

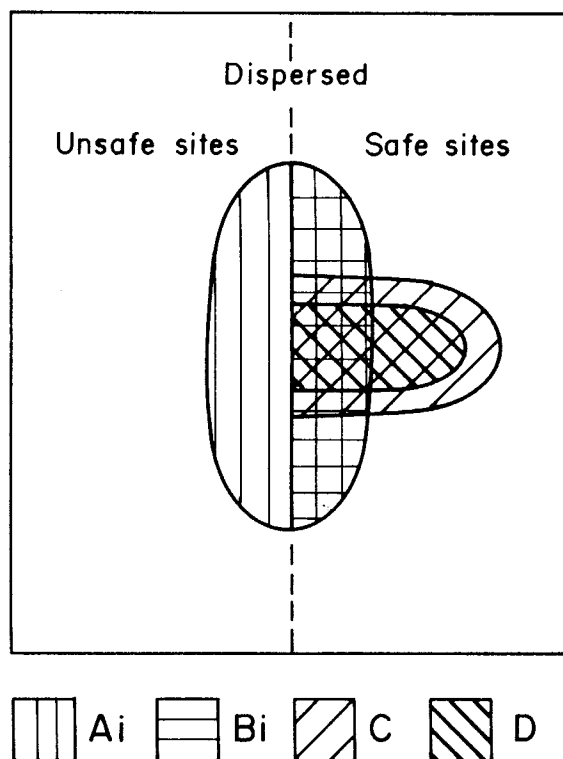
Dispersal quality in plants: how to measure efficiency and effectiveness of a seed disperser

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Seed dispersal by animals is often used as a classical example of animal-plant mutualism (Snow 1971, Mckey 1975, van der Pijl 1983). Although this interaction has received much attention (Wheelwright and Orians 1982, Herrera 1985, Howe 1989), the consequences of seed dispersal on plant demography and evolution remain poorly understood (Howe 1989, Jordano 1992). Many studies have attempted to evaluate the effect of different members of a disperser's coterie on a plant's performance (Mckey 1975, Herrera and Jordano 1981, Wheelwright and Orians 1982). None of these studies however, have used a clearly and well defined metric that allows making quantitative statements about the relative benefits for the plant derived from the disperser services. McKey (1975), for example, used the term dispersal quality, but did not provide a way to measure this quantity. More recently, Reid (1989) proposed that the quality of a disperser could be partitioned into two components: efficiency and effectiveness. Efficiency is the probability that a seed dispersed by a vector will lodge in a safe site and germinate; on the other hand, effectiveness is the proportion of seedlings in a plant population that a particular seed vector is responsible for disseminating. These definitions, although very precise, have not been expressed quantitatively. Here, we use Reid's definition to propose a quantitative metric to evaluate the effect of seed vectors on plant demography. In addition, we derive some properties of these metrics and apply them to a published data set to appraise their utility.

established seedling, a disperser's efficiency (G_i) can be defined as:

$$G_i = P(B_i | nC) = P(B_i) \times P(C|B_i) \quad (1)$$



Definitions

Given the following events, represented in a Venn diagram (Fig. 1): A_i : a seed is dispersed by agent i ($i = 1, 2, \dots, k$), B_i : a seed is dispersed to a safe site by agent i , C : a seed germinates, and D : a germinating seed becomes an

Fig. 1. Venn diagram to represent the probabilistic events which define efficiency (G_i) and effectiveness (S_i). A_i : a seed is dispersed by agent i ; B_i : a seed is dispersed to a safe site by agent i ; C : a seed germinates; and D : a germinating seed becomes an established seedling.

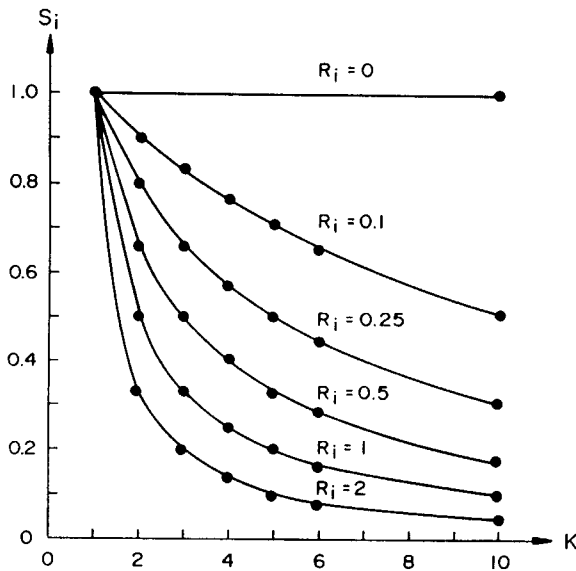


Fig. 2. Relationship between effectiveness of frugivore i (S_i , $i = 1, 2, 3 \dots k$) and the size of the frugivores guild (k), at different values of R_i ($R_i = G_0/G_i$); G_0 = average efficiency of the $k-1$ other frugivores, G_i = efficiency of frugivore i .

Assuming that germination success and dispersal to a safe site are independent events, a disperser's effectiveness (S_i) can be defined

$$S_i = P(A_i|D) \quad (2)$$

If all dispersed seeds of a focal plant are partitioned among k members of the frugivore coterie, then we can use Bayes theorem, to rewrite S_i as,

$$S_i = \frac{P(D|A_i) \times P(A_i)}{\sum_{i=1}^k (P(D|A_i) \times P(A_i))} \quad (3)$$

Efficiency and effectiveness have been defined independently (Reid 1989). We shall use eq. (3) to show that these concepts are related. Assume that 100% of the seeds germinating in safe sites survive to become seedlings (in the Venn diagram $C = D$; see Fig. 1), then

$$P(D|A_i) = P(D \cap A_i)/P(A_i) \quad (4)$$

and

$$G_i = P(B_i \cap C) = P(D \cap A_i) \quad (5)$$

Consequently, eq. (3) may be rewritten as

$$S_i = \frac{G_i}{G_i + \sum_{j \neq i} G_j} \quad (6)$$

which can be transformed into

$$S_i = \frac{1}{1 + G_0/G_i(k-1)} = \frac{1}{1 + R_i(k-1)} \quad (7)$$

where G_0 equals

$$\sum_{j \neq i} G_j/k-1,$$

i.e., the average efficiency of dispersers excluding disperser i and the ratio $R_i = G_0/G_i$, compares the efficiency of disperser i relative to the average efficiency of the $k-1$ other dispersers. The value R_i is 0 when all effective dispersal is achieved by disperser i , and is infinity when species i deposits all seeds in unsuitable places. Note that S_i decreases as k , the size of the disperser's coterie, increases. The impact of a given frugivore is always decreased as the size of the coterie of dispersers increases. However, the rate of decrease in S_i as k increases is modulated by R_i . When the efficiency of disperser i is high (i.e., R_i is small), adding dispersers to the coterie will have a small effect on S_i (Fig. 2). Conversely, for dispersers with low efficiency (i.e., R_i is large), adding species to the coterie will have a strong decreasing effect on S_i (Fig. 2).

Application

Effectiveness is difficult to estimate in the field. Dispersed seeds must be assigned to the agent (s) responsible for their dissemination and they must be tagged and monitored up to seedling establishment (Wheelwright and Orians 1982, Reid 1989). Our model enables a more easy (but indirect) estimation of effectiveness. In fact, eq. (6) establishes that in order to evaluate S_i , we only need to know the efficiency of each frugivore ($i = 1, 2, \dots k$) in the guild. To evaluate G_i , we use eq. (1) which is expressed in terms of $P(B_i)$ and $P(C|B_i)$.

$$P(B_i) = \frac{\text{no. seeds dispersed by disperser } i \text{ to safe sites}}{\text{no. total of seeds dispersed by disperser } i} \quad (8)$$

$$P(C|B_i) = \frac{\text{no germinated seeds}}{\text{no. seeds dispersed by agent } i \text{ to safe sites}} \quad (9)$$

The knowledge of the safe sites, that is, such microsites that maximize germination and establishment (Harper et al. 1981) is an essential requisite to estimate effectiveness with our method. In some cases, this kind of knowledge may be difficult to obtain because we must measure the environment at the scale of a seed (Harper 1977). However, we may have a gross estimation of safe sites if we

Table 1. Dispersal quality of *Dicaeum hirundinaceum* (mistletoebird) and *Acanthagenys rufogularis* (spiny-checked honeyeater) on the mistletoe *Amayema quadrang*. Estimations were obtained from the original data set of Reid (1989).

	$P(B_i)^1$	$P(C B_i)^2$	G_i^3	S_i^4	S_i^5
Mistletoebird	0.077	0.88	0.067	0.98	0.834
Honeyeater	0.002	0.76	0.0015	0.02	0.166

(1) proportion of seeds deposited on live branches (safe sites) of *Acacia papyrocarpa* (Reid 1989: Table 1).

(2) mean percentage of germination of mistletoe seeds obtained under lab conditions. These estimates were obtained from experiments made on four different dates (Reid 1989: Table 2).

(3) Values obtained by multiplying $P(B_i) \times P(C|B_i)$.

(4) Values obtained from eq. (6) of this study.

(5) Values obtained from the proportion of seedlings 0–1 month old, observed on live branches of *A. papyrocarpa* (Reid 1989: Table 6).

know the regeneration niche (sensu Grubb 1977) of the focal plant, that is if it is shade-tolerant and/or shade-intolerant (Bustamante et al. 1992). Once we obtain this information, we may evaluate the number of seeds dispersed by disperser i to safe sites and finally to obtain S_i .

The only data set available to evaluate S_i empirically is that of Reid (1989). We will use it to illustrate how our method works. Reid (1989) compared the efficiency and effectiveness of two frugivores birds: *Dicaeum hirundinaceum* (mistletoebird) and *Acanthagenys rufogularis* (spiny-checked honeyeater). These birds are the main dispersal agents of the mistletoe *Amyema quadrang* which parasitizes the western myall *Acacia papyrocarpa* (Leguminosae) in South Australia.

Estimation of $P(B_i)$

The safe sites for seeds of mistletoe are the thin young stems of the western myall *Acacia papyrocarpa* (see Reid 1989). Therefore, we may estimate $P(B_i)$ by using Reid's data which describe the proportion of seeds deposited on live branches for the two bird species (Table 1).

Estimation of $P(C|B_i)$

To estimate $P(C|B_i)$, for each bird species, we used the average proportion of germination reported from four experiments performed by Reid (1989) in November 1981, January 1982, March 1982 and September 1982 (Table 1). By multiplying $P(B_i)$ and $P(C|B_i)$, we obtain G_i . Finally, using eq. (6) we obtain S_i for each bird species (Table 1). Our results show that the mistletoebird is by far the most efficient and effective compared with the spiny-checked honeyeater. These results do not agree with those of Reid (1989) who concluded that both birds were equally efficient, but the honeyeater was the most effective. More recently, however, the results obtained by Murphy et al. (1993) working with the same system, are concordant with our estimations.

In order to test our method, we compared our estimated S_i with the observed proportion of mistletoe seedlings coming from each bird species (Reid 1989: Table 8). We

only used the seedlings of the first age class (0–1 month; $n = 32$), because we assumed that as seedlings become older, the effect of frugivores on recruitment is diluted and other ecological factors (e.g., competition, herbivory) become more important.

The seedlings developing from seeds dispersed by the mistletoebird were recruited in a higher proportion than that for the honeyeater (Table 1). Clearly, the two procedures (i.e., the method advanced in this study and the observed seedling survival pattern of Reid's data) exhibit the same pattern: the mistletoebird are more effective at dispersing seeds than the honeyeater. Thus, the concordance between an estimation derived from a probabilistic model and an empirical evaluation lends support to our method to compare effectiveness of dispersal agents in other studies.

Conclusions

We have put forward a quantitative method which relates two important concepts of common use in dispersal ecology: efficiency and effectiveness. This method serves to evaluate S_i indirectly. We think that the definitions and the procedure advanced in this note can be used in field studies in order to clarify the effects of frugivory on the demography of plants.

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