Distinctive inter-annual patterns of tree seed production can include spatial synchronicity, periodicity, and high variability among individuals within a population. Synchronicity and high variability are now commonly used to define mast seeding, with ‘strict’ mast seeding further distinguished by annual seed production that is either often large or nil and thus bimodal. Here we test for synchronicity, periodicity, and bimodality using 43 years of annual total and viable seed counts, along four transect lines, sampling an elevation gradient (480–1340 m) in a monospecific New Zealand mountain beech Nothofagus solandri var. cliffortioides forest. We expect most support for periodicity and bimodality at relatively high elevation sites that are most resource limited and known to have the greatest variability in seed production. While there was weak evidence for differences in viable seed counts along the elevation gradient, this was not the case for total seed counts. A significant year-effect on seed counts provided some evidence for synchronization, but the correlations of total or viable seed counts rapidly declined (from 0.96 to 0.58) with increasing elevation difference among transect lines. Although we detected a seven-year periodicity in total and viable seed counts at each elevation, we also detected other period lengths at most elevations. We did not find evidence for our expectation of increased period length and bimodality in relatively unproductive high elevation mountain beech forests because they would take more time to recover from seeding events. As a consequence, if resource limitation is an important driver of mountain beech seed production its influence must be strongly regulated by other factors to determine the distinctive characteristics (periodicity and synchronicity but not bimodality) of inter-annual variation in seed production.

Seed production by perennial plants has vital consequences for population demography, consumer dynamics, and ecosystem processes (Janzen 1971, Kelly and Sork 2002, Wardle 2002). Distinctive inter-annual patterns of tree seed production can include spatial synchronicity (Burrows and Allen 1991, Koenig and Knops 2000, Schaub et al. 2002, Liebhold et al. 2004, LaMontagne and Boutin 2007, Fearer et al. 2008), periodicity (Caron and Powell 1989, Sork et al. 1993, but see Greene and Johnson 2004), and high variability (Kelly 1994, Herrera et al. 1998, Greene and Johnson 2004) by individuals within a population. The patterns of synchronicity and high variability are now commonly used to define mast seeding, with ‘strict’ mast seeding further distinguished by annual seed production that is often large or nil and thus bimodal (Kelly 1994). Bimodality is a characteristic of seeding that implies resource allocation switching (Kelly and Sork 2002). Few studies have provided strong statistical tests for bimodality in seed crop size frequency distributions, or periodicity, and such analyses also require suitably long time-series data (Herrera et al. 1998, Kelly and Sork 2002, Greene and Johnson 2004). So, for example, although Koenig and Knops (2000) showed seed production was generally not bimodal in Northern Hemisphere trees their data sets had timespans of as few as six years.
seed production at higher elevations should accentuate any seeding bimodality. We expect any shifts in periodicity or bimodality with elevation should cause a related decay in synchronicity (Allen and Platt 1990).

We use 43 years of seed counts in a population-level (sensu Kelly 1994) test of synchronicity, periodicity, and bimodality along an elevation gradient in a New Zealand mountain beech Nothofagus solandri var. cliftonioides forest. Mountain beech forms monospecific stands that dominate extensive areas in the drier montane and subalpine forests in eastern parts of New Zealand between 36°S and 46°S (Wardle 1984). The wind-pollinated mountain beech trees are considered to seed periodically (e.g. 4–6 years in Wardle (1984); 3–5 years in White and King (2006)). Three factors make our mountain beech forest elevation gradient ideal for examining synchronicity, periodicity, and bimodality in seed production. First, CVs of inter-annual seed production are among the highest for any species in the world, particularly near treeline (Webb and Kelly 1993). Second, a simple forest structure allows population-level comparisons along an elevation gradient without the confounding effects of compositional variation in tree species. Third, net annual primary production of mountain beech at the stand level (Benecke and Nordmeyer 1982, Richardson et al. 2005), stemwood production (Harcombe et al. 1998), and individual tree growth (Coomes and Allen 2007) all decline with increasing elevation. We test: 1) for decay in seeding synchronicity with elevation, 2) whether seeding periodicity or bimodality is more apparent at relatively high elevations, and 3) whether synchronicity, periodicity, or bimodality is more distinct for total rather than viable annual seed counts. We expect total seed production (somewhat equivalent to number of flowers) to be more strongly synchronized and bimodal, as a consequence of pollination benefits (Kelly and Sork 2002), than viable seed production, as viable seed production also reflects the influence of post-pollination factors during the reproductive period (e.g. nutrition, climate; Allen and Platt 1990). As Kelly et al. (2001) have shown greater pollination benefits to mountain beech from mating at higher elevations, we also hypothesize that total seed production would not decline with elevation.

Material and methods

Study site

Three mountain beech stands were selected in the Craigieburn Range (43°13´S, 171°69´E) and one stand at Mt Thomas Forest (43°09´S, 172°16´E), South Island, New Zealand. Mountain beech is the only tree species forming the natural forest of the Craigieburn Range up to treeline at ca 1370 m elevation while Mt Thomas Forest is dominated by trees of intermediate form between mountain beech and black beech N. solandri var. solandri. Two climate stations are located within 2 km of the Craigieburn Range stands: Craigieburn Forest (914 m elevation) and Ski Basin (1550 m elevation). Mean annual temperature at Craigieburn Forest is 8.0°C, with the highest mean monthly temperature occurring in February (13.9°C) and the lowest in July (2.0°C; McCracken 1980). The lapse rate of mean annual temperature between Craigieburn Forest and Ski Basin is 0.66°C per 100 m of elevation. Mean annual precipitation at Craigieburn Forest is 1447 mm, with February, March, and June receiving <100 mm (McCracken 1980). Mean annual precipitation at Ski Basin is 139 mm higher than at Craigieburn Forest. Ashley Forest climate station (107 m elevation) is located ca 25 km east of the Mt Thomas Forest stand. At this station mean annual temperature is 11.4°C, with a February maximum of 16.1°C and July minimum of 6.2°C (New Zealand Meteorological Service 1980). Mean annual precipitation is 825 mm, with all months having less than 100 mm. The rainfall at Mt Thomas Forest is at least 200 mm year\(^{-1}\) higher than at Ashley Forest. Soils in the study area are acidic, and low in nitrogen and cation availability (Allen et al. 1997, Clinton et al. 2002). Soil nutrient availability is also known to decline with increasing elevation (Coomes and Allen 2007). Competition for soil nutrients (nitrogen) limits growth of individual mountain beech plants and population-level seed production (Davis et al. 2004, Platt et al. 2004, Smaill et al. 2011).

Mountain beech is a long-lived (250–350 years) evergreen tree species, stands of which exhibit a decline in biomass, net productivity, height, and mortality with increasing elevation, but a small increase in stem density and basal area (Benecke and Nordmeyer 1982, Harcombe et al. 1998, Coomes and Allen 2007). For example, Benecke and Nordmeyer (1982) showed that net annual primary production at the stand level declines from 33.6 ton ha\(^{-1}\) year\(^{-1}\) at 1000 m elevation to 18.0 ton ha\(^{-1}\) year\(^{-1}\) at 1320 m elevation in the Craigieburn Range. The summer optimal temperature for photosynthesis is ca 17°C at 890 m elevation near the study site where, as is commonly the case, photosynthesis is unconstrained by moisture deficits. Summer temperatures are usually below this optimum at the study site and the influence of cool air temperatures as a factor restricting net photosynthesis increases with elevation (Benecke and Nordmeyer 1982). The species is monoeccious, with wind-pollinated flowers, and produces a nut enclosed in a cupule. Each nut is one-seeded. Reproduction spans two growing seasons. In the first season, floral primordia are laid down in the dormant buds soon after they begin to form. Flowering occurs in the second season, and the timing is strongly influenced by site conditions, so that flowering can occur in late October at 450 m elevation and in early January at treeline (Wardle 1984). The nuts ripen and seeds are shed ca 6 months after pollination. Mountain beech annual total seed production (at a site) ranges from <10 (15% of years) to >6000 (15% of years) seeds m\(^{-2}\) (Allen and Platt 1990, Richardson et al. 2005). This large inter-annual variation in seed production is strongly correlated with climatic variation over the reproductive period (Poole 1948, Wardle 1984, Allen and Platt 1990, Schuber et al. 2002, Richardson et al. 2005). Smaill et al. (2011) show that such climatic variation can influence inter-annual resource availability (soil nitrogen availability), and that nitrogen availability in turn regulates the synchronicity in mountain beech seed production. Resource depletion from mountain beech seeding events is indicated by a tendency for trees not to seed in consecutive years (Wardle 1984, Allen and Platt 1990), which is in turn overcome, to some degree, by experimental nitrogen additions (Smaill et al. in 2011).
Data collection

We collected mountain beech seedfall along transect lines in stands representing a strong productivity gradient at 1340, 1190 and 1050 m elevation (each approximately 0.3 km apart) in the Craigieburn Range (High-, Mid-, and Low-elevations respectively) and from a Mt Thomas Forest stand at 480 m elevation (Low-elevation; approximately 50 km from Craigieburn). Each line included eight seed trays arranged ca 40 m apart. Seed trays were funnel-shaped with a catch area of 0.28 m². Seedfall was measured from 1965 to 2007 at Craigieburn and from 1966 to 2007 at Mt Thomas (see details in Allen and Platt 1990). We counted the number of nuts in the seed catch of each tray, for each year. The number of viable nuts (intact endosperm) was determined in most years by cutting each nut with a scalpel. However, in years with high seed production viability was instead determined by floating the nuts in 99% ethanol (tested against cutting by Ledgard and Cath 1983).

Data analysis

Synchronicity

We used an ANOVA approach to examine synchrony in annual total and viable seed counts, where the model included year and line as random factors. Levene's test revealed significant heterogeneity in variance between groups, whether groups were formed according to year or line, and thus violates an assumption of the F-test. Therefore, we chose Welch's W-test for its insensitivity to heterogeneity in variance when there are at least 10 observations per group (Krishnamurthy et al. 2007). This test is, however, sensitive to non-normality, with non-normal data giving inflated type I errors. To accommodate this, we used Monte Carlo randomizations to test the significance of observed Welch W-values. Given that both year and line were random factors, the appropriate randomization groups data within levels of both factors (i.e. by year and by line). These groups (rather than individual observations) were then randomly allocated within the same level as in the observed data for the factor not being tested and across levels of the factor being tested (Anderson and ter Braak 2003). In our case, when testing the effect of year on seed counts, we randomized groups of counts from the same line and year, within the line in which they were observed, but across years. p-values were calculated as the proportion of permutations giving a W as large, or larger, than that observed.

Periodicity

Periodicity was analysed initially using Spearman's rank correlations of total and viable seed counts from each tray for period lengths from two to 10 years (Bandt 2005). So for a period length of two years the rank correlation is between all pairs of \( t \) and \( t+2 \), and for a period of 10 years the correlations are between all pairs of \( t \) and \( t+10 \). p-values were generated from Monte Carlo simulations where seed counts were randomly allocated to the same line, but different years, ensuring that the null model retained all the processes that generated the observed data, except the temporal order of observations.

We also used an ordinal approach (Groth 2002) to examine periodicity, which is based on methods developed for generating recurrence plots describing the dynamics of complex systems (Marwan et al. 2007), and is closely related to those used by Bandt (2005). This approach was adopted as it makes no assumption about the amplitude or shape of fluctuations in time series (cf. Fourier transformation). Further, ordinal methods 1) are not affected by long-term trends in amplitude and 2) allow comparison of three or more values simultaneously and, in so doing, provide more information than the pairwise comparisons inherent in correlative approaches (Bandt 2005). These properties enable detection of periods of different lengths and thus permit examination of time series where phase changes occur. The fact that ordinal methods are insensitive to changes in the amplitude of peaks is a great advantage in analysing temporally variable ecological phenomena, such as seeding, where peaks can vary greatly in amplitude.

Our ordinal method estimates the probability that a time series has period length \( T(P^T) \) by simultaneous comparisons of seed counts from four different years. This is achieved by calculating the proportion of \( t \) values that satisfy conditions 1A–1D (i.e. each term represents a seed count for a particular year), then summing these proportions (Groth 2002):

\[
P_e = P[t(t) \leq x(t+T) \leq x(t+v) \leq x(t+v+T)] \quad (1A)
\]

\[
P_b = P[t(t+T) \leq x(t) \leq x(t+v+T) \leq x(t+v)] \quad (1B)
\]

\[
P_c = P[t(t) \geq x(t+T) \geq x(t+v) \geq x(t+v+T)] \quad (1C)
\]

\[
P_d = P[t(t+T) \geq x(t) \geq x(t+v+T) \geq x(t+v)] \quad (1D)
\]

where: \( x(t) \) is the response value at time \( t \), \( v \) is the delay value. All values of \( t \) between \( 1 \leq t \leq L \cdot T \cdot v \) inclusive (where \( L \) is the length of the time series) were analysed, to ensure that every datum in the time series is included.

In the case where a time series exhibits a noiseless periodic signal, a delay value \( (v) \) of 1 would be used, since this gives the highest precision in estimating period length. However, when noise occurs, the signal may be locally disrupted, so that it is necessary to try a range of delay values. \( P^T \) estimates for different delay values may be integrated by multiplying the probabilities obtained for each delay value to give a more general estimation of the probability that a time series has period length \( T \):

\[
P^T = \prod_{v=1}^{N} P(T,v),
\]

where \( N \) is the number of delay values used, and \( P(T,v) \) is the probability that a time series has period length \( T \) given a delay value of \( v \). For a noiseless signal of period length \( T \) all \( P(T,v) \) take a value of 1, so that \( P^T \) has an upper limit of 1. \( P^T \) will approach 0 for signals with no periodicity. At least two cycles are needed for a period to be detected, which limits us to examining period lengths less than half the total length of the time series. In our case, the maximum period length examinable was 21 years. As the delay value should not exceed \( 0.25 \times T \) (A. Groth pers. comm.) and \( T \) has a maximum value of 21 in our case, we decided to use delay values ranging from 1 to 5 in Eq. 2.
Analyses were performed for viable and total counts from each seed tray separately. We then pooled results for each line to give an average probability for each period length for each line. The Monte Carlo simulation, as for the rank correlation analyses, was used to test whether observed probabilities were significantly different from random expectation. This constitutes a test of whether the observed probability for a given period length, in a given line, differs from that expected when observations are randomly ordered. Two-tailed p-values were calculated by doubling the proportion of randomizations giving a probability as or more extreme than that observed. An expected probability was calculated as the mean taken across randomizations. This was used to calculate a standardized effect size (SES) value, which allows comparison of effect sizes from tests of differing power (Gotelli and McCabe 2002):

\[ \text{SES} = \left( \frac{\text{Observed} - \text{Expected}}{\sigma_{\text{Expected}}} \right) \]

where Observed is the observed \( P^T \), and Expected and \( \sigma_{\text{Expected}} \) are respectively the mean and standard deviation of randomised \( P^T \) values. Artificially generated datasets confirmed that the ordinal periodicity method and Monte Carlo simulation test gave appropriate type 1 error rates.

**Bimodality**

To test for bimodality, we used the dip test of Hartigan and Hartigan (1985). This is a commonly employed test of bimodality and has recently been used in ecological studies including tests for bimodality in the body size of mammal assemblages (Kelt and Meyer 2009). The dip statistic is the maximum distance between the observed probability distribution and the

Figure 1. Mean annual total and viable seed counts for High-, Mid- and Low-elevation Craigieburn Forest seed trays along each transect line, as well as for the Low-elevation Mt Thomas transect line, for each year.
The significant effect of year on total and viable seed counts provides strong evidence for a level of synchronicity in both total and viable seed production at different elevations (Table 1). All Spearman’s rank correlations of annual total or viable seed counts among elevations were significant ($p < 0.001$), although correlations declined from 0.96 for total seed production between the adjacent High- and Mid-elevation Craigieburn lines to 0.58 for viable seed production between the High-elevation Craigieburn line and the Low-elevation Mt Thomas line. While the ANOVA gave weak evidence ($p < 0.1$) of between-line (elevation) differences in viable seed counts, this was not the case for total seed counts (Table 1).

Median (with 5th and 95th percentile values) annual viable seed counts were 1.0 (0, 1264), 3.3 (0, 1202), 5.9 (0, 1307), and 3.2 (0, 1177) for High-, Mid- and Low-elevation Craigieburn, and Low-elevation Mt Thomas lines, respectively.

**Table 1.** ANOVA of viable and total seed counts with year and seed tray transect line as random factors. Permutation test results for Welch’s $W$ are given. SES is standardized effect size (Gotelli and McCabe 2002) and $p$ is the proportion of permutations giving a $W$ equal to or greater than that observed.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$W_{\text{observed}}$</th>
<th>$W_{\text{expected}}$</th>
<th>SES</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Viable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Line</td>
<td>4.585</td>
<td>2.236</td>
<td>1.216</td>
<td>0.093</td>
</tr>
<tr>
<td>Year</td>
<td>24.493</td>
<td>1.073</td>
<td>38.999</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Line</td>
<td>1.842</td>
<td>2.082</td>
<td>-0.141</td>
<td>0.445</td>
</tr>
<tr>
<td>Year</td>
<td>36.455</td>
<td>0.987</td>
<td>73.933</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

unimodal distribution function that minimizes this distance. The dip test is non-parametric and makes no assumptions about the shape of the probability distribution of either the best univariate fit to the observed data or the best empirical fit to the data. $p$-values for observed dip statistics were taken from tables of critical values available in the function ‘dip’ in the R package ‘diptest’ (R Development Core Team 2009).

**Results**

**Synchronicity**

Annual total and viable seed counts exhibited ongoing year-to-year variation throughout the period of study (Fig. 1). The periodicity

Using the ordinal approach, a seven-year period yielded significantly higher probability ($P^r$) than expected at random for total seed counts on all lines, and there was also evidence of a two-year period for all but the Low-elevation Craigieburn line (Fig. 2). This two-year period probably represents the need for trees to recover resources after a seeding year, but its occurrence at higher elevations is surprising given an expectation that trees would take longer to recover from seeding on such sites. The seven-year period was supported by significant Spearman’s rank correlations of total seed counts using a delay
of seven years ($0.01 < p < 0.05$ in all cases). Rank correlation analyses also revealed significant negative correlations between consecutive years in total seed production for all lines, suggesting that resource limitation severely decreases potential seed production following a seeding event. The power of the ordinal approach was apparent through its detection of a number of other period lengths for total seed counts, including for the Low-elevation Mt Thomas line a 14-year period as a multiple of 7 (Fig. 2). The detection of multiple period lengths, particularly the low-elevation Mt Thomas line, suggests either that drivers of differing periodicity are interacting with each other, or that the periodicity of these drivers has changed throughout the study period.

For viable seed counts, a seven-year period was the only period length to give a significant result for all four lines (using ordinal and correlative methods), although it was only clearly dominant for the Low-elevation Craigieburn line (Fig. 3). A nine-year period length was the only other to give a significant result for more than one line (High-elevation Craigieburn line and Low-elevation Mt Thomas line). At least one longer period-length was identified using the ordinal method for each line, except the Low-elevation Craigieburn line, with the Low-elevation Mt Thomas line again having a 14-year period as a multiple of 7 (Fig. 2). A two-year period was apparent for viable seed counts from the Mid-elevation Craigieburn line. Overall our results indicate greater significance of a seven-year period length for total seed counts than viable seed counts (Fig. 2 vs Fig. 3). That some evidence was obtained for multiple period lengths for both total and viable seed counts suggests that the observed periodicity in seed production is unlikely to be due to periodicity in any single driving variable.

### Bimodality

There was very little evidence from the dip test for bimodality in total seed counts for any of the lines (Fig. 4, 5). The only significant dip-test result was for viable seed counts in the Mid-elevation Craigieburn line. The binomial probability of receiving one significant result from eight tests is 0.33 (with $\alpha = 0.05$), indicating that the evidence for bimodality did not exceed that expected at random. The overwhelming pattern is of highly skewed distributions for total and viable seed counts with many years having low seed counts, even for the single significant result. There was little apparent difference in the form of the frequency distributions among lines.

### Discussion

We show, using a data set that is relatively long term by global standards, that mountain beech seedfall is to some degree synchronous, can have several dependable time intervals, and that frequency declines monotonically with seed crop size. In addition, we did not detect a decline in mountain beech total seed counts (somewhat equivalent to number of flowers) with increasing elevation and suggest this restricts the effect of greater pollen limitation with increasing elevation (Kelly et al. 2001).

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Figure 3. Standardized effect size (SES) values of each period length for annual viable seed counts from each of the four seed-tray transect lines. Each tray, within each line, was analysed separately with observed and expected probability for each period being calculated as the mean across all trays within a line ($p < 0.05$, ***$p < 0.01$, ****$p < 0.001$). It should be noted that SES values are for the probability that the time series has the period length in question, as derived from Eq. 2.
Synchronicity

Population-level synchronicity in seed production, as found in mountain beech, has been widely demonstrated (Kelly 1994, Fearer et al. 2008). In this study, we show strong local synchronicity (e.g. Spearman’s rank correlations > 0.90) in total and viable seed production among adjacent Craigieburn seed tray lines (0.3 km apart). This reflects synchronized responses to inter-annual climatic variation (Allen and Platt 1990, Richardson et al. 2005). Elsewhere, seed production correlation coefficients at this scale, performed in various ways, rarely exceed 0.80 (Lázaro et al. 2006, LaMontagne and Boutin 2007). Certainly pollination efficiency arguments support high local synchrony in mountain beech seed production as selection appears to act strongly against unsynchronized individuals (Kelly et al. 2001). However, there are barriers to pollen flow along the elevation gradient as phenology is progressively delayed at higher elevations, with no overlap in flowering time with low elevations (Wardle 1984). This would weaken selective pressures for synchrony along the elevation gradient. Physiographic gradients have also been shown to affect spatial synchrony in Quercus alba acorn production (Fearer et al. 2008).

Periodicity

Mountain beech (Wardle 1984, White and King 2006) is one of many species (Fowells 1965, Sork et al. 1993) for which a dependable periodicity has previously been suggested. Our analyses support periodicity for both total and viable seed counts on all lines. This is intriguing as inter-annual variability in seed production is often the consequence of inter-annual variability in climate (Houle 1999, Richardson et al. 2005, Newbery et al. 2006), and sometimes climate is not periodic (Robinson and Henderson-Sellers 1999). The climate variables with by far the strongest correlations with mountain beech total and viable seed counts are summer temperatures at the time of floral primordial development and summer rainfall a year prior to that (Allen and Platt 1990, Richardson et al. 2005, Smaill et al. 2011). To test periodicity in climate, we applied the ordinal method used on the seeding data to summer mean daily maximum temperature and mean daily temperature (January to April), as well as summer mean monthly rainfall (December to March) at Craigieburn Forest over the study period. That test distinguished a four-year periodicity for mean daily temperature (p < 0.01). While that is a poor match to the seeding periodicity, it does represent the cycle of 3–6 years observed in the El Niño–Southern Oscillation (Gordon 1986, Sturman and Wanner 2001). The El Niño–Southern Oscillation is known to influence, to some degree, inter-annual variation in temperature (Gordon 1986, Mullan 1995). Notwithstanding that, correlations between inter-annual variation in seed production and the Southern Oscillation index are weak in New Zealand when compared with temperature correlations (Schauber et al. 2002). In tropical forests inter-annual variability in seed production is related to the El Niño–Southern Oscillation (Curran and Leighton 2000, Wright and Candefon 2006).
While Greene and Johnson (2004) found no evidence for cycles in annual seed production for a range of North American tree species, our study instead found evidence for multiple period lengths between seeding events for most seed-tray lines (Fig. 2, 3). However, there was no evidence for our hypothesis that period length would increase with elevation, and longer period lengths were associated with the lowest elevation line (Fig. 2, 3). A feature of periodicity was greater statistical significance, at most elevations, for total seed production periods rather than for viable seed production periods. We suggest total seed production may be linked to one (or more) periodically varying factor(s) (White and Tourre 2003), while viable seed production is also sensitive to processes during reproduction (e.g. tree carbohydrate balance), or to stochastic events disrupting seeding cycles (e.g. cool temperatures in a year when trees have abundant carbohydrate reserves; Lyles et al. 2009). In summary, the periodicity of seeding is not well matched to periodicity of any particular variable (e.g. climatic or recovery period) but is dependent on the periodicity with which all conditions necessary for seeding events are satisfied.

Bimodality

Although Kelly and Sork (2002) considered that bimodality occurs in many species, few studies have adequately long time-series data to robustly test for bimodality. Those that do either show no bimodality (Koenig and Knops 2000) or have had their methods questioned (Greene and Johnson 2004). We adopted an approach that overcomes some limitations of earlier methods and we did not pool different species in an attempt to create a suitably long time-series (cf. Herrera et al. 1998). We found no evidence for bimodality, even at high elevations with variable seed production, beyond that expected by chance for the number of tests performed (Fig. 4, 5). Instead frequency distributions were monotonically declining and highly right skewed such that mean seed production would rarely be achieved (Greene and Johnson 2004).

Conclusions

Our analyses did not support our expectation that periodicity and bimodality would be more apparent on unproductive high elevation sites, where mountain beech has highly variable seed production (Kelly et al. 2001). As a consequence, if resource limitation is an important driver of mountain beech seed production its influence must be strongly regulated by other factors to determine the distinctive characteristics (periodicity and synchronicity but not bimodality) of inter-annual variation in seed production (Richardson et al. 2005, Smaill et al. 2011).

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