Comparing two ground-based seed count methods and their effect on masting metrics

Jessie J. Foest (1, 5), Michal Bogdziewicz (1), Thomas Caignard (2), Martin Hadad (3), Peter A. Thomas (4), Andrew Hacket-Pain (5)

(1) Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland.
(2) BIOGECO, INRAE, University of Bordeaux, Cestas, France
(3) Laboratorio de Dendrocronología de Zonas Áridas-Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, CIGEOBIO (CONICET-UNSJ), San Juan, Argentina.
(4) School of Life Sciences, Keele University, Staffordshire ST5 5BG
(5) Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom

Abstract

Masting, i.e. interannually variable and synchronized seed production, plays a crucial role in forest ecosystems, influencing wildlife dynamics, pathogen prevalence, and forest regeneration. Accurately capturing masting variability is important for effective forest management, conservation efforts, and predicting ecosystem responses to environmental changes. The adoption of low-cost methods facilitates the large-scale data acquisition needed in this time of unprecedented environmental upheaval, but it is important to understand the reliability of such methods. We investigated the relationship between the timed count method and the quadrat-based method for monitoring seed production in European beech (*Fagus sylvatica*). The timed count method is fast, cost-effective, and suitable for areas with public access. These characteristics make time counts a practical choice for large-scale seed monitoring. However, the method has not been cross-calibrated with more traditional ground-based methods like quadrat sampling, which involves exhaustive seed collection from designated plots under tree canopies. Our research reveals a loglinear relationship between seed counts obtained by the two methods, and shows that the timed count is an effective method of estimating seed production. We also found that seed production exhibits greater dispersion in patchiness at lower levels of seed fall, which explains why the timed count method, covering a larger area, captures greater variability in seed fall compared to the quadrat method in such contexts. This highlights the importance of choosing an appropriate sampling strategy to accurately assess seed fall. The differences between the two methods introduce variability into derived masting metrics, such as the coefficient of variation and synchrony, with individual-level seed production variability metrics being more affected than population-level ones. The findings underscore the importance of understanding how different sampling methods can impact long-term ecological studies, particularly those focused on masting behaviour.

Introduction

Researchers have long been counting seeds to estimate the interannual variability of seed production in a population (i.e. masting), since this seed production variability has important applied and ecological consequences (Ascoli et al., 2017a; Hilton and Packham, 2003; Koenig, 2021). For instance, the resource pulses associated with high seeding years affect the population dynamics and behaviour of wildlife including insects, rodents, larger mammals, and birds (Jones et al., 1998; Maag et al., 2024; Ostfeld and Keesing, 2000; Touzot et al., 2020). Via cascading effects, masting also influences the prevalence of pathogens, including Lyme disease, and haemorrhagic fever (Bregnard et al., 2021; Clement et al., 2009; Reil et al., 2016; Tersago et al., 2009). Moreover, masting dictates seedling emergence, recruitment and forest regeneration (Maringer et al., 2020; Zhang et al., 2022; Zwolak et al., 2016). Effective management of natural systems therefore relies on our understanding of masting (Pearse et al., 2021).

Our grasp of the spatio-temporal variability in masting, and its effects on the ecosystem, depends on the availability of extensive records of both seed quantity and quality. Increasing seed sampling across climate change gradients, for instance, is particularly important as it can reveal the drivers of changes in masting and help to predict the response of masting to further environmental change (Foest et al., 2024; Hacket-Pain and Bogdziewicz, 2021). Moreover, unpredictable seed supply is a challenge for forest restoration and afforestation projects (Kettle, 2012; Pearse et al., 2021; Whittet et al., 2016). Models which forecast masting, built on seed monitoring data, can help improve the timing of seed sourcing for such projects (Journé et al., 2023b; Pearse et al., 2021). Thus, there is a demand for reliable, well-understood and cost-effective seed production monitoring methods.

The adoption of low-cost methods can improve large scale data acquisition, and support the longevity of seed monitoring projects (Koenig et al., 2020, 1994b). Yet, it is important to understand the reliability of such methods, and cross-calibrate them with reference methods. One easy to implement, time-effective, and low-cost monitoring method which requires no infrastructure is the timed count used to monitor seed production in European beech (*Fagus sylvatica*) since 1980 in the United Kingdom (Packham et al., 2008). This time-efficient method is easily learned and takes only 3.5 minutes per tree. Moreover, it is suitable for monitoring in areas with public access and areas where seed traps cannot be deployed. Its low cost and speed facilitate the acquisition of large sample sizes – a trait especially important when seed production is variable between years and individuals, as is the case for masting seeding (Koenig et al., 1994b). In contrast to another well established and efficient method, namely the 30-second binocular count of fruit in the canopy (the 'Koenig method'; Koenig et al., 1994a; Touzot et al., 2018), the timed count method can be used when branches are difficult to see (including in closed canopy forest), and allows for further assessment of seed quality post-sampling. This is highly relevant as, for example, UK beech seeds collected with the timed count can be examined to measure rates of seed predation and pollination. Such efforts have revealed that due to temporal changes in masting associated with climate warming, the number of viable seeds declined by up to 83% over the last four decades, despite increasing total seed production (Bogdziewicz et al., 2023, 2020). Crucially, the joint monitoring of seed quantity and quality uncovered a highly concerning process that would have otherwise remained hidden, and opened further research avenues to mitigate the impacts of decreased viable seed supply (Bogdziewicz et al., 2024). Here, we investigate how this timed count method relates to a more traditional ground-plot method, which is performed by collecting all seeds from quadrats placed under the tree canopy.

We predicted that the relationship between timed and quadrat seed counts is loglinear because a degree of saturation can occur when using effort-based methods such as timed counts. That is, there are physical limits to how many seeds can be collected within a certain time frame (Koenig et al., 1994a; Touzot et al., 2018). Exhaustive counts within quadrats would not feature such saturation. Although logarithmic functions do not include a plateau parameter for the maximum number of seeds collected with the timed count, they are particularly useful to describe processes where the rate of change slows down as the quantity being measured increases. In contrast to more complex nonlinear models, logarithmic transformations within the context of linear models are versatile and can easily be incorporated regardless of the directionality (i.e. from timed counts to quadrat counts or vice versa).

Another reason we anticipated nonlinearity arises from the potential impact of seed fall patchiness on seed count estimates derived from the two methods. Generally, comparing estimates obtained with different methods can improve insights on the properties of the system in which we obtain data. Touzot et al. (2018), for instance, found evidence of predation satiation by contrasting estimates obtained with exposed ground plots and seed trap nets (which offer some protection against predation). Here, we expected to observe differences related to sampling area. The timed count method covers a larger sampling area than is typical for an area-based count (whole or large canopy nets can be used but such nets are highly intensive; (Fleurot et al., 2023; Touzot et al., 2018), and seeds are picked up from multiple locations under the crown of each individual. Where the observer collects seeds from is unlikely to be random – while care is taken to sample from multiple areas, the observer could be drawn to patches of seeds. In plants which produce clusters of heavy fruits, the comparatively small seed shadow can feature strong aggregation (Cousens et al., 2008). When seed production is patchy, the observer might sample more seeds from seed fall patches that would be missed by the quadrat sampling method as this method samples only a fraction of the surface area. Possibly, seed fall is patchier at lower levels of seed fall than at higher levels. At low seed fall levels only some branches may produce seeds (resulting in patchiness), while at higher seed fall, more or most branches participate (resulting in random to uniform seed fall). However, it is also possible that total seed fall affects the dispersion of patchiness. For example, at low seed fall levels, the seed fall distribution may be uniform (in the extreme: there are zero seeds, falling in zero plots) or random (i.e. there are a few seeds falling randomly from across the canopy), but in some trees, a limited number of branches produce a relatively large seed crop, resulting in a patchy distribution of seed fall.

Alongside the need to cross-calibrate seed sampling methods, it is important to investigate how the use of different sampling methods translates into measures of masting variability. Long-term seed production records are becoming increasingly available (Hacket-Pain et al., 2022), and seed sampling methods vary among time series. This is unsurprising, as methods vary in terms of collecting effort (i.e. time), required infrastructure, and their usefulness for particular species and habitats (e.g. small or large seeded species, closed canopy or savanna). Masting research increasingly uses integrated datasets which combine multiple methods (e.g. Ascoli et al., 2017b; Dale et al., 2021; Journé et al., 2023a; Lobry et al., 2023; Pearse et al., 2020), but we have a limited understanding of the effects of such collation; seed collection methods can affect seed production estimates (Koenig et al., 1994a; Touzot et al., 2018), which may translate into metrics derived from such data.

The aim of this study was to establish the relationship between the timed count and a reference method, i.e. quadrat counts. Subsequently, we aimed to test how the choice of method influences masting metrics. Specifically, we examined (1) if the relationship between timed counts and area-based counts is loglinear in nature, rather than linear, (2) if patchiness and the dispersion of patchiness vary as a function of total seed fall, and (3) the effect of sampling method on masting metrics at the individual and population level.

Methods

To test how estimates of seed fall obtained with a timed count and a quadrat-based count relate to each other, we collected seeds from European beech (*Fagus sylvatica*) in early October in 2022 and 2023. We subsequently used this relationship between the two methods to test the effect of the collection method on individual and population-level masting metrics using a dataset spanning 43 years of observation (the English Beech Mast Survey dataset, EBMS; Packham et al., 2008).

Species and sites

We sampled seed production under 59 beech canopies in early October of 2022 (N = 30) and 2023 (N = 29), across 5 sites. The sampled individuals are part of the English Beech Mast Survey, and grow at sites near Woodbury, Killerton, Buckholt, Painswick, and Portway. A detailed description of sites can be found in Packham et al. (2008), and an overview of the EBMS sites can be found in Fig. S1.

Sampling designs

To limit interference between sampling methods, quadrats were laid out before the timed count was conducted, and seeds found inside quadrats were not collected with the timed count method. Typically, the quadrats covered between 0.2 – 3% of the projected crown area, so the timed count was not significantly affected by the presence of the quadrats. Collected seeds were counted in the lab.

Quadrat count

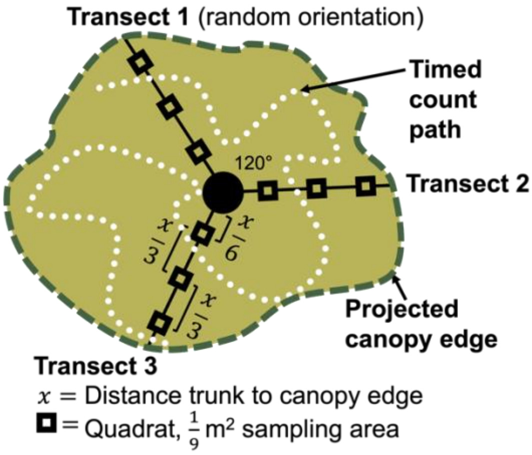


Figure 1: Graphical example of sampling layout under a tree canopy (dashed line). Quadrats were sampled along three transects, and a representation of a timed count sampling path is shown in a white dotted line. The black circle represents the tree trunk. Figure not to scale. Increasing canopy size reduces the relative sampling area covered by the methods, particularly when using the quadrat sampling method.

Under each tree, 9 quadrats (surface area: 1/9 m^2 each) were laid out along three transects, 120° apart (Fig. 1). Along each transect, three quadrats were placed at 1/6th, 1/2nd and 5/6th of the distance between the tree trunk and the canopy edge, starting at the tree trunk. All current-year seeds were collected from each quadrat by one observer, and another observer then checked that no seeds were missed.

Timed count

The timed count method was performed by collecting seeds under a tree for 3.5 minutes, and doubling the number of collected nuts (to obtain a 7-minute count for historical reasons; doubling may theoretically inflate counts, particularly during low-seeding years, but also increase the frequency of zeros. It was implemented to reduce fieldwork time, ensuring the feasibility of this long-term, large-scale study). This effort-based method has been used since 1980 in the EBMS (Packham et al., 2008). When performing the timed count, particular attention is paid to searching as much of the below-canopy area as possible, instead of sampling in a particular area. Moreover, when sampling, each seed is picked up and placed in the sample bag separately.

Statistical analyses

Analyses were performed in R (v. 4.4.1; R Core Team, 2023). Regression models were constructed with glmmTMB (v. 1.1.9; Brooks et al., 2017), unless differently indicated. Models were validated with DHARMa (v. 0.4.6; Hartig and Lohse, 2022).

Comparing seed count estimates

We tested the nature of the relationship between seed counts obtained with the two methods by constructing two linear mixed models and comparing their fit with AICc. The input consisted of raw seed count observations (X_{ij}), where each observation represented counts from a specific tree ($_i$) in a given year ($_j$). In the first model, the dependent variable 'Timed seed count' was modelled as a function of 'Quadrat seed count'. In the second model, the dependent variable was considered to be a function of ln(1 + Quadrat seed count).

To account for non-independence, we included tree ID nested with site as random intercept. To test if sampling year should be included in the model, we added year as a predictor, as well as a two-way interaction term of year with the quadrat seed count. Neither additive and interaction terms were significant, thus we removed the sampling year from the final model.

To convert timed count estimates into quadrat count estimates (i.e. seeds/m^2), we constructed a third model, with the natural log of 1 + 'Quadrat seed count' as the dependent, and 'Timed seed count' as the independent variable. The same random intercepts were included in this model.

Using a linear model, we tested if seed fall is patchier at lower levels of seed production (i.e. lower tree level quadrat count), and if seed fall levels affect the dispersion of patchiness. Patchiness was calculated with

Lloyd's index of patchiness (I_p; Lloyd, 1967; Wade et al., 2018), using nine quadrats for each sampled canopy. It is obtained as follows (Lloyd, 1967; Wade et al., 2018):

$$I_p = \frac{m + \left(\frac{V}{m} - 1\right)}{m} = 1 + \frac{(V - m)}{m^2}$$

where 'm' is the mean seed count across samples (i.e. quadrats) and 'V' is the variance of seed counts. An index of 1 signifies that seed fall across quadrats follows a random distribution, values below one signify uniformity, and values over 1 indicate a patchy distribution.

Effects on masting metrics

Since calculation of masting metrics requires many years of observation, it is not possible to use the two years of data we collected to calculate and compare the timed- and ground-based derived masting metrics. Therefore, we used the relationship between timed seed counts and quadrat counts derived from the linear mixed model described under 'Comparing seed count estimates' to convert timed seed counts to quadrat seed counts. These estimated quadrat seed count and observed timed seed count series were then used to investigate how individual and population-level estimates of masting metrics (specifically, CV, kCV, AR(1), Psd, and S; see below) would differ between methods, using data from the EBMS (3663 annual observations; 15 sites with sample sizes > 3 individuals; Packham et al., 2008). Loess models were fitted with the 'geom_smooth' function of the ggplot2 package (v. 3.5.1) to aid visual interpretation of the relationships between metrics (Wickham, 2016), and for each metric (obtained with two methods) the Spearman rank correlation was calculated.

CV is the coefficient of variation of seed production and is the most used metric to describe masting (Kelly and Sork, 2002). It is the standard deviation divided by the mean of seed production. kCV is a newly proposed bounded alternative to CV (Lobry et al., 2023). The kCV can be obtained by dividing CV^2 by 1 + CV^2, and subsequently taking the square root (Lobry et al., 2023). AR(1) captures the temporal autocorrelation of seed production at lag 1 year, and can be considered as a deterministic component of year-to-year variability (Bogdziewicz, 2022; Schermer et al., 2020). It was obtained with the 'Acf' function in the forecast package (v. 8.23; Hyndman and Khandakar, 2008). The Psd is calculated by taking the proportion of high seed years to all years, as proposed by LaMontagne and Boutin (2007) (note that we use 'high seed years' rather than 'mast years' as recommended by the Bogdziewicz, et al. (2024) review on masting). High seed years are the years where the standardised annual deviate of reproductive effort exceeds the absolute magnitude of the largest deviate below the mean. Synchrony of seed production (S) captures the average synchrony between an individual tree and conspecifics at a site at the individual level (Si), and at the population level (Sp), it describes the site-level average between-individual synchrony. Synchrony was calculated at the individual level (i.e. Si) with the average Pearson correlation between a tree's seed production and the seed production of all other trees at a site. The population-level estimate of synchrony (Sp) was obtained by calculating individual-level synchrony for all trees in a site, and then taking the average. For all metrics other than synchrony, individual-level and population-level estimates were obtained by using individual-level and population-level average seed production time series respectively.

When quadrat counts show a loglinear relationship with timed counts, small differences in timed counts at high seed fall levels can be transformed into unrealistically large quadrat counts. Therefore, we refrained from extrapolating beyond the maximum value on which the relationship between methods is based. Years in individual-level time series which had seed count values larger than the largest observation in our field study (i.e. 270 seeds; 4% of observations in the UK beech dataset) were excluded from the analyses comparing the masting metrics from the timed-and quadrat count data. Since individual-level time series were used to calculate population-level time series (i.e. by taking the average timed count per site per year), these large observations were also removed prior to the calculation of population-level time series.

Individual-level time series were split into 10-year segments to increase sample sizes and capture more variation, starting from the first year of observation. Since masting behaviour in UK beech has changed over time due to climate warming, dividing long time series into shorter segments is also justified biologically (Bogdziewicz et al., 2020). Any years where fewer than three individuals were sampled at a site were removed from population-level time series. Individual or population time series segments comprising fewer than six annual observations were excluded from the analysis. This approach resulted in 359 individual-level segments (3116 annual observations), and 45 population-level segments (446 annual observations).

Results

We collected a total of 11,109 seeds with the quadrat seed count (average: 188.3 seeds/m^2, range: 12-886 seeds/m^2). A total of 8,312 seeds were collected with the timed count (average: 140.9 seeds/individual, range: 12-270 seeds/individual). We found that the relationship between the two sampling methods was loglinear and had a good fit across sites (Fig. 2). Additionally, collected evidence supports the prediction that seed fall can be patchier at lower levels of seed production (Fig. 3). Lastly, we show that seed collection methods result in variation in masting metrics, particularly for individual-level metrics (Fig. 4).

Comparing seed count estimates

Nature of the relationship

In both the linear and loglinear model predicting timed seed counts using quadrat counts, the quadrat seed count predictor was statistically significant (linear model: 0.27 ± 0.03 SE, z = 8.88, $p < 0.001$; natural log model: 56.63 ± 4.23 SE, z =13.39, $p < 0.001$). Nonetheless, the model with a logarithmic relationship better fit the data (ΔAICc: -33.57; Model fit of natural log model of timed counts: marginal $R^2 = 0.74$, conditional $R^2 = 0.79$), matching our predictions. Timed counts (T) can be estimated from quadrat seed counts (Q) using this formula:

$$T \approx -130.374 + 56.632 \times ln(1 + Q)$$

Similarly, the model estimating quadrat seed counts using timed counts showed a significant relationship with timed seed counts (Table 1, Fig. 2), and a good model fit (marginal $R^2 = 0.77$, conditional $R^2 = 0.78$). Estimated quadrat seed counts can be obtained from timed counts (T) as follows:

$$ln(1 + Q) \approx 2.95 + 0.013 \times T$$

Therefore,

$$Q \approx e^{2.955 + 0.013 \times T} - 1$$

The minor differences between the marginal and conditional R^2 indicate that site and tree exerted little influence on the estimated quadrat seed counts. In the natural log model of timed counts, site and tree explained 2.135×10^{2} and 1.857×10^{-7} of the variance respectively, and the residual variance was 9.983×10^{2}. In the natural log model of quadrat counts, the variance explained by site and tree were 1.012×10^{-2} and 6.504×10^{-10} respectively, with a residual variance of 2.446×10^{-1}.

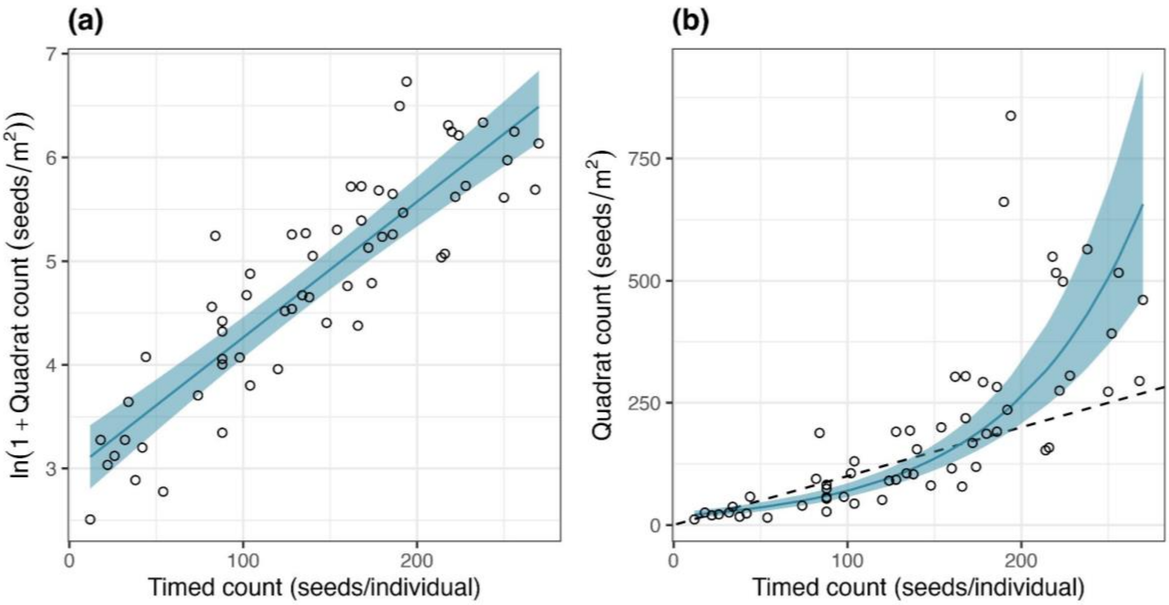


Figure 2: Relationship between the two ground-based sampling methods, the timed count and the quadrat count method. Partial residuals of tree-level observations are shown as points. (a) The relationship is shown with the quadrat counts on a natural logarithmic (ln) scale, and (b) with back-transformed quadrat counts. The

dashed line shows the bisector. Prediction lines (blue) and shaded 95% confidence intervals were obtained with a linear mixed model.

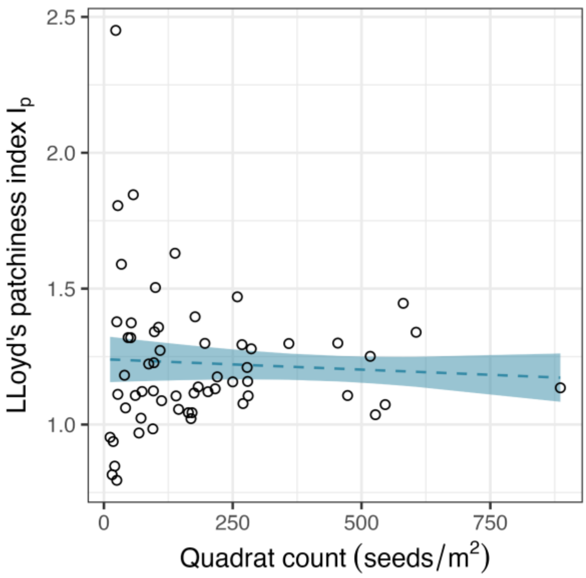


Figure 3: Seed production patchiness across levels of seed production. Points show tree-level partial residuals. Most canopies show a patchy seed production of seed fall ($I_p > 1$). The blue dashed non-significant prediction line and shaded 95% confidence interval were obtained with a linear model.

Table 1: Summary of linear mixed model showing how logarithmic quadrat count estimates (i.e. ln(1 + quadrat count)) can be obtained from timed counts.

Effect	Group	Term	Estimate	SE	z	P-value
Random	Residual	sd Observation	0.495			
Random	Site	sd (Intercept)	0.101			
Random	Tree: Site	sd (Intercept)	< 0.001			
Fixed		(Intercept)	2.955	0.166	17.752	< 0.001
Fixed		Timed count	0.013	0.001	12.352	< 0.001

N: 59, Sites: 5, Trees: 48, Marginal R^2: 0.774, Conditional R^2: 0.783, sd = standard deviation.

Patchiness of seed fall

As is evident from Fig. 2b, the timed count detects more variation in seed production at lower levels of quadrat counts. Most canopies show a patchy seed production of seed fall (i.e. Lloyd's index of patchiness exceeds 1; Fig. 3, For seed fall patterns per tree, see Fig. S2). While patchiness does not decrease with seed fall ($-7.65 \times 10^{-5} \pm 8.43 \times 10^{-5}$ SE, $z = -0.91$, $p = 0.36$), the decrease in the dispersion of patchiness is statistically significant ($-2.07 \times 10^{-3} \pm 3.70 \times 10^{-4}$, $z = -5.59$, $p < 0.001$).

Effects on masting metrics

Individual level

Not all masting metrics are similarly sensitive to the seed collection method (Fig. 4). The spearman rank correlations range between 0.55 (Psd) and 0.94 (S). Moreover, loess regression lines cross the bisector, indicating that for lower levels of the timed count metrics, the timed count underestimates the reference metrics, and at higher levels they tend to overestimate them. However, this is less pronounced for Ari and Si than for the other metrics.

Fig. 5 allows for a closer inspection of time series segments which differ substantially in their CVi values obtained with the two methods. The lower CVi can be explained by two processes, both associated with the shape of the estimated relationship between seed counts obtained via the two methods at the low levels of timed counts. Firstly, the maximal timed counts in these segments are relatively low (see Fig. 2, quadrat seed counts associated with timed counts ≤ 164 are below the bisector), and are therefore scaled down during the conversion to quadrat counts. Secondly, the model predicts some seeds in quadrats even if timed counts are zero, which decreases the number of very low-seeding years. Together, these processes decrease the amplitude of variation between high and low seeding years, resulting in lower CVi. In contrast, synchrony (Si) and temporal autocorrelation at lag 1 year (ARi(1)) are comparable between the two methods.

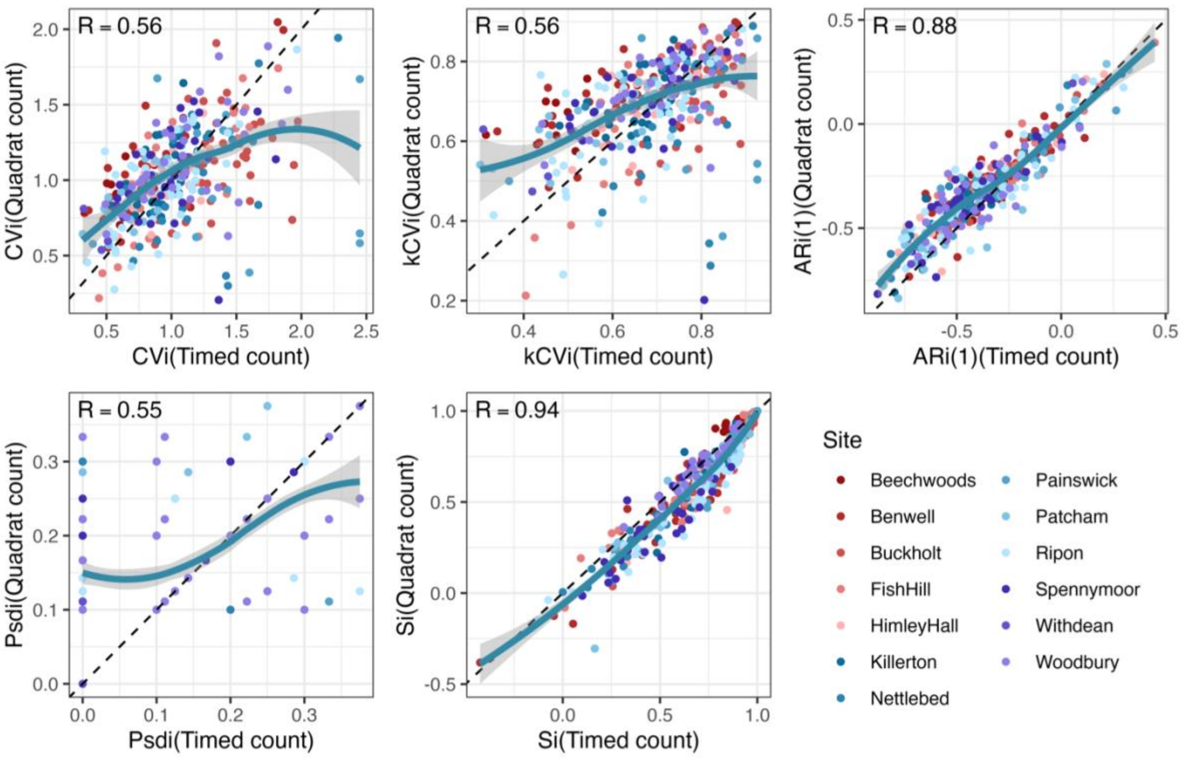


Figure 4: Relationships between metrics (CV, kCV, AR, Psd, S) obtained with two different methods, at the individual level (i). CV: coefficient of variation, kCV: Kvalseth coefficient of variation, AR(1): temporal autocorrelation at lag 1 year, Psd: proportion of high seeding years, S: synchrony. The thin black dashed line represents the bisector. The thicker blue loess regression lines and 95% confidence interval are added for visual interpretation. Points represent time series segments, where the colour indicates the site. The spearman rank correlation (R) is shown in the top-left of each subplot.

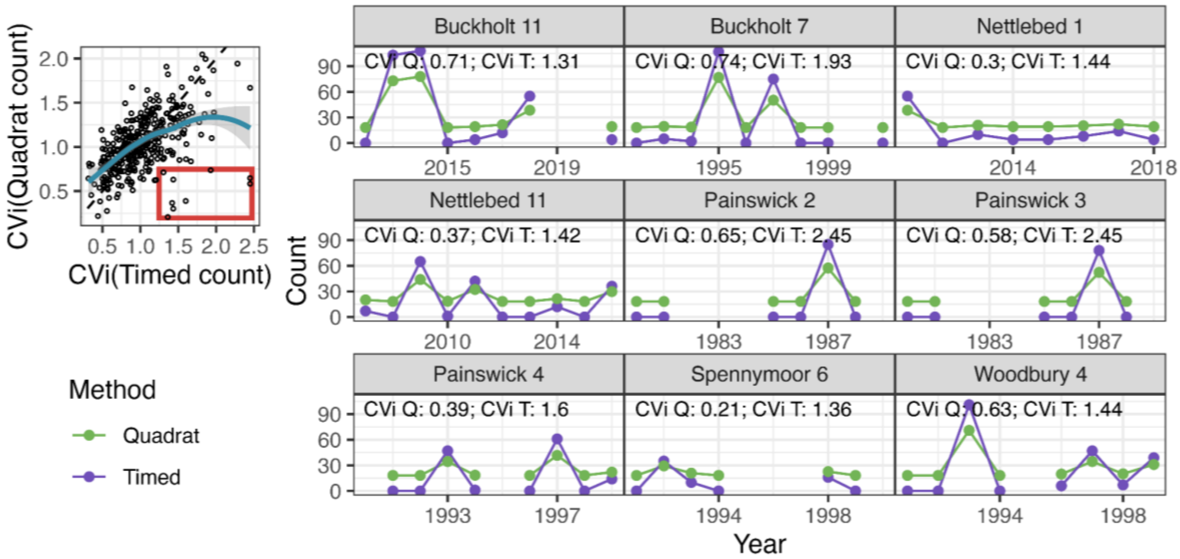


Figure 5: Illustration of differences between level of temporal variability measured with the CVi (coefficient of variation at the individual level) of timed count (CVi T) and quadrat count (CVi Q) time series. Nine time series segments (faceted by Site and Tree ID) are plotted over time, with colour specifying the counting method. These time series match the points which fall within the red rectangle in the top-left plot (i.e. the first subplot of Fig. 4). Note that missing values either represent missing data, or measured values from the timed count that fell beyond the range of values to develop the conversion model.

Population level

The differences between seed production variability metrics (i.e. CVp, kCVp) obtained with the two seed collection methods are less pronounced at the population level (Fig. 6). Spearman rank correlations range between 0.54 for Psd and 0.92 for S. Psd is the only metric with a relatively poor fit between metrics of the two seed collection methods at the population level.

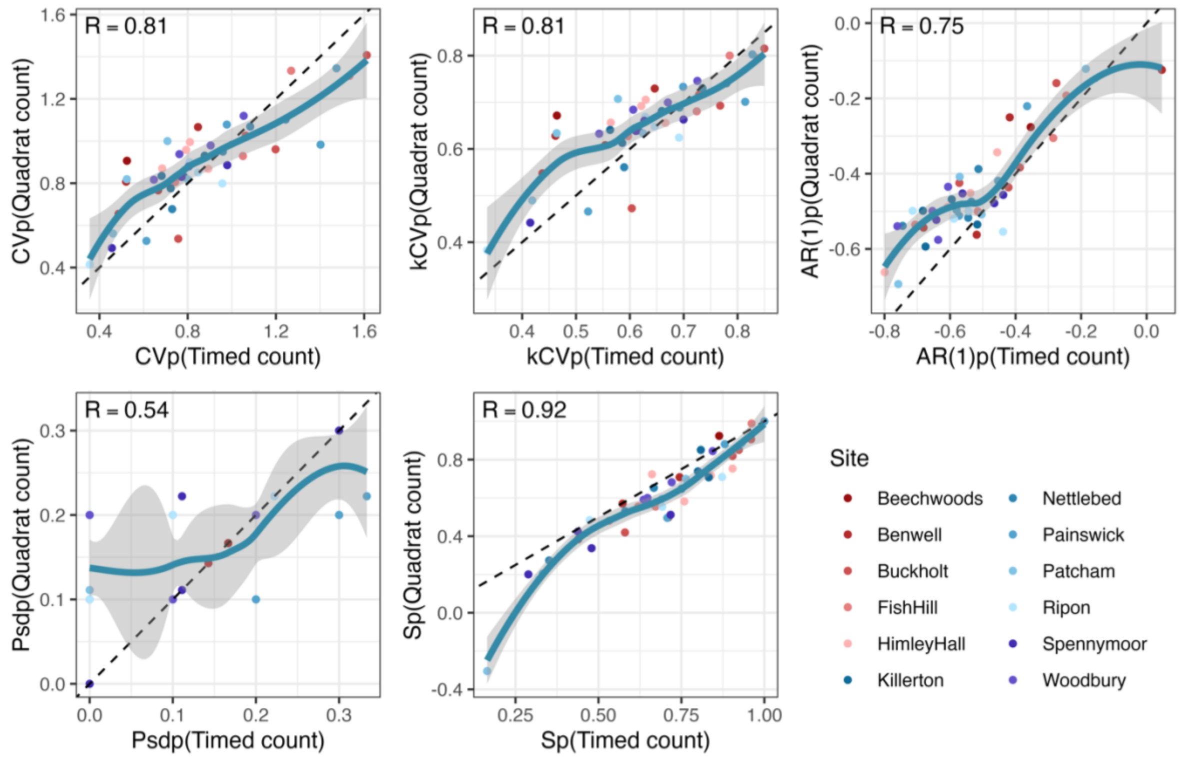


Figure 6: Relationships between metrics (CV, kCV, AR(1), Psd, S) obtained with two different methods, at the population level (p). CV: coefficient of variation, kCV: Kvalseth coefficient of variation, AR(1): temporal autocorrelation at lag 1 year, Psd: proportion of high seeding years, S: synchrony. The thin black dashed line represents the bisector. The thicker blue loess regression lines and 95% confidence interval are added for visual interpretation. Points represent time series segments, where the colour indicates the site. The spearman rank correlation (R) is shown in the top-left of each subplot.

Discussion

The timed count has been used for multiple decades (Packham et al., 2008), and data obtained with this method has been used in several publications on the ecology of seed production in perennial plants (Bogdziewicz et al., 2023, 2020; Foest et al., 2024; Journé et al., 2024, 2023b). Until now, it remained unclear how this method relates to the more commonly used area-based methods. Our study showed that the relationship between seed counts obtained with the two methods is loglinear and has a good fit across sites, allowing for translation between the two sampling methods. Since timed counts are considerably faster than quadrat counts, those interested in measuring seed production over time more efficiently might consider adopting this method. To illustrate, a single observer employing the timed count sampled around six trees per hour. This estimate includes conducting the seed count, labelling and storing bags, taking notes and moving between trees. To conduct the quadrat counts under the same canopies, two to three observers managed to sample around nine trees per 8-hour working day (~1.13 trees per hour). This equates to over a tenfold difference in sampling speed. Differences in seed counting time in the lab were also substantial; on average we counted 141 seeds per tree for the timed count, and 188 per tree for the quadrat count, resulting in a lab effort that was one-third greater for quadrat counts.

While the presented formulas can be used to translate between timed and quadrat counts, some caution is warranted. Firstly, we advise recalibrating the loglinear relationship to local conditions (or, when site conditions have changed substantially over time) when seeking to convert timed seed counts into quadrat counts (Tattoni et al., 2021). This is because the exact relationship may differ between plant species (e.g. different seed sizes resulting in different ease of sampling with timed counts, and therefore, different counts), site conditions (i.e. we measured trees in mature, relatively open, limited understory stands, but timed counts may be lower in more challenging sites compared to quadrat counts), and possibly observers. Regardless, an important insight resulting from this work is that the timed count is broadly equivalent to log converted quadrat counts, and, by extension, ln(seeds/m^2). Generally, caution is warranted when converting between methods which are characterised by a loglinear relationship (and extrapolating may yield unrealistic results). Namely, small changes in timed counts at high seed fall levels would be transformed into large changes in quadrat count estimates. Further work is required to expand the current dataset, incorporating timed seed counts > 270 seeds/7 minutes.

When using timed counts to predict quadrat counts, the goodness of fit (i.e. marginal $R^2 = 0.77$) is comparable with another quick and easy referenced seed count method. Namely, Koenig et al. (1994a) and

Perry and Thill (1999), who compared the Koenig 30-second visual count method with seed traps found an R^2 of 0.72 and 0.76 respectively. We could not contrast the timed count with seed traps (which are generally considered to be the 'gold standard' as they limit post-dispersal seed predation; Perry and Thill, 1999; Touzot et al., 2018), since these traps can easily be vandalised in publicly accessible stands. We therefore stress that to minimise bias from post-dispersal seed predation in estimating tree seed production from either quadrats or timed counts, sampling must be well-timed: too early, and few nuts will have fallen; too late, and seed consumers like squirrels may have removed many (Packham et al., 2008). However, the reference method we used, i.e. ground plots, have recently been compared to seed traps, and they are themselves strongly related (Chianucci et al., 2021; Tattoni et al., 2021; Touzot et al., 2018).

Secondly, by contrasting the two methods with different strengths, we show that seed production patchiness might explain why the timed method picks up more variation under low-seed production canopies than the quadrat (Fig. 3). We found that most seed fall is patchy, and the dispersion of seed fall patchiness decreases with increasing seed crop size. This indicates that especially at low seed crop sizes, there are at least some trees with highly patchy seed fall. When seed fall is variable underneath a canopy, it is crucial to sample from across the seed fall shadow (Perry and Thill, 1999). While the quadrats were placed along multiple transects, their surface area was small (i.e. 1/9 m^2 per quadrat). The smallest canopy under which we sampled was 36 m^2 whereas the largest canopy was 403 m^2. This means that the combined quadrats only captured between 3% and 0.2% of the seed fall area, which makes it probable that many aggregations of seeds were missed. In contrast, the timed count covered substantially more ground. This likely enabled the observer to collect seeds from more aggregations when present, and consequently pick up more variation in seed production at low seed fall levels.

The observed patchiness underscores the general importance of sampling a sufficient proportion of the canopy (Perry and Thill, 1999). In the field, it is customary for area-based seed collection methods to sample 1 m^2 to obtain an individual-level seed production estimate (e.g. Ida, 2021; Koenig et al., 1994a; Patterson et al., 2023; Rodríguez-Ramírez et al., 2021). This is most likely done for practical reasons. Increasing the sampling area while using seed traps or quadrats comes at the cost of increased infrastructure or time. However, our findings show that it is advisable to increase this sampling area if resources permit and if individual-level variation of seed production is of interest (as done in e.g. Fleurot et al., 2023). Adopting methods which sample a larger area at a low cost such as the Koenig method, which samples approximately 13% of the canopy (Koenig et al., 1994a), or the timed count is a possible solution when resources are limited. The timed count method may be preferable for beech since beech produces fruits regardless of pollination. Unlike the Koenig method, which would require additional estimation on the proportion of filled seeds, the timed count allows for accurate discrimination between filled and unfilled seeds. It is worth noting that it is not currently known which of the two methods tested here better captures the 'true' value of whole-plant seed supply. Further research into the small-scale spatial structure of seed fall is required to establish the optimal sampling area given the observed patchiness.

Our findings reveal that seed sampling differences translate into variation in masting metrics, measured at the individual and population level. The differences between the often-used variability metric CV tended to be larger for individual-level time series than for population-level time series. Regardless, the findings underpin the need to understand the underlying characteristics of the specific data collection method chosen on seed counts and masting metrics. Refining our grasp on the effects of sampling methods on masting metrics is becoming increasingly pressing, as large-scale research on masting ecology gains momentum with the availability of large, combined datasets (e.g. Foest et al., 2024; Hacket-Pain et al., 2022; Journé et al., 2024, 2023a; Szymkowiak et al., 2024). While such datasets are invaluable resources for studying the wide-ranging impacts of masting on ecosystems (Pearse et al., 2021), comparisons of masting metrics across datasets obtained via different seed collection methods likely contain additional variation associated with the method used. Such variation may obscure ecologically relevant patterns (Mason et al., 2018). In the light of our results, we advise that modelling in such studies should include sampling method as a covariate, especially if individual-level masting metrics are compared.

While our study sheds light on how seed sampling methods impact masting metrics at both individual and population levels, important challenges remain. Seed production is measured with a wide variety of other methods (Hacket-Pain et al., 2022), and one gap in our understanding is how population-level estimates derived from individual-level data differ from stand-based estimates. In other words, do we obtain similar population-level estimates of masting if seed fall is sampled not directly under tree canopies, but systematically or at randomised locations in stands (Chianucci et al., 2021)? Both methods may yield different time series and metrics, as the relative individual-plant contributions to the population-level mean can vary (Minor and Kobe, 2017). If population-level seed crop is calculated from individual-level seed production, then each individual contributes equally to the population-level mean. In contrast, in stand-based estimates, the relative contribution is affected by the fecundity of trees and the location of seed traps. This could affect masting metrics, as dominant and fecund trees can show different masting patterns (Szymkowiak et al., 2023), and can be responsible for a disproportionate fraction of the overall population-level seed production (Minor and Kobe, 2017). It is important for the research communities interested in seed production to prioritise efforts to better understand the variation associated with measurement methods and mitigate for it.

Recommendations

In summary, we recommend using timed counts for seed production sampling due to its efficiency, information on seed viability, and good fit with traditional quadrat counts through a loglinear relationship. Although further research is needed to determine the optimum sampling area for whole-plant seed supply, it is advised to sample areas larger than 1 m^2 per tree. Lastly, using sampling methods as covariates in regeneration studies is crucial to account for variation between different seed collection techniques, and the effects of other sampling methods on seed counts and masting metrics is necessary.

Acknowledgements

We would like to thank Dr. Rebecca Snell and Dr. Samantha Patrick for their insightful comments on the manuscript. This work was supported by a PhD studentship to JJF under Natural Environment Research Council grant no. NE/S00713X/1and by the European Union (ERC, ForestFuture, 101039066). Views and opinions expressed are however those of the authors only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them. For the purpose of Open Access, the author has applied a CC-BY public copyright licence to any Author Accepted Manuscript (AAM) version arising from this submission.

Conflict of interest statement

None declared.

Author contributions

The study was conceptualised by JJF, MB, and AH-P, and supervised by AH-P. JJF wrote the initial draft, conducted the analysis and visualisation. JJF, AH-P, TC, MH and PT collected data. All authors contributed critically to the interpretation of the analysis and drafts, and gave final approval for publication.

References

Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R., Cirolli, M., Kantorowicz, W., Zang, C., Schueler, S., Croisé, L., Piussi, P., Berretti, R., Palaghianu, C., Westergren, M., Lageard, J.G.A., Burkart, A., Gehrig Bichsel, R., Thomas, P.A., Beudert, B., Övergaard, R., Vacchiano, G., 2017a. Two Centuries of Masting Data for European Beech and Norway Spruce across the European Continent. Ecology 98, 1473–1473. https://doi.org/10.1002/ecy.1785

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J., Motta, R., Hacket-Pain, A., 2017b. Inter-Annual and Decadal Changes in Teleconnections Drive Continental-Scale Synchronization of Tree Reproduction. Nat. Commun. 8, 2205. https://doi.org/10.1038/s41467-017-02348-9

Bogdziewicz, M., 2022. How Will Global Change Affect Plant Reproduction? A Framework for Mast Seeding Trends. New Phytol. 234, 14–20. https://doi.org/10.1111/nph.17682

Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E., Fleurot, E., Foest, J.J., Gratzer, G., Hagiwara, T., Han, Q., Journé, V., Keurinck, L., Kondrat, K., McClory, R., LaMontagne, J.M., Mundo, I.A., Nussbaumer, A., Oberklammer, I., Ohno, M., Pearse, I.S., Pesendorfer, M.B., Resente, G., Satake, A., Shibata, M., Snell, R.S., Szymkowiak, J., Touzot, L., Zwolak, R., Zywiec, M., Hacket-Pain, A.J., 2024. Evolutionary Ecology of Masting: Mechanisms, Models, and Climate Change. Trends Ecol. Evol. 0. https://doi.org/10.1016/j.tree.2024.05.006

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P., Foest, J., Lageard, J., Hacket-Pain, A., 2023. Reproductive Collapse in European Beech Results from Declining Pollination Efficiency in Large Trees. Glob. Change Biol. 29, 4595–4604. https://doi.org/10.1111/gcb.16730

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A., Hacket-Pain, A., 2020. Climate Warming Disrupts Mast Seeding and Its Fitness Benefits in European Beech. Nat. Plants 6, 88–94. https://doi.org/10.1038/s41477-020-0592-8

Bregnard, C., Rais, O., Voordouw, M.J., 2021. Masting by Beech Trees Predicts the Risk of Lyme Disease. Parasit. Vectors 14, 168. https://doi.org/10.1186/s13071-021-04646-0

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. R J. 9, 378–400.

Chianucci, F., Tattoni, C., Ferrara, C., Ciolli, M., Brogi, R., Zanni, M., Apollonio, M., Cutini, A., 2021. Evaluating Sampling Schemes for Quantifying Seed Production in Beech (Fagus Sylvatica) Forests Using Ground Quadrats. For. Ecol. Manag. 493, 119294. https://doi.org/10.1016/j.foreco.2021.119294

Clement, J., Vercauteren, J., Verstraeten, W.W., Ducoffre, G., Barrios, J.M., Vandamme, A.-M., Maes, P., Van Ranst, M., 2009. Relating Increasing Hantavirus Incidences to the Changing Climate: The Mast Connection. Int. J. Health Geogr. 8, 1. https://doi.org/10.1186/1476-072X-8-1

Cousens, R.D., Wiegand, T., Taghizadeh, M.S., 2008. Small-Scale Spatial Structure within Patterns of Seed Dispersal. Oecologia 158, 437–448. https://doi.org/10.1007/s00442-008-1150-7

Dale, E.E., Foest, J.J., Hacket-Pain, A., Bogdziewicz, M., Tanentzap, A.J., 2021. Macroevolutionary Consequences of Mast Seeding. Philos. Trans. R. Soc. B Biol. Sci. 376, 20200372. https://doi.org/10.1098/rstb.2020.0372

Fleurot, E., Lobry, J.R., Boulanger, V., Debias, F., Mermet-Bouvier, C., Caignard, T., Delzon, S., Bel-Venner, M.-C., Venner, S., 2023. Oak Masting Drivers Vary between Populations Depending on Their Climatic Environments. Curr. Biol. S0960982223000684. https://doi.org/10.1016/j.cub.2023.01.034

Foest, J.J., Bogdziewicz, M., Pesendorfer, M.B., Ascoli, D., Cutini, A., Nussbaumer, A., Verstraeten, A., Beudert, B., Chianucci, F., Mezzavilla, F., Gratzer, G., Kunstler, G., Meesenburg, H., Wagner, M., Mund, M., Cools, N., Vacek, S., Schmidt, W., Vacek, Z., Hacket-Pain, A., 2024. Widespread

Breakdown in Masting in European Beech Due to Rising Summer Temperatures. Glob. Change Biol. 30, e17307. https://doi.org/10.1111/gcb.17307

Hacket-Pain, A., Bogdziewicz, M., 2021. Climate Change and Plant Reproduction: Trends and Drivers of Mast Seeding Change. Philos. Trans. R. Soc. B Biol. Sci. 376, 20200379. https://doi.org/10.1098/rstb.2020.0379

Hacket-Pain, A., Foest, J.J., Pearse, I.S., LaMontagne, J.M., Koenig, W.D., Vacchiano, G., Bogdziewicz, M., Caignard, T., Celebias, P., van Dormolen, J., Fernández-Martínez, M., Moris, J.V., Palaghianu, C., Pesendorfer, M., Satake, A., Schermer, E., Tanentzap, A.J., Thomas, P.A., Vecchio, D., Wion, A.P., Wohlgemuth, T., Xue, T., Abernethy, K., Aravena Acuña, M.-C., Daniel Barrera, M., Barton, J.H., Boutin, S., Bush, E.R., Donoso Calderón, S., Carevic, F.S., de Castilho, C.V., Manuel Cellini, J., Chapman, C.A., Chapman, H., Chianucci, F., da Costa, P., Croisé, L., Cutini, A., Dantzer, B., Justin DeRose, R., Dikangadissi, J.-T., Dimoto, E., da Fonseca, F.L., Gallo, L., Gratzer, G., Greene, D.F., Hadad, M.A., Herrera, A.H., Jeffery, K.J., Johnstone, J.F., Kalbitzer, U., Kantorowicz, W., Klimas, C.A., Lageard, J.G.A., Lane, J., Lapin, K., Ledwoń, M., Leeper, A.C., Vanessa Lencinas, M., Lira-Guedes, A.C., Lordon, M.C., Marchelli, P., Marino, S., Schmidt Van Marle, H., McAdam, A.G., Momont, L.R.W., Nicolas, M., de Oliveira Wadt, L.H., Panahi, P., Martínez Pastur, G., Patterson, T., Luis Peri, P., Piechnik, Ł., Pourhashemi, M., Espinoza Quezada, C., Roig, F.A., Peña Rojas, K., Micaela Rosas, Y., Schueler, S., Seget, B., Soler, R., Steele, M.A., Toro-Manríquez, M., Tutin, C.E.G., Ukizintambara, T., White, L., Yadok, B., Willis, J.L., Zolles, A., Żywiec, M., Ascoli, D., 2022. MASTREE+: Time-series of Plant Reproductive Effort from Six Continents. Glob. Change Biol. 28, 3066–3082. https://doi.org/10.1111/gcb.16130

Hartig, F., Lohse, L., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.

Hilton, G.M., Packham, J.R., 2003. Variation in the Masting of Common Beech (Fagus Sylvatica L.) in

Northern Europe over Two Centuries (1800–2001). For. Int. J. For. Res. 76, 319–328. https://doi.org/10.1093/forestry/76.3.319

Hyndman, R.J., Khandakar, Y., 2008. Automatic Time Series Forecasting: The Forecast Package for R. J. Stat. Softw. 26, 1–22.

Ida, H., 2021. A 15-Year Study on the Relationship between Beech (Fagus Crenata) Reproductive-Organ Production and the Numbers of Nuisance Japanese Black Bears (Ursus Thibetanus Japonicus) Killed in a Snowy Rural Region in Central Japan. Landsc. Ecol. Eng. 17, 507–514. https://doi.org/10.1007/s11355-021-00472-9

Jones, C.G., Ostfeld, R.S., Richard, M.P., Schauber, E.M., Wolff, J.O., 1998. Chain Reactions Linking Acorns to Gypsy Moth Outbreaks and Lyme Disease Risk. Science 279, 1023–1026. https://doi.org/10.1126/science.279.5353.1023

Journé, V., Hacket-Pain, A., Bogdziewicz, M., 2023a. Evolution of Masting in Plants Is Linked to Investment in Low Tissue Mortality. Nat. Commun. 14, 7998. https://doi.org/10.1038/s41467-023-43616-1

Journé, V., Hacket-Pain, A., Oberklammer, I., Pesendorfer, M.B., Bogdziewicz, M., 2023b. Forecasting Seed Production in Perennial Plants: Identifying Challenges and Charting a Path Forward. New Phytol. 239, 466–476. https://doi.org/10.1111/nph.18957

Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D., Bogdziewicz, M., 2024. Summer Solstice Orchestrates the Subcontinental-Scale Synchrony of Mast Seeding. Nat. Plants 10, 367–373. https://doi.org/10.1038/s41477-024-01651-w

Kelly, D., Sork, V.L., 2002. Mast Seeding in Perennial Plants: Why, How, Where? Annu. Rev. Ecol. Syst. 33, 427–447. https://doi.org/10.1146/annurev.ecolsys.33.020602.095433

Kettle, C.J., 2012. Seeding Ecological Restoration of Tropical Forests: Priority Setting under REDD+. Biol. Conserv., REDD+ and Conservation 154, 34–41. https://doi.org/10.1016/j.biocon.2012.03.016

Koenig, W.D., 2021. A Brief History of Masting Research. Philos. Trans. R. Soc. B Biol. Sci. 376, 20200423. https://doi.org/10.1098/rstb.2020.0423

Koenig, W.D., Knops, J.M.H., Carmen, W.J., 2020. Can Mast History Be Inferred from Radial Growth? A Test Using Five Species of California Oaks. For. Ecol. Manag. 472, 118233. https://doi.org/10.1016/j.foreco.2020.118233

Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T., Mumme, R.L., 1994a. Estimating Acorn Crops Using Visual Surveys. Can. J. For. Res. 24, 2105–2112. https://doi.org/10.1139/x94-270

Koenig, W.D., Mumme, R.L., Carmen, W.J., Stanback, M.T., 1994b. Acorn Production by Oaks in Central Coastal California: Variation within and among Years. Ecology 75, 99–109. https://doi.org/10.2307/1939386

LaMontagne, J.M., Boutin, S., 2007. Local-Scale Synchrony and Variability in Mast Seed Production Patterns of \emphPicea\emph Glauca. J. Ecol. 95, 991–1000. https://doi.org/10.1111/j.1365-2745.2007.01266.x

Lloyd, M., 1967. `Mean Crowding'. J. Anim. Ecol. 36, 1–30. https://doi.org/10.2307/3012

Lobry, J.R., Bel-Venner, M.-C., Bogdziewicz, M., Hacket-Pain, A., Venner, S., 2023. The CV Is Dead, Long Live the CV! Methods Ecol. Evol. 14, 2780–2786. https://doi.org/10.1111/2041-210X.14197

Maag, N., Korner-Nievergelt, F., Szymkowiak, J., Hałas, N., Maziarz, M., Neubauer, G., Luepold, S.B., Carlotti, S., Schaub, M., Flade, M., Scherrer, D., Grendelmeier, A., Riess, M., Stelbrink, P., Pasinelli, G., 2024. Wood Warbler Population Dynamics in Response to Mast Seeding Regimes in Europe. Ecology 105, e4227. https://doi.org/10.1002/ecy.4227

Maringer, J., Wohlgemuth, T., Hacket-Pain, A., Ascoli, D., Berretti, R., Conedera, M., 2020. Drivers of Persistent Post-Fire Recruitment in European Beech Forests. Sci. Total Environ. 699, 134006. https://doi.org/10.1016/j.scitotenv.2019.134006

Mason, N.W.H., Holdaway, R.J., Richardson, S.J., 2018. Incorporating Measurement Error in Testing for

Changes in Biodiversity. Methods Ecol. Evol. 9, 1296–1307. https://doi.org/10.1111/2041-210X.12976

Minor, D.M., Kobe, R.K., 2017. Masting Synchrony in Northern Hardwood Forests: Super-producers Govern Population Fruit Production. J. Ecol. 105, 987–998. https://doi.org/10.1111/1365-2745.12729

Ostfeld, R.S., Keesing, F., 2000. Pulsed Resources and Community Dynamics of Consumers in Terrestrial Ecosystems. Trends Ecol. Evol. 15, 232–237. https://doi.org/10.1016/S0169-5347(00)01862-0

Packham, J.R., Thomas, P.A., Lageard, J.G.A., Hilton, G.M., 2008. The English Beech Masting Survey 1980–2007: Variation in the Fruiting of the Common Beech (\emphFagus\emph Sylvatica L.) and Its Effects on Woodland Ecosystems. Arboric. J. 31, 189–214. https://doi.org/10.1080/03071375.2008.9747535

Patterson, T.W., Greenberg, C.H., Hacket-Pain, A., 2023. Acorn Production, Climate, and Tree-Ring Growth of Five Oak Species in Southern Appalachian Forests. For. Ecol. Manag. 546, 121310. https://doi.org/10.1016/j.foreco.2023.121310

Pearse, I.S., LaMontagne, J.M., Lordon, M., Hipp, A.L., Koenig, W.D., 2020. Biogeography and Phylogeny of Masting: Do Global Patterns Fit Functional Hypotheses? New Phytol. 227, 1557–1567. https://doi.org/10.1111/nph.16617

Pearse, I.S., Wion, A.P., Gonzalez, A.D., Pesendorfer, M.B., 2021. Understanding Mast Seeding for Conservation and Land Management. Philos. Trans. R. Soc. B Biol. Sci. 376, 20200383. https://doi.org/10.1098/rstb.2020.0383

Perry, R.W., Thill, R.E., 1999. Estimating Mast Production: An Evaluation of Visual Surveys and Comparison with Seed Traps Using White Oaks. South. J. Appl. For. 23, 164–169. https://doi.org/10.1093/sjaf/23.3.164

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for

Statistical Computing, Vienna, Austria.

Reil, D., Imholt, C., Drewes, S., Ulrich, R.G., Eccard, J.A., Jacob, J., 2016. Environmental Conditions in Favour of a Hantavirus Outbreak in 2015 in Germany? Zoonoses Public Health 63, 83–88. https://doi.org/10.1111/zph.12217

Rodríguez-Ramírez, E.C., Williams-Linera, G., Díaz-Ávalos, C., Luna-Vega, I., 2021. Masting Effect on Canopy Greenness and Climate Response on Seed Production of \emphFagus\emph Grandifolia Subsp. \emphMexicana across the Sierra Madre Oriental, Mexico. Clim. Change Ecol. 2, 100035. https://doi.org/10.1016/j.ecochg.2021.100035

Schermer, É., Bel-Venner, M.C., Gaillard, J.M., Dray, S., Boulanger, V., Le Roncé, I., Oliver, G., Chuine, I., Delzon, S., Venner, S., 2020. Flower Phenology as a Disruptor of the Fruiting Dynamics in Temperate Oak Species. New Phytol. 225, 1181–1192. https://doi.org/10.1111/nph.16224

Szymkowiak, J., Foest, J., Hacket-Pain, A., Journé, V., Ascoli, D., Bogdziewicz, M., 2024. Tail-Dependence of Masting Synchrony Results in Continent-Wide Seed Scarcity. Ecol. Lett. 27, e14474. https://doi.org/10.1111/ele.14474

Szymkowiak, J., Hacket-Pain, A., Kelly, D., Foest, J., Kondrat, K., Thomas, P., Lageard, J., Gratzer, G., Pesendorfer, M., Bogdziewicz, M., 2023. Masting Ontogeny: The Largest Masting Benefits Accrue to the Largest Trees. https://doi.org/10.21203/rs.3.rs-3407832/v1

Tattoni, C., Chianucci, F., Ciolli, M., Ferrara, C., Marchino, L., Zanni, M., Zatelli, P., Cutini, A., 2021. A Comparison of Ground-Based Count Methods for Quantifying Seed Production in Temperate Broadleaved Tree Species. Ann. For. Sci. 78, 1–14. https://doi.org/10.1007/s13595-020-01018-z

Tersago, K., Verhagen, R., Servais, A., Heyman, P., Ducoffre, G., Leirs, H., 2009. Hantavirus Disease (Nephropathia Epidemica) in Belgium: Effects of Tree Seed Production and Climate. Epidemiol. Infect. 137, 250–256. https://doi.org/10.1017/S0950268808000940

Touzot, L., Bel-Venner, M.-C., Gamelon, M., Focardi, S., Boulanger, V., Débias, F., Delzon, S., Saïd, S., Schermer, E., Baubet, E., Gaillard, J.-M., Venner, S., 2018. The Ground Plot Counting Method: A Valid and Reliable Assessment Tool for Quantifying Seed Production in Temperate Oak Forests? For. Ecol. Manag. 430, 143–149. https://doi.org/10.1016/j.foreco.2018.07.061

Touzot, L., Schermer, É., Venner, S., Delzon, S., Rousset, C., Baubet, É., Gaillard, J.-M., Gamelon, M., 2020. How Does Increasing Mast Seeding Frequency Affect Population Dynamics of Seed Consumers? Wild Boar as a Case Study. Ecol. Appl. 30, e02134. https://doi.org/10.1002/eap.2134

Wade, M.J., Fitzpatrick, C.L., Lively, C.M., 2018. 50 Year Anniversary of Lloyd's "Mean Crowding": Ideas on Patchy Distributions. J. Anim. Ecol. 87, 1221–1226. https://doi.org/10.1111/1365-2656.12854

Whittet, R., Cottrell, J., Cavers, S., Pecurul, M., Ennos, R., 2016. Supplying Trees in an Era of Environmental Uncertainty: Identifying Challenges Faced by the Forest Nursery Sector in Great Britain. Land Use Policy 58, 415–426. https://doi.org/10.1016/j.landusepol.2016.07.027

Wickham, H., 2016. Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Zhang, H., Yan, C., Niu, H., Li, H., Zhang, Z., 2022. Masting Benefits Seedling Recruitment of Armeniaca Sibirica through Directed Dispersal by Rodents. For. Ecol. Manag. 513, 120200. https://doi.org/10.1016/j.foreco.2022.120200

Zwolak, R., Bogdziewicz, M., Wróbel, A., Crone, E.E., 2016. Advantages of Masting in European Beech: Timing of Granivore Satiation and Benefits of Seed Caching Support the Predator Dispersal Hypothesis. Oecologia. https://doi.org/10.1007/s00442-015-3511-3

Supporting information

Comparing two ground-based seed count methods and their effect on masting metrics

Jessie J. Foest (1,5), Michal Bogdziewicz (1), Thomas Caignard (2), Martin Hadad (3), Peter Thomas (4), Andrew Hacket-Pain (5)

(1) Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland.
(2) BIOGECO, INRAE, University of Bordeaux, Cestas, France
(3) Laboratorio de Dendrocronología de Zonas Áridas CIGEOBIO (CONICET-UNSJ), Gabinete de Geología Ambiental (INGEO-UNSJ), 5400, San Juan, Argentina
(4) Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, United Kingdom.
(5) Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom

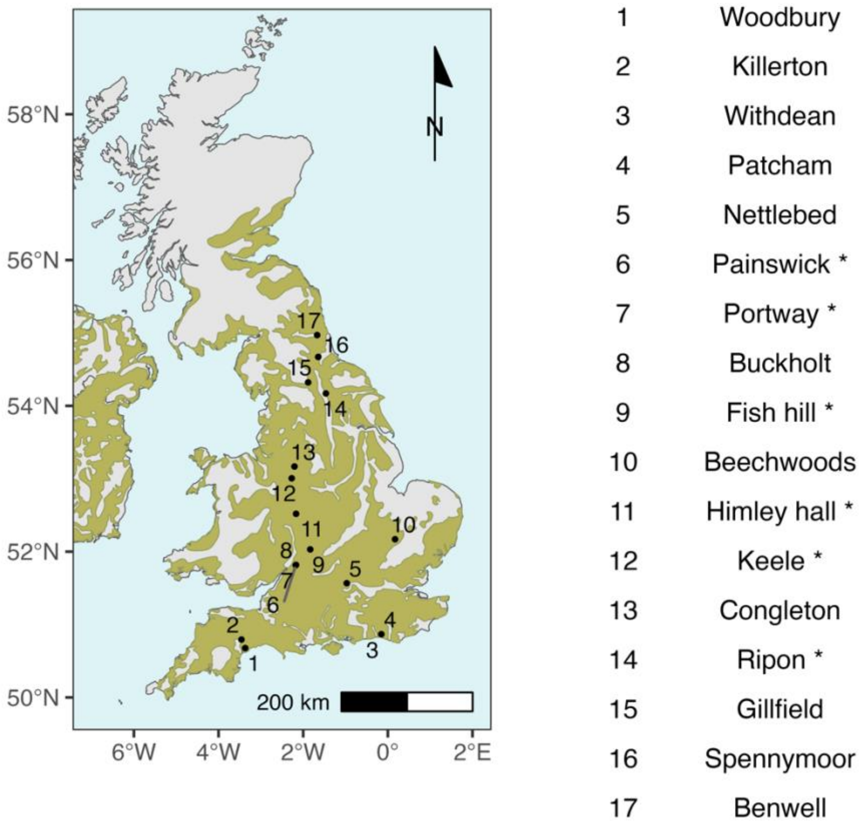
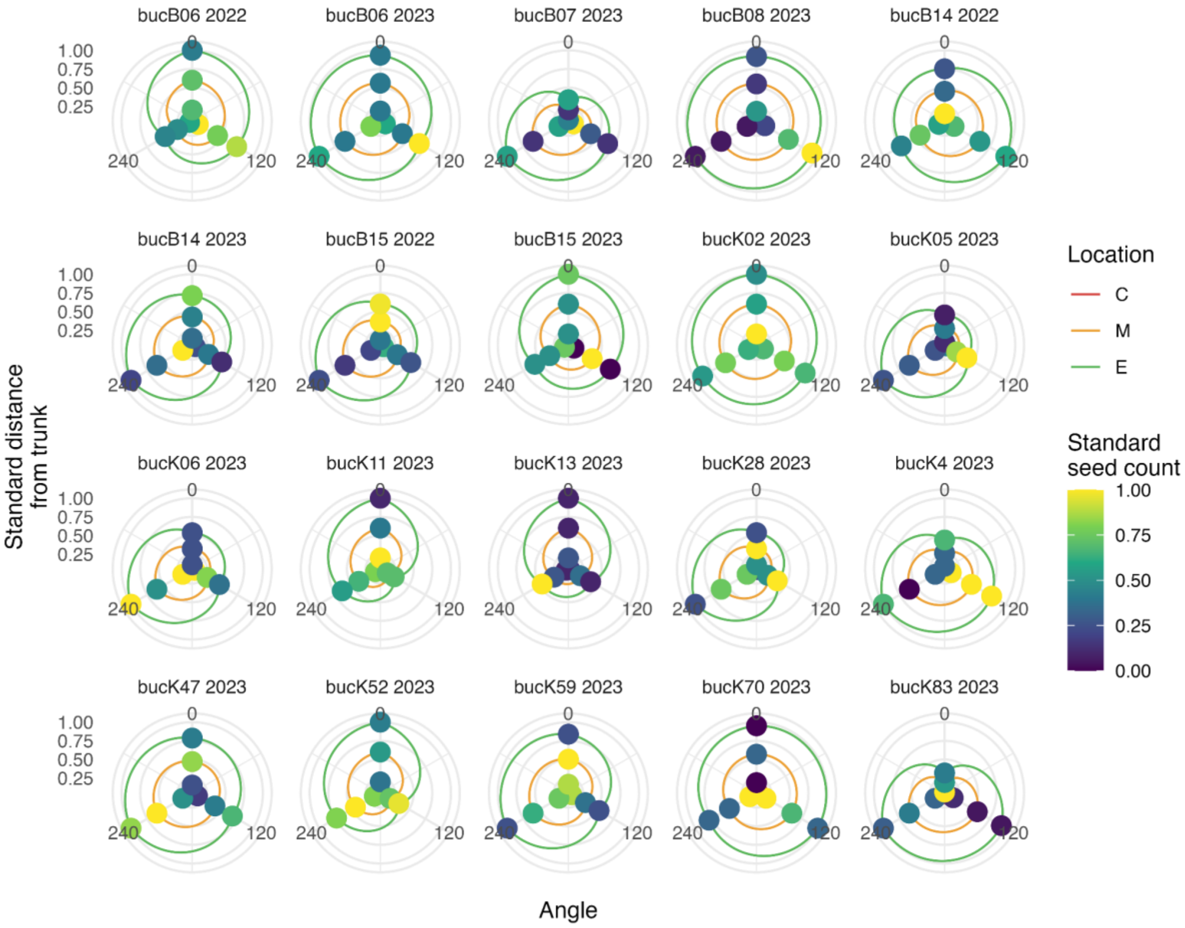
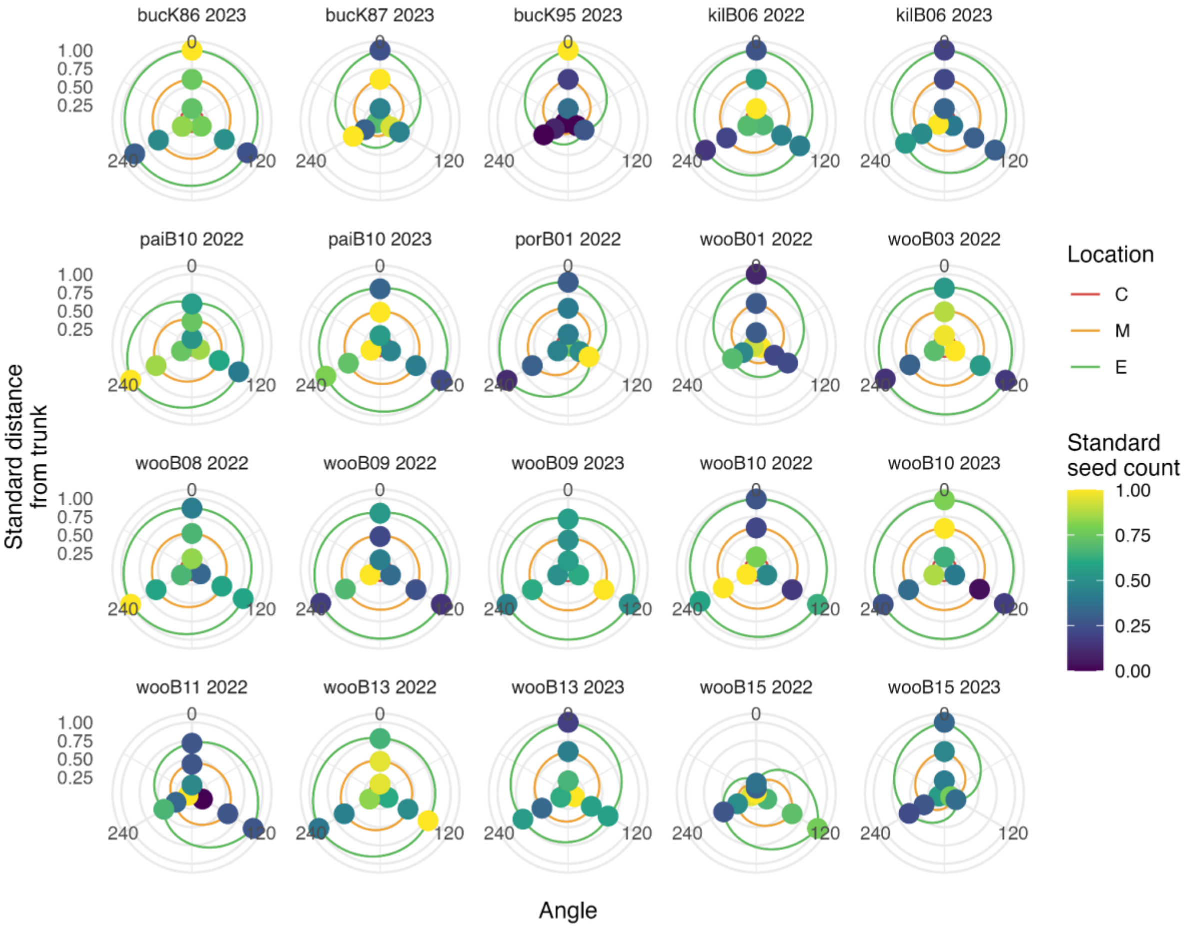


Figure S1: An overview of the EBMS sampling sites in the United Kingdom. An asterisk (*) was added to the site name to indicate locations where the survey was initiated after the original EBMS sites, and in some cases subsequently retired from the survey. These shorter records have not been included in prior studies using the EBMS record. Quadrat sampling was conducted in sites 1, 2, 6, 7, and 8.


bucB06 2022
bucB06 2023
bucB07 2023
bucB08 2023
bucB14 2022
bucB14 2023
bucB15 2022
bucB15 2023
bucK02 2023
bucK05 2023
bucK06 2023
bucK11 2023
bucK13 2023
bucK28 2023
bucK4 2023
bucK47 2023
bucK52 2023
bucK59 2023
bucK70 2023
bucK83 2023
Standard distance from trunk
1.00
0.75
0.50
0.25
0
120
240
Angle
Location
C
M
E
Standard seed count
1.00
0.75
0.50
0.25
0.00

634



bucK86 2023
bucK87 2023
bucK95 2023
kilB06 2022
kilB06 2023
paiB10 2022
paiB10 2023
porB01 2022
wooB01 2022
wooB03 2022
wooB08 2022
wooB09 2022
wooB09 2023
wooB10 2022
wooB10 2023
wooB11 2022
wooB13 2022
wooB13 2023
wooB15 2022
wooB15 2023
0
120
240
1.00
0.75
0.50
0.25
Standard distance from trunk
Angle
Location
C
M
E
Standard seed count
1.00
0.75
0.50
0.25
0.00

635

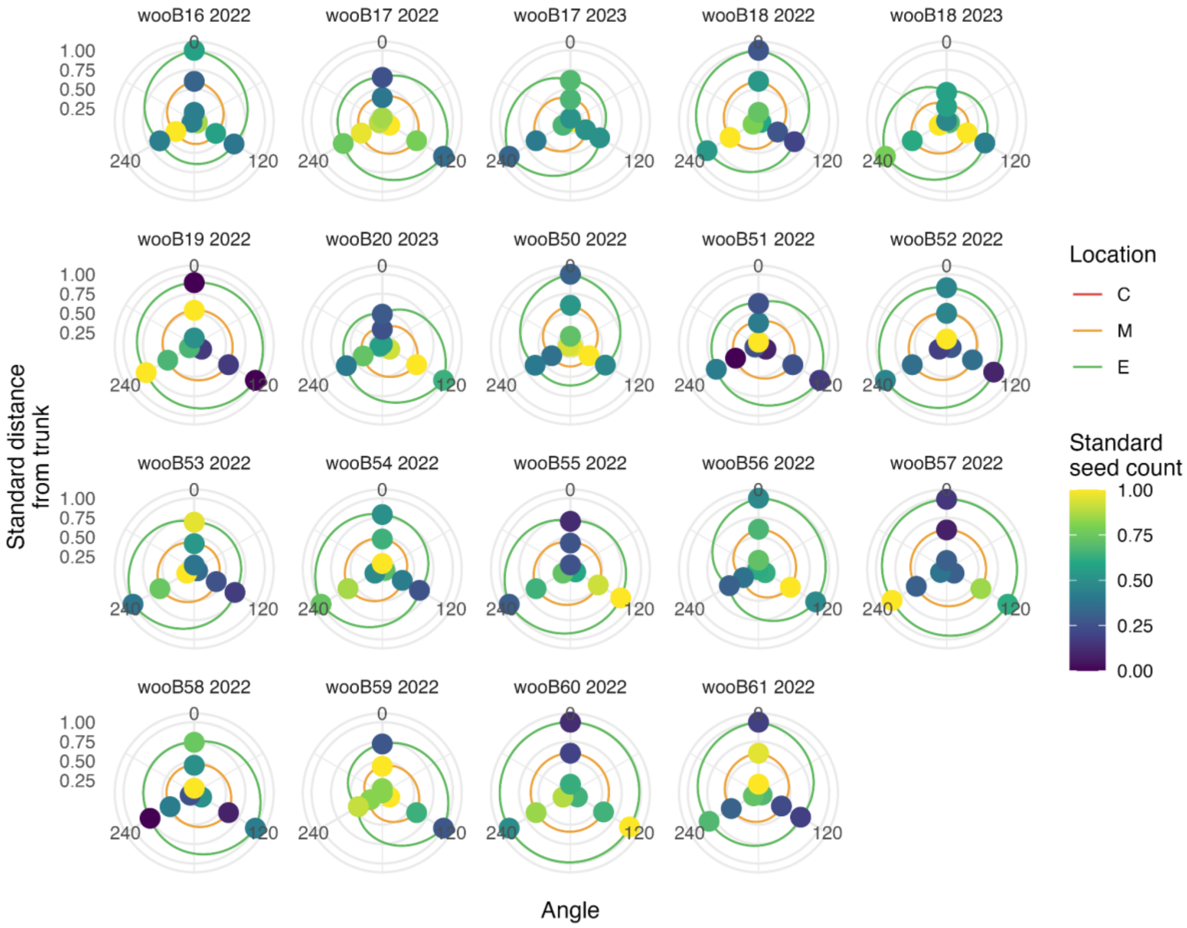


Figure S2: Seed production estimates under all tree canopies obtained with quadrat counts. Panel titles show 3-letter site code, the Tree ID preceded by the letter B or K, and year. Coloured points indicate standardised seed counts (at the tree level, using the maximum). The three sampling transects are shown, where the randomised orientation of the first transect is plotted at an angle of 0 degrees. The coloured lines indicate the relative distance from the canopy edge (i.e. Core (C), Middle (M), (Edge).