The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis

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The Janzen-Connell hypothesis explains the maintenance of tropical diversity through the interacting effects of parent-centered dispersal patterns and distance- and density-dependent propagule survival. These effects were thought to support regular spacing of species within tropical forest, enhancing diversity. One of the predictions of the hypothesis is that seed and seedling survival should improve with increased parental distance. Although there are many independent tests of this hypothesis for individual species, there are few synthetic studies that have brought these data together to test its validity across species. This paper reports the results of a meta-analysis of the effect of distance on enhancing propagule survival, employing an odds-ratio effect size metric. We found no general support for the distance-dependent prediction of the hypothesis, and conclude that further testing to explore this hypothesis as a diversity-maintaining mechanism is unnecessary. However, we did find that distance from parent slightly reduces survivorship in the temperate zone, as contrasted with the tropics, and we saw stronger evidence in support of the hypothesis for seedlings than for seeds. The phenomenon of enhanced propagule survival with distance from the parent may be important for the population biology of particular species, but it is not a general phenomenon across communities, life history stages or life forms.

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Thirty years ago, two papers were published that proposed a suite of testable hypotheses about the processes maintaining diversity in tropical forests. At the time, it was thought that within a forest, individuals from each species of tropical tree were more regularly spaced than would be expected by a random process (Black et al.

1950, Pires et al. 1953) and that this facilitated the maintenance of high tree diversity. Janzen (1970) and Connell (1971) proposed that this pattern was the result of the interacting effects of clumped seed dispersal patterns focused on parent trees and the top-down effects of density- and distance-dependent behavior of seed, seedling and sapling predators. Under the hypothesis, recruitment only occurs under a small "population recruitment curve" (Janzen 1970) that is centered at some distance from parent trees. At this distance, seeds are available for germination and some germinating juveniles may survive. It was hypothesized that this process prevents the recruitment of offspring in close proximity to parent plants and promotes regular tree spacing. Of the five general predictions that Janzen made, the first was that the probability of survival of seeds to adulthood should increase with distance from the parent plant (Janzen 1970 p. 517, General prediction No. 1).

Connell (1971) further suggested that this effect should be stronger in seedlings than in seeds. His reasoning was that very few seeds are ever likely to survive, regardless of their location, given the multitude of processes that contribute to their deaths. However, insects and disease organisms with pathogenic effects on adults can have terminal, predatory effects on smaller seedlings with fewer resources to offset loss to damage. This process, he suggested, reduces the likelihood of offspring recruitment in areas of high surviving seed density which occur in close proximity to the parent and enhances regular spacing in tropical forests. He supported this contention with observational studies showing that seedlings located in clumps of conspecifics were less likely to survive than those in mixed species clumps. He also showed that the effect declined with increasing plant height (Connell 1971, Connell et al. 1984), suggesting that distance-dependent mortality is strongest at the seedling stage.

Does this process support species diversity in the same way everywhere? Janzen (1970) suggested that host specificity of seed consumers, herbivores and plant pathogens is greater in the tropics than it is in the temperate zone. Because a greater proportion of the temperate herbivore complex is composed of generalists (Harper 1977, Howe and Westley 1988) foraging should be less directed to specific targets. In contrast, the increased specificity of pathogens and predators should enhance the regular spacing of trees in the tropics. If true, this would predict that parental distance has a weaker effect on offspring survival in the temperate zone than in the tropics.

Howe and Smallwood (1982), whose work focused on plant population dynamics rather than overall community diversity, expanded on the idea that distance enhances survival, not just in the tropics, but in general. They suggested that not only does the dis-

tance a propagule moves from the parent enhance the probability of recruitment (escape hypothesis, a general form of prediction 4 of the Janzen-Connell hypothesis) but that propagule dispersal by trees to newly created forest gaps, which have both low adult density and altered seed predation probabilities, reduces the overall probability of juvenile predation (colonization hypothesis). Similarly, directed dispersal to habitats favoring seedling growth is also hypothesized to increase the chances of recruitment (directed dispersal hypothesis). Although targeted towards population rather than community dynamics, these ideas are components of the general predictions made by Janzen (1970). Data investigating these somewhat different hypotheses also contribute to an effective exploration of the distance-dependent component of the Janzen-Connell hypothesis.

The survival-enhancing effects of distance from parent plants have been explored by many researchers. The vast majority of tests have focused on single species, either experimentally examining how seed and seedling mortality rates change with distance from adults or comparing mortality rates between adjacent environments (e.g. intact forest and gaps or open fields). Such experimental and observational tests have taken place in both the tropical and temperate zones, and are designed to explore influences on the distribution of adult plants within a community. The studies have explored survival patterns for trees as well as shrubs and herbs and vary widely in duration and experimental seed or seedling density. All these factors may contribute to variation in the effect of distance on propagule survival.

Syntheses of the results from these numerous studies have met with mixed results. Clark and Clark (1984) tallied the numbers of studies that supported either density-dependent or distance-dependent components of the hypothesis and concluded that both components were supported. Willson (1988), examining the Howe and Smallwood (1982) escape hypothesis, compared seed mortality in intact and exposed or disturbed habitats for a variety of species and found virtually no patterns in seed predation intensity in either temperate or tropical habitats. Given the differing conclusions that these approaches have yielded, it is clear that a different strategy is required to explore the validity of this component of the Janzen-Connell hypothesis.

Meta-analysis is an emerging statistical tool in the ecological sciences that facilitates synthesizing the research results of multiple empirical studies that explore the same general question (Gurevitch and Hedges 1993, Arnquist and Wooster 1995). By devising a metric to summarize experimental results across many different experiments, meta-analyses statistically explore the magnitude of support for the hypothesis

under consideration. Thus the technique is superior to traditional vote-counting methods because it makes it possible to generalize results across experiments and systems and quantify the magnitude of particular ecological effects, such as how strongly distance from parent influences propagule survival or how the magnitude of the effect differs across functional groups. Meta-analysis is quantitative, objective and embraces the inherent variation present in most ecological processes.

Some workers have objected to the application of meta-analysis because its results are confounded by publication bias; it has been shown in some settings that studies showing significant results are more likely to be published than those not showing significant results (Csada et al. 1996, but see Bachau 1997). However, it is possible to explore publication bias within data sets for meta-analysis using a variety of graphical, modeling and statistical techniques. These approaches allow for quantification of bias if it exists.

The distance aspect of the Janzen-Connell hypothesis is very amenable to testing through meta-analysis for several reasons. There are a large number of experiments in the literature addressing whether distance enhances propagule survival using a wide variety of plants. The spatial patterns of seed and seedling predation and survival have been explored from both animal and plant perspectives, exploring many independent hypotheses and reducing the potential for publication bias. Further, because this group of experiments is so large, excluding data sets with incomplete details (missing N, variance, replication) or poor design does not reduce the number of experiments included below a useful level. This situation is ideal for exploring the hypothesis as well as axillary, related questions.

Our primary objective was to use meta-analysis to examine the hypothesis that seed and seedling survival is enhanced with increasing distance from parent plants. Because we included studies considering distance from parent plants both literally, in terms of meters from a target parent plant, and figuratively, comparing survival of seeds in a habitat where adults are found (often under intact plant canopies) to one where adults are less dense (often in gaps or adjacent fields), we were able to examine the relative magnitude of support for the escape hypothesis with that for the colonization and directed dispersal hypotheses. We also compared the magnitude of this effect on seeds and seedlings, in the temperate and tropical zones, and on different life forms (trees, shrubs and herbaceous species). A regression approach was used to explore the effects that distance from parent plant (in meters), experimental propagule density, and study duration had on propagule survival. We also examined the role that publication bias might have in altering our conclusions.

Methods

Literature search

We chose ten major journals that we expected to publish field experiments on seed and seedling predation. We examined issues of the American Journal of Botany, American Midland Naturalist, American Naturalist, Biotropica, Canadian Journal of Botany, Ecology, Journal of Ecology, Journal of Tropical Ecology, Oecologia, and Oikos published between 1970 and 1998 for appropriate articles. Internet searches were also conducted using online versions of the Science Citation Index and Biological Abstracts, searching for the terms "seed" or "seedling" and "predation." This search led to a large number of articles that were then examined for suitability of inclusion in the meta-analysis.

Criteria were devised a priori to avoid personal bias in selecting articles. Articles were included if all criteria applied to at least one experiment reported. For inclusion, the study had to be quantitative and the data reported in a usable form, allowing us to compute the number of seeds or seedlings surviving in each distance category and the number of seeds used in the test. Often, data were only reported in graphical form. To use these data, graphs were scanned with Deskscan II cx v 2.0 (Hewlett-Packard Co. 1993) software and analyzed with the data-grabbing software TechDig v1.1b (Jones 1995). Further, some experimental manipulation by the observer was required; experiments conducted with natural seedfall or naturally occurring seedlings were excluded. Studies had to report at least two contrasting conditions, either near/far from parent plant ("distance"), or two habitats with conspecific adults present in one habitat but generally not in the other ("habitat"). We also required studies to be conducted on native plants in their natural habitat and to use experimental designs that allowed predation on propagules by the full complement of native animals. This led us to reject data from portions of experiments that excluded groups of predators (insect or vertebrate exclosures) or only examined the effects of disease or pathogens on propagule survival.

Data analysis

Experimenters generally placed a known number of propagules in depots which were located either near or far from the parent plant. After a given amount of time had passed, the number of survivors was counted and recorded. The number of individuals consumed was then inferred through subtraction. Thus, the data from each study can be arranged in a 2×2 contingency table, with columns corresponding to distance (near or far), and rows corresponding to seed or seedling fate (survival or predation, see Fig. 1). For studies involving

	Near	Far	
Predated	P_{near}	P_{far}	$N_{predated}$
Survived	S_{near}	S_{far}	$N_{survived}$
	N_{near}	N_{far}	N

$$R_{near} = \frac{P_{near}}{N_{near}}$$

$$Odds_{near} = \frac{R_{near}}{(1-R_{near})}$$

$$OddsRatio = \frac{Odds_{near}}{Odds_{far}}$$

Fig. 1. Diagram of odds ratio calculation methods. The setup of the data structure for a 2×2 contingency table and the calculation of an odds ratio. P is the number consumed, S is the number surviving, and R is the predation rate or risk. An odds ratio < 1 [ln (OR) > 0] indicates the odds of predation are greater near to the parent than far away; an odds ratio > 1 [ln (OR) < 0] indicates the odds of predation increase with increasing parental distance.

multiple distances, we compared the closest and furthest depots and for studies with repeated measurements, we used a collective measure, selecting the number of individuals surviving and consumed at the final census interval as the values for the contingency table. The closest (near) depots were usually within the canopy of the focal plant, while the far distances were as noted in Appendix 1.

To compare results across experiments we used an odds ratio (or relative odds) metric computed from the 2×2 contingency table which is the ratio of the odds of propagule survival when near the parent to the odds of propagule survival when far from the parent (Fig. 1, Sokal and Rohlf 1995, Haddock et al. 1998). Using the same metric to quantify the results of multiple experiments across studies allows unbiased comparisons within meta-analysis. Because there were some studies in which all or none of the propagules survived, and this could produce odds ratio values that would require division by 0, we calculated the odds ratio by adding 0.5 to the numbers of seeds in each category for every study. The odds ratio ranges from 0 to infinity and indicates the degree to which seed or seedling predation changes with distance from a parent plant. If it is greater than 1, this indicates that in that experiment, predation was higher close to the parent plant. If the value of the odds ratio is less than 1, it indicates that predation was higher away from the parent plant. The meta-analysis was performed on the natural logarithm of this ratio for all experiments, with positive values supporting the hypothesis and negative values refuting it.

We believe this to be the first use of the odds ratio as a metric in meta-analysis in ecology. The odds ratios were calculated using the Mantel-Haenszel procedure (Mantel and Haenszel 1959, Yusuf et al. 1985), and studies were combined using traditional meta-analysis methodology (Rosenberg et al. 2000). Although there were many different metrics we could have chosen to calculate from our contingency tables (rate differences, rate ratios, or odds ratios; Berlin et al. 1989, Normand 1999, Rosenberg et al. 2000), we chose the odds ratio because it is a common metric in the medical meta-analysis literature and seemed to best represent the type of comparison we wished to make.

All of the analyses was conducted using MetaWin (Rosenberg et al. 2000). For specific details on meta-analysis and its calculations, see Hedges and Olkin (1985), Gurevitch and Hedges (1993), and Rosenberg et al. (2000). Mean effect sizes were calculated using a random-effects model (Raudenbush 1994, Hedges and Vevea 1998); we felt the fixed-effects model assumption that all observed variation is due to sampling error was unrealistic for such a broad based meta-analysis. Their confidence intervals were calculated using bootstrap resampling procedures as described in Adams et al. (1997).

We examined the heterogeneity of effect sizes using Q statistics (Hedges and Olkin 1985), which are essentially weighted sums of squares which follow a χ^2 distribution. The corresponding P-value indicates whether the variance among effect sizes is greater than would be expected from chance. For our categorical tests (seeds vs seedlings, tropical vs temperate, etc.), we examined the P-values associated with $Q_{Between}$, which describes the variation in effect size between groups. The effects of continuous independent variables such as study duration, distance, and depot size on effect size were explored using a weighted least squares regression adjusted for meta-analysis (Hedges and Olkin 1985, Greenland 1987, Rosenberg et al. 2000). Because in meta-analysis the standard errors of the slope and intercept cannot be determined through normal least squares procedures, different formulas are required to adjust the weighted least squares regression (Hedges and Olkin 1985).

The possibility of publication bias was explored through the examination of weighted histograms (Greenland 1987) and funnel plots (Light and Pillemer 1984, Palmer 1999). Publication bias occurs when studies showing significant results enjoy a greater possibility of publication than those showing non-significant results. If the distribution of a weighted histogram (where weight is the inverse of the variance of the effect size in each study) is depressed around 0, it suggests that a publication bias exists against publishing nonsignificant studies. A funnel plot, which graphs effect size against sample size or variance, can also indicate if bias exists in the data set if it is skewed in shape or direction. We also conducted Spearman rank correlation tests, examining the relationship between the standardized effect size and the sample size across studies (Begg 1994, Begg

and Mazumdar 1994). Significance of such a test indicates that larger effect sizes in either direction are more likely to be published than smaller effect sizes.

Results

After all available studies were examined for suitability, 40 papers remained, yielding 152 data points based on 75 unique species (Appendix 1). Some studies were rejected because they were not experimental or used non-native seeds in studies of mammal behavior. Others were rejected because it was not possible to obtain the needed data from the published material (missing N, numbers of surviving or consumed seeds). A third group of studies were rejected because they involved predispersal seed predation or explored the effects of varying parent density. Although these studies address aspects of the Janzen-Connell hypothesis, they did not relate to our question of interest. The retained studies were heavily weighted towards examining seed predation, with 129 data points derived from experimental data on seed survival. The remaining 23 data points concerned experimental seedling studies. One hundred and four of the data points were derived from studies conducted in the tropics, and the remainder were taken from temperate zone data. 82 data points were based on distance data and 70 were derived from experiments contrasting survival in different habitat types.

Overall effect

There were no individual outliers or groups of points with significantly different effect sizes than all the data points together; i.e. the test of overall heterogeneity was not significant ($Q_{total} = 152.21$, $P = 0.45$). The 95% confidence interval (corrected for bias introduced through resampling) for the mean effect size for all data points together significantly overlapped zero, suggesting that, on average, across all studies, distance from parent plant does not enhance propagule survival (Fig. 2).

Distance versus habitats

Studies that explicitly tested the effect of distance on survival showed no significant effect of distance (average effect = 0.13, Fig. 2). Studies that tested the effect of habitat also had no effect (average effect = 0.04, Fig. 2). Further, the mean effect sizes for the two sub-sets did not significantly differ from each other ($Q_{between} = 0.13$, $P = 0.71$) and they did not differ in any of the subsequent analyses (data not reported). For this reason, results below are reported for the distance and habitat sets combined.
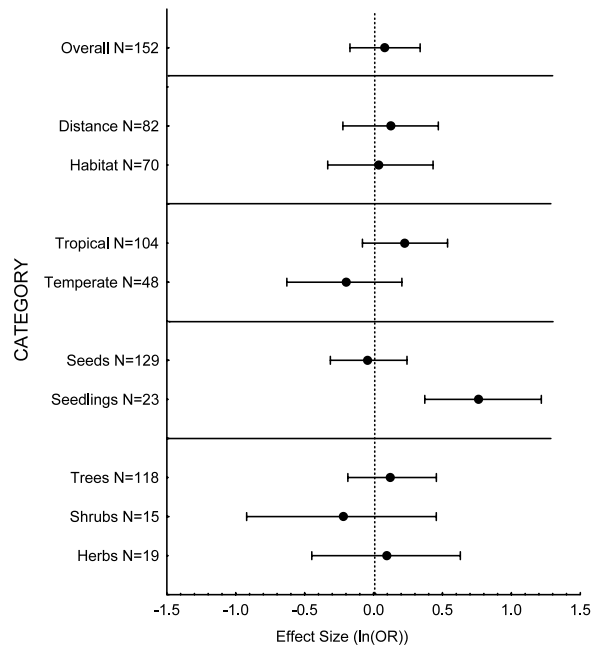
Fig. 2. Confidence intervals for study categories. Points show means and bars show 95% bias-corrected confidence interval ranges for all studies as well as each study category. Sample sizes and categories indicated on figure; dotted line shows ln(OR) = 0, indicating the absence of an effect.

Temperate versus tropical

The tropical and temperate sub-sets of the data set did not have average effect sizes that significantly differed from each other, or from 0 ($Q_{between} = 2.62$, $P = 0.10$, Fig. 2). However, examination of the means and confidence intervals (Fig. 2) suggests that propagules of tropical species may show a slight tendency for increased probability of survival at a distance from parent plants (average effect = 0.23) and temperate propagules may show slight tendency for decreased survival with distance from parent plants (average effect = −0.2).

Seeds versus seedlings

For seeds, there was no effect of distance on survival but for seedlings, distance appeared to have a positive effect on survival (predation was higher near the parent, average effect = 0.76, Fig. 2). The mean effects on seeds and seedlings were significantly different from each other ($Q_{between} = 5.07$, $P = 0.024$).

Life forms

There was no detectable effect of distance on propagule survival for trees, shrubs or herbs ($Q_{between} = 0.66$, $P = 0.71$). Further, the mean effects for any of the groups

did not differ significantly from 0 (Fig. 2). Thus, the inclusion of non-tree species (n = 15 for shrubs, n = 19 for herbs) did not mask any effect that might be seen considering trees alone.

Distance, density, duration

None of the regressions explained a significant portion of the variation in effect among studies and the slopes did not differ from zero (meters from parent [distance]: $Q_{regression} = 0.88$, $P = 0.34$, slope = 0.01, $P = 0.34$; seeds per depot [density]: $Q_{regression} = 2.04$, $P = 0.15$, slope = 0.01, $P = 0.15$; study length in days [duration]: $Q_{regression} = 1.12$, $P = 0.28$, slope = 0.01, $P = 0.10$;). Thus, there was no significant association between any of these factors and propagule survival.

Publication bias and mean effects

The fact that the weighted histogram of effect sizes was not depressed around 0 suggested that there was no bias in reporting results from these studies; studies with exclusively positive or negative effects of distance on propagule survival are not more frequently published (Fig. 3). This result is further emphasized by a non-skewed funnel plot (not shown) and non-significant results of the rank correlation test (Rs = − 0.174, P = 0.07).

Discussion

The distance-dependent prediction of the Janzen-Connell hypothesis was not borne out by the data we examined. The lack of support is probably not due to insufficient data; we are confident of the generality of this conclusion, as our result is based on data from five continents and at least 35 plant families. There is no
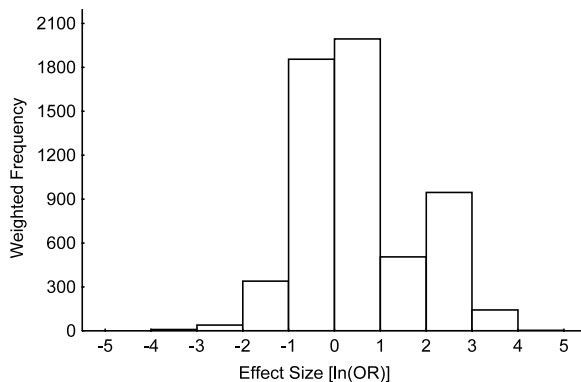
Fig. 3. Histogram of effect aize values weighted by 1/variance. Based on 151 of the 152 studies; one study with an effect of − 8.21 and a weight of 2.18 is not shown on this figure.

general evidence that enhanced distance from conspecific adults enhances seed survival, although there is some suggestion that seedlings might benefit from increased distance. Individual cases of conformity to the hypothesis appear to be special cases and are balanced by cases where the hypothesis is not supported. Effect sizes for individual studies ranged above and below 0, suggesting that escaping the vicinity of parents benefits some species while it harms others (for examples see Aguiar and Sala 1994, Blundell and Peart 1998). Because we used a random model to analyze effect sizes, we took random variation into consideration and the lack of heterogeneity in the data (non-significant Q values) suggests that no general Janzen-Connell distance effect exists. Further, the fact that we find no evidence for publication bias suggests that support will not be yielded by increasing the number of studies on this topic. Because studies were motivated by questions involving both animals and plants, communities and populations, it is clear that further studies on this general prediction will not yield a more supportive result. This is not to say that distance-dependence is not an important ecological factor for the population biology of some species; clearly there are a range of species that respond in dramatically different ways to parental distance.

Still, the possibility remains that examining other subsets of the data or other predictions may yield more support for the hypothesis. When he originally posed the hypothesis, Janzen suggested that the pattern should be more apparent in species with regularly distributed adult populations than for those with random or clumped distributions (Janzen 1970, p. 517, General prediction No. 5). One would assume that studies purporting to test this aspect of the hypothesis would provide data on adult distributions, but such information is rarely provided. As we did not examine adult distributions, this factor, along with interannual timing and magnitude of reproduction (masting patterns) may have affected propagule survival in ways we did not detect. However, those factors were beyond the scope of this study.

These results do support the findings of workers who have explored the Janzen-Connell model mathematically. Implicit in the model is the idea that the existence of some minimum critical recruitment distance will necessarily lead to regular spacing of adult trees. Such a pattern was assumed to describe tropical forests at the time (Black et al. 1950, Pires et al. 1953), although many forests that have been examined explicitly are better described by random or clumped models than uniform ones (Condit et al. 1992, Wills et al. 1997, Hubbell et al. 1999).

Hubbell (1980) tested the potential role of distance-dependence in maintaining tree diversity through modeling and showed that spacing patterns can account for only a very small fraction of observed tree diversity. His model suggested that under this hypothesis, only a

very few species could be maintained. Adding annual and interspecific variation in seed dispersal and recruitment to the model further increases heterogeneity in adult spacing, reducing the likelihood of regular species distributions sustaining excess diversity.

We were surprised to find that in general, offspring survivorship was not enhanced by moving to habitats at a distance from parents (Fig. 2; distance vs habitat; range for habitat findings not different from 0). Species selected for such studies would most likely be those suspected to enjoy some kind of benefit from moving to less shaded habitats than those occupied by their parents. Our finding suggests that at this scale, directed dispersal to gaps or adjacent but different habitats does not generally enhance recruitment. For individual species, specialization on gap environments may enhance fitness, but at this scale it is not possible to make general conclusions (Hubbell et al. 1999). Although directed dispersal may play a role in the dynamics of colonization by some ruderal, invading, or early successional species, on average, directed dispersal to gaps or other habitats did not significantly improve offspring survival.

The lack of an effect of distance on survival in tropical settings and a slight negative effect of distance on survival in the temperate zone suggests that Janzen's (1970) ideas about the specificity of granivores and herbivores in the two regions bear further examination. It should be noted that we were able to use only two studies of temperate zone seedling survival in our meta-analysis (Appendix 1), and thus these results pertain more strongly to granivory than herbivory. Studies of the interactions of foraging behavior of temperate zone seed predators and plant population dynamics may bear further examination.

Connell (1971) argued that if propagule distance or density were to impact diversity, it should be seen most strongly in individual species at the seedling stage. Our results (Fig. 2, seeds vs seedlings), combined with some recently reported data analysis from the Forest Dynamics Project in Panama on seedling density (Harms et al. 2000) support this contention. Clearly, because they grow larger, as seedlings age they are more detectable by visually-oriented specialist predators. Dense clumps of seedlings, often found at short distances from parent plants, are very apparent to specialist predators who cue on adults. As individuals within these clumps age and self-thin, not only are they less apparent to specialists, but they also have more resources to fend off the effects of herbivores and specialized pathogens.

The lack of significant differences among life forms is not surprising. There is no reason to suspect that tree seeds or seedlings of the same size are subject to different pressures or have different kinds of defenses from those of herbs or shrubs. However, correcting our analysis for seed size might reveal interesting trends. Although the original hypothesis was constructed to explain tree diversity, it could also explain the diversity of other life forms as well, albeit at different scales.

The lack of significance for the continuous-variable regressions (study duration, distance and depot size) associated with effect sizes was somewhat surprising. We were motivated to explore aspects of experimental design with the regression approach because design can strongly influence results. However, none of the regressions explained a significant amount of variation in effect size. There are several explanations for this lack of effect. One might expect to see a positive relationship between distance and survival in a regression of meters on effect size. However, if predation processes scale to parent height, we might have combined data in such a way as to mask any significant effect, if it exists. The lack of significant study duration effects on survival may also have been an issue of scale, with seeds in different ecosystems experiencing different time lags between seed production and germination. If experiments were conducted on time scales that matched recruitment constraints, a simple regression might not capture this effect. Finally the effect of depot density on survival may actually scale to seed size and nutritional value rather than density per se. We would not rule out the possible effects of these covariates on seed survival, but we have no evidence to support the role of any of these experimental design issues on measured propagule survival in relation to distance from a parent.

Although we found no support for the first prediction of Janzen and Connell's model, we have only tested one of its four specific predictions. The other three predictions: 1) an inverse relationship between predispersal predation and the distance between adults, 2) a positive relationship between predispersal predation and the density of reproducing adults, and 3) density-dependence in offspring survival also bear further examination. These predictions have also been broadly tested in a variety of systems and as such, are highly amenable to testing by the application of similar meta-analytical approaches.

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Appendix 1. Experimental design and outcome seed and seedling predation for 147 experiments in 40 studies.

Study	Authors and year	Env.	Life form	Stage	Dur.	Dens.	Dist.	Near total	Near No. surviving	Far total	Far No. surviving	ln OR	var ln OR
1.1	Augspurger and Kitajima 1992	1	T	1	77	10	100	7433.5	1963.8	588.6	245.9	0.770	0.009
1.2	Augspurger and Kitajima 1992	1	T	1	77	10	100	7433.5	1432.4	588.6	188.3	0.790	0.011
1.3	Augspurger and Kitajima 1992	1	T	1	77	10	100	1250	574.5	2500	857.9	−0.493	0.005
1.4	Augspurger and Kitajima 1992	1	T	1	77	6	100	4676.19	1969.4	611.92	148.0	−0.745	0.008
1.5	Augspurger and Kitajima 1992	1	T	1	77	6	100	4563.72	1773.2	541.19	88.9	−0.965	0.009
1.6	Augspurger and Kitajima 1992	1	T	1	77	6	100	750	319.7	1500	205.3	−1.615	0.011
1.7	Augspurger and Kitajima 1992	1	T	2	700	10	100	1963.84	278.4	245.96	37.8	0.107	0.037
1.8	Augspurger and Kitajima 1992	1	T	2	700	10	100	1432.36	189.2	188.27	20.9	−0.170	0.053
1.9	Augspurger and Kitajima 1992	1	T	2	700	10	100	574.45	61.8	856.85	185.6	0.759	0.020
1.10	Augspurger and Kitajima 1992	1	T	2	700	6	100	1969.43	107.7	147.986	23.7	1.832	0.123
1.11	Augspurger and Kitajima 1992	1	T	2	700	6	100	1773.15	133.8	88.87	7.1	0.125	0.166
1.12	Augspurger and Kitajima 1992	1	T	2	700	6	100	319.68	49.6	205.31	20.9	−0.450	0.068
2.1	Bermejo et al. 1998	2	S	1	4.5	50		1250	342.5	2500	725.0	0.078	0.006
2.2	Bermejo et al. 1998	2	S	1	4.5	50		1250	567.5	2500	905.0	−0.386	0.005
2.3	Bermejo et al. 1998	2	H	1	4.5	50		1250	315.0	2500	490.0	−0.332	0.007
3.1	Boman and Casper 1995	2	T	1	21	1		24	7.1	24	0.0	−2.048	0.579
3.2	Boman and Casper 1995	2	T	1	24	1		24	16.4	24	1.2	−2.552	0.336
3.3	Boman and Casper 1995	2	T	1	21	1		24	3.0	24	0.0	−1.606	1.054
3.4	Boman and Casper 1995	2	H	1	21	3		72	5.2	72	35.4	2.015	0.133
3.5	Boman and Casper 1995	2	H	1	24	3		72	1.4	72	49.7	2.866	0.119
3.6	Boman and Casper 1995	2	T	1	21	2		48	9.9	48	2.1	−1.385	0.351
3.7	Boman and Casper 1995	2	T	1	24	2		48	43.3	48	4.1	−3.169	0.162
3.8	Boman and Casper 1995	2	S	1	21	5		120	10.3	120	56.2	1.876	0.082
3.9	Boman and Casper 1995	2	S	1	24	5		120	35.5	120	89.3	1.773	0.066
3.10	Boman and Casper 1995	2	S	1	21	1		24	16.5	24	0.0	−2.842	0.345
3.11	Boman and Casper 1995	2	S	1	24	1		24	21.0	24	3.6	−2.745	0.314
4.1	Burkey 1994	1	T	1	20	1	25	28	11.9	70	38.4	0.473	0.193
5.1	Caccia and Ballare 1998	2	T	1	5	30		960	299.7	960	536.9	1.004	0.009
5.2	Caccia and Ballare 1998	2	T	1	3	50		500	36.0	500	217.3	1.908	0.021
6.1	Casper 1987	2	H	1	2	10	2.5	470	315.0	480	408.0	0.984	0.023
6.2	Casper 1987	2	H	1	3	10	2.5	920	497.0	920	488.0	−0.039	0.009
6.3	Casper 1987	2	H	1	3	10	2.5	960	787.0	970	786.0	−0.063	0.014
7.1	Casper 1988	2	H	1	21	75	1.5	750	456.0	750	428.0	−0.154	0.011
7.2	Casper 1988	2	H	1	21	75	1.5	750	184.0	750	297.0	0.690	0.012
8.1	Chapman and Chapman 1996	1	T	1	58		n/f	60	2.4	1515	181.8	0.701	0.164
8.2	Chapman and Chapman 1996	1	T	1	170		n/f	100	99.0	225	139.5	−1.860	0.073
8.3	Chapman and Chapman 1996	1	T	1	122		n/f	80	76.0	60	60.0	1.384	0.840
8.4	Chapman and Chapman 1996	1	T	1	143		n/f	16	12.0	720	136.8	−3.363	0.372
8.5	Chapman and Chapman 1996	1	T	1	63		n/f	180	0.0	90	0.0	0.743	4.492
8.6	Chapman and Chapman 1996	1	T	1	103		n/f	20	20.0	560	50.4	−8.213	0.458
8.7	Chapman and Chapman 1996	1	T	2	100	1	n/f	60	58.0	54	50.5	−0.585	0.652
8.8	Chapman and Chapman 1996	1	T	2	112	1	n/f	25	22.0	64	57.6	0.278	0.526
8.9	Chapman and Chapman 1996	1	T	2	127	1	n/f	15	10.0	56	54.5	3.297	0.855
8.10	Chapman and Chapman 1996	1	T	2	92	1	n/f	15	11.0	64	62.2	3.164	1.002
9.1	Cintra and Horna 1997	1	T	1	140	8	n/f	1024	12.0	1024	41.0	1.103	0.076
9.2	Cintra and Horna 1997	1	T	1	140	8	n/f	1024	67.0	1024	95.0	0.373	0.027
9.3	Cintra and Horna 1997	1	T	2	112	4	n/f	512	221.0	512	233.0	0.095	0.016

Appendix 1 (Continued).

Study	Authors and year	Env.	Life form	Stage	Dur.	Dens.	Dist.	Near total	Near No. surviving	Far total	Far No. surviving	ln OR	var ln OR
9.4	Cintra and Horna 1997	1	T	2	84	4	n/f	64	42.0	64	45.0	0.209	0.140
10.1	Coates-Estrada and Estrada 1988	1	T	1	46		50	100	0.0	30	20.0	4.869	0.313
10.2	Coates-Estrada and Estrada 1988	1	T	1	46	10	50	100	0.0	100	10.0	1.913	0.383
10.3	Coates-Estrada and Estrada 1988	1	T	2	730	5	50	50	5.0	50	20.0	1.533	0.205
11.1	Dalling et al. 1998	1	T	1	1	500	30	8000	3520.0	8000	3600.0	0.041	0.001
12.1	Forget 1997	1	T	1	28	20	100	160	6.0	160	0.0	−1.747	0.582
12.2	Forget 1997	1	T	1	28	20	100	160	11.0	160	3.0	−1.115	0.279
12.3	Forget 1997	1	T	1	28	20	100	160	1.0	160	0.0	−1.003	2.006
13.1	Forget 1993	1	T	1	155	1		100	24.0	100	48.0	1.025	0.085
13.2	Forget 1993	1	T	1	155	1		100	40.0	100	47.0	0.281	0.080
13.3	Forget 1993	1	T	2	730	1		24	1.0	48	13.0	1.316	0.369
13.4	Forget 1993	1	T	2	730	1		40	18.0	47	33.0	1.004	0.184
14.1	Gryj and Dominguez 1996	1	S	1	10		20	270	37.8	270	10.8	−1.196	0.089
15.1	Hart 1995	1	T	1	28	30	200	300	0.0	300	0.0	0.000	4.000
15.2	Hart 1995	1	T	1	28	15	100	375	34.1	150	10.1	−0.283	0.118
15.3	Hart 1995	1	T	1	28	50	100	500	242.0	1250	185.0	−1.818	0.015
16.1	Holl and Lulow 1997	1	T	1	30	5		90	55.0	90	2.0	−2.668	0.101
16.2	Holl and Lulow 1997	1	S	1	30	5		90	26.1	90	1.8	−1.988	0.164
16.3	Holl and Lulow 1997	1	S	1	30	5		90	20.7	90	39.6	0.925	0.098
16.4	Holl and Lulow 1997	1	H	1	30	5		90	23.4	90	28.8	0.285	0.106
16.5	Holl and Lulow 1997	1	T	1	30	5		90	55.8	90	78.3	1.286	0.114
16.6	Holl and Lulow 1997	1	T	1	30	5		90	0.9	90	19.8	1.967	0.208
16.7	Holl and Lulow 1997	1	T	1	30	5		90	0.0	90	0.0	0.000	4.000
16.8	Holl and Lulow 1997	1	T	1	30	5		90	64.8	90	68.4	0.203	0.113
16.9	Holl and Lulow 1997	1	T	1	30	5		90	21.6	90	1.8	−1.864	0.188
16.10	Holl and Lulow 1997	1	T	1	30	5		90	43.2	90	69.3	1.215	0.093
16.11	Holl and Lulow 1997	1	T	1	18	5		30	15.0	30	0.0	−2.486	0.332
16.12	Holl and Lulow 1997	1	S	1	18	5		30	8.1	30	5.1	−0.539	0.360
16.13	Holl and Lulow 1997	1	S	1	18	5		30	8.1	30	20.1	1.529	0.255
16.14	Holl and Lulow 1997	1	H	1	18	5		30	5.1	30	9.9	0.796	0.332
16.15	Holl and Lulow 1997	1	T	1	18	5		30	5.1	30	21.9	2.153	0.256
16.16	Holl and Lulow 1997	1	T	1	18	5		30	3.0	30	0.0	−1.578	1.052
16.17	Holl and Lulow 1997	1	T	1	18	5		30	24.9	30	24.9	0.000	0.429
16.18	Holl and Lulow 1997	1	T	1	18	5		30	12.9	30	0.9	−2.096	0.349
16.19	Holl and Lulow 1997	1	T	1	18	5		30	15.9	30	21.9	0.813	0.271
17.1	Howe 1993	1	T	1	42	1	45	680	20.9	680	103.1	1.447	0.035
17.2	Howe 1993	1	T	2	42	1	45	325	8.4	325	36.2	1.308	0.094
18.1	Howe et al. 1985	1	T	1	42	1	49	839	39.0	351	58.0	1.578	0.053
18.2	Howe et al. 1985	1	T	2	42	1	49	400	8.0	175	23.0	2.141	0.156
19.1	Hulme 1997	2	T	1	3			22	12.3	22	10.7	−0.266	0.341
20.1	Hyatt 1998	2	H	1	150	25		925	738.0	1000	307.0	−1.975	0.008
21.1	Itoh et al. 1995	1	T	1	7	10	30	10	9.0	10	4.0	−1.875	0.750
21.2	Itoh et al. 1995	1	T	1	7	10	30	10	10.0	10	3.0	−2.625	0.750
22.1	Janzen 1982	1	T	1	10	100		1500	1482.0	1500	1495.0	1.092	0.168
22.2	Janzen 1982	1	T	1	10	500		7500	345.0	7500	5645.0	2.946	0.001
22.3	Janzen 1982	1	T	1	10	25		225	218.0	225	225.0	1.778	0.508
22.4	Janzen 1982	1	T	1	10	125		1125	144.0	1125	1067.0	3.297	0.007

Appendix 1 (Continued).

Study	Authors and year	Env.	Life form	Stage	Dur.	Dens.	Dist.	Near total	Near No. surviving	Far total	Far No. surviving	ln OR	var ln OR
22.5	Janzen 1982	1	T	1	10	1		12	11.0	12	12.0	1.042	2.083
22.6	Janzen 1982	1	T	1	10	5		60	41.0	60	59.0	2.054	0.228
23.1	Louda and Zedler 1985	1	T	1	249	5		5	2.8	5	2.8	0.025	1.233
23.2	Louda and Zedler 1985	1	T	1	249	5		5	1.0	5	0.0	−1.123	2.170
23.3	Louda and Zedler 1985	1	T	1	249	5		5	0.0	5	0.0	0.000	4.000
23.4	Louda and Zedler 1985	1	T	1	249	5		5	1.3	5	1.7	0.247	1.378
24.1	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1862.6	1920	1918.5	1.894	0.068
24.2	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1849.6	1920	1849.9	0.004	0.029
24.3	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1856.9	1920	1885.5	0.597	0.042
24.4	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1729.1	1920	1847.6	0.963	0.016
24.5	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1567.5	1920	1240.1	−0.867	0.005
24.6	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1438.6	1920	1136.3	−0.712	0.005
24.7	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1895.1	1920	1899.9	0.209	0.088
24.8	Manson and Stiles 1998	2	T	1	0.5	20	10	1920	1695.7	1920	1574.2	−0.500	0.008
25.1	Masaki et al. 1998	2	T	1	395	20	n/f	200	92.7	200	56.1	−0.776	0.043
25.2	Masaki et al. 1998	2	T	1	395	20	n/f	200	29.4	200	33.9	0.166	0.074
26.1	Molofsky and Fisher 1993	1	T	2	365	5		20	4.1	20	8.1	0.866	0.431
26.2	Molofsky and Fisher 1993	1	T	2	365	5		20	0.6	20	1.4	0.539	1.419
26.3	Molofsky and Fisher 1993	1	T	2	365	5		20	16.0	20	14.8	−0.309	0.506
27.1	Myster and McCarthy 1989	2	T	2	455	1		10	1.0	10	5.5	1.738	0.772
28.1	Notman et al. 1996	1	T	1	21	10	20	20	0.3	20	0.6	0.398	2.161
28.2	Notman et al. 1996	1	T	1	23	5	20	20	18.5	20	14.2	−1.244	0.584
28.3	Notman et al. 1996	1	T	1	18	5		50	19.1	50	16.0	−0.259	0.170
28.4	Notman et al. 1996	1	T	1	18	5		50	35.2	50	29.8	−0.459	0.170
29.1	Parker 1982	2	S	2	90			215	134.4	138	63.2	−0.674	0.048
30.1	Peres et al. 1997	1	T	1	25	4	300	40	7.9	138	106.3	2.428	0.136
30.2	Peres et al. 1997	1	T	1	25	4	300	40	2.9	213	71.1	1.205	0.139
31.1	Pizo 1997	1	T	1	6	50	50	150	37.7	200	28.2	−0.714	0.075
31.2	Pizo 1997	1	T	1	6	50	50	100	20.8	150	62.6	0.926	0.074
32.1	Roberts and Heithaus 1986	1	T	1	1	50		200	68.5	200	36.5	−0.818	0.051
33.1	Russell and Schupp 1998	2	T	1	70	9		135	127.4	135	97.5	−1.560	0.104
33.2	Russell and Schupp 1998	2	T	1	70	9		135	132.0	135	85.5	−2.159	0.093
34.1	Schupp 1988	1	T	1	196	16	5	624	58.2	624	214.0	1.458	0.019
34.2	Schupp 1988	1	T	2	14	12	5	468	296.1	468	356.1	0.605	0.020
35.1	Schupp and Frost 1989	1	T	1	35	5	10	40	15.0	25	4.0	−0.964	0.296
35.2	Schupp and Frost 1989	1	T	1	35	5	10	40	12.0	40	28.0	1.542	0.193
36.1	Smith et al. 1989	2	H	1	2	20		20	1.7	20	1.7	0.000	0.976
36.2	Smith et al. 1989	2	H	1	2	20		20	10.2	20	2.8	−1.549	0.418
36.3	Smith et al. 1989	2	H	1	2	20		20	10.7	20	16.3	1.168	0.417
36.4	Smith et al. 1989	2	H	1	2	18		18	9.3	20	3.8	−1.333	0.429
36.5	Smith et al. 1989	2	H	1	2	18		18	7.5	20	5.9	−0.485	0.424
36.6	Smith et al. 1989	2	H	1	2	18		18	11.6	20	3.6	−1.796	0.406
37.1	Terborgh et al. 1993	1	T	1	365	75	25	150	4.0	150	14.0	1.120	0.224
37.2	Terborgh et al. 1993	1	T	1	365	75	25	150	2.0	150	4.0	0.583	0.583
37.3	Terborgh et al. 1993	1	T	1	365	16	50	64	0.0	64	0.0	0.000	4.000
37.4	Terborgh et al. 1993	1	T	1	365	16	50	48	0.0	48	0.0	0.000	4.000
37.5	Terborgh et al. 1993	1	T	1	365	3	50	12	0.0	12	0.0	0.000	4.000

Appendix 1 (Continued).

Study	Authors and year	Env.	Life form	Stage	Dur.	Dens.	Dist.	Near total	Near No. surviving	Far total	Far No. surviving	ln OR	var ln OR
37.6	Terborgh et al. 1993	1	T	1	365	3	50	12	0.0	12	0.0	0.000	4.000
37.7	Terborgh et al. 1993	1	T	1	365	9	50	36	1.0	36	1.0	0.000	1.371
37.8	Terborgh et al. 1993	1	T	1	365	9	50	36	3.0	36	4.0	0.277	0.553
37.9	Terborgh et al. 1993	1	T	1	365	16	50	32	10.0	32	6.0	−0.624	0.312
37.10	Terborgh et al. 1993	1	T	1	365	16	50	32	23.0	32	16.0	−0.875	0.250
37.11	Terborgh et al. 1993	1	T	1	365	75	25	150	4.0	150	14.0	1.120	0.224
38.1	Verdu and Garcia-Fayos 1996	2	S	1	28	3		180	45.0	180	67.0	0.565	0.051
38.2	Verdu and Garcia-Fayos 1996	2	S	1	28	3		180	45.0	150	44.0	0.219	0.061
39.1	Willis et al. 1997	2	H	1	8	335	1	1340	1214.0	1349	1106.8	−0.722	0.013
39.2	Willis et al. 1997	2	H	1	8	335		1340	1081.4	1340	1245.4	1.067	0.013
40.1	Willson 1989	2	S	1	14	100	8	300	187.5	300	159.3	−0.383	0.027

Parameters and their possible states are as follows:

Parameter	States
Study	First value indicates study number, second value indicates experiment number within study
Environment	1 = Tropical, 2 = Temperate
Life form	T = tree, S = shrub, H = herb
Stage	1 = seed, 2 = seedling
Dur.	Duration; number of days the experiment was monitored
Dens.	Density; number of seeds per depot. Note empty cells indicate experimenter varied density among treatments
Dist.	Distance of 'far' treatment, in meters. n/f indicates distance experiments without explicit distances reported, generally reported as "near" and "far." Empty cells indicate experiments that used habitat treatments, not distance treatments
Near total	Number of units placed in the near (or parent habitat) treatment
Near No. surviving	Number of surviving units in the near treatment
Far total	Number of units place in the far (or alternative habitat) treatment
Far No. surviving	Number of surviving units in the far treatment
ln OR	Natural logarithm of the odds-ratio for adjusted data
var ln OR	Variance of lnOR