curve within a certain range does not change the area. This is shown by the two dispersal curves, labeled a_1 and a_2 respectively, which yield the same number of safe sites that can be occupied

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An alternative model

It is assumed that safe sites are distributed uniformly or randomly. Safe sites may also be moderately clumped on a scale that is much smaller than the scale on which dispersal distances are measured. Then, the distribution curve of safe sites is a linear function through the origin (Fig. 2.I) and the safe site density is a constant when measured on the same scale as dispersal. It is also assumed that no appreciable overlap of safe sites, nor a measurable gradient of propagules within a single safe site exists.

For any dispersal curve, the expected number of propagules that land in safe sites between distances r and $r+h$ from the parent, where h is small, is given by

$$z \cdot N_r \cdot p \cdot A \cdot h \tag{1}$$

where z denotes the total seed production of the parent, N_r any distribution of relative frequencies of distances travelled by propagules, p the density of safe sites and A the area of a single safe site (in m^2). The expected number of safe sites between these distances is

$$2\pi \cdot p \cdot r \cdot h. \tag{2}$$

The ratio of (1) to (2) gives the expectation of the number of propagules per safe site as a function of distance from the parent:

$$N_r \cdot \frac{z \cdot A}{2\pi r} \; \mathit{def} \; L_r \tag{3}$$

When propagules do not adhere to each other and do not land or stay with different readiness in safe sites, the number of propagules in a safe site will be approximately Poisson distributed with an expectation L_r. Multiplication of (2) with the fraction of safe sites that are occupied by at least one propagule gives the distribution of the expected number of offspring.

$$2\pi \cdot p \cdot r \cdot (1\text{-}e^{-L_r}). \tag{4}$$

Integration over all distances from the parent gives the total numbers of offspring

$$2\pi \cdot p \cdot \int_0^\infty r \cdot (1-e^{-L_r}) dr. \tag{5}$$

If we consider two dispersal curves with different values of z and A, the curve that yields the largest offspring at a given density of safe sites will do so at any safe site density, because the integral in (5) does not depend on the value of p. The optimal dispersal is not influenced by the safe site density because the probability that a safe site contains a seed is not influenced by the density of safe sites. Of course the number of progeny does depend on the density of safe sites.

Since by definition no more than one plant per safe site will become established, the density of propagules must be reduced to diminish the number of multiple occupation of safe sites and increase the number of safe sites that are occupied by at least one propagule which is equal to the number of offspring. The probability of a seed to land in a safe site, and concomitantly the fraction of propagules that land in safe sites, is given by the product of safe site density and the area of a safe site, and does not depend on the shape of the dispersal curve, the probability of a seed to land in a safe site that has not already been occupied however does. Low densities of propagules are accomplished by dispersal curves with long tails. A plant should therefore disperse as far away as possible to maximize the number of progeny, no matter what the safe site density may be. This reasoning holds when safe sites are distributed within an area that is wider than any distance that could ever be covered by propagules.

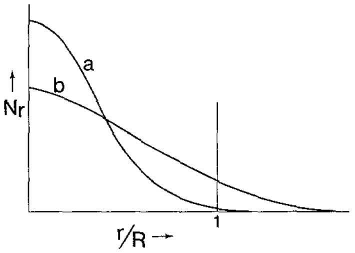

Fig. 3. Optimal dispersal curves at different values of $z \cdot A/R^2$. The curves labeled *a* and *b* represent Gaussian dispersal curves that have been optimized at $z \cdot A/R^2 = 0.01$ and 1.00 respectively, by varying the variance. Since R has been used as unit of distance, the vertical line at $r/R=1$ denotes the distance to which safe sites are confined

When safe sites are largely confined to a restricted area around the parent, dispersal should not be too far to prevent a major loss of seeds that land in an area almost depleted of safe sites. Dispersal should neither be too close to prevent mortality of seeds caused by multiple occupation of safe sites.

For mathematical conveniency it is assumed that safe sites are strictly confined within a radius R from the parent. The expected number of offspring is equal to (4) integrated over distances from zero to R. Maximization of this number by varying any parameter χ in N_r gives the highest efficacy. The solution of χ from

$$2\pi \cdot p \cdot \frac{\delta}{\delta\chi} \cdot \int_0^R r \cdot (1-e^{-L_r}) dr = 0 \tag{6}$$

gives the value of χ that is most efficacious. The factor p can be eliminated from (6). Maximization of efficacy is therefore independent of safe site density but depends on the total number of propagules produced and the size of a safe site because z and A cannot be eliminated.

We have not been able to solve Eq. (6) analytically. The shape of the dispersal curve that is most efficacious must be calculated by means of numerical integration under specified values of z, A and R. The effect of the total number of seeds produced or the area of a safe site can be investigated simultaneously, because both emerge as a single factor $z \cdot A$ in (3), (4) and (6).

Using R as unit of distance, the variance of dispersal that is most efficacious was calculated at different values of $z \cdot A/R$ for a normal (Gaussian) distribution of propagules. From Fig. 3 it follows that when safe sites are small or when a plant produces few propagules, distributions with a small variance, i.e. with a short tail, are most efficacious. When safe sites are larger or when more propagules are produced, distributions with longer tails are more suitable.

Discussion

Our model allows us to calculate optimal dispersal curves as a function of seed production, safe site area and boundary of the habitat. Optimal dispersal curves will also be influenced by other processes affecting the probability of seed survival or seedling establishment. Reduced establishment near the parent may be the result of, for instance, accumulation of autotoxic substances, interspecific competition or depletion of a nutrient supply.

Furthermore, Janzen (1970) has pointed out that seed predation is often higher close to the parent plant. This may be so if seed predators are either distance- or density-responsive. Although Janzen originally framed his hypothesis in relation to the abundance of tree species in the tropics and at first evidence was collected in this region (Janzen 1970, 1971), the validity of the hypothesis may be more general and the idea may also apply to trees or herbaceous plants in temperate regions (see examples in Howe and Smallwood 1982).

If we know the shape of the seed predation curve as a function of seed density or distance to the parent, we may proceed in a fashion analogous to Janzen (1970) and multiply the seed dispersal curve with the probability that a seed will escape from predation, to calculate the expectation of the number of propagules per safe site (L_r). We may then proceed as above to calculate the population recruitment curve. In general, density- or distance responsive predation will have the effect of shifting optimal dispersal curves to the right (more dispersal).

Pre-dispersal seed predation has the effect of decreasing Z and therefore shifting optimal dispersal curves to the left (less dispersal).

The situation may become different in the case of seedling predation. If the seedlings grow older the distribution of seedlings will become more alike Eq. (4) due to intraspecific competition. We can multiply the seedling distribution with the probability that a seedling will be missed by a predator to calculate the distribution of the expected number of offspring. If seedling predation is density dependent, the density of safe sites (p) cannot eliminated from the integral in Eq. (6). This is because p occurs both in Eq. (4) and in the density dependent probability that a seedling will mature.

Therefore the conclusion that safe site density is irrelevant to the optimization of dispersal curves holds in all mentioned cases of predation, except in the case of density dependent predation on seedlings.

The model presented in this paper is formulated under rather rigid conditions. Probably the most important one is the assumption that for safe sites occupied by seeds there is no relation between the number of seeds in a safe site and the probability, that an individual eventually will mature.

In nature such a relation may exist. It is likely, however, that the mean number of seedlings that mature per seed will diminish with increasing number of seeds per safe site. The model will therefore still be useful for a qualitative comparison of dispersal curves.

Green (1980) investigated the dispersal curves of ashes (Fraxinus spp.) and maples (Acer spp.). The dispersal curve of ash is long-tailed and the dispersal curve of maple has a broad peak and declines gently. Green (1983) tried to explain the difference between the dispersal curves by the difference in safe site density. Our analysis shows that this is incorrect and offers an alternative explanation.

Green (1983) notes that the mean safe site area for maples is smaller than for ashes, maples also produce less seeds than ashes (maples: 80,000–300,000; ashes 150,000–450,000; Schalk pers. com., 1983). The difference between the dispersal curves of the two species may therefore be explained by differences in seed production and safe site area and not by differences in safe site density.

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