

Research



Cite this article: Bogdziewicz M, Kuijper D, Zwolak R, Churski M, Jędrzejewska B, Wysocka-Fijorek E, Gazda A, Miścicki S, Podgórski T. 2022 Emerging infectious disease triggered a trophic cascade and enhanced recruitment of a masting tree. *Proc. R. Soc. B* **289**: 20212636.
<https://doi.org/10.1098/rspb.2021.2636>

Received: 4 December 2021

Accepted: 2 February 2022

Subject Category:

Ecology

Subject Areas:

ecology

Keywords:

mast seeding, post dispersal seed predation, top-down control, tree recruitment, trophic cascades, forest dynamics

Author for correspondence:

Michał Bogdziewicz

e-mails: michalbogdziewicz@gmail.com,

micbog@amu.edu.pl

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5859707>.

Emerging infectious disease triggered a trophic cascade and enhanced recruitment of a masting tree

Michał Bogdziewicz^{1,2}, Dries Kuijper³, Rafał Zwolak¹, Marcin Churski³, Bogumiła Jędrzejewska³, Emilia Wysocka-Fijorek⁴, Anna Gazda⁵, Stanisław Miścicki⁶ and Tomasz Podgórski^{3,7}

¹Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University in Poznań, Ulica Uniwersytetu Poznańskiego 6, Poznań 61-614, Poland

²INRAE, LESSEM, University Grenoble Alpes, 2 rue de la Papeterie, BP 76, Saint-Martin-d'Hères 38400, France

³Mammal Research Institute, Polish Academy of Sciences, Ul. Stoczek 1, 17-230 Białowieża, Poland

⁴Department of Forest Resources Management, Forest Research Institute-Sękoćin Stary, ul. Braci Leśnej 3, 05-090 Raszyn, Poland

⁵Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture, al. 29 Listopada 46, 31-425 Kraków, Poland

⁶Department of Forest Management Planning, Dendrometry and Forest Economics, Institute of Forests Sciences, Warsaw University of Life Sciences (SGGW), Nowoursynowska Str. 159, Warszawa 02-776, Poland

⁷Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, 165 00 Prague, Czech Republic

id MB, 0000-0002-6777-9034; DK, 0000-0002-0324-5893; RZ, 0000-0002-7665-5033; EW-F, 0000-0002-4838-8169; AG, 0000-0001-9806-1159; SM, 0000-0002-0252-5121

There are several mechanisms that allow plants to temporarily escape from top-down control. One of them is trophic cascades triggered by top predators or pathogens. Another is satiation of consumers by mast seeding. These two mechanisms have traditionally been studied in separation. However, their combined action may have a greater effect on plant release than either process alone. In 2015, an outbreak of a disease (African swine fever, ASF) caused a crash in wild boar (*Sus scrofa*) abundance in Białowieża Primeval Forest. Wild boar are important consumers of acorns and are difficult to satiate relative to less mobile granivores. We hypothesized that the joint action of the ASF outbreak and masting would enhance regeneration of oaks (*Quercus robur*). Data from ungulate exclosures demonstrated that ASF led to reduction in acorn predation. Tree seedling data indicated that oak recruitment increased twofold relative to pre-epidemic period. Our results showed that perturbations caused by wildlife disease travel through food webs and influence forest dynamics. The outbreak of ASF acted synergistically with masting and removed herbivore top-down control of oaks by mobile consumers. This illustrates that the ASF epidemic that currently occurs across Europe can have broad effects on forest dynamics.

1. Introduction

High interannual variability in seed production synchronized among plants within populations, called masting or mast seeding, is a widespread reproductive strategy that evolved multiple times in the plant kingdom [1,2]. According to a general consensus, masting allows successful regeneration by starving specialist seed predators in years of seed scarcity and satiating them in years of high seed production [1,3]. The starvation and satiation cycle works well against small specialist seed consumers with restricted mobility, such as insects or rodents whose population dynamics are largely affected by the masting cycles [4,5]. By contrast, large, mobile and more generalist species can sustain themselves on alternative food sources during low seed years, avoiding numerical reductions. Moreover, they move freely across habitats, which creates a risk

of consumer attraction in periods with large-seed crops [4,6,7]. Thus, abundant generalist and mobile seed predators can resist predator satiation and jeopardize plant recruitment [5]. Yet, in contrast with generally well-known satiation dynamics in specialists seed consumers [5,8], the ecological context under which masting can satiate generalist and mobile seed predators is rarely studied.

Crashes in the abundance of generalist seed predators can create periods when satiation is more likely, and seeds can escape consumer control. For example, predation by carnivores can lead to declines in ungulates numbers, which can cascade down to affect plant populations [9,10]. Recolonization of the Banff National Park by wolves led to increased willow and aspen recruitment [11]. Lethal infectious agents can cause similar top-down trophic cascades [12,13]. For example, anthrax epidemics drastically reduced impala populations in northern Tanzania and narrow windows of opportunity for tree establishment leading to even-aged stands [12]. Thus, trophic cascades and mast seeding are among the key mechanisms that allow temporary escape of plants from herbivore control. These two mechanisms have been traditionally studied separately. However, in certain systems, only their combined effect may release plants from top-down control by consumers.

Disease-induced population crashes of an important seed consumer are recently being observed across Europe. African swine fever (ASF) infects wild boar with lethality reaching 95–100%, leading to local population crashes [14,15]. Concerns related to the ASF outbreaks are largely focused on threats to the pork industry [16]. By contrast, the impact of ASF-induced decline of wild boar abundance on ecosystem functioning is largely unexplored. Nonetheless, the ecological consequences can be substantial, as variation in wild boar population size affects a range of ecosystem processes including understory plant species composition, bird nest success and tree recruitment [17–19]. Wild boar are also voracious seed predators, especially of large seeds such as oak acorns [20]. High acorn availability in mast years increases the reproductive success of wild boar, but populations of this omnivorous ungulate are less responsive to masting cycles relative to seed consumers with more restricted mobility and shorter generation time, such as rodents [21–23]. At the same time, the high mobility of wild boar compared to rodents allows aggregating in seed-rich sites [24,25], which makes satiation less likely [4,26]. These traits suggest that masting is unlikely to be successful in satiating wild boar unless populations of this consumer crashes.

Here, we describe the synergistic effects of satiation by masting and disease-related herbivore mortality on oak recruitment in a temperate European forest system. We used the ASF-caused population crash in wild boar in the Białowieża Primeval Forest (Poland) as a natural experiment to test whether periods of population declines of the facultative seed predator are necessary to allow consumer satiation and increase recruitment of masting plants. Two types of consumer exclusions allowed us to disentangle the role of masting and ASF-induced wild boar decline on seed predation and the consequences for tree recruitment. In the first, we separated seed predation of oak (*Quercus robur*) acorns by small mammals (rodents) and large ungulates. In the second, we monitored natural *Q. robur* recruitment with and without access of large herbivores. Both experiments covered the period from 2009 until 2020, which allowed us

to compare patterns of seed predation and sapling recruitment pre- and post-ASF. We tested the following predictions: (1) oak masting is effective at satiating small mammals, (2) but not large mammals such as wild boar. (3) Targeting high-seeding trees by foraging wild boar is responsible for lack of satiation in pre-ASF period. Finally, (4) the decline of wild boar, caused by the ASF epidemic, and associated decrease in seed predation rates translate into higher oak recruitment.

2. Methods

(a) Study site

Our study site is in Białowieża Primeval Forest, one of the last natural forests in Central Europe [27]. It is a large, generally flat, continuous forest composed of mixed deciduous stands located in eastern Poland and western Belarus (52°45'0" N, 23°50'0" E). The Białowieża Primeval Forest covers in total 1450 km² (including the Belarussian part of the forest) and consists of a mosaic of forest types, dominated by deciduous oak–lime–hornbeam forest. The climate is continental with mean temperature of 6.8°C and mean annual precipitation of 641 mm.

(b) Study species

Pedunculate oak, *Q. robur*, is a large broad-leaved tree, widespread and often dominating in temperate forests of Europe. Acorns are large (1–6 g) and consumed by a wide range of animals. Oak seed production is characterized by high interannual variation and interindividual synchronization of seed production [28,29]. Masting helps to satiate pre-dispersal, specialist seed predators such as weevils, but appears to be less effective at satiating mobile consumers such as hares [30].

Eurasian wild boar, *Sus scrofa*, is a medium-sized ungulate widely distributed across Europe and particularly abundant in forested habitats [31]. Wild boar are omnivorous and opportunistic in their food preferences. Their diet composition reflects local and seasonal food availability with plant matter constituting over 90% [32]. Oak acorns are attractive, energy-rich food items which are targeted by wild boar [20]. Acorns can make up most (up to 70%) of the wild boar diet during mast years [33,34]. Trees masting cycles and winter severity are major natural factors shaping population dynamics of wild boar [35]. Wild boar spatial requirements show high intraspecific variation, with home range size varying between 4 and 60 km² depending on the habitat and averaging 4.2 km² in our study area [24,36]. Daily distance travelled by wild boar in the study area averages 6.8 km [24].

(c) Wild boar population crash following African swine fever outbreak

The first official cases of ASF in Białowieża Primeval Forest were reported in March 2015 [15]. From being the most abundant ungulate [35] with widespread occurrence across the Białowieża forest landscape [10], the abundance of wild boar dropped by approximately 90% within 1 year following ASF invasion [15]. A similar decline was reported by the Polish State Forest Office (electronic supplementary material, figure S1). Wild boar culling increased in the managed parts of the Białowieża forest (and not in the Białowieża National Park) during the ASF outbreak as part of national strategy to limit the spread of the disease. Nonetheless, the comparison between the two management regimes showed that ca 90% of the decline in wild boar abundance was associated with the ASF epidemic [15].

(d) Experimental enclosures I: acorn production and seed predation

We have monitored acorn production and predation at 29 oaks for 12 years (2009–2020). At each tree, we installed a seed trap (a cloth bag on a 50 × 50 × 50 cm stand) that excluded all seed predators. We also installed an ungulate enclosure constructed of wire mesh that allowed rodent access (50 × 50 × 50 cm, hole size 10 cm) (electronic supplementary material, figure S2). Data were collected every two weeks, from mid-August (when acorns start to fall) to December (first heavy snow). At each visit, we counted all acorns in the seed trap and in the ungulate enclosure. Moreover, beneath each tree, we counted acorns on the forest floor on 10 randomly placed 50 × 50 cm squares accessible for all seed predators. Acorns counted in the seed trap were removed at each visit, while those counted in the enclosure and on the forest floor were left intact. Moreover, at each visit, we recorded whether fresh wild boar rooting was present or absent at the focal tree. From that data, we calculated tree-level, annual seed predation rates by three sets of seed predators (electronic supplementary material, table S1). Predation by all post-dispersal seed predators was calculated as a difference between acorn production (the number of acorns in the seed trap under focal tree) and the number of acorns remaining on the forest floor (the average number of acorns counted on the floor during the last visit at the focal tree each year). Predation by small mammals was calculated as a difference between the number of acorns in the seed trap and the number of acorns in the ungulate enclosure during the last visit at focal tree each year. Predation by ungulates was calculated as a difference between the number of acorns to which all post-dispersal seed predators had an access and the number of acorns in the enclosures.

(e) Experimental enclosures II: oak recruitment

We used 29 paired enclosure–control plots that were erected as part of a long-term experiment in Białowieża National Park in July 2000 [37]. Each enclosure consisted of a 2 m-high fence with mesh size of ca 15 cm, surrounding 7 × 7 m sample plots. This fence excluded all ungulate species (roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, moose *Alces alces*, European bison *Bison bonasus* and wild boar) from entering, while allowing all small mammals free access. Each enclosure had a paired control plot (unfenced) of 7 × 7 m as close as possible to the enclosure, with comparable habitat characteristics, such as canopy tree species composition, forest type, tree sapling density, herbaceous vegetation cover and canopy openness. Control plots were situated on average 20 m away from their paired enclosure plot, with a minimum distance of 5 m. See Kuijper *et al.* [37] for a more detailed description.

Surveys of oak recruitment were done four times: in 2011, 2013, 2015 and 2019. At each survey, oaks seedlings and saplings were counted and classified into eight size classes (less than 10 cm, 11–25 cm, 26–50 cm, 51–75 cm, 76–100 cm, 101–130 cm, 131–200 cm, greater than 200 cm). A 50 cm buffer zone along the borders of the sample plot was included, in which no measurements were taken, to prevent potential fence effects. In this study, we used oak counts from size classes up to 25 cm, as this is the relevant class for oaks that recruited during the post-ASF period (i.e. post 2015, surveyed in 2019).

(f) Statistical analysis

We analysed data in R v. 4.0.3. We fitted models using the glmmTMB package v. 1.0.2.1 [38]. Models were validated using the DHARMA package v. 0.3.3.0 [39]. The validation included testing for heterogeneity of model residuals, overdispersion,

zero-inflation and temporal autocorrelation. No significant issues were detected.

To test whether oak masting decreased seed predation by different groups of predators, we constructed three binomial-family generalized linear mixed models (GLMMs). The three models corresponded to the three groups of seed predators. The details of calculation of predation for each group is provided above (Methods: Acorn production and predation; electronic supplementary material, table S1). In each model, proportion of predated seeds under a given tree *i* in the year *k* was used as the response variable, while seed production by tree *i* and year *k* in the interaction term with ASF period were used as predictors. We used period as a categorical variable (pre-ASF: 2009–2015, and post-ASF: 2016–2020), because of the clear-cut difference in wild boar abundance between the periods (electronic supplementary material, figure S1). Each model included tree ID as a random intercept. We did not include year as a random factor because it would have restricted the assessment of predation to variation in acorns within each year, while the among-year variation is essential for the predator satiation in masting [3].

To test whether targeting high-seeding trees by foraging wild boar could be responsible for lack of satiation during the pre-ASF period, we used binomial-family GLMM with the same structure of random and fixed effects as the model above. We used the proportion of visits at which rooting was present as a response. The proportion was calculated as an average of fresh rooting occurrences recorded during the resurveys at tree *i* and year *k*.

Finally, to estimate whether ASF created a window of opportunity for oak recruitment, we used Poisson family GLMM. Here we used seedling counts (summed over two categories: less than 10 cm, 11–25 cm) at each plot *j* and year *k* as a response, and period (pre-ASF versus post-ASF) in the interaction time with treatment (enclosure versus control) as predictors. Random intercepts included plot pair ID and year.

3. Results

Seed production in oaks exhibited fluctuations typical of mast seeding trees (figure 1). Post-dispersal seed predation was high, with annual means ranging from 71% to 90%. Ungulates were a major seed predator and excluding them led to predation rates ranging annually from 21% to 78% (figure 1).

Masting satiated rodents during pre- and post-ASF period, while ungulates were satiated only during the post-ASF period. During the pre-ASF period, seed predation by all predators was not related to acorn production (β [s.e.] = 0.11 [0.07], $z = 1.56$, $p = 0.12$) (figure 2a). However, predation by all seed predators decreased with increasing acorn production during the post-ASF period (β [s.e.] = -0.11 [0.05], $z = -2.21$, $p = 0.03$). This change in the relationship between acorn production and total predation between periods was driven by differences in ungulate satiation. Pre-ASF, seed predation by ungulates was not related to acorn production (β [s.e.] = 0.02 [0.08], $z = 0.27$, $p = 0.79$). However, post-ASF, seed predation by ungulates decreased with increasing acorn production (β [s.e.] = -0.15 [0.05], $z = -2.77$, $p = 0.005$). By contrast, oak masting efficiently satiated seed predation by rodents, both pre-ASF (β [s.e.] = -0.20 [0.06], $z = -3.61$, $p = 0.003$) and post-ASF (β [s.e.] = -0.18 [0.05], $z = -3.94$, $p < 0.001$; figure 2c).

Variation in seed production during the pre-ASF period, but not post-ASF period, was associated with a strong response of foraging wild boar to trees with the highest acorn production. Pre-ASF, the proportion of visits at which

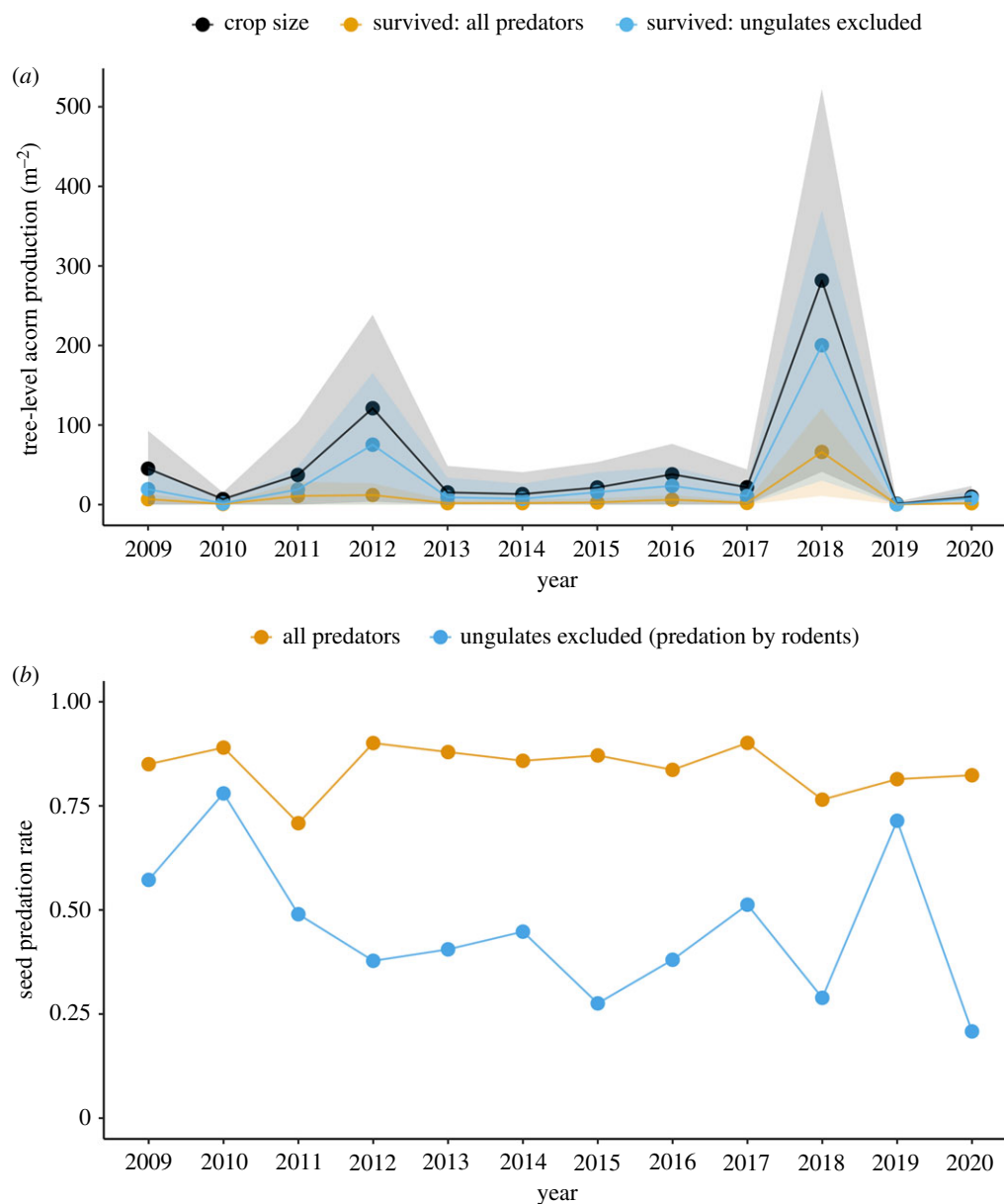


Figure 1. Annual variation in seed production and seed predation. (a) Mean number of acorns produced each year (black), mean number of acorns surviving on the forest floor (yellow) and number of acorns surviving in the exclosures (blue). (b) Seed predation in the same categories. Shading shows standard deviations. (Online version in colour.)

rooting was recorded increased 2.8-fold with acorn production (from 18% under low-seeding tree-years to 48% under high-seeding tree-years) (β [s.e.] = 0.29 [0.05], $z = 5.64$, $p < 0.001$) (figure 3). Post-ASF, the proportion of visits at which rooting was recorded dropped to 7% and was no longer correlated with acorn production (β [s.e.] = 0.01 [0.06], $z = 0.01$, $p = 0.99$).

Long-term oak recruitment was higher inside exclosures (excluding wild boar and other ungulates), represented by the higher number of oak saplings in all size classes including the smallest size classes (figure 4*a,b*). The ASF-driven decline in wild boar abundance and corresponding reduction in acorn predation was associated with a peak increase in oak recruitment. In control plots, i.e. where the wild boar could access, the number of recruited oak seedlings increased two-fold between pre- and post-ASF period (β [s.e.] = 0.71 [0.32], $z = 2.27$, $p = 0.02$). At the same time, no such increase in oak recruitment was recorded inside the exclosures, where the change in wild boar abundance could not have an effect

(β [s.e.] = 0.46 [0.32], $z = 1.48$, $p = 0.14$) (figure 4*a*). Distribution of size classes of seedlings in the control plots and in the exclosures further supported a release of oak recruitment from the top-down control by wild boar (figure 4*b*). A prominent peak in number of small oaks (less than 10 cm and 11–25 cm) occurred in the post-ASF control plots, whereas oak recruitment in the exclosures was more evenly distributed. Results are summarized in table 1.

4. Discussion

Bottom-up effects of masting on seed consumer populations are assumed to be delayed and therefore to have negligible effects on seed survival during mast years [26]. However, the immediate behavioural response to increased seed availability by mobile, large consumers can jeopardize satiation [5,26,40]. In accordance with this reasoning, our research shows that masting is effective at satiating relatively less

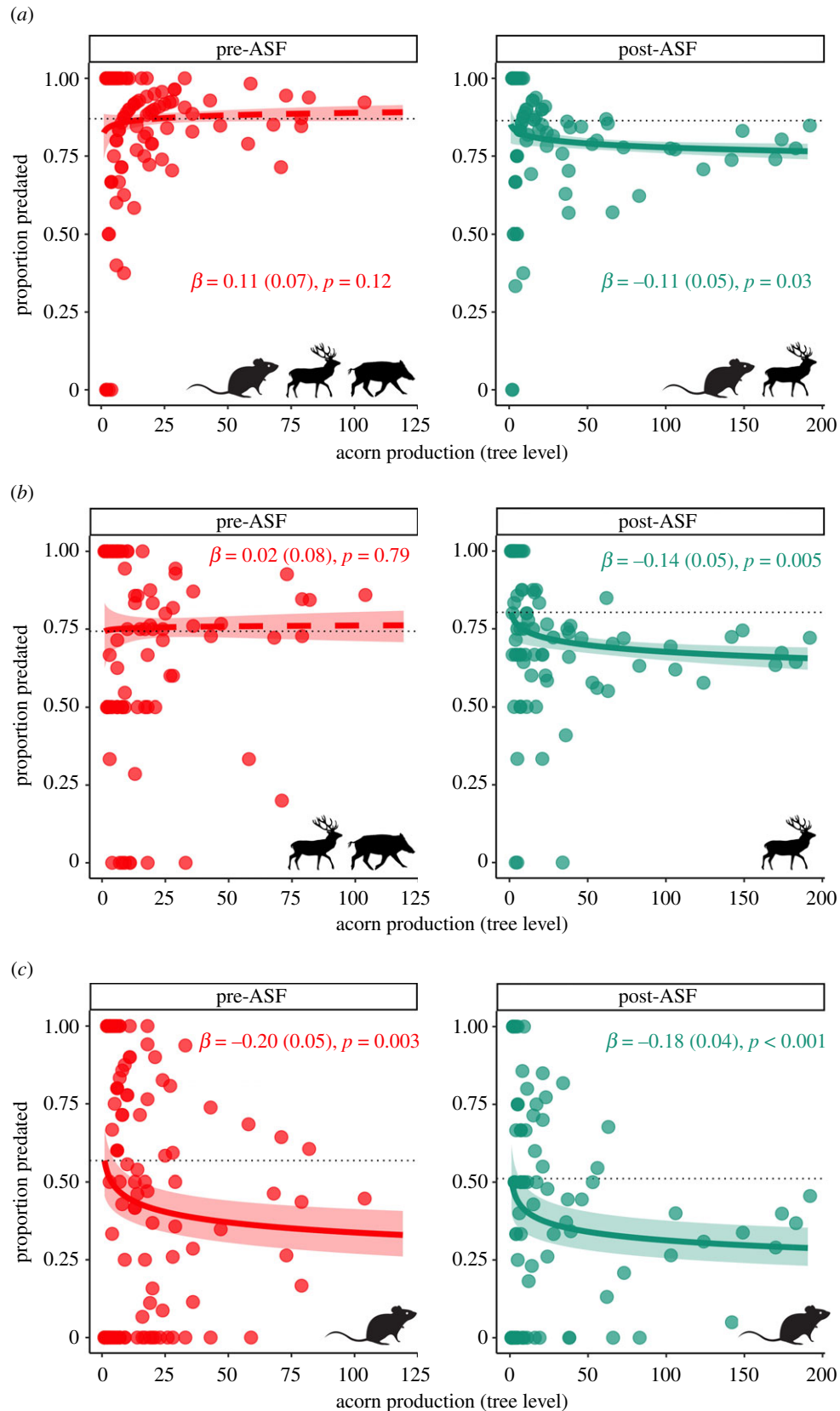


Figure 2. Predator satiation in different predator subgroups. (a) All seed predators; (b) ungulates only; (c) rodents only. Points are annual tree-level observations, lines are binomial GLMM predictions with associated 95% CI. Slopes not significantly different from zero are dashed. Slopes (β) are provided with standard errors and p -value. Horizontal lines at each graph represent intercepts. (Online version in colour.)

mobile rodents. At the same time, mobile wild boar mount rapid behavioural response to increased seed availability, which prevents their satiation. Following the dramatic crash in wild boar abundance induced by the ASF epidemic, the sparse population of wild boar was no longer able to target high-seeding trees during mast years. Lack of the behavioural

response made consumer satiation possible, seed predation declined and oak recruitment increased twofold. Thus, our study provides evidence that a synergistic effect of bottom-up resource pulse (mast) and a top-down impact by a pathogen can be necessary to release trees from a control by mobile, generalist consumers. We showed that a disease

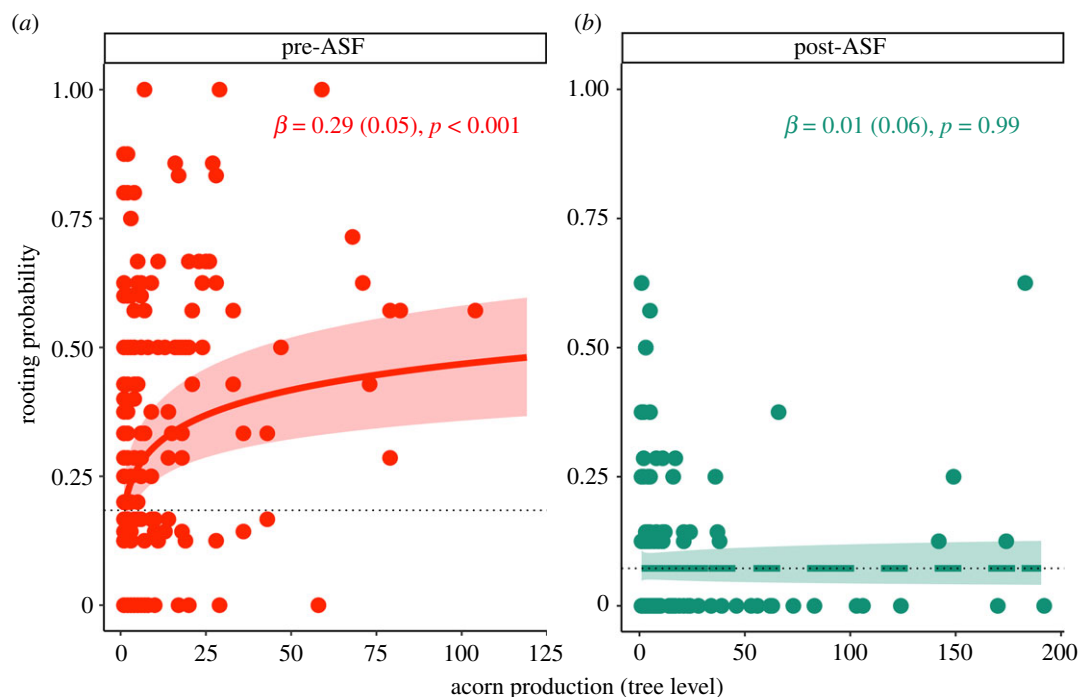


Figure 3. Foraging of wild boar in relation to acorn production. Each data point represents acorns produced in a given year at a given tree (seed trap), lines are binomial GLMM predictions with associated 95% CI. Slopes not significantly different from zero are dashed. Slopes (β) are provided with standard errors and p -value. Horizontal lines at each graph represent intercepts. (Online version in colour.)

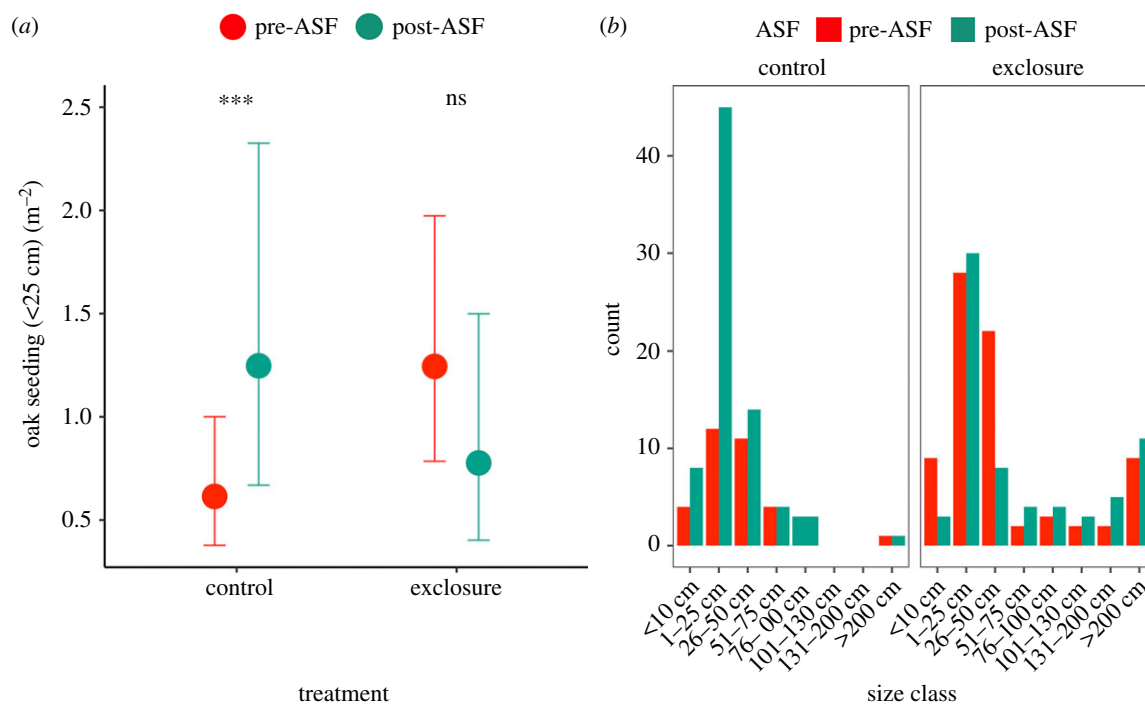


Figure 4. Higher oak recruitment in the post-ASF period compared to pre-ASF. (a) Oak seedling abundance (up to 25 cm tall) estimated with Poisson GLMM and associated 95% CI. The model compared surveys conducted in 4 years (2011, 2013, 2015 and 2019) and categorized into two categories (pre- and post-ASF). (b) Seedling counts across size classes in pre- and post-ASF period. For meaningful comparisons of seedling sums at (b), pre-ASF period is limited to 1 year (here, 2015), while post-ASF period is 2019. Changing the pre-ASF reference year to any other year does not change the trend. (Online version in colour.)

outbreak, via cascading interactions, enhances recruitment of masting oaks and potentially leads to changes in forest regeneration patterns.

We recorded a twofold increase in oak recruitment outside ungulate enclosures after the ASF epidemic had reduced wild boar numbers by approximately 90% [15]. By

contrast, no such peak occurred within enclosures, where seed predation by wild boar was excluded and therefore did not show fluctuations in relation to the ASF outbreak. Together, these results provide experimental evidence that an epidemic, through top-down effects on generalist host abundance, can indirectly affect regeneration of a masting

Table 1. Results summary.

prediction	result
(1) oak masting is effective at reducing predation by specialist seed consumers (small mammals)	masting reduced seed predation from approximately 60–75% to approximately 35%
(2) satiation of mobile and generalist seed predators, such as wild boar, operates only after the abundance of wild boar is reduced by ASF	no satiation in pre-ASF period; post-ASF masting reduced seed predation by ungulates by up to 15%
(3) targeting high-seeding trees by foraging wild boar is responsible for lack of satiation in pre-ASF period	rooting probability increased with acorn production pre-ASF (18% to 48%), but not post-ASF
(4) wild boar decline together with rodent satiation creates window of opportunity for oak recruitment	oak recruitment increased twofold post-ASF in control plots, but not in ungulate exclosures

tree species. Epidemics are usually considered in the light of their direct negative effects on hosts. However, just like predators, viruses or other infectious agents can also shape ecosystem structure and function through their indirect effects on plant communities [13,41]. Indeed, our study implies that ASF can have broad ecological implications. In addition to the consequences for oak recruitment, wild boar predation is likely to have varying impact on recruitment across different tree species, depending on the tree species susceptibility to seed predation and herbivory. Such species-specific variation in the response to wild boar population reduction has the potential to affect forest community structure, biodiversity and carbon sequestration through changes in species dominance [42,43]. Considering the longevity of trees, the community-wide changes in recruitment can be discernible for a long time after the disease outbreak has passed, leaving a permanent footprint of the virus in the forest structure [41,44]. The exact changes in forest regeneration trajectories represent an urgent area for future investigations. One of the key questions is whether the observed peak in oak regeneration overcomes the documented ungulate ‘herbivory trap’ that strongly limits tree recruitment into taller size classes [37,45]. If such a satiation of ungulate browsers occurs [46], then it is more likely that the forests will bear the ASF marks for hundreds of years to come. Another unresolved question is whether wild boar mortality represented a brief window of opportunity for tree regeneration, or a true regime shift, where ASF becomes endemic and wild boar abundance remains at a low level, leading to permanently change in tree regeneration patterns.

Theory predicts that satiation of highly mobile seed predators requires high interindividual synchrony of mast

seeding to counter the immediate aggregation of consumers at high-seeding trees [4,5]. Our study implies that this may not be sufficient to satiate this group of seed predators as in our region *Q. robur* masting is well synchronized [47]. Among all major forest-forming species from the region, interindividual synchrony in *Q. robur* was the highest [48]. Our study showed that satiation additionally required a crash in the numbers of mobile predators, which allowed high-seeding trees to avoid being targeted. We hypothesize that the low abundance and resulting patchy distribution of seed predators over the landscape is a key prerequisite for satiation of mobile and generalist seed consumers [40]. Such patchy distribution can be created either by elevated top-down control or by other factors. For example, coarse woody debris can create patches with restricted consumer access [49], allowing plants to escape from their large-seed predators [20]. Another possibility is the presence of large apex carnivores that create spatial variation in large herbivore presence [10,50]. Thus, trees growing in proximity to numerous woody debris or locations with frequent predator presence can be more efficient at satiating large mobile seed predators. Until now, behavioural responses of generalist seed consumers to masting received little attention in studies of seed predator satiation, despite both evidence and theory implying their important role [4,5,8]. Incorporating temporal (e.g. population crashes) or spatial (e.g. patchy distribution over the landscape) variation in seed predator pressure into predator satiation models appears to be a promising avenue for future research.

One limitation to our study is that high-seeding years occurred only twice during our 12-year-long study, with the post-epidemic 2018 mast year being relatively larger compared to 2012. Separation of the effect of epidemic from the effect of differences in mast year size on seed predation is therefore not possible. However, if the larger recruitment was driven by differences in mast year sizes, but not by changes in wild boar pressure, we would record similar patterns within and outside exclosures, which was not the case.

In closing, our study has two general results. First, masting can be ineffective as an antipredator strategy for highly mobile seed predators if these consumers are abundant, in contrast with less mobile small predators. In multispecies communities, periodical population crashes in these mobile seed predators are then required to allow satiation during mast years through preventing consumer aggregations at high-seeding trees. Hence, only their joint action (masting and population crash) can release plants from top-down control of their seed consumers. The second general insight is experimental evidence that the virus can indirectly affect forest regeneration dynamics. There are at least two major implications that follow. First, more complete understanding of regeneration dynamics in masting trees requires more intense studies on facultative and mobile seed predators to disentangle the context under which satiation and regeneration will occur. Second, our study shows a consequence of the ongoing ASF epidemic in Europe that received little attention so far and point that ASF may indirectly affect long-term tree species dynamics in forest systems. The exact direction and consequences of these effects call for urgent research.

Data accessibility. The data associated with this study can be found at <https://doi.org/10.17605/OSF.IO/H6725>.

Authors' contributions. M.B.: conceptualization, formal analysis, visualization, writing—original draft and writing—review and editing; B.J.: data curation, funding acquisition, investigation, methodology, project administration and writing—review and editing; E.W.-F.: investigation, methodology and writing—review and editing; A.G.: investigation, methodology, writing—review and editing; S.M.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration and writing—review and editing; D.K.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, visualization and writing—review and editing; R.Z.: conceptualization and writing—review and editing; M.C.: data curation, funding acquisition, investigation, project administration and writing—review

and editing; T.P.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, visualization and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. M.B. was supported by the (Polish) National Science Centre (grant no. 2019/35/D/NZ8/00050) and the Polish National Agency for Academic Exchange Bekker programme (PPN/BEK/2020/1/00009/U/00001).

Acknowledgements. We thank Andrzej Waszkiewicz for his help in data collection.

References

- Kelly D, Sork VL. 2002 Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* **33**, 427–447. (doi:10.1146/annurev.ecolsys.33.020602.095433)
- Dale EE, Foest JJ, Hacket-Pain A, Bogdziewicz M, Tanentzap AJ. 2021 Macroevolutionary consequences of mast seeding. *Phil. Trans. R. Soc. B* **376**, 20200372. (doi:10.1098/rstb.2020.0372)
- Fletcher QE, Boutin S, Lane JE, LaMontagne JM, McAdam AG, Krebs CJ, Humphries MM. 2010 The functional response of a hoarding seed predator to mast seeding. *Ecology* **91**, 2673–2683. (doi:10.1890/09-1816.1)
- Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD. 2003 Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* **102**, 581–591. (doi:10.1034/j.1600-0706.2003.12272.x)
- Kelly D. 2021 Mast seeding: the devil (and the delight) is in the detail. *New Phytol.* **229**, 1829–1831. (doi:10.1111/nph.16990)
- Curran LM, Webb CO. 2000 Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipteroocarpaceae. *Ecol. Monogr.* **70**, 129–148. (doi:10.1890/0012-9615(2000)070[0129:ETOTSS]2.0.CO;2)
- Bogdziewicz M, Szymkowiak J, Tanentzap AJ, Calama R, Marino S, Steele MA, Seget B, Piechnik Ł, Żywiec M. 2021 Seed predation selects for reproductive variability and synchrony in perennial plants. *New Phytol.* **229**, 2357–2364. (doi:10.1111/nph.16835)
- Zwolak R, Celebias P, Bogdziewicz M. In press. Global patterns in the predator satiation effect of masting—a meta-analysis. *Proc. Natl Acad. Sci. USA*.
- Ripple WJ *et al.* 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)
- Bubnicki JW, Churski M, Schmidt K, Diserens TA, Kuijper DP. 2019 Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *eLife* **8**, e44937. (doi:10.7554/eLife.44937)
- Hebblewhite M, White CA, Nietvelt CG, McKenzie JA, Hurd TE, Fryxell JM, Bayley SE, Paquet PC. 2005 Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**, 2135–2144. (doi:10.1890/04-1269)
- Prins HHT, van der Jeugd HP. 1993 Herbivore population crashes and woodland structure in East Africa. *J. Ecol.* **81**, 305–314. (doi:10.2307/2261500)
- Buck JC, Ripple WJ. 2017 Infectious agents trigger trophic cascades. *Trends Ecol. Evol.* **32**, 681–694. (doi:10.1016/j.tree.2017.06.009)
- Gallardo MC, Reoyo AdIT, Fernández-Pinero J, Iglesias I, Muñoz MJ, Arias ML. 2015 African swine fever: a global view of the current challenge. *Porc. Health Manag.* **1**, 21. (doi:10.1186/s40813-015-0013-y)
- Morelle K, Bubnicki J, Churski M, Gryz J, Podgórski T, Kuijper DPJ. 2020 Disease-induced mortality outweighs hunting in causing wild boar population crash after African Swine fever outbreak. *Front. Vet. Sci.* **7**, 378. (doi:10.3389/fvets.2020.00378)
- Sánchez-Córdón PJ, Montoya M, Reis AL, Dixon LK. 2018 African swine fever: a re-emerging viral disease threatening the global pig industry. *Vet. J.* **233**, 41–48. (doi:10.1016/j.tvjl.2017.12.025)
- Gómez JM, Hódar JA. 2008 Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). *Forest Ecol. Manag.* **256**, 1384–1389. (doi:10.1016/j.foreco.2008.06.045)
- Burrascano S, Copiz R, Vico ED, Fagiani S, Giarrizzo E, Mei M, Mortelliti A, Sabatini FM, Blasi C. 2015 Wild boar rooting intensity determines shifts in understory composition and functional traits. *Community Ecol.* **16**, 244–253. (doi:10.1556/168.2015.16.2.12)
- Cocquelet A, Mårell A, Bonthoux S, Baltzinger C, Archaux F. 2019 Direct and indirect effects of ungulates on forest birds' nesting failure? An experimental test with artificial nests. *Forest Ecol. Manag.* **437**, 148–155. (doi:10.1016/j.foreco.2019.01.025)
- van Ginkel HAL, Kuijper DPJ, Churski M, Zub K, Szafrńska P, Smit C. 2013 Safe for saplings not safe for seeds: *Quercus robur* recruitment in relation to coarse woody debris in Białowieża Primeval Forest, Poland. *Forest Ecol. Manag.* **304**, 73–79. (doi:10.1016/j.foreco.2013.04.037)
- Bogdziewicz M, Zwolak R, Crone EE. 2016 How do vertebrates respond to mast seeding? *Oikos* **125**, 300–307. (doi:10.1111/oik.03012)
- Gamelon M, Focardi S, Baubet E, Brandt S, Franzetti B, Ronchi F, Venner S, Sæther BE, Gaillard JM. 2017 Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. *Oecologia* **183**, 1065–1076. (doi:10.1007/s00442-017-3821-8)
- 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. (doi:10.1002/eap.2134)
- Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H. 2013 Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *J. Mammal.* **94**, 109–119. (doi:10.1644/12-MAMM-A-038.1)
- Bisi F, Chirichella R, Chianucci F, Von Hardenberg J, Cutini A, Martinoli A, Apollonio M. 2018 Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study. *Ann. Forest Sci.* **75**, 46. (doi:10.1007/s13595-018-0726-6)
- Bogdziewicz M, Marino S, Bonal R, Zwolak R, Steele MA. 2018 Rapid aggregative and reproductive responses of weevils to masting of North American oaks counteract predator satiation. *Ecology* **99**, 2575–2582. (doi:10.1002/ecy.2510)
- Jaroszewicz B, Cholewińska O, Gutowski JM, Samojlik T, Zimny M, Latałowa M. 2019 Białowieża forest—a relic of the high naturalness of European forests. *Forests* **10**, 849. (doi:10.3390/f10100849)
- Bogdziewicz M *et al.* 2017 Masting in wind-pollinated trees: system-specific roles of weather and pollination dynamics in driving seed production. *Ecology* **98**, 2615–2625. (doi:10.1002/ecy.1951)
- Schermer É *et al.* 2019 Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecol. Lett.* **22**, 98–107. (doi:10.1111/ele.13171)
- Crawley MJ, Long CR. 1995 Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *J. Ecol.* **83**, 683–696. (doi:10.2307/2261636)
- Bosch J, Iglesias I, Muñoz MJ, de la Torre A. 2017 A cartographic tool for managing African swine fever

- in Eurasia: mapping wild boar distribution based on the quality of available habitats. *Transboundary Emerging Dis.* **64**, 1720–1733. (doi:10.1111/tbed.12559)
32. Schley L, Roper TJ. 2003 Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mamm. Rev.* **33**, 43–56. (doi:10.1046/j.1365-2907.2003.00010.x)
33. Groot Bruinderink GWTA, Hazebroek E, Van Der Voot H. 1994 Diet and condition of wild boar, *Sus scrofa scrofa*, without supplementary feeding. *J. Zool.* **233**, 631–648. (doi:10.1111/j.1469-7998.1994.tb05370.x)
34. Herrero J, Irizar I, Laskurain NA, García-Serrano A, García-González R. 2005 Fruits and roots: wild boar foods during the cold season in the Southwestern Pyrenees. *Italian J. Zool.* **72**, 49–52. (doi:10.1080/1125000509356652)
35. Jedrzejewska B, Jedrzejewski W, Bunevich AN, Milkowski L, Krasinski ZA. 1997 Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica* **42**, 399–451.
36. Keuling O, Stier N, Roth M. 2008 Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *Eur. J. Wildl. Res.* **54**, 403–412. (doi:10.1007/s10344-007-0157-4)
37. Kuijper DPJ, Cromsigt JPGM, Jędrzejewska B, Miścicki S, Churski M, Jędrzejewski W, Kweczlich I. 2010 Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *J. Ecol.* **98**, 888–899. (doi:10.1111/j.1365-2745.2010.01656.x)
38. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400.
39. Hartig F. 2020 DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. See <https://cran.rproject.org/web/packages/DHARMA/vignettes/DHARMA.html>.
40. Curran LM, Leighton M. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128. (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2)
41. Dobson A, Crawley M. 1994 Pathogens and the structure of plant communities. *Trends Ecol. Evol.* **9**, 393–398. (doi:10.1016/0169-5347(94)90062-0)
42. Vesterdal L, Clarke N, Sigurdsson BD, Gundersen P. 2013 Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecol. Manag.* **309**, 4–18. (doi:10.1016/j.foreco.2013.01.017)
43. Courbaud B *et al.* 2021 Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. *J. Appl. Ecol.* **59**, 492–503. (doi:10.1111/1365-2664.14068)
44. Scheffer M, van Nes EH, Holmgren M, Hughes T. 2008 Pulse-driven loss of top-down control: the critical-rate hypothesis. *Ecosystems* **11**, 226–237. (doi:10.1007/s10021-007-9118-8)
45. Churski M, Bubnicki JW, Jędrzejewska B, Kuijper DPJ, Cromsigt JPGM. 2017 Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. *New Phytol.* **214**, 158–168. (doi:10.1111/nph.14345)
46. Kuijper DPJ, Jędrzejewska B, Brzeziecki B, Churski M, Jędrzejewski W, Żybura H. 2010 Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. *J. Veget. Sci.* **21**, 1082–1098. (doi:10.1111/j.1654-1103.2010.01217.x)
47. Pucek Z, Jędrzejewski W, Jędrzejewska B, Pucek M. 1993 Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica* **38**, 199–232. (doi:10.4098/AT.ARCH.93-18)
48. Pesendorfer MB, Bogdziewicz M, Szymkowiak J, Borowski Z, Kantorowicz W, Espelta JM, Fernández-Martínez M. 2020 Investigating the relationship between climate, stand age, and temporal trends in masting behavior of European forest trees. *Glob. Change Biol.* **26**, 1654–1667. (doi:10.1111/gcb.14945)
49. Smit C, Kuijper DPJ, Prentice D, Wassen MJ, Cromsigt JPGM. 2012 Coarse woody debris facilitates oak recruitment in Białowieża Primeval Forest, Poland. *Forest Ecol. Manag.* **284**, 133–141. (doi:10.1016/j.foreco.2012.07.052)
50. Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B. 2013 Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* **36**, 1263–1275. (doi:10.1111/j.1600-0587.2013.00266.x)