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The ground plot counting method: A valid and reliable assessment tool for quantifying seed production in temperate oak forests?

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ABSTRACT

Masting, or mast-seeding, defined as a synchronized and highly variable seed production from year-to-year within a population of plants, is one of the most common example of pulsed resources in terrestrial ecosystems. In oaks, the dramatic fluctuations of acorn production impact its reproductive success and regeneration, the dynamics of a large diversity of seed consumers that rely on it, and, by cascade effects, the dynamics of the entire forest community. However, reproductive effort is difficult to quantify and there is therefore an urgent need of a reliable assessment of the dynamic of acorn production based on a low-cost, unbiased, and robust tool. One of the most commonly used method, the "visual on-tree" method, is very easy and quick to carry out, but is biased under high seed production or when branches are difficult to see. We here assessed the robustness of an alternative method, the "ground plot" (GP), based on a unique annual ground survey after peak of acorn fall, which has not been tested so far. We compared this method at tree and site levels (10 forests throughout France) with the costly and time-consuming trap acorn collection (TNR) method (used here as a reference method). We show that results from the GP method closely matched with those obtained using the TNR method, which demonstrates the efficiency and robustness of the GP method at both tree and forest site levels. Despite some limitations in specific environmental contexts we review, this GP method offers a powerful tool to quantify acorn production and should be deployed to understand mechanisms underlying oak masting and/or to assess its ecological or economic consequences.

1. Introduction

The dynamics of many terrestrial and aquatic ecosystems are characterized by pulsed resources, typically defined as low frequency, large magnitude, and short duration episodes of increased resource availability (Yang et al., 2008, 2010). These events are known to affect a wide range of communities at multiple trophic levels (i.e. individual, population and community) (Ostfeld and Keesing, 2000; Schmidt and Ostfeld, 2008). Masting, or mast-seeding in perennial plants, which involves the synchronous production of large seed crops within a tree population (Silvertown, 1980; Kelly, 1994; Pearse et al., 2016) is one of the most common type of pulsed resources in terrestrial ecosystems (Ostfeld and Keesing, 2000). By affecting the demography of seed consumers, masting not only impacts the reproductive success of plants, but also drives their recruitment and regeneration success, and as a result, forest plant species assembly (Loftis and McGee, 1993; Alejano et al., 2011). One well-supported selective advantage of masting is the predator satiation hypothesis, which states that when seed production is low, seed consumers are maintained at low density. However, when seed production is unpredictably high, seed consumers are satiated and a large proportion of seeds are likely to escape from predation

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(Janzen, 1971; Kelly, 1994; Kelly and Sork, 2002; Bogdziewicz et al., 2018). Oak trees are found in both temperate and Mediterranean regions (McShea, 2000; Gea-Izquierdo et al., 2006) and provide an illustrative case study of the dramatic among-year variation in seed production (Koenig et al., 1994b; Koenig and Knops, 2000; Liebhold et al., 2004a, 2004b). The high fluctuation of oak acorn production shapes the dynamics of acorn consumers such as insects (Venner et al., 2011; Bogdziewicz et al., 2018), birds (Haney, 1999; McShea, 2000), rodents (Wolff, 1996; Stapp and Polis, 2003; Bergeron et al., 2011) and ungulates (Servanty et al., 2009; Gamelon et al., 2017), and impacts by cascade effects the dynamics of the entire community (Ostfeld and Keesing, 2000; Yang et al., 2010; Bogdziewicz et al., 2016). Moreover, by influencing the regeneration of oak forests (Loftis and McGee, 1993; Alejano et al., 2011), masting affects the production of wood of high economic value, and has thereby a strong socio-economic impact (Ostfeld and Keesing, 2000).

Considering the high scientific and societal significance of acorn dynamics, a lot of efforts have been devoted to measure acorn crops (e.g. Graves, 1980; Koenig et al., 1994a; Perry and Thill, 1999). Up to now, two main methods for counting mature acorns have been used. The "trap acorn collection" (named hereafter TNR) corresponds to a method where acorns fall into collectors (e.g. nets, buckets, cans) evenly located beneath the crown (Carevic et al., 2014). This method prevents post-acorn fall seed predation by using protection devices and performing frequent collects during the acorn fall period but does not account for the removal of acorns in the canopy pre-fall. It seems to be the most accurate method to estimate acorn crop (Perry and Thill, 1999; Gea-Izquierdo et al., 2006), but has several drawbacks: the equipment required to collect and protect acorns from consumers may be costly (Perry and Thill, 1999), the conspicuous devices have to be frequently visited to ensure these are not subject to human disturbance, and exhaustive counting of the collected seeds is time consuming (Gea-Izquierdo et al., 2006). The second method, the "visual on-tree" (VOT) method, involves direct counting of mature acorns while still on trees (Koenig et al., 1994a). For this method, observers stand beneath the crown of the focused tree and count as many acorns as possible during a timed period. As used in California oak woodlands, two observers count separate parts of the tree, each for 15 s (Koenig et al., 1994a). This method requires very little equipment (Carevic et al., 2014) and is quick to apply. However, the number of acorns counted in any given period of time is limited by the counting speed of the observer, which may bias the results especially on mast years (Koenig et al., 1994a; Perry and Thill, 1999; see Supplementary Material Appendix 1; Fig. S1; and Table S1). Furthermore, visual access to branches could be compromised either by the location of the acorns inside the tree or by high tree density leading branches from different trees mixing up and canopy closure, which can generate biases when assessing the acorn production in forest landscape (Koenig et al., 1994a; Perry and Thill, 1999; see Supplementary Material Appendix 2; Fig. S2; and Table S2).

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.061.

As these limitations are inherent to any TNR or VOT method previously used, we aimed to set up a new low-cost method that would be easily and quickly applicable in any forest landscape to obtain accurate estimates of acorn production at both tree and population scales. To do so, we proposed and tested the efficiency of the "ground plot" counting method (GP). This sampling method is based on counting acorns on the ground under the tree crown, in quadrats of known area, with no protection against seed predators. The survey took place during a single annual visit soon after main acorn fall. We applied this new GP method on one hundred oak trees from 10 forests (i.e. 10 trees per study site) and we compared the estimates of acorn production with the ones obtained with the TNR reference method deployed on the same individual trees. We assessed the robustness of the GP method at both individual tree and site scales.

2. Methods

2.1. Study sites and selection of oak trees

To test the performance of the GP counting method, we selected 10 forest sites widely distributed throughout France (see Supplementary Material Appendix 3; Fig. S3), with the sessile oak tree (*Quercus petraea*) as the dominant species. The distribution of the studied forests allowed encompassing a large range of environmental conditions with contrasting density and diversity of seed predators. At each site, 10 mature and reproductive trees (i.e. at least 45 cm in diameter) were randomly selected. Every year from 2013 to 2016, a single observer surveyed every tree by applying both TNR and GP methods.

2.2. The Trap-Net reference method (TNR)

Seed traps (i.e. nets of 20 m^2 (4 × 5 m)) were laid under the crown of the studied trees to collect mature acorns falling from mid-August to mid-November. Acorns that dropped in the net were forced, once a week, to fall into a collecting device (80 cm in height and diameter) closed with a lid and surrounded by a wooden fence, thus preventing seed consumption by predators (i.e. birds, rodents and ungulates) (see Supplementary Material Appendix 4; Fig. S4). Each year, acorns were collected in December and counted. The annual acorn production of a tree was estimated as the number of acorns collected per square meter.

2.3. The ground plot counting method (GP)

Soon after the main drop of mature acorns (from mid-October to early November), four sampling points were evenly distributed under the half canopy that was free of any seed trap device (used for the TNR method). To do so, the observer placed himself between two and four meters (depending on crown size) away from the tree trunk and defined four evenly spaced counting points following a circular transect fitting the crown shape (see Supplementary Material Appendix 5; Fig. S5). At each counting point, a quadrat of 0.25 m^2 (50 × 50 cm) was settled on the ground and the number of acorns inside was recorded by a single observer, who remained the same throughout the study period. A unique visit made at each tree was required to implement the method. The acorn production was estimated as the number of acorns per square meter.

2.4. Statistical analyses

2.4.1. Assessment of the GP method performance to estimate the number of acorns produced by a tree

We compared the number of acorns produced by individual trees as estimated by the GP and the TNR methods. First, we explored the ability of the GP method to detect very low amounts of acorns produced by trees. To do so, we fitted a logistic regression to estimate the probability for acorns to be detected by the GP method (i.e. presence or absence of acorns in the quadrats) from the number of acorns harvested with the TNR method. Second, we examined the relationship between the number of acorns counted using the GP and the TNR methods for every tree and year. Trees for which no acorn was found in the quadrat a given year were analyzed separately from the other trees having at least one acorn. This allowed us to account for the lack of power of the GP method when very low amounts of acorns are produced. For non-null GP counts, we explored the relationship between the production of the GP method and the one of the TNR method by fitting constant, linear, and quadratic models. To account for repeated measures performed on the same trees over several years and then avoid pseudo-replication issues (sensu Hurlbert, 1984), we included in the model the tree identity as random effect. Year was not included as a random effect because acorn production is synchronized at the population scale and varies among years within a given population (Koenig et al., 1994b).

We used the Akaike Information Criterion corrected for small sample size (AICc) for model selection and retained the model with the lowest AICc (Burnham and Anderson, 2002). When the AICc difference between two competing models was less than 2, we retained the model including the lowest number of parameters according to parsimony rules. Parameter estimates ± standard errors (SE) are provided for the selected model. For null GP counts, we examined the distribution of the corresponding TNR counts and fitted Poisson, zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB) distributions using the "fitdistrplus" R package (Delignette-Muller and Dutang, 2015). The theoretical distribution best fitting the data was then used to validate the GP method (see below). All analyses were performed with R (version 3.3.1, R Development Core Team, 2011).

2.4.2. Assessment of the robustness of the GP method when applied to a discarded site

The robustness of the GP method was tested through its ability to predict the number of acorns produced by trees (i.e., TNR counts) on a discarded site, at both individual tree and site scales. To do so, we performed a leave-one-out cross-validation analysis that was repeated rotationally for all the 10 study sites (Cawley and Talbot, 2003). Hence, for a given step of the analysis, we discarded one (considered as the discarded site) of the ten study sites at a time from the dataset and assessed the relationship between GP and TNR methods from the nine remaining study sites. For non-null GP values, the same set of models (i.e. constant, linear and quadratic) was fitted to determine the shape of the relationship between the GP and TNR methods (see the previous section for the model selection). For each tree and each year of the survey of the discarded site, whenever the GP count was non-null, we estimated the number of acorns expected under the TNR method using the selected model. When no acorn was counted with the GP method, we estimated the TNR count by randomly sampling within the selected distribution fitted on the 9-site dataset. Finally, we compared predicted and observed TNR acorn production by fitting a linear model forced through the origin and tested whether the slope departed from 1. We repeated this analysis excluding sequentially the ten sites from the dataset, so as to check whether there could be variation in the accuracy of the method among sites. Finally, this analysis was repeated using two out of the four counting points per tree with the GP method. All possible combinations were tested (i.e. A and B, A and C, A and D, B and C, or C and D) as to test the GP method robustness when implemented with a reduced sampling effort.

2.4.3. Assessment of the GP method performance to estimate the number of acorns at a given site

In a wildlife and forest management context, it might be more informative to get estimates of acorn production at the site scale (i.e., a forest plot) rather than at the tree scale. Thus, we used the TNR estimates at each tree and each year of the discarded site (see above) to compute the arithmetic mean for the ten trees each year of the four-year survey. We repeated this for the ten sites sequentially discarded from the dataset and plotted the estimated average TNR values against the observed ones. We tested whether these values fitted a linear model forced through the origin with a slope of 1. Then, this analysis was repeated using only two counting points per tree with the GP method (see above).

3. Results

3.1. Assessment of the GP method performance to count the number of acorns

In 51 out of the 400 acorn productions measured during the 4 years of the survey, acorns were collected in the traps while under the same trees no acorn was found in the quadrats (Fig. 1). This suggests that post-dispersal seed removal may have occurred, thus preventing in some cases the detection of acorn production. Using a logistic regression, we found, however, that the GP method could detect non-null fruiting event from very few numbers of acorns collected in the net with the TNR method (Figs. 1 and 2a). For null GP counts, we found that the zero-inflated binomial negative distribution best described the data (Poisson: AIC = 3687.30; ZIP: AIC = 2576.51; ZIBN: AIC = 498.44), meaning that almost every time, the number of acorns actually collected with the TNR method was null or residual (Fig. 2b; 80% of the null counts with the GP method correspond to less than 2 acorns per m^2 counted with the TNR method). Moreover, the GP method was successful at detecting acorns from very low acorn crops (from 12 fruits or more per m^2 counted with the TNR method; Fig. 2b; see Supplementary Material Appendix 6; Fig. S6 for the cumulative fruiting distribution).

When at least one acorn was counted using the GP method, the correlation between the production estimated with the GP and the TNR methods was very strong (R^2 = 0.89), with the best description using the convex quadratic model (Table 1; Fig. 2a). This curve was located below the first bisector, which indicates that the rate of seed removal by consumers on the ground was higher than in the trap (see Supplementary Material Appendix 7; Fig. S7 for further details). Together with the absence of acorn in some quadrats at low seed production, this result confirms that seed predation actually occurred on the ground in our study sites and that the rate of seed removal decreased with increasing intensity of fruiting. However, whenever acorns are detected with the GP method, the acorn production estimates from TNR and GP methods are very close to each other.

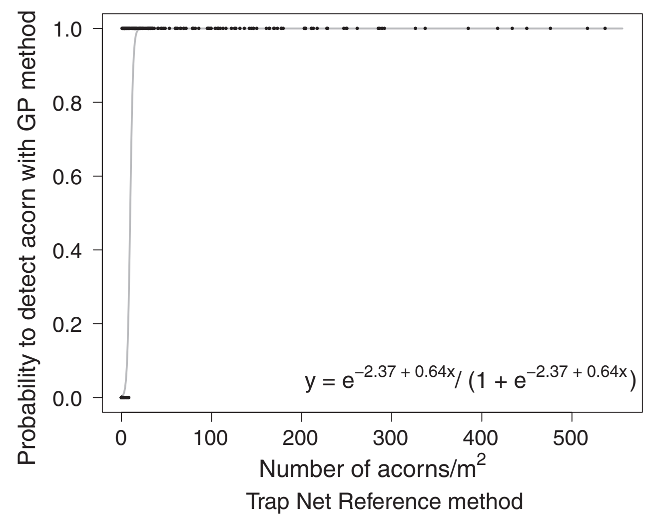

Fig. 1. Probability to detect an acorn production using the GP method according to the number of acorns collected using the TNR method in 1 m^2 net. The solid line represents the logistic regression that best fitted the data. Dots represent the number of acorns harvested in the nets using the TNR method for which absence or presence of acorns has been reported when using the GP method.

3.2. Efficiency of the GP method when applied to a new site

For non-null GP counts, the relationship between the acorn production obtained from GP and TNR methods was consistently best described by quadratic models when analyzing 9 out of the 10 selected study sites at the tree scale (see Supplementary Material Appendix 8; Table S3). From these models (see Supplementary Material Appendix 8; Table S4), we estimated the number of acorns expected with the TNR method from the number of acorns counted with the GP method for the 10th site. For null GP counts, we randomly sampled values from the ZIBN distribution observed for the study sites left in the dataset. By combining those results, we found strong linear relationships (Table 2)

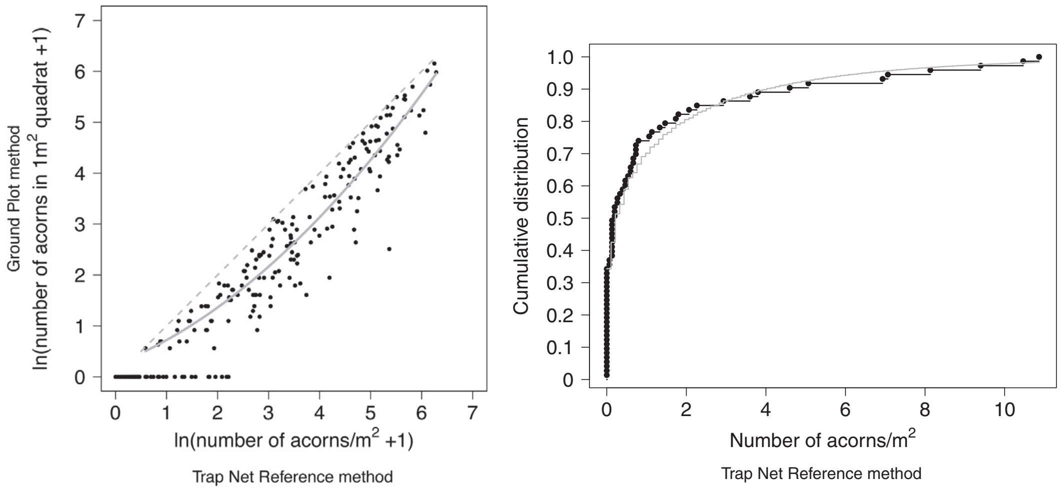

Fig. 2. (a) Relationship between acorn productions from the GP and TNR counting methods (on a log-log scale) implemented on the randomly selected trees in forest landscapes. The tree scale was considered. The solid line represents the quadratic model that best fitted the data when acorns were detected using the GP method; the broken line represents the linear relationship of slope 1 expected in absence of seed predation - (b) Cumulative distribution of the number of acorns collected in 1 m^2 using the TNR method when no acorn were detected using the GP method. The grey line represents the zero-inflated negative binomial distribution that best fitted the data.

Table 1
Model selection for the relationship between the acorn production estimated from the GP method for non-null counts and the reference TNR method. The tree scale was considered. Displayed are the number of parameters (Np), Akaike Information Criterion corrected for small sample size (AICc), AICc difference between a given model and the model with the lowest AICc (ΔAICc) and Akaike weight measuring the likelihood that a given model will be the best among the candidate models (ω). The selected model occurs in bold.

Model	Np	AICc	ΔAICc	Dev	ω
Quadratic	**4**	**591.75**	**0.00**	**583.75**	**1.00**
Linear	3	631.23	39.48	625.23	0.00
Constant	2	965.71	373.96	961.71	0.00

Table 2
Parameter estimates of the linear models forced to pass through the origin that best fitted the relationship between the number of acorns estimated for the new study site being tested and the number of acorns observed using the TNR method for this given site. Parameter estimates ± SE and R^2 are provided.

Site	Parameter estimates ± SE	R^2
Site 1	1.07 ± 0.04	0.96
Site 2	0.97 ± 0.02	0.98
Site 3	0.85 ± 0.04	0.95
Site 4	1.05 ± 0.05	0.94
Site 5	0.92 ± 0.03	0.96
Site 6	0.95 ± 0.03	0.96
Site 7	1.07 ± 0.06	0.88
Site 8	0.89 ± 0.04	0.93
Site 9	0.89 ± 0.04	0.94
Site 10	0.89 ± 0.04	0.94

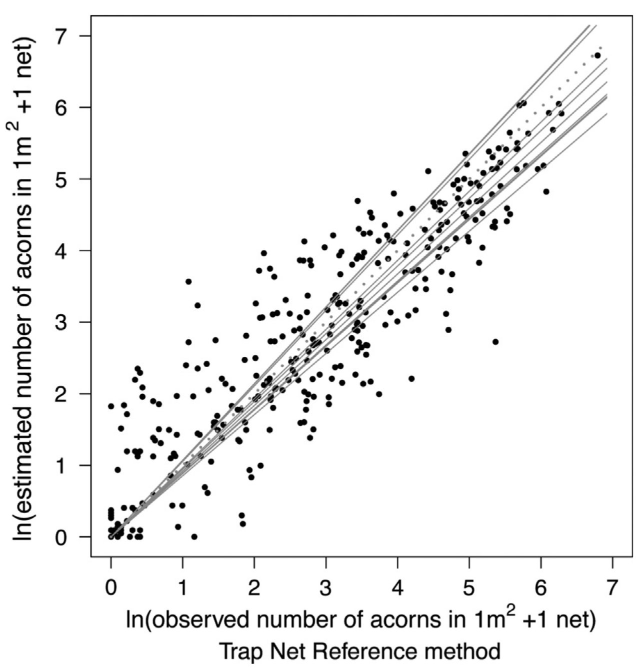

Fig. 3. Relationship between the predicted number of acorns that should have been caught in a 1 m^2 net and the observed number of acorns collected in 1 m^2 net using the TNR method when estimated from results obtained using the GP counting method (on a log-log scale). For null GP counts, the predicted number of acorns that should have been caught in a 1 m^2 net has been estimated from the zero-inflated negative binomial distribution that best fitted the acorn productions observed for the 9 study sites left in the dataset. The tree scale was considered. Solid and broken lines represent the linear models that best fitted the data and the linear model of slope 1, respectively. Models were all forced to pass through the origin.

between the expected and the observed number of acorns using the TNR method (Fig. 3), with R^2 ranging from 0.88 to 0.98 (Table 2). These results showed no site-specific relationship between GP and TNR at any of the 10 sites and thereby suggest that GP counts provide highly reliable estimates of acorn production at the individual tree scale. Furthermore, at the site scale, we found strong linear relationship between the expected and the observed number of acorns when using the TNR method, with a R^2 of 0.98 and a slope not statistically different from 1 ($\beta = 0.98 \pm 0.023$) (Fig. 4), which indicates that the GP counts provide highly reliable estimates of acorn production at both tree and site scales. Finally, using only two counting points per tree with the GP method still provided well-fitted linear relationships between the expected and observed number of acorns using the TNR method, with R^2 ranging from 0.86 to 0.98 and from 0.89 to 0.99, when considering tree

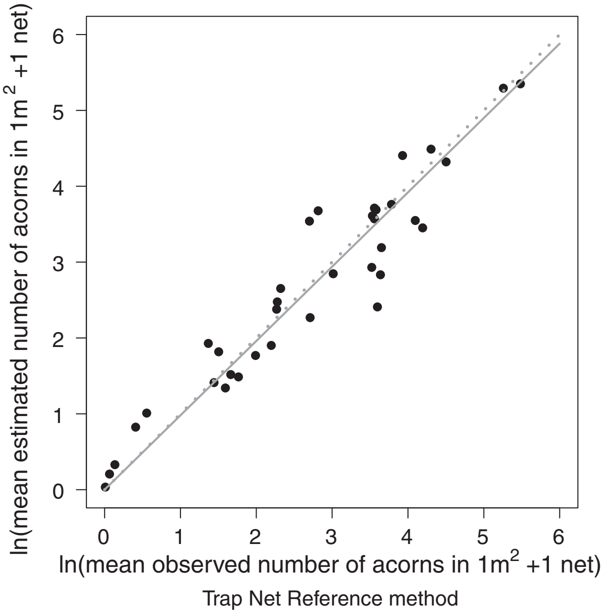

Fig. 4. Relationship between the predicted number of acorns that should have been caught in a 1 m^2 net and the observed number of acorns collected in 1 m^2 net using the TNR method when estimated from results obtained using the GP counting method (on a log-log scale). The site scale was considered. Solid and broken lines represent the linear model that best fitted the data and the linear model of slope 1, respectively. Models were all forced to pass through the origin.

and site scales, respectively (see Supplementary Material Appendix 9; Figs. S8 and S9).

4. Discussion

Despite long-standing *a priori* against GP-like methods due to potential biases induced by the lack of protection of counting devices against acorn consumers (Gysel, 1956; Koenig et al., 1994a; Perry and Thill, 1999), our findings demonstrate that the GP method is reliable when applied in distinct French temperate forests, regardless of the scale of the analysis (i.e. tree or site). Indeed, when conducted at numerous study sites and years encompassing a large range of acorn productions, levels of predation, and environmental conditions, the GP crop size estimates closely matched the ones obtained with the TNR method.

When applied to forest stands, the GP counting method allowed successfully detecting acorn production in quadrats in 87% of the cases. In 13% of the cases, there was no acorn in the quadrats, which could either be due to no or very low acorn production, or to seed predation (Fig. 1; Fig. 2a and b). In absence of seed predation, a proportional (i.e. with a slope of 1) linear relationship should occur between measures obtained with the GP method (that do not protect acorns against predation) and measures obtained with the reference method (that does). Interestingly, when acorns are detected with the GP method, the relationship was not linear but displayed a convex quadratic shape and was located below the first bisector (Fig. 2a). Together with the absence of acorn in quadrats at low seed production, such a relationship indicates that seed predation did occur on the ground in absence of protection. This led less acorns to be found with the GP method than with the reference method and suggests that the level of seed predation was higher at low seed production. Thus, the rate of seed predation (i.e. the proportion of the total acorn production removed by seed predators) decreased with the increase of seed production (see also Supplementary Material Appendix 7; Fig. S7), as expected under the predator satiation hypothesis (Janzen, 1971; Kelly, 1994; Kelly and Sork, 2002; Bogdziewicz et al., 2018). Our results are thus in line with those reported by Crawley and Long (1995) (see Fig. S10 in the Supplementary Material Appendix 10). Our study demonstrates that, despite the occurrence of acorn consumption on the ground, the GP method provides an accurate assessment of acorn production both at the individual and population levels (Figs. 3 and 4).

Beside empirical evidence of seed consumption on the ground, we show that (i) finding no acorn in the quadrats (GP method) corresponds to very low fruiting for the tree under consideration (80% of the trees with no acorn in the quadrats had less than 2 acorns per m^2 with the TNR method); (ii) a strong, positive relationship occurs between the number of acorns detected with the TNR and GP method run at the same trees (Fig. 2a); and (iii) finally the number of acorns in the trap net, when estimated from the GP count at both tree and site scales (when removing one site at a time), always fit well the observed counts, with slopes close to 1 (Figs. 3 and 4). Interestingly, we found similar results when using either two or four sampling points per tree (see Supplementary Material Appendix 9; Fig. S8 and S9), suggesting that even a reduced sampling effort provides reliable estimates and allows the survey of large numbers of trees and sites within the same year. All these results indicate that, when conducted in French oak forests and despite potential among-site and among-year variation in the diversity and density of acorn consumers, the GP counting method is robust at providing accurate estimates of acorn production and, as such, can be reliably used by forest managers and scientists.

From a practical viewpoint, a good knowledge of the temporal dynamics of acorn drop within and between study sites is required to implement the GP method successfully. Indeed, to minimize seed removal by predators and thus provide an accurate estimate of the acorn crop size, the GP count has to take place immediately after the main seed fall period, which is known to occur between late October and early November in temperate Northern regions (Pérez-Ramos et al., 2008; Caignard et al., 2017). In French forests, the acorn drop commonly spreads over a two-month period (early September-late October) with only marginal drop in November (see Appendix 11; Fig. S11). It seems therefore that the GP method, which was successfully applied in ten sites, does not require extremely synchronized acorn drop. Furthermore, seed retention on trees for an extended period of time -the so-called serotiny-, which has been sometimes reported in populations of California oak trees (Koenig et al., 2014), would lead both TNR and GP methods to be inefficient. However, this phenomenon has not been reported yet in any European forest. Obviously, all the three methods we discussed (i.e. TNR, VOT and GP counting methods) present pro and cons that depend on both the needs of users and the environmental context in which they are implemented. Table 3 provides a detailed review of these advantages and disadvantages for quickly and objectively identifying which method is the most appropriate according to the ecological context, as well as some possible arrangements (see also Koenig et al. (2013) for a discussion of different acorn counting methods).

In temperate regions of Europe, forest ecosystem functioning and community dynamics often depend on oak tree reproduction. The mechanisms involved in oak masting and its ecological, evolutionary and economic consequences are still largely unknown (Ostfeld and Keesing, 2000; Alejano et al., 2011), making difficult any relevant prediction about the future of forest ecosystems in the current context of global change (Bogdziewicz et al., 2017). Because it is cheap, quick and easy to implement, the GP method proposed here provides a turn-key tool for surveying fruiting dynamics of many trees across several sites and for analyzing oak tree reproduction and its consequences at both tree and forest scales. As this method can be widely applied to various research and management contexts, it might help better identifying the economic, ecological and evolutionary issues based on acorn production dynamics in European temperate forests.

Table 3
Review of the pro and cons of the Trap Net Reference, Visual On-Tree and Ground Plot counting methods.

Methods		Trap Net Reference (TNR)	Visual On Tree (VOT)	Ground Plot (GP)
Costs & risks	Implementation time	High	Low	Low
	Device cost	Medium or high (depending on the sampling area covered by the collecting devices and the protection level)	Low	Low
	Vulnerability to vandalism	Yes	No	No
Potential biases related to seed consumption by predators	Sensitivity to seed removal in the canopy during summer	Yes	Yes	Yes
	Sensitivity to seed removal in the canopy during fruit fall	Yes	No	Yes
	Sensitivity to seed removal on the ground	No or low. Reliability of the method depends on the protective devices, density and diversity of seed predators and fruiting intensity - further work required	No	Low in our study. But reliability of the method could depend on the density and diversity of seed predators and fruiting intensity - further work required
Efficiency of the methods to provide reliable estimate of acorn crop size in various contexts	Open stand locations with high visual access to branches	High	Medium or high depending on fruiting intensity (see Fig. S1)	Further work required
	Forest landscape	High	Low (lack of visual access to branches due to canopy closure and trees mixing up; see Fig. S2)	High (see Figs. 3 and 4)
	Very low seed crop	High	Medium (risk of no detection)	Medium (risk of no detection, see Fig. 1)
	Very large seed crop	High	Low (saturation effect; see Fig. S1)	High
Requirements for tree selection		Depending on the devices; often relatively flat and unencumbered topography, trees spaced enough and low human attendance	Visual access to branches and trees spaced enough to assign branches to their tree unambiguously	Relatively flat topography; trees spaced enough to assign seeds to their tree unambiguously
Possible adaptation		Complementary devices protecting against different seed predators Adjustment of trap surface	Extending counting time (up to 1 min) and use “time to count an acorn” as a metric to assess acorn production	Sloping ground: use of permanent quadrats fixed on the ground (e.g., board enclosure) keeping acorns within quadrats
References		Perry and Thill, 1999; this work	Koenig et al., 1994a,b this work (Appendices 1 and 2)	Crawley and Long, 1995, this work

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References

Alejano, R., Vázquez-Piqué, J., Carevic, F., Fernández, M., 2011. Do ecological and silvicultural factors influence acorn mass in Holm Oak (southwestern Spain)? Agrofor. Syst. 83 (1), 25–39.
Bergeron, P., Réale, D., Humphries, M.M., Garant, D., 2011. Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. Ecology 92 (11), 2027–2034.
Bogdziewicz, M., Zwolak, R., Crone, E.E., 2016. How do vertebrates respond to mast seeding? Oikos 125 (3), 300–307.
Bogdziewicz, M., Crone, E.E., Steele, M.A., Zwolak, R., 2017. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. J. Ecol. 105 (2), 310–320.
Bogdziewicz, M., Espelta, J.M., Muñoz, A., Aparicio, J.M., Bonal, R., 2018. Effectiveness of predator satiation in masting oaks is negatively affected by conspecific density. Oecologia. 1–11.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New-York.
Carevic, F.S., Alejano, R., Fernández, M., Martín, D., 2014. Assessment and comparison of the visual survey method for estimating acorn production in Holm oak (*Quercus ilex* ssp. ballota) open woodland of southwestern Spain. Arid Land Res. Manage. 28 (1), 102–108.
Caignard, T., Kremer, A., Firmat, C., Nicolas, M., Venner, S., Delzon, S., 2017. Increasing spring temperatures favor oak seed production in temperate areas. Sci. Rep. 7 (1), 8555.
Cawley, G.C., Talbot, N.L., 2003. Efficient leave-one-out cross-validation of kernel fisher discriminant classifiers. Pattern Recogn. 36 (11), 2585–2592.
Crawley, M., Long, C.R., 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. J. Ecol. 683–696.
Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: An R package for fitting distributions. J. Stat. Softw. 64 (4), 1–34.
Gamelon, M., Focardi, S., Baubet, E., Brandt, S., Franzetti, B., Ronchi, F., Gaillard, J.M., 2017. Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. Oecologia 183 (4), 1065–1076.
Gea-Izquierdo, G., Cañellas, I., Montero, G., 2006. Acorn production in Spanish holm oak woodlands. For. Syst. 15 (3), 339–354.
Gysel, L.W., 1956. Measurement of acorn crops. For. Sci. 2 (4), 305–313.
Graves, W.C., 1980. Annual oak mast yields from visual estimates. In: Plumb, T.R., tech. coord. Proceedings of the symposium on the ecology, management, and utilization of California oaks. Gen. Tech. Rep. Rep. PSW-44. Berkeley, CA: US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, pp. 270–274.
Haney, J.C., 1999. Numerical response of birds to an irruption of elm spanworm (*Ennomos subsignarius* [Hbn.]; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. For. Ecol. Manage. 120 (1), 203–217.
Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54 (2), 187–211.
Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. 2 (1), 465–492.
Kelly, D., 1994. The evolutionary ecology of mast seeding. Trends Ecol. Evol. 9 (12), 465–470.
Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: why, how, where? Annu. Rev. Ecol. Syst. 33 (1), 427–447.
Koenig, W.D., Knops, J.M., Carmen, W.J., Stanback, M.T., Mumme, R.L., 1994a. Estimating acorn crops using visual surveys. Can. J. For. Res. 24 (10), 2105–2112.
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 (1), 99–109.
Koenig, W.D., Knops, J.M., 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. Am. Nat. 155 (1), 59–69.
Koenig, W.D., Díaz, M., Pulido, F., Alejano, R., Beamonte, E., Knops, J.M., 2013. Acorn production patterns. In: Mediterranean Oak Woodland Working Landscapes. Springer, Dordrecht, pp. 181–209.
Koenig, W.D., Walters, E.L., Pearse, I.S., Carmen, W.J., Knops, J.M.H., 2014. Serotiny in California oaks. Madroño 61 (2), 151–158.
Liebhold, A., Koenig, W.D., Bjørnstad, O.N., 2004a. Spatial synchrony in population dynamics. Annu. Rev. Ecol. Evol. Syst. 35, 467–490.
Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjørnstad, O.N., Westfall, R., Knops, J.M., 2004b. Within-population spatial synchrony in mast seeding of North American oaks. Oikos 104 (1), 156–164.
Loftis, D.L., McGee, C.E., 1993. Oak regeneration: Serious problems practical recommendations (symposium proceedings). Gen. Tech. Rep. SE-84. Asheville, NC: US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, 319 p., 84.
McShea, W.J., 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81 (1), 228–238.
Ostfeld, R.S., Keesing, F., 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol. Evol. 15 (6), 232–237.
Pearse, I.S., Koenig, W.D., Kelly, D., 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. New Phytol. 212 (3), 546–562.
Pérez-Ramos, I.M., Urbieta, I.R., Maranón, T., Zavala, M.A., Kobe, R.K., 2008. Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. Oikos 117 (9), 1386–1396.
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 (3), 164–169.
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing.
Schmidt, K.A., Ostfeld, R.S., 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. Ecology 89 (3), 635–646.
Servanty, S., Gaillard, J.M., Toïgo, C., Brandt, S., Baubet, E., 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. J. Anim. Ecol. 78 (6), 1278–1290.
Silvertown, J.W., 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. 14 (2), 235–250.
Stapp, P., Polis, G.A., 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102 (1), 111–123.
Venner, S., Pélisson, P.F., Bel-Venner, M.C., Débias, F., Rajon, E., Menu, F., 2011. Coexistence of insect species competing for a pulsed resource: toward a unified theory of biodiversity in fluctuating environments. PLoS One 6 (3), e18039.
Wolff, J.O., 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. J. Mammal. 77 (3), 850–856.
Yang, L.H., Bastow, J.L., Spence, K.O., Wright, A.N., 2008. What can we learn from resource pulses. Ecology 89 (3), 621–634.
Yang, L.H., Edwards, K.F., Byrnes, J.E., Bastow, J.L., Wright, A.N., Spence, K.O., 2010. A meta-analysis of resource pulse–consumer interactions. Ecol. Monogr. 80 (1), 125–151.