Natural and anthropogenic drivers of brown bear damage occurrence

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Naturalne i antropogeniczne czynniki wpływające na występowanie szkód powodowanych przez niedźwiedzie brunatne

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ENGLISH SUMMARY

The conflicts arising from wildlife damage to human property are a main challenge for biodiversity conservation worldwide. Damages can result in substantial economic and emotional losses to people, which can trigger persecution and retaliatory killing of wild animals, and ultimately threat their conservation. A cost-effective way to reduce the impact of this conflict is to predict when and where are damages more likely to occur to inform damage preventive programmes.

The occurrence of wildlife damage varies widely across space and time. Although many studies link this variability mostly to how damages are managed, evidence shows that damages also vary spatially and temporally under the same management conditions. To what extent do natural and anthropogenic factors drive the observed variability in damage occurrence remains still unresolved in the literature. Holistic approaches that integrate socioeconomic and management factors with the ecological mechanisms underlying the occurrence of wildlife damage at different scales are needed to answer these questions, but rarely followed (see general introduction in Chapter I).

The main objective of this dissertation is to improve the understanding of the factors that drive the occurrence of wildlife damage in different socio-ecological systems. By taking the brown bear (*Ursus arctos*) as a model species, I aim at disentangling the natural and anthropogenic factors associated with damage occurrence based on spatial-temporal analysis at different scales, and analyzing damage data from different habitats, populations and management scenarios.

In a first study (Chapter II), I evaluated current programs to compensate and prevent large carnivore damage in 27 European countries as well as the economic factors related to the costs of these programs. I found large differences in the compensation costs among countries and species. Overall, high compensation costs are associated with free-ranging livestock (68% of the total costs) and with national economic wealth. Contrary to the general belief, the return of large carnivores does not always translate into higher compensation costs. This lack of pattern is related to the type of compensation program, to the abundance of livestock and the type of husbandry practices present in the places that large carnivores have recolonized. Half of the studied countries do not invest in prevention programs and just a few wealthy countries pay the majority of the money allocated for prevention programs in Europe. Certain subsidized preventive measures seem ineffective to prevent damage. I discuss that programs mainly focused on paying large amounts for compensation, not conditioned to the use of effective preventive measures may fail to build tolerance towards large carnivores.

In a second study (Chapter III) I used 406 records of brown bear damage to apiaries occurring in 2010-2017 in the North-eastern Carpathians (SE Poland) to model the risk of bear predation on beehives. I used generalized additive models at three nested spatial scales to analyze the factors related to the occurrence of bear damage to beehives I found that the habitat preferences of bears and beekeepers together with bear's tendency to avoid humans determine the risk of bear damage at multiple scales. Damage risk at fine scales increased when the broad landscape context also favored damage occurrence. The results from this study suggest that principles of resource selection by animals can be used to understand the occurrence of damage and help mitigate conflicts in a proactive and preventive manner.

Finally, in a third study (Chapter IV) I used a novel combination of remote sensing indicators of forest productivity and phenology and weather cues to predict tree masting and, ultimately, conflicts related to food shortages. To that end, I used a 14-years-long dataset on the production of European beech (*Fagus sylvatica*) seeds (beechnuts) and brown bear damage in the North-eastern Carpathians. Beech masting events were best predicted by a combination from on-the-ground measures of beechnut production and meteorological variables with remotely-sensed indicators of forest productivity and phenology, which, in turn, can predict years of high intensity of human-bear conflicts. These years of increased bear damage are associated with beech crop failure.

The present dissertation provides new insights into the ecological processes and management actions underlying bear damage occurrence. It represents an important contribution to human-wildlife conflict research, both from theoretical and applied perspectives. Furthermore, it contributes with a novel application of vegetation indices to model and predict crop failure in masting plants related to an increased occurrence of bear damage. The use of freely available satellite data in predicting drivers of bear damage can become a breakthrough in conflict management as it has the potential to reduce damage and optimize the costs-effectiveness of management actions.

STRESZCZENIE – POLISH SUMMARY

Konflikty wynikające ze szkód w mieniu ludzkim wyrządzanych przez dzikie zwierzęta stanowią główne wyzwanie dla ochrony różnorodności biologicznej na całym świecie. Szkody mogą powodować znaczne straty ekonomiczne i emocjonalne u ludzi, co może wywołać prześladowania i odwetowe zabijanie dzikich zwierząt, a w efekcie zagrozić ich ochronie. Efektywnym pod względem kosztów sposobem ograniczenia wpływu tego konfliktu jest przewidywanie, kiedy i gdzie prawdopodobieństwo wystąpienia szkód jest największe, co pozwoli na opracowanie programów zapobiegania szkodom.

Występowanie szkód wyrządzanych przez dzikie zwierzęta jest silnie zróżnicowane w czasie i przestrzeni. Chociaż wiele badań wiąże tę zmienność głównie ze sposobem zarządzania szkodami, dowody wskazują, że występowanie szkód jest zróżnicowane przestrzennie i czasowo również gdy sposoby zarządzania nimi są takie same. W literaturze nadal nie rozstrzygnięto, w jakim stopniu czynniki naturalne i antropogeniczne wpływają na obserwowaną zmienność w zakresie występowania szkód. Podejścia holistyczne, które uwzględniają zarówno czynniki społeczno-ekonomiczne i sposoby zarządzania, jak i mechanizmy ekologiczne leżące u podstaw występowania szkód wyrządzanych przez dzikie zwierzęta w różnych skalach są niezbędne by odpowiedzieć na te pytania, ale rzadko stosowane (zob. ogólne wprowadzenie w rozdziale I).

Głównym celem tej dysertacji jest próba lepszego zrozumienia czynników, które wpływają na występowanie szkód wyrządzanych przez dzikie zwierzęta w różnych systemach społeczno-ekologicznych. Przyjmując niedźwiedzia brunatnego (*Ursus arctos*) jako gatunek modelowy, staram się rozdzielić naturalne i antropogeniczne czynniki związane z występowaniem szkód w oparciu o analizę przestrzenno-czasową w różnych skalach i analizując dane dotyczące szkód w różnych siedliskach, populacjach i systemach zarządzania.

W pierwszym badaniu (rozdział II) oceniłem aktualne programy kompensacji i zapobiegania szkodom powodowanym przez duże drapieżniki w 27 krajach europejskich, a także Czynniki ekonomiczne związane z kosztami tych programów. Stwierdziłem duże różnice w kosztach kompensacji pomiędzy krajami i gatunkami. Ogólnie ujmując, wysokie koszty odszkodowań są związane ze zwierzętami gospodarskimi żyjącymi na wolności (68% całkowitych kosztów) oraz z sytuacją ekonomiczną danego kraju. Wbrew powszechnemu przekonaniu, powrót dużych drapieżników nie zawsze przekłada się na wyższe koszty odszkodowań. Brak takiej zależności związany jest z rodzajem obowiązującego programu kompensacyjnego, liczebnością zwierząt gospodarskich i rodzajem praktyk hodowlanych stosowanych w miejscach ponownego

skolonizowania przez duże drapieżniki. Połowa badanych krajów nie inwestuje w programy prewencyjne, a większość pieniędzy przeznaczanych na programy prewencyjne w Europie przypada na zaledwie kilka bogatych krajów. Niektóre dotowane działania prewencyjne wydają się nieskuteczne w zapobieganiu szkodom. Wskazuję, że programy skoncentrowane głównie na wypłacaniu dużych kwot odszkodowań, nie uwarunkowane stosowaniem skutecznych środków zapobiegawczych, nie budują tolerancji wobec dużych drapieżników.

W drugim badaniu (rozdział III) wykorzystałem 406 odnotowanych przypadków szkód wyrządzonych w pasiekach przez niedźwiedzia brunatnego, które miały miejsce w latach 2010-2017 w północno-wschodnich Karpatach (SE Polska) do modelowania ryzyka drapieżnictwa niedźwiedzi na ulach. Do analizy czynników związanych z występowaniem uszkodzeń uli przez niedźwiedzie wykorzystałem uogólnione modele addytywne w trzech zagnieżdżonych skalach przestrzennych. Stwierdziłem, że tendencja niedźwiedzia brunatnego do unikania ludzi oraz preferencje siedliskowe niedźwiedzi i pszczelarzy determinują ryzyko wystąpienia szkód powodowanych przez niedźwiedzie w różnych skalach. Ryzyko wystąpienia szkód w małych skalach wzrastało, gdy szeroki kontekst krajobrazowy również sprzyjał występowaniu szkód. Wyniki tego badania sugerują, że zasady wyboru zasobów przez zwierzęta mogą być wykorzystane do zrozumienia występowania szkód i pomóc w łagodzeniu konfliktów w sposób proaktywny i prewencyjny.

W trzecim badaniu (rozdział IV) wykorzystałem nowatorską kombinację teledetekcyjnych wskaźników produktywności i fenologii lasu oraz danych pogodowych do przewidywania produktywności drzew, a w konsekwencji konfliktów związanych z niedoborem pokarmu. W tym celu wykorzystałem 14-letni zbiór danych dotyczących produkcji nasion buka zwyczajnego (*Fagus sylvatica*), czyli bukwi i szkód wyrządzanych przez niedźwiedzia brunatnego w północno-wschodnich Karpatach. Zdarzenia związane z wyrządzaniem szkód przez niedźwiedzie były najlepiej przewidywane dzięki połączeniu naziemnych pomiarów produktywności buka i zmiennych meteorologicznych ze zdalnie monitorowanymi wskaźnikami produktywności fenologii lasu, co pozwala przewidzieć lata o wzmożonej intensywności konfliktów na linii człowiek-niedźwiedź. Lata charakteryzujące się większą liczbą szkód wyrządzanych przez niedźwiedzie związane są z latami o niskiej produkcji bukwi.

Niniejsza rozprawa doktorska dostarcza nowego spojrzenia na procesy ekologiczne i działania związane z zarządzaniem środowiskiem leżące u podstaw występowania szkód wyrządzanych przez niedźwiedzie. Stanowi ona ważny wkład w badania nad konfliktami na linii człowiek-dzikie zwierzęta, zarówno z perspektywy teoretycznej, jak i praktycznej. Ponadto, wnosi nowatorskie zastosowanie indeksów wegetacyjnych do modelowania i przewidywania lat nienasiennych, związanych ze zwiększonym występowaniem szkód wyrządzanych przez niedźwiedzie. Wykorzystanie ogólnodostępnych danych satelitarnych w przewidywaniu czynników powodujących szkody wyrządzane przez niedźwiedzie może stać się przełomem w zarządzaniu konfliktami ze względu na potencjał do redukcji szkód i zoptymalizowanie opłacalności systemów zarządzania.

CHAPTER I
INTRODUCTION

Everything is a matter of perspective:

“The tiger, the lion and the panther are harmless animals. Instead, chickens, geese and ducks, they are highly dangerous animals, a worm said to his children.”

Bertrand Russell (1872-1970)

1. GENERAL INTRODUCTION

The conflicts arising from wildlife damage are a complex ecological issue shaped by multiple factors acting at different scales and interlinked with management policies and socioeconomic factors (Redpath et al., 2015a). These conflicts (hereafter human-wildlife conflicts) are becoming more frequent, serious and widespread at the global scale (Ripple et al., 2016, 2014; Wolf and Ripple, 2016) and represent an increasing challenge for wildlife conservation worldwide (Frank et al., 2019; Redpath et al., 2015b; Woodroffe et al., 2005).

The occurrence of wildlife damage varies widely across space and time (Boitani et al., 2010; Kaczensky et al., 2012; Newsome et al., 2016; Petra Kaczensky, 1999; Swenson and Andrén, 2005). Although a number of studies link this variability mostly to how damages are managed (e.g., Petra Kaczensky, 1999; Swenson and Andrén, 2005), evidence shows that damages also vary spatially and temporally under the same management conditions (Artelle et al., 2016; Bautista et al., 2017, 2015; Hoare, 1999; Johnson et al., 2015). To what extent the observed variation in damage occurrence is driven by natural or anthropogenic factors, remains an unresolved question. However, to design management policies that tackle the root causes of conflicts, we need to understand the underlying ecological mechanisms driving wildlife damage under different management situations and at multiple spatial and temporal scales.

The main objective of this thesis is to improve our understanding of the factors that drive damage occurrence by wildlife in different socio-ecological scenarios. By taking the brown bear (*Ursus arctos*) as a model species, I aim at disentangling the natural and anthropogenic factors associated with damage occurrence through an integrative and comprehensive approach based on spatial-temporal analysis at multiple scales, and analyzing damage data from different habitats, populations and management scenarios.

2. STATE OF THE ART

The complexity of human-wildlife conflicts relies on its diverse components, including social (Dickman, 2010; Naughton-Treves et al., 2003), political (Darimont et al., 2018; Treves et al., 2017), economic (Barua et al., 2013; Dickman et al., 2011), ecological (Artelle et al., 2016; Honda, 2013; Tveraa et al., 2014) and even psychological (Barua et al., 2013; Bruskotter and Wilson, 2014). Many studies on this topic highlight the link between damage incidence and human factors, such as the management of wildlife and livestock (Baker et al., 2008; Bautista et al., 2017; Fernández-Gil et al., 2016; Pettigrew et al., 2012). Other studies focus on the economical and social aspects, assessing people’s attitudes towards damage-causing species (Dressel et al., 2015; Treves, 2008) and estimating the costs derived from conflicts (Bautista et al., 2015; Berger, 2006; Schwerdtner and Gruber, 2007). Recently, an ecological approach has also been taken, and aspects like landscape features, habitat selection, food availability, climatic factors and individual features and their role in human-wildlife conflicts have just started to be considered (Artelle et al., 2016; Chiyo et al., 2011; Kissling et al., 2009; Morehouse, 2016; Treves et al., 2011). Yet, more holistic approaches that integrate both human and management factors with the ecological mechanisms underlying the occurrence of wildlife damage are scarce in the literature. This thesis uses an integrative, multidisciplinary and multi-scale approach to the study of human-wildlife conflicts under different socio-ecological scenarios to get a better understanding of the proximate and ultimate factors underlying conflict occurrence.

The study of conflicts generated by brown bear damages is particularly interesting. After centuries of persecution and decline, most populations in Europe and North America have experienced a recent recovery (Chapron et al., 2014; Clark et al., 2002; Gompper et al., 2015; Kasworm et al., 2007). The brown bear is currently the large carnivore species most abundant in Europe (Chapron et al., 2014) and in spite of historical range contractions, it is the large carnivore with the second largest distribution in the world (Wolf and Ripple, 2017). Bears inhabit a wide range of habitats and its broad diet often includes anthropogenic food, such as livestock, crops and beehives (Bojarska and Selva, 2012; Can et al., 2014).

Multiple factors affect the occurrence of conflicts arising from bear damage (Bautista et al., 2017; Can et al., 2014). At the continental scale, policies to manage bear damage greatly influence the occurrence of conflicts; lower levels of conflict are found when the use of effective prevention measures is a precondition to receive compensation (Bautista et al., 2017). Good husbandry practices are proven to be the most effective and widespread technique to prevent conflict with bears (Van Eeden et al., 2017). Reintroduced populations expand into areas where bears were extirpated and where traditional prevention and husbandry practices no longer exist, leading to high damage incidence (Stahl et al., 2002). Finally, wealthier countries and regions could more easily afford the costs of wildlife conservation (Balmford et al., 2003; Barnes et al., 2016), which also include high subsidies for damage management policies (Agarwala et al., 2010; Bautista et al., 2017; Dickman et al., 2011) that can ultimately affect conflict occurrence.

European brown bear populations mostly occur in human dominated landscapes, yet bears avoid areas of high human density (Chapron et al., 2014). In temperate ecosystems, bears mainly select forest dominated areas with high forest cover and low human disturbance (i.e., low density of roads and settlements) (Fernández et al., 2012; Pop et al., 2018; Ziółkowska et al., 2016). To a lower extent, bears also roam in agricultural fields (Bartoń et al., 2019; Pop et al., 2018), where they find important natural food resources, such as insects and herbaceous vegetation (Bojarska, 2014; Roellig et al., 2014) but also anthropogenic ones, like maize crops and livestock (Mertens and Promberger, 2001; Skuban et al., 2016). Previous studies in Europe and North America about bear-related conflicts showed that the density of humans and the availability of pastures and other agriculture land types is directly related to the occurrence of damages (Baruch-Mordo et al., 2008; Gastineau et al., 2019; Northrup et al., 2012; Wilson et al., 2006). The abundance of farms and apiaries also increases the risk of bear damage, especially when not fenced and unprotected against bears (Wilson et al., 2006, 2005). Another important aspect is the presence of forest edges, which facilitates to bears the access to anthropogenic food (Northrup et al., 2012). To sum up, bears tend to live in relatively undisturbed forest habitats, but they also use agricultural lands, and when they do, they can enter in conflicts with humans.

The occurrence of human-bear conflicts may also be related to different climatic events and ecological processes. Various climatic and meteorological events have been associated with an increasing trend in human-wildlife conflicts. For instance, an increase in the frequency of crop raiding and approaches to people by sun bears (*Helarctos malayanus*) in Indonesia and American black bears (*Ursus americanus*) in New Mexico (USA) was reported during drought periods associated with the El Niño-Southern Oscillation (Fredriksson, 2012; Zack et al., 2003). Climate change is predicted to increase the severity of meteorological events, such as late-spring frosts that are associated with natural food failures in temperate regions and then a higher use of urban areas by American and Asiatic black bears (Honda, 2013; Laufenberg et al., 2018). The frequency of bears using or searching for anthropogenic foods seems to increase when natural bear food sources become scarce. For instance, human-grizzly bear conflicts increased in British Columbia, Canada, in years of low availability of salmon biomass (Artelle et al., 2016). On the other hand, years of high mast production can increase bear reproductive rates (Costello et al., 2003), which in turn can also lead to increased level of conflicts in subsequent years due to a larger number of mothers with cubs and young individuals that look for shelter and food near humans (Elfström et al., 2014; Obbard et al., 2014).

3. RESEARCH QUESTIONS AND SPECIFIC GOALS

I divided the thesis in three non-excluding and complementary research questions, each of them covered by a separate chapter (see Fig. 1).

Research question 1: How damage compensation programs influence the variability of damage caused by bears and other large carnivore species across European countries?

The occurrence of conflicts arising from brown bear damage is determined by multiple factors, including the type of damage compensation schemes, human land use and management practices, and shows a high variation at the continental scale (Bautista et al., 2017). Here, I aimed at conducting a comparative analysis of the damages caused by brown bears and other large carnivore species across different European populations. Particularly, I investigated the role of several factors, including economic indexes (e.g. gross domestic product), management measures (e.g. husbandry practices and damage management policies) and population dynamics (e.g. increase range of large carnivore populations), on the costs of damage compensation. I hypothesized that compensation costs are higher in countries (i) where livestock is free ranging and husbandry practices are not adapted to the presence of large carnivores, (ii) that are wealthy and can provide a large support for wildlife conservation and management, (iii) that invest little money in preventive measures, (iv) that have experienced higher expansion rates of large carnivore's distribution, and (v) where the tolerance towards large carnivore species is low and people are more prone to show their discomfort regarding the presence of predators.

Research question 2: Which factors shape the spatial variability in bear damage occurrence at the landscape, local and household scales?

Human-wildlife conflicts do not occur randomly in the landscape (Bautista et al., 2015; Gubbi, 2012; Treves et al., 2011, 2004). In this study, I focused on the brown bear population segment in the North-eastern Carpathians (SE Poland) to investigate the spatial variation of damage occurrence, which comprises almost exclusively damage to beehives (Bautista et al., 2017, 2015). I hypothesized that bear damage to beehives would mostly occur in areas of high bear habitat suitability with low human influence (i.e. areas of high probability of bear occurrence, Ziółkowska et al. 2016), and with a high availability and accessibility of apiaries. To evaluate this hypothesis, I modelled the risk of damage at multiple scales independently based on a priori specified scale-dependent predictions (e.g., the risk of damage is higher in areas of interspersion between forest patches and agricultural land). I used a multiscale approach to capture possible scale-specific differences underlying the occurrence of bear damage (Hebblewhite and Merrill, 2007) and to include the different scales at which farmers and the administrations manage livestock and wildlife (Miller, 2015). I integrated the results into a multi-scale risk map aiming to identify conflict "hotspots" (Wilson et al., 2006, 2005). I ran an additional model at the household scale to evaluate to what extent the use of preventive measures decreases the risk of damage. Finally, I aimed at assessing whether the risk of damage follows a spatially hierarchical structure, in which the broader landscape context can shape bear damage response to household conditions.

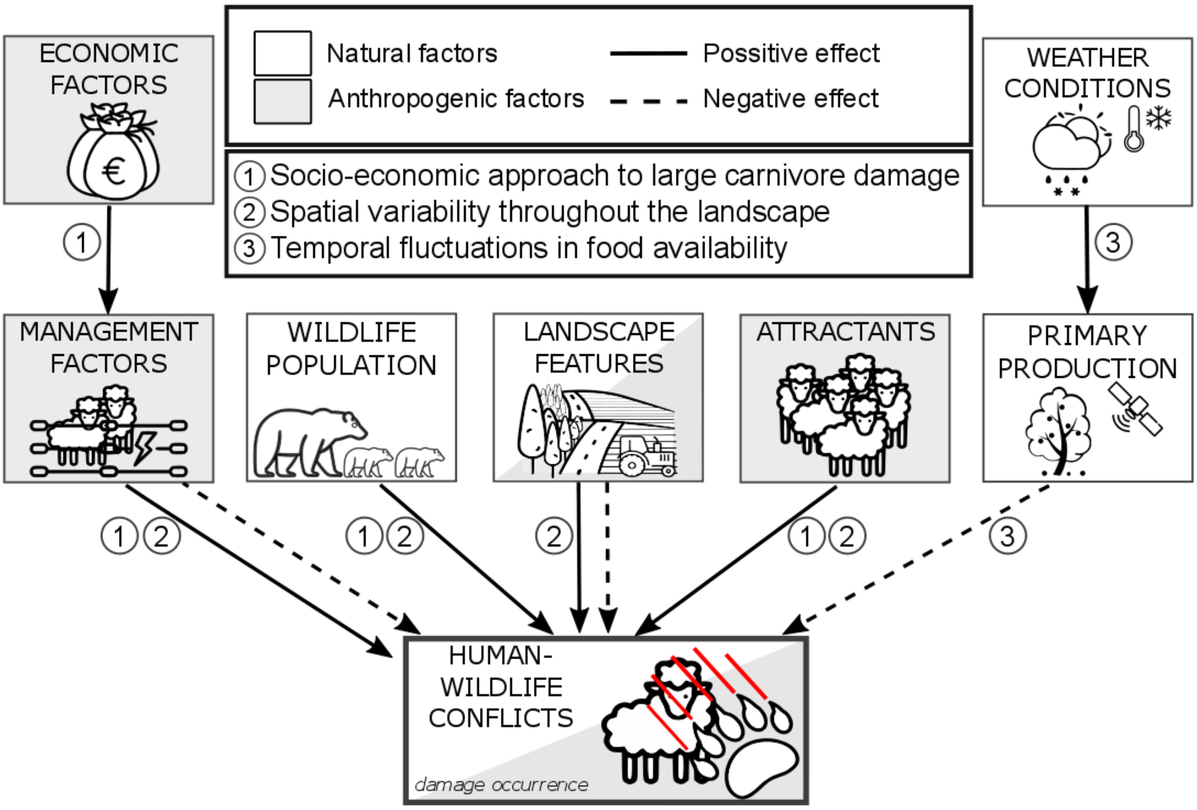

Figure 1. Conceptual diagram showing the structure and content of the thesis. The thesis follows an integrative approach to the study of human-wildlife conflicts based on a broad socio-ecologic context taking into account the expected impacts of different natural and anthropogenic drivers. The numbers in the circles indicate each study included in the thesis.

Research question 3: To what extent the temporal fluctuations in natural resource availability influence bear damage occurrence?

Masting events affect many ecological processes through different trophic levels (see Ostfeld and Keesing, 2000); therefore, resource pulses can potentially influence human-bear interactions. In temperate Europe, brown bears rely primarily on vegetal matter and are affected by fluctuations in resource availability (Bojarska and Selva, 2012; Ciucci et al., 2014; Naves et al., 2006; Vulla et al., 2009). Specifically, hard mast, such as beechnuts, are a critical food resource for bears before and after hibernation (Ciucci et al., 2014; Naves et al., 2006). I hypothesized that the number of bear damages increases in years of low production of food resources in general, and of hard mast in particular. To test this hypothesis, I used a novel combination of remote sensing indicators of forest productivity and phenology and weather cues to predict masting events and, ultimately, conflicts related to food shortages. Specifically, I used a 14-year dataset including weather variables, satellite-derived indices of photosynthesis activity at different temporal scales, on-the-ground measurements of beechnut production and brown bear damage reports in the north-eastern Carpathians.

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CHAPTER II

LARGE CARNIVORE DAMAGE IN EUROPE: ANALYSIS OF COMPENSATION AND PREVENTION PROGRAMS

with

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SUMMARY

The mitigation of conflicts associated with large carnivore damage to livestock and agriculture is pivotal to their conservation. We evaluate current programs to compensate and prevent large carnivore damage in 27 European countries and the factors related to the economic costs of these programs. Overall, high compensation costs are associated with free-ranging livestock (68% of total costs) and with national economic wealth. Contrary to general belief, the return of large carnivores does not always translate into higher compensation costs. We identify a tendency towards prioritizing compensation over prevention; only a few wealthy countries pay the majority of the money allocated for prevention programs to adapt husbandry practices to the presence of large carnivores. We conclude that programs mainly focused on paying large compensation amounts will often fail to build tolerance towards predators. To mitigate conflicts and optimize the cost-effectiveness of publicly funded measures, responsible agencies should be proactive, focus on prevention-based policies and periodically evaluate the effectiveness of compensation and prevention programs in an adaptive manner. With this purpose and to identify further solutions for conflict mitigation, we call for a pan-European database of damage occurrence, management actions and associated costs.

1. INTRODUCTION

After centuries of decline, the density, abundance, and distribution of large carnivore populations have increased in most European countries during the last decades (Chapron et al., 2014). This recent recovery is due to legal protection, reforestation, the recovery of wild prey populations, and an increased social tolerance towards wildlife (Boitani and Linnell, 2015). Nevertheless, many of these populations are still threatened and their long-term viability relies on effective conservation efforts. A key conservation issue is the socio-political conflict that arises from the presence of large carnivores and the damage they do to human property, such as livestock (Can et al., 2014). This is a particularly sensitive problem when large carnivores return to areas where people have abandoned husbandry practices, which prevented damage (Linnell, 2013). Such situations can lead to high economic losses and intense social conflicts between conservationists and the farmers that feel threatened by the presence of large carnivores (Redpath et al., 2013). Accordingly, we define damage to human property (and the associated economic losses) as a wildlife impact on human livelihood that may fuel conflicts between different stakeholder groups over the desired conservation or management targets for damage-causing species.

Negative attitudes towards carnivores can hinder conservation efforts as they can result in illegal killings and public opposition to management policies (see Dressel et al., 2015).

However, attitudes towards carnivores and their management are likely to change as circumstances change (e.g., Majić et al., 2011). In Europe, for instance, there is a trend for attitudes to become less positive with perceived increases in the abundance of large carnivores and risk of damage (Dressel et al., 2015; Eriksson et al., 2015; Heberlein and Ericsson, 2003; Majić et al., 2011). Thus, successful carnivore conservation largely depends on management policies that aim to maintain accepted population size of carnivores and enhance tolerance through ensuring low damage occurrence.

Wildlife agencies often implement compensation programs to mitigate conflicts emerging from damage-related losses and, therefore, to increase tolerance towards large carnivores of the local stakeholders sharing the landscape with these species (Boitani et al., 2010). Even though these programs have been operating since 1970 in many European countries (Bautista et al., 2017; Boitani et al., 2010), their conservation outcomes have been rarely evaluated and their effectiveness is still under debate (Ravenelle and Nyhus, 2017). Major flaws in compensation programs are insufficient and/or delayed payments, inefficient administrative procedures, failure to assess damage verification protocols, failure to condition compensation to prevention and ignoring the opinion of local stakeholders (Bulte and Rondeau, 2003; Marino et al., 2016; Nyhus et al., 2005; Ravenelle and Nyhus, 2017). Indeed, when responsible agencies tackle these limitations, compensation programs can successfully reduce the occurrence of damage and improve tolerance (Dalmasso et al., 2012; Stone, 2009).

In Europe, most large carnivore populations are transboundary, spanning up to eight countries (e.g., Carpathian lynx population; see Tables A1 and A2 in the supplementary material). Yet, the legal responsibility to conserve large carnivores falls on national and regional administrative levels. Despite the efforts to coordinate the management of large carnivores in Europe at the population level (Trouwborst, 2015), improving transboundary cooperation is still a key action for the conservation of large carnivores in the European Union (Boitani et al., 2015). In terms of damage management there is no common policy in Europe; policies differ among and within countries, even for shared carnivore populations. Compensation programs are part of damage management policies and they differ between countries, leading to differences in the quantity of damage compensation across Europe (Bautista et al., 2017).

The main goal of this policy analysis is to identify weaknesses and strengths of current policies to manage large carnivore damage in Europe and to give recommendations for effective conflict mitigation. To this end, we provide an overview of the damage compensation programs in 27 European countries involving four species of large carnivores: the brown bear

(Ursus arctos), the Eurasian lynx (Lynx lynx), the grey wolf (Canis lupus), and the wolverine (Gulo gulo). We compiled data on the type and costs of compensation programs and analyzed these costs in relation to different socioeconomic metrics. We quantified the costs of compensation programs in each country, based on Kaczensky et al. (2012). We standardized the costs of compensation across countries using purchasing power parities and divided the compensation expenditures by the estimated number of each species in each country or region separately (see supplementary material for detailed explanation of the methods). We investigated the link between compensation expenditures and husbandry practices, the countries' economic status, the rate of large carnivore recolonization and tolerance towards large carnivores. In a second step, taking the brown bear as a case study, we compiled information about the type and costs of the measures subsidized in damage prevention programs. As for compensation expenditures, we standardized prevention costs using purchasing power parities and evaluated their relationship with compensation expenditures, the countries' economic status, and the rate of large carnivore recolonization. Finally, we proposed strategies to optimize the effectiveness of compensation and prevention programs to reduce damage-related economic losses and encourage coexistence between large carnivores and people.

2. LARGE CARNIVORES AND DAMAGE COMPENSATION PROGRAMS IN EUROPE

Europe harbours approximately 17,000 brown bears, 12,000 wolves, 9000 Eurasian lynx and 1200 wolverines (excluding Belarus, Russia and Ukraine, Chapron et al., 2014). Lynx occur in eleven populations, bears and wolves in ten populations each, and wolverines in two populations (Fig. 1). Of these 33 large carnivore populations, eight are small and highly isolated (of which six are reintroduced or augmented), whereas 14 have>1000 individuals each. Altogether, large carnivores occur in 27 countries in Europe and 25 of the 33 populations are transboundary (Tables A1 and A2). All but seven countries have compensation programs for one or more large carnivore species (Table A2). In most countries, compensation is paid a posteriori, based on damage verification. Only Swedish authorities implement a different approach for reindeer, paying Sámi reindeer herders a priori based on the estimated large carnivore abundance or reproduction, regardless of the amount of the damage-related economic losses (Zabel and Holm- Müller, 2008).

3. THE COSTS OF COMPENSATION FOR LARGE CARNIVORE DAMAGE: A CONTINENTAL OVERVIEW

The annual compensation for large carnivore damage in Europe comprises approximately 28.5 million Euros. The average cost per year and individual carnivore during 2005–2012 was over

6300 Euros for wolverines, 2400 Euros for wolves, 1800 Euros for bears, and 700 Euros for lynx (valued at 2011 purchasing power parity, hereafter PPS; see Supplementary methods and Table A2). However, there is a lot of variation among and within countries depending on the species. For instance, in Italy and Poland the costs of compensation per animal are higher for bears than for wolves (see Table A2). In the case of Poland, the occurrence of wolf damage is rare in most of the species' range because livestock density is low and wild ungulates are highly abundant (Nowak et al., 2011), whereas bear damage occurs across most of its range (Bautista et al., 2017). In Italy, the occurrence of wolf damage may be underestimated because many regional administrations do not keep formal records on the compensation schemes and some just do not compensate at all (Boitani et al., 2010). Currently, the brown bear in Italy is fully protected and occurs in two separated small populations, which are the focus of large conservation efforts, also in the form of damage compensation (Bautista et al., 2017; Kaczensky et al., 2012).

3.1. The toll of free-ranging livestock

Differences in compensation costs among species and countries are largely related to husbandry practices. The amount paid per individual carnivore differed by up to three orders of magnitude between countries (e.g., ca 9400 PPS per bear in Norway vs. 9 PPS per bear in Croatia, Table A2). Whereas compensation for lynx depredation on livestock was zero in six countries, Sámi communities raising semi-domestic reindeer in Fennoscandia received up to 75% of the total compensation paid for lynx damages in Europe (Fig. 1, Table A2). Reindeer herding is deeply anchored in the culture of Sámi people and represents a key component of their livelihood. Depredation on reindeer by all large carnivore species together accounted for 41% of the total compensation costs in Europe (approximately 9.2 million PPS annually, half of which is paid a priori in Sweden). Nordic authorities implement damage management policies to build tolerance towards large carnivores, either as a priori (Zabel and Holm-Müller, 2008) or a posteriori compensation (Sippola et al., 2005). However, they rarely implement techniques to prevent reindeer predation (e.g., artificial feeding in sensitive periods to protect reindeer, Table 1). National laws specify different management policies for large carnivores inside and outside reindeer herding areas. For example, the law permits wolf extermination in reindeer herding areas in Finland, Norway and Sweden (Kojola et al., 2005; Wabakken et al., 2010). As a consequence, resident packs do not occur in reindeer areas (see Fig. 1).

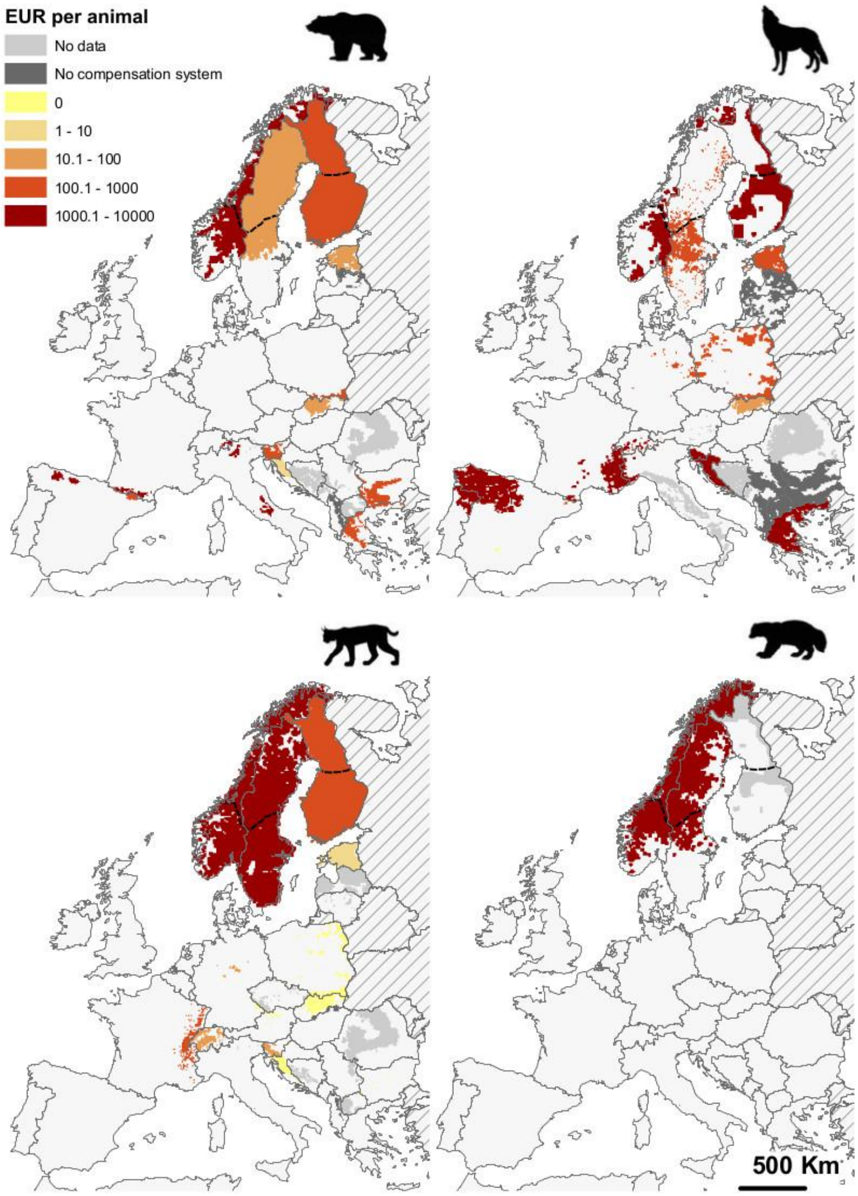

Figure 1. Compensation costs for damage caused by the brown bear, wolf, Eurasian lynx and wolverine in Europe. Costs are expressed in PPS per animal (supplementary methods in supplementary material). Black dashed lines show the southern edge of the semi-domestic reindeer husbandry area. Countries with grey dashed lines were not included in this study. Species distributions were extracted from Chapron et al. (2014).

Next in magnitude is the predation on free-ranging sheep in Norway, which represented almost 25% of total compensation payments in Europe. Despite the disproportionate amount paid, the conflict around free-ranging sheep predation remains chronic, resulting in very low population goals for large carnivores set by the Norwegian Parliament. For instance, in 2016 authorities approved plans to kill over two-thirds of the Norwegian wolf population (Immonen and Husby, 2016), disregarding that wolf experts had previously indentified the very small population size as the main threat to wolves in Norway (Kaczensky et al., 2012).

3.2. Wealthier countries pay more

The annual compensation cost per individual carnivore is positively related to national economic wealth measured as gross domestic product per capita in PPS (model 1 in Table A3). This association is not due to differences in the price of livestock or agricultural products across countries, because we expressed both variables at a uniform price level (Supplementary methods). The link between wealth and conservation expenditures has been reported globally (Balmford et al., 2003; Barnes et al., 2016). Our findings suggest that, in wealthier countries, damage management policies receive more institutional support to cover the costs of damage compensation. However, spending more money for damage management does not necessarily imply an effective reduction of damage occurrence and its costs (see below).

3.3. The return of large carnivores does not always translate into higher compensation costs

The rate of carnivores' range change (calculated for each country/region as the ratio of the species' range sizes in the year 2012 in relation to the species' range sizes in the 1950–70s based on maps published by Chapron et al. (2014); supplementary material) was larger in wealthier countries, which tend to pay more for compensation (model 5 in Table A3; see also Kojola et al., 2018). This may suggest that compensation costs tend to be higher in countries with higher recolonization rates. However, our analysis shows that, at the European scale, this positive relationship only occurs in the case of the brown bear (Fig. 2 and model 7, 12 and 15 in Table A3). It seems that the costs of bear damage compensation are higher in countries where bears have returned or expanded after decades of absence than in countries with a long history of coexistence and where the use of preventive measures was never abandoned (Linnell, 2013).

The lack of relationship between recolonization rates and compensation costs for wolf and lynx damages may be related to land-use dynamics in the areas of expansion. Land abandonment in Europe and the decline of the rural population (17% since 1961) have resulted in an increase in forest and scrubland cover (Pereira and Navarro, 2015). These changes have favoured an increase in the abundance of wild prey, which has likely further promoted the expansion of large carnivores into abandoned lands (Boitani and Linnell, 2015), and may have helped to keep livestock predation at very low rates. This is the case in Western and Central Poland and Eastern Germany, where wolves have expanded into areas with low farming activity, high forest cover and high abundance of wild prey (Nowak et al., 2011; Wagner et al., 2012). Furthermore, costs can be kept low in recolonized rural areas if responsible authorities help farmers to adapt husbandry practices to the presence of large carnivores, by ensuring financial support for preventive measures (e.g., wolf expansion in

Piedmont, NW Italy; Dalmasso et al., 2012). On the contrary, when these expansions occur into areas where husbandry practices are not adapted to the presence of large carnivores and where proper prevention is not a precondition for compensation, the costs of damage compensation tend to be high. These are the cases of bear recolonization in Norway (Swenson and Andrén, 2005), wolf expansion in most of Italy (Boitani et al., 2010), and lynx reintroduction in the Jura Mountains in France (Stahl et al., 2001). Finally, in the case of reintroduced and/or reinforced populations, compensation expenditures tend to be higher due partly to authorities' huge efforts to increase tolerance as a critical component for the success of reintroduction programs (Clark et al., 2002; Tosi et al., 2015).

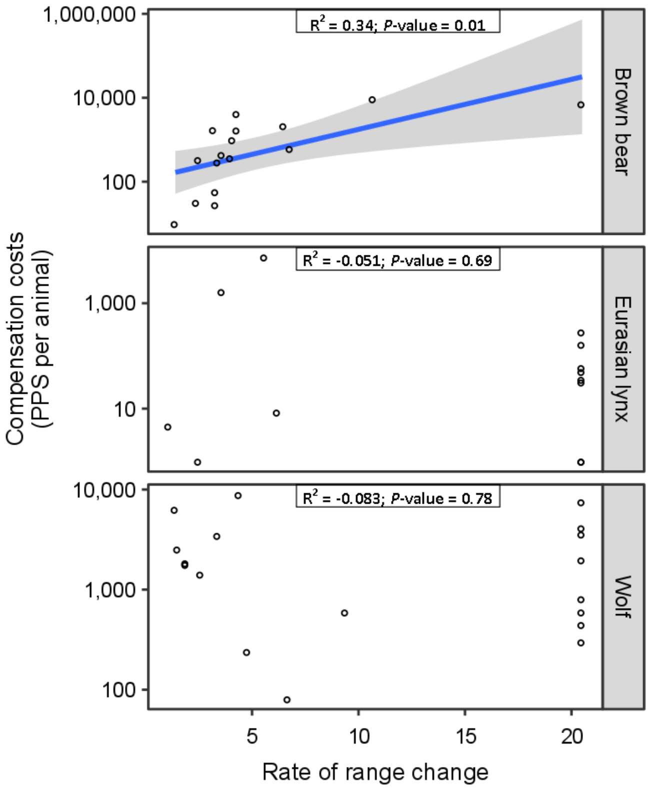

Figure 2. Annual costs of compensation for large carnivore damage in relation to the rate of large carnivore range change over the last five decades in Europe (see supplementary methods in supplementary material). Costs are log-scaled and expressed in PPS per animal (see supplementary methods). Complete return and reintroduction to places with no population a few decades ago were given the maximum value of range change rate, which corresponds to a 20-fold lynx range increase in Finland. No wolf population has been reintroduced in Europe (Table A2).

3.4. Compensation alone is not enough to improve tolerance towards large carnivores

The tolerance for large carnivores is a highly complex and context-dependent issue (Linnell and Boitani, 2012). The attitudes towards different species involved in conflict situations are taxonomically biased (Kansky et al., 2014). Farmers in Europe tend to have more negative attitudes towards wolves than towards other predators (Dressel et al., 2015), even though in a few countries compensation costs are lower for the wolf than for other species (see France, Italy, Norway and Poland in Table A2). Attitudes are usually more strongly associated with intangible costs (e.g., risk perception) than with economic costs (e.g., livestock predation) (Kansky and Knight, 2014). This can partly explain why the return of extirpated populations is often unwelcome by local communities (independent of economic losses), whereas decades of human-carnivore coexistence result in a greater tolerance (Kaczensky et al., 2004; Majić and Bath, 2010; see the previous section). In addition, tolerance towards large carnivores is strongly linked to cultural values (Dickman, 2010). There are great cultural differences across Europe that play a role in how various societies deal with and tolerate carnivores. For instance, levels of tolerance seem to be lower in Norway than in Sweden, and especially low in rural areas with free-ranging sheep and strong hunting traditions (Gangaas et al., 2013).

Moreover, compensation programs can sometimes further motivate negative attitudes and can be a source of conflict over large carnivore management. For instance, programs that aim to improve tolerance by only paying compensation can perpetuate a negative perception of carnivores (Berger, 2006). When prevention payments are not used efficiently, damage incidence does not decrease and conflicts over large carnivore conservation escalate (Boitani et al., 2010). Furthermore, poorly functioning compensation programs, in which damage verification processes are unreliable and slow, may discourage people from claiming damage and fail to promote positive attitudes (Dickman et al., 2011; Nyhus et al., 2005). Finally, compensation programs can benefit from an adaptive approach and should adjust to changes in the conflict situations over time (e.g., increase of damage occurrence) and being integrated in participatory processes (i.e., engaging stakeholders to manage conflicts) (Anthony and Swemmer, 2015). Failing to do so can hamper efforts to improve tolerance (Marino et al., 2016) and to achieve effective conflict mitigation (Redpath et al., 2013, 2017). In such participatory processes, providing information about benefits stemming from the presence of predators to the parties involved can also help to build tolerance (Slagle et al., 2013).

There are some examples of low costs of compensation and high tolerance that partly relate to the prerequisite of using effective prevention practices in order to receive compensation. In Sweden, compensation payments outside the reindeer herding area are among the lowest in Europe because compensation is conditional on the proper protection of livestock and wildlife agencies strongly focus on subsidizing preventive measures (Widman and Elofsson, 2018). The management of brown bear damage in Croatia is another example. Hunter organizations are responsible for damage compensation and stipulate the use of protection measures as a condition for compensation (Bautista et al., 2017). The members of hunting organizations are local people (mainly farmers) who profit from hunting bears, are involved in bear management, and protect well their livestock to avoid a conflictive coexistence (Hipólito et al., 2018). As a result, costs for compensation of bear damage are among the lowest in Europe (Fig. 1) and local communities accept and value the presence of bears (Majić et al., 2011).

4. THE COSTS OF PREVENTION PROGRAMS: THE CASE OF BROWN BEARS

4.1. Heterogeneity in prevention programs

National administrations routinely compensate for brown bear damage in most of Europe, whereas only half of the countries systematically subsidize preventive measures (Tables 1, A4 and A5). The majority of the funds for preventive measures come from public agencies at the national or regional level, and in some cases from the European Union (mostly through LIFE NATURE projects) and non- governmental organizations (Tables A4 and S5).

In almost every country and region damage prevention programs cover the costs of electric fences and livestock guarding dogs, which represented ca 20% of the overall annual cost to prevent bear damage in Europe (Fig. 3, Table A4). These measures are effective in preventing damage only if properly implemented and maintained (Van Eeden et al., 2017). Improper use of these measures, such as inadequate fence design, uncharged batteries, or chained dogs, can result in up to 40% of the funded measures being ineffective (di Vittorio et al., 2016; Rigg et al., 2011). We identified a substantial portion of the prevention subsidies allocated to assist in restructuring husbandry practices in places where extensive farming has emerged after the temporary absence of large carnivores (Linnell, 2013). Payments for shepherd dog food or relocation of herds to areas where large carnivores are absent were among these husbandry-supportive measures (Table 1). Together with the cost of the salaries for shepherds in the French Pyrenees (23% of the total), husbandry-supportive measures represented ca 56% of the total annual expenditures allocated for damage prevention in Europe (Fig. 3). These measures were subsidized in prevention programs implemented in countries or regions with reintroduced bear populations (France, Catalonia in Spain, and Trentino in Italy) and in Norway, where the bear range has increased tenfold in the last decades (Kaczensky et al., 2012; Tables 1, A2 and A4).

In the case of Norway, additional measures included in damage prevention programs do not involve guarding or active herding, but other actions rather related to damage verification and compensation; e.g., patrolling of the grazing area to look for signs of dead or injured sheep (Mabille et al., 2015; Tables 1 and A4). These measures represented as much as 20% of the total annual expenditures incurred on prevention programs in Europe (Fig. 3).

Table 1. List of measures subsidized in prevention programs to mitigate brown bear damage across 14 European countries in 2003-2015.

Measures subsidized in prevention programs*	Countries and regions in which the measure is subsidized on a yearly basis	Countries and regions in which the measure is occasionally subsidized
Electric fences	CM, CAT, EST†, FR, NO, SLO, SW, TR	CI, CR, PO
Livestock guarding dogs	CAT, FR, GR, NO, SLO, TR	CI, PO
Physical barriers (i.e., fences and gates)	CAT	CI, CM, PO
Alarm pistols and firecrackers	-	PO
Public awareness with documents (e.g., leaflets)	-	CM
Shepherds‡	CAT, FR	-
Helicopter transportation of cabins and other equipment to the summer pastures‡	FR, TR	-
Food for livestock guarding dogs‡	CAT	-
Late release and early removal of sheep from the summer pastures‡	NO	-
Translocation of livestock to areas free of large carnivores‡	NO	-
Facilitation of grazing areas near villages protected with predator-proof fences‡	NO	-
Supplementary feeding in sensitive periods to protect reindeer‡	NO	-
Patrolling of grazing areas to look for signs of dead or injured livestock§	NO	-
Electronic surveillance (i.e., GPS-radio collar for livestock) in grazing areas§	NO	-
Dogs to find livestock carcasses§	NO	-

Countries and regions as follows: CM: Cantabrian Mountain (NW Spain); CAT: Catalonia (NE Spain); CI: Central Italy; CR: Croatia; EST: Estonia; FR: France; GR: Greece; NO: Norway; PO: Poland; SLO: Slovenia; SW: Sweden; TR: Trentino (N Italy)

*Citations for the subsidized measures available in Tables A4 and A5 in the supplementary material.

†Starting from 2013

‡Measures related to restructuring husbandry practices

§Measures related to damage verification and compensation

4.2. Payments for bear damage prevention almost double compensation costs

On average, the annual costs for prevention of brown bear damage were almost twice the costs for compensation of bear damage in Europe (ca 5 million vs. ca 3 million PPS; Table A5). Prevention costs per bear differed by four orders of magnitude among countries: ca 56,000 vs. 1 PPS paid per bear and year in France and Croatia, respectively (Fig. 3). Approximately 90% of the total prevention costs in Europe were paid in Norway and France, where free-ranging sheep herding is an important socio-economic activity (Kaczensky et al., 2012).

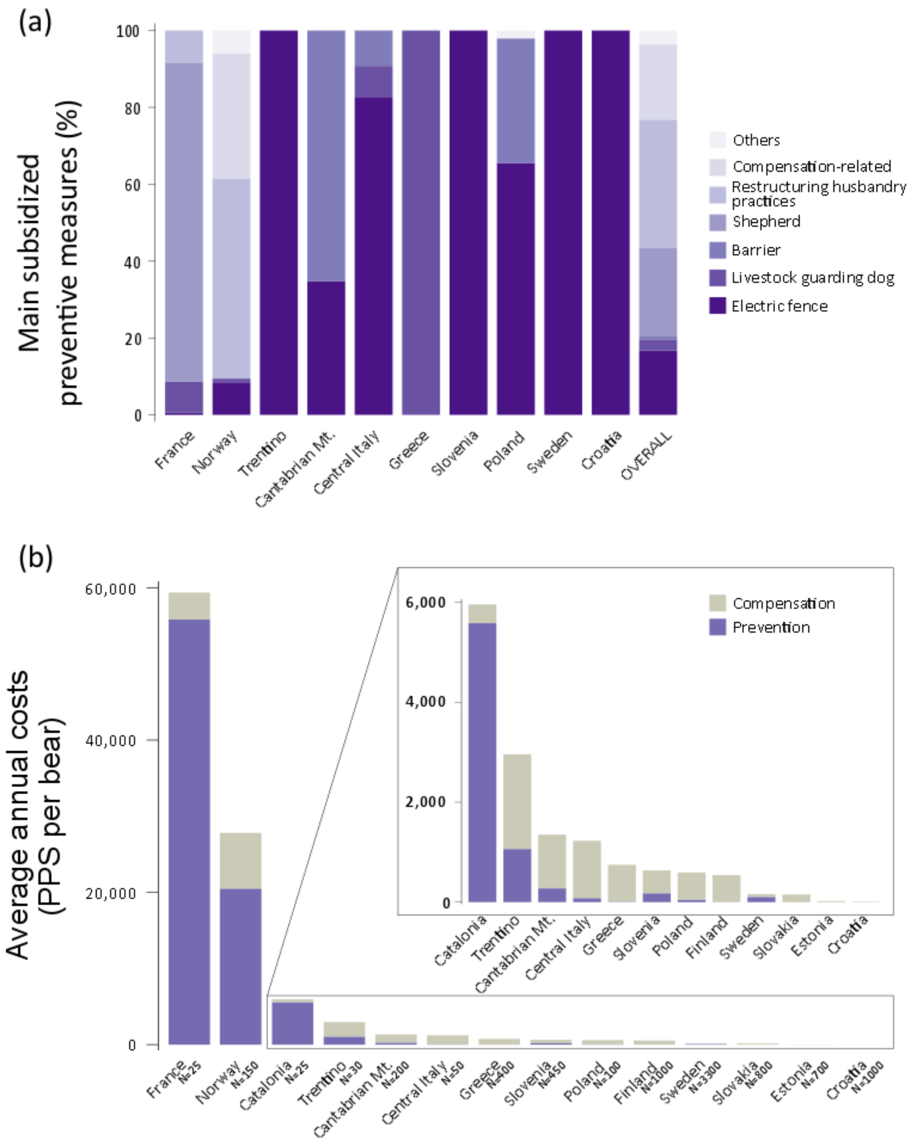

Figure 3. Relative distribution of the average annual costs of the main measures officially subsidized to prevent brown bear damage (a); and average annual compensation and prevention expenditures for brown bear damage in Europe in 2005–2012 (b). In (b), N indicates the bear population estimation (see details in Table A5). No data were available for Catalonia about the cost of each subsidized measure, neither about prevention costs for Finland and Slovakia (Table A4). Costs are expressed in PPS per bear (supplementary methods in supplementary material). Detailed information about the different measures included in each category in (a) is presented in Tables 1 and A4.

Our analyses indicate that the annual costs of compensation per individual bear are positively related to costs of prevention per individual bear, which, in turn, tend to be higher in wealthy countries (Models 16 and 24 in Table A3). However, only the costs of compensation, but not prevention, are positively related to the rate of the bear's range change (Models 16 and 25 in Table A3). The lack of relationship between prevention costs and bear recolonization rate is probably due to a lack of systematic prevention before the "problem appears", especially in countries where the bear populations have increased considerably during the last decades (e.g., Cantabrian Mountains in Spain, see Tables A2 and A5). This indicates a tendency to prioritize compensation over prevention programs in Europe and a lack of proactive approaches to mitigate conflict (i.e. act before the problem appears).

We did not find any relationship between compensation costs and previous investments in prevention (Model 29 in Table A3), probably due to the heterogeneity of measures classified and subsidized as prevention (Tables 1, A4 and A5). Additional local-scale analyses would help to test whether prevention has actually reduced compensation costs in resident bear populations and whether administrations have sufficiently subsidized preventive measures to mitigate damage in recently recolonized areas. For example, in an area of the Cantabrian bear population in Spain, where the species' range has quadrupled in the last 30 years, an investment of around 1000 PPS in prevention of damage to apiaries reduced compensation costs more than threefold. Therefore, a small investment in prevention reduced compensation costs in that area by 30,000 PPS, which is equivalent to a 30–50% reduction compared to previous years (Seijas et al., 2016).

5. IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

Effective conflict mitigation implies facilitating coexistence and reducing damage to human property and associated economic losses (Van Eeden et al., 2017). To achieve that, responsible agencies should focus on damage-prevention programs that help to adapt husbandry practices to the presence of large carnivores. Because large carnivore populations are expected to expand further across Europe (Milanesi et al., 2017; Scharf and Fernández, 2018), damage management strategies need to be proactive and anticipate emerging conflicts to ensure the success of large carnivore recolonization. For this purpose, responsible agencies should integrate compensation and prevention programs into participatory processes that consider socio-cultural aspects at the national, regional and local levels (Anthony and Swemmer, 2015; Marino et al., 2016; Redpath et al., 2017; Tosi et al., 2015).

In Europe, research studies and LIFE NATURE projects sometimes evaluate the outcome of compensation and prevention programs (e.g., di Vittorio et al., 2016), but these evaluations are rarely led by the responsible authorities. Examples of the latter include the assessment of programs to compensate and prevent bear damage in Asturias in northern Spain and the evaluation of measures to prevent wolf damage in the French Alps funded by the regional and national Ministries of Environment, respectively (Naves et al., 2010; de Roincé, 2016). Such assessments are not compulsory in LIFE projects and they only occasionally evaluate whether compensation programs succeed to improve attitudes towards large carnivores or whether subsidized preventive measures are effectively reducing damage to human property. To ensure that damage management policies alleviate conflicts, responsible agencies should be obliged to evaluate the effectiveness of compensation and prevention programs periodically and adapt these programs according to the results of such evaluations.

Finally, to enable a proper assessment of the effectiveness of compensation and prevention programs, we encourage the administrations and organizations working on damage mitigation to establish a common pan-European database of damage occurrence, management actions and associated costs. A common criterion to properly classify measures as compensative, preventive or supportive would be desirable. Such efforts would allow for optimizing the cost-effectiveness of public funds invested in damage management and the identification of the most adequate solutions for conflict mitigation in Europe in a more adaptive manner.

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SUPPLEMENTARY MATERIAL FOR
Large carnivore damage in Europe: Analysis of compensation and prevention programs

SUPPLEMENTARY METHODS

Data collection and standardization

Compensation of large carnivore damage in Europe

We collected all available information on current policies and programs for the management of damage caused by the brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*) and wolverine (*Gulo gulo*) in Europe. We extracted information from the most recent and comprehensive report published by the IUCN/SSC Specialist Group-Large Carnivore Initiative for Europe (Kaczensky et al. 2012). Specifically, we collected information for 27 European countries (except Belarus, Russia and Ukraine due to lack of reliable information) about 1) the existence of damage compensation schemes; 2) specific characteristics of the compensation schemes; and 3) expenditures on damage compensation (Table S2). Additional information was collected by the collaborators from public administrations and official reports.

We standardized the costs of compensation using purchasing power parities (PPPs) to allow for a direct comparison of expenditures across countries in a uniform price level. According to Eurostat & OECD (2012) "*PPPs convert different currencies to a common currency and, in the process of conversion, equalise their purchasing power by eliminating the differences in price levels between countries*". Values of PPPs were extracted from the Eurostat database (http://ec.europa.eu/eurostat/data/database) for all countries included in our study and for each year during the period 2005 – 2012. We, then, averaged each country's PPPs across its specific data period (see Table S2). We used this approach to convert all expenditures into a single artificial currency called purchasing power standard (hereafter PPS), which is equivalent to euros valued at average EU price levels in the reference year 2011. PPS are euros that have the same purchasing power across the entire European Union. Their purchasing power is a weighted average of the purchasing power of the national currencies of EU Member States. They reflect the average price level in the European Union or, more precisely, the weighted average of the price levels of Member States (Eurostat & OECD 2012)). Finally, to allow comparisons among species after conversion to PPS, we divided the compensation expenditures in each country or regional administration by the estimated number of bears, lynx, wolves and wolverines separately. Estimates of large carnivore abundance were extracted from Kaczensky et al. (2012).

National economic wealth

We used the gross domestic product per capita (GDP) as an indicator of economic wealth in order to assess whether the costs of the total compensation paid (already standardized to PPS) correlate with economic wealth. We extracted the national GDP per capita valued in PPS from the Eurostat database for each year in 2005 – 2012 and then averaged each country's GDP per capita across its specific data period (see period in Table S2).

Costs of compensation and prevention of brown bear damage in Europe

We searched for detailed information on programs to prevent brown bear damage in 14 countries and regional administrations in 2003-2015. Specifically, we looked for 1) the type of measures included in prevention programs; 2) their associated costs; 3) the funding organization or institution; and 4) whether preventive measures were funded every year (see Table S4 & S5). As we aimed to examine the effectiveness of damage prevention programs in reducing compensation costs, we also collected detailed data on expenditures to compensate bear damages in the studied countries and regions. Finally, we converted prevention and compensation expenditures into PPS and then standardized them by dividing the total costs in PPS by the estimated number of bears in each country and region. We obtained data on compensation and prevention costs, and estimates of bear population sizes from national and regional wildlife agencies, published literature and reports, as well as from researchers and practitioners (see Table S5). Data on prevention costs for Norway and Sweden were available for all large carnivores together (i.e, one expenditure for all the species combined), and at the national and county level, respectively. We estimated the prevention costs paid within the distributional range of the bear to avoid overestimating the costs of measures that can actually prevent bear damage. Specifically, we calculated the percentage of the areas occupied by bears relative to the total area occupied by all large carnivores at the county level and applied that percentage to the amount paid for prevention per county. For Norway, we extracted the relative weight of prevention subsidies in each county based on data detailed at the county level from 2009 (extracted from http://www.rovviltportalen.no/).

Rate of carnivores' range changes in the last 40-60 years

The incidence of large carnivore damage and the level of related social conflict are expected to be higher in areas where large carnivores have returned after prolonged absence, compared with areas in which people are adapted to the presence of large carnivores after many years of coexistence (Stahl et al. 2001, Redpath et al. 2013, Chapron et al. 2014). We calculated the rate of carnivores' range change from the 1950-70s to 2012 based on the data published by Chapron et al. (2014). In that study, the authors compiled European distribution maps for the four large carnivores for the year 2012 and for the 1950-1970s by pooling all available country-specific data on the basis of a 10x10 km grid. We calculated the rate of range change as the ratio of the number of occupied grid cells in 2012 in relation to the number of occupied grid cells in the period 1950-1970s (Table S2). We calculated this ratio for each large carnivore species and country/region. In some areas, the calculation of these rates was impossible because the historical range was zero (see *Reintroduced* or *Returned* in Table S2). We valued these areas with the maximum value obtained for all species and areas (see Table S2). We used ArcGIS 10.1 (ESRI, Redlands, CA, USA) to calculate the ratio.

The methods used to estimate the distribution maps in the original data set are based on a diverse array of monitoring techniques, including genetic analysis, telemetry, camera trapping, snow tracking, field signs, density extrapolation, coordinated counts (e.g., bear females with cubs of the year), dead animals, damage reports, harvest data, observation indices from hunter and forester organizations, questionnaires and expert opinion. In most cases, distribution maps for each country and each species are based on a combination of the above-mentioned monitoring techniques and they differ among countries and from the historic to the most recent estimates. This variability in the data and methods implies differences in uncertainty in the distribution maps at the national level. Yet, these data represent the most comprehensive consensus of current and historical ranges of large carnivores in Europe. Therefore, to the best of our knowledge, these data provide the most reliable source of information to quantify country-specific range changes of large carnivores at a European level.

Statistical analyses

We assessed whether the amount of compensation expenditures was related to the countries' economic wealth and to the rate of carnivores' range change, both calculated as explained in the above sections, using linear mixed-effects models (see Table S3). We used data from the period 2005-2012. The period was selected based on the availability of data on compensation and prevention costs. In these models, we included the compensation costs per individual large carnivore averaged for the study period in each country or region as a response variable, while the economic wealth (GDP per capita averaged across the study period) and rate of carnivores' range change were included as fixed explanatory variables. We fitted every model using a normal error distribution and included the species (brown bear, Eurasian lynx, grey wolf or wolverine) as a random intercept.

We analyzed the association between expenditures for brown bear damage prevention and compensation during 2005-2012 (Table S5). We used linear mixed-effects models in which the compensation cost per bear individual in each year was treated as the response variable, while the explanatory variables included expenditures on prevention per bear in each year, the GDP per capita in each year and the rate of bear range change in that country/region (Table S5). Similarly, we used linear mixed-effects models with the prevention expenditures per bear in each year as a response of the GDP per capita and the rate of bear range change. Because the number and location of damage events vary across time (Bautista et al. 2015), prevention programs may need to be implemented systematically for a number of years to really reduce compensation costs at the national or lower administrative level. We tested this hypothesis by assessing the cumulative effect of prevention expenditures on compensation costs. To do so, we used linear mixed effects models, in which we modelled the compensation cost per bear in a given year as a response of the cumulative sum of prevention costs per bear of all previous years within the study period. To calculate the 'accumulated prevention' we first standardized the prevention costs per bear individual and then summed the per capita prevention costs across the period of interest (e.g., the cumulative per capita prevention costs from 2005 to 2009 to model the per capita compensation cost of 2010). We added the rate of bear range change as an explanatory variable. In all the models, we used a normal error distribution and included the studied country or region as a random intercept (Table A3). We calculated marginal and conditional R^2 for each model to assess the variance explained by the fixed and the random factors, respectively (Nakagawa & Schielzeth 2013).

In all models, the compensation and prevention expenditures and the GDP per capita were expressed in PPS. We transformed compensation and prevention expenditures to their natural logarithm before analysis to meet the assumption of normality. We excluded highly correlated explanatory variables in the same model ($r > 0.7$). We standardized the explanatory variables to zero mean and unit variance to allow for a comparison of effect sizes across variables. We used the small sample corrected Akaike Information Criterion (AIC_c) to compare the importance of each model across the set of candidate models including all possible combinations of explanatory variables. We did that for each response variable separately. All statistical analyses were performed in R (R Development Core Team 2016) using the packages *nlme* for fitting linear mixed-effect models (Pinheiro et al. 2016), *MuMIn* for model selection and calculation of marginal and conditional R^2-values (Bartoń 2015).

SUPPLEMENTARY TABLES

Table A1.Summary of economic and demographic information in 2012 of European countries with presence of large carnivores.

Country	Country area (km^2)*	Human population	GDP per capita (PPS)	Large carnivores species
Albania	27,400	2,900,247*	7,800	bear, lynx, wolf
Austria	82,540	8,408,121	34,700	bear, lynx, wolf
Bosnia&Herzegovina	51,200	3,839,265	12,786†	bear, lynx, wolf
Bulgaria	108,560	7,327,224	12,200	bear, lynx, wolf
Croatia	55,960	4,275,984	15,900	bear, lynx, wolf
Czech Republic	77,230	10,505,445	21,800	bear, lynx, wolf
Estonia	42,390	1,325,217	19,500	bear, lynx, wolf
Finland	303,890	5,401,267	30,600	bear, lynx, wolf, wolverine
France	547,561	65,276,983	28,400	bear, lynx, wolf
FYR Macedonia	25,220	2,059,794	9,000	bear, lynx, wolf
Germany	348,540	80,327,900	33,000	lynx, wolf
Greece	128,900	11,086,406	19,600	bear, wolf
Hungary	90,530	9,931,925	17,200	lynx
Italy	294,140	59,394,207	26,800	bear, lynx, wolf
Latvia	62,180	2,044,813	16,000	bear, lynx, wolf
Lithuania	62,674	3,003,641	18,500	lynx, wolf
Montenegro	13,450	620,308	18,907†	bear, wolf
Norway	365,245	4,985,870	49,500	bear, lynx, wolf, wolverine
Poland	306,220	38,063,792	17,600	bear, lynx, wolf
Portugal	91,590	10,542,398	20,500	wolf
Romania	230,020	20,095,996	14,300	bear, lynx, wolf
Serbia	87,460	7,216,649	9,800	bear, lynx, wolf
Slovakia	49,035‡	5,407,579‡	19,700	bear, lynx, wolf
Slovenia	20,140	2,055,496	21,600	bear, lynx, wolf
Spain	500,210	46,818,219	24,300	bear, wolf
Sweden	407,340	9,482,855	33,600	bear, lynx, wolf, wolverine
Switzerland	39,516	7,954,662	43,200	bear, lynx, wolf

Gross Domestic Product (GDP) expressed in Euros valued a 2011 purchasing power parities (PPS)
Human population and GDP were extracted from Eurostat http://ec.europa.eu/eurostat/data/database
Information on large carnivore presence was extracted from Kaczensky et al. (2012)
*Data extracted from World DataBank http://databank.worldbank.org/data/
†Value extrapolated from World DataBank estimates. We calculated a "PPP to PPS exchange rate" by dividing the GDP PPS per capita by the GDP PPP in USD (reference year 2011) in all the studied countries. Then, we multiply the figures presented by the World DataBank in the country of interest by the average "PPP to PPS exchange rate" (1.37; SD = 0.63)
‡Data extracted from Statistical Office of the Slovak Republic www.statistics.sk

Table A2. Summary of large carnivore populations, damage management policies and compensation costs in European countries in 2005-2012.

Country	Population*	Period	Distribution area (km^2)	Rate of range change	Estimated no. of individuals	Compensation system	Compensation costs per year (EUR)	Compensation costs per year (PPS)†	Compensation costs per individual (PPS)†
BROWN BEAR									
EUROPEAN SUMMARY		2005-2011	1,200,000	-	17,000	-	4,200,000	3,400,000	1,800
Albania	DP	2006-2010	13,400	NA	180-200	no	NA	NA	NA
Austria	A	2007-2011	2,300	Returned	5	yes	NA	NA	NA
Bosnia&Herzegovina	DP	2005	33,200	1.3	550	NA	NA	NA	NA
Bulgaria	EB	2007-2011	32,800	2.5	530-590	yes	81,850	186,142	332
Croatia	DP	2005-2011	11,824	1.4	1,000	yes	6,000	8,976	9
Estonia	Blt	2011	37,000	3.3	700	yes	13,200	18,998	27
Finland	K	2007-2011	357,900	3.4	1,600-1,800	yes	922,700 *81% reindeer‡*	496,075	292
France	P	2006-2011	8,400	4.3 (Reinf.)	22§	yes	103,000	91,964	4,180
FYR Macedonia	DP	2006-2011	17,200	NA	160-200	yes	NA	NA	NA
Greece	EB, DP	2006-2011	25,000	4.0	400-450	yes	140,725	156,361	368
Italy	A	2006-2011	5,500	6.5 (Reinf.)	33-36	yes	48,000	72,727	2,139
Italy	CA	2006-2011	6,400	3.2	37-52	yes	50,000	75,758	1,722
Latvia	Blt	2010	1,400	7.9	10-15	no	NA	NA	NA
Montenegro	DP	2008-2011	7,000	NA	270	NA	NA	NA	NA
Norway	K, S	2007-2011	194,200	10.7	151	yes	2,035,000 *2% reindeer‡*	1,418,852	9396
Poland	Cpt	2007-2010	10,400	6.8	80	yes	29,891	49,041	613
Romania	Cpt	2011	89,900	1.4	6000	yes	NA	NA	NA
Serbia	DP	2010	9,600	NA	58-78	yes	NA	NA	NA
Slovakia	Cpt	2006-2010	21,200	2.4	800-1,100	yes	18,700-20,400	29,412	31
Slovenia	A, DP	2006-2011	13,700	3.6	396-480	yes	156,000	192,593	440
Spain	Cnt	2010	7,700	4.3	195-210	yes	321,000	341,479	1,691
Spain	P	2010	5,100	4.1(Reinf.)	22§	yes	20,500	21,808	991
Sweden	S	2007	316,300	3.3	2,968-3,667	yes	220,000 *86% reindeer‡*	185,847	56
Switzerland	A	2006-2011	1,200	Returned	0-2	yes	0-38,000	14,271	7,136

Table A2. Continued

Country	Population*	Period	Distribution area (km^2)	Rate of range change	Estimated no. of individuals	Compensation system	Compensation costs per year (EUR)	Compensation costs per year (PPS)†	Compensation costs per individual (PPS)†
EURASIAN LYNX									
EUROPEAN SUMMARY		2006-2012	1,300,000	-	9,000	-	8,900,000	6,400,000	700
Albania	Blkn	2006-2010	4,800	1.0	5-10	no	NA	NA	NA
Austria	A, BB	2006-2011	3,800	Returned	8-15	yes	0	0	0
Bosnia&Herzegovina	D	2000-2012	14,800	Returned	70	NA	NA	NA	NA
Bulgaria	Cpt	2000-2012	13,00	Returned	11	yes	0	0	0
Croatia	D	2006-2012	12,332	Returned	50	yes	0	0	0
Czech Republic	BB	2009-2012	10,900	Reintroduced	30-45	yes	NA	NA	NA
Czech Republic	Cpt	2009-2012	2,100	1.5	20	yes	NA	NA	NA
Estonia	Blt	2011	46,800	1.1	790	yes	2,000	2,878	4
Finland	K	2011	141,600	20.5	2,430-2,610	yes	842,722 *98% reindeer‡*	700,371	283
France	A, J, VP	2008-2010	50,800	Reintroduced	108	yes	20,000	17,699	164
FYR Macedonia	Blkn	2011	12,700	1.0	23	NA	NA	NA	NA
Germany	BB	2010-2011	4,200	Reintroduced	12	yes	0	0	0
Germany	HM	2010	2,400	Reintroduced	11	yes	399	382	35
Hungary	Cpt	2011	4,100	Returned	1-3	no	NA	NA	NA
Italy	A	2012	700	Returned	10-15	NA	NA	NA	NA
Latvia	Blt	2010	61,200	Returned	600	NA	NA	NA	NA
Lithuania	Blt	2011	6,700	2.0	40-60	NA	NA	NA	NA
Norway	S	2012	298,200	5.6	384-408	yes	3,200,000-6,300,000 *47% reindeer‡*	2,972,493	7506
Poland	Blt, Cpt	2012	34,000	2.5	200	yes	0	0	0
Romania	Cpt	2011	92,600	2.0	1,200-1,500	yes	NA	NA	NA
Serbia	Cpt	2010	7,500	NA	50	NA	NA	NA	NA
Slovakia	Cpt	2010	30,800	6.2	300-400	yes	0	0	0
Slovenia	A, D	2011	7,900	Reintroduced	15-25	yes	975	1175	58.7
Sweden	S	2006-2011	428,700	3.6	1,400-1,900	yes	3,010,000-3,525,000 *99% reindeer‡*	2,725,580	1652
Switzerland	A, J	2006-2011	19,400	Reintroduced	124-143	yes	6,500-25,000	6,563	49

Table A2. Continued

Country	Population*	Period	Distribution area (km^2)	Rate of range change	Estimated no. of individuals	Compensation system	Compensation costs per year (EUR)	Compensation costs per year (PPS)†	Compensation costs per individual (PPS)†
WOLF									
EUROPEAN SUMARY		2006-2012	1,300,000	-	12,000	-	7,900,000	7,900,000	2,400
Albania	DB	2010	21,200	NA	200-250	no	NA	NA	NA
Austria	A	2009-2011	2,900	Returned	2-8	yes	NA	NA	NA
Bosnia&Herzegovina	DB	2010	48,500	1.0	650	NA	NA	NA	NA
Bulgaria	DB	2011	87,100	5.0	1000	no	NA	NA	NA
Croatia	DB	2010	27,800	2.6	168-216	yes	194,000	275,672	1,421
Czech Republic	Cpt	2006-2010	1,100	Returned	4-8¶	yes	1,800	2,671	445
Estonia	Blt	2010-2011	42,500	9.4	200-260	yes	95,000	136,726	595
Finland	K	2007-2012	141,600	3.4	150-165	yes	532,688-1,404,302 *91% reindeer‡*	547,578	3,466
France	A, P	2011-2012	50,600	Returned	250	yes	1000,000	893,463	3,574
FYR Macedonia	DB	2010	18,600	1.5	267	NA	NA	NA	NA
Germany	CEL	2011-2012	7,800	Returned	43	yes	26,584	25,586	595
Greece	DB	2006-2009	71,500	1.9	700**	yes	800,000-1,500,000	1,292,134	1,846††
Italy	IP	2006-2011	59,600	5.8	600-800	yes	NA	NA	NA
Italy	A	2010-2011	5,800	Returned	70	yes	92,656	138,327	1,976
Latvia	Blt	2010	29,200	Returned	200-400	no	NA	NA	NA
Lithuania	Blt	2011	26,700	5.0	300	no	NA	NA	NA
Montenegro	DB	2010-2012	8,100	NA	NA	NA	NA	NA	NA
Norway	S, K	2007-2012	94,800	Returned	45-49‡‡	yes	120,000-500,000 *11% reindeer‡*	193,994	4,128
Poland	Cpt, Blt, CEL	2008-2010	65,800	4.8	576-723	yes	94,900	155,325	239
Portugal	NWI	2006-2011	22,300	1.52§§	220-430¶¶	yes	674,925	823,079	2,533[a]
Romania	Cpt	2011	125,900	1.5	2,300-2,700	yes	NA	NA	NA
Serbia	DB	2011	44,200	1.4	750-850	no	NA	NA	NA
Slovakia	Cpt	2010	25,500	6.7	200-400	yes	16,000	23,932	80
Slovenia	DB	2007-2011	9,000	4.4	32-43	yes	269,000	328,049	8,866
Spain	NWI	2008-2010	99,800	1.9	1196[b]	yes	2,000,000[c]	2,127,660	1,779
Spain (Asturias)	NWI	2006-2010	8,800	1.4	133[d]	yes	789,713[d]	840,120	6,317

Table A2. Continued

Country	Population*	Period	Distribution area (km^2)	Rate of range change	Estimated no. of individuals	Compensation system	Compensation costs per year (EUR)	Compensation costs per year (PPS)†	Compensation costs per individual (PPS)†
Spain	SM	2010-2012	800	0.1	2	yes	0	0	0
Spain	P	2010-2012	700	Returned	1-2	yes	1,500	1,613	805
Sweden	S	2010	95,400	Returned	238-305[e]	yes	100,000 *0% reindeer‡*	80,916	299
Switzerland	A	2006-2011	7,800	Returned	8	yes	40,000-120,000	60,089	7,511
WOLVERINE									
EUROPEAN SUMMARY		2006-2011	73,000	-	1,200	-	7,500,000	5,600,000	6,300
Finland	K, S	2011	21,200	4.0	165-175	yes	NA	NA	NA
Norway	S	2006-2011	2,900	6.0	339-431	yes	4,500,000-6,000,000 *38% reindeer‡*	3,749,763	9,740
Sweden	S	2006-2011	48,500	4.9	580-780	yes	2,000,000-2,500,000 *100% reindeer‡*	1,876,834	2,760

Data extracted from Kaczensky et al. (2012)

EUR: Euros; PPS: Purchasing power standard; NA: no information available; Returned: populations established by dispersal individuals after prolonged absence of their presence; Reinf.: populations reinforced before extinction by translocating individuals from other populations; Reintroduced: populations reintroduced after extinction.

*Populations as follows. A: Alpine; Blkn: Balkan; Blt: Baltic; BB: Bohemian-Bavarian; Cnt: Cantabrian; Cpt: Carpathian; CA: Central Apennine; CEL: Central European Lowland; D: Dinaric; DB: Dinaric-Balkan; DP: Dinaric-Pindos; EB: Easter-Balkan; HM: Harz Mountains; IP: Italian Peninsula; J: Jura; K: Karelian; NWI: NW Iberia; P: Pyrenean; S: Scandinavia; SM: Sierra Morena; VP: Vosges Palatinian

†Calculated using data extracted from Eurostat http://ec.europa.eu/eurostat/data/database, see Supplementary Methods for further information

‡Percentage of compensations paid for semi-domestic reindeer predation in Sami regions. In Norway, the rest of compensations were paid for free-ranging sheep predation

§Number of individuals estimated for the whole Pyrenean bear population

¶Data extracted from Kovařík et al. (2014)

**No updated data, national estimate from 1999

††Calculated with estimate from 1999

‡‡23-24 individuals shared in the Scandinavian population and included in estimates for both Norway and Sweden

§§Only considers the wolf population in the north of the Tagus river. In the south the wolf population became extinct

¶¶No updated data, national estimate from 2002/2003

[a] Calculated with estimates from 2002/2003

[b] No updated data at the national level, guess estimate from different periods between 1997 and 2011. The number of wolf individuals was calculated by multiplying the number of packs by the average number of wolves per pack in different European countries (4.6 wolves per pack; SD = 1.45; calculated with the data available in Kaczensky et al. (2012)).

[c] Guess estimate calculated by adding (1) compensation payment for all damages throughout the territory, (2) compensation payment of wolf damage only in hunting reserves, and (3) reimbursement to farmers who have taken out private insurance

[d] Data extracted from Fernández-Gil et al. (2016).The number of wolf individuals was calculated by multiplying the number of pack by the average number of wolves per pack in different European countries (4.6 wolves per pack; SD = 1.45; calculated with the data available in Kaczensky et al. (2012)).

[e] Calculated by subtracting the number of wolves present only in Norway (i.e. 22-25 wolves after excluding “border packs” and pairs) to the total estimation for the Scandinavian population (i.e. 260-330 wolves)

Table A3. Summary of linear and linear mixed-effects models testing for the effect of different ecological and socioeconomic variables on (1) the compensation costs for large carnivore damage in Europe averaged across 2005-2012, (2) the rate of large carnivore range change and (3) the annual costs of prevention measures subsidized within the bear range in the period 2005-2012 (see *STATISTICAL ANALYSES* section in Methods S1). Compensation and prevention costs were divided by the estimated population sizes of the respective large carnivore species (Table S5). The explanatory variables were standardized to zero mean and unit variance to allow for comparison of effect sizes. ΔAIC_c was calculated across the set of models for each response as the difference between the AIC_c value of a given model and the minimum AIC_c value of all the candidate models. The models and results discussed in the main text are highlighted in bold face type.

*RESPONSE: Average costs of compensation per large carnivore individual and per year** *SAMPLE SIZE, n_{obs} = 49; RANDOM INTERCEPT, n_{spec} = 4 species of large carnivore*								
Model	Variable	df	β	SE	*P*-value	Marginal R^2†	Conditional R^2	ΔAIC_c
1	GDP per capita	5	**1.42**	**0.26**	**<0.001**	**0.29**	**0.59**	0.00
	Range change		-0.50	0.28	0.084			
2	GDP per capita	4	1.24	0.25	<0.001	0.24	0.59	0.72
3	*Intercept only*	3	-	-	-	0.00	0.47	19.08
4	Range change	4	0.07	0.33	0.80	0.01	0.47	21.42
RESPONSE: Rate of large carnivore's range change *SAMPLE SIZE, n_{obs} = 51; RANDOM INTERCEPT, n_{spec} = 4 species of large carnivore*								
5	GDP per capita	4	**7.16**	**3.11**	**0.026**	**0.10**	**0.15**	0.00
6	*Intercept only*	3	-	-	-	0.00	0.06	2.90
RESPONSE: Average costs of compensation for brown bear damage per bear individual and per year ‡ *SAMPLE SIZE, n_{obs} = 16*								
7	Range change	3	**1.27**	**0.43**	**0.010**	0.34	-	0.00
8	GDP per capita	3	1.23	0.43	0.012	0.32	-	0.49
9	*Intercept only*	2	-	-	-	-	-	4.73
RESPONSE: Average costs of compensation for lynx damage per lynx individual and per year ‡ *SAMPLE SIZE, n_{obs} = 13*								
10	GDP per capita	3	2.05	0.58	0.005	0.48	-	0.00
11	*Intercept only*	2	-	-	-	-	-	6.35
12	Range change	3	**0.24**	**0.84**	**0.78**	-0.08	-	9.72
RESPONSE: Average costs of compensation for wolf damage per wolf individual and per year ‡ *SAMPLE SIZE, n_{obs} = 18*								
13	GDP per capita	3	0.56	0.29	0.07	0.14	-	0.00
14	*Intercept only*	2	-	-	-	-	-	0.80
15	Range change	3	**-0.13**	**0.32**	**0.69**	-0.05	-	3.52
*RESPONSE: Annual costs of compensation for brown bear damage per bear individual ** *SAMPLE SIZE, n_{obs} = 62; RANDOM INTERCEPT, n_{reg} = 12 countries or regions*								
Model	Variable	df	β	SE	*P*-value	Marginal R^2†	Conditional R^2	ΔAIC
16	Prevention costs per bear*	5	**0.40**	**0.19**	**0.037**	**0.51**	**0.91**	0.00
	Range change		**1.22**	**0.39**	**0.010**			
17	Range change	4	1.39	0.44	0.010	0.43	0.91	1.88
18	GDP per capita	6	-0.08	0.40	0.85	0.51	0.91	2.42
	Prevention costs per bear*		0.42	0.21	0.049			
	Range change		1.27	0.46	0.020			
19	GDP per capita	5	0.20	0.39	0.60	0.44	0.91	3.98
	Range change		1.26	0.50	0.030			
20	Prevention costs per bear*	4	0.40	0.19	0.042	0.04	0.90	5.42
21	GDP per capita	5	0.37	0.39	0.36	0.13	0.89	7.05
	Prevention costs per bear*		0.35	0.21	0.10			
22	*Intercept only*	3	-	-	-	0.00	0.92	7.14
23	GDP per capita	4	0.60	0.37	0.11	0.10	0.89	7.50

Table A3. Continued

<table>
<tr><td colspan="9"><i>RESPONSE: Annual costs of prevention measures subsidized within bear range per bear individual*</i>
<i>SAMPLE SIZE, n_{obs} = 62; RANDOM INTERCEPT, n_{reg} = 12 countries or regions</i></td></tr>
<tr><td>Model</td><td>Variable</td><td>df</td><td>β</td><td>SE</td><td><i>P</i>-value</td><td>Marginal R^2†</td><td>Conditional R^2</td><td>ΔAIC_c</td></tr>
<tr><td>24</td><td>GDP per capita</td><td>4</td><td>3.42</td><td>0.77</td><td><0.001</td><td>0.49</td><td>0.83</td><td>0.00</td></tr>
<tr><td>25</td><td>GDP per capita</td><td>5</td><td>3.61</td><td>0.96</td><td><0.001</td><td>0.48</td><td>0.83</td><td>2.26</td></tr>
<tr><td></td><td>Range change</td><td></td><td>-0.36</td><td>1.09</td><td>0.75</td><td></td><td></td><td></td></tr>
<tr><td>26</td><td>Range change</td><td>4</td><td>2.02</td><td>1.16</td><td>0.11</td><td>0.17</td><td>0.81</td><td>12.13</td></tr>
<tr><td>27</td><td><i>Intercept only</i></td><td>3</td><td>-</td><td>-</td><td>-</td><td>0.00</td><td>0.81</td><td>12.63</td></tr>
<tr><td colspan="9"><i>RESPONSE: Annual costs of compensation per brown bear individual</i>
<i>SAMPLE SIZE, n_{obs} = 50; RANDOM INTERCEPT, n_{reg} = 12 countries or regions</i></td></tr>
<tr><td>28</td><td>Range change</td><td>4</td><td>1.44</td><td>0.45</td><td>0.009</td><td>0.44</td><td>0.92</td><td>0.00</td></tr>
<tr><td>29</td><td>Cumulative prevention*§</td><td>5</td><td>-0.03</td><td>0.25</td><td>0.92</td><td>0.43</td><td>0.92</td><td>2.47</td></tr>
<tr><td></td><td>Range change</td><td></td><td>1.44</td><td>0.46</td><td>0.011</td><td></td><td></td><td></td></tr>
<tr><td>30</td><td><i>Intercept only</i></td><td>3</td><td>-</td><td>-</td><td>-</td><td>0.00</td><td>0.92</td><td>5.28</td></tr>
<tr><td>31</td><td>Cumulative prevention*§</td><td>4</td><td>-0.10</td><td>0.26</td><td>0.71</td><td>0.001</td><td>0.93</td><td>7.54</td></tr>
</table>

df, degrees of freedom; β, estimate; SE, standard error

*variable transformed to its natural logarithm

†Adjusted R^2 for simple linear regressions

‡Simple linear regression

§highly correlated to the *GDP per capita* and to the *Prevention costs per bear* (r > 0.7)

Table A4. Detailed summary of funded measures officially classified as damage prevention within bear range in Europe in 2003-2015.

Country/region	Years	Funding source	Funded preventive measures	Cost (EUR)*
Central Italy	2004-2008	LIFE Nature project "Coex"	Electric fences: 28	18,363
			Livestock guarding dogs: 8	3,464
		National park authorities	Physical barriers: 43 bear-proof metal gates	3,922
	2010-2014	LIFE project "Arctos"	Electric fences: 245	68,129
Cantabrian Mt. (Spain)‡	2005-2009	Asturian regional government	Electric fences: 11	29,826
			Physical barriers: 40 closures for apiaries, orchards and farms	183,498
			Physical barriers: Construction of 5 “cortines”† to protect apiaries	25,653
			Electric fences: 1643	164,835
	2001-2015	Fundacion Oso Pardo	Public awareness: 4250 leaflets for beekeepers	
Catalonia (Spain)‡	2007-2010	Catalonian regional government	Electric fences, livestock guarding dogs, shepherds, coordination of grouping different livestock herds	1,048,952
Croatia	2006-2008	LIFE Nature project "Coex"	Electric fences: 14	2,146
Estonia‡	2013-2015§	Estonian Environmental Board	Electric fences: ca 40 fences for 34 beneficiaries	10,544
France‡	2007-2012	National government and European Funds (FEDER & FEADER)	Shepherds: salaries for 350 shepherds per year	6,966,964
			Livestock guarding dogs: ca 1200 dogs for 250 beneficiaries	671,429
			Electric fences: ca 80 electric fences for 62 beneficiaries	50,893
			Restructuring of husbandry practices: Transport of preventive measures and other equipment to the summer pastures by helicopter and with mules	716,071
Greece‡,¶	2007-2010	NGO "ARCTUROS"	Livestock guarding dogs: 126	27,692
Norway‡	2007-2010	National government	Electric fences, livestock guarding dogs, patrolling of herding areas, herding-related measures and other measures	12,383,868
	2015**	National government	Electric fences	211,934
			Sheep guarding dogs	24,670
			Restructuring of husbandry practices:	
			Early bring back of sheep in fall	390,025
			Late release of sheep in spring	53,435
			Moving sheep to other grazing areas	138,224
			Moving reindeer to other grazing areas	137,721
			Sheep grazing in fenced areas	411,275
			Sheep emergency area	32,201
			Calving reindeer in fenced areas	1,542
			Artificial feeding in sensitive periods to protect reindeer	132,615
			Compensation-related:	
			Increase surveillance in sheep grazing areas	310,303
			Increase surveillance in reindeer grazing areas	129,543
			Electronic surveillance in sheep grazing areas	330,049
			Dogs to find sheep carcasses	47,276

Table A4. Continued

Country/region	Years	Funding source	Funded preventive measures	Cost (EUR)*
			Technical equipment to protect reindeer	35,387
			Other measures to protect sheep	79,297
Norway‡	2015**	National government	Others:	
			Other measures to protect reindeer	34,138
Poland	2011-2015	Regional governments	Electric fences: 56	17,822
			Physical barriers: 3 km of game fencing	10,333
			Others: 10 alarm pistols and 30 boxes of firecrackers	806
	2012-2015	WWF Poland	Electric fences: 44	9,217
Slovenia‡	2006-2012	Slovenia Forest Service	Electric fences: 31	57,407
	2006-2010	Slovenian Environmental Agency	Electric fences: 488	346,541
	2011-2013	LIFE Nature project "SloWolf"	Electric fences: 13	20,610
			Livestock guarding dogs: 9	5,488
Sweden‡	2003-2015	National government	Mostly electric fences and related material to protect livestock, sometimes covering also a part of the labour cost for fence installation	4,594, 378
Trentino (Italy)‡	2005-2015	Regional government	Mostly electric fences and related material	254,283
			Livestock guarding dogs: 7 livestock guarding dogs (2014-2015)	N.A.
			Restructuring of husbandry practices: Helicopter transportation of shepherd cabins to summer pastures, and additional electric fences for herds in summer pastures	N.A.
	2010-2014	LIFE Nature project "Arctos"	Electric fences: 278	142,990

*Euros valued at 2011 purchasing power standards (PPS)

†Cortines is the name of traditional small fortifications built of stone

‡Countries and regions in which prevention is funded systematically on a yearly basis

§Systematic prevention program started on the year 2013

¶Additional electric fences were eventually subsidized

**1,743,038 EUR were additional invested for preventive culling, education, local research and development

Table A5. Summary of the estimated numbers of brown bears in European countries or regions, and average costs (± 1 SD) of bear damage compensation and funded measures classified for damage prevention within bear range per year in 2005-2012. The period was selected based on the availability of data on compensation and prevention costs. Data compiled by the authors. The costs are valued in euros at purchasing power parities in 2011 (see Methods S1).

Country/region	Years	No bears*	Cost type	Average cost in EUR	Funding organization or body
Central Italy†	2005-2010	51	Compensation	58,483 ± 20,620	Regional government
			Prevention	4,124 ± 2,306	LIFE Nature project "Coex" and National Park authorities
Cantabrian Mt. (Spain)‡	2005-2010	222	Compensation	238,215 ± 61,956	Regional governments
			Prevention	61,350 ± 45,746	Asturias regional government and Fundacion Oso Pardo
Catalonia (Spain)‡	2007-2010	25¶	Compensation	9,368 ± 3,002	Catalonian regional government
			Prevention	139,531 ± 6,075	Catalonian regional government
Croatia	2005-2011	1000	Compensation	8,420 ± 6,926	National government and hunter associations
			Prevention	1,188 ± 1,617	LIFE Nature project "Coex"
Estonia†,‡,§	2007-2011	700	Compensation	14,665 ± 9247	National government
			Prevention	0	-
France‡	2007-2010	25¶	Compensation	88,784 ± 32,615	National government
			Prevention	1,395,737**	National government and European funds
Finland	2007-2010	1037††	Compensation	542,230 ± 83,595	National government
			Prevention	NA	-
Greece‡	2007-2010	410	Compensation	302,010 ± 31,111	Semi-public organization "ELGA"
			Prevention	3,818 ± 2,598	NGO "ARCTUROS"
Norway‡	2007-2010	151	Compensation	1,103,692 ± 174,098	National government
			Prevention	3,095,967 ± 671,931	National government
Poland†	2007-2012	95	Compensation	51,480 ± 33,471	Regional governments
			Prevention	4,793 ± 7,517	Regional governments and WWF Poland
Slovakia	2007-2012	800	Compensation	122,850 ± 5,4017	Regional government
			Prevention	NA	-
Slovenia‡	2006-2010	440	Compensation	201,694 ± 69,100	National government
			Prevention	78,445 ± 7,502	National government and LIFE Nature project "SloWolf"
Sweden‡	2007-2010	3300	Compensation	177,510 ± 17,733	National government
			Prevention	258,549 ± 141,489	National government
Trentino (Italy)‡	2005-2012	30	Compensation	58,790 ± 33,239	Regional government
			Prevention	31,843 ± 14,667	Regional government and LIFE nature project "Arctos"

NA, Not available information
*Extracted from Bautista et al. (2017)
†Costs of measures to prevent other large carnivore damage within bear range not included
‡Prevention funded systematically every year
¶Total number of estimated bears are shared by Catalonia and France
§Preventive measures started to be subsidized systematically by the Environmental Board of Estonia in 2013
**Calculated from total expenditures in 2007-2012 and divided by the number of years in the period
††Extracted from Wikman (2008a, 2008b, 2009, 2010)

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CHAPTER III

SPATIAL ECOLOGY OF CONFLICTS:
UNRAVELLING PATTERNS OF WILDLIFE DAMAGE
AT MULTIPLE SCALES

with

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SUMMARY

Human encroachment into natural habitats is typically followed by conflicts derived from wildlife damages to agriculture and livestock. Spatial risk modelling is a useful tool to gain understanding of wildlife damage and mitigate conflicts. Although resource selection is a hierarchical process operating at multiple scales, risk models usually fail to address more than one scale, which can result in the misidentification of the underlying processes. Here, we addressed the multi-scale nature of wildlife damage occurrence by considering ecological and management correlates interacting from household to landscape scales. We studied brown bear (*Ursus arctos*) damage to apiaries in the North-eastern Carpathians as our model system. Using generalized additive models, we found that brown bear tendency to avoid humans and the habitat preferences of bears and beekeepers determine the risk of bear damage at multiple scales. Damage risk at fine scales increased when the broad landscape context also favoured damages. Furthermore, integrated-scale risk maps resulted in more accurate predictions than single-scale models. Our results suggest that principles of resource selection by animals can be used to understand the occurrence of damages and help mitigate conflicts in a proactive and preventive manner.

1. INTRODUCTION

Conflicts arising from wildlife damage to livestock and agriculture are one of the most urgent and complex challenges for conservationists today (Frank et al., 2019; Redpath et al., 2015). To mitigate these conflicts, public administrations often compensate farmers for the economic losses caused by wildlife damages (Ravenelle and Nyhus, 2017) and eventually encourage measures to prevent these damages (Bautista et al., 2019). However, compensation and prevention programs systematically neglect landscape heterogeneity in damage risk (Miller, 2015).

An approach to effectively reduce the impact of wildlife damage is to model risk across space (Miller, 2015). From an ecological perspective, the risk of damage can be described as the probability of selection of anthropogenic food resources by wild animals. Resource selection is a scale-dependent process, i.e., inference at a broad scale may not adequately explain resource use at a finer scale (Boyce, 2006). For example, the distance to forest may be a strong predictor of livestock predation at intermediate scales but weak at finer ones (Searle et al., 2006). In addition, multiscale resource selection studies show that broader-scale features can constrain selection at finer scales; i.e., fine-scale foraging decisions depend on the spatial heterogeneity of resources at broader scales (Searle et al., 2006). That implies the need to integrate inferences across scales to understand the landscape characteristics that determine the probability of resource selection by animals.

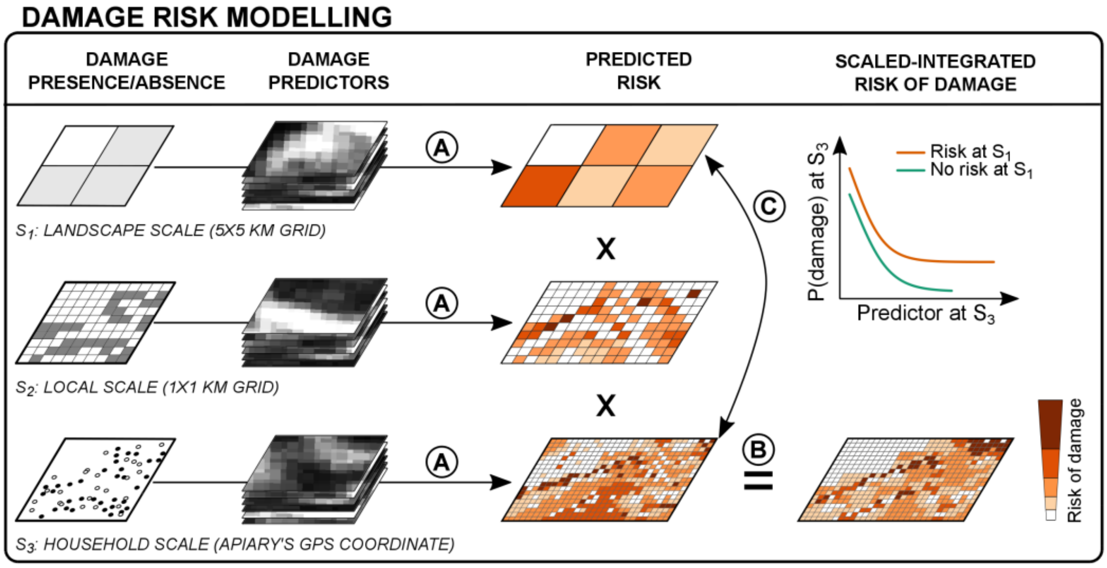

Figure 1. Conceptual diagram showing a multi-scale approach to model the risk of wildlife damage. The risk of damage is modelled at multiple scales independently based on a priori specified scale-dependent predictions that test one or more general hypotheses. At each scale, the risk of damage can be extrapolated to a larger spatial extension to inform about potential conflict zones in the case of dispersing individual and/or future population increases (A). The resulting predicted probabilities of damage are multiplied at the smallest scale to produce a scale-integrated risk map (B). Finally, it is assessed if the damage risk at fine scale depends on whether the context at larger scales favours damage or not (C).

Integrating the output of scale-dependent resource selection functions provides the relative probability of selection at a lower scale (e.g., selection of a farm) conditional upon the relative probability of selection at a higher scale (e.g., selection of home range). This is useful for conservation and management because it allows predicting and mapping the probability of selection with higher accuracy than single-scale models (Lipsey et al., 2017). In the case of conflict mitigation, public administrations and farmers try to prevent damages at different levels, ranging from the national administrative levels to the household (Miller, 2015). Providing scale-integrated risk maps has big potential to understand the ecological processes underlying damage occurrence and providing an effective tool for conflict mitigation.

In this study, we assessed the scale-dependent probability of brown bear (*Ursus arctos*) damage to apiaries in the Polish Carpathian Mountains (Fig. 1 & Fig. 2). The brown bear is the most abundant terrestrial large carnivore in Europe (Chapron et al., 2014). Its distribution range has been increasing in the last decades in Europe (Chapron et al., 2014) and is expected to continue growing in the near future (Scharf and Fernández, 2018). Brown bear predation on domestic beehives is widespread and in some countries (e.g. Poland) it is nearly the only type of human property that bears damage (Bautista et al., 2017).

In the Carpathian population, bears mainly select forest-dominated areas with low density of roads and human settlements (Fernández et al., 2012; Ziółkowska et al., 2016). The species sometimes roam in the surroundings of agricultural fields, where they may find natural food resources, such as berries and herbaceous vegetation (Pop et al., 2018) as well anthropogenic resources like beehives (Bautista et al., 2017). We hypothesized that bear damages to beehives would mostly occur in areas of high bear habitat suitability with low human influence (Ziółkowska et al., 2016) but with a high availability and accessibility of apiaries.

To evaluate this hypothesis we modelled the risk of bear damage to beehives at three scales encompassing (1) the scale of a bear home range (hereafter landscape scale); (2) the habitat selection of bears within their home ranges and the distribution of apiaries at the local scale (hereafter local scale); and (3) the microhabitat preferences of bears and the preferences of beekeepers in locating their apiaries (hereafter household scale). We fitted one risk model at each scale and integrated the results into a multiscale risk map. We run an additional model at the household scale to evaluate to what extent the use of preventive measures decreases the risk of damage. We finally assessed whether the risk of damage follows a spatially hierarchical structure, in which the broader landscape context can shape bear damage response to household conditions.

2. METHODS

2.1. Study area

This study covers the Carpathian Mountain range in the Podkarpackie Province, Poland (Fig. 2). This area is characterized by gentle slopes and low to medium altitude mountains ranging from 199 to 1199 meters above sea level. The land is mainly covered by forest (62%) and agriculture (32%). Human density averages 44 inhabitants/km^2, while the average density of roads is 3.2 km/km^2. Honey production is an important economic activity in the area, mostly carried out in domestic exploitations. Many apiaries are unprotected against bear damage. Others are close to buildings or fenced with mesh fence, and only a few of them are well protected with electric fencing (see Fig. A1 in the supplementary material). The average number of beehives per apiary is 17.8 (SD= 18.21), ranging from just one to over a hundred (Fig. A1).

2.2. Bear damage data

We compiled data on bear damages to apiaries from official records collected through the damage compensation program in 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. After a preliminary exploration of the data we decided to use only data from 2010 to avoid potential omissions and biases associated to a limited knowledge by farmers of the compensation scheme at the initial period of the program implementation. Finally, we filtered out records with imprecise or missing location of the attacked beehives.

We obtained data from 406 bear damages to apiaries from 2010 to 2017. All these records contained geographic information in the form of geographic coordinates (68% records) or the name of the nearest village- the latter were mapped to the village (Fig. 2).

Damages to apiaries were transferred to 5x5 and 1x1 km grids for the landscape and the local scale analyses. At the landscape scale we used the same 5x5km grid as Fernández et al. (2012), who provided modelled probabilities of bear occurrence based on habitat characteristics in the Northern Carpathians, including our study area. From that grid, we selected 338 cells covering the Carpathian Mountain range within Podkarpackie Province. At the local scale we used a grid of 8,450 1–km cells nested in the 5x5km grid. Finally, at the household scale we used the GPS locations of apiaries sampled during 99 days of field work specifically conducted for this study between August 2014 and June 2015 (see Appendix A in the supplementary material). In addition to these locations, we used data of damaged apiaries from compensation records for the period 2014-2017, since during these years the damage inspectors systematically collected GPS locations at damage sites. In total, we gathered information from 293 apiaries, of which 123 were damaged.

2.3. Predictors of damage at different scales

We analyzed the occurrence of bear damage to apiaries based on scale-specific predictions within the bear range in Podkarpackie Province (see Table B1). Specifically, we run one spatial correlation model per each scale, plus an extra model at the household scale to assess the effect of preventive measures on damage risk; i.e. four models: landscape model, local model, household model and preventive model. To delimit the bear range we selected the 5x5 km cells with bear presence based on (Fernández et al., 2012) and on the location of damage events occurring in 2010-2017. We also added cells that had over 40% of forest cover and were adjacent to at least three cells with bear presence to include places where bears could potentially occur but be undetected. This selection resulted in 159 (out of 338) and 3,355 (out of 8,450) cells of the 5x5 and 1x1 km grids, respectively. All the apiaries used for the household and the preventive models were located within this selected area. To assess the probability of damage occurrence at each scale, we classified all cells and apiaries with binary values, with 0 and 1 for undamaged and damaged cells/apiaries, respectively.

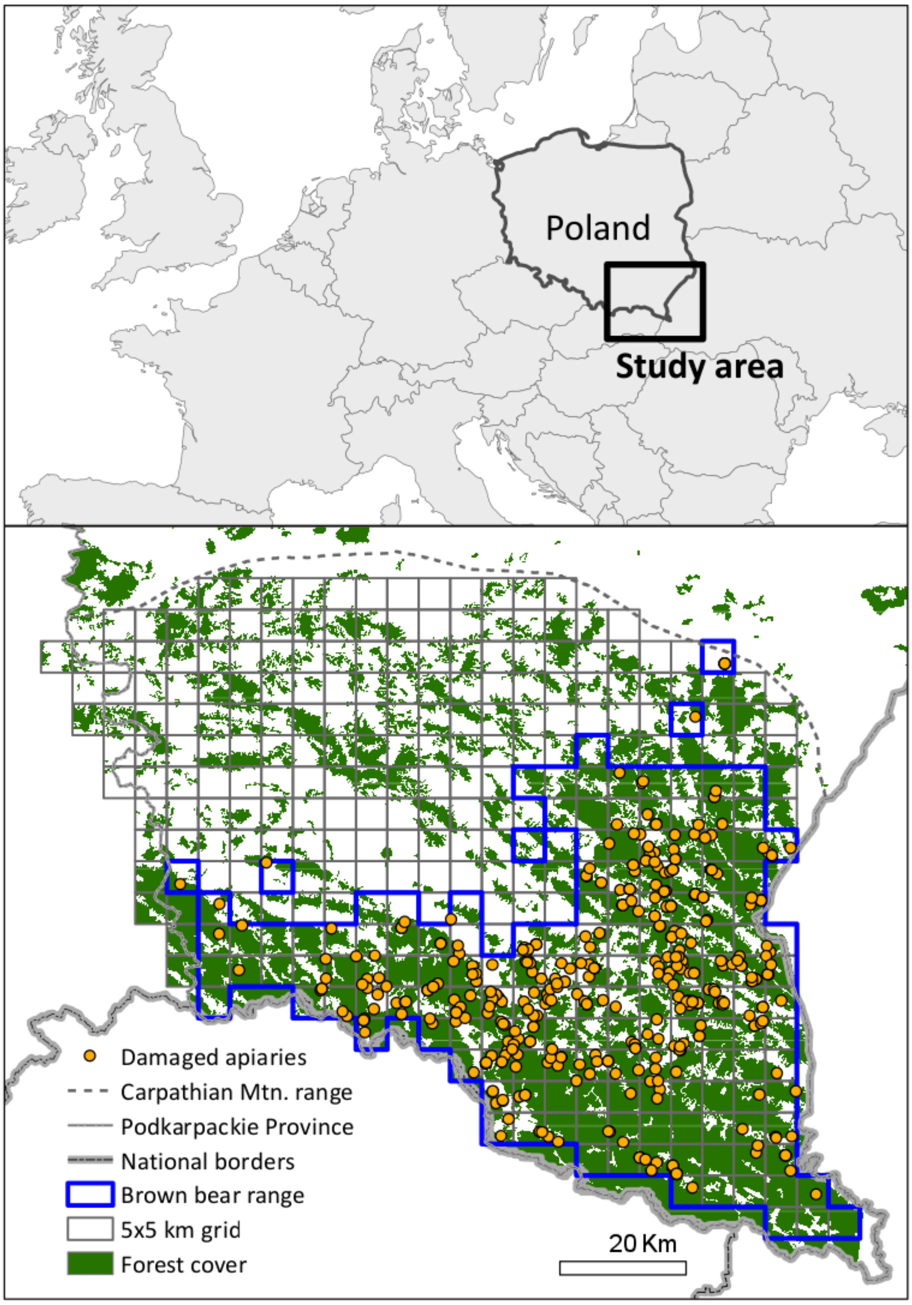

Figure 2. Location of study area showing the apiaries damaged by the brown bear (*Ursus arctos*) in the Northern Carpathian Mountains (SE Poland, Podkarpackie Province) in the period 2010-2017.

At the landscape scale, we expected the probabilities of bear and apiary presence to be inversely correlated, i.e., bears occurring in forested areas with relatively little human influence and apiaries in more altered landscapes dominated by agriculture (Table B1). For each 5x5 km cell we extracted the probability of bear presence from (Fernández et al., 2012). We, then, calculated the probability of apiary presence by modelling the location of apiaries recorded during our fieldwork as a response to different environmental and socioeconomic predictors (see Appendix A). Finally, we calculated the damage probability as a function of bear presence probability and apiary presence probability.

At the local scale we calculated in each 1x1 km cell 12 predictors expected to influence the risk of bear damage to beehives (Table B1). Specifically, we predicted that damage occurrence is directly related to the densities of humans, settlements and roads, to the proportion of agricultural cover and to the length of forest edges, all of which are higher at low altitudes and gentle slopes (Table B1). We also expected that the above predicted relationships would have non-linear effects on damage occurrence. For example, we expected damage risk to have a positive relationship with human population density until a certain threshold in which high human densities would deter bears and shift the relationship into negative.

Finally, at the household scale, we predicted that the apiaries that are more exposed to bears are more vulnerable to bear damage, i.e., far from buildings and located within areas of high probability of bear presence. Accordingly, for each apiary we calculated the probability of bear presence, the distance to the nearest forest patch, the distance to the nearest building, the number of buildings in a radius of 200 meters around the apiary and the forest cover in the same 200-meters radius. At this scale, we also aimed to assess the influence of preventive measures in damage occurrence. For that, we used a subsample of 151 apiaries (32 of them damaged) for which we had information about the type of measures used to protect apiaries against bear damage. We only considered as preventive measures properly installed and working electric fences (see Fig. A1). Other types of fencing, such as wooden or simple wires, were classified as no prevention. Since the immediate surroundings of apiaries may also influence the occurrence of damage (e.g., less damage occurring in apiaries far from the forest and surrounded by buildings), we also expected an interaction effect between the presence of electric fences and the above explained predictors.

2.4. Damage risk models

We used generalized additive models (GAMs) to analyse the occurrence of bear damage to apiaries and predict the probability of damage at the three scales (landscape, local, household) and to assess the effect of preventive measures on damage risk at the household scale (preventive model). We fitted all GAMs with a binomial error distribution and a logarithmic link with damage occurrence (1) versus absence (0) as a response to different environmental and socioeconomic predictors (see above). For the landscape and local models we used data from the period 2010-2015 to build the models and data from 2016-2017 to evaluate our predictions. For the household model we used all available data about apiaries located with GPS in the period 2014-2017. We used a maximum likelihood method to estimate smoothing parameters. We added a second penalty in the null space for each smooth term in each model to allow the model to reject the least relevant terms for predictions (Marra and Wood, 2011). To avoid collinearity, we excluded the highly correlated variables through a stepwise procedure based on variance inflation factor (Naimi et al., 2014). We only included the predictors with a variance inflation factor lower than two using a correlation threshold of 0.60. We included in all models an interaction term of the geographical coordinates to account for spatial trends in the data across large geographical distances (Dormann, 2007). For the preventive model we included the main term ‘prevention’ (as a categorical linear predictor) plus two smothers for each significant predictor in the household model (one smother for the group ‘prevention=yes’ and another for ‘prevention=no’). This allowed assessing the compounding effect of the presence of preventive methods and the immediate landscape characteristics of the apiaries on damage risk. We run spline correlograms on the occurrence of predation events and on the residuals of all models to assess for the remaining spatial autocorrelation. All statistical analyses were performed in R (version 3.5.1, R Development Core Team 2018) using the packages mgcv to run GAMs (Wood, 2017), ncf to assess the spatial autocorrelation and mgcViz to visualize the results of GAMs (Fasiolo et al., 2019).

2.5. Model evaluation

We measured the predictive capacity of the models on damage occurrence using the area under the receiver operating characteristics curves (AUC); the overall rate of correct classifications (accuracy); and the proportions of correctly classified presences (sensitivity) and absences (specificity) of damage to apiaries. For each model, we set the optimal threshold for discriminating damage using the maximized sum of sensitivity and specificity in the receiver operating characteristic (ROC) curve. For the landscape and local models, we carried out an internal evaluation by computing the performance metrics using data from 2010 to 2015 used to fit the model. We also performed an external evaluation considering the ability of the model to predict bear damages to apiaries using independent data for the period 2016-2017. For the household and preventive models we only performed the internal evaluation because we used all the observations for which we had data on the described predictors to fit them.

2.6. Scale-integrated risk mapping

We extrapolated the risk of bear damage across the Carpathian mountain range within the Podkarpackie Province (Fig. 1, Fig. 2 & Fig. 3). We performed this extrapolation beyond the bear distribution area to inform about potential conflict zones in the case of dispersing individual bears and/or future population increases (Ziółkowska et al., 2016). Specifically, we predicted the risk of damage at each scale based on the coefficients of its corresponding risk model. To extrapolate the risk of damage at the household scale we divided each of the 8,450 cells of 1 km side into 16 cells of 0.25 km side (i.e., 135,200 cells of 0.25x0.25 km) and calculated the predictors used in the household model at the centroid of each 0.25 km-side cell.

We integrated the predicted risk of damage across scales at the 0.25 x 0.25 km resolution. To that end, we characterized each 0.25 km-side cell with the probability of damage estimated at each of the three study scales; i.e., three values of damage probability for each cell. We then scaled the predicted probabilities in each cell between 0 and 1 based on the following formula:

$$P(damage) = \frac{(P(x) - P_{min})}{(P_{max} - P_{min})}$$

We scaled the probabilities between zero and one to give equal weight to the predicted risk at every scale. Finally, we calculated the scaled-integrated probability of damage to apiaries at each cell by multiplying the damage probabilities at the landscape, local and household scales following DeCesare et al., (2012) as follows:

$$Scale - integrated\ probability\ of\ damage = P(S_1) \times P(S_2) \times P(S_3)$$

where $P(S_1)$, $P(S_2)$, and $P(S_3)$ are the relative probabilities of damage for a given 0.25 km-side cell at the landscape, local and household scales, respectively.

2.7. Assessing whether the landscape context shapes bear damage response to household conditions

We assessed if the damage risk at a fine scale depends on whether the context at larger scales favours or not damage. For that, we first selected the 0.25 km side cells encompassing damaged and undamaged apiaries (i.e., 272 cells). Then, we characterized the selected cells according to whether they were located within an area predicted as risky or safe in the risk maps at the landscape and local scales (Fig. 3). As a result, we had four subsets of the

0.25x0.25km grid, comprising apiaries located in (1) risky landscape conditions, (2) safe landscape conditions, (3) risky local conditions and (4) safe local conditions. We used GAMs to predict the probability of damage for each subset of data. We included as predictors the variables previously identified as significant in the household model.

Table 1. Results from generalized additive models analyzing the occurrence of brown bear damage to apiaries in the Northern Carpathians (SE Poland) at three scales: landscape (5x5 km), local (1x1 km) and household (apiary's GPS coordinates). The estimated degrees of freedom (*Edf*) for each smooth term are provided. Generally, the higher the Edf the more non-linear is the smoothing spline with Edf =1 indicating a linear function. However, since we added a second penalty in the null space for each smooth term, Edfs ≤ 1 are not necessarily linear and an Edf near zero indicates that the effect of that smooth term is removed from the model. The smoother effect of the interaction of the geographical coordinates is provided in the Appendix B of the electronic supplementary material.

Spline fits	*Edf*	Smooth effects
LANDSCAPE MODEL (N = 157, Adjusted R^2 = 0.224, Deviance explained = 21.3%)		
s(Probability of bear presence)	1.60*	
s(Probability of apiary presence)	0.91***	
s(X-coordinate, Y-coordinate)	5.75**	Figure B2
LOCAL MODEL (N = 3925, Adjusted R^2 = 0.040, Deviance explained = 12.5%)		
s(slope)	~0	no effect
s(agricultural cover)	0.90	
s(density of major roads)	1.23**	
s(density of minor roads)	~0	no effect
s(density of very small roads)	~0	no effect
s(forest edge)	3.36***	
s(X-coordinate, Y-coordinate)	12.8***	Figure B3
HOUSEHOLD MODEL (N = 293, Adjusted R^2 = 0.379, Deviance explained = 36.4%)		
s(Probability of bear presence)	~0	no effect
s(distance to nearest building)	~0	no effect
s(distance to nearest forest patch)	1.28*	
s(number of buildings in a 200 meters radius)	1.80***	
s(forest cover in a 200 meters radius)	1.05^	
s(X-coordinate, Y-coordinate)	16.97***	Figure B4

s=spline; Approximate significance of smooth terms based on p-values: 0 *** 0,001 ** 0,01 * 0,05 ^ 0,1

~0 = values <0.1;

3. RESULTS

3.1. Correlates of brown bear damage risk

The results from the landscape model showed that the probability of damage occurrence steadily increased with the probability of apiary presence and, to a lesser extent, with high probabilities of bear presence (Table 1 & Fig. B2 in the supplementary material). At the local scale, the damage probability increased with the length of forest edge and with low densities of major roads. It also increased with low values of agricultural cover (Table 1 & Fig. B3 in the supplementary material). At the household scale we found that the risk of damage decreased with increasing density of buildings in a 200-meters radius around the apiaries and increased in apiaries located near forest patches and surrounded by forests (Table 1 & Fig. B4 in the supplementary material). Overall, the occurrence of damage had a negative relationship with the distance to the nearest forest patch (Fig. B4). Results from the preventive model showed that apiaries with preventive measures were those with higher risk of being attacked (Table 1 & Fig. B5 in the supplementary material). Also, increasing density of buildings in a 200-meters radius decreased the probability of damage in apiaries with no preventive measures (Table 2 & Fig. B5).

Risk models showed medium to high predictive accuracy according to the internal evaluation: AUC = 0.79-0.95. The predictive accuracy was lower for the external evaluation: AUC= 0.68-0.63 (see table B2 in supplementary material).

Table 2. Results from a generalized additive model analyzing the compounding effect of preventive measures and the surroundings of the apiaries on the occurrence of brown bear damage to apiaries in the Northern Carpathians (SE Poland). The estimated degrees of freedom (*Edf*) for each smooth term are provided. The smoother effect of the interaction of the geographical coordinates is provided in the Appendix B of the supplementary material.

Spline fits	*Edf*	Smooth effects
PREVENTION MODEL (N = 151, Adjusted R^2 = 0.449, Deviance explained = 49.1%)		
prevention (yes)[a]	1.70 (± 0.73)*	-
s(distance to nearest forest patch): prevention=no	~0	no effect
s(distance to nearest forest patch): prevention=yes	~0	no effect
s(number of buildings in a 200 meters radius): prevention=no	0.92**	╲
s(number of buildings in a 200 meters radius): prevention=yes	~0	no effect
s(forest cover in a 200 meters radius): prevention=no	~0	no effect
s(forest cover in a 200 meters radius): prevention=yes	~0	no effect
s(X-coordinate, Y-coordinate)	14.13**	Figure SB5

[a] linear fit for which is reported the estimate ± standard error instead of the Edf

s=spline; Approximate significance of smooth terms based on p-values: 0 *** 0,001 ** 0,01 * 0,05 ^ 0,1

~0 = values <0.1; [a] linear fit for which is reported the estimate ± standard error instead of the Edf

3.2. Scale-integrated risk map

The scale-integrated risk map predicted that 66% of the bear range in Podkarpackie Province is at some level of risk of bear damage to apiaries, of which 1% is considered to be at high or very high risk (Fig. 3 & Table B2 in the). The spatial location of high-risk zones within the bear range was consistent across scales. Considering the potential bear habitat within the Podkarpackie

Province, 32.7% of the area was at moderate risk, and 0.3% at high risk. The scaled-integrated risk map had a high classification accuracy (AUC = 0.856, see Fig. 3).

3.3. Landscape context can shape bear damage response to household conditions

The predicted risk of damage at the household scale depended on the risk predicted at larger scales. In other words, broad landscape characteristics determined to what extent the immediate surroundings of the apiary influence its vulnerability. Specifically, an apiary surrounded by several buildings and more than 80 meters away from the forest edge is up to three times more likely to be damaged by a bear when it is inside (vs outside) a landscape that favours damage (see Fig. 4). To a lesser extent, the probability of damage at the household scale also increased when the environmental characteristics at the local scale favour damage (Fig. 4).

4. DISCUSSION

4.1. Patterns and correlates of damage risk

Our results illustrate that the spatial patterns of bear damage to apiaries are a complex ecological issue modulated by multiple environmental factors and their interactions across several scales. We found that high risk of damage is associated with areas of interface between agricultural landscapes that are suitable for beekeeping (landscape scale) and forest patches that facilitate the movement of bears within their home range (Bartoń et al., 2019) (local and household scales). In addition, we found that a high building density in the immediate surroundings of an apiary (household scale) was related to low risk of damage. The overall interpretation of these results confirms, as we hypothesized, that the habitat preferences of bears (to find resources) and beekeepers (to install apiaries) together with the bear's natural tendency to avoid humans determine the risk of bear damage to apiaries at multiple scales.

Our results showed that local-scale patches with high density of forest edges, roads and agricultural land are susceptible to host bear damage. Similar patterns have been observed for other wildlife in different landscapes. For instance, the risk of livestock predation by leopards (*Panthera pardus*) in Bhutan or of crop predation by Asian elephants (*Elephas maximus*) in India also increased in agricultural fields and near roads, respectively (Goswami et al., 2015; Rostro-García et al., 2016). Overall, this pattern shows that the risk of damage at medium scales depends directly on the availability and accessibility of farms and crops, both of which are higher in the surroundings of rural human settlements. Conversion of natural ecosystems to agricultural land has steadily increased over the XX century and is projected to keep increasing globally (Dobrovolski et al., 2011). As wilderness keeps converting into agriculture lands, conflicts arising from damage are also expected to increase (Ripple et al., 2015, 2014). Conversely, and in spite of the general trend of agriculture expansion, many regions (e.g. Europe) have experienced a conversion from agriculture into forest habitat mainly as a result of socio-political dynamics like the rural exodus (Levers et al., 2018). Land abandonment in rural areas can facilitate conflicts. For example, the decrease and aging of local population in central Japan has enhanced leaving unattended fruit trees and unharvested crops, which attracts Asiatic black bears (*Ursus thibetanus*), and Japanese macaques (*Macaca fuscata*) to villages (Yamazaki et al., 2009).

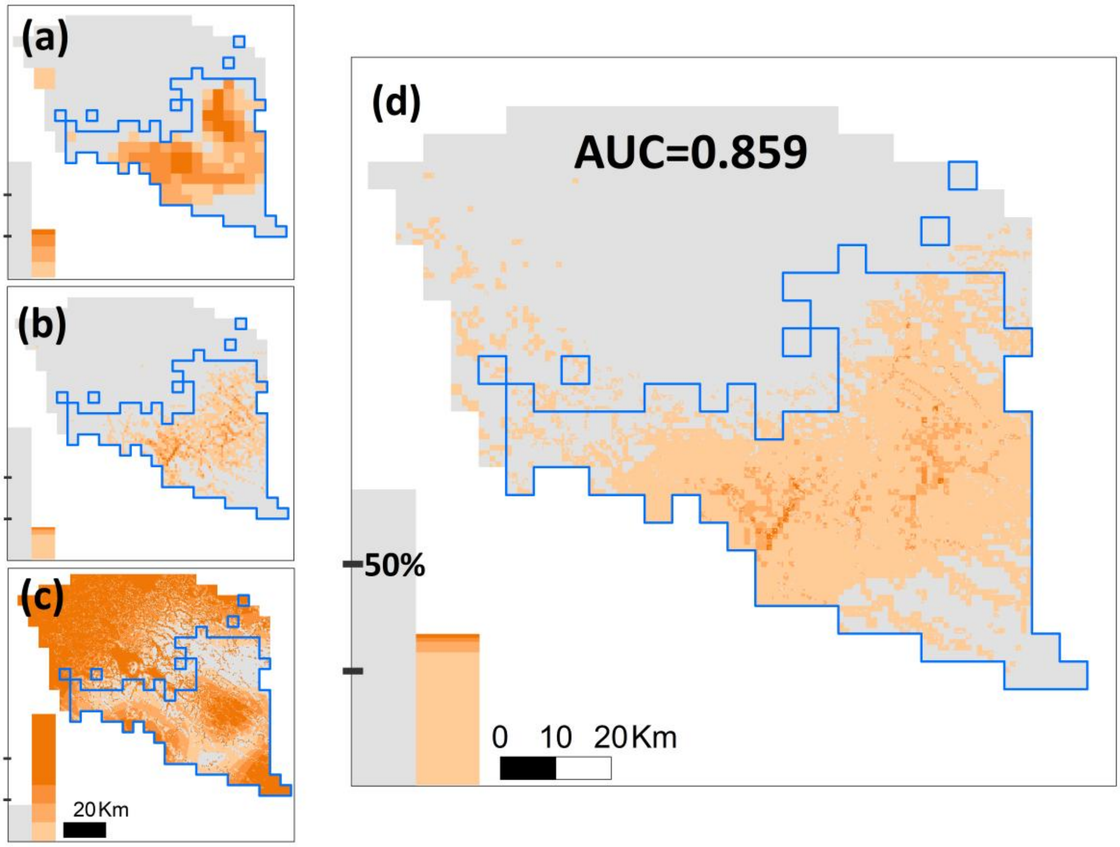

Figure 3. Risk maps showing the relative probabilities of brown bear damage to apiaries in the Northern Carpathians (SE Poland) at three scales: 5x5 km (a), 1x1 km (b) and 0.25x0.25 km (c). The relative probability of damage was predicted at each scale based on the coefficients of generalized additive models run within the bear distribution range (cells delimited by the blue line). That probability was then extrapolated to the potential bear habitat within the Podkarpackie Province to inform about potential conflict zones in the case of future population increases. The relative probabilities of bear damage were multiplied at the smallest scale to produce a scale-integrated risk map (d). Predicted risk of damage for all maps was classified using the maximized sum of sensitivity-specificity. The values below the threshold are considered as predicted absence of damage (grey colour). The values above the thresholds were divided into four equal-interval classes of damage risk (the darker the orange colour,

the higher the risk). The bar plots at the bottom-left of each panel show the relative frequency of the different risk classes in the map.

Yet, the accessibility of farms and agricultural land (and, thus, the risk of damage) may well be compromised by the landscape characteristics in their most immediate surroundings. Results from our household model showed that the risk of damage was at its minimum when apiaries were surrounded by several buildings and located far enough from forest patches (Table 1, Fig. 4 & Fig. B4). This evidences that the fear associated to human presence influences the decisions of bears to feed on available energy-rich resources, such as honey and larvae from beehives. Similar patterns have been observed in the use of human-derived foods by other conflict-prone species, such as tigers (*Panthera tigris*) and African elephants (*Loxodonta africana*) (Graham et al., 2009; Rostro-García et al., 2016). This trade-off between energy demands and fear (i.e, using accessible and abundant food resource vs avoiding dangerous situations) has been suggested to shape the spatial ecology and decision-making of wild animals (Gallagher et al., 2017) and seems to also shape animal behaviours driving the occurrence of damage. That could explain why the apiaries without electric fences but surrounded by buildings (something relatively common in the study area), tend to have lower damage probability than apiaries with electric fence but installed inside or very close to forest patches and with no buildings around (Table 1, Fig. B6 & Fig. B7 in the supplementary material). Although electric fences can be very effective in preventing damage (Van Eeden et al., 2017), their effectiveness is significantly reduced when they are poorly maintained and they are not reinforced with additional preventive measures (di Vittorio et al., 2016; Naves et al., 2018), which is frequent in our study area (Fig. A1). Furthermore, animals with high cognitive abilities, like the brown bear, are known to damage the same farms repeatedly across years and to be able to learn how to skip preventive measures at particular farms (Naves et al., 2018). This suggests that, in the absence of effective prevention, anthropized areas (e.g., urban settlements) can act as a protective shield for farms against wildlife damage.

Although our risk models at the landscape and local scales were accurate in extrapolating the risk of damage to the potential bear habitat within the Podkarpackie Province (AUC>=0.9, Fig. B9), they were limited in predicting the presences and absences of damage for the two subsequent years (AUC between 0.65 and 0.68, Table B2). That limitation is likely connected to spatio-temporal variation in missing covariates (Johnson et al., 2015) that can also influence the movement and behaviour of bears (e.g., the availability of food resources; Johnson et al., (2015). Indeed, we found that the geographical coordinates used to account for spatial structure in damage patterns in our risk models were significant at every scale (see Table 1), which can be an indication of missing relevant, spatially structured covariates. For example, the presence of supplementary food provided in natural habitats for wildlife is known to alter the movement behaviour of many animals (including bears in temperate forest ecosystems; Selva et al., (2017), and can sometimes increase, instead of decrease, the occurrence of damage (Newsome et al., 2015). That may be the case when feeding sites, which attract wildlife, and beehives are located close to each other. Other factors that can influence the spatiotemporal patterns of damage occurrence are related to the dispersal movements of juveniles (Bartoń et al., 2019) or to the search of human infrastructure by female with cubs to prevent infanticides (Steyaert et al., 2016). Including data on species demography and individual movements can help gaining a better understanding on the processes shaping the occurrence of damage, as well as achieving more accurate predictions.

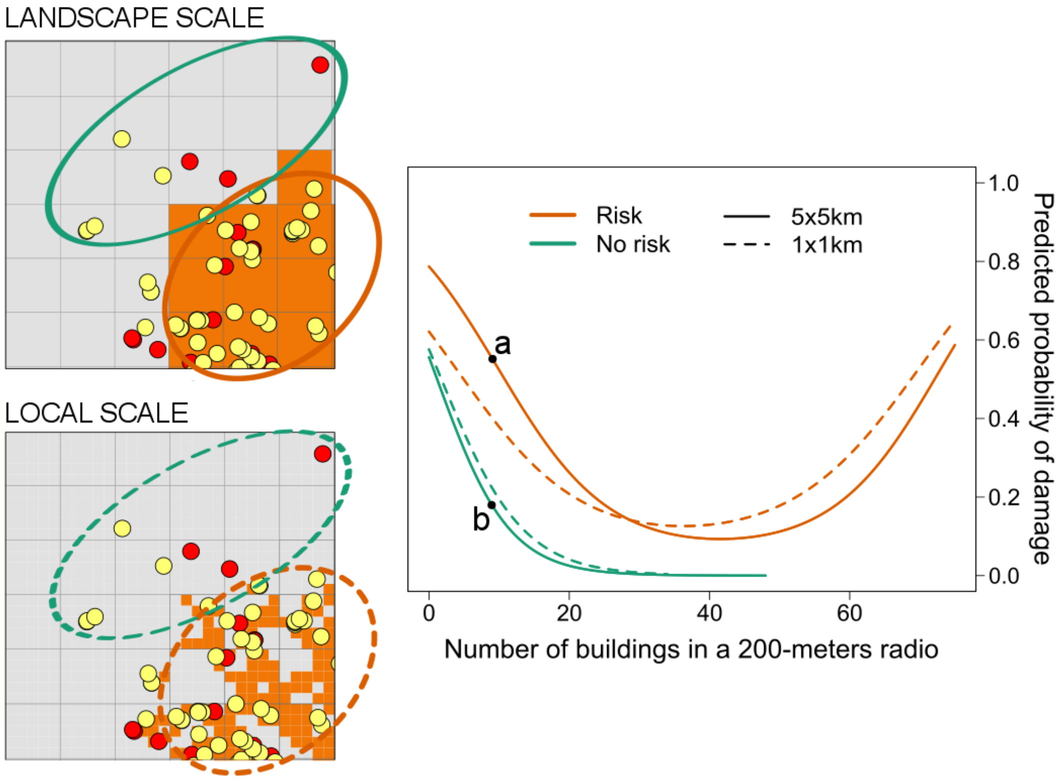

Figure 4. Predicted probability of brown bear damage to apiaries as a response to the number of buildings in a 200-meters radius around the apiary in the Northern Carpathians (SE Poland). Responses are conditioned to whether the landscape characteristics at large scales favour damage or not. Orange and green lines show the probability of damage in apiaries located in landscapes that favoured (orange cells) and did not favour damage (grey cells), respectively. Solid lines indicate landscape classification (favouring damage or not) at the landscape scale (5x5km), and dashed lines at the local scale (1x1km). Red and yellow dots represent damaged and undamaged apiaries, respectively. The damage probabilities were predicted with average values of the distance to the nearest forest patch, forest cover around the apiary (in a 200-meters radius), longitude and latitude. An apiary located in a landscape that

favours damage (a) can be up to three times more at risk of being damaged than an apiary located in a safe landscape (b).

4.2. Integrating damage response to habitat characteristics across scales

By combining the results of risk models across multiple scales, we have demonstrated that the broader landscape context can shape animal response to the immediate environmental characteristics of a farm. For example, the probability of damage to an apiary greatly increased (up to three times; 0.6 *vs* 0.2) when it was located in cells predicted at risk at the landscape scale (see Fig. 4). This supports previous findings showing that resource selection at fine scales can be constrained by habitat selected at coarser scales. For example, Lipsey et al., (2017) demonstrated that the fine-scale probability to select grasslands by Sprague's Pipit (*Anthus spragueii*) increased with the proportion of grass at broader landscapes. These conditional relationships in resource selection among scales are rarely tested in risk mapping, and yet, help to gain a more integrative understanding of how animals select different types of resources and are prone to conflict.

To the best of our knowledge, this is the first study integrating scale-dependent responses of animals in the use of farm products. The majority of damage risk assessments up to date are based on scale-specific models (Miller, 2015). Just a few studies have assessed the probability of damage at multiple scales by identifying scale-dependent patterns of livestock predation (Rostro-García et al., 2016) or the best grain to improve damage predictions (Miller et al., 2015). Here, we showed that combining the extrapolations from single-scale risk models into an integrated-scale risk map greatly improved the spatial prediction accuracy (Fig. 3, Fig. B9 & Table B7) and overcame the limitations of single-scale risk mapping on predicting conflicts from other time lapses (Fig. B10). Previous studies integrating the scale-dependent response of animals to the availability of natural resources also resulted in more accurate predictions than traditional, scale-specific models (DeCesare et al., 2012; Lipsey et al., 2017). Our study adds evidence that scale integration can be applied to the particular case of wildlife damage to farm products to predict more accurately where conflicts are more likely to occur.

The recommendations derived from scale-integrated risk maps can avoid wasting resources in management actions based on inaccurate recommendations from scale-specific risk maps. For example, the map based on the landscape model wrongly identified a small region in the north-west part of our study area as a priority for conflict mitigation (Fig. 3). The north-west has in fact an optimal habitat to install apiaries (see Fig. A4), however, it is relatively far from the current bear distribution and its local context does not favour damage (see local scale risk map in Fig. 3). Accordingly, the joint probability of damage rescaled to the landscape scale (Fig. B9 & Fig. B10) reduced by 75% the area identified as at risk in the north-west. Furthermore, rescaling the risk of damage from the integrated-risk map at the finest scale to the broadest landscape scale increased the prediction sensitivity in comparison with the predictions derived from the single-scale map (i.e, 90% -vs 82%- of damage locations were identified correctly, see Fig. B10). Although the management and decisions on conflict mitigation strategies are taken on broad scales, these scales do not accurately reflect the spatial heterogeneity of damage occurrence (Gastineau et al., 2019; Miller, 2015). Summarizing the results from scale-integrated risk maps from fine to large scales can help to avoid mismatches between the scales of inference and management action and thus, provide better information to managers and policymakers for damage prevention (Montgomery et al., 2018).

4.3. Implications for conservation

Proactive and preventive approaches to mitigate conflicts arising from wildlife damage are proven to be more successful over time than reactive approaches (Van Eeden et al., 2017). Yet, most efforts invested in conflict mitigation around the world are allocated to reactive approaches (e.g, compensation programs), thus, compromising the real success of conflict mitigation actions (Bautista et al., 2019; Ravenelle and Nyhus, 2017). Given that resources for conflict mitigation are usually limited, prioritizing the areas in the landscape and the particular farms that should be protected first would be highly beneficial for damage prevention. Our multiscale approach allows identifying risk areas on the broad landscape context and, in there, selecting the most vulnerable households where to subsidize preventive measures. Following our case study, beekeepers working in landscapes that favour damage could reduce more than threefold the probability of experiencing bear damage if they would locate their beehives at least 300 meters away from the forest patches and in the vicinity of several buildings (see Fig. 4 & Fig. B4). We believe that our approach may be used as a guideline for future damage risk assessments of other wildlife species and in other parts of the world and, thus, help to effectively reduce damage occurrence and enhance human-wildlife coexistence.

Conflicts arising from wildlife damage are predicted to grow due to the recovery and expansion of some wild animal populations into human-dominated landscapes (Chapron et al., 2014) and due to the increasing transformation of natural areas into agriculture fields (Dobrovolski et al., 2011; Ripple et al., 2015, 2014). The use of agriculture lands and suburban areas by wild animals can become an ecological trap for them, impacting species demography and even leading to local extinctions (Lamb et al., 2020). Indeed, conflict with humans is one of the main threats for the survival of many species of large carnivores and herbivores (Ripple et al., 2015, 2014). That is worrying because they play an essential role in ecosystem functioning worldwide (Estes et al., 2011). Unfortunately, given the current human population growth, stopping agriculture expansion into natural areas and the conflicts arising from it may be an unrealistic short-term goal (Ripple et al., 2017). However, using risk models to predict where damages are more likely to occur and have a proactive and preventive attitude towards conflicts is something that farmers, conservation practitioners and policy makers can start doing today.

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SUPPLEMENTARY MATERIAL FOR:
The spatial ecology of conflicts:
Unravelling patterns of wildlife damage at multiple scales

APPENDIX A– MODELING THE PROBABILITY OF APIARY OCCURRENCE WITHIN THE BROWN BEAR RANGE IN THE POLISH CARPATHIAN MOUNTAINS, SE POLAND.

A.1. Apiary field data

We collected information on the location of apiaries during 99 days of field work conducted by the team between August 2014 and June 2015. We established the study area based on the records of bear presence from 1985 to 2012, such as direct observations, collected samples, observed tracks or registered damages, based on (Fernández et al., 2012). Point locality data were aggregated into a grid of 5x5 km cells (Fernández et al., 2012), where species was recorded as present or absent. To account for possible expansion and to obtain a continuous area, we additionally included neighboring cells with no evidence of bear presence, but suitable for bears, i.e. with at least 40% of forest cover (Fernández et al., 2012), and surrounded by at least six suitable cells. Finally, we excluded cells which have more than 30% of its surface outside Poland and the Podkarpackie territory.

We registered the location of 308 apiaries with a GPS during transects on foot conducted in each 5x5 km cell and also while driving between cells during fieldwork. All cells were visited at least on five occasions in different days during the sampling period and often by different observers. Some apiaries were detected more than once in different sampling days and by different research team members. We identified these duplicated observations based on the coordinates of the apiary, the description of the apiary, observer id and the date. We retained only one observation per apiary in the database, resulting in 182 detected apiaries (Fig. A1). We recorded the walking and driving tracks with the GPS device and estimated the total length covered by both types of tracks in each sampled grid cell.

A.2. Predictors to model the occurrence of apiaries

To model the probability of apiary presence we used the same 1x1km grid used to model the predation risk model at the local scale (see Methods section in the article). For that, we used the number of sampled apiaries as a response to different environmental predictors (hereafter apiary model, see Table 1 and section 2.5). We selected a subsample of the grid including only the cells in which we had actively sampled apiaries; i.e., we excluded the cells in which the length of the driving and walking transects was almost equal to zero. That resulted in a subsample of 1,609 1x1km cells. We categorized each cell with the number of detected apiaries, ranging from zero to five. Because apiaries are mainly located in places accessible to humans, we predicted that the probability of apiary presence is positively associated with human density, urban infrastructure (including roads and buildings), and the proportion of agricultural cover. To increase the quality of the honey and to produce forest honey, beekeepers often locate apiaries in the vicinity of forest patches. Accordingly, we predicted that the probability of apiary presence is positively related to the length of ecotone between forest and agricultural land. We modeled the abundance of apiaries in the selected 1,609 cells and then extrapolated that probability of apiary presence across the 8,450 cells covering the Carpathian range within the Podkarpackie Province based on the coefficients of the model. To include the resulting probability of apiary presence in the risk model at the landscape scale (see *(c) Predictors of damage at different scales* in the Methods section of the article), we averaged the probability of apiary presence in the 25 cells of 1km side within each cell of 5km side.

A.3. The apiary model

We fitted zero inflated Poisson Generalized Additive Models (GAMs) to predict the probability of apiary presence in relation to different environmental and socioeconomic predictors (see Table B1) in the 1x1 km grid. The zero inflated structure allowed us to model the excess of zeroes due to apiaries potentially present in the cells but undetected during the field transects. We included the length covered by the field transects as an offset in all models to account for the heterogeneity in the sampling effort. To avoid extreme estimates due to the excess of zeroes we included low order penalties for one-dimensional smooths and Duchon splines with one order penalty for the isotropic smooth included in the interaction between the longitude and latitude (Wood, 2017). We added a second penalty in the null space for each smooth term to allow the model selecting for the most relevant variables (Marra and Wood, 2011).

To evaluate the results of the apiary model we used data on the number of beehives registered by the beekeepers association with municipality as a spatial resolution (29 in total). For that, we averaged the probability of apiary presence predicted for each 1km-side cell within each municipality. We fitted Generalized Linear Models (GLMs) with a Poisson error distribution to model the total number of registered beehives in each municipality as a response to the averaged probability of apiary presence. We did not use GAMs here because we expected a linear relationship.

A.4. Results

Results from the apiary model showed that apiaries in Podkarpackie tend to be located in agriculture fields, in areas with higher densities of major and minor roads and with gentle slopes (see Table A1 and Fig. A2). Our model evaluation showed that the average probability of apiary presence was positively correlated to the number of registered beehives by beekeepers association at the municipality level (see Fig. A3 and section 2.6).

Figure A1. Bar plots showing the frequency of beehives per apiary and the number of detected apiaries conditional on the type of fences and measures that the apiaries had to prevent brown bear predation in the Northern Carpathians, SE Poland. The red dashed line indicates the average number of beehives per apiary.

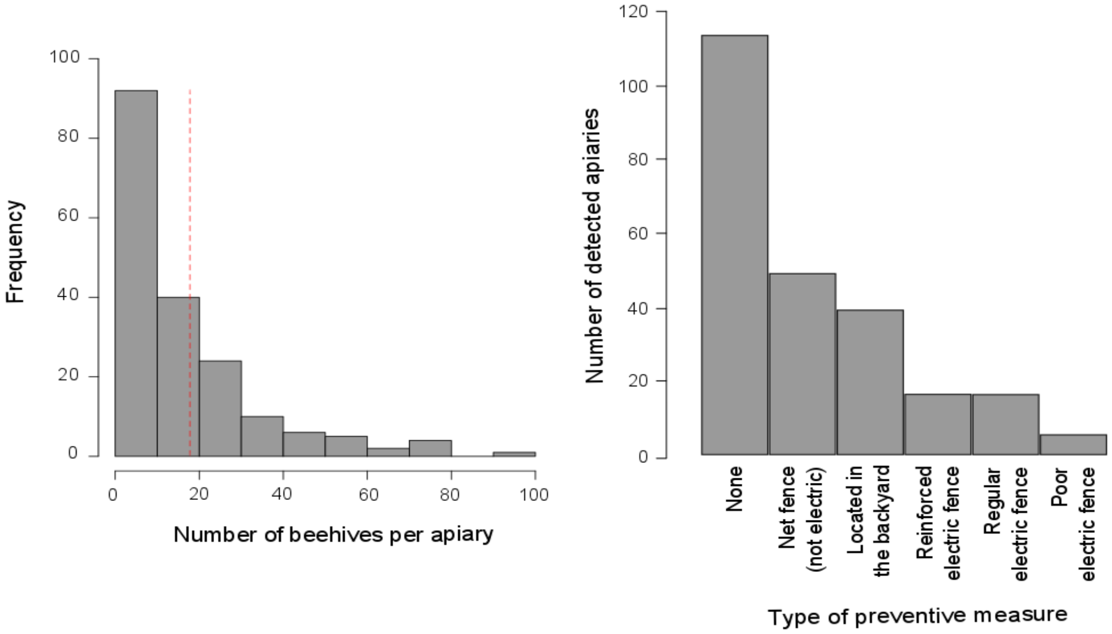


Table A1. Results from zero inflated Generalized Additive Models analysing the occurrence of apiaries in a 1x1km grid covering the brown bear range within the Northern Carpathians (SE Poland). The estimated degrees of freedom (*Edf*) for each smooth term are provided. Generally, the higher the Edf is, the more non-linear is the smoothing spline (Edf =1 indicates a linear function). However, since we added a second penalty in the null space for each smooth term, Edfs ≤ 1 are not necessarily linear and a Edf near zero indicates that the effect of that smooth term is removed from the model.

N= 1907, Deviance explained = 15%

Spline fits	*Edf*
COUNT-MODEL COEFFICIENTS (POISSON WITH IDENTITY LINK)	
s(slope)	0.72^
s(agricultural cover)	0.85**
s(human density)	~0
s(density of major roads)	0.89**
s(density of minor roads)	1.12*
s(density of very small roads)	~0
s(forest edge)	~0
s(X-coordinate, Y-coordinate)	2.0
ZERO-INFLATED-MODEL COEFFICIENTS (BINOMIAL WITH IDENTITY LINK)	
s(slope)	3.43***
s(agricultural cover)	1.83**
s(human density)	1.91*
s(density of major roads)	3.39**
s(density of minor roads)	0.82*
s(density of very small roads)	~0
s(forest edge)	0.48^
s(X-coordinate, Y-coordinate)	15.76***

s=spline; Approximate significance of smooth terms based on p-values: 0 *** 0,001 ** 0,01 * 0,05 ^ 0,1

~0 = values <0.1

Figure A2. Smooth splines showing the relative probability of occurrence of apiaries on a 1x1 km-grid in the Northern Carpathians, SE Poland, in relation to different predictors. The probability of apiary occurrence was estimated based on zero inflated Generalized Additive Model. Solid lines represent the estimated smooth functions of different predictors and the dashed lines indicate the 95% confidence interval. The value given in brackets in each Y-axis is the effective degree of freedom estimated for the spline; when it equals zero indicates no relevance of the predictor for the model. Predictors as follows: latitude (lat), longitude (long), slope (slope), human density (hum_den), major roads (MaR), minor roads (MiR), very small roads (VsR), agricultural cover (agri), length of forest edge (f_edge). For further information about the predictors see Table B1.

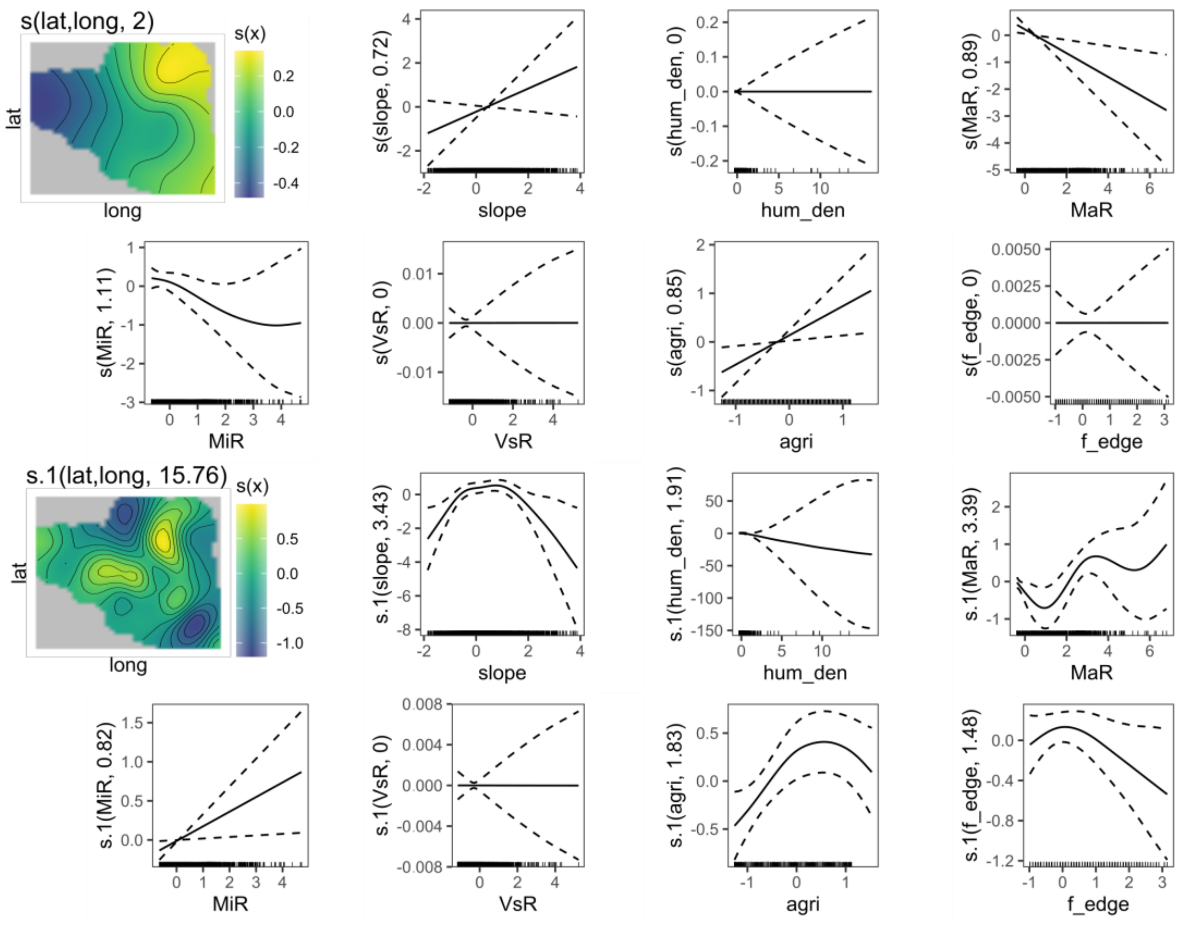


Figure A3. Spline correlograms showing the spatial independency in the residuals from the generalized additive model run to predict the relative probability of apiary occurrence in the Northern Carpathians, SE Poland.

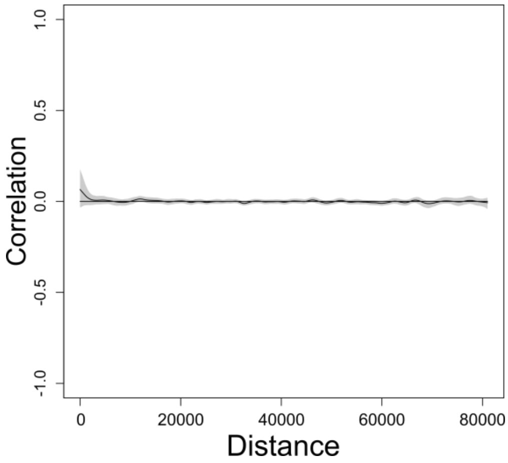


Figure A4. Relationship between the predicted probability of apiary and the number of registered beehives in 29 municipalities in the Northern Carpathians, SE Poland (see section A.3 in this Appendix).

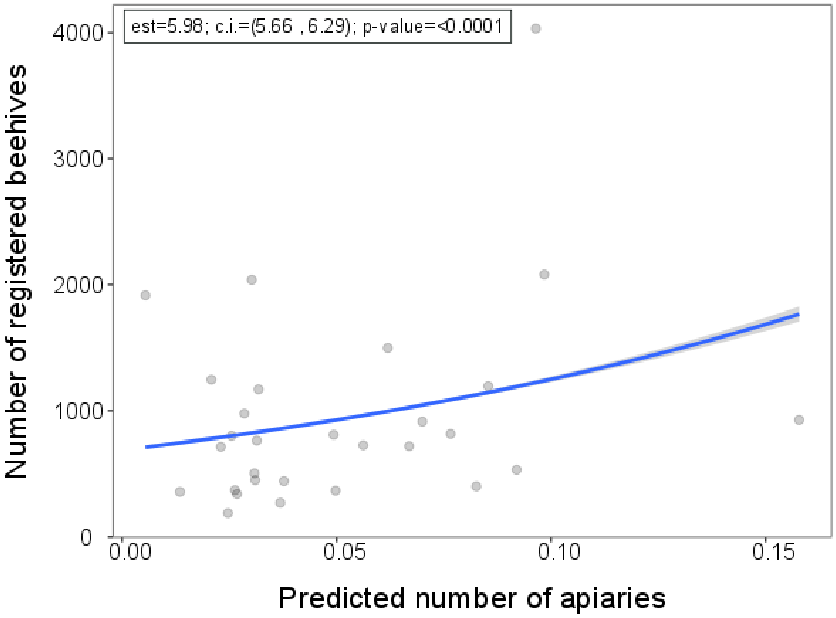
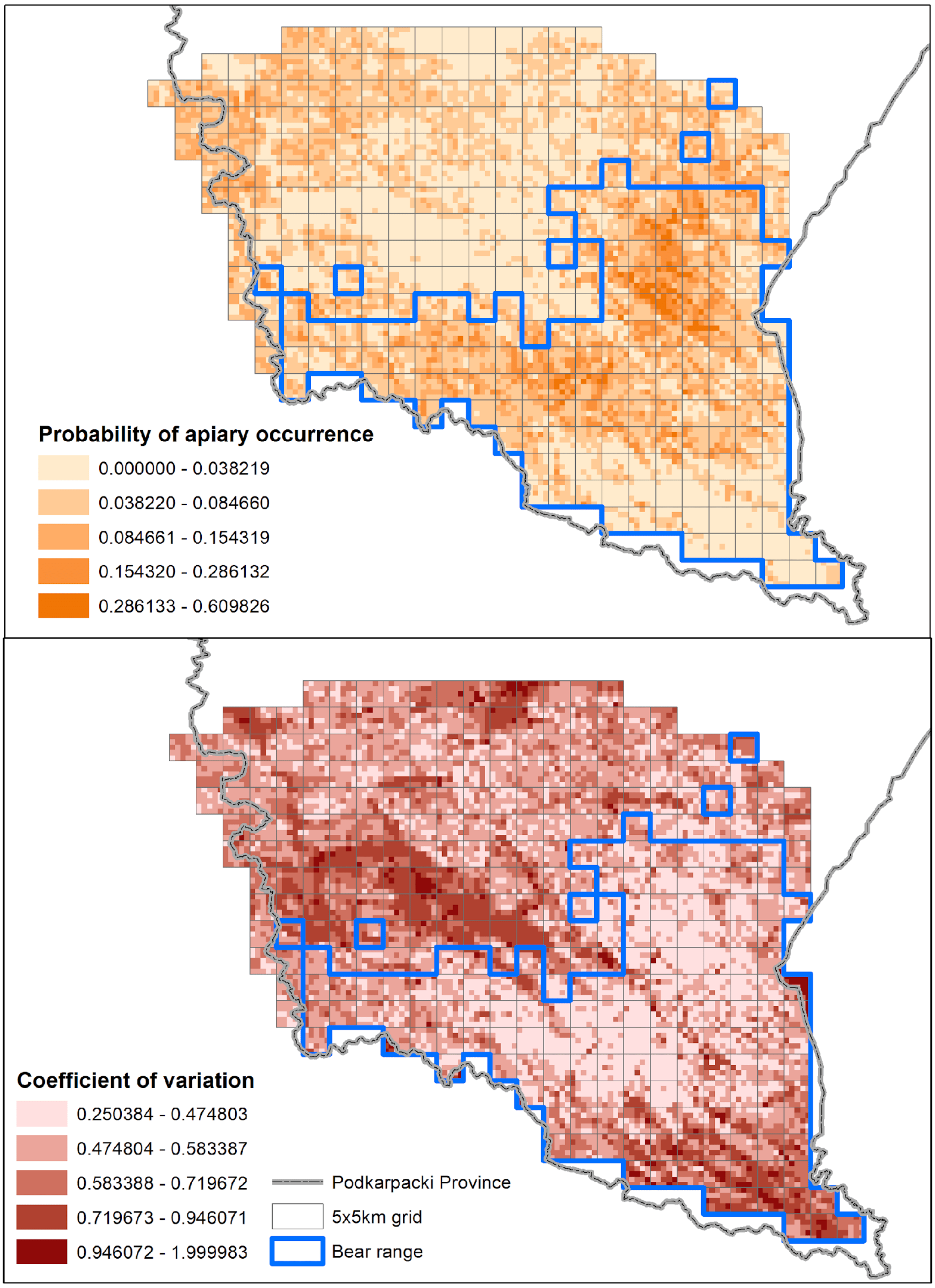


Figure A4. Relative probability of apiary presence in the Northern Carpathians, SE Poland (Podkarpackie Province) and associated coefficient of variation.



APPENDIX B – RESULTS FROM RISK MODELS

Table B1. Variables considered for modeling the probability of brown bear damage to apiaries within the bear range in the Northern Carpathians, SE Poland (Podkarpackie Province). For each predictor we present a brief description, the justification for the selection as predictor and the source of data. Predictors are classified by study scales.

Variable name	Description	Expected effect	Data source
LANDSCAPE SCALE (risk model at a spatial resolution of 5x5km)			
Probability of bear presence	Probability of bear occurrence (from 0 to 1)	We expected that damage occurrence would occur mostly in cells where relatively high probabilities of bear and apiary occurrences overlap	Fernandez et al., 2012
Probability of apiary presence	Probability of apiary occurrence (from 0 to 1)		Estimated in this study (see the Appendix A)
LOCAL SCALE (risk model at a spatial resolution of 1x1km)			
Human population density	Number of inhabitants per km^2	Expected to positively affect apiary presence and, thus, the risk of damage. Apiaries are mostly located closer to villages where people live. The risk of damage could decrease when the number of inhabitants is relatively high because bears would tend to avoid those areas	Population and Housing Census 2011 (NSP 2011) www.geo.stat.gov.pl
Density of buildings	Area covered by buildings (%)		Open Street Map (OSM codes of the road categories used as follows: 5113 and 5114 for major roads; 5115 and 5121 for minor roads; 5122, 5142, 5143, 5144, 5145, 5147 and 5154 for very small roads) www.openstreetmap.org
Density of major roads	Length of major roads including main national and regional roads (m/km^2)	Roads provide human access to forests and crop areas and facilitate the transport and installation of apiaries. Therefore, we expected that roads positively affect the presence of apiaries and, thus, the risk of damage. However, bears avoid intensively modified landscapes where human activity and disturbance is high, and are known to avoid roads. We expected that the risk of damage is more likely in cells with high density of minor and small roads that facilitate beehive operations but is not affected by major roads with high traffic volume	
Density of minor roads	Length of local roads (m/km^2)		
Density of small roads	Length of small roads including unpaved agricultural and forest roads, and roads to access farms and other agricultural and forest roads, which in the study area include residential roads and unspecified paths (m/km^2)		
Forest cover	Area of the cell covered by forests (%)	In highly forested areas the probability of apiary presence is less likely and thus the risk of damage	Corine land cover (CLC) 2012, EEA www.eea.europa.eu
Agricultural cover	Area of the cell covered by agricultural land (%)	We expect many apiaries to be located within agricultural lands. Accordingly and based on the results of Bautista et al,	

		(2019) for all Europe, we expected higher risk in cells with higher cover of agricultural land	Corine land cover (CLC) 2012, EEA www.eea.europa.eu
Density of forest edge	Number of pixels of 100m representing the edge of forest (ha/km^2)	Bears mainly live in forested areas and use forest patches to travel (Bartoń et al., 2019). Also, forest ecotones provide food for bears (Fernandez et al., 2012). We expect that risk of damage to apiaries will be positively affected by the length of the forest edge	
Density of forest ecotone with agriculture	Number of pixels of 100m representing the ecotone between forests and agricultural fields (ha/km^2)	Since we expect that apiaries will be mainly located in agricultural land and bears mainly live in, and move across, forested areas we expect that the risk of damage is higher in cells with higher interspersion between forest and agriculture fields	
Altitude	Average elevation (m above sea level)	We expect fewer apiaries located at high altitudes and high slopes, thus, meaning lower risk of bear damage	Digital Elevation Map 50m (EEA 2016) www.eea.europa.eu
Slope	Average slope (%)		
HOUSEHOLD SCALE (risk model at a spatial resolution of 250x250m)			
Probability of bear presence	Probability of bear occurrence (from 0 to 1)	We expected that risk of damage will be higher in apiaries located in areas of high probability of bear occurrence	Fernandez et al., 2012
Distance to buildings	Distance to the nearest building (m)	Because bears tend to avoid people and areas that are more disturbed by human activities, we expected that the risk of damage will be lower in apiaries located closer to buildings or with a high density of buildings around the apiary	Open Street Map www.openstreetmap.org
Building density	Number of buildings in a 200 meters radius		
Distance to forest	Distance to the nearest forest patch (m)	Because bears mainly use forest patches for their daily movements, we expected that risk of damage to apiaries will be higher in apiaries located closer to forests or with a high forest cover around the apiary	Corine land cover www.eea.europa.eu
Forest cover	Proportion of land covered by forest in a 200 meters radius (from 0 to 1)		
Apiary protection	Information about whether the apiary was protected with electric fences against bear predation or not	We expected protected apiaries to have a low risk of damage	Field data (see Appendix A)

Table B2. Performance of models predicting the occurrence of bear damage to apiaries in 2010-2017 at three different scales in the Northern Carpathians, SE Poland. Performance was assessed through AUC, accuracy (overall correct classification rate), sensitivity (true positive rate) and specificity (true negative rate). Performance metrics were computed considering the ability of each model to predict the observed damage occurrence in the studied period (internal evaluation) and in the two subsequent years (external evaluation). Data to perform the external evaluation at the household scale was not available.

		Internal				External (2016-2017)			
Model	Period	AUC	Balanced accuracy	Sensitivity	Specificity	AUC	Balanced accuracy	Sensitivity	Specificity
Landscape	2010-15	0.797	0.75	0.79	0.70	0.683	0.67	0.45	0.88
Local	2010-15	0.790	0.75	0.79	0.71	0.651	0.62	0.70	0.54
Household	2014-17	0.884	0.81	0.86	0.75	-	-	-	-
Preventive	2014-17	0.946	0.91	0.94	0.88	-	-	-	-

Figure B1. Predicted probabilities of bear and apiary occurrences in the Northern Carpathians, SE Poland. Each point represents a 5x5 km cell.

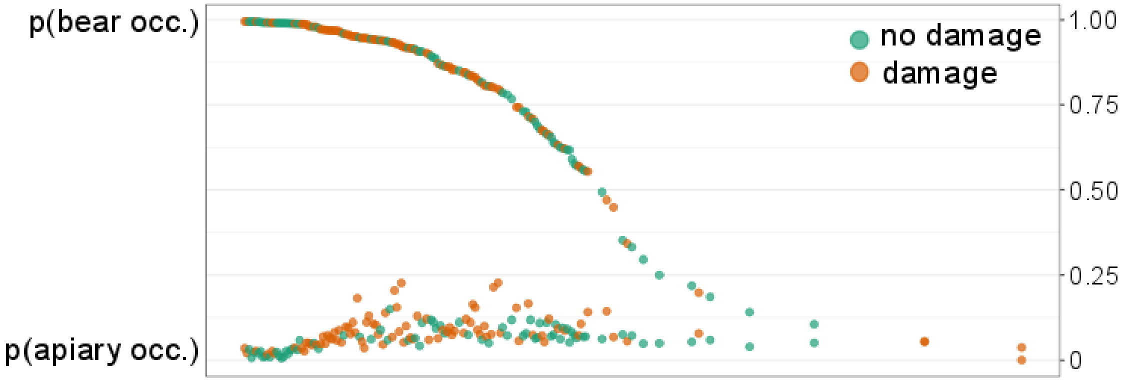


Figure B2. Smooth splines showing the relative probability of occurrence of bear damage to apiaries at the landscape scale (5x5km grid) in the Northern Carpathians, SE Poland, in relation to the interaction between the longitude and latitude and the probabilities of apiary presence and bear presence based on the coefficients of generalized additive models. The value given in brackets in each y-axis is the effective degree of freedom estimated for the spline and when is close to or equals zero indicates no relevance of the predictor for the model. Dashed lines represent 95% confidence intervals. For further information on the predictors see Table B1.

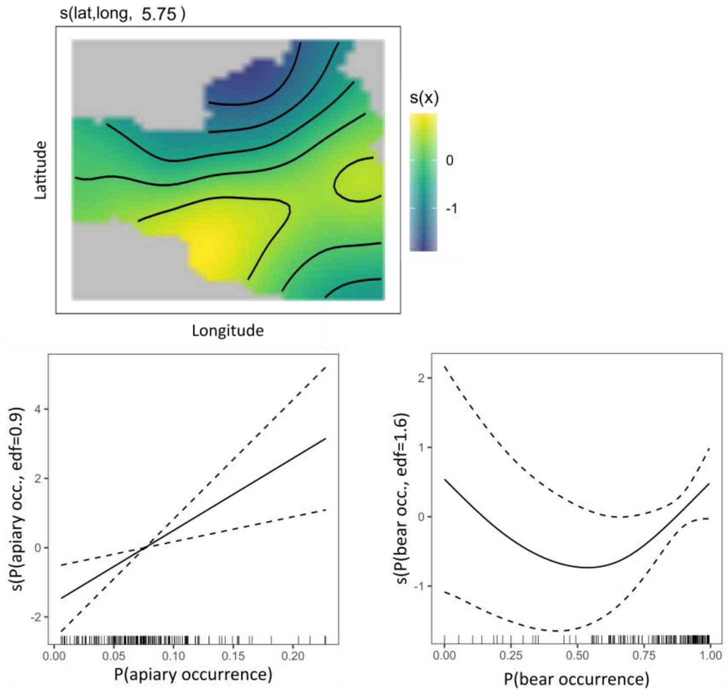


Figure B3. Smooth splines showing the relative probability of occurrence of bear damage to apiaries in relation to different predictors. The probability of bear damage occurrence was estimated in a 1x1 km-grid (N= XX cells) covering the brown bear range in the Northern Carpathians, SE Poland, based on a binomial generalized additive model. Solid lines represent the estimated smooth functions of different predictors and the dashed lines indicate the 95% confidence intervals. The value given in brackets in each y-axis is the effective degree of freedom estimated for the spline and when equal or closer to zero indicates no or little relevance of the predictor for the model. Predictors as follows: density of major roads (MaR), density of minor roads (MiR), density of very small roads (VsR), slope (slope_), agricultural cover (agri), length of forest edge (f_edge). For further information on the predictors see Table B1.

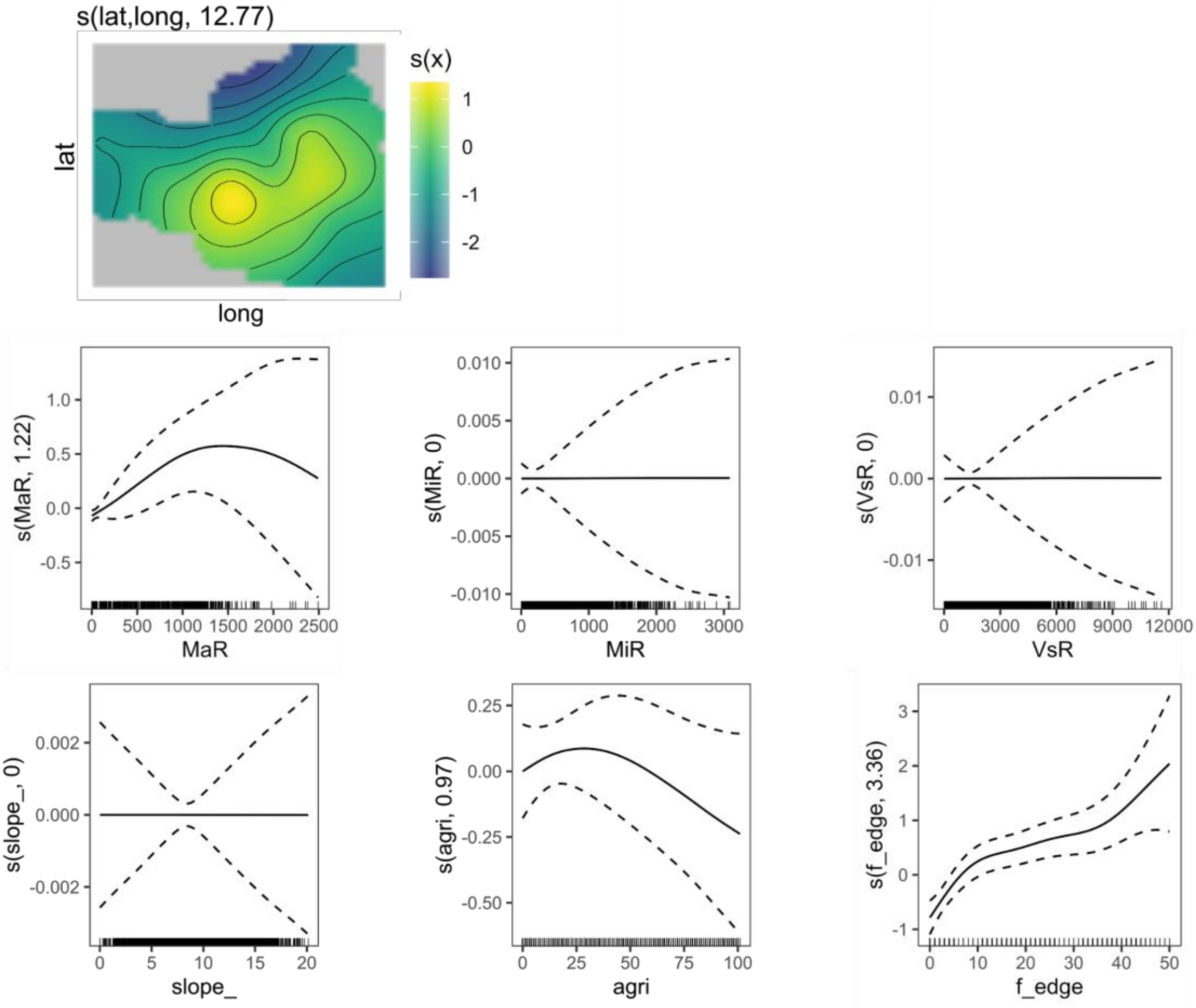


Figure B4. Smooth splines showing the relative probability of occurrence of bear damage to apiaries at the household scale (actual location of the apiary) in relation to different predictors. The probability of bear damage occurrence was estimated with information from 293 apiaries distributed within the bear range in the Northern Carpathians, SE Poland, and based on a binomial generalized additive model. Solid lines represent the estimated smooth functions of different predictors and the dashed lines indicate the 95% confidence interval. The value given in brackets in each y-axis is the effective degree of freedom estimated for the spline and when equal or closer to zero indicates no or little relevance of the predictor for the model. Predictors as follows: probability of bear presence (P(bear)), distance to the nearest building (D_build), distance to the nearest forest patch (D_forest), forest cover in a 200 meters radius (forest200), number of buildings in a 200 meters radius (build200). For further information on the predictors see Table B1.

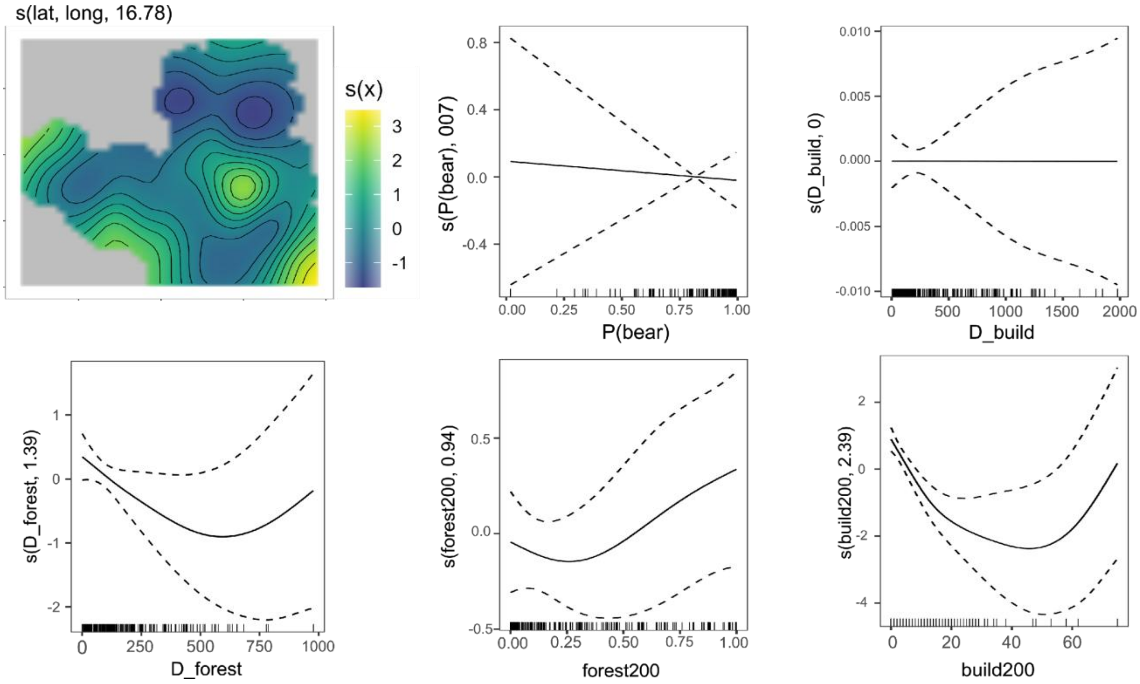


Figure B5. Results from Generalized Additive Models assessing the effect of preventive measures in the occurrence of bear damage to apiaries in relation to different predictors. The probability of bear damage occurrence was estimated with information from 151 apiaries distributed within the bear range in Northern Carpathians, SE Poland, and based on a binomial generalized additive model. Solid lines represent the estimated smooth functions of different predictors and the dashed lines indicate the 95% confidence interval. The value given in brackets in each y-axis is the effective degree of freedom estimated for the spline and when is close to or equals zero indicates no or little relevance of the predictor for the model. Predictors as follows: distance to the nearest building (D_build), distance to the nearest forest patch (D_forest). Prev0 and prev1 indicate apiaries unprotected and protected against bear damage, respectively. For further information on the predictors see Table B1.

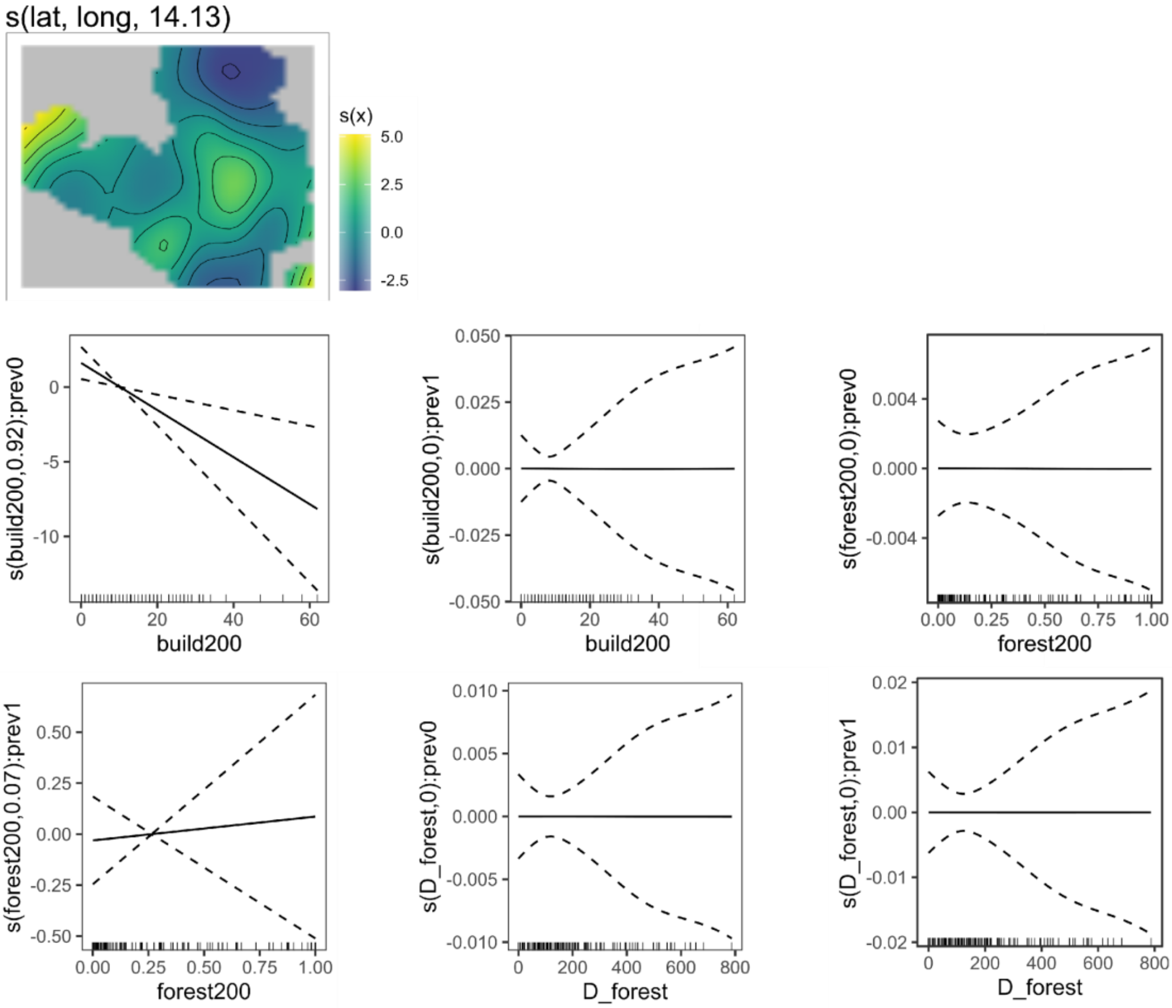


Figure B6. Number of apiaries used in the preventive model grouped by being damaged or not and conditional to the use of preventive measures. We considered as preventive measures installed electric fences.

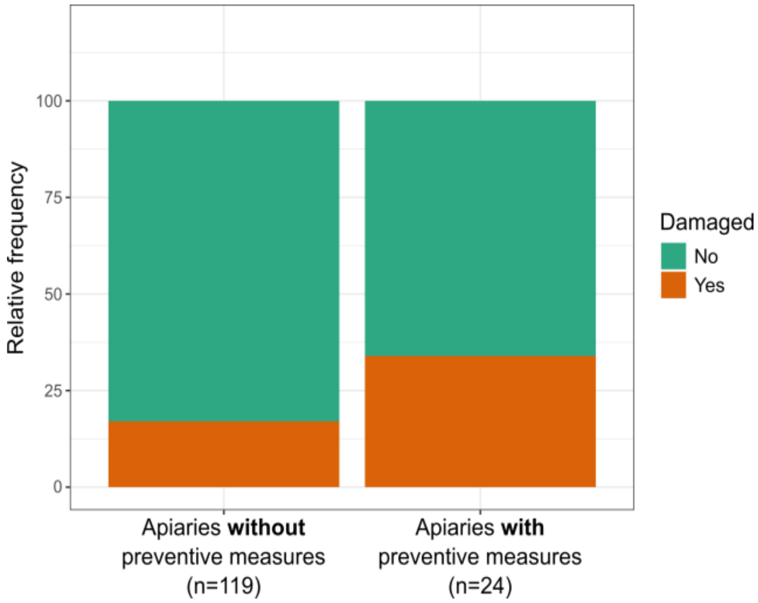


Figure B7. Distribution of the number of apiaries in relation to the density of buildings surrounding the apiaries in a 200-meters radius in areas predicted to be at very low, moderate and high risk of bear damage. The apiaries are classified according to the presence or absence of measures to prevent damage. Note that in the apiaries located in areas predicted to be at moderate or high risk the density of buildings is relatively low. Note, as well, that the majority of apiaries with preventive measures are surrounded by less than three buildings.

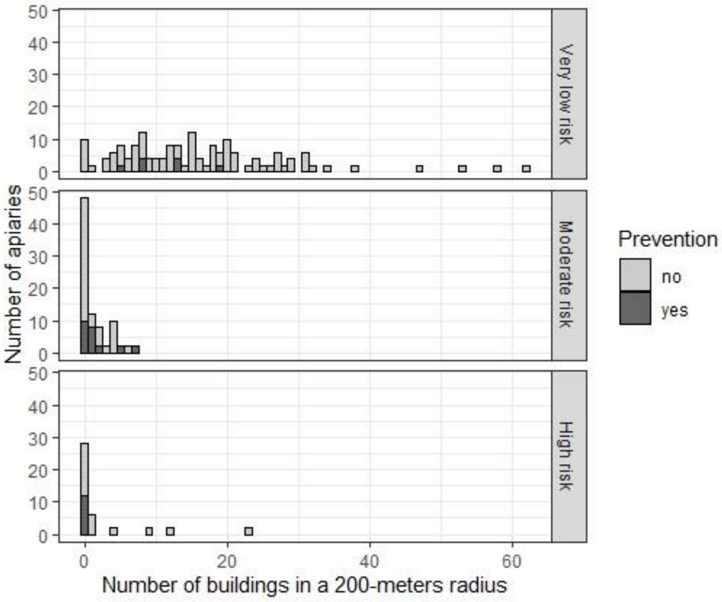


Figure B8. Spline correlograms of the occurrence of bear damage on beehives and the residuals of Generalized Additive Models run to predict the relative probability of bear predation at multiple scales.

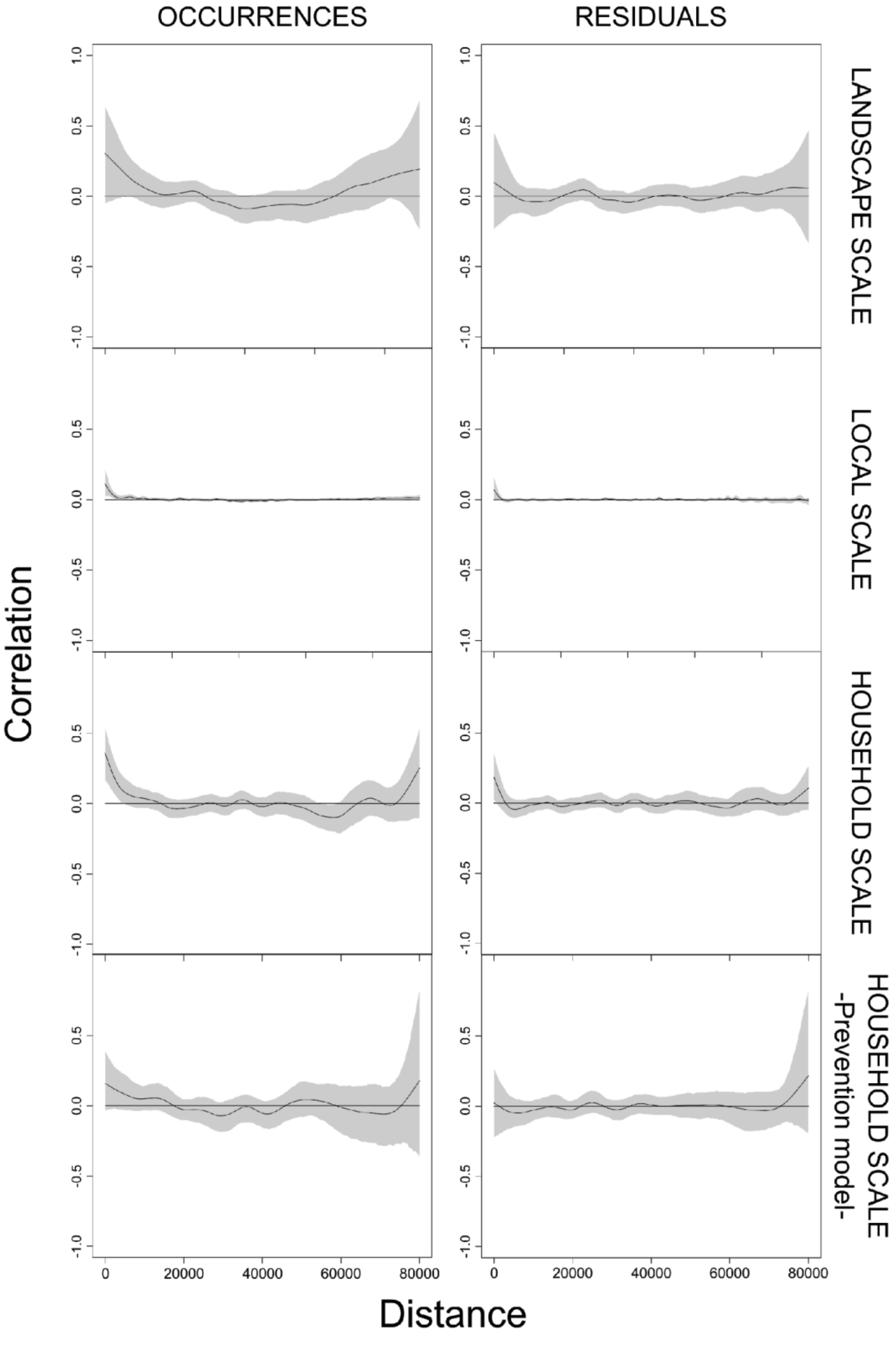


Figure B9. Risk maps showing the relative probabilities of bear damage to apiaries in the Northern Carpathians (SE Poland) at three nested scales (left panels). The relative probability of damage was predicted at each scale based on the coefficients of generalized additive models run within the bear distribution range (cells highlighted with blue line) and then extrapolated to the entire Carpathian Mountain range in the Podkarpackie Province. Multiscale risk maps (right panels) were predicted based on the joint probability of damage across scales, which was calculated at the smallest scale (bottom-right panel) and then rescaled it to the upper levels (mid and top right panels). Predicted risk of damage for all maps was classified using the maximized sum of sensitivity-specificity. The values below the threshold are considered as predicted absence of damage (grey colour). The values above the threshold were divided into four equal-interval classes of damage risk (the darker the orange colour, the higher the risk). The bar plots at the bottom-left of each panel show the relative frequency of the different risk classes in the map. The predictive accuracy for each risk map was measured with the area under the curve (AUC).

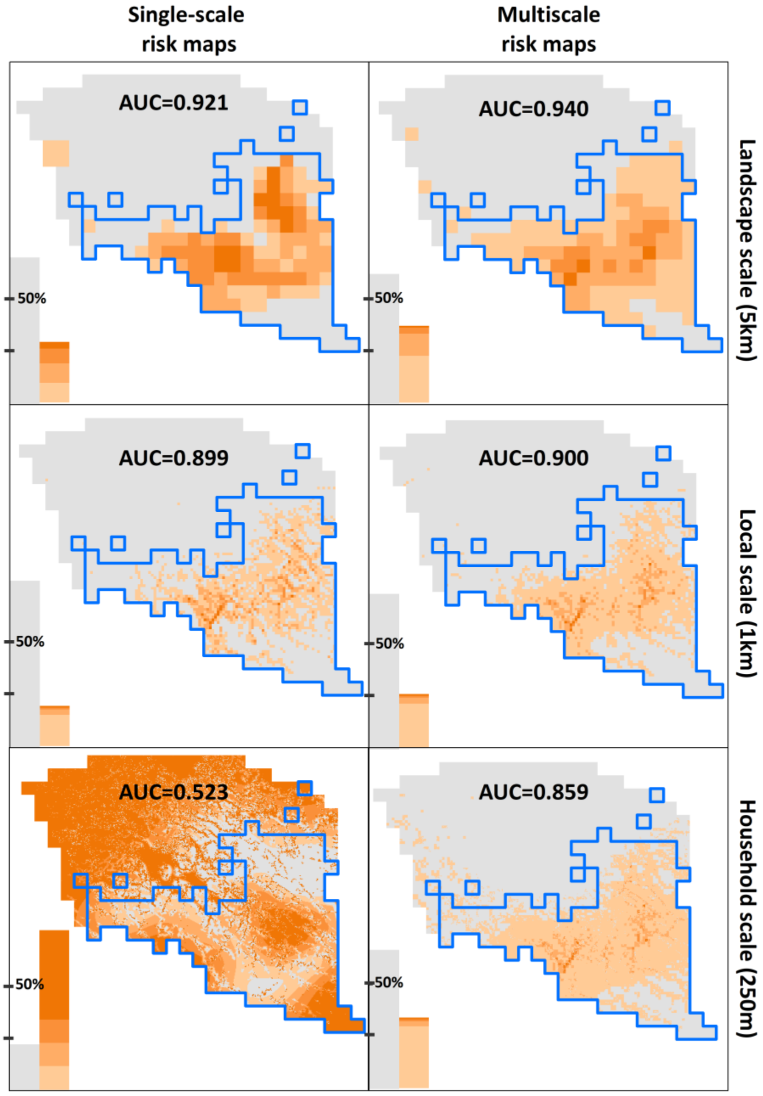
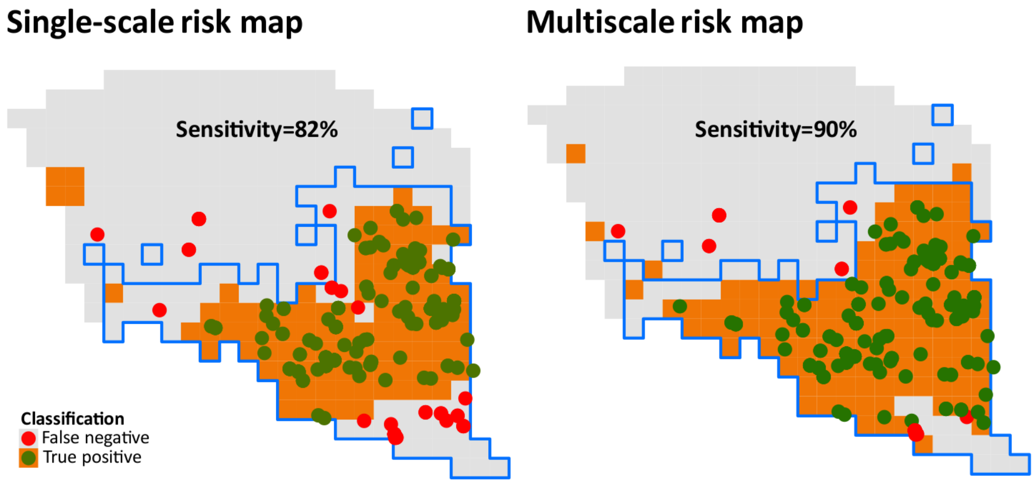


Table B2. Relative frequency (%) of the area covered by different categories of risk of brown bear damage to apiary in the Northern Carpathian Mountains, SE Poland. The risk of damage was predicted by generalized additive models at multiple scales and then categorized based on the maximized sum of specificity and sensitivity (see Fig. B9).

	Single-scale risk maps		Multiscale risk maps	
LANDSCAPE SCALE	Full study area	Bear range	Full study area	Bear range
Very low risk	70.7	39.5	62.7	22.3
Moderate risk	29.3	59.9	37.3	76.4
High risk	10.0	21.7	3.8	7.6
LOCAL SCALE				
Very low risk	80.6	59.2	75.1	47.2
Moderate risk	19.4	40.7	24.9	52.8
High risk	0.7	1.6	0.4	0.9
HOUSEHOLD SCALE				
Very low risk	22.1	29.5	67.3	35.2
Moderate risk	77.9	70.5	32.7	64.8
High risk	54.8	34.8	0.3	0.7

Figure B10. Risk maps based on the joint probability of damage across scales are more sensitive to the occurrence of damage than risk maps based on the extrapolation from single-scale analysis. This figure presents two maps showing the risk of brown bear damage to apiaries in the Northern Carpathian. The map on the left resulted from projecting across the space the probability of damage based on a generalized additive model analyzing the occurrence of damage in a grid of 5x5km grid. The map in the right resulted from combining the estimated probabilities of damage calculated separately at three nested scales (5x5 km, 1x1 km and 0.25x0.25 km) into an integrated-scale risk map at the finest resolution and then rescaling it into the coarser resolution. The blue line delimits the bear distribution range. Orange and grey cells represent predicted presences and absences of bear damage, respectively. Dots represent locations of damaged apiaries in the years 2000 to 2009 and that were not used in the predictive models. Green and red colours indicate correctly and wrongly classified damages to apiaries, respectively.



APPENDIX C – EVALUATING THE PREDICTIONS FROM THE LOCAL-SCALE MODEL WITH SLIGHT SPATIAL AUTOCORRELATION IN ITS RESIDUALS.

A widely accepted approach to control for autocorrelation is directly modeling it using correlation structures and removing its effect (Zuur et al., 2009). However, autocorrelation can reflect underlying ecological processes (Keitt et al., 2002; McIntire and Fajardo, 2009), and by removing it we may miss patterns of interest. Accordingly, instead of removing the autocorrelation, we aimed to guarantee that the slight spatial autocorrelation in the residuals of the model at the local-scale (see previous Fig. B8) did not lead to wrong predictions. For that, we compared the predictions from the model with slight spatial autocorrelation in the residuals with the averaged predictions from 1000 models built with subsamples that were balanced (same number of absences and presences), had spatially thinned absences (separated by at least 1km), were randomly selected and presented no spatial autocorrelation in the residuals. We compared the contributions of the fitted values by predicting the trend for each of the terms (predictors) included in the model. We did that for the spatially autocorrelated model and the 1000 models. Specifically, and based on the coefficients of each model, for each term we predicted 100 evenly-spaced values over its range and left the other variables on their mean value. Then, we averaged the predictions from the 1000 models with no spatial autocorrelation. We repeated this operation for the 6 terms included in the local-scale analysis (see Fig. A10). We also compared the capacity of the prediction from our main model (local model) and from the averaged predictions to discriminate between presences and absences of damage and we obtained almost identical results (Fig. C2).

Figure C1. Contribution from different predictors to the fitted values of generalized additive models used to predict the probability of bear damage to apiaries in a 1x1km grid in the Northern Carpathians, SE Poland. Black lines represent the contribution of the predictors from the model containing all the data and the red lines the averaged contribution from 1000 models built with subsamples from the data.

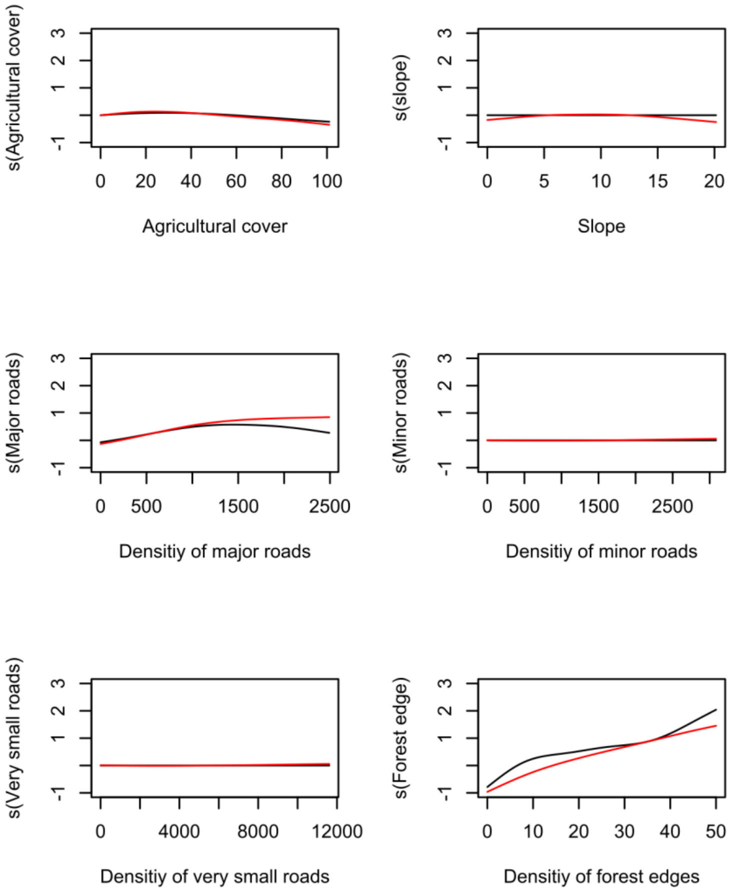
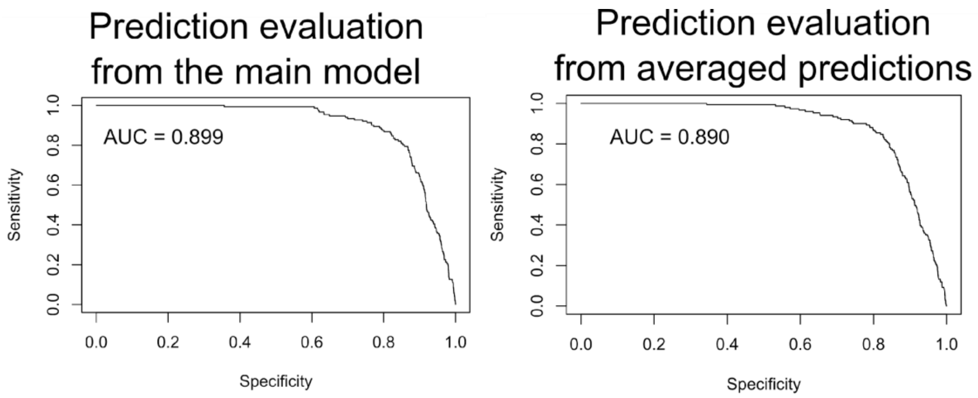


Figure C2. Evaluation of the prediction from the main model (local-scale model) and from averaged predictions analysing the occurrence of brown bear damage to apiaries in a 1x1km grid in the Northern Carpathians, SE Poland.



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CHAPTER IV

RESOURCE PULSES AND HUMAN-WILDLIFE CONFLICTS: LINKING SATELLITE INDICATORS AND GROUND DATA ON FOREST PRODUCTIVITY TO PREDICT BROWN BEAR DAMAGES

with

Julian Oeser, Tobias Kuemmerle & Nuria Selva

(submitted to *Remote Sensing in Ecology and Conservation*)

SUMMARY

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, 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 parts of the globe, 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.

1. 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 and 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 and 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 and Jedrzejewski, 1998; McShea, 2000; Ostfeld and 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 and 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 (Jędrzejewska and Jędrzejewski 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 and 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 and Roper, 2003). A scarce primary production can also result in increased conflicts through indirect bottom-up effects in higher trophic levels. For example, grey wolves (*Canis lupus*) can switch their diet towards livestock (Ciucci et al., 2018; Jedrzejewski et al., 2011; Meriggi et al., 1996; Salvador and Abad, 1987) as a response to decreasing abundance of wild prey after years of low primary productivity (Kiffner and 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 et al., 2020a; 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 and

Sork, 2002; Piovesan and Adams, 2001). Common cues of masting include temperature, precipitation, and evapotranspiration in different phenological seasons, both in the year of masting and up to two years before (Bogdziewicz et al., 2020b; Nussbaumer et al., 2018; Piovesan and 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 resources 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; Pettorelli et al., 2005a, 2011). Vegetation indices also appear promising to predict mast seeding events (Bajocco et al., 2021; Camarero et al., 2010; Fernández-Martínez et al., 2015; 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., 2005a, 2011). 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; Pettorelli et al., 2005b), 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 north-eastern Carpathians 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 beehives (Bojarska and 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 (Ciucci et al., 2014; Naves et al., 2006). In temperate ecosystems, brown bears are known to strongly rely on tree crops, such as beechnuts, 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, beechnuts can remain available under the snow until the end of the following winter, allowing bears to consume beechnuts after they emerge from their dens (Bojarska 2014). However, beech masting and years of crop failure occur at highly irregular intervals (Hilton and Packham, 2003; Nussbaumer et al., 2018). Since beechnuts are a key food resource for bears (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 (Bautista et al., 2021, 2017). We tested this hypothesis using novel remote-sensing indicators of vegetation growth and phenology, weather cues, and a unique time series of human-bear conflict occurrence.

2. MATERIAL AND METHODS

2.1. Study area

Our study area is located in the Carpathian Mountains in the Podkarpackie Province, Poland (Fig. 1). This area is characterized by gentle slopes and low to medium elevation mountains ranging from about 200 to 1200m. 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 zone (<500m) which is nowadays mostly occupied by human settlements and agriculture, with a limited cover of mixed deciduous forests; (2) the lower montane zone (500–1150m) primarily consisting of forests dominated by beech and silver fir (*Abies alba*); and (3) the zone above the upper tree line (>1150m), 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 (s.d. = 0.8) in July and −3°C (s.d. = 0.8) in January. Annual precipitation for the same period ranged between 790 and 1,200mm, with a maximum during the summer (average precipitation between 100-150mm, maximum of 320mm in July) and a minimum in winter (average precipitation between 50-60mm, with a minimum of 10mm in January; data provided by the Polish Institute of Meteorology and Water Management, https://dane.imgw.pl/data/).

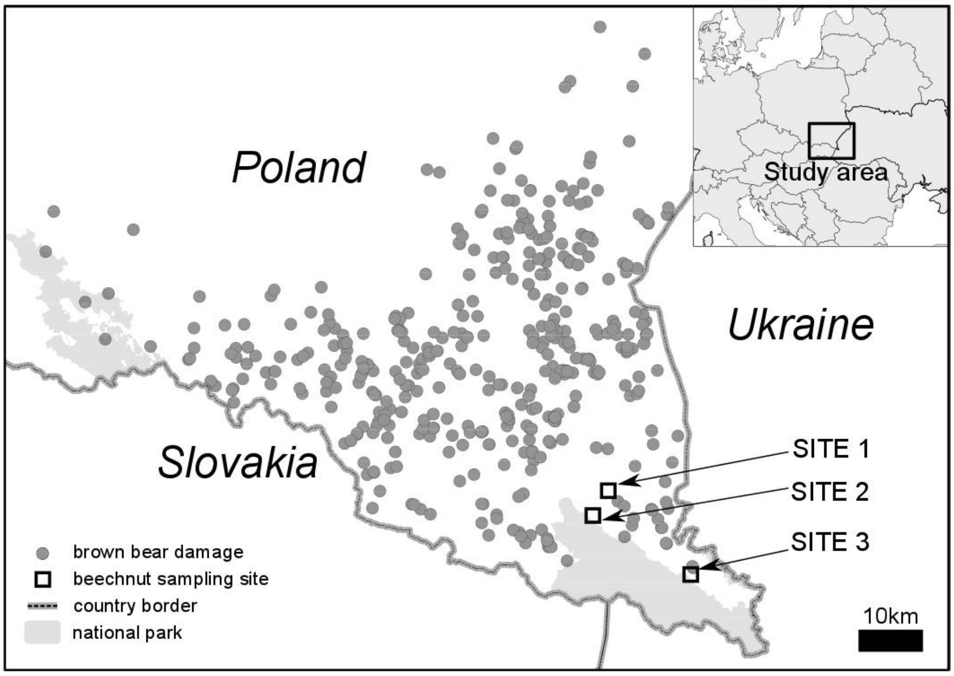


Figure 1. Map of the study area showing the locations of the three beechnut sampling sites and brown bear (*Ursus arctos*) damages in the northe-astern Carpathians (SE Poland) in 2007-2020.

2.2. 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 (Fig. 1). The annual number of recorded damages ranged from 15 to 104 (mean of 47 damages annually, s.d. = 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).

2.3 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 1x1 m^2on the ground of beech forests at three sites, 10 plots per site (Fig. 1 & Fig. 2). 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 in the supplementary material). This was due to weather, field conditions and logistics. Traditional approaches that measure beech productivity by collecting seed crops from October to November risk to overlook 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).

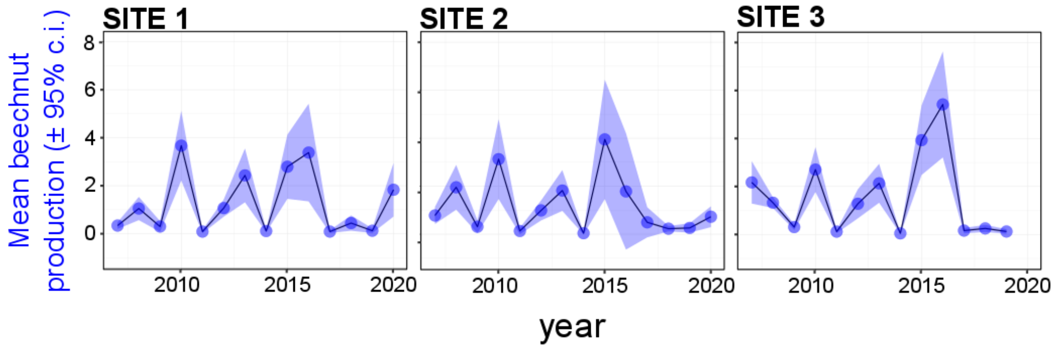


Figure 2. Temporal trends in European beech (*Fagus sylvatica*) seed production in three sampling sites in the north-eastern Carpathians (SE Poland) in 2007-2020. Beechnut production was sampled yearly in 30 1x1m^2 plots distributed evenly across three sampling sites and was measured in number of seeds per m^2 and standardized by the duration in days of the sampling session (see Table S1 for details).

2.4. 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 two years before masting, (2) a dry and warm summer one year before masting and/or (3) a warm spring in the masting year (Bogdziewicz et al., 2020b; Nussbaumer et al., 2018; Piovesan and Adams, 2001). Accordingly, we extracted the mean maximum temperature and summed precipitation in summer (June and July) for one and two 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 growing season (May–August), since raising temperatures can enhance beechnut production (Bogdziewicz et al., 2020b), 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 and 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).

As remote sensing indicators of beechnut productivity and phenology, we tested two types. First, we used spectral-temporal metrics derived from Landsat imagery at a 30m spatial resolution (Oeser et al., 2019), using the Tasseled Cap (TC) greenness index as a proxy of vegetation productivity (Crist and 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 250m resolution. MODIS-based phenological metrics have been shown to be useful to analyse 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 2005-2020 (extent of the field sampling and two 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 in the supplementary material.

2.5. Statistical analyses

2.5.1 Temporal fluctuations of damage in relation to beechnut production

We hypothesized that the number of bear damages decreases in masting years or years of high beechnut production, and increases in years of low beechnut production or crop failure. To test our hypotheses 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 slowly to feed (January – June) as responses to different categories of beechnut production (i.e., crop failure, common crop and masting). 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). For all analyses, we used Generalized Linear Models with a negative binomial distribution to avoid overdispersion.

2.5.2. 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 autocorrelation 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 (ΔAIC_c= 36). We did not include 'site' as a fixed effect because this decreased the model fit (ΔAIC_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 fixed. To find the most parsimonious models, we compared candidate models according to Akaike's Information Criterion, adjusted for small sample sizes (AIC_c; Supplementary 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. Finally, 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* (Bartoń, 2014) for model selection, model averaging and prediction of averaged models, and *ggplot2* (Wickham, 2016) for data visualization.

3. 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, Fig. 3). 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 conditions explained mast years in beech forests: (1) a cold summer two years before masting, (2) a low beechnut production and high yearly forest productivity one year before masting, and (3) low summer productivity in the masting year (Table 2; Table S3, S4). The fact that beechnut production was negatively correlated to 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, 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, df=70, Fig. S2) and their yearly means across plots correctly classified the seed failure in 2019 (Fig. 3).

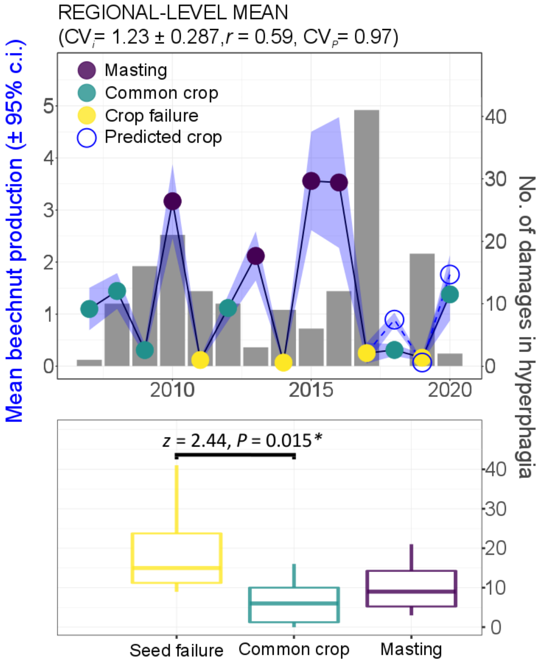
Table 1. Summary of negative binomial generalized linear models analyzing the number of brown bear damages at different seasons as a response to beechnut production in the north-eastern Carpathians (SE Poland) in 2007-2020. The beechnut production was categorized as crop failure, common crop and masting 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.

	Responses	
Predictors	**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
	** p<0.05 ** p<0.01 *** p<0.001*	

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 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.

Figure 3. The effect of European beech (*Fagus sylvatica*) seed production on the occurrence of brown bear (*Ursus arctos*) damages in the north-eastern Carpathians (SE Poland) in 2007-2020. The upper plot in shows the regional-level mean beechnut production (blue lines) and the number of confirmed and compensated bear damages during hyperphagia (September-December; grey bars). Masting behavior is measured in terms of mean interannual variability in beechnut production (CV_i) 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.



This study provides important evidence that temporal fluctuations in bear damage occurrence are sensitive to the year-to-year variation of mast pulses in Europe. The previous available literature on the topic 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 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 include anthropogenic food such us beehives and livestock (Bautista et al., 2021, 2017), and, as proven here, they can cover food shortages consuming them. 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 and 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). 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 Fig. 3). 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 success of conflict prevention programs also 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 unlikely a heavy reproduction in the following year (Pearse et al., 2015). In terms of weather cues, we found that masting occurs two years after cold summers, which can prime resource accumulation for floral induction in the following year (Nussbaumer et al., 2018; Piovesan and 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 one year after a high yearly forest productivity, and low summer forest productivity in the masting year. High forest productivity one 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 two years before masting primes trees to accumulate resources.

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

Predictor	**Estimate**	**SE**	**Adj. SE**	***p*-value**	**AICc***
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 lag1	-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

* Relative 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 in the supplementary material.

Additionally, these finding 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 et al., 2020a; Kelly and Sork, 2002). Accordingly, the high forest productivity one 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 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; Vergotti et al., 2019) and that, combined with other correlates, can adequately explain and predict seed production (see Fig. 3). 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 filed data can help to increase the forecasting ability and to deepen into the understanding of ecological dynamics governed by resource pulses (Bjørnstad and 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 et al., 2020b).

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 et al., 2020b; Hacket-Pain and 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 and 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 and 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 et al., 2020b; 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 and 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 towards 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., 2015, 2014) 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.

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SUPPLEMENTARY MATERIAL FOR
Resource pulses and human-wildlife conflicts: Linking satellite indicators and ground data on forest productivity to predict brown bear damages

SUPPORTING TABLES AND FIGURES

Table S1. Summary statistics on beech seed production in the Northern Carpathians (SE Poland) obtained in 30-1m^2 sample plots in different sampling sessions in 2007-2020. The sampling sessions selected to analyze the impact of weather cues and remotely sensed indicators of forest productivity and phenology on the production of beechnuts are shaded with grey color.

	sampling session			seed production (seeds m^{-2} day^{-1})			
year	cleaning day	collecting day	duration (days)	MIN	MAX	MEAN	SD
2007	28-Aug	19-Oct	53	0.08	3.83	1.10	1.09
2008	04-Aug	07-Oct	64	0.09	2.66	0.69	0.60
2008	07-Oct	12-Nov	36	0.33	4.53	1.44	0.92
2009	05-Aug	11-Sep	37	0.03	1.32	0.31	0.29
2009	11-Sep	12-Nov	62	0.00	0.20	0.05	0.05
2010	15-Aug	15-Sep	31	0.03	0.81	0.38	0.23
2010	15-Sep	15-Oct	30	0.68	8.42	3.17	1.91
2010	16-Oct	13-Nov	28	0.07	3.89	1.40	1.11
2011[a]	31-Aug	30-Sep	30	0.00	1.10	0.22	0.26
2011[a]	30-Sep	28-Oct	28	0.00	0.61	0.12	0.13
2012[a]	19-Aug	27-Sep	39	0.05	3.18	1.12	0.66
2012[a]	27-Sep	17-Nov	51	0.04	1.27	0.57	0.36
2013[a]	13-Sep	19-Nov	67	0.45	4.84	2.12	1.26
2014	25-Aug	29-Oct	65	0.00	0.27	0.07	0.07
2015	19-Sep	10-Oct	21	0.43	11.29	3.56	2.53
2015	10-Oct	07-Dec	58	0.03	2.12	0.92	0.52
2016	17-Sep	24-Oct	37	0.19	11.38	3.53	3.36
2016	24-Oct	23-Nov	30	0.00	2.24	0.60	0.51
2017	16-Sep	15-Oct	29	0.00	2.83	0.25	0.53
2017	15-Oct	25-Nov	41	0.00	0.22	0.03	0.05
2018	19-Sep	30-Oct	41	0.02	1.32	0.31	0.30
2019[b]	18-Aug	24-Sep	37	0.00	0.19	0.05	0.05
2019[b]	24-Sep	19-Oct	25	0.00	0.76	0.16	0.18
2020[c]	30-Aug	05-Oct	36	0.11	4.68	1.38	1.35

[a], 28 plots; [b], 27 plots; [c], 17 plots

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

Predictor	Abbreviation	Time lag	Description
WEATHER CUES – described by meteorological variables measured in the Stuposiany meteorological station and extracted from the Polish Institute of Meteorology and Water Management			
Mean maximum temperature in summer (June and July)	*sum*T	2yr, 1yr	Commonly indentified weather cues for European beech seeding are a cold and wet summer two years before a masting year, a dry and warm summer one year before a masting year and a warm and dry spring in the masting year (Piovesan and Adams 2001, Kasprzyk and Ortyl 2014, Nussbaumer et al. 2018, Bogdziewicz et al. 2020)
Summed precipitation in summer (June and July)	*sum*P	2yr, 1yr	
Mean maximum temperature in spring (April and May)	*spr*T	0yr	
Summed precipitation in spring (April and May)	*spr*P	0yr	
Mean temperature in the growing season (May-August)	*gs*T	0yr	Increasing temperatures during the growing season can enhance higher beechnut production (Bogdziewicz et al. 2020)
Minimum absolute temperature in late spring (May and June)	*spr*$\mathrm{T}_{\mathrm{min}}$	0yr	Late spring frost is associated to crop failure in masting plants (Neilson and Wullstein 1980, Honda 2013)
FOREST PRODUCTIVITY – The productivity was measured by Tasseled Cap greenness values extracted from Landsat satellite imagery			
Start of the season	*spr*Prod	2yr, 1yr, 0yr	Median TC greenness in spring (March-May)
Peak of the season	*sum*Prod	2yr, 1yr, 0yr	Median TC greenness in summer (June-August)
End of the season	*aut*Prod	2yr, 1yr, 0yr	Median TC greenness in autumn (September-November)
FOREST PHENOLOGY – The canopy photosynthetic capacity was measured by Enhanced Vegetation Index values, extracted from MODIS satellite imagery, and plotted against the day of the year to calculate different phenological metrics			
Start of the growing season	SOS	2yr, 1yr, 0yr	The day of the year on which the peak green-up rate occurs (being the peak green-up rate the largest growth rate of canopy photosynthetic capacity during the growing season) (Gu et al. 2009)
Peak of the growing season	POP	2yr, 1yr, 0yr	The day on which peaks the canopy photosynthetic capacity and thus when the peak of the growing season occurs (Gu et al. 2009)
End of the growing season	EOS	2yr, 1yr, 0yr	The day of the year on which the peak senescence rate occurs (being the peak senescence rate the most negative growth rate of canopy photosynthetic capacity during the growing season) (Gu et al. 2009)

Table S2. Continued

Predictor	**Abbreviation**	**Time lag**	**Description**
FOREST PHENOLOGY (continued)			
Upturn day	UD	2yr, 1yr, 0yr	The day on which the green-up line intercepts with the x -axis. Around the upturn day, the canopy photosynthetic capacity often starts to increase sharply (Gu et al. 2009)
Stabilization day	SD	2yr, 1yr, 0yr	The day on which the peak canopy photosynthetic capacity is predicted to occur based on the recovery line (Gu et al. 2009)
Downturn day	DD	2yr, 1yr, 0yr	The day on which the peak canopy photosynthetic capacity is predicted to occur based on the senescence line. Around the downturn day, canopy photosynthetic capacity often starts to decrease sharply (Gu et al. 2009)
Recession day	RD	2yr, 1yr, 0yr	The day on which the senescence line intercepts with the x –axis (Gu et al. 2009)
Green-up slope	greenup slope	2yr, 1yr, 0yr	A line that closely approximates the linear feature within the green-up phase of the seasonal dynamics of plant community photosynthesis and is defined by the canopy photosynthetic capacity and its growth rate on the start of the growing season (Gu et al. 2009)
Green-up length	senescence slope	2yr, 1yr, 0yr	Length of the green-up phase, determined by the number of days elapsed between the upturn day and the stabilization day (Gu et al. 2009)
Senescence slope	greenup length	2yr, 1yr, 0yr	A line that closely approximates the linear feature during the senescence phase of the seasonal dynamics of plant community photosynthesis and is defined by the canopy photosynthetic capacity and its growth (decline) rate (negative) on the end of the growing season (Gu et al. 2009)
Senescence length	senescence length	2yr, 1yr, 0yr	Length of the senescence phase, determined by the number of days elapsed between the downturn day and the recession day (Gu et al. 2009)
Yearly total produtivity	Integral	2yr, 1yr, 0yr	The integration of canopy photosynthetic capacity over a year (the area under the curve of canopy photosynthetic capacity in a plot of canopy photosynthetic capacity vs. day of year, which serves as a measure of the yearly total productivity) (Gu et al. 2009)

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 North-eastern Carpathians (SE Poland) in 2007-2020. All models included the sampling plot and the year as random intercepts and the seed crop in lag1 (β= -0.28, CI= -0.41 – -0.15, p-value < 0.001). The sampling duration (i.e., numbers of days between plot cleaning and seed collection) was added as an offset in all models. We fitted every model using negative binomial error distribution. The 95% confidence intervals are shown in brackets below the estimates. The predictor variables (including seed crop in lag1) were standardized to zero mean and unit variance, and, therefore, the estimates are comparable. Estimates highlighted in bold indicate significant predictors of seed production and were then combined in a global model for prediction proposes (see Table S4).

WEATHER CUES

Predictors	**Lag2**	**Lag1**	**Lag0**
*sum*T	**-0.96 **** **(-1.65 – -0.28)**	0.44 (-0.23 – 1.10)	NA
*sum*P	0.45 (-0.29 – 1.18)	-0.33 (-1.04 – 0.38)	NA
*spr*T	NA	NA	-0.38 (-1.15 – 0.38)
*spr*P	NA	NA	0.15 (-0.69 – 0.98)
*gs*T	NA	NA	0.08 (-0.69 – 0.84)
sprT_{min}	NA	NA	**0.86** **(-0.03 – 1.74)**

FOREST PRODUCTIVITY

Predictors	**Lag2**	**Lag1**	**Lag0**
*spr*Prod	0.11 (-0.04 – 0.26)[a]	**-0.18 *** **(-0.33 – -0.03)**[a]	-0.01 (-0.15 – 0.13)[a]
*sum*Prod	-0.09 (-0.23 – 0.05)	0.05 (-0.07 – 0.16)	**-0.18 **** **(-0.30 – -0.07)**
*aut*Prod	-0.15 (-0.35 – 0.06)[b]	**0.23 *** **(0.01 – 0.45)**[b]	-0.06 (-0.24 – 0.12)

FOREST PHENOLOGY

Predictors	**Lag2**	**Lag1**	**Lag0**
SOS	-0.06 (-0.16 – 0.04)	**-0.31** * **(-0.60 – -0.03)**	0.11 (-0.06 – 0.28)
POP	-0.04 (-0.16 – 0.08)	**-0.23** ** **(-0.39 – -0.08)**	-0.10 (-0.25 – 0.04)
EOS	-0.04 (-0.18 – 0.11)	-0.10 (-0.24 – 0.04)	-0.03 (-0.18 – 0.11)
UD	-0.05 (-0.15 – 0.05)	-0.02 (-0.23 – 0.18)	**0.14** **(-0.01 – 0.28)**
SD	-0.07 (-0.18 – 0.04)	**-0.25** * **(-0.45 – -0.05)**	-0.01 (-0.16 – 0.14)
DD	-0.02 (-0.17 – 0.13)	**-0.15** * **(-0.28 – -0.01)**	0.01 (-0.15 – 0.17)
RD	-0.06 (-0.20 – 0.08)	0.04 (-0.11 – 0.18)	-0.04 (-0.17 – 0.08)

Table S3. Continued

FOREST PHENOLOGY			
Predictors	**Lag2**	**Lag1**	**Lag0**
integral	0.04 (-0.08 – 0.16)	**0.28** ** **(0.08 – 0.49)**	-0.14 (-0.32 – 0.04)
greenup slope	-0.06 (-0.17 – 0.04)	**0.17** ** **(0.06 – 0.28)**	0.01 (-0.11 – 0.13)
senescence slope	0.02 (-0.10 – 0.15)	0.07 (-0.06 – 0.19)	-0.05 (-0.18 – 0.09)
greenup length	-0.01 (-0.13 – 0.10)	-0.08 (-0.20 – 0.03)	-0.10 (-0.23 – 0.03)
senescence length	-0.02 (-0.17 – 0.13)	**0.14** * **(0.00 – 0.27)**	-0.04 (-0.19 – 0.11)
Observations	362	362	362

[a], 352 observations; [b], 332 observations; [c], 387 observations

** p<0.05 ** p<0.01 *** p<0.001*

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 North-eastern Carpathians (SE Poland) in 2009-2020. Data on beechnut production in 2007 and 2008 were not included in the model because some remote sensing predictors were missing due to cloud cover. The offset (duration in days of the sampling session) was kept fixed during the model selection procedure to account for any potential effects of sampling intensity between years and is not shown in the table. Conditional (cond) and marginal (marg) R^2 as well as the Root Mean Square Error (RMSE) are given for each model. The tables shows the models with delta AIC_c <4 (8 out of 8,192 models).

Variables	df	logLik	AIC_c	Delta	AIC_c Weight	R^2 (cond)	R^2 (marg)	RMSE
*sum*T$_{lag2}$ + Integral$_{lag1}$ + DD$_{lag1}$ + Seeds$_{lag1}$ + *sum*Prod	9	-1335.75	2690.07	0.00	0.080	0.726	0.308	46.794
*sum*T$_{lag2}$ + Integral$_{lag1}$ + DD$_{lag1}$ + SenesL$_{lag1}$ + Seeds$_{lag1}$ + *sum*Prod	10	-1335.51	2691.73	1.65	0.035	0.722	0.318	47.062
*sum*T$_{lag2}$ + Integral$_{lag1}$ + DD$_{lag1}$ + Seeds$_{lag1}$ + *spr*Tmin + *sum*Prod	10	-1335.52	2691.75	1.68	0.034	0.737	0.297	46.791
*sum*T$_{lag2}$ + Integral$_{lag1}$ + Seeds$_{lag1}$ + *sum*Prod	8	-1338.12	2692.69	2.62	0.022	0.718	0.317	48.099
Integral$_{lag1}$ + DD$_{lag1}$ + Seeds$_{lag1}$ + *spr*Tmin + *sum*Prod	9	-1337.43	2693.43	3.36	0.015	0.735	0.191	46.734
*sum*T$_{lag2}$ + Integral$_{lag1}$ + DD$_{lag1}$ + SenesL$_{lag1}$ + Seeds$_{lag1}$ + *spr*Tmin + *sum*Prod	11	-1335.31	2693.48	3.41	0.015	0.732	0.307	47.052
Integral$_{lag1}$ + DD$_{lag1}$ + Seeds$_{lag1}$ + *sum*Prod	8	-1338.61	2693.67	3.60	0.013	0.710	0.051	46.765
*sum*T$_{lag2}$ + SOS$_{lag1}$ + Integral$_{lag1}$ + DD$_{lag1}$ + Seeds$_{lag1}$ + *sum*Prod	10	-1336.57	2693.85	3.78	0.012	0.731	0.305	46.862

*sum*T$_{lag2}$, mean maximum summer (June–July) temperature in lag2 (i.e., two years before the assessment year); Integral$_{lag1}$, Carbon assimilation potential in lag1 (one year before the assessment year); DD$_{lag1}$, Downturn day in lag1; Seeds$_{lag1}$, beechnut production in lag1; *sum*Prod, summer productivity measured by TC greenness; SenesL$_{lag1}$, length of the senescence phase in lag1; *spr*Tmin, absolute minimum spring (May-June) temperature; SOS$_{lag1}$, day of the start of the growing season in lag1.

The set of candidate models also included the median TC greenness in spring and autumn in lag1 and the upturn day in lag0

Figure S1. Observed temporal trend in European beech (*Fagus sylvatica*) seed production in 30 sampling plots in the north-eastern Carpathians (SE Poland) in 2007-2020. Beechnut production was measured as the number of seeds per m^2 and standardized by the duration in days of the sampling session (see Table S1 for details). Each line and point within each year represents a different plot. This figure shows a moderate synchrony in the observed beechnut production between plots (mean of all pairwise Pearson between plots (r) = 0.59, see Koenig et al. (2003) for reference levels of synchrony in mast plants).

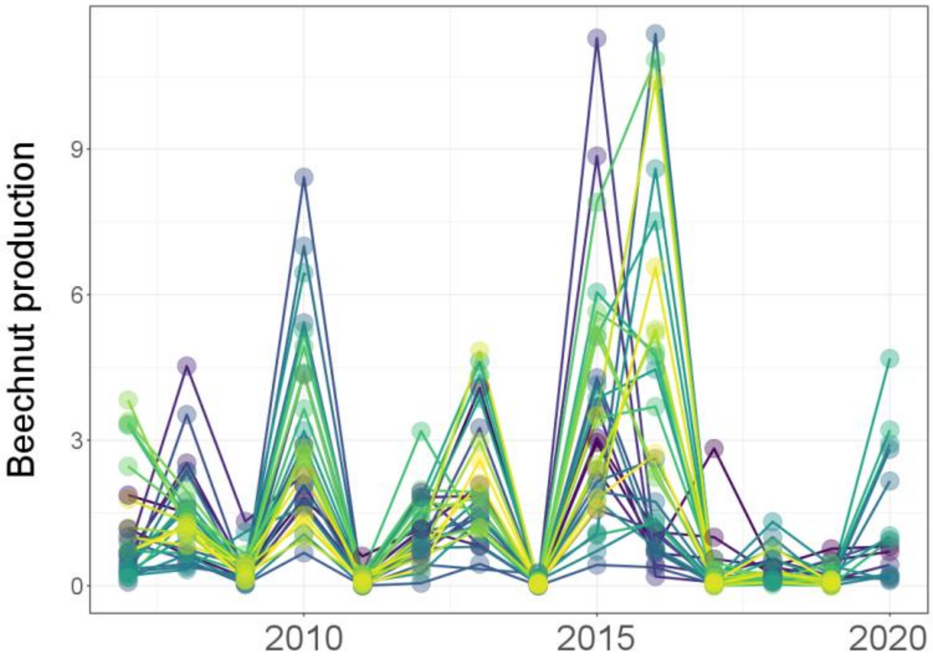
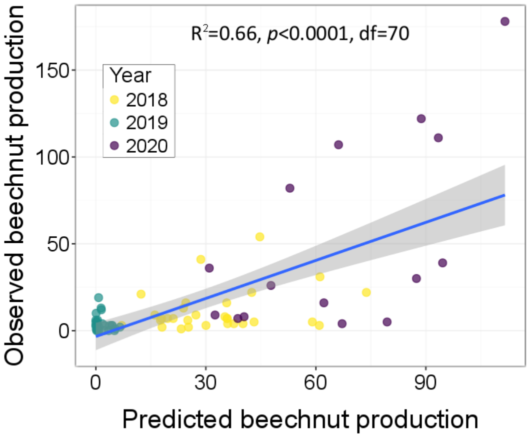


Figure S2. Linear relationship between the observed and predicted beechnut production in the north-eastern Carpathians (SE Poland) in 2018-2020.



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CHAPTER V

CONCLUSIONS

Problems and solutions are two sides of the same coin:

“The man is the most intelligent animal – and the most silly”

Diogenes (412 BC - 323 BC)

GENERAL CONCLUSIONS

1. **The occurrence of brown bear damage and associated conflicts is a complex issue determined by multiple anthropogenic and natural factors.** Anthropogenic factors include socio-economic variables, such as (i) the characteristics of compensation and prevention programs, (ii) husbandry practices and (iii) the economic wealth at the national level, as well as variables linked to human modification of the landscape such as (iv) the presence of free-ranging livestock, apiaries and agricultural fields or (v) the density of buildings around particular farm locations (in the case of damage to apiaries in the Northern Carpathians). Natural factors affecting damage occurrence include (vi) the availability of and proximity to forest patches, (vii) the natural behavior of bears to avoid humans and (viii) the availability of crucial food resources, such as hard mast.
2. **Anthropogenic factors play a primary role in conflicts arising from bear damage** to **human properties at several spatial scales.** At the continental scale, the occurrence of damage increases when the economic wealth at the national level is high, the husbandry practices are not adapted to the presence of large carnivores and prevention is not a precondition to compensation. At the landscape scale, the occurrence of damage increases in areas of interface between agricultural fields that are suitable for beekeeping or farming and forest patches, a suitable habitat for bears. Finally, at the local scale, a low density of buildings and short distance to forest patches are associated with high damage occurrence.
3. **Human tolerance towards large carnivores has an important role in damage management and can influence the costs of compensation.** In general, strong negative attitudes towards large carnivores are associated with high costs for compensation and prevention and can even prevent the recolonization of large carnivore populations. That is especially true in areas of extensive livestock farming, which receive 68% of the total costs invested in the compensation for large carnivore damage in Europe. However, when negative attitudes are not an obstacle, the cost of damage compensation and prevention associated with these recolonizations is often negligible. At the European scale, the costs of damage compensation do not always increase when the rate of large carnivore recolonization was high. Low compensation costs and high recolonization rates can happen in areas with little human influence and high availability of natural preys, but also in human-dominated landscapes when proactive preventive programs readapt husbandry practices to the presence of large carnivores.
4. **The conditional relationships in resource selection among spatial scales** (commonly described in habitat selection by wildlife species) also **apply to how animals select anthropogenic resources and thus, how they are prone to be involved in conflicts with humans**. The risk of damage follows a spatially hierarchical structure, in which the broader landscape context determines to what extent the immediate surroundings of an apiary influence its vulnerability to bear damage. Beekeepers working in landscapes that favor damage could reduce the probability of experiencing bear damage by more than threefold if they would locate their beehives at least 300 m away from the forest patches and in the vicinity of buildings.

5. **Natural resource pulses, such as tree masting, can percolate through food webs and mediate human-wildlife conflict in human-dominated landscapes.** The temporal fluctuation in damage occurrence is influenced by the year-to-year variation of beechnut production, a crucial food resource for brown bears. Bear damages increase in years of beechnut crop failure, which usually occur just after masting years.
6. **A trade-off between bear's fear to humans and the availability of natural foods seems to shape the occurrence of bear damage**. Bears damage more apiaries when the availability of beechnut is low, and when they are located in remote areas, where human presence is low.
7. **Wildlife agencies rarely evaluate the success of compensation and prevention programs in order to improve tolerance and reduce damage costs**. The creation of a pan-European database of damage occurrence, management actions and associated costs could help to fill that gap, to make comparative analysis of the cost-effectiveness of the measures and to implement an adaptive management that will identify best solutions for conflict mitigation.
8. **Efforts to prevent and mitigate conflicts in a proactive manner, and thus to foster coexistence of wildlife and people, must be prioritized.** Given that resources for conflict mitigation are usually limited, prioritizing the areas in the landscape and the particular time periods in which farms are more vulnerable to damage would optimize the cost-effectiveness of damage prevention programs. To that end, it is fundamental to properly predict when and where damages are more likely to occur. The scale-integrated approach to predict the spatial risk of damage allows identifying risk areas on the broad landscape context and, in those areas, selecting the most vulnerable households in which to subsidize preventive measures. Furthermore, such integrated approach results in more accurate predictions than traditional, scale-specific models and can increase prediction sensitivity from 82% to 90%. Moreover, the novel application of freely available satellite and meteorological data in predicting mast failures can be a useful tool for responsible agencies to forecast when conflicts are more likely to escalate and, thus, measures have to be taken. This proactive and adaptive management approach can also be applied to other species prone to cause damage and in other parts of the world.

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