# Acorn availability reduces agricultural damage by ungulates

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- 9 human-wildlife conflict

10 Abstract

Human-wildlife conflicts, particularly the damage to agricultural crops caused by 11 ungulates, pose significant ecological and economic challenges. Understanding the 12 role of natural food availability in driving these conflicts is important for developing 13 effective management strategies. We investigated how the pulsed availability of for-14 est tree seeds, i.e., mast seeding, influences the extent of agricultural crop damage in Poland. Using a 19-year national dataset (2001–2020), we analyzed the relationship 16 between oak (Quercus spp.) and European beech (Fagus sylvatica) seed production, 17 the abundance of wild boar (Sus scrofa) and red deer (Cervus elaphus), and the 18 area of damaged agricultural crops. We found a negative relationship between oak 19 seed production and the level of crop damage, with estimated damage decreasing by 30% from years of seed failure to years of abundant seed production, supporting 21 the hypothesis that a diet shift occurs in ungulates during years of seed abundance 22 that averts ungulates from damaging the crop. In contrast, beech seed production showed no significant effect on crop damage. Our findings demonstrate that pulsed 24 resource dynamics in forests are an important driver of human-wildlife conflict in adjacent agricultural landscapes.

## Introduction

Anthropogenic change has led many taxa to supplement natural foods with agricultural crops, including insects, birds, and especially ungulates (Bereś 2015; Vergin et al. 2025; Jacob et al. 2014; Blount et al. 2021; Montràs-Janer et al. 2019; Brown et al. 2007). In wild boar, a synthesis of 11 studies across eight European countries 31 showed frequent and often large consumption of crops with strong seasonal and geographic variation (Schley and Roper 2003). Crop damage is now a major form of 33 human-wildlife conflict with ecological and socioeconomic costs. Habitat conversion increases animal-human contact, and large-bodied species commonly damage fields, livestock, orchards, and other property, fueling financial losses and negative 36 attitudes (McKee et al. 2021; Hill 2018; Hulme et al. 2020; Distefano 2005; Basak et al. 2023). Because farmland provides accessible, energy-rich food, wildlife turns 38 to anthropogenic sources when natural resources are limited. For example, a 15-year study in Italy reported fewer bear attacks on livestock in years of abundant beech masting but 67% higher attacks in poor mast years (Tattoni et al. 2025). These 41 patterns show how fluctuations in natural food modulate the severity of conflict, 42 highlighting the importance of identifying the ecological drivers of crop damage for better prediction and management. Financial compensation schemes have been introduced in many countries to support those affected (Ravenelle and Nyhus 2017), reaching tens of millions of euros annually (Coordination Rurale 2024; Bleier et al. 46 2012; Schley, Dufrêne, et al. 2008). Such losses burden farmers, institutions, and 47 taxpayers, and mitigation strategies such as fencing, repellents, regulated hunting (Geisser and Rever 2004), and supplementary feeding (Calenge et al. 2004) require further investment. Compensation records illustrate the scale of the problem: in 2000/2001 these amounted to nearly 26 million PLN in Poland ( $\sim 6$  mln EUR), rising to 104 million PLN (~ 24 mln EUR) in 2019/2020 (Główny Urzad Statystyczny 52 2006; Główny Urząd Statystyczny 2021). Analysis of compensation records from the 2005/2006–2019/2020 hunting seasons showed that, on average, 1.72 thousand PLN was paid per hectare of damaged cropland nationwide (Figure S1 in Supplementary Materials). Pinpointing the environmental drivers of damage is thus important for both ecological understanding, forecasting, and cost-effective management. 57 Ungulates are major contributors to crop damage due to their large body size, 58 high energy demands, social foraging, and mobility. Wild boar (Sus scrofa) and red

deer (*Cervus elaphus*) trample fields and consume large amounts of maize, cereals, potatoes, and rapeseed (Massei, Kindberg, et al. 2015; Dzięciołowski 1979; Schley and Roper 2003; Picard et al. 1991). Behaviors such as grubbing alter soil structure (Mohr et al. 2005; Risch et al. 2010), while group foraging increases the spatial extent of damage (Maselli et al. 2014). Yet, agricultural plants supplement rather than replace forest foods. Red deer are herbivorous, shifting seasonally among grasses, shrubs, and conifer needles, and in autumn consume acorns and beechnuts (Gebert and Verheyden 2008; Barrere et al. 2020). Wild boar are omnivorous generalists but depend on energy-dense resources such as acorns, turning to crops or alternative foods when mast is scarce (Massei, Kindberg, et al. 2015). Thus, both species combine forest and agricultural foods, with mast availability shaping their autumn diets (Picard et al. 1991; Schley and Roper 2003).

Masting, the highly interannually variable and synchronized production of large 72 seed crops, is a widespread strategy among European trees, including large-seeded oaks (Quercus spp.) and European beech (Fagus sylvatica) (Kelly 1994; Bogdziewicz, Kelly, et al. 2024; Szymkowiak et al. 2024). By concentrating reproduction in highseeding years, trees enhance pollination and reduce seed predation (Zwolak et al. 2022). The resulting pulses of acorns and beechnuts provide critical resources for 77 insects, birds, rodents, and ungulates (Thomas 2008; Myczko et al. 2014; Ruscoe et al. 2005; Schley and Roper 2003). While abundance of invertebrate seed predators is strongly regulated by mast cycles, large-bodied vertebrates such as ungulates 80 can compensate for poor seed years by shifting to alternative foods (Bogdziewicz, Kuijper, et al. 2022; Curran and Leighton 2000). Nevertheless, fluctuations in seed 82 abundance are expected to alter their foraging behavior, space use, and the degree to which they exploit agricultural crops (Zwolak et al. 2022; Pucek et al. 1993; Touzot et al. 2020; Gamelon, Focardi, et al. 2017). 85

Mast-generated resource pulses also affect ungulate population dynamics. Wild boar depend on at least one energy-rich food source throughout the year, whether mast or crops (Schley and Roper 2003). In high-seeding years, acorn and beechnut availability improves body condition, advances reproduction (Drimaj et al. 2019; Touzot et al. 2020; Cachelou et al. 2022), increases the proportion of breeding females (Gamelon, Touzot, et al. 2021), and leads to larger litters (Touzot et al. 2020), thereby promoting population growth (Massei, Genov, et al. 1996). Access to crops alongside mast can further enhance body size and condition (Merta et al. 2014). In contrast, mortality may increase when mast resources are unavailable, as observed in wild boar from Białowieża Forest, whereas red deer showed no such pattern (Okarma et al. 1995). Thus, while masting has particularly strong demographic effects on wild boar, it also shapes the feeding preferences of both species and modulates their reliance on agricultural foods.

Previous studies show that ungulates preferentially consume mast when available.

In France, Picard et al. (1991) found that during oak high-seeding year, acorns 100 comprised 51% of red deer diet and occurred in 56% of rumen samples, while maize 101 (12%), twigs (9%), and grasses (6%) were secondary. In the preceding poor seed 102 production year, diets shifted toward grasses (20%), maize (12%), leaf stalks (13%), 103 and beechnuts (9%). Long-term data from La Petite Pierre Reserve in northeastern 104 France support these patterns: over 30 years, both red and roe deer increased acorn 105 intake in mast years, with red deer consuming up to 52% of diet compared to 34% 106 in roe deer; in poor years, acorns dropped to 4% and 1% respectively (Barrere et al. 107 2020). Wild boar show similar responses. A review by Schley and Roper (2003) highlights mast (e.g., seeds of oaks and beech) as a preferred food, with other items 109 taken opportunistically. In the Czech Republic, stomach contents of 182 wild boar 110 collected during a strong oak mast year showed acorns and maize dominating diets, with acorns reaching up to 95% of intake (Mikulka et al. 2018). As acorns declined 112 in winter, maize consumption rose, and acorn presence disappeared. Together, these 113 studies demonstrate that mast abundance strongly shapes ungulate diets. Yet most 114 work has focused on dietary shifts, while the direct link between seed production 115 and the extent of crop damage remains poorly quantified, despite its relevance for anticipating and mitigating human-wildlife conflict. 117

In this study, we tested whether oak and beech masting influences agricultural damage in Poland by altering ungulate foraging after seedfall. We predicted reduced crop damage in high-seeding years and elevated damage when seed production failed. To examine this, we combined 19 years of national data (2001–2019) on oak and beech seed production, ungulate abundance, and reported crop damage. Our aim was to clarify whether mast seeding modulates conflict intensity and to assess its potential value as an early-warning indicator for targeted, cost-effective management.

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## Material and Methods

#### $_{\scriptscriptstyle{126}}$ Research area

Poland offers a suitable setting to study interactions between masting and crop 127 damage due to its extensive coverage by both forests and farmland. Oaks (Quercus robur, Q. petraea) are widespread, while beech (Fagus sylvatica) reaches its north-129 eastern range limit and is locally scarce (Eaton et al. 2016; Durrant et al. 2016). 130 Forest cover increased modestly from 28.4% in 2001 to 29.5% in 2020 (Główny Urząd 131 Statystyczny 2002; Główny Urząd Statystyczny 2020), but connectivity remains low 132 compared to other European countries (Estreguil et al. 2013). Agricultural land dominates the landscape, exceeding 50% of the national area, with sown fields de-134 clining from 12.3 to 10.7 million has over the study period. 135 Ungulates are widespread across Poland (Borowik et al. 2013), occupying forests, 136 farmland, and even urban areas (Kowalewska 2019). The main ungulate species 137 are wild boar (Sus scrofa), red deer (Cervus elaphus), roe deer, and fallow deer, 138 with moose and bison present regionally (Michalska et al. 2023; Mysterud et al. 139 2007). Wild boar populations increased for decades (Massei, Kindberg, et al. 2015) 140 but declined recently due to African Swine Fever (Szymańska and Dziwulaki 2022), whereas deer populations continue to expand across Europe (Burbaitė and Csányi 142 2010). Poland is divided into hunting districts managed by local associations, which also administer compensation for crop damage. For this study, we used voivodeship-144 level (N = 16) population estimates reported by the Polish Hunting Association 145 (PZŁ).

#### Seed production data

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We extracted seed production data from MASTREE+, a data set that collects an-148 nual reproductive time series data from all over the world and makes these data 149 freely available (Hacket-Pain et al. 2022; Foest et al. 2024). We used data on Eu-150 ropean beech (Fagus sylvatica) and two types of oaks merged under one category 151 (Quercus robur and Quercus petraea, grouped together as Quercus spp.) from 2001 152 to 2019. This particular data set of seed production from Poland is a part of a long-153 term monitoring program that began in 1954, covering 17 areas of the Regional 154 Division of State Forests (RDLP) and presenting seed production as the percentage 155 of reproducing trees in a population (Pesendorfer et al. 2020). To spatially match the seed production data (collected at the level of RDLP) 157 to voivodeships (the level at which crop damage and animal abundance data are 158 collected), we transformed and weighted the seed production data to align with 159

$$SP_{v,t} = \sum (SP_{f,t} * wt_f)$$

crop damage and animal abundance data, applying the following equation:

Seed production in a given voivodship in a given year  $(SP_{v,t})$  is calculated as a sum of seed production in each forest division within that year  $(SP_{f,t})$ , multiplied by the proportion of the forest division overlapping with the voivodship  $(wt_f)$ .

Seed production exhibited considerable interannual variation across years for both beech (mean coefficient of variation, CV = 1.02, and standard deviation, SD = 23) and oak (CV = 0.66, SD = 17) (Figure 1).

#### Damaged crops and ungulate count data

We obtained data on reduced crop damage area (hectares) and ungulates populations 168 (number of individuals) spanning 19 hunting seasons from 2000/2001 to 2019/2020 169 at the voivodeship level, from the Research Station of the Polish Hunting Associa-170 tion (PZŁ) in Czempiń. Their main objective since 1990 has been to monitor game species in Poland. Damaged crop data is a set of annual records of reduced area 172 of damaged agricultural crops for each voivodeship, calculated as the damaged crop 173 area multiplied by the percentage of its destruction. Damaged crop areas and com-174 pensation withdrawals for these damages are documented by the divisions of PZŁ 175 and aggregated in annual reports. The number of individuals for each ungulate species is also recorded by hunters across Poland based on year-round observations, 177 and this data is used to create annual hunting plans for the season ahead. It is there-178 fore the estimated number of individuals present in a given area (for our purpose, 179 grouped by voivodeships). We focused on two ungulate species that are widespread 180 and known for damaging crops and consuming beech nuts and acorns: wild boars (Sus scrofa) and red deer (Cervus elaphus). 182 Crop damage area showed an increasing trend, rising from under 1000 ha in 183 2001 to approximately 2500 ha in 2020 and was also characterised by relatively 184 large interannual variation (CV=0.77, SD = 1248, Figure 1). Regarding animal 185 populations, ungulate numbers generally increased over the studied period; however, after 2014, the wild boar population declined sharply due to African Swine Fever 187

(ASF) (Figure 1).

#### Statistical analysis

We modeled the relationship between crop damage and seed production, taking into account ungulate abundance. We used a generalized linear mixed model with reduced damaged crop area as a response variable, and predictors including two ungulate species abundance (wild boar and red deer, separately) and seed produc-tion from two species (beech and oak, separately). All predictors were scaled to enable direct comparisons between them. After visual inspection of the relationships, animal abundance variables were fitted as cubic splines to allow for non-linear relationships. We log-transformed the crop damage records to address skewness in the data (see Figure S2 in Supplementary Materials). The region (voivodeship) was included as a random intercept to account for spatial variations in crop damage and repeated sampling. 

We lagged both the ungulate counts and seed production by one year to match the timing of the hunting season, which runs from April 1st to March 31st. The reduced damage area data is referenced to the hunting season (e.g. the 2000/2001 season is recorded as 2001), while the ungulate counts represent the estimated population as of the end of March, which is then used to create the annual hunting plans for the upcoming season (beginning of hunting season e.g. 2000 record is a prediction for 2000/2001 hunting season). Seed production is estimated in a given year, and reflects the food availability for ungulates after the seedfall (within the hunting season, e.g., seeds produced in 2000 are a food source in 2000/2001 hunting season).

To assess the potential impact of African Swine Fever (ASF) on crop damage, we additionally ran models on a shortened time span, using 2015 as a cutoff year (responding to the 2014/2015 hunting season, within which the first known ASF outbreak that happened in Poland). Due to insufficient post-2015 data and the progressive nature of the disease, a classical before—after analysis was not feasible. Therefore, we limited the analysis to the pre-outbreak period and compared it with results from the full dataset. To avoid issues of multicollinearity between the two ungulate species, which were highly correlated (r = 0.68 for the full period; r = 0.91 before ASF), we fitted separate models for wild boar and red deer.

All analyses were conducted in R (version 4.4.2). We fitted the models via the lme4 package (version 1.1.35.5) (Bates et al. 2015). To generate model-based predictions, we used the ggeffects package (Lüdecke 2018).

## Results

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In both models, oak seed production was negatively related to agricultural crop
    damage, while beech seed production showed no significant effect (p > 0.1).
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      In the model including wild boar abundance, oak masting significantly reduced
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    crop damage (\beta = -0.07, SE = 0.02, p < 0.01), while wild boar abundance had a
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   strong positive effect (\beta_1 = 0.647, SE = 0.153, p < 0.001, \beta_2 = 1.820, SE = 0.234,
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    p < 0.001, \beta_3 = 1.226, SE = 0.226, p < 0.001). Assuming average conditions,
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    predicted damage decreased from \sim 1828 ha at low oak seed production to \sim 1295
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   ha at maximum acorn production (Figure 2 A.), representing a \sim 29\% reduction
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    in actual area damaged. In contrast, wild boar abundance had a strong positive
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    effect, where predicted crop damage increased from \sim 452 ha at low abundance to
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    \sim 1925 ha (Figure 2 B.) at high abundance, corresponding to more than a threefold
   increase.
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      In the red deer model, oak seed production again had a negative effect (\beta = -0.10,
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    SE = 0.02, p < 0.001), where assuming average conditions predicted crop damage
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    decreased from \sim 2977 ha at low oak seed production to \sim 1828 ha, which accounted
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    for a \sim 38\% reduction. Red deer abundance was a strong positive predictor of crop
    damage (\beta_1 = 2.133, SE = 0.133, p < 0.001, \beta_2 = 4.483, SE = 0.206, p < 0.001,
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    \beta_3 = 2.553, SE = 0.168, p < 0.001). Predicted damage increased from \sim 224 ha at
   low abundance to \sim 6135 ha at highest values - a more than twentyfold rise (Figure 2
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      Across both model configurations, oak masting reduced crop damage, while un-
    gulate abundance remained the dominant positive driver. The negative effects of
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    oak masting on crop damage persisted when analyzing only the period before the
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    ASF outbreak (Table S1 in Supplementary Materials).
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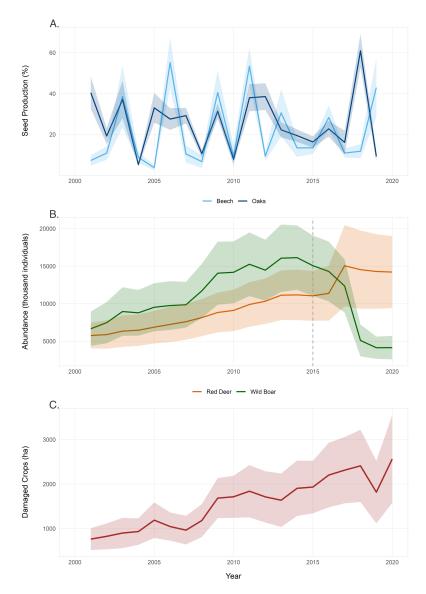


Figure 1: Temporal trends in seed production, ungulate populations and crop damage across all study regions. A) Annual seed production of beech and oaks over time. B) Annual crop damage area across all regions. C) Population trends of red deer and wild boar across all districts. Solid lines represent means and shaded areas indicate one standard deviation around the mean. The vertical dashed line indicates the African Swine Fever (ASF) outbreak (2015).

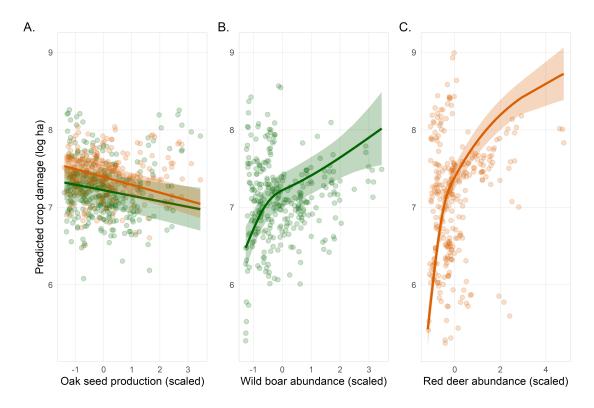


Figure 2: Estimated relationships between crop damage and ecological predictors across the full study period. Panels show estimated crop damage (ha) in relation to (A) oak seed production, (B) wild boar abundance, and (C) red deer abundance. Beech seed production was not a significant predictor of crop damage (Table S1). Lines represent estimated mean values with 95% confidence intervals (shaded areas), and points show partial residuals. Colors show predictions derived from separate models (green - that included wild boar abundance as a predictor; orange - red deer abundance). Predictors were scaled before entering the model. Estimates were derived from linear mixed models with voivodeship included as a random intercept. The conditional  $R^2$  of the model that included wild boar abundance and seed production of both species as predictors was 0.65, while the marginal  $R^2$  was 0.25. The conditional  $R^2$  of the model that included red deer abundance and seed production of both species as predictors was 0.90, while the marginal  $R^2$  was 0.76.

## **Discussion**

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Our results show that interannual variation in natural food, specifically oak masting, modulates the intensity of human-wildlife conflict. We found a negative relationship 250 between acorn availability and the area of damaged crops, with predicted damage decreasing by over 30% between years of lowest and highest oak seed production. 252 This indicates that high-seeding years buffer conflict by reducing the need for un-253 gulates to forage in fields. The pattern suggests that energy-rich acorns act as a 254 substitute resource, lowering reliance on agricultural foods when abundant, while 255 poor mast years intensify pressure on farmland. By linking dietary flexibility of ungulates to a direct, management-relevant outcome, these results extend earlier work 257 that focused mainly on diet composition. Practically, acorn availability emerges as a 258 useful indicator of conflict risk: integrating mast seeding with regional factors such as forest composition, proximity of farmland to oak stands, and animal movements 260 across administrative borders could support more targeted deployment of mitigation 261 strategies. The fact that we detected this effect using broad-scale, non-targeted data 262 suggests that in oak-rich landscapes with strong fruiting, the local strength of this 263 relationship may be even greater.

In contrast to oak, beech seed production did not show a significant influence on crop damage in our analyses. This could due to the lower nutritional value and smaller size of beechnuts compared to acorns (Rivero et al. 2019). Even during mast years, beechnuts may not constitute a sufficient resource to become a primary food source for large ungulates. From a management perspective, our results imply that monitoring oak flowering intensity can be a valuable forecasting tool, whereas tracking beech flowering may be less critical given its negligible impact. Indeed, reports from other countries indicate that beech masting impacted ungulate population dynamics to a lesser extent than oak masting (Gamelon, Focardi, et al. 2017). It is worth noting, though, that the positive correlation (r=0.28) we observed between oak and beech seed production during our study might have partially masked any potential, separate effect of the latter species.

Our analysis indicates that the abundance of key game species had a substantial impact on the extent of crop damage, and it has been shown in previous studies in Poland that agricultural crops are a significant component of their diet (Gebert and Verheyden 2008; Kniżewska and Rekiel 2015). It is important to acknowledge,

however, that our analysis of animal abundance, based on hunter observations, is subject to methodological limitations, as observer expertise and financial incentives can introduce biases into population estimates (Kamieniarz et al. 2023). These limitations prevented us from assessing a direct numerical response of ungulates to seed production, but it remains evident that animal abundance is a critical factor intensifying human-wildlife conflicts.

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We observed that recent (since 2015), drastic shifts in the ungulate community structure, i.e., rising deer numbers and the decline of wild boar due to African Swine Fever (ASF) did not erase the overall significant influence of oak seed production. It is, however, important to note that the wild boar population decline was driven by several interconnected factors: direct mortality from the disease, extensive sanitary culling, and intensified hunting pressure related to management policies, with spatially variable intensity across regions The subsequent spatiotemporal spread of the epidemic (Wojewódzki Inspektorat Weterynarii 2019) likely had profound and regionally varied effects. However, the limited number of observations in the post-ASF period prevented us from conducting a formal statistical comparison between the two periods.

The species analyzed are game animals, and hunting remains the primary pop-298 ulation management tool in Europe. However, high hunting pressure can induce 299 fear, altering animal behavior—potentially creating "refugee effects" (Amici et al. 300 2012) where animals avoid certain areas—and influencing their use of agricultural 301 landscapes (Sütő et al. 2023). Hunting pressure can also drive evolutionary conse-302 quences, such as earlier reproduction in wild boars (Gamelon, Besnard, et al. 2011). 303 Furthermore, hunting pressure might obscure the effects of seed production on pop-304 ulation dynamics at local scales, for example, by maintaining animal populations at low levels. Management recommendations should therefore integrate these environ-306 mental factors to better forecast potential crop losses. While the ongoing recovery 307 of large predators like wolves in Poland (Chapron et al. 2014; Di Bernardi et al. 308 2025) could theoretically help regulate ungulate populations, habitat fragmentation 309 and other anthropogenic influences may limit their effectiveness in keeping ungulate numbers under control (van Beeck Calkoen et al. 2023). Therefore, it could 311 be beneficial to align hunting strategies with oak seed production, as masting can 312 influence not only the extent of wildlife impact on agriculture, but also population dynamics in the subsequent months. In conclusion, our findings demonstrate that 314 oak seed production plays a significant role in shaping crop damage by altering un-315 gulate foraging behavior. This interaction occurs within a complex socio-ecological 316 context influenced by climate, habitat structure, and human management, suggest-317 ing that integrating regional seed production forecasts with landscape composition data and adaptive wildlife management practices may provide substantial benefits 319 for mitigating human-wildlife conflicts. 320

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## 328 Supplementary Materials

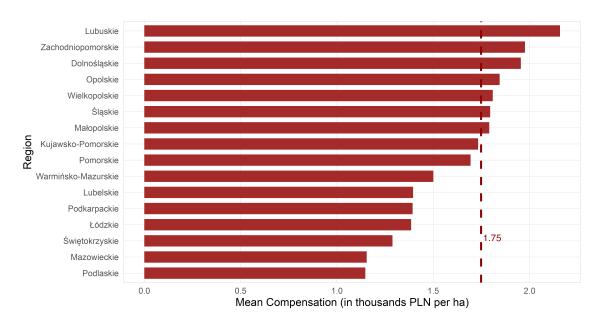


Figure S1: Mean compensations per 1 hectare of damaged crop area for all regions in hunting seasons 2005/2006-2019/2020. The red line represents the calculated mean for the whole of Poland.

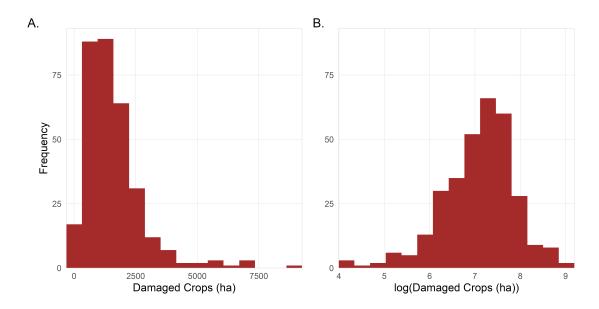


Figure S2: Distribution of damaged crop area (ha) before (A.) and after (B.) log-transformation.

Model	Predictors	Estimates	Std. E.	df	p-value
Wild boar full period	Beech seed production	0.03	0.02	281.73	0.24
	Oak seed production	-0.07	0.02	283.66	0.003
	Wild boar abundance <sub>1</sub>	0.65	0.15	297.81	> 0.001
	Wild boar abundance <sub>2</sub>	1.82	0.23	297.87	> 0.001
	Wild boar abundance <sub>3</sub>	1.23	0.23	296.27	> 0.001
Red deer full period	Beech seed production	0.01	0.02	283.76	0.64
	Oak seed production	-0.10	0.02	284.32	> 0.001
	Red deer abundance <sub>1</sub>	2.13	0.13	282.94	> 0.001
	Red deer abundance <sub>2</sub>	4.48	0.21	290.99	> 0.001
	Red deer abundance <sub>3</sub>	2.55	0.17	297.77	> 0.001
Wild boar before ASF	Beech seed production	-0.03	0.01	205.95	0.02
	Oak seed production	-0.05	0.01	205.29	> 0.001
	Wild boar abundance $_1$	1.60	0.09	217.15	> 0.001
	Wild boar abundance <sub>2</sub>	4.33	0.15	216.79	> 0.001
	Wild boar abundance <sub>3</sub>	2.48	0.12	217.04	> 0.001
Red deer before ASF	Beech seed production	0.01	0.02	204.54	0.72
	Oak seed production	-0.09	0.02	204.23	> 0.001
	$Red deer abundance_1$	1.95	0.15	207.39	>0.001
	Red deer abundance <sub>2</sub>	4.56	0.27	204.79	>0.001
	Red deer abundance <sub>3</sub>	2.71	0.20	213.41	>0.001

Table S1: Linear Mixed-Effects Regression fixed effects for seed production and ungulate abundance for full period and before the ASF outbreak. Animal abundance variables were fitted as cubic splines to allow for non-linear relationships.

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