

NEWS AND VIEWS

PERSPECTIVE

The full path of Janzen–Connell effects: genetic tracking of seeds to adult plant recruitment

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The Janzen–Connell (J-C) model (Janzen 1970; Connell 1971) has been a dominant yet controversial paradigm for forest community dynamics for four decades, especially in the tropics. With increasing distance from the parent plant, the density of dispersed seeds decreases and, because of a reduced impact of distance- and density-responsive seed and seedling enemies, propagule survival increases, resulting in peak recruitment at some distance from the parent and little recruitment near adult conspecifics. This spacing generates gaps near adult trees for the recruitment of heterospecifics, enhancing species coexistence and species richness. Field studies, primarily focused on seeds and young seedlings, have repeatedly demonstrated increasing survival with increasing distance from parents or decreasing density of propagules (e.g. Clark & Clark 1984; Gilbert *et al.* 1994; Swamy & Terborgh 2010). Yet a meta-analysis of distance-dependent propagule survival failed to support a general pattern of survival increasing with distance from adult conspecifics, suggesting that there is no need for further experimental tests of the J-C hypothesis in terms of diversity enhancement—results are species-specific, not general (Hyatt *et al.* 2003). However, a lack of consistent experimental results is not surprising. The outcome of tests of the hypothesis can vary as a function of many factors that can affect successive recruitment stages differently (Schupp 1992; Hyatt *et al.* 2003; Swamy & Terborgh 2010). This highlights a critical gap—a full test of the J-C model requires data demonstrating that effects carry over to recruitment of new reproductive adults, yet few studies have gone beyond early stages. There is strong inferential evidence that adult trees can show the imprint of J-C effects (e.g. Nathan *et al.* 2000; Howe & Miriti 2004), and focal individual modelling has clearly demonstrated that J-C effects can operate from sapling

through adult stages in a significant number of species (Peters 2003). It is likely that such results are not unusual, but there have been few attempts to demonstrate J-C spacing at the adult stage. In this issue of *Molecular Ecology*, Steinitz *et al.* (2011) studied the Mediterranean pine *Pinus halepensis* (Aleppo pine) and combined a unique situation with an innovative approach to provide the most elegant demonstration yet that adult recruits are spaced further from parents than expected from the initial seed distribution, clear evidence of a J-C effect carrying over to reproductive adults. A major advancement of this study is that it incorporates estimates of the initial patterns of seed dispersal and parentage analysis of adult–offspring relationships, illustrating the value of combined field and genetic approaches.

Keywords: density dependence, distance dependence, effective seed dispersal, Janzen–Connell model, microsatellites, plant recruitment

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The unique situation was an isolated natural Aleppo pine population that expanded from five trees early in the 20th century to about 2000 individuals now (Fig. 1). The study effectively extended previous parentage analyses (e.g. Robledo-Arnuncio & García 2007; Grivet *et al.* 2009) by assessing multiple cohorts and demographic stages. The innovative approach was to combine genetic analysis to determine spatial patterns of effective dispersal with a mechanistic model to determine the original pattern of seed dispersal. Microsatellite markers were used to assign parentage to offspring that recruited between 1944 and 1957, a period when only the five original trees were reproductive and before large-scale planting of Aleppo pine began in the area. For recruits that could be unambiguously assigned two parents, the maternal parent was determined based on a chloroplast marker that is paternally inherited in this gymnosperm. The authors then calculated an ‘effective seed dispersal kernel’—that is, the distance distribution of adult recruits around the parents—and compared this kernel with an initial seed dispersal kernel derived from a validated mechanistic model of wind dispersal. With these two kernels, the authors could then calculate the survival kernel. Results clearly showed that the mode of the effective dispersal kernel (20 m) was shifted substantially further from the parents than the mode of the seed dispersal kernel (4 m). Interestingly, although the probability of survival increased with distance from the parent up to 45 m, after that point, survival slowly declined with increasing distance, a result not predicted by the J-C model but also one that did not negate a J-C

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Fig. 1 The Aleppo pine (*Pinus halepensis*) population on Mt. Pithulim, Israel, used by Steinitz *et al.* (2011) in their genetic study of Janzen–Connell effects (top) and a close-up of an Aleppo pine with both open and closed cones (bottom) (Top Photo: Ofer Steinitz; Bottom Photo: Maayan Harel).

recruitment effect. The decline in survival with greater distances from parents might be due to declining suitability of the abiotic conditions (real decline) or perhaps simply because of bias from a reduced accuracy of estimating the tail of the dispersal kernel, which is based on only a small number of long-distance dispersal events (apparent decline). The use of parentage analysis for multiple cohorts allowed the authors to overcome a frequent problem in J-C tests, namely the limited time span for the recruits considered and thus lack of appropriate extrapolations for delayed effects on adult recruitment.

The problems arising from a lack of insight into recruitment of new adults have implications well beyond tests of the J-C model. In particular, the overall framework of seed dispersal effectiveness (SDE) is founded on the consequences of seed dispersal for the recruitment of new adults (Schupp *et al.* 2010). And perhaps even more so than in tests of the J-C model, empirical studies of SDE have fallen short, almost entirely limited to the consequences of seed dispersal for the success of seeds and/or seedlings and

assuming this reflects the consequences for adult recruitment. Unfortunately, this is likely untrue for many species exhibiting life-stage conflicts; that is, when sites suitable for some life stages, such as seed survival, are unsuitable for other stages, such as seedling survival (Schupp *et al.* 2010; Steinitz *et al.* 2011). To understand the ecology and evolution of seed dispersal, it is critical to really follow the consequences of dispersal through all stages from dispersed seed to recruited adults, but this is a huge challenge, especially with long-lived woody species (Schupp *et al.* 2010). Several recent modelling approaches have potential (Schupp *et al.* 2010), but can the general framework developed by Steinitz *et al.* (2011) and applied to Aleppo pine be broadly applicable to assessing SDE and its associated J-C effects? The authors suggest that the approach can be applied to a wide range of seed dispersal systems, but the extent that this is true is not completely clear. While some of the four stages of their framework, such as assigning maternal plants to adult recruits, are potentially feasible for a wide variety of species, the ability to broadly apply other stages of the framework is uncertain. Perhaps the biggest constraint is estimating the pattern of seedfall during a time frame relevant to the studied recruits in fleshy-fruited animal-dispersed species with diverse assemblages and moderate to high frequency of difficult-to-detect long-distance dispersal events. While patterns of seed dispersal by wind are probably moderately consistent across years, patterns of seed dispersal by frugivore assemblages potentially vary dramatically across years. Different dispersal agents in an assemblage differ in distances seeds are dispersed, microhabitats to which seeds are dispersed, the degree of seed clumping and more, all of which will affect the population-level pattern of seedfall (Schupp *et al.* 2010). Year-to-year changes in the composition of disperser assemblages that differentially contribute to total dispersal kernels (Jordano *et al.* 2007; Nathan 2007) can dramatically alter the patterns of seed dispersal and the outcome of J-C effects (Schupp *et al.* 2010). An analogous scenario for wind-dispersed species would be the role of different wind regimes in generating asymmetric dispersal kernels away from the seed sources, as revealed by Steinitz *et al.* (2011) (also see Robledo-Arnuncio & Gil 2005; García *et al.* 2007). These processes likely drive local-scale variations in dispersal kernels that can be of interest in relation to specific environmental settings. Despite these difficulties inherent to the complex process of seed dispersal, the expected conceptual breakthroughs of the framework are highly promising, particularly by suggesting ways to combine the genetic analysis of seed shadows within explicitly experimental J-C tests.

On a final note, this study highlights a common problem in ecological research: to really understand the system, we need to apply a variety of approaches. While the Steinitz *et al.* (2011) framework shows potential for accurately assessing the consequences of seed dispersal for adult recruitment, at least for some types of dispersal systems, it only assesses outcomes, not mechanisms. In contrast, the typical experimental tests of the J-C model clearly assess

potential mechanisms (e.g. seed predation), but they have failed to adequately address the final outcome: the effects on adult recruitment. The time is ripe for an effective combination of both approaches.

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