

SPECIAL FEATURE – STANDARD PAPER
META-ANALYSIS IN PLANT ECOLOGY

Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival

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Summary

1. The Janzen–Connell hypothesis proposes that specialist natural enemies, such as herbivores and pathogens, maintain diversity in plant communities by reducing survival rates of conspecific seeds and seedlings located close to reproductive adults or in areas of high conspecific density. Variation in the strength of distance- and density-dependent effects is hypothesized to explain variation in plant species richness along climatic gradients, with effects predicted to be stronger in the tropics than the temperate zone and in wetter habitats compared to drier habitats.

2. We conducted a comprehensive literature search to identify peer-reviewed experimental studies published in the 40+ years since the hypothesis was first proposed. Using data from these studies, we conducted a meta-analysis to assess the current weight of evidence for the distance and density predictions of the Janzen–Connell hypothesis.

3. Overall, we found significant support for both the distance- and density-dependent predictions. For all studies combined, survival rates were significantly reduced near conspecifics compared to far from conspecifics, and in areas with high densities of conspecifics compared to areas with low conspecific densities. There was no indication that these results were due to publication bias.

4. The strength of distance and density effects varied widely among studies. Contrary to expectations, this variation was unrelated to latitude, and there was no significant effect of study region. However, we did find a trend for stronger distance and density dependence in wetter sites compared to sites with lower annual precipitation. In addition, effects were significantly stronger at the seedling stage compared to the seed stage.

5. *Synthesis.* Our study provides support for the idea that distance- and density-dependent mortality occurs in plant communities world-wide. Available evidence suggests that natural enemies are frequently the cause of such patterns, consistent with the Janzen–Connell hypothesis, but additional studies are needed to rule out other mechanisms (e.g. intraspecific competition). With the widespread existence of density and distance dependence clearly established, future research should focus on assessing the degree to which these effects permit species coexistence and contribute to the maintenance of diversity in plant communities.

Key-words: determinants of plant community diversity and structure, herbivory, maintenance of diversity, natural enemies, pathogens, plant population and community dynamics, review, seed predation, species coexistence, tropical forest

Introduction

Explaining the maintenance of diversity in plant communities has long been a challenge for ecologists. Species coexistence results from a mix of equalizing forces, that is, those that

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reduce average fitness differences between species, and stabilizing forces, that is, those that increase negative intraspecific interactions relative to negative interspecific interactions, such that species can recover from low density (Chesson 2000; Adler, HilleRisLambers & Levine 2007). Theoretical work has shown that stabilizing mechanisms are necessary for long-term, stable coexistence (Chesson 2000). Empirical research to identify such stabilizing mechanisms has traditionally focused on resource niche partitioning (Schoener 1974), which results in stronger intraspecific than interspecific competition for shared resources. However, since all plant species ultimately depend on the same suite of resources for survival, namely light, water and soil nutrients, resource niche partitioning is unlikely to be the only mechanism contributing to species coexistence in diverse plant communities (Barot 2004; Silvertown 2004).

Another potential explanation is that species coexistence is promoted by specialist natural enemies that keep the density of each species in check. The most well-known hypothesis invoking specialist natural enemies to explain species coexistence is that proposed independently by Janzen (1970) and Connell (1971). Their hypothesis posits that host-specific seed predators, herbivores and pathogens act in a density- and/or distance-dependent manner to reduce the survival of seeds, seedlings and juvenile plants close to conspecific adult trees or in areas of high conspecific density. In both cases, plants would have a greater negative impact on conspecifics than on heterospecifics, meeting the requirements of a stabilizing mechanism capable of promoting species coexistence and maintaining diversity (Chesson 2000).

Over the 40 years since it was first proposed, the Janzen–Connell hypothesis has received much attention (Fig. 1). There have been numerous tests of its predictions, the majority of which have focused on whether plant performance during early life stages (i.e. seed germination, seedling and sapling recruitment, growth and survival) is lower close to versus far from parent trees and at high versus low conspecific densities. Over the years, studies testing the Janzen–Connell hypothesis have periodically been summarized in review papers (Clark & Clark 1984; Hammond & Brown 1998; Carson *et al.* 2008; Terborgh 2012), which have generally found support for the hypothesis. For example, Carson *et al.* (2008) found that 50 out of 53 articles examined found some evidence consistent with the density or distance dependence predictions of the Janzen–Connell hypothesis, with

40% of 125 species showing negative density dependence and 36% of 129 species showing distance dependence. However, there are methodological concerns with such ‘vote-counting’ studies, and a more rigorous approach is to pool results from each independent study in an overall meta-analysis (Gurevitch & Hedges 1993).

Despite the large number of published studies testing the Janzen–Connell hypothesis, only a single meta-analysis utilizing the results of these studies has been conducted to date. Hyatt *et al.* (2003) used meta-analysis to examine experimental evidence for the distance dependence prediction of the Janzen–Connell hypothesis from 40 published studies. In contrast to other reviews, they found no general support for distance dependence and concluded that further testing was not necessary. Nonetheless, additional tests of the Janzen–Connell hypothesis have been conducted in the 10 years since the Hyatt *et al.* (2003) analysis was published, providing additional data with which to test the distance dependence prediction. Furthermore, a meta-analysis of the density dependence prediction of the Janzen–Connell hypothesis has yet to be conducted.

Meta-analysis offers several advantages over traditional reviews that simply tally the number of studies with significant versus non-significant results (Gurevitch & Hedges 1993). Most importantly, it allows for an estimate of the magnitude of the hypothesized effect across all available studies, providing a synthetic quantitative measure with which to evaluate the weight of evidence for a particular prediction (Koricheva, Gurevitch & Mengersen 2013). In addition, it allows for comparisons of the magnitude of the effect among different groups (e.g. different ecological guilds), or for statistical analysis of how effect size varies with continuous variables (e.g. temperature, elevation). This is particularly relevant for tests of the Janzen–Connell hypothesis, since the strength of Janzen–Connell effects is hypothesized to vary with a number of different factors.

First, Janzen–Connell effects are hypothesized to vary with latitude (Hille Ris Lambers, Clark & Beckage 2002). Both Connell (1971) and Janzen (1970) speculated that distance- and density dependence caused by natural enemies should be stronger in the tropics. Janzen (1970) hypothesized that this was due to ‘lowered efficiency of the predators... brought about by the increased severity and unpredictability of the physical environment’ outside of the wet lowland tropics. Consistent with this prediction, biotic interactions are often

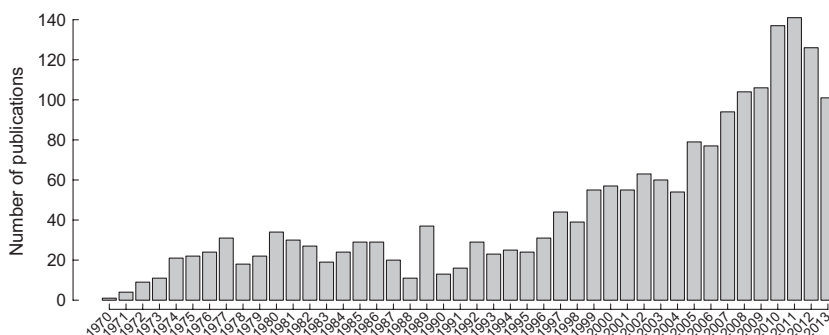


Fig. 1. Number of articles citing Janzen (1970) or Connell (1971) between 1970 and 2013 (total = 1976).

more important in tropical than temperate regions (reviewed by Schemske *et al.* 2009). For example, herbivory rates tend to be lower in temperate than tropical forests (Coley & Barone 1996). In addition, there is evidence that herbivorous insects are more specialized in the tropics (Dyer *et al.* 2007).

Within latitudes, the strength of distance- and density-dependent effects may also be weaker in drier, more seasonal habitats, because of lower pest pressure when resource availability is intermittent and survival of natural enemies is reduced (Janzen 1970; Givnish 1999). Even in forests with similar climate, the strength of Janzen–Connell effects may vary due to differences in biogeographic history or local idiosyncrasies. For example, Southeast Asian forests exhibit supra-annual, community-wide mast fruiting. Mast fruiting is thought to have evolved in part to satiate seed predators (Kelly & Sork 2002), and species that mast are therefore unlikely to experience strong distance- and density-dependent predation (Janzen 1970; Bagchi *et al.* 2011). Thus, we may expect weaker Janzen–Connell effects in Asia compared to other regions. Despite these hypothesized differences both within and among regions, a large proportion of studies testing the Janzen–Connell hypothesis are from just a handful of study sites. In particular, as noted by Carson *et al.* (2008), the literature is dominated by studies conducted in the lowland tropical forest of Barro Colorado Island (BCI) and nearby areas in central Panama. Whether results from this one study site are representative of plant communities world-wide, or even of other tropical forests, remains to be tested.

Differences in the strength of Janzen–Connell effects may also occur both within and among species. Within species, Janzen–Connell effects are thought to be most prevalent at early life stages, when individuals are more vulnerable to natural enemy attack and tend to be highly clumped because of limited seed dispersal (Nathan & Muller-Landau 2000; Comita *et al.* 2007). Janzen (1970) hypothesized that effects should be strong at both the seed and seedling stages, while Connell (1971) observed distance and density dependence at the seedling, but not at the seed stage. Within a species, the strength of density- and distance-dependent effects may also vary with local population density as a result of predator satiation in high, but not low, density areas (Schupp 1992). In addition, the cumulative impact of density- and distance-dependent effects likely increases with the amount of time an individual is exposed to natural enemies. Thus, longer studies should be more likely to detect significant effects of distance and density on survival compared to shorter studies (Terborgh 2012).

Among species, the strength of Janzen–Connell effects may vary among ecological guilds with differing life-history strategies, reflecting trade-offs between vulnerability to predation versus competitive ability or allocation of resources to defence versus rapid growth (Janzen 1970; Connell 1971; Coley & Barone 1996; Carson *et al.* 2008). In addition, recent studies have found that rare species are more sensitive to species-specific pathogens (Klironomos 2002; Mangan *et al.* 2010), resulting in stronger negative density dependence for rare versus common species within plant communities (Comita *et al.* 2010; Johnson *et al.* 2012). Therefore, even at a single study site, the strength of distance- and

density-dependent effects is expected to vary depending on the species being tested.

In the present study, we conducted a comprehensive literature search to identify peer-reviewed experimental studies testing the Janzen–Connell hypothesis in the four decades since the hypothesis was proposed. We then used meta-analysis to assess the weight of evidence for both the distance- and density dependence predictions made by Janzen (1970) and Connell (1971). In addition, we tested whether distance- and density-dependent mortality varies along climatic gradients related to latitude and precipitation. We also tested for differences among regions and between life stages and for a relationship between the strength of distance and density dependence and study duration.

Materials and methods

LITERATURE SEARCH

We conducted a comprehensive literature search using the academic citation indexing and search service Web of Knowledge (<http://thomsonreuters.com/web-of-knowledge/>) in April 2013 to identify experimental tests of the distance and density dependence predictions of the Janzen–Connell hypothesis. We performed three separate searches, with the following conditions:

Search 1 (Yielded 558 results):

Condition 1: cites Janzen (1970), and

Condition 2: contains in title, abstract or keywords: experiment*.

Search 2 (Yielded 91 results):

Condition 1: contains in title, abstract or keywords: 'plant-soil feedback*', and

Condition 2: contains in title, abstract or keywords: experiment*.

Search 3 (Yielded 463 results):

Condition 1: contains in title, abstract or keywords: ('density depend*' or 'density-depend*' or 'distance-depend*' or 'distance depend*'), and

Condition 2: contains in title, abstract or keywords: (plant* or tree* or grass* or herb* or forest* or forb* or prairie* or tundra*), and

Condition 3: contains in title, abstract or keywords: experiment*, and

Condition 4: contains in title, abstract or keywords: (herbivor* or pathogen*).

Searches 2 and 3 were designed to capture studies that were not necessarily explicit tests of the Janzen–Connell hypothesis, but nonetheless tested predictions about enemy-mediated distance- and density-dependent plant survival. We combined the results from all three searches and removed duplicates, yielding a total of 1038 studies. In addition, we searched the lists of articles included in the meta-analysis of Hyatt *et al.* (2003) and the comprehensive review by Carson *et al.* (2008) and included any applicable articles that were missed by our literature search.

We then examined each article to determine whether studies met the following criteria: (i) main text was written in English, (ii) the study experimentally manipulated conspecific plant density or distance

from conspecific adult trees (by transplanting seeds or seedlings, or by thinning naturally occurring plants), (iii) the article reported number of individuals surviving in treatments with high versus low conspecific density or treatments with near versus far from conspecific adult (either in the main text, tables or figures; in a handful of cases, numbers were obtained by contacting authors directly), (iv) study species were native plants in their natural habitat and (v) plants were accessible to the full range of natural enemies occurring in their natural environment (i.e. no glasshouse or laboratory experiments). For condition (v), we did not completely exclude field studies that had enemy exclusion treatments (e.g. cages, fungicide, insecticides), but rather only used data from control treatments in which the full range of enemies had access to the plants. In addition, we excluded experiments in which seeds or seedlings in one treatment were moved into a different habitat (e.g. the 'far' treatment involved moving seeds into canopy gaps, or from the forest interior to the forest edge or adjacent pasture area).

DATA ANALYSIS

For each species examined in each publication, we recorded the following information: article title, year, journal, study site information (country, latitude and annual precipitation), growth form (tree, shrub, herb or palm), life-history stage (fruit, seed or seedling), study duration (number of days) and the prediction tested (distance or density). We also classified each site as temperate, subtropical or tropical based on latitude, using the guidelines in Corlett (2013). In the few cases where studies provided a range of precipitation, we used the midpoint of the range. We also assigned each site to one of the four regions, Africa, Europe, Asia (including Oceania) and the Americas (including North, Central and South America).

For tests of the distance prediction, we extracted the total number of survivors and total number of deaths near to and far from conspecific adult trees. If multiple distances were tested, we only used data from the nearest and furthest distances. For tests of the density prediction, we extracted the total number of survivors and total number of deaths in the highest and lowest conspecific density treatments reported. Data presented in graphs were extracted using the freely available software program Plot Digitizer (<http://plotdigitizer.sourceforge.net/>). For articles that contained multiple experiments, we considered experiments to be separate tests when they were conducted on different species, at different life stages, or tested different predictions. A list of all articles included in the meta-analysis and data for each test are provided in Appendix S1 and Table S1, respectively, in Supporting Information.

Analyses were conducted in the statistical software environment R 3.0.2 (R Core Team 2013), using the 'metafor' package version 1.9-2 (Viechtbauer 2010). For each test, we calculated the log odds ratio and estimated sampling variances using the function `escalc()`. Using a random effects model, we tested whether log odds ratios were significantly less than zero, which would indicate that survival was significantly lower in near versus far treatments or in high density versus low density treatments. We then included modifiers in the random effects model and ran separate models to test whether the following factors influenced the log odds ratio: (i) distance from equator (i.e. absolute latitude), (ii) zone (temperate versus tropical, the 1 subtropical study was pooled with temperate studies), (iii) annual precipitation, (iv) region (Asia versus Africa versus Europe versus the Americas), (v) life-history stage (seed versus seedlings, the few studies on fruit were pooled with studies of seed) and (vi) study duration. In addition, we tested whether effect sizes were significantly different

for the two best-studied sites in our meta-analysis, BCI (Panama) and Cocha Cashu (Peru), compared to all other sites and to all other tropical sites. We had also planned to test for differences in growth form, but most studies were conducted on tree species and sample sizes of other growth forms were too small to make valid inferences about differences among them (trees, $N = 130$; shrubs, $N = 8$; herbs, $N = 8$; and palms, $N = 8$). Precipitation (range: 260–5100) and absolute latitude (range: 0.22–58.3) were both centred around the mean and scaled by the standard deviation prior to entering the models.

As in any review of existing literature, and meta-analysis in particular, there is concern that results could be confounded by publication bias (Csada, James & Espie 1996). We therefore used several standard approaches for assessing whether a bias existed against publication of non-significant results. Specifically, we examined a weighted histogram of effect sizes (Greenland 1987) and also constructed a funnel plot and tested for funnel plot asymmetry using the rank correlation test of Begg & Mazumdar (1994).

Results

PUBLISHED STUDIES OF DISTANCE- AND DENSITY-DEPENDENT MORTALITY

We found a total of 63 articles containing tests that met all our criteria. Combined, these articles included 154 separate tests of distance- or density dependence (mean = 2.44, range = 1–16): 120 for distance and 34 for density (see Table S1). The majority of tests were conducted at tropical sites (95 tests, 38 papers), but the temperate zone was also well represented (59, 25). Only a single test from the subtropics was found, which was pooled with temperate studies in analyses. The tests covered a wide breadth of taxonomic and phylogenetic diversity, with tests on 108 unique species and 44 families.

OVERALL

We found an overall significant negative effect of density and proximity on survival when pooling all tests ($Z = -3.481$, $P = 0.0005$; Figs 2 and 3a). The estimated log odds ratio of seeds and seedlings located at high density or close to conspecifics compared to those at low density or far from conspecifics was -0.43 (CI: -0.67 to -0.19), that is, the probability of survival of offspring in high/near treatments was 39% that of offspring in low/far treatments. There was wide variation in effect sizes among tests (range = -7.48 – 6.53 , $QE = 2985.54$, d.f. = 153, $P < 0.0001$; Figs 3a and 4).

When we separated the papers into studies testing only density effects and studies testing only distance effects, we again found a similar significant negative effect in each group (density: log OR = -0.4 ± 0.14 (SE), $Z = -2.9$, $P = 0.004$; distance: log OR = -0.43 ± 0.16 (SE), $Z = -2.743$, $P = 0.006$; Fig. 2). There was no significant difference between density and distance tests in their effect size ($Q_M = 0.014$, d.f. = 1, $P = 0.906$). Thus, in all subsequent analyses, we pooled studies investigating distance and density effects, equating 'near' with 'high' and 'far' with 'low', unless otherwise stated.

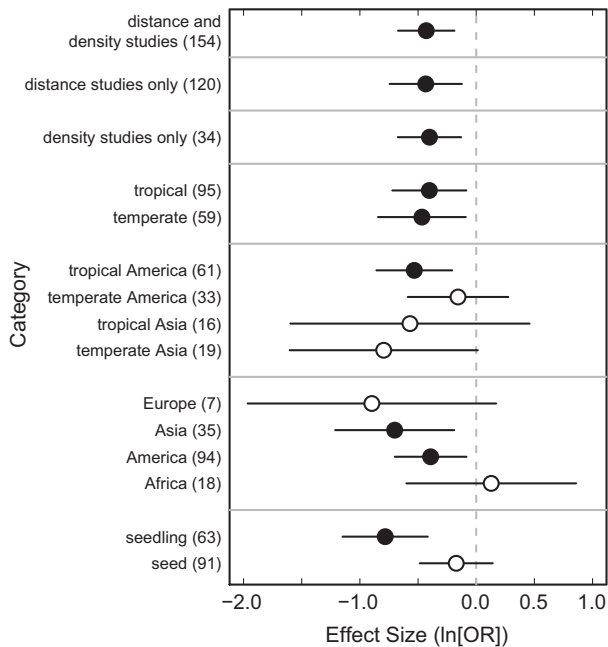


Fig. 2. Effect sizes and confidence intervals for study categories. Effect sizes are indicated by points [filled circles are significantly different from 0 ($P < 0.05$), empty circles are not]. Error bars are estimated 95% confidence intervals. Significant differences within categories are indicated in the main text.

VARIATION WITH LATITUDINAL AND PRECIPITATION GRADIENTS

We found no significant effect of absolute latitude on effect size ($Q_M = 1.69$, d.f. = 1, $P = 0.194$; Fig. 5a). Similarly, there was no significant difference between studies located in the tropics versus studies from the temperate zone ($Q_M = 0.064$, d.f. = 1, $P = 0.8$). Even when comparing studies within a single region (possible only for studies from the Americas and Asia), we found no significant difference between tropical and temperate studies in the Americas ($Q_M = 1.858$, d.f. = 1, $P = 0.173$; Fig. 2) or Asia ($Q_M = 0.114$, d.f. = 1, $P = 0.735$; Fig. 2), and

no significant correlation of effect size with latitude within these two regions (America: $Q_M = 1.081$, d.f. = 1, $P = 0.298$; Asia: $Q_M = 1.421$, d.f. = 1, $P = 0.233$).

We found a marginally significant correlation of effect size with overall precipitation (slope = -0.24 ± 0.12 , $Q_M = 3.698$, d.f. = 1, $P = 0.054$; Fig. 5b). When we examined tropical and temperate studies separately, the correlation was significant in both cases (tropical: slope = -0.32 ± 0.16 , $Q_M = 4.08$, d.f. = 1, $P = 0.04$; temperate: slope = -1.02 ± 0.45 , $Q_M = 5.05$, d.f. = 1, $P = 0.02$; Fig. 5b).

VARIATION AMONG REGIONS AND STUDY SITES

Of the four regions, only America and Asia had significantly negative effect sizes (overall model with all four regions testing difference of effect size from zero: $Q_M = 16.284$, d.f. = 3, $P = 0.003$; Fig. 2). There was no significant difference among regions in their effect sizes ($Q_M = 4.13$, d.f. = 3, $P = 0.25$). However, there were relatively few tests from Europe and Africa.

There was no significant difference in effect size for studies from BCI, Panama ($n = 14$), compared to all other studies ($Q_M = 1.27$, d.f. = 1, $P = 0.26$) or all other tropical studies ($Q_M = 1.73$, d.f. = 1, $P = 0.19$). Likewise, there was no significant difference in effect size for studies from Cocha Cashu, Peru ($n = 16$), compared to all other studies ($Q_M = 0.05$, d.f. = 1, $P = 0.82$) or all other tropical studies ($Q_M = 0.03$, d.f. = 1, $P = 0.87$).

VARIATION AMONG LIFE-HISTORY STAGES

We found a significant difference between life-history stages in effect size ($Q_M = 6.192$, d.f. = 1, $P = 0.013$; Fig. 2). Seedlings showed a significantly lower odds ratio than seeds (seedlings: log OR = -0.78 ± 0.19 ; seeds: log OR = -0.17 ± 0.16), indicating stronger negative effects of conspecific density and proximity at the seedling stage. In fact, when the two life stages were tested separately, significant negative effects of conspecific density and proximity were only found

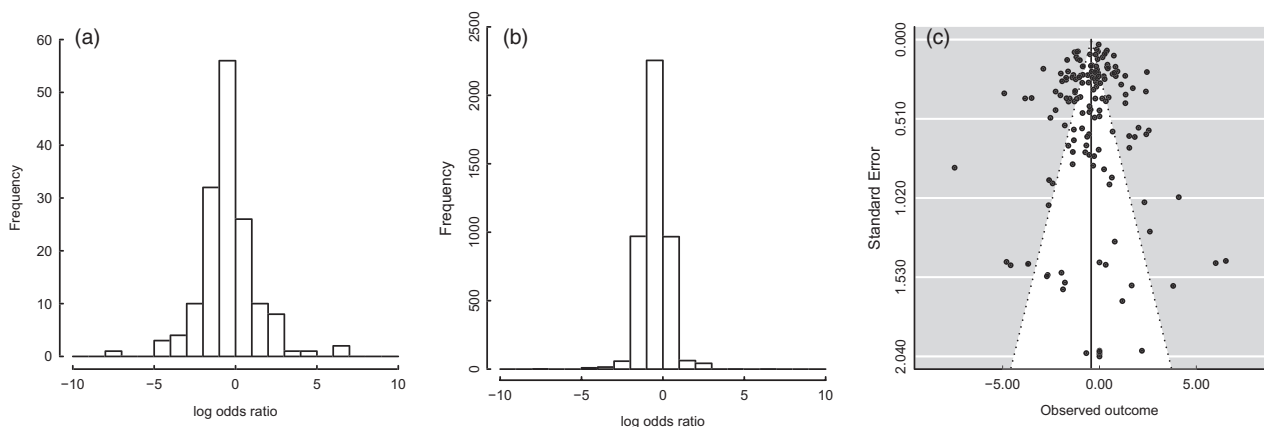


Fig. 3. Checks for publication bias. (a) Histogram of log odds ratios; (b) histogram of log odds ratios weighted by $1/\text{variance}$; (c) funnel plot. No evidence of publication bias is shown.

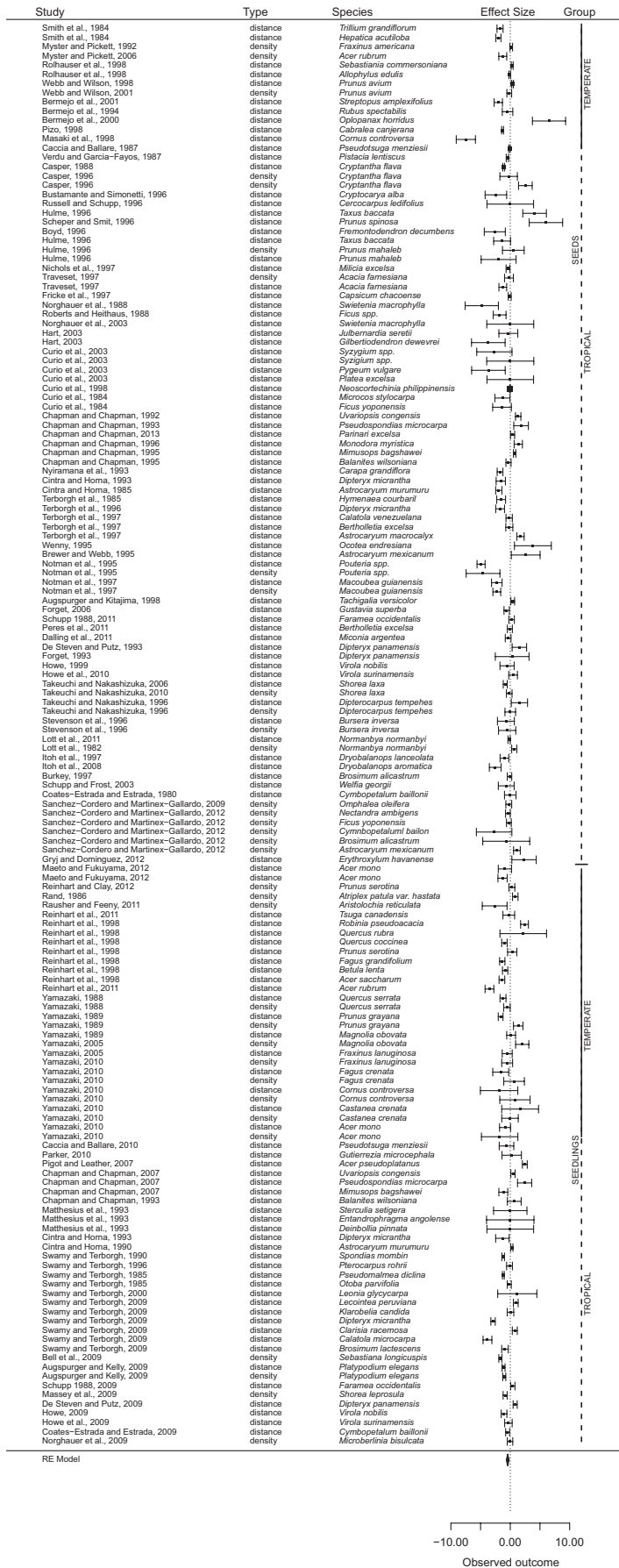


Fig. 4. Forest plot of all experimental studies investigating density and/or distance dependence included in the meta-analysis. Each point depicts the effect size for each article with 95% estimated confidence intervals. The size of each point is proportional to the study precision. ‘RE Model’ indicates the overall effect size weighted for each study in a random effects model. Studies are ordered as indicated by the Group column in the following order: seed stage – temperate (upper solid line), seed stage – tropical (upper dashed line), seedling stage – temperate (lower solid line), seedling stage – temperate tropical (lower dashed line). Within each group, studies are sorted by increasing precipitation going down the figure.

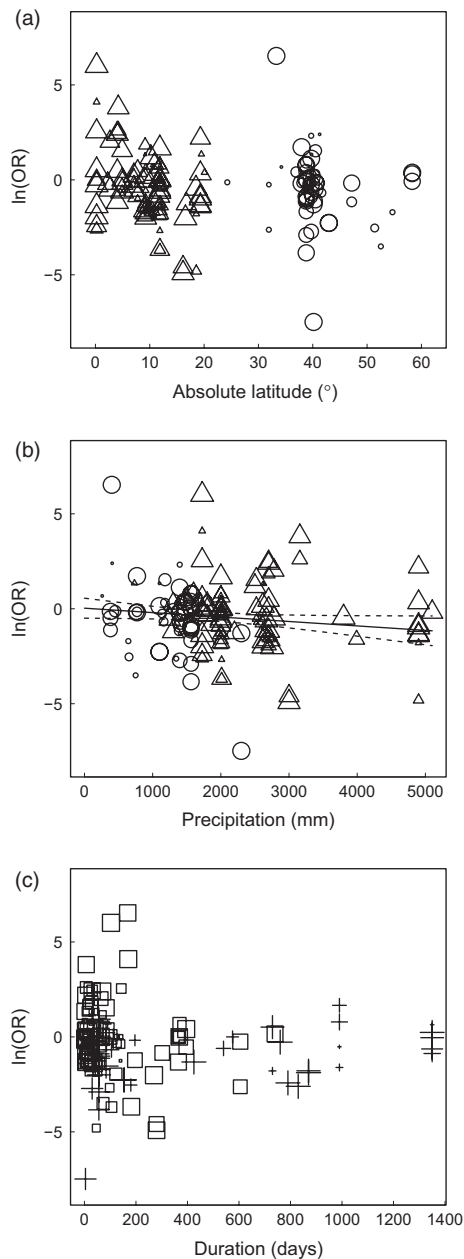


Fig. 5. The effect of (a) absolute latitude, (b) precipitation and (c) study duration on the log odds ratio of survival of seeds and seedlings in a meta-analysis of experimental tests of density and distance dependence. The size of each point is proportional to the precision of the estimate. In panels (a) and (b), tropical (circles) and temperate (triangles) studies are indicated. In panel (c), studies of seeds (squares) and seedlings (pluses) are indicated. No significant effects of latitude (a) or study duration (c) were detected. Precipitation (b) had a marginally significant effect for all studies combined ($P = 0.054$) and a significant effect ($P < 0.05$) when tropical and temperate studies were analysed separately.

for the seedling stage (Fig. 2). When we tested whether seeds and seedlings responded differently to density and distance treatments, we found a significant interaction ($Q_M = 9.048$, d.f. = 3, $P = 0.029$), with seedlings showing a significantly greater negative response to distance than seeds (seeds: log OR = -0.09 ± 0.2 ; seedlings: log OR = -0.94 ± 0.24 ;

$Q_M = 7.476$, d.f. = 1, $P = 0.006$), but no difference between seedlings and seeds with regard to density (seeds: log OR = -0.46 ± 0.19 ; seedlings: log OR = -0.34 ± 0.2 ; $Q_M = 0.17$, d.f. = 1, $P = 0.68$).

EFFECT OF STUDY DURATION

We found no significant effect of study duration on effect size ($Q_M = 0.6$, d.f. = 1, $P = 0.44$, Fig. 5c), and there was no significant difference between seeds and seedlings in terms of the slope of this non-significant correlation (seeds: slope = -0.0015 ± 0.0012 ; $Q_M = 1.675$, d.f. = 1, $P = 0.196$; seedlings: slope = 0.0002 ± 0.0004 ; $Q_M = 0.339$, d.f. = 1, $P = 0.56$).

PUBLICATION BIAS

The weighted histogram was not depressed around zero (Fig. 3b), suggesting that there was no bias in reporting results of Janzen–Connell effects; studies with exclusively positive or negative results of density or distance on seed or seedling survival were not more frequently published (Fig. 3b). Furthermore, the funnel plot of standard error on effect size was not skewed (Fig. 3c), and the rank correlation test of asymmetry in the funnel plot was not significant (Kendall's $\tau = -0.01$, $P = 0.83$).

Discussion

OVERALL PATTERNS OF DENSITY- AND DISTANCE-DEPENDENT MORTALITY

Our meta-analysis revealed significant support for both the distance- and density-dependent predictions of the Janzen–Connell hypothesis. Overall, the probability of survival was significantly reduced for individuals located near conspecific plants compared to those located far from conspecifics, and for individuals located in areas with high densities of conspecifics compared to areas with low conspecific densities. We found no indication that our finding of significant effects was due to publication bias (Fig. 3b,c). In fact, there was large, continuous variation in the strength of distance- and density dependence across studies (Fig. 3a), suggesting that the significance and impact of such effects varies widely in nature. Variation among studies may also reflect methodological differences. For example, differences among studies in minimum and maximum distances or densities could result in different effect sizes. Nonetheless, for all studies combined, we found significant distance- and density-dependent mortality, consistent with predictions of the Janzen–Connell hypothesis.

MECHANISMS DRIVING DISTANCE- AND DENSITY-DEPENDENT MORTALITY

It is important to stress that while our results support these predictions made by Janzen (1970) and Connell (1971), they

do not demonstrate that the observed patterns of distance- and density-dependent survival are a result of attack by distance- and density-responsive natural enemies, which is key to the Janzen–Connell hypothesis (Terborgh 2012). For the seed stage, studies predominantly measured seed removal, which was assumed to result in mortality. This is not necessarily the case, however, since some organisms that remove fruit or seeds may not consume the seed itself or may cache seeds and not return to them. Thus, seed removal may simply result in secondary dispersal, and not necessarily death. For seedlings, distance and density dependence could result from strong intraspecific competition for resources rather than natural enemies, which would be consistent with resource niche partitioning, not with Janzen–Connell effects. However, there is little evidence for strong seedling–seedling competition, at least in tropical forests (Wright 2002; Paine *et al.* 2008; Terborgh 2012). Such effects could also result from chemical interference, although there is only limited support in the literature for that as a mechanism of distance or density dependence (McCarthy-Neumann & Kobe 2010). In contrast, a large number of studies have demonstrated that natural enemies are responsible for density- and distance-dependent seedling mortality (Bell, Freckleton & Lewis 2006; Mangan *et al.* 2010; Swamy & Terborgh 2010). In particular, pathogens have been implicated as agents of negative density and distance dependence in a number of recent experimental studies from both temperate and tropical forests (Packer & Clay 2000; Freckleton & Lewis 2006; Bagchi *et al.* 2010, 2014; Mangan *et al.* 2010; Liu *et al.* 2012). Furthermore, a meta-analysis of plant–soil feedbacks by Kulmatiski *et al.* (2008), which included mostly glasshouse studies of grassland species, found strong support for the hypothesis that soil pathogens contribute to the maintenance of plant diversity through negative frequency dependence.

Of the 56 experiments showing significant distance or density dependence based on our analysis (i.e. negative log odds ratios and 95% confidence intervals not overlapping zero; Fig. 3), 33 (59%) explicitly tested for density- or distance-dependent natural enemy impacts, either through experimental exclusion of one or more classes of natural enemies (e.g. via fungicide application or cages to exclude herbivores) or by quantifying damage caused by natural enemies (e.g. percentage leaf loss due to herbivory). Of those 33 studies, 28 (85%) found support for natural enemies as a driving force behind the observed density- or distance-dependent mortality patterns. This is likely an underestimate, however, since individual studies usually did not test for all natural enemies that could potentially be causing distance and density dependence.

COMPARISON WITH PREVIOUS REVIEWS OF THE JANZEN–CONNELL HYPOTHESIS

Our results are consistent with past reviews of the Janzen–Connell hypothesis (Clark & Clark 1984; Carson *et al.* 2008), which have largely relied on tallying numbers of studies supporting the hypothesis and found strong support for the

distance- and density-dependent predictions. However, our finding of significant distance-dependent effects on survival sharply contrasts with the non-significant results of the meta-analysis of Hyatt *et al.* (2003). There are a number of reasons why our results may have differed from those of Hyatt *et al.* (2003). First, our study included an additional decades worth of peer-reviewed articles, providing more data with which to evaluate the hypothesis. We also conducted a broader search, including all journals indexed by Web of Knowledge, whereas Hyatt *et al.* (2003) restricted their search to 10 major ecological journals. Another potential explanation may have to do with the number of experiments on seeds versus seedlings included in the respective meta-analyses. In both our study and Hyatt *et al.* (2003), effects were found to be significantly stronger at the seedling than the seed stage (discussed below). In our meta-analysis, ca. 40% of studies were conducted on seedlings, compared to only 15% in Hyatt *et al.* (2003). Thus, we may have been more likely to detect significant effects due to the better representation of seedling studies in our analysis.

Also, in contrast to Hyatt *et al.* (2003), we excluded experiments in which seeds or seedlings were moved into a different habitat, since these studies were not appropriate tests of the Janzen–Connell hypothesis. In their study, the ‘far’ treatment often involved moving seeds into a distinct habitat, such as from the forest interior to the forest edge or adjacent pasture area. In most of these cases, the extreme differences in microenvironmental conditions between treatments likely far outweighed effects of conspecific density or distance to a conspecific adult.

Finally, we took a more conservative approach when determining what was considered a separate study in the meta-analysis. Specifically, Hyatt *et al.* (2003) treated each replicate within a paper as a separate study (if data for each replicate were reported). For example, if effect of distance from conspecific adult tree on seedling survival was assessed for a single species using three different conspecific adult trees, the results from each tree were entered as if each were a separate study. In our analysis, we combined numbers from replicates in which the species, life stage and prediction being tested were the same, in order to avoid pseudoreplication. Regardless of the reasons why our results differed from those of Hyatt *et al.* (2003), our finding of significant support for the distance dependence prediction of the Janzen–Connell hypothesis indicates that their conclusion that ‘further testing to explore this hypothesis as a diversity-maintaining mechanism is unnecessary’ was premature.

VARIATION WITH LATITUDE: ARE DENSITY AND DISTANCE DEPENDENCE STRONGER IN THE TROPICS?

Both Janzen (1970) and Connell (1971) hypothesized that distance and density dependence would be stronger in the tropics than in temperate regions. However, we found no relationship between the strength of density- or distance-dependent survival and absolute latitude (i.e. distance from the equator) in our meta-analysis. Likewise, we found no significant

difference in the strength of density or distance effects when comparing tropical versus temperate studies. Hille Ris Lambers, Clark & Beckage (2002) examined the relationship between latitude and density-dependent mortality, based on 10 published studies, and found no evidence that the *proportion* of tree species in a community exhibiting significant density dependence was higher in tropical than temperate forests (they could not assess the *strength* of density dependence with their methods). Together, these results suggest that there is little support for the idea that Janzen–Connell effects are stronger in the tropics. Conversely, a recent study using extensive forest inventory data found evidence for a decrease in the strength of negative density dependence from subtropical to boreal forests in eastern USA (Johnson *et al.* 2012), suggesting that latitudinal gradients in the strength of density dependence do exist within some regions. Nonetheless, in the current study, we found little evidence for differences in the strength of density- or distance dependence with latitude even when restricting analyses to a single region (e.g. only Asia or only the Americas; Fig. 2).

Overall, our results suggest that distance dependence and density dependence play a significant role in shaping patterns of survival at early life stages in both temperate and tropical plant communities. While such effects likely contribute to species coexistence and the maintenance of diversity within these communities, variation in the strength of distance and density dependence among sites does not appear to explain the latitudinal gradient in diversity since stronger effects were not detected for highly diverse tropical forests compared to lower diversity temperate plant communities. However, each study in our meta-analysis included only a handful of species present at the study site. Since experimental manipulation of distance and density requires collection of a large number of seeds or seedlings in order to have sufficient replication, it is likely that the majority of the species used in the experiments were relatively common. Recent studies have found that common species are less sensitive to conspecifics and experience weaker negative density dependence on a per-neighbour basis compared to species that are rare within the community (Comita *et al.* 2010; Mangan *et al.* 2010; Johnson *et al.* 2012). Thus, our estimates of the strength of density and distance dependence at a site may be underestimated, especially for tropical forests where most species are rare. Furthermore, differences among species in the strength of distance- or density dependence occur due to variation in life-history strategy, such as species' shade tolerance (Kobe & Vriesendorp 2011). Thus, studies that contain only one or a few species are unlikely to accurately reflect the true strength of (and variation in) density and distance dependence at a site. Furthermore, although we found that the strength of density and distance dependence did not differ between tropical and temperate sites, we did not assess the underlying causes. Therefore, it is possible that distance- and density-responsive natural enemies do play a more important role in the tropics, as predicted by Janzen (1970) and Connell (1971), while intraspecific competition for resources is more important in driving distance and density dependence in the temperate zone.

VARIATION WITH PRECIPITATION: DO WETTER FORESTS EXPERIENCE STRONGER DISTANCE AND DENSITY DEPENDENCE?

In contrast to latitude, we found evidence for a relationship between annual precipitation and the strength of distance and density dependence. In all cases, the strength of distance and density effects tended to be stronger at wetter sites. Givnish (1999) hypothesized that survival of, and therefore attack by, small-bodied, desiccation-intolerant natural enemies, such as fungi and insects, should increase with increasing precipitation, resulting in stronger density dependence at wetter sites, both within and outside of the tropics. Although we cannot definitely attribute our finding of increased distance- and density-dependent mortality in wetter sites to natural enemies, pest pressure has been shown to increase with water availability. In a transplant study involving seedlings of 24 tropical plant species, Brenes-Arguedas, Coley & Kursar (2009) found higher insect herbivore damage and pathogen-mediated mortality in wet relative to drier forest in central Panama. Further evidence comes from the experimental study of Swinfield *et al.* (2012), in which higher watering frequency and volume led to higher pathogen-induced seedling mortality for a tropical tree species. Nonetheless, rates of herbivory and pathogen attack are not always higher in forests with higher annual precipitation, since insect herbivores and pathogens may respond more strongly to dry season length/severity, which is often, but not always, correlated with total annual precipitation (Leigh *et al.* 2004). In addition, while pest pressure may be higher at wetter sites, species at those sites may invest more in defences, reducing damage and mortality caused by natural enemies (Coley & Barone 1996). Additional studies are needed to determine whether the relationship between precipitation and distance/density dependence is due to increased natural enemy attack at wetter sites, or to other mechanisms, such as competition. Regardless of the specific mechanisms involved, our results suggest that predicted shifts in precipitation patterns due to anthropogenic climate change (Christensen *et al.* 2007) may alter biotic interactions that underlie density and distance dependence, with ensuing consequences for species composition and diversity in ecological communities.

VARIATION AMONG REGIONS AND STUDY SITES

We found no evidence for significant differences in the strength of density- or distance-dependent mortality among regions. Rather, wide variation within regions resulted in overlapping confidence intervals when comparing studies from Africa, Asia, Europe and the Americas (Fig. 2). We had originally hypothesized that Janzen–Connell effects would be weaker in Asia due to the supra-annual community-wide masting events, which are thought to result in predator satiation (Janzen 1974). However, distance and density dependence do not appear to be weaker in Asia relative to other regions, even when comparing only studies from the tropics. However, there was only a single seedling study in the Asian tropics

(versus 15 tropical seed studies in Asia) and only a single seed study in temperate Asia (versus 18 temperate seedling studies in Asia). Given the significant difference we found between the two life stages, additional studies of density and distance dependence in Asia for tropical seedlings and temperate seeds are needed to fully assess patterns in that region.

In their review of the Janzen–Connell hypothesis, Carson *et al.* (2008) expressed concern over the fact that a large numbers of the studies had been conducted at a single study site. Specifically, they reported that 63% of the species included in their review were studied on or near BCI, Panama. A large proportion of studies from a single site can be cause for concern if that site is not representative. In our meta-analysis, two Neotropical sites, BCI and Cocha Cashu (Peru), combined accounted for nearly 20% of the studies. However, we found no evidence to suggest that either site is an outlier in terms of the strength of distance or density dependence. Thus, while studies from additional sites are clearly needed, there is no reason to believe that existing evidence from well-studied sites should be discounted.

The observed variation among study sites may reflect differences in the density and composition of natural enemies present. In particular, studies have found that patterns of density and distance dependence can be altered when vertebrate seed disperser and seed predator populations are reduced due to poaching and other human disturbances (Wright & Duber 2001; Wyatt & Silman 2004). Future studies of Janzen–Connell effects should therefore consider whether intact communities of seed dispersers and predators exist at the study site.

VARIATION WITHIN AND AMONG SPECIES

At his study site in North Queensland, Australia, Connell (1971) observed that the impact of density and distance dependence was evident at the seedling and sapling stages, but not at the seed stage. Consistent with his observations, we found significantly stronger effects at the seedling stage compared to at the seed stage. Specifically, mortality at the seedling stage was more strongly impacted by distance to conspecifics than at the seed stage, although both life stages responded similarly to conspecific density. This may reflect differences in the host-specificity and behaviour of natural enemies that attack seeds versus seedlings. For example, mammals, which tend to forage over large areas and be polyphagous, are less likely to contribute to Janzen–Connell effects than insects or pathogens (Wright 2003) and may cause a higher proportion of mortality at the seed stage compared to at the seedling stage (Paine & Beck 2007). It is important to note that all of the experiments on seeds included in our meta-analysis quantified post-dispersal seed predation (or removal). However, rates of pre-dispersal seed predation can be high and may be density-dependent, with pre-dispersal seed predators attracted by the high density of fruits and seeds on individual adult plants or to neighbourhoods with high densities of fruiting individuals (Janzen 1970; Jones & Comita 2010). Therefore, studies looking only at post-dispersal seed predation may underestimate density-

dependent mortality at the seed stage. In addition, none of the studies in our meta-analysis examined later life stages, presumably because of the logistical difficulties associated with manipulating density of larger plants. Observational studies have reported negative density-dependent recruitment, growth and survival for saplings and adult plants (Peters 2003; Uriarte *et al.* 2004; Stoll & Newbery 2005; Steinitz *et al.* 2011; Piao *et al.* 2013). Thus, the impacts of density and distance on plant performance likely persist beyond the seedling stage. However, a recent analysis by Zhu, Y., Comita, L.S., Hubbell, S.P. & Ma, K. (in review) found a monotonic decrease in the strength of negative conspecific density effects on survival from the seedling to the adult stage for tropical trees in the BCI forest, providing support for the idea that density dependence is most important at earlier stages.

Our analysis revealed wide variation among species in the strength of distance- and density-dependent effects (Fig. 4), even for species from the same study site that were analysed in the same publication (e.g. Chapman & Chapman 1996). Among species, the strength of negative conspecific effects has been shown to vary with life-history strategy (e.g. shade tolerance; Kobe & Vriesendorp 2011), growth form (e.g. shrub versus tree; Hubbell *et al.* 2001) and relative abundance (Comita *et al.* 2010; Mangan *et al.* 2010) within plant communities. In the majority of studies included in our meta-analysis, however, information on life-history strategy and relative abundance was not reported for the study species. Growth form, on the other hand, was regularly reported, but ~85% of the experiments were performed on tree species, precluding analysis of differences in distance- and density dependence among growth forms. Thus, at this point, few generalizations can be made about potential drivers of variation in distance- and density-dependent mortality among species. Consistent reporting of species relative abundances, life-history strategies and related functional trait values (e.g. seed mass), along with additional experiments on growth forms besides trees, would help clarify which factors determine species sensitivity to conspecific density and distance.

Conclusions

We found significant overall effects of conspecific density and distance on survival in plant communities world-wide. While we cannot currently attribute these effects to density- and distance-responsive seed predators, herbivores and/or pathogens, available evidence suggests that natural enemies are frequently the cause of such patterns. Future studies should assess the mechanisms underlying distance- and density-dependent mortality in order to determine whether Janzen (1970) and Connell (1971) were correct in their focus on natural enemies. We also found support for a relationship between density/distance dependence and precipitation, but not latitude. Nonetheless, we are hesitant to conclude that Janzen–Connell effects do not vary with latitude or contribute to the latitudinal gradient in species richness. Each site in our study was represented by one or only a handful of species from the community, and thus, our estimates do not represent

overall impacts at the community level for a given study site. Observational studies of density dependence typically include a much larger proportion of species in the community and may better reflect the strength of distance- and density-dependent mortality at a site. A meta-analysis of community-level observational studies would help shed light on the variation in density and distance dependence among regions, including any relationship with latitude. Finally, the wide variation in effect size among studies included in our meta-analysis suggests that not all species experience density and distance dependence at early life stages. However, density and distance dependence can contribute to the maintenance of diversity even if only some of the species within a community are impacted, especially if competitively dominant species are most strongly affected (Carson *et al.* 2008). Few studies have attempted to test the degree to which observed density or distance dependence contribute to species coexistence (Carson *et al.* 2008). This is no simple task, but recent studies using a combination of empirical data and population models to assess contributions to species coexistence (Levine & HilleRisLambers 2009; Adler, Ellner & Levine 2010) may point to a way forward.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Study information and survival data for each test used in the meta-analysis.

Appendix S1. Reference list for articles used in the meta-analysis.

Appendix S2. R code used to conduct statistical analyses.

Appendix S3. R code used to make figures.