

RESEARCH ARTICLE

Resource pulses and human–wildlife conflicts: linking satellite indicators and ground data on forest productivity to predict brown bear damages

Carlos Bautista^{1,2} , Julian Oeser² , Tobias Kuemmerle^{2,3}  & Nuria Selva¹ ¹Institute of Nature Conservation of the Polish Academy of Sciences (IOP PAN), Adama Mickiewicza 33, 31-120 Kraków, Poland²Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany³Integrative Research Institute on Transformations of Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

Keywords

Fagus sylvatica, human–wildlife conflict, masting, remote sensing, resource pulses, *Ursus arctos*

Correspondence

Tobias Kuemmerle, Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany. Tel: +49 (0) 30 2093-9372; Fax: +49 (0) 30 2093-6848; E-mail: tobias.kuemmerle@hu-berlin.de

Funding Information

This study was funded by the National Science Centre in Poland under agreement nos. UMO-2020/36/T/NZ8/00571 and UMO-2017/25/N/NZ8/02861.

Editor: Nathalie Pettorelli

Associate Editor: Abdulhakim Abdi

Received: 9 December 2021; Revised: 14 July 2022; Accepted: 21 July 2022

doi: 10.1002/rse2.302

Abstract

Pulsed resources have prominent effects on community and ecosystem dynamics; however, there is little research on how resource pulses affect human–wildlife interactions. Tree masting is a common type of pulsed resource that represents a crucial food for many species and has important bottom-up effects in food webs. In anthropogenic landscapes, years of food shortage after mast years can have negative outcomes for both people and wildlife, for instance when an increased use of anthropogenic foods by animals exacerbates human–wildlife conflicts. Here, we used novel remote sensing indicators of forest productivity and phenology, together with weather cues and ground measures of mast production, to assess whether years of masting and crop failures lead to changes in human–wildlife conflict occurrence. We used a unique 14-year dataset including the production of European beech *Fagus sylvatica* seeds and brown bear *Ursus arctos* damage in the northeastern Carpathians as our model system. Linking these data in a panel regression framework, we found that temporal fluctuations in damage occurrence were sensitive to the year-to-year variation in beechnut production. Specifically, the number of damages during bear hyperphagia (i.e., September to December, when bears need to accumulate fat reserves prior to hibernation) was significantly higher in years with low beechnut production than in normal or mast years. Furthermore, we provide evidence that beech masting and failure can be predicted through a combination of remote-sensing, weather, and field indicators of forest productivity and phenology. We demonstrate how pulsed resources, such as tree masting, can percolate through food webs to amplify human–wildlife conflict in human-dominated landscapes. Given the recent range expansion of large carnivores and herbivores in many regions, including Europe, predicting years of natural food shortage can provide a pathway to proactive damage prevention, and thus to foster coexistence between wildlife and people.

Introduction

Pulses in primary production, defined as infrequent, large-magnitude, and short-duration events of increased resource availability (Yang et al., 2008), have major impacts on consumer communities, with bottom-up effects that affect species interactions across trophic levels (Ostfeld & Keesing, 2000). Mast seeding (synchronized

and intermittent production of a large seed crop by a population of plants) is one of the most common type of resource pulses, impacting food webs in terrestrial ecosystems in major ways (Kelly & Sork, 2002; Yang et al., 2008). For instance, the fluctuation of seed production in temperate forests has a direct influence on the abundance of seed consumers such as rodents which, in turn, affects the density of generalist predators such as

owls and mesocarnivores (Jedrzejewska & Jedrzejewski, 1998; McShea, 2000; Ostfeld & Keesing, 2000). Furthermore, resource pulses trigger functional responses at both population and community level. For example, generalists can be supported by nonmast resources during periods of low seed availability and switch back to seeds during the resource pulse (Ostfeld & Keesing, 2000; Selva et al., 2012). At the community level, predators may switch their diet to alternative prey following the decrease of seed consumers after seed depletion (Jedrzejewska & Jedrzejewski, 1998; Yang et al., 2008). Although there is an increasing understanding of the different ways in which pulsed resources shape trophic dynamics in ecosystems, much of this understanding has come from studying ecosystem with little human influence (Jedrzejewska & Jedrzejewski, 1998; Kelly et al., 2008; McShea, 2000; Selva et al., 2012). How resource pulses drive species interactions in human-dominated landscapes, and whether they can also mediate the intensity and occurrence of human–wildlife interactions, are open questions.

In human-dominated landscapes, many wild animal species rely, to some extent, on anthropogenic food resources (Newsome et al., 2015). Any shortage of natural food may increase the use of anthropogenic food, which can translate into an increase in human–wildlife interactions and potential conflicts. For instance, wild boar *Sus scrofa* increase their home ranges in years of low availability of hard mast (Bisi et al., 2018) and can eventually cause severe damage to agricultural crops (see Schley & Roper, 2003). A scarce primary production can also result in increased conflicts through indirect bottom-up effects in higher trophic levels. For example, gray wolves *Canis lupus* can switch their diet toward livestock (Ciucci et al., 2018; Jedrzejewski et al., 2011; Meriggi et al., 1996; Salvador & Abad, 1987) as a response to decreasing abundance of wild prey after years of low primary productivity (Kiffner & Lee, 2019). Often, such conflicts lead to the persecution of wild animals and can jeopardize the conservation of their populations (Bautista et al., 2019). Thus, understanding and predicting temporal variations in natural food resources, and how they translate into conflict, can help prevent the occurrence of damage to human properties, and ultimately promote human–wildlife coexistence.

Due to the overall importance of masting events in shaping trophic interactions in ecosystems, there is an extensive literature about the proximate drivers of masting (Bogdziewicz, Ascoli, et al., 2020; Pearse et al., 2015; Pesendorfer et al., 2021). The predominant approach is to model the occurrence of masting events as a response to weather cues, which are known to trigger the production and accumulation of resources that plants need for reproduction (Kelly & Sork, 2002; Piovesan & Adams, 2001).

Common cues of masting include temperature, precipitation, and evapotranspiration in different phenological seasons, both in the year of masting and up to 2 years before (Bogdziewicz, Kelly, et al., 2020; Nussbaumer et al., 2018; Piovesan & Adams, 2001). Some studies have suggested that seed production depends on carbon resources derived from short-term photosynthetic production during the months prior to seeding (Hoch et al., 2013; Ichie et al., 2013). However, measuring seed production or resource accumulation at the plant level is time-consuming, expensive and difficult to perform at broad spatial and temporal scales (Fernández-Martínez et al., 2015). These scales, in turn, are most relevant for conservation planning and wildlife management.

Satellite-based vegetation indices (e.g., the Normalize Difference Vegetation Index -NDVI) provide a promising avenue to scale up information about masting. Vegetation productivity can be routinely measured by these indices using freely available imagery, yielding a systematic, repeatable, and verifiable monitoring method to measure changes in resource availability across space and time (Pettorelli et al., 2011). Indeed, these vegetation indices have been widely used to monitor primary productivity, vegetation biomass or carbon uptake in forests and other ecosystems (Garbulsky et al., 2013; Pettoelli et al., 2011; Pettoelli, Vik, et al., 2005). Vegetation indices also appear promising to predict mast seeding events (Bajocco et al., 2021; Camarero et al., 2010; Fernández-Martínez et al., 2015; Garcia et al., 2021; Vergotti et al., 2019), although applications of this kind are still rare. Furthermore, vegetation indices can reveal how changes in vegetation phenology and productivity affect higher trophic levels (Pettorelli et al., 2011; Pettoelli, Vik, et al., 2005). For example, fluctuations in resource availability explain spatio-temporal variation in rutting and calving of European red deer *Cervus elaphus* (Loe et al., 2005), body mass, calf survival and the location of calving grounds of reindeer *Rangifer tarandus* (Griffith et al., 2002; Kuemmerle et al., 2014; Pettoelli, Weladji, et al., 2005), locust *Schistocerca gregaria* outbreaks (Despland et al., 2004), migrations in Mongolian gazelles *Procapra gutturosa* (Mueller et al., 2008) or seasonal variation of habitat use in red deer, roe deer *Capreolus capreolus* and Eurasian lynx *Lynx lynx* (Oeser et al., 2019). Altogether, this suggests a considerable potential of vegetation indices to explain how crop failure in natural vegetation might translate into conflicts between wildlife and people, and to improve the prediction of conflict occurrence.

Here, we investigated the use of remote sensing indicators of vegetation growth, along with weather cues, to predict masting events and, ultimately, conflicts related to mast failures. We used a unique 14-year dataset (2007–2020) comprising the production of European beech

Fagus sylvatica seeds (beechnuts) and brown bear *Ursus arctos* damage in the northeastern Carpathians (southeastern Poland) as our model system. Conflicts arising from brown bear damage are predicted to grow due to the recovery and expansion of many bear populations into human-dominated landscapes (Chapron et al., 2014). Indeed, brown bears inhabit a wide range of habitats and have a broad diet, which also includes anthropogenic foods, such as livestock, crops and honey (Bojarska & Selva, 2012; Can et al., 2014; García-Rodríguez et al., 2021). As a generalist species, the brown bear can adapt well to fluctuations in food availability (Bojarska & Selva, 2012). Brown bears are known to rely strongly on the seeds of masting trees, such as white bark pine *Pinus monticola* in northwestern North America (Mattson et al., 1992), pine nuts from Siberian pine *Pinus sibirica* in boreal forest of north-central Asia (Niedziałkowska et al., 2019), or beechnuts in temperate Europe (Ciucci et al., 2014; Naves et al., 2006). Bears rely on mast seeding particularly during hyperphagia (September–December), when they need to accumulate fat reserves prior to hibernation (Bojarska, 2014; Ciucci et al., 2014; Naves et al., 2006). During mast years, these resources are particularly abundant. Additionally, after masting years, seeds can remain available under the snow until the end of the following winter, allowing bears to consume them after they emerge from their dens (Bojarska, 2014). However, masting and years of crop failure occur at highly irregular intervals (Hilton & Packham, 2003; Nussbaumer et al., 2018). Since beechnuts are a key food resource for bears in temperate Europe (Bojarska, 2014; Ciucci et al., 2014; Naves et al., 2006), we hypothesized that the availability of beechnuts shapes the consumption of other food resources, including human foods (Figure 1). We tested this hypothesis using a unique time series of human–bear conflict occurrence and ground measures of beechnut production. Finally, we modeled the temporal changes in beechnut production using novel remote-sensing indicators of vegetation growth and phenology and weather cues as a means to forecast years when beechnut production will be low and conflicts intense.

Materials and Methods

Study area

Our study area is located in the Carpathian Mountains in the Podkarpackie Province, Poland (Figure 2). This area is characterized by gentle slopes and low-to medium-elevation mountains ranging from about 200 to 1200 m. The land is mainly covered by forest (62%) and agriculture (32%) (Bautista et al., 2021). The natural vegetation can be divided into three altitudinal zones: (1) the foothill

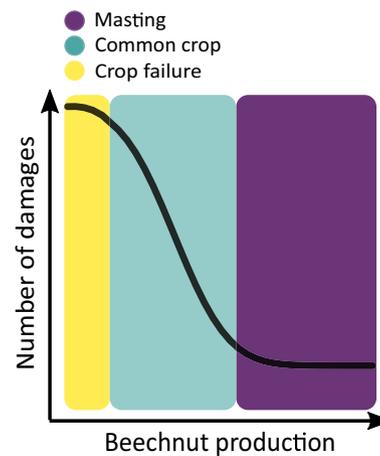


Figure 1. Conceptual diagram showing the partial expected effect of beechnut production on brown bear damage occurrence. In masting years bears will feel satiated and the number of damages will be low. In turn, in years of crop failure bears are expected to damage more human properties in their search for alternative food resources.

zone (<500 m), which is nowadays mostly occupied by human settlements and agriculture, with a limited cover of mixed deciduous forests; (2) the lower montane zone (500–1150 m) primarily consisting of forests dominated by beech and silver fir *Abies alba* and (3) the zone above the upper tree line (>1150 m), where subalpine and alpine communities are typical. The climate is continental with cold winters and mild summers. The mean temperature between 2005 and 2020 was 18°C (SD = 0.8) in July and –3°C (SD = 0.8) in January. Annual precipitation for the same period ranged between 790 and 1200 mm, with a maximum during the summer (average precipitation between 100 and 150 mm, maximum of 320 mm in July) and a minimum in winter (average precipitation between 50 and 60 mm, with a minimum of 10 mm in January; data provided by the Polish Institute of Meteorology and Water Management, <https://dane.imgw.pl/data/>).

Bear damage data

We compiled data on bear damage to livestock, apiaries and fruit tree plantations from official claims collected through the damage compensation program in the Podkarpackie Province by the Regional Directorate for Environmental Protection in Rzeszów. The compensation scheme has been in place since 1999 and includes damage inspection and verification by trained personnel (Bautista et al., 2017). Each damage record contained information about the type and date of damage (day/month/year). We obtained data from 654 bear damage events (mostly to apiaries) from 2007 to 2020 (Figure 2). The annual

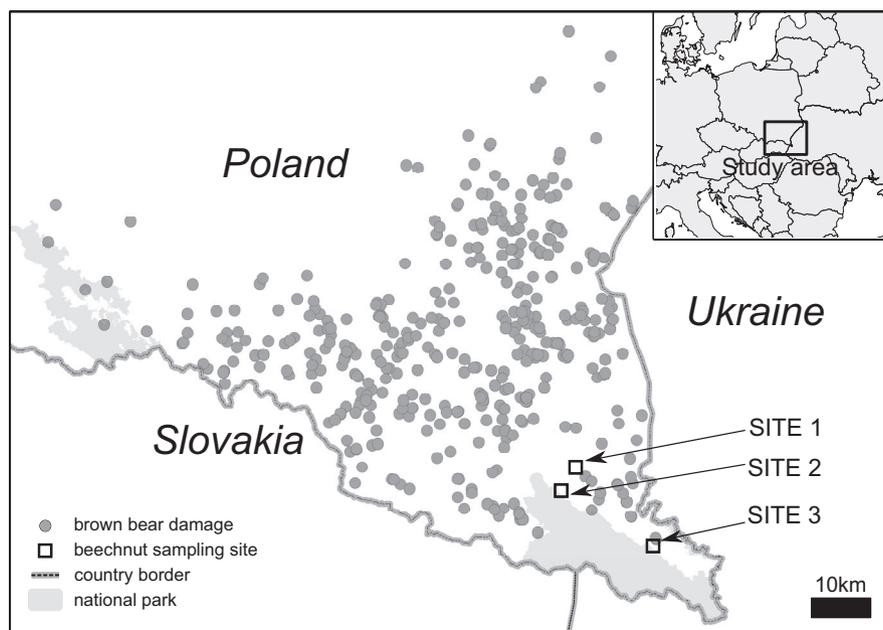


Figure 2. Map of the study area showing the locations of the three beechnut sampling sites and brown bear *Ursus arctos* damages in the northeastern Carpathians (SE Poland) in 2007–2020.

number of recorded damages ranged from 15 to 104 (mean of 47 damages annually, $SD = 28.8$), with a maximum in July (ranging from 2 to 30 damages) and a minimum in the winter months, when most bears hibernate (ranging from 0 to 4 damages).

Beechnut production data

We assessed beechnut availability by counting seeds on 30 sampling plots every year in the period 2007–2020. To sample the beechnuts, we installed 30 sampling plots of $1 \times 1 \text{ m}^2$ on the ground in beech forests at three sites, 10 plots per site (Figs. 2 and 3). Beechnut sampling consisted of counting all beechnuts in each plot and distinguishing intact from non-intact beechnuts. While counting beechnuts on the ground might underestimate seed fall, because some beechnuts are immediately removed by animals, it reliably distinguished mast from non-mast years (Zwolak et al., 2016) and gives a proxy of the beechnuts available to brown bears. Every year, the plots were cleaned in late summer before sampling and also after collecting the beechnuts for subsequent sampling sessions within the same year. The number of sampling sessions differed among years, as did the number of days elapsed between cleaning the plots and collecting the beechnuts (hereafter sampling duration; see Table S1). This was due to weather, field conditions and logistics. Traditional approaches that measure beech productivity by collecting seed crops from October to November risk

overlooking wide interannual variation in phenological stages in deciduous forests (Melaas et al., 2013; Senf et al., 2017). To avoid this pitfall and to minimize post-dispersal loss of beechnuts to predators (Packham et al., 2008), we selected for each year the sampling sessions that had (1) the minimum sampling duration, and (2) included the days of maximum seed fall in our data (i.e., from late August to the end of October, depending on the year; Table S1). For years when the sampling sessions had similar duration, we selected the session in which the seed fall was higher (see years 2010 and 2016 in Table S1).

Predictors of beechnut production

To model and predict beechnut production, we obtained weather data identified as important for beech seeding in previous studies. Specifically, the production and accumulation of resources that beech trees need for reproduction is commonly related to (1) a cold and wet summer 2 years before masting, (2) a dry and warm summer 1 year before masting and/or (3) a warm spring in the masting year (Bogdziewicz, Kelly, et al., 2020; Nussbaumer et al., 2018; Piovesan & Adams, 2001). Accordingly, we extracted the mean maximum temperature and summed precipitation in summer (June and July) for one and 1 years before the assessment year (lag1 and lag 2) and in spring (April and May) of the actual assessment year (lag 0). We also included mean temperature of the

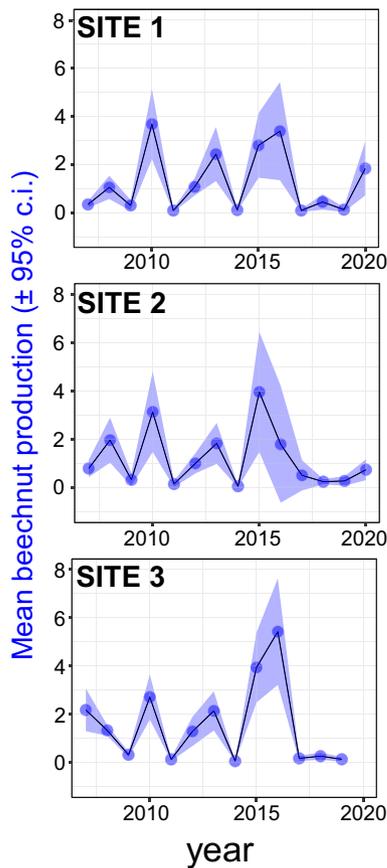


Figure 3. Temporal trends in European beech *Fagus sylvatica* seed production in three sampling sites in the north-eastern Carpathians (SE Poland) in 2007–2020. Beechnut production was sampled yearly in 30 1 × 1 m² plots distributed evenly across three sampling sites and was measured in the number of seeds per m² and standardized by the duration in days of the sampling session (see Table S1 for details).

growing season (May–August), since raising temperatures can enhance beechnut production (Bogdziewicz, Kelly, et al., 2020), and the minimum absolute temperature in late spring (May and June) because late spring frost is associated to crop failure in masting plants (Bogdziewicz, 2021; Neilson & Wullstein, 1980). We extracted all weather data from the Polish Institute of Meteorology and Water Management (<https://dane.imgw.pl/data/>), and used data from the nearest meteorological station with available data to our three sampling sites (see Table S2).

We tested two types of remote-sensing indicators of beechnut productivity and phenology. First, we used spectral-temporal metrics derived from Landsat imagery at a 30-m spatial resolution (Oeser et al., 2019), using the Tasseled Cap (TC) greenness index as a proxy of vegetation productivity (Crist & Cicone, 1984). Specifically, we

calculated TC greenness for all Landsat pixels covering the sampling sites for every image within our study period and then summarized index values over time by calculating median values. To capture phenological variations throughout the year, we calculated separate median values for three temporal windows, representing key phenological stages in European temperate forests (Oeser et al., 2019): start-of-season (day of year 60–151, 42 images), peak-of-season (day of year 152–243, 53 images), and end-of-season observations (day of year 244–334, 54 images). Second, to better capture the timing of phenological stages and their year-to-year variations, we additionally derived phenological metrics (i.e., phenometrics) from MODIS satellite imagery at a 250 m resolution. MODIS-based phenological metrics have been shown to be useful to analyze beech masting events (Bajocco et al., 2021). In total, we calculated 12 phenometrics based on the Enhanced Vegetation Index (EVI), including measures of the date of the start, peak and end of the growing season, the start and end dates, as well as the length and slope of both the vegetation green-up and senescence stages, and the yearly total productivity (measured as the integral of the growth curve: Table S2). We calculated all Landsat- and MODIS-based metrics for every year between 2005 and 2020 (extent of the field sampling and 2 years prior). We used the Google Earth Engine (Gorelick et al., 2017) for calculating Landsat metrics (see Oeser et al., 2019 for more details on the satellite image processing and metric calculation) and derived MODIS-based metrics using the R-package *phenofit* (Kong, 2020). For further details about the predictors of beechnut production, we refer to Table S2.

Statistical analyses

Temporal fluctuations of damage in relation to beechnut production

We hypothesized that the number of bear damages decreases in masting years (i.e., years of high beechnut production) and increases in years of crop failure (i.e., low beechnut production). To test our hypotheses, we used Generalized Linear Models with a negative binomial distribution, with the number of damages as the dependent variable and beechnut production as the predictor variable. Specifically, we analyzed the number of damages in (1) bear hyperphagia (September–December, which covers the period of seed fall in beech forests); and (2) after bears emerge from their dens in the following year and start to feed (January–June) as responses to different categories of beechnut production (i.e., crop failure, common crop and masting). We decided to categorize beechnut production because beyond a certain threshold of

production the response of bears and other seed consumers to masting remains the same (Zwolak et al., 2022, see also Figure 1). That is because masting satiates consumers to reduce seed losses and enhance survival and recruitment (Kelly & Sork, 2002). Consequently, beyond a threshold of production the rate of seed consumption reaches a plateau at which it remains constant irrespective of the size of the seed surplus (Zwolak et al., 2022). A similar logic is expected for years of crop failure; below a certain threshold, seed consumers (e.g., the brown bear) would be forced to feed on alternative food resources (e.g., honey and larvae from beehives) (Bogdziewicz et al., 2016). To create these categories, we first standardized the predicted values of beechnut production by the sampling duration and then calculated the yearly average across plots. Then, we classified each year as crop failure (i.e., production below the first quartile), common crop (i.e., between the first and the third quartile) and masting (i.e., above the third quartile).

Predicting seed failure in European beech

We first explored the best predictors of temporal trends in beechnut production. We used Generalized Linear Mixed Models with the plot ID as a random intercept and a negative binomial error distribution to control for overdispersion. We also included the year as a random intercept and the beechnut production in lag1 as fixed effect to control for (1) within year dependency and (2) possible temporal autotony to the first order. We included beechnut production in lag1 instead of an autocorrelation structure, because this allowed to directly compare the effect of seed crop from the previous year with other predictors of beechnut production. Moreover, in preliminary analyses, we found this model to be more parsimonious than a first-order autoregressive model ($\Delta AIC_c = 36$). We did not include 'site' as a fixed effect, because this decreased the model fit ($\Delta AIC_c = 6$) and there was no heterogeneity detected in the residuals across different sites. To account for any potential effects of differences in sampling intensity, we used the sampling duration as an offset.

To identify the main predictors of beechnut production, we first constructed single-variable models to avoid overfitting and to reduce the risk of finding spurious correlations. Then, we constructed a global model including all predictors for which the confidence intervals of standardized coefficients in the single-variable models excluded zero. This global model included data on beechnut production for the period 2009–2020 (data in 2007 and 2008 were not included in the model because we could not calculate some remote-sensing predictors due to persistent cloud cover). Based on this model, we

generated candidate models for all possible combinations of predictor variables, while keeping the offset (sampling duration) fixed. To find the most parsimonious models, we compared candidate models according to Akaike's Information Criterion, adjusted for small sample sizes (AIC_c ; Table S2). Then, we calculated a weighted average of the coefficient estimates present in the most parsimonious candidate models (i.e., $\Delta AIC_c < 4$). To assess the relative importance of each predictor included in all candidate models, we calculated the Akaike weight for each model and summed weights per predictor across models including that variable. For prediction purposes, we constructed a second global model using a subset of the data for the period 2009–2017. We used the same predictors and the same fitting procedure as for the global model using all data. We predicted beechnut production per plot and year in the period 2018–2020, based on the averaged coefficients from the set of the most parsimonious models. To predict the beechnut production in the years 2019 and 2020 we used the predicted value of beechnut production in the previous year instead of the observed values. We standardized the predicted values of beechnut production by the sampling duration and calculated the averaged and associated confidence across plots for each year.

All analyses were conducted in R version 4.0.2 (R Core Team, 2020) using the packages *glmmTMB* (Brooks et al., 2017) for generalized linear models and mixed-effects models, *MuMIn* (Barton, 2014) for model selection, model averaging and prediction of averaged models and *ggplot2* (Wickham, 2016) for data visualization.

Results

We found that temporal fluctuations in the occurrence of bear damage during hyperphagia were sensitive to the year-to-year variation of beechnut production. Specifically, the number of damages in hyperphagia was significantly and consistently higher in years with very low beechnut production (i.e., crop failure) in comparison to the number of damages occurring in masting years and years of common crop (Table 1, Figure 4). We did not find any relationship between the number of damages during hypophagia and the beechnut production in the previous year (Table 1).

Overall, our results showed that year-to-year variation in beechnut production at the population level can be predicted by a combination of remote-sensing indicators of forest productivity and phenology, weather cues and the beechnut production from previous years (range of the conditional and marginal R^2 from the set of most parsimonious models = 0.71–0.74 and 0.05–0.32, respectively; Table S4). We found that three combinations of

Table 1. Summary of negative binomial generalized linear models analyzing the number of brown bear damages at different seasons as a response to beechnut production in the north-eastern Carpathians (SE Poland) in 2007–2020.

Predictors	Responses	
	Damages hyperphagia (September–December)	Damages after winter (January–June)
Intercept (common crop)	1.83*** (1.03–2.64)	2.86*** (2.42–3.48)
Crop failure	1.18* (0.23–2.13)	0.23 (–0.66–1.11)
Masting	0.62 (–0.41–1.65)	0.58 (–0.24–1.40)
Observations	14	14

The beechnut production was categorized as crop failure, common crop and masting year based on percentiles values of the mean temporal trend (see Methods for details). The 95% confidence intervals are shown in brackets below the estimates.

* $P < 0.05$.

*** $P < 0.001$.

conditions explained mast years in beech forests: (1) a cold summer 2 years before masting, (2) a low beechnut production and high yearly forest productivity 1 year before masting, and (3) low summer productivity in the masting year (Table 2; Table S3 and S4). The fact that beechnut production was negatively correlated with the production in the previous year (i.e., negative temporal autocorrelation) indicated that crop failure occurrence was most likely after a masting year (Table 2). Other predictors also present in the most parsimonious models, but of lesser importance, included (in decreasing order of importance) the start day of the senescence phase in lag1, the absolute minimum spring temperature in lag0, the starting day of the growing season, and the length of the senescence phase in lag1 (Table 2, Table S3 and Table S4). The predicted values of beechnut production in each plot for the period 2018–2020 were significantly correlated with the observed values ($r = 0.66$, $P < 0.0001$, d.f. = 70, Fig. S2) and their yearly means across plots correctly classified the seed failure in 2019 (Figure 4).

Discussion

Human–wildlife conflicts are a major challenge for the coexistence of people and wildlife, yet how variation in natural food availability increases the reliance on anthropogenic foods, and through this, conflicts, remains poorly understood. Here, we provide evidence that bear damages in temperate ecosystems increase in years of beechnut crop failure using a combination of remote-sensing and field-measured productivity indicators. Our study provides empirical evidence on how bottom-up effects of resource pulses, such as masting, shape the interactions

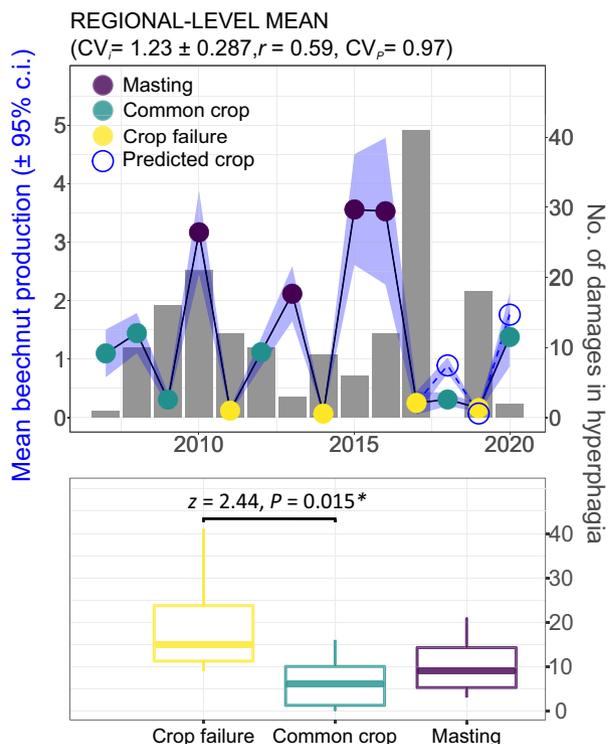


Figure 4. The effect of European beech *Fagus sylvatica* seed production on the occurrence of brown bear *Ursus arctos* damages in the northeastern Carpathians (SE Poland) in 2007–2020. The upper plot shows the regional-level mean beechnut production (blue lines) and the number of confirmed and compensated bear damages during hyperphagia (September–December; gray bars). Masting behavior is measured in terms of mean interannual variability in beechnut production (CV_T) and synchrony (r) at the plot level and interannual variability at the population level (CV_P) (Kelly & Sork, 2002). Boxplots show the distribution of the number of brown bear damages conditional on different categories of beechnut production (see Methods for details). Results from generalized linear models show that the number of damages is significantly higher in years with very low beechnut production (i.e., crop failure) in comparison with years of common crop (see Table 1). Boxplots indicate range, quartiles and median of distributions.

between wildlife and humans. To the best of our knowledge, this is the first study linking human–wildlife conflicts with a combination of data on primary productivity measured from the space and on the ground. Furthermore, we demonstrate that combining weather cues and remote-sensing indicators of vegetation growth and phenology can explain and predict year-to-year variation in beechnut production linked to wildlife damage. This opens up new opportunities to forecast years when conflicts will likely be intense and, thus, to improve conflict management and proactively reduce conflicts.

This study provides important evidence that temporal fluctuations in bear damage occurrence are sensitive to

TABLE 2. Summary of the averaged model coefficients across the set of most parsimonious models relating beechnut production to weather cues and remote-sensing indicators of forest productivity and phenology in the north-eastern Carpathians (SE Poland) in 2009–2020.

Predictor	Estimate	SE	Adj. SE	P-value	AICc ¹
Beechnut production in lag1	−0.255	0.0700	0.0703	0.0003	0.937
Mean maximum summer temperature in lag2	−0.869	0.5098	0.5109	0.0891	0.810
Median summer TC greenness in lag0	−0.235	0.0707	0.0709	0.0009	0.755
Yearly total productivity in lag 1	0.325	0.0897	0.0900	0.0003	0.668
Start day of the senescence phase in lag1	−0.238	0.1473	0.1475	0.1067	0.610
Absolute minimum spring temperature in Lag0	0.045	0.3063	0.3071	0.8828	0.352
Starting day of the growing season in lag0	−0.005	0.0392	0.0393	0.9010	0.336
Length of the senescence phase in lag1	−0.050	0.1167	0.1169	0.6671	0.259

Observations of sampled beechnuts in 2007 and 2008 could not be included in the model because some RS variables were missing due to cloud cover.

¹Relative importance of each predictor included in all candidate models, calculated as the sum of the Akaike weights of all models including the respective variable. A summary of the model selection is presented in the Table S2.

the year-to-year variation of mast pulses in Europe. Mast failure is known to increase the occurrence of conflicts related to bears in the urban-wildlife interface in other parts of the world. For instance, the use of human facilities by grizzly bears *Ursus arctos horribilis* in North America and by Asiatic black bears *Ursus thibetanus* in Japan increases in years when the availability of hard mast is small (Fujiki, 2021; Mattson et al., 1992). However, the previous available literature on the topic for the European brown bear had shown mixed support for this relationship. In Scandinavia, conflicts related to bears using residential areas did not increase in years of berry scarcity, their primary food in hyperphagia (Hertel, Zedrosser, et al., 2018). Similarly, although an overall pattern of increasing damages in years of low food availability was found in Northern Spain, this relationship varied strongly among and even within bear populations (Zarzo-Arias et al., 2020). This can be related to the fact that bears are generalists with a broad diet that can easily adapt to temporal changes in food availability. Although bears can track pulsed resources (Schindler et al., 2013), masting events occur synchronously over hundreds or even thousands of kilometers (Pearse et al., 2021), which may force bears to switch their diet to other food resources in years of crop failure. For example, in temperate ecosystems, they can rely on berries and other fleshy fruits to avoid the nutritional stress induced by annual failures in beechnut production (Ciucci et al., 2014). However, bear diet also includes anthropogenic food such as honey and livestock (Bautista et al., 2017, 2021), and, as proven here, they can cover food shortages consuming them (see also Mori et al., 2021). Accordingly, guaranteeing the availability of alternative natural foods in years of crop failure, for example through berry picking control (García-Rodríguez et al., 2021), can be an effective way to mitigate conflicts.

In spite of bears' diet flexibility (Bojarska & Selva, 2012), hard mast is known to be key food for bears in temperate ecosystems (Ciucci et al., 2014; Naves et al., 2006), with aggregative and reproductive responses to masting reported in some bear populations (Bogdziewicz et al., 2016). For example, reproductive rates in American black bears *Ursus americanus* can increase in years of high mast production (e.g., Costello et al., 2003). Similarly, reproductive rates and body mass in Scandinavian female brown bears increase in years of high abundance of bilberry *Vaccinium myrtillus* (Hertel, Bischof, et al., 2018). That, in turn, can lead to more conflicts in subsequent years related to a larger number of females with cubs and young dispersers seeking shelter and food near humans (Elfström et al., 2014; Obbard et al., 2014). The existence of similar dynamics in our model system could also explain the observed pattern of more damages in years of crop failure, which usually occur after a mast year (see Figure 4). Unfortunately, we lacked reliable demographic data for our study system to explore this further. Understanding the compounding effect of crop failure and animal population increase after masting events on conflict occurrence would be interesting to explore in future studies.

The fact that the occurrence of bear damage to beehives does not solely depend on the availability of beechnuts can be inferred from the variation in the number of damages within each category of beechnut production; for example, from 9 to 41 damages in years of crop failure (see Figure 4). Besides changes in the bear population size over time, other factors that can influence the temporal patterns of damage occurrence are the dispersal of juveniles (Bartoń et al., 2019) or the occurrence of so-called “problem bears” (i.e., individuals that cause repeated damage to apiaries) (Krofel et al., 2020). Also, the annual variation in the production of other food

resources could interfere in the effect of mast failures on damage occurrence. For instance, during years of low beechnut production, high availability of fleshy fruits can act as a buffer and deter bears from raiding apiaries, whereas a high production of honey can possibly attract bears to apiaries and amplify the impact of the mast failure. The presence of these other sources of temporal variation in damage occurrence compromises finding a non-linear, threshold-type response of bear damage occurrence to variation in the beechnut production as shown in Fig. 1 (see also Fig. S3). Yet, categorizing beechnut production in masting, common crop and years of crop failure has helped us to capture a significant effect of mast failures on increased damage occurrence. Similar approaches have been proven useful to, for example, understand how numerical responses to masting by rodents influence their patterns of habitat selection (Zwolak et al., 2016) and interspecific interactions (Selva et al., 2012) or how masting influences wild boar reproductive rates (Bieber & Ruf, 2005).

Although the observed positive relationship between years of mast failure and damage occurrence in our data is relatively small, we argue that this effect is highly relevant. On average, the number of damages in years of crop failure is twice as high as the number of damages in masting years, and this difference can be up to 13 times high (a minimum of 3 damages in a masting year vs. a maximum of 41 in a year of crop failure, see Figure 3). The number of damages in our study area is low in comparison to other bear populations in Europe (Bautista et al., 2017). This is partly due to the low densities of both bears and farms in a rather large and productive forest (Bautista et al., 2015, 2017, 2021). Accordingly, although, the observed effect may not be of extreme relevance for wildlife managers in our study area at present, it can be very relevant in the future due to, for example, an increase in the bear population (Zarzo-Arias et al., 2020), in the amount of natural areas transformed into agriculture fields (Dobrovolski et al., 2011) and/or due to changes in species interaction and productivity in forest ecosystems related to climate change (e.g., Bogdziewicz, Kelly, et al., 2020). Similarly, the effect of masting on bear damage occurrence is likely an important warning for managers working in other areas where the forest productivity is lower and/or the food competition is enhanced by a population at carrying capacity or a second sympatric bear species (see Hertel, Zedrosser, et al., 2018).

The success of conflict prevention programs depends on our ability to forecast when conflicts will be more likely to occur. Our results suggest that in our beechnut-bear model system, predicting crop failure is a pathway to predict when bear damages will increase. We showed that

combining remote-sensing indicators with weather cues, together with a moderately long time series of beechnut production ground data, can successfully predict beechnut crop failure. The most important predictor of beechnut production in our data was the beechnut production in the previous year with a negative effect (see Table 2), which indicates that a crop failure is more likely occurring after a masting year. This finding supports the hypothesis that a large seed crop depletes internal resources and makes a heavy reproduction unlikely in the following year (Pearse et al., 2015). In terms of weather cues, we found that masting occurs years after cold summers, which can prime resource accumulation for floral induction in the following year (Nussbaumer et al., 2018; Piovesan & Adams, 2001). Likewise, crop failures seem to be linked to years when minimum spring temperatures are high, which avoids the environmental veto that catkin frost impose upon reproduction (Bogdziewicz et al., 2019). Regarding the remote-sensing predictors used, we showed that beechnut production increases 1 year after a high yearly forest productivity, and low summer forest productivity in the masting year. High forest productivity 1 year before masting supports the hypothesis that resources for reproduction are accumulated in the years preceding masting events (resource budget model, see Abe et al., 2016), which furthermore could explain that a cold summer 2 years before masting primes trees to accumulate resources.

Additionally, these findings also converge well with the resource switching hypothesis, which predicts that a variable fraction of current-year resource acquisition is allocated to seed production (Bogdziewicz, Ascoli, et al., 2020; Kelly & Sork, 2002). Accordingly, the high forest productivity 1 year before masting could also be related to a higher vegetative growth before reproduction. Furthermore, a low summer productivity can be connected to a smaller leaf area index in beech during masting years, which indicates a resource allocation shift from leaf to fruit production in masting years (Müller-Haubold et al., 2015). Altogether, that gives strength to the idea that both plant growth and reproduction exploit the same plant resources, which are mostly allocated to one of them in a given year (Bajocco et al., 2021; Vergotti et al., 2019). Thus, our models have plausible results that resonate well with ecological theory, building trust in using our methodology as a monitoring and forecasting tool.

Because masting depends on resources accumulated through photosynthesis, it seems reasonable to use remote-sensing indicators of vegetation growth to gain a better mechanistic understanding of the causes of masting events. Indeed, our results suggest that combining remote sensing indicators with weather cues can adequately

capture internal plant dynamics of resource acquisition and allocation driving masting. Furthermore, our results corroborate that remote-sensing indicators can be among the best predictors of mast seeding (Bajocco et al., 2021; Fernández-Martínez et al., 2015; García et al., 2021; Vergotti et al., 2019) and that, combined with other correlates, can adequately explain and predict seed production (see Figure 4). Because wild animals can switch their diet to anthropogenic food resources in years of crop failure, our approach can be a really useful tool for responsible agencies to forecast when conflicts are more likely to escalate, and, accordingly optimize efforts to prevent and mitigate conflicts in a proactive manner. Yet, in the present study we used a moderately long time-series, which could have potentially compromised the proper modeling and forecasting of masting events. In that sense, long-term field data can help to increase the forecasting ability and to deepen our understanding of ecological dynamics governed by resource pulses (Bjørnstad & Grenfell, 2001). Such long-term datasets can be especially suitable to anticipate the possible ways in which climate change can alter masting events and eventually influence community and ecosystem dynamics (Bogdziewicz, Kelly, et al., 2020).

Global change is already altering masting events, with warming temperatures enhancing seed predation rates and, thus, compromising plant recruitment in the long term (Bogdziewicz, 2021; Bogdziewicz, Kelly, et al., 2020; Hacket-Pain & Bogdziewicz, 2021). Because masting has bottom-up effects on trophic interactions, followed by cascading effects throughout the trophic web, altered masting behavior will have profound impacts on forest ecosystem dynamics (Hacket-Pain & Bogdziewicz, 2021). Accordingly, gaining a better understanding of the mechanisms driving masting and improving our predictions on how masting will respond to climate change is important for the management of natural resources and biodiversity conservation (Hacket-Pain & Bogdziewicz, 2021; Pearse et al., 2021). Finally, we highlight the need to further assess how resource pulses, such as masting, shape trophic interactions and through this the occurrence of human–wildlife conflicts. For instance, warming temperatures are predicted to reduce seed production variability and increase masting frequency (Bogdziewicz, Kelly, et al., 2020; Touzot et al., 2020). A more constant and higher supply of seeds can increase the reproductive success and, thus, the population of seeds consumers, such as bears and wild boars (Bieber & Ruf, 2005; Costello et al., 2003; Touzot et al., 2020). Under that scenario, could an overabundant population of seed consumers potentially increase the use of anthropogenic food resources in the short-term through enhanced competition for natural food resources? May an increased predation pressure on seeds compromise seed recruitment and

regeneration in forest ecosystems in the long term and eventually force the community of consumers to shift their diet toward anthropogenic foods? Conflicts are already growing in different parts of the world due to the increasing transformation of natural habitats (Dobrovolski et al., 2011; Ripple et al., 2014, 2015) and the parallel recovery and expansion of wildlife populations in some human-dominated landscapes (Chapron et al., 2014). A better understanding of how altered interactions in food webs can dampen or intensify conflict occurrence in the landscape undoubtedly would provide a pathways to proactive damage prevention, and thus to foster coexistence of wildlife and people.

Acknowledgments

This study was funded by the National Science Centre in Poland under agreement nos. UMO-2020/36/T/NZ8/00571 and UMO-2017/25/N/NZ8/02861. We thank the Regional Direction of Environmental Protection in Rzeszow, Teresa Berezowska-Cnota, Robert Gatzka, Marta Josa, Gabriel Pérez, and all the volunteers from the Carpathian Brown Bear Project for helping in data collection. We thank two anonymous reviewers and editor Abdulhakim Abdi for very helpful and encouraging remarks. Open Access funding enabled and organized by Projekt DEAL. WOA Institution: HUMBOLDT-UNIVERSITÄT ZU BERLIN Consortia Name : Projekt DEAL

REFERENCES

- Abe, T., Tachiki, Y., Kon, H., Nagasaka, A., Onodera, K., Minamino, K. et al. (2016) Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. *Ecology Letters*, **16**, 1129–1139. <https://doi.org/10.1111/ele.12651>
- Bajocco, S., Ferrara, C., Bascietto, M., Alivernini, A., Chirichella, R. & Cutini, A. (2021) Characterizing the climatic niche of mast seeding in beech: evidences of trade-offs between vegetation growth and seed production. *Ecological Indicators*, **121**, 107139. <https://doi.org/10.1016/j.ecolind.2020.107139>
- Barton, K. (2014) *MuMIn: multi-model inference*. <https://r-forge.r-project.org/projects/mumin/>
- Bartoń, K., Zwijacz-kożica, T., Zięba, F., Sergiel, A. & Selva, N. (2019) Bears without borders: long-distance movement in human-dominated landscapes. *Global Ecology and Conservation*, **17**, e00541. <https://doi.org/10.1016/j.gecco.2019.e00541>
- Bautista, C., Naves, J., Revilla, E., Fernández, N., Albrecht, J., Scharf, A.K. et al. (2017) Patterns and correlates of claims for brown bear damage on a continental scale. *Journal of Applied Ecology*, **54**, 282–292. <https://doi.org/10.1111/1365-2664.12708>

- Bautista, C., Olszańska, A., Berezowska-Cnota, T., Fedyń, H., Jastrzębski, T., Nowakowski, R. et al. (2015) Compensations for brown bear damages in the Podkarpackie Voivodeship in 1999–2014. *Chrońmy Przyrodę Ojczystą*, **71**, 442–453.
- Bautista, C., Revilla, E., Berezowska-cnota, T., Fernández, N., Naves, J. & Selva, N. (2021) Spatial ecology of conflicts: unravelling patterns of wildlife damage at multiple scales. *Proceedings of the Royal Society B*, **288**, 20211394. <https://doi.org/10.1098/rspb.2021.1394>
- Bautista, C., Revilla, E., Naves, J., Albrecht, J., Fernández, N., Olszańska, A. et al. (2019) Large carnivore damage in Europe: analysis of compensation and prevention programs. *Biological Conservation*, **235**, 308–316. <https://doi.org/10.1016/j.biocon.2019.04.019>
- Bieber, C. & Ruf, T. (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications. *Journal of Applied Ecology*, **42**, 1203–1213. <https://doi.org/10.1111/j.1365-2664.2005.01094.x>
- Bisi, F., Chirichella, R., Chianucci, F., Von Hardenberg, J., Cutini, A., Martinoli, A. et al. (2018) Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study. *Annals of Forest Science*, **75**, 1–9. <https://doi.org/10.1007/s13595-018-0726-6>
- Bjørnstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–644.
- Bogdziewicz, M. (2021) How will global change affect plant reproduction? A framework for mast seeding trends. *New Phytologist*, **1–7**, 14–20. <https://doi.org/10.1111/nph.17682>
- Bogdziewicz, M., Ascoli, D., Hackett-Pain, A., Koenig, W.D., Pearse, I.S., Pesendorfer, M. et al. (2020) From theory to experiments for testing the proximate mechanisms of mast seeding: an agenda for an experimental ecology. *Ecology Letters*, **23**, 210–220. <https://doi.org/10.1111/ele.13442>
- Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hackett-pain, A. (2020) Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants*, **6**, 88–94. <https://doi.org/10.1038/s41477-020-0592-8>
- Bogdziewicz, M., Zwolak, R. & Crone, E.E. (2016) How do vertebrates respond to mast seeding? *Oikos*, **125**, 300–307. <https://doi.org/10.1111/oik.03012>
- Bogdziewicz, M., Żywiec, M., Espelta, J.M., Fernández-Martinez, M., Calama, R., Ledwoń, M. et al. (2019) Environmental veto synchronizes mast seeding in four contrasting tree species. *American Naturalist*, **194**, 246–259. <https://doi.org/10.1086/704111>
- Bojarska, K. (2014) *Trophic ecology of the brown bear: from biogeographical to individual point of view*. PhD thesis. Kraków, Poland: Jagellonian University, p. 97.
- Bojarska, K. & Selva, N. (2012) Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Review*, **42**, 120–143. <https://doi.org/10.1111/j.1365-2907.2011.00192.x>
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, **9**, 378–400.
- Camarero, J.J., Albuixech, J., López-Lozano, R., Casterad, M.A. & Montserrat-Martí, G. (2010) An increase in canopy cover leads to masting in *Quercus ilex*. *Trees*, **24**, 909–918. <https://doi.org/10.1007/s00468-010-0462-5>
- Can, Ö.E., D’Cruze, N., Garshelis, D.L., Beecham, J. & Macdonald, D.W. (2014) Resolving human-bear conflict: a global survey of countries, experts, and key factors. *Conservation Letters*, **7**, 501–513. <https://doi.org/10.1111/conl.12117>
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H. et al. (2014) Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science*, **346**, 1517–1519. <https://doi.org/10.1126/science.1257553>
- Ciucci, P., Artoni, L., Crispino, F., Tosoni, E. & Boitani, L. (2018) Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. *European Journal of Wildlife Research*, **64**, 5.
- Ciucci, P., Tosoni, E., Di Domenico, G., Quattrociochi, F. & Boitani, L. (2014) Seasonal and annual variation in the food habits of Apennine brown bears, Central Italy. *Journal of Mammalogy*, **95**, 572–586. <https://doi.org/10.1644/13-MAMM-A-218>
- Costello, C.M., Jones, D.E., Inman, R.M., Inman, K.H., Thompson, B.C. & Quigley, H.B. (2003) Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus*, **14**, 1–16. <https://doi.org/10.2307/3872951>
- Crist, E.P. & Cicone, R.C. (1984) A physically-based transformation of thematic mapper data—the TM tasseled cap. *IEEE Transactions on Geoscience and Remote Sensing*, **22**, 256–263.
- Despland, E., Rosenberg, J. & Simpson, S.J. (2004) Landscape structure and locust swarming: a satellite’s eye view. *Ecography*, **27**, 381–391. <https://doi.org/10.1111/j.0906-7590.2004.03779.x>
- Dobrovolski, R., Diniz-Filho, J.A.F., Loyola, R.D. & Júnior, P.D.M. (2011) Agricultural expansion and the fate of global conservation priorities. *Biodiversity and Conservation*, **20**, 2445–2459. <https://doi.org/10.1007/s10531-011-9997-z>
- Elfström, M., Zedrosser, A., Støen, O.-G. & Swenson, J.E. (2014) Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review*, **44**, 5–18. <https://doi.org/10.1111/j.1365-2907.2012.00223.x>
- Fernández-Martínez, M., Garbulsky, M., Peñuelas, J., Peguero, G. & Espelta, J.M. (2015) Temporal trends in the enhanced vegetation index and spring weather predict seed production in Mediterranean oaks. *Plant Ecology*, **216**, 1061–1072. <https://doi.org/10.1007/s11258-015-0489-1>

- Fujiki, D. (2021) A model to predict the occurrence of Asiatic black bears at the municipal level using mast production data. *Ursus*, **32e6**, 1–11. <https://doi.org/10.2192/URSUS-D-19-0008.1>
- Garbulsky, M.F., Peñuelas, J., Ogaya, R. & Filella, I. (2013) Leaf and stand-level carbon uptake of a Mediterranean forest estimated using the satellite-derived reflectance indices EVI and PRI. *International Journal of Remote Sensing*, **34**, 37–41.
- Garcia, M., Zuckerberg, B., Lamontagne, J.M. & Townsend, P.A. (2021) Landsat-based detection of mast events in white spruce (*Picea glauca*) forests. *Remote Sensing of Environment*, **254**, 112278. <https://doi.org/10.1016/j.rse.2020.112278>
- García-Rodríguez, A., Selva, N., Zwijacz-Kozica, T., Albrecht, J., Lionnet, C., Rioux, D. et al. (2021) The bear-berry connection: ecological and management implications of brown bears' food habits in a highly touristic protected area. *Biological Conservation*, **264**, 109376. <https://doi.org/10.1016/j.biocon.2021.109376>
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017) Remote sensing of environment Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, **202**, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>
- Griffith, B., Douglas, D.C., Walsh, N.E., Young, D.D., McCabe, T.R., Russell, D.E., et al. (2002) *The porcupine caribou herd, arctic refuge coastal plain terrestrial wildlife research summaries*.
- Hacket-Pain, A. & Bogdziewicz, M. (2021) Climate change and plant reproduction: trends and drivers of mast seeding change. *Philosophical Transactions of the Royal Society B*, **376** (1839), 20200379.
- Hertel, A.G., Bischof, R., Langval, O., Myrsterud, A., Kindberg, J., Swenson, J.E. et al. (2018) Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos*, **127**, 197–207. <https://doi.org/10.1111/oik.04515>
- Hertel, A.G., Zedrosser, A., Kindberg, J., Langvall, O. & Swenson, J.E. (2018) Fluctuating mast production does not drive Scandinavian brown bear behavior. *The Journal of Wildlife Management*, **83**, 657–668. <https://doi.org/10.1002/jwmg.21619>
- Hilton, G.M. & Packham, J.R. (2003) Variation in the masting of common beech (*Fagus sylvatica* L.) in northern Europe over two centuries (1800–2001). *Forestry*, **76**, 319–328. <https://doi.org/10.1093/forestry/76.3.319>
- Hoch, G., Siegwolf, R.T.W., Keel, S.G., Körner, C. & Han, Q. (2013) Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia*, **171**, 653–662. <https://doi.org/10.1007/s00442-012-2579-2>
- Ichie, T., Igarashi, S., Yoshida, S., Kenzo, T., Masaki, T. & Tayasu, I. (2013) Are stored carbohydrates necessary for seed production in temperate deciduous trees? *Journal of Ecology*, **101**, 525–531. <https://doi.org/10.1111/1365-2745.12038>
- Jedrzejewska, B. & Jedrzejewski, W. (1998) *Predation in Vertebrate Communities. The Białowieża Primeval Forest as a case study, Ecological Studies*. Białowieża, Poland: Springer Science & Business Media.
- Jedrzejewski, W., Apollonio, M., Jedrzejewski, B. & Kojola, I. (2011) Ungulate – large carnivore relationships in Europe. In: Putman, R., Apollonio, M. & Andersen, R. (Eds.) *Ungulate management in Europe: problems and practices*. Cambridge: Cambridge University Press, pp. 284–318. <https://doi.org/10.1017/CBO9780511974137>
- Kelly, D., Koenig, W.D. & Liebhold, A.M. (2008) An intercontinental comparison of the dynamic behavior of mast seeding communities. *Population Ecology*, **50**, 329–342. <https://doi.org/10.1007/s10144-008-0114-4>
- Kelly, D. & Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**, 427–447. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095433>
- Kiffner, C. & Lee, D.E. (2019) Population dynamics of browsing and grazing ungulates in the Anthropocene. In: Gordon, I.J. & Prins, H.H.T. (Eds.) *The ecology of browsing and grazing II*. Cham: Springer International Publishing, pp. 155–179. https://doi.org/10.1007/978-3-030-25865-8_6
- Kong, D. (2020) eco-hydro/phenofit: phenofit v0.3.1. Zenodo <https://doi.org/10.5281/zenodo.5150204>
- Krofel, M., Elfström, M., Ambarlı, H., Bombieri, G., González-Bernardo, E., Jerina, K. et al. (2020) Human–bear conflicts at the beginning of the twenty-first century: patterns, determinants, and mitigation measures. In: Penteriani, V. & Melletti, M. (Eds.) *Bears of the world: ecology*. Cambridge: Conservation and Management. Cambridge University Press, pp. 213–226. <https://doi.org/10.1017/9781108692571.016>
- Kuemmerle, T., Baskin, L., Leitão, P.J., Prishchepov, A.V., Thonicke, K. & Radeloff, V.C. (2014) Potential impacts of oil and gas development and climate change on migratory reindeer calving grounds across the Russian Arctic. *Diversity and Distributions*, **20**, 416–429. <https://doi.org/10.1111/ddi.12167>
- Loe, L.E., Bonenfant, C., Myrsterud, A., Gaillard, J.-M., Langvant, R., Klein, F. et al. (2005) Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and. *Journal of Animal Ecology*, **74**, 579–588. <https://doi.org/10.1111/j.1365-2656.2005.00987.x>
- Mattson, D.J., Blanchard, B.M. & Knight, R.R. (1992) Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management*, **56**, 432–442. <https://doi.org/10.2307/3808855>
- McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, **81**, 228–238. <https://doi.org/10.2307/177146>

- Melaas, E.K., Friedl, M.A. & Zhu, Z. (2013) Detecting interannual variation in deciduous broadleaf forest phenology using Landsat TM/ETM + data. *Remote Sensing of Environment*, **132**, 176–185. <https://doi.org/10.1016/j.rse.2013.01.011>
- Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. (1996) The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography*, **19**, 287–295.
- Mori, T., Sugiura, R., Kato, M., Miura, K., Ogawa, H., Umamo, S. et al. (2021) Relationship between diet and occurrence around human settlements in Asiatic black bears. *Ursus*, **32e11**, 1–10. <https://doi.org/10.2192/URSUS-D-19-00024.2>
- Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G. & Leimgruber, P. (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, **45**, 649–658. <https://doi.org/10.1111/j.1365-2664.2007.01371.x>
- Müller-Haubold, H., Hertel, D. & Leuschner, C. (2015) Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. *Ecosystems*, **18**, 1083–1100. <https://doi.org/10.1007/s10021-015-9885-6>
- Naves, J., Fernández-Gil, A., Rodríguez, C. & Delibes, M. (2006) Brown bear food habits at the border of its range: a long-term study. *Journal of Mammalogy*, **87**, 899–908. <https://doi.org/10.1644/05-MAMM-A-318R2.1>
- Neilson, R.P. & Wullstein, L.H. (1980) Catkin freezing and acorn production in gambel oak in Utah, 1978. *Botanical Society of America*, **67**, 426–428.
- Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. et al. (2015) The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, **24**, 1–11. <https://doi.org/10.1111/geb.12236>
- Niedziałkowska, M., Hayward, M.W., Borowik, T., Jędrzejewski, W. & Jędrzejewska, B. (2019) A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in Eurasia. *Mammal Research*, **64**, 1–9. <https://doi.org/10.1007/s13364-018-0396-7>
- Nussbaumer, A., Waldner, P., Apuhtin, V., Aytar, F., Benham, S., Bussotti, F. et al. (2018) Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *Forest Ecology and Management*, **429**, 336–350. <https://doi.org/10.1016/j.foreco.2018.07.011>
- Obbard, M.E., Howe, E.J., Wall, L.L., Allison, B., Black, R., Davis, P. et al. (2014) Relationships among food availability, harvest, and human–bear conflict at landscape scales in Ontario, Canada. *Ursus*, **25**, 98–110. <https://doi.org/10.2192/URSUS-D-13-00018.1>
- Oeser, J., Heurich, M., Senf, C., Pflugmacher, D., Belotti, E. & Kuemmerle, T. (2019) Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat. *Remote Sensing in Ecology and Conservation*, **1**–18, 52–69. <https://doi.org/10.1002/rse2.122>
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.
- Packham, J.R., Thomas, P.A., Lagueard, J.G.A. & Hilton, G.M. (2008) The English beech masting survey 1980 – 2007: variation in the fruiting of the common beech (*Fagus sylvatica* L.) and its effects on woodland ecosystems. *Arboricultural Journal*, **31**, 189–214. <https://doi.org/10.1080/03071375.2008.9747535>
- Pearse, I.S., Koenig, W.D. & Kelly, D. (2015) Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, **212**, 546–562.
- Pearse, I.S., Wion, A.P., Gonzalez, A.D. & Pesendorfer, M.B. (2021) Understanding mast seeding for conservation and land management. *Philosophical Transactions of the Royal Society B*, **376**, 20200383.
- Pesendorfer, M.B., Ascoli, D., Bogdziewicz, M., Hackett-pain, A., Pearse, I.S., Vacchiano, G. et al. (2021) The ecology and evolution of synchronized reproduction in long-lived plants. *Philosophical Transactions of the Royal Society B*, **376**, 20200369.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. et al. (2011) The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Climate Research*, **46**, 15–27. <https://doi.org/10.3354/cr00936>
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, **20**, 503–510. <https://doi.org/10.1016/j.tree.2005.05.011>
- Pettorelli, N., Weladji, R.B., Holand, Ø., Mysterud, A., Breie, H. & Stenseth, N.C. (2005) The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biology Letters*, **1**, 24–26. <https://doi.org/10.1098/rsbl.2004.0262>
- Piovesan, G. & Adams, J.M. (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*, **1047**, 1039–1047. <https://doi.org/10.1139/cjb-79-9-1039>
- R Core Team. (2020) *R: a language and environment for statistical computing*.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M. et al. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484. <https://doi.org/10.1126/science.1241484>
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M. et al. (2015) Collapse of the world's largest herbivores. *Science Advances*, **1**, e1400103. <https://doi.org/10.1126/sciadv.1400103>
- Salvador, A. & Abad, P.L. (1987) Food habits of a wolf population (*Canis lupus*) in León province, Spain. *Mammalia*, **51**, 45–52. <https://doi.org/10.1515/mamm.1987.51.1.45>

- Schindler, D.E., Armstrong, J.B., Bentley, K.T., Jankowski, K., Lisi, P.J. & Payne, L.X. (2013) Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, **9**, 20130048. <https://doi.org/10.1098/rsbl.2013.0048>
- Schley, L. & Roper, T.J. (2003) Diet of wild boar *sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, **33**, 43–56. <https://doi.org/10.1046/j.1365-2907.2003.00010.x>
- Selva, N., Hobson, K.A., Cortés-Avizanda, A., Zalewski, A. & Donazar, J.A. (2012) Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. *PLoS One*, **7**, 3–8. <https://doi.org/10.1371/journal.pone.0051267>
- Senf, C., Dirk, P., Heurich, M. & Krueger, T. (2017) Remote sensing of environment a Bayesian hierarchical model for estimating spatial and temporal variation in vegetation phenology from Landsat time series. *Remote Sensing of Environment*, **194**, 155–160. <https://doi.org/10.1016/j.rse.2017.03.020>
- Touzot, L., Schermer, E., Venner, S., Delzon, S., Rousset, C., Baubet, E. et al. (2020) How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. *Ecological Applications*, **30**, 1–11. <https://doi.org/10.1002/eap.2134>
- Vergotti, M.J., Fernández-Martínez, M., Kefauver, S.C., Janssens, I.A. & Peñuelas, J. (2019) Weather and trade-offs between growth and reproduction regulate fruit production in European forests. *Agricultural and Forest Meteorology*, **279**, 107711. <https://doi.org/10.1016/j.agrformet.2019.107711>
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.
- Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008) What can we learn from resource pulses? *Ecology*, **89**, 621–634. <https://doi.org/10.1890/07-0175.1>
- Zarzo-Arias, A., Delgado, M.M., Palazón, S., Afonso Jordana, I., Bombieri, G., González-Bernardo, E. et al. (2020) Seasonality, local resources and environmental factors influence patterns of brown bear damages: implications for management. *Journal of Zoology*, **313**, 1–17. <https://doi.org/10.1111/jzo.12839>
- Zwolak, R., Bogdziewicz, M., Wróbel, A. & Crone, E.E. (2016) Advantages of masting in European beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, **180**, 749–758. <https://doi.org/10.1007/s00442-015-3511-3>
- Zwolak, R., Celebias, P. & Bogdziewicz, M. (2022) Global patterns in the predator satiation effect of masting: a meta-analysis. *Proceedings of the National Academy of Sciences*, **119**, e2105655119. <https://doi.org/10.1073/pnas.2105655119>

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary statistics on beech seed production in the northeastern Carpathians (SE Poland) obtained in 30–1 m² sample plots in different sampling sessions in 2007–2020.

Table S2. Description of the predictors used to analyze the temporal trend in beechnut production in the Northeastern Carpathians (SE Poland) in 2007–2020.

Table S3. Summary of generalized linear mixed models analyzing beech productivity as a response to meteorological variables and satellite-based measures of forest productivity and phenology in northeastern Carpathians (SE Poland) in 2007–2020.

Table S4. List of the most parsimonious models included in the set of linear mixed-effects models to analyze the impact of weather cues and remotely sensed forest productivity and phenology on the production of beechnuts in the northeastern Carpathians (SE Poland) in 2009–2020.

Figure S1. Observed temporal trend in European beech *Fagus sylvatica* seed production in 30 sampling plots in the northeastern Carpathians (SE Poland) in 2007–2020.

Figure S2. Linear relationship between the observed and predicted beechnut production in the northeastern Carpathians (SE Poland) in 2018–2020.

Figure S3. Relationship between the number of bear damages and the beechnut production in the northeastern Carpathians (SE Poland) in 2007–2020.