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## TESTING THE DISPERSION OF JUVENILES RELATIVE TO ADULTS: A NEW ANALYTIC METHOD<sup>1</sup>

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**Abstract.** When there are two types of points in a plane, their "relative dispersion" is the tendency for one type to be located near or far from the other. We present a method for describing and testing relative dispersion. Our motivation in developing this test was the need to analyze the dispersion of juvenile plants relative to conspecific adults. To demonstrate the usefulness of the method, we simulated plant populations under randomness and under five alternative "dispersion-generating processes." The results from analyses of these populations illustrate the method and its use in the interpretation of dispersion pattern. In addition, these results provide insight into the types of patterns resulting from these dispersion-generating processes.

**Key words:** adults; clumping; dispersion; edge effects; juveniles; maps; multitype; null distribution; overdispersion; pattern; point; seed predator.

### INTRODUCTION

The "dispersion" of points in a plane (e.g., plants in a mapped plot) describes their tendency to be located near or far from one another. When two types of points can be recognized, "relative dispersion" can be defined as this tendency for one type relative to the other. Our particular interest here is in the dispersion of juvenile plants relative to conspecific adults. We present a method for describing and testing randomness of relative dispersion of two types of points in a bounded plane. We will refer to these types as juvenile and adult plants, but the analysis is applicable whenever multitype patterns are of interest. Examples include different species of plants or animals, cell types in a tissue sample, and objects in archaeological sites. Plant ecologists are interested in dispersion largely because knowledge of dispersion patterns can provide insight into processes affecting the distributions of plants. We will demonstrate here how such insight can be improved by analysis of relative dispersion.

### THE METHOD

It is assumed that the data set to be analyzed consists of a map of juvenile and adult locations. The juveniles must be in a bounded area, but adults may be outside that area. It will further be assumed that the area or plot is rectangular, but the method can be adapted to any shape. Even areas which are not contiguous can be subjected to a single analysis.

The proposed measure of relative dispersion is the observed cumulative distribution of distances from ju-

veniles to respective nearest adults. When this distribution is plotted on the same axes as an appropriate null distribution, it is easy to see where, and by how much, relative dispersion deviates from that expected under the null hypothesis. The null distribution of primary interest here is the distribution of juvenile-to-nearest-adult distances expected under the random hypothesis. This hypothesis states that juveniles are located in the mapped area independently and at random, i.e., that each location in the plot is equally likely to contain a juvenile, and that the presence of a juvenile at one location does not influence the probability of occurrence of juveniles at other locations. This null distribution can be used not only for comparison in the descriptive graph, but also in a test of the random hypothesis.

#### *The null distribution*

Under the random hypothesis the probability that a juvenile will be less than or equal to a given distance  $s$  from its nearest adult neighbor is equal to the proportion of the total area that is within that distance of any adult. Thus, the cumulative distribution function of juvenile-to-nearest-adult distances under the random hypothesis is:

$$F(s) = \frac{1}{A} \int_{x=0}^{x_{\max}} \int_{y=0}^{y_{\max}} I(s) dy dx, \quad (1)$$

where  $A$  is the total area in the  $x_{\max}$  by  $y_{\max}$  plot, and  $I(s)$  is the indicator function:

$$I(s) = \begin{cases} 1, & \text{Min } \{\sqrt{(x-a_i)^2 + (y-b_i)^2} \\ & i = 1, 2, \dots, n\} \leq s; \\ 0, & \text{otherwise.} \end{cases} \quad (2)$$

<sup>1</sup> Manuscript received 25 March 1985; revised and accepted 14 November 1985.

Here  $(a_i, b_i)$  are the coordinates of the  $i^{\text{th}}$  adult, and there are  $n$  adults. For simplicity it is assumed that the plot is oriented such that two of its sides form the positive  $x$  and  $y$  axes.  $I(s) = 1$  for all  $(x, y)$  values in the plot which have a nearest adult distance  $\leq s$ ; thus, the integral in Eq. 1 computes the area in the plot within which all points are less than or equal to each distance  $s$  from the nearest adult. Dividing by the total area results in the desired probabilities. Since  $F(s)$  is a function of  $x_{\text{max}}, y_{\text{max}}$ , and all  $(a_i, b_i)$ , it is conditional on the plot dimensions and adult locations. This conditional property is advantageous, eliminating problems with "edge effects" and dependency among observed distances such as those present in the Clark and Evans (1954) nearest neighbor test of single type dispersion (Ripley 1981).  $F(s)$  requires numerical integration, but can be calculated to any degree of accuracy.

The null hypothesis that juveniles are located at random with respect to adults can be tested using a Kolmogorov-Smirnov (KS) test. This test compares  $D$ , the maximum difference between the observed and null distributions, with a critical value based on the number of distances used in calculating the observed distribution (the number of juveniles in the data set). Because the KS test assumes that  $D$  is the maximum over all differences, the difference between the distributions should be checked as often as possible. Infrequent comparison of the distribution reduces the power of the test.

When there are distances at which the observed number of juvenile-to-nearest-adult distances is greater than expected under the random hypothesis, we refer to juveniles as being "relatively clumped" at that distance (scale). For example, if half of the juvenile-to-adult distances were  $\leq 20$  m, and the expected proportion was only 30%, we would describe juveniles as clumped relative to adults at 20 m. "Relative overdispersion" at a given distance describes the condition where fewer of the juvenile-to-nearest-adult distances than expected are within the given distance. Relative dispersion has meaning only with respect to a specific scale. As will be seen, juveniles can be overdispersed relative to adults at one distance and clumped relative to adults at another. We will refer to relative clumping as "significant" if the maximum excess by the observed distribution is at least the critical value of  $D$ . Similarly, significant relative overdispersion describes the condition where the observed distribution falls below the null by at least the critical  $D$ . Single type dispersion patterns will be described simply as "clumped" or "overdispersed," but juveniles exhibiting single type clumping can also be referred to as "juveniles clumped relative to juveniles."

When dispersion at a particular scale is of interest a priori, a chi-square test is preferable to the KS test. The KS test must be able to detect nonrandomness at all scales, thus will be less powerful than a chi-square test when addressing only a finite (small) set of scales.

For example, if one believes that juveniles tend to be within 50 m of adults, the expected number of juveniles each  $\leq 50$  m from an adult can be calculated using the null distribution, and the observed number tested against this expectation using a chi-square test.

#### *Summary of the method of analysis*

The procedure can be summarized as follows.

- 1) Calculate the null distribution from plot dimensions and adult coordinates.
- 2) Calculate the observed distribution from juvenile and adult coordinates.
- 3) Graph the observed and null distributions for descriptive purposes.
- 4) Test the maximum difference between observed and null distributions using the KS test (or a chi-square test if a particular scale has been specified).

A BASIC language program which performs steps 1, 2, and 4 is available.<sup>2</sup>

#### ANALYSIS OF SIMULATED POPULATIONS

To investigate the usefulness of this method of analysis we have applied it to a series of populations of adults and juveniles simulated under the random hypothesis and under five alternative hypotheses. The populations were constructed as follows. In a  $400 \times 200$  m rectangular plot, 40 adults were located independently and at random. For each of the six cases, 200 juveniles were located according to the rules of the case. This produced a set of six populations, each with the same adult locations but different juvenile locations. The dispersion patterns in each population were analyzed using two approaches. First, single type dispersion (juveniles relative to juveniles) was tested using Morisita's (1959) index and  $20 \times 20$  m quadrats. Second, the dispersion of juveniles relative to adults was tested using the approach proposed here. This entire procedure was repeated 100 times, i.e., 100 adult populations were simulated, each with six different sets of juveniles. The same adults were used for each set of six juvenile alternatives in order to minimize any effects chance variation in adult pattern might have on the comparative results. Fig. 1 presents maps of a representative set of six simulated populations. The results from analyses of these six populations are shown in Fig. 2.

#### *The six cases of juvenile distribution*

The six juvenile distributions, with possible biological interpretations, follow.

<sup>2</sup> See ESA Supplementary Publication Service Document No. 8632 for 9 pages of supplementary material listing two versions of this program. For a copy of this document, contact the senior author or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853-2701 USA.

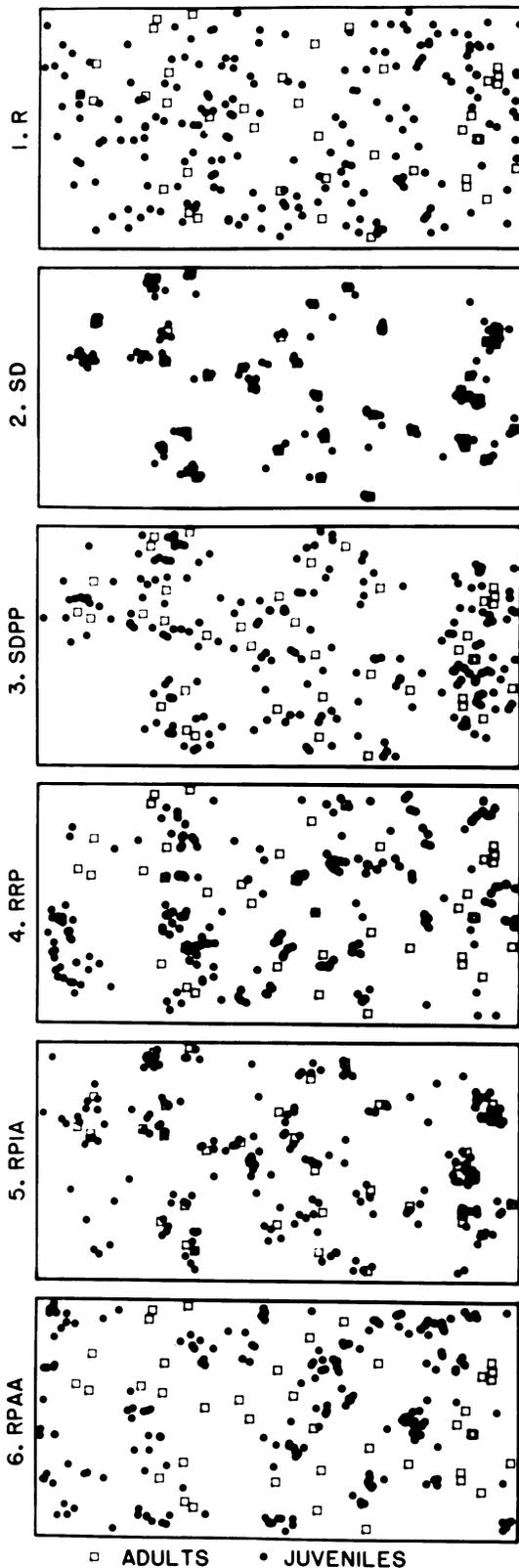


FIG. 1. Maps of a representative set of populations, plotted on a  $400 \times 200$  m area, resulting from the six different processes generating simulated juvenile (●) populations. The adults

1) *Randomness* (R). This is the “null” case. The  $x$  and  $y$  coordinates of each juvenile were chosen, independently, from uniform distributions. It is difficult to suggest plausible natural causes of such dispersion patterns. One scenario which could produce such a pattern requires dependence for establishment of seedlings on resource patches which are: (1) randomly and independently distributed, (2) sufficiently ephemeral to be located independently and randomly with respect to patch locations at the time of establishment of earlier generations, and (3) each too small to support more than one juvenile at the size mapped. In addition, seed fall in the mapped plot would have to be dense enough, and widespread enough, to insure that each resource patch contains enough seeds to make all patches equally likely to “produce” a juvenile. Random pattern is more likely the result of unlikely outcomes of nonrandom processes, or population sizes too small to permit an investigator to detect nonrandomness.

2) *Seed dispersal* (SD). Patterns of seed dispersal result in initial distributions of juveniles which are unlikely to be random. When seeds tend to fall near, rather than far, from their parent, the expected result is clumping of juveniles relative to both other juveniles and adults. Such patterns were simulated by locating five juveniles from each adult via an artificial seed dispersal distribution. The direction from the “parent” adult was chosen at random. The distance ( $w$ ) was chosen from the exponential distribution,

$$F(w) = 1 - \exp[0.1 \cdot \ln(0.2) \cdot w], \quad (3)$$

with parameters selected such that 80% of juveniles would be expected to lie within 10 m of their “parents.” Here, as in all subsequent cases, any juveniles falling outside the plot were replaced.

3) *Seed dispersal plus a seed or seedling predator* (SDPP). In nature, initial distributions of juveniles due to seed dispersal are subsequently modified by any nonrandom mortality. One possible source of such mortality which has received much attention is predation by a seed or seedling predator which is more likely to kill juveniles located near adults (Janzen 1970, Hubbell 1979, 1980, Howe and Smallwood 1982). This alternative was simulated by first locating five juveniles per adult according to the seed dispersal distribution used in case 2. Juveniles within 10 m of any adult were, however, replaced if they failed to survive the effects of a seed predator. The probability of surviving the predator was .001 if the nearest adult distance was  $< 8$  m, .01 between 8 and 10 m, and .15 between 10 and 12 m. The dispersion patterns which might result in this case are not easy to predict. Janzen (1970) sug-

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(□) have the same locations in each population in the set. The six processes are: R = random, SD = seed dispersal, SDPP = seed dispersal plus a seed or seedling predator, RRP = random resource patches, RPIA = resource patches include adults, RPAA = resource patches avoid adults.

gested that such a seed predator would result in overdispersion of the population. However, as Hubbell (1980) pointed out, such a result may require very good seed dispersal and/or a very efficient predator. Depending on the parameters chosen to simulate dispersal and predation, the result may be clumping close to adults, overdispersion, or perhaps clumping away from adults.

4) *Random resource patches (RRP)*. If juveniles are unlikely to survive unless they happen to be located in patches of some resource or collection of resources, clumped patterns of juveniles may result. Here we simulated the possibility that such resource patches were located independently of each other and randomly with respect to adults. Since juveniles are likely to depend on the same types of resources as did their parents, this alternative requires a scenario similar to that suggested for case 1. In the present case, however, each resource patch must be capable of supporting more than one juvenile, and seed fall must be uniform enough to permit the number of juveniles per patch to be independent of proximity to adults. Simulations located 40 patch centers independently and at random in the plot. Four juveniles were located independently and at random within 10 m of each patch center (all locations within the patch were equally likely). Forty additional juveniles were located independently and at random within the plot. Thus, the dispersion patterns of juveniles simulated here (and in cases 5 and 6) are analogous to those in case 2 in that  $\approx 80\%$  of the juveniles were located in 20 m diameter clumps, and  $\approx 20\%$  were more widely distributed.

5) *Resource patches include adults (RPIA)*. Here it is assumed that resource patches are permanent, so that adults and juveniles tend to be located in the same clumps. Patchy edaphic or topographic factors favorable to a particular species could lead to this situation. Simulated juveniles were located as in case 4, except that centers of resource patches were located at random within 10 m of adults. Patch centers outside the plot were replaced. Dispersion patterns resulting from these assumptions should be analogous to those in the "seed dispersal" case (case 2); juveniles should be clumped with respect to both juveniles and adults.

6) *Resource patches avoid adults (RPAA)*. This final alternative would result if resource patches which favor juveniles, such as light-gaps favoring tree seedlings, could not include adults. Juvenile locations were simulated as in case 4, except that any patch centers within 20 m of an adult were replaced. Locating the edge of patches at least 10 m from adults simulated, e.g., the effect of adult canopies which preclude light-gaps. The expectation here is that juveniles will be clumped with respect to other juveniles, but overdispersed with respect to adults.

## RESULTS

The questions addressed in analyses of these simulated populations (Table 1) were: (1) does the proposed

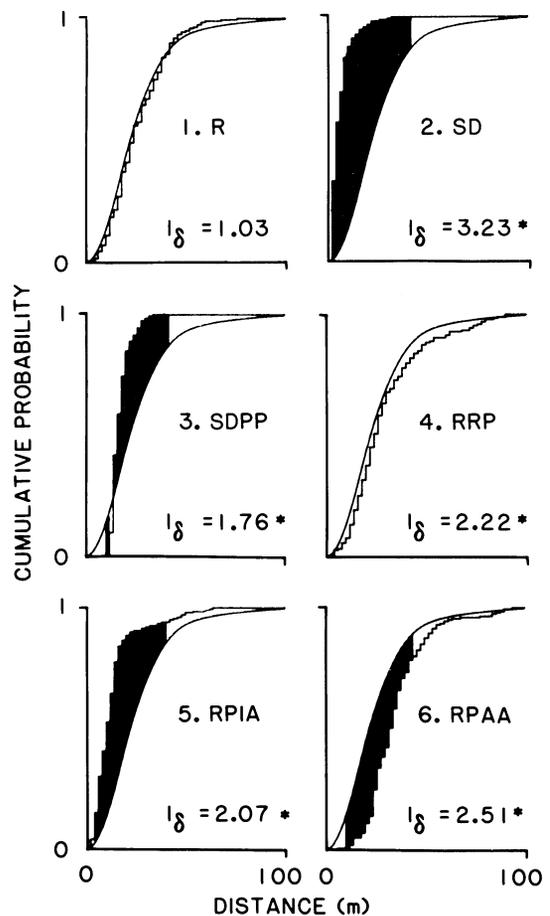


FIG. 2. Results of analyses of the populations in Fig. 1. The null distribution of nearest adult distances is the same in each case. The observed distribution is the step function. When the difference between the distributions is larger than the critical value of the Kolmogorov-Smirnov statistic  $D$  ( $P < .05$ ), the area between the two curves has been represented as filled. \* indicates significance ( $P < .05$ ) of Morisita's index ( $I_\delta$ ).

test of nearest adult distances reject the correct proportion of the time when the null hypothesis is true? (2) does it reject when the null is false? and (3) does it provide information useful in interpretation of dispersion pattern? These results should also tell us something about the type of dispersion patterns resulting from the six simulated "dispersion-generating processes."

The random null hypothesis is true only in case 1. Here Morisita's index applied to juveniles averaged nearly its theoretical value of 1. For both this index and the test of nearest adult distances, the number of rejections was less than the five expected, but for each method the difference was not significant (chi-square tests,  $P > .05$ ).

The proposed test also performed well when the null hypothesis was false. In case 2, seed dispersal resulted in significant clumping relative to juveniles (Morisita's

TABLE 1. Results from analyses of simulated population.

Case*	Morisita's index†		Test of nearest adult distances‡								
	MMI	VMI	Rejections		Significant clumping			Significant overdispersion			Both
			C	O	RC	MSRC	VSRC	RO	MSRO	VSRO	
1. R	0.98	0.01	0	2	3	22.0	8.00	0	...	...	0
2. SD	3.11	0.13	100	0	100	10.8	1.69	0	...	...	0
3. SDPP	1.56	0.04	93	0	100	20.7	1.49	100	10.5	0.77	100
4. RRP	2.30	0.07	100	0	11	23.1	39.54	10	21.4	68.84	0
5. RPIA	2.21	0.05	100	0	100	14.9	1.47	0	...	...	0
6. RPAA	2.59	0.12	100	0	0	...	...	100	21.5	5.49	0

\* Cases named in Fig. 1 legend, and detailed in Analysis of Simulated Populations: The Six Cases of Juvenile Distribution.

† Statistics: mean (MMI) and variance (VMI) of Morisita's (1959) index for all populations, and number of clumped (C) and overdispersed (O) rejections.

‡ Statistics: RC is the number of populations with significant relative clumping, and RO is the number with significant relative overdispersion. For the populations with significant relative clumping, MSRC is the mean of the distances at which the maximum positive difference (D) between the distributions occurred, and VSRC is the variance of those distances. MSRO and VSRO are the mean and variance of the analogous distances where populations show significant overdispersion.

index) and adults (test of nearest adult distances) in all populations. When the effects of a predator were added (case 3), an interesting result was obtained. Juveniles were significantly clumped in 93 populations; however, the test of nearest adult distances revealed that relative to adults they were clumped at some scales, and overdispersed at others. Fig. 2 shows a case 3 population exhibiting this pattern. The seed predator was effective enough close to adults to result in relative overdispersion, but the clumping effect of seed dispersal was dominant at greater distances.

The six cases can be viewed as two parallel groups; the first three assume a homogeneous "environment," while the last three assume heterogeneity which could result in clumping of juveniles. Case 4 is analogous to case 1 in that juveniles are located at random relative to adults. In case 4, however, dependence on patchy resources results in a lack of independence among juvenile locations. The random hypothesis for relative dispersion is false here only because of this lack of independence. Of course, juveniles are located nonrandomly with respect to other juveniles, and Morisita's index always detected significant clumping. Relative to adults, however, lack of independence resulted in rejection of the null hypothesis only 21% of the time. This relatively low rate of rejection is not surprising, since the dependency is weak in these populations. (On average, a juvenile location is dependent on only 1.2% of the other locations.)

The final two cases resulted in the expected dispersion patterns. Juveniles were always clumped according to Morisita's index; relative to adults they were clumped when resource patches included adults, and overdispersed when patches avoided adults.

Comparison of results from different cases demonstrates the usefulness of the test of nearest adult distances for interpretation of dispersion pattern. When juveniles were nonrandom relative to adults (cases 2, 3, 5, 6) the test always reached this conclusion. When they were random relative to adults but not indepen-

dently distributed (case 4), the test rejected 21% of the time. It was also able to differentiate between juveniles clumped (cases 2 and 5) versus overdispersed (cases 3 and 6) relative to adults. However, relative clumping or overdispersion due to biological processes such as seed dispersal or predation cannot, in general, be distinguished from similar dispersion patterns resulting from patchy resources. A different choice of seed dispersal distributions for the simulated populations in case 2 could produce dispersion patterns closely matching those resulting from dependence on permanent resource patches in case 5.

In consideration of these simulations, two final points should be made. First, detection of nonrandomness with Morisita's index is dependent on the relationship between quadrat size and scale of clumping or overdispersion. Here 20 × 20 m quadrats were "aimed" at the scale of clumping simulated; thus, the near-perfect performance of Morisita's index when the null hypothesis was false is almost certainly better than could be expected when the scale is not known. Finally, this analysis of simulated populations should not be viewed as a power analysis of the proposed test. A power analysis would vary the numbers of both adults and juveniles, the parameters and distributions generating simulated populations, and the plot shape. The results with simulated populations presented here, however, demonstrate the ability of the test to correctly reject or fail to reject the null hypothesis, and to provide a useful description of relative dispersion pattern.

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