

# Mapping the pressure of natural predators on pest arthropods

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## Abstract

Natural predators of arthropods provide an important ecosystem service by preying on crop-damaging species. However, measuring the positive impact of natural pest predators is still challenging. We present a framework to estimate the pest-consumption pressure by natural predators across space and project it onto geographical maps. We use DNA metabarcoding and species distribution modelling to integrate predator density estimations with their energetic requirements and direct pest predation, which yields a comprehensive measure of pest-consumption pressure per time-frame and area. We showcase it on a European bat assemblage, and show that bats consume a variety of pests whose predation pressure varies throughout space. We also report that the impact of different predators depends on spatial scale, and that pest predation pressure is negatively correlated with agricultural intensity. Our framework can be used to estimate broad-scale effects of natural predators on pest arthropods as well as to design research and management strategies.

## Introduction

Arthropods cause a yearly damage estimated at over \$540 billion on crops worldwide (Paini *et al.* 2016), an impact that is expected to increase under warming climatic conditions (Deutsch *et al.* 2018). While historically tackled through active physical, chemical and biological measures (Thacker 2002), the economic cost and environmental impact of these control measures have led to the recognition of the need for more sustainable solutions to improve the quality and yield of crops (Pickett & Bugg 1998). Natural enemies of crop-damaging arthropods are essential allies for pest control (Thomson & Hoffmann 2010), and as such, there is an increasing interest in developing efficient strategies to maximise the ecosystem service they provide (Gurr & Wratten 2012).

The large abundance and spatio-temporal variability of pest arthropod populations complicate measuring the impact natural predators have on their populations and affected crops (Rhainds & English-Loeb 2003). However, acknowledging the pest-consumption pressure natural predators exert on pest arthropods is a first step to identify target predators and geographic areas in which natural predator-based management strategies could be prioritised. The estimation of the predation pressure on pest populations requires quantifying the average absolute consumption of pest arthropods by individual natural predators coupled with the density of predators across landscape (Maine & Boyles 2015). Conducting such estimations is complicated, as predator population densities and dietary habits vary across taxa, time and space (Krauel *et al.* 2018; Baroja *et al.* 2019; Weier *et al.* 2019). Nevertheless, the combined use of recently developed molecular and spatial ecology tools might enable conducting large-scale approximations with a resolution never seen before. Species distribution modelling allows refining continental-level predator density estimations across space, while DNA metabarcoding enables detecting and quantifying the large-scale consumption of pest species by predators (Aizpurua *et al.* 2018; Kamenova *et al.* 2018).

Here we present a new analytical framework that uses such technological developments to model pest-consumption pressure by natural predators across space (and potentially time) and project it into high-resolution geographical maps. Our approach relies on predator energy budget estimations, molecular dietary data, regional population density estimates and species distribution modelling to estimate the pest-consumption pressure, which is expressed as the mass of pest prey consumed by predators per time-period and area (e.g. grams/day/km<sup>2</sup>). The framework integrates strategies to account for the uncertainty of the data, so that the reliability of the final measurements can also be assessed.

We showcase the potential of our framework by combining DNA metabarcoding-derived pest consumption data, species distribution modelling, demographic information and energy budget estimates of a European bat assemblage. Bats are one of the taxa with the highest potential for pest control, as nearly all species in temperate regions are insectivorous and many can form aggregations of thousands of individuals (Fenton & Simmons 2014). We analyse the spatial variability of pest predation pressure, and overlay the spatial estimations with agricultural intensity maps to identify zones with different ecosystem service provision potential by the analysed bats. We report the details of the employed model including full code, showcase it with real data, discuss strategies to improve the predation pressure estimates and suggest potential practical applications of the proposed framework.

## Materials and methods

We present a methodological framework that relies on i) spatial distribution of population densities derived from region- or country-specific population size estimates refined with spatial distribution models, ii) the daily mass of insect intake estimated for each species based on energy budgets and average energy contribution of arthropods, and iii) proportion of consumed pest species as determined by DNA metabarcoding (Fig. 1). The model yields estimates of daily pest consumption in terms of consumed pest mass per time period and area, following Equation 1:

$$C_{x,y} = N_{x,y} * I * P_{x,y} \text{ Equation 1}$$

In which  $C_{x,y}$  is consumption of pest arthropods (g) per area,  $N_{x,y}$  is the density of bats in each cell (individuals/km<sup>2</sup>),  $I$  is the total intake of arthropods (g) per day and  $P_{x,y}$  is the proportion of pest species in respect to the total consumed prey (0-1).  $C$ ,  $N$  and  $P$  values vary across grid cells, while  $I$  is constant for each predator species. We have implemented all functions required to perform the calculations in a new R package, namely P3Mapper. The entire pipeline used for generating all the data shown in this manuscript has been added to Appendix S1 in Supporting Information.  $N_{x,y}$  is calculated using the function `predator_density()`,  $I$  is calculated using `food_intake()` and  $P_{x,y}$  is generated using `pest_proportion()`. All three elements can be inputted as value distributions (e.g. average and standard distribution). The modelling approach makes a number of assumptions: (i) all values (e.g. predator body mass, prey energy content) are normally distributed, (ii) the habitat suitability projections derived from the species distribution models reflect demographic variation across space, (iii) prey detection reflects prey consumption, and (iv) the dietary profiles obtained in a location are representative of the surrounding area and change linearly across space between characterised locations. The implications of these assumptions and the precautions required to interpret the data are addressed in the discussion section.

We showcase our framework using dietary and spatial data of seven European insectivorous bat species: *Miniopterus schreibersii* (MSc), *Myotis capaccinii* (MCa), *Myotis daubentonii* (MDa), *Myotis emarginatus* (MEem), *Myotis myotis* (MMy), *Rhinolophus euryale* (REu) and *Rhinolophus ferrumequinum* (RFe). For our analyses, we iterated the analysis of each predator species 100 times to account for the data uncertainty and natural variability of the analysed features, and thus measure the dispersion of the conducted estimates. In each iteration one value was randomly chosen from each of the distributions, so after the iteration process 100 different pest consumption estimates were generated. The resulting mean value represents the most probable estimation, while the dispersion quantifies the uncertainty of the estimation. The normalised dispersion of the data was measured by means of the coefficient of variation (CV), which was obtained by dividing standard deviation by the corresponding average value. All GIS procedures, statistical analyses

and visualisations were carried out in the R statistical environment, and all general estimates are shown as average and standard distribution values ( $X \pm SD$ ).

#### Spatial predator density estimates

The *predator\_density()* function estimates spatial predator density across space by combining population estimates with species distribution models (Fig. 1). This function transforms georeferenced population estimates into smooth spatial data using inverse distance weighted (IDW) interpolation, as implemented in the R package *gstat*. IDW determines cell values using a linearly weighted combination of a set of sample points in which weight is a function of inverse distance (Pebesma 2004). As the distribution of predators across space is not homogeneous, but depends on a range of environmental conditions, spatial density distributions are refined through combining them with species distribution models (Araújo & Guisan 2006) and cropping them with IUCN-recognised distribution ranges (IUCN 2010).

For our analyses, we generated population density estimations from bat species population sizes per country or region, retrieved from journal articles, books, IUCN website and technical reports (Table S1). The number of estimated individuals per country was divided by the total area of the country to obtain density estimation distributions of number of bats per  $\text{km}^2$ , and the values were georeferenced to geographic centroids for each country or region before mapping them across space. Species distribution models generated through an ensemble approach using *biomod2* (Thuiller *et al.* 2013) were obtained from Alberdi *et al.* (2020). Models included between 113 and 591 occurrence records per species and multiple filters to minimise the impact of spatial autocorrelation and erroneous identifications, as detailed in the original publication.

#### Food intake estimates

The *food\_intake()* function estimates the daily ingested mass of arthropod prey per predator individual based on the relationship between the daily energy requirement of the predator and energy content of dietary items (Equation 2). Daily energy requirements are estimated following the mass-independent normalisation constant and allometric scaling exponent determined by Nagy *et al.* (1999). The function requires a value distribution (average and standard deviation) of the body mass of the predator, a value distribution of the energy content of prey and the ‘a’ and ‘b’ constants determined for the predator taxa in the allometric equations proposed by Nagy *et al.* (1999). It yields a vector of prey consumption estimations of the length specified by the number of iterations.

$$I = (a * w_{\text{predator}}^b) / e_{\text{prey}} \text{ Equation 2}$$

In which  $I$  is the daily food intake mass,  $w_{\text{predator}}$  is the body mass of the predator, ‘a’ and ‘b’ are the constants from the allometric equations proposed by (Nagy *et al.* 1999) and  $e_{\text{prey}}$  is the energy content of prey.

For our analyses, we retrieved energy content of dry matter and water percentage estimations of 11 arthropod orders from the literature (Table S2), from which mean and standard deviation values were generated and inputted into the model. We also obtained predator body mass values from the literature, while the ‘a’ and ‘b’ constants for the energy budget estimates of predators were obtained from Equation 4 by Nagy *et al.* (1999) on Chiropterans.

#### Relative pest consumption estimates

The *pest\_proportion()* function generates spatial estimates of the proportion of pest insects consumed by interpolating DNA metabarcoding-based georeferenced prey consumption data. The function incorporates a bootstrapping step that generates value distributions that reflect uncertainty of the data by randomly incorporating one sample from a different location in each iteration. Relative pest consumption measurements per site are then converted into a spatial raster of relative pest consumption using IDW interpolation. The function requires a count (i.e. OTU, ASV) table that specifies the relative detection of prey in each sample, a binary raster that delimits the geographic range of the predator, and tables specifying the relation between

OTUs and pest species, characterised samples and their sampling sites, and the geographic coordinates of the sites.

For our analyses, pest consumption information was obtained from the dietary metabarcoding data (Alberdi *et al.* 2020) generated using ZBJ-ArtF1c/ZBJ-ArtR2c primers (Zeale *et al.* 2011). The dataset includes dietary information of over 350 individual bats belonging to the seven analysed species sampled in 40 locations distributed throughout Europe. The technical procedures employed to obtain the samples and generate the data are explained in the original publication. Of critical relevance for this study, the employed procedures ensured maximum reliability of taxonomic identifications, as only high quality ( $Q_{avg} > 30$ ) sequences that appeared in at least two of the three PCR replicates per sample were retained, and sequences identical to those detected in the extraction and library blanks of the corresponding processing batch of each sample were removed. In addition, taxonomy assignment was based on two reference databases, BOLD (Ratnasingham & Hebert 2007) and Genbank (Benson *et al.* 2013), limited to matches over 99% identity between query and reference sequences, and ambiguous identifications were discarded. Pest arthropods were identified through a thorough bibliographical research that included scientific journal articles, books, specialised websites and technical reports (Table S3). Prey identified at species level were classified in two groups: *Innocuous*, species that do not regularly affect agricultural activities; and *Pests*, species that regularly affect agricultural productivity with varying economic impacts.

### Ecosystem service indices

We computed two spatial indices to analyse different features of pest predation pressure and its potential impact on agricultural productions. The Ecosystem Service Evenness (ESE) index measures whether the ecosystem service is evenly provided by the analysed assemblage of predators or majorly concentrated in a single predator. It is calculated as shown in Equation 3, in which,  $D_{x,y}$  is the Shannon diversity, or Hill number of q-value 1 (Alberdi & Gilbert 2019), calculated from the relative contribution of each predator to the total pest predation pressure in each grid cell, and  $R_{x,y}$  is the predator richness calculated as the number of predators present in each grid cell. When the ecosystem service is provided by a single predator the ESE value is 0, while ESE approaches 1 as the service becomes more evenly distributed across multiple predators.

The Ecosystem Service Potential (ESP) index measures the potential of the analysed predators to provide an ecosystem service by quantifying the joint incidence of agricultural activity and pest predation pressure. It is calculated as shown in Equation 4, in which  $A_{x,y}$  is agriculture intensity,  $C_{x,y}$  is the pest predation pressure in each grid cell,  $C_{min}$  is the minimum pest predation pressure in the considered area, and  $C_{max}$  is the maximum pest predation pressure in the considered area. When both the presence of agricultural intensity and predation pressure are maximum ESP takes a value of 1, while approaching 0 when both variables decrease. In our showcasing system agricultural intensity was characterised as the fraction of cropland area (FCA) retrieved from earthstat.org (Ramankutty *et al.* 2008). Overall ESE index, ESP index and predator richness were computed by averaging the values across the considered region.

$$ESE_{x,y} = ({}^1D_{x,y} - 1) / (R_{x,y} - 1) \text{ Equation 3}$$

$$ESP_{x,y} = AI_{x,y} * ((C_{x,y} - C_{min}) / (C_{max} - C_{min})) \text{ Equation 4}$$

## Results

We generated a map of total pest predation pressure provided by the seven studied bats (Fig. 2a), as well as species-specific maps (Fig. 2b-h), with which we analysed the spatial and predator-species variation of the ecosystem service they provided. Using DNA metabarcoding 103 prey taxa were identified as pests. Predation pressure on crop-damaging arthropods was mainly exerted on Lepidopterans, as 14 out of the 15 most consumed pest arthropods revealed by DNA metabarcoding were moths (Table S4). These included mostly lepidopterans whose larval phase damage a wide range of agricultural systems, including vegetable gardens (e.g. *Agrotis segetum*, *Spodoptera exigua*), citrus plantations (e.g. *Prays citri*), ornamental gardens (e.g.

*Noctua pronuba*), cereal fields (e.g. *Helicoverpa armigera*), corn fields (e.g. *Agrotis ipsilon*) and coniferous plantations (e.g. *Thaumetopoea pityocampa*). The relative pest predation estimates showed that *Miniopterus schreibersii* and *Rhinolophus euryale* have the highest proportion (around 80%) of pest prey in their diet, followed by *Myotis emarginatus* and *R. ferrumequinum* (slightly over 50%) and the rest of species (*Myotis daubentonii*, *M. capaccinii* and *M. myotis*) below 50% of their diet (Fig. 2m). Absolute pest consumption was calculated based on daily food intake of predators (Fig. 2l) estimated from their body mass (Table S5) and energy content estimations of prey (Table S2).

The total estimated daily pest predation pressure of bats for the entire analysed area was  $63.3 \pm 13.9$  metric tonnes ( $=10^6$  grams) of pest arthropods, with  $12.1 \pm 5.85$  grams on average per  $\text{km}^2$ . *M. daubentonii* contributed the most ( $31.7 \pm 12.8$  tonnes), followed by *M. schreibersii* ( $14.1 \pm 3.01$ ) and *M. myotis* ( $8.28 \pm 2.31$ ) (Fig. 2i). The contribution of the different features considered for estimating the total predation pressure differed across the analysed species. The large contribution of *M. daubentonii* was driven by its large distribution area and density (Fig. 2n), as it is one of the species with the lowest pest predatory pressure per bat (Fig. 2k). The contribution of the second ranked *M. schreibersii* was due to a mixture of high relative proportion of pest prey (Fig. 2m), medium food intake (Fig. 2l) and moderate density and distribution range (Fig. 2n). In contrast, *M. myotis* exhibited large food intake, low relative proportion of pest prey and moderate distribution area.

The average Ecosystem Service Evenness (ESE) index was  $0.59 \pm 0.15$ , which shows that pest predation pressure was typically provided by multiple, yet not all, predators, though ESE index values varied across space (Fig. 3). Although in most of the regions pest predation pressure was provided by many predator species (high ESE index; Fig. 3a), in some others the ecosystem service was provided by a few (Fig. 3b-c) or just a single (ESE index of 0; Fig. 3d) species. Total pest predation pressure exhibited an inverse correlation with the fraction of cropland area ( $r = -0.23$ ;  $t = -23.34$ ,  $df = 9998$ ,  $p\text{-value} < 0.001$ ; Fig. 4a). This pattern was observed in all predators, yet with different intensities (Fig. 4b-c). Finally, the Ecosystem Service Potential (ESP) index enabled identifying the factors that enabled the uncommon joint presence of intensive agriculture and large pest predation pressure (Fig. 4e). The highest values were achieved in small agriculturally intense patches surrounded by heterogeneous landscape (Fig. 4f-h), while lowest values were observed in large cropland-dominated areas (Fig. 4i).

## Discussion

The novel methodological framework we introduce enables scrutinising the spatial and predator-specific variation of pest predation across space. Similar approaches have been recently employed to generate global prey consumption estimates of birds and spiders (Nyffeler & Birkhofer 2017; Nyffeler *et al.* 2018), yet this is the first time that high-resolution dietary information derived from DNA metabarcoding and spatially refined predator density data are implemented in a single framework.

### Possibilities and limitations of P3Mapper

Our framework is grounded on simplified relationships between energy budget of predators, energy content of prey, and relative consumption of pest prey. As any other approach that models a complex system it makes a number of assumptions. The model could be further refined to better reflect the complexity of the analysed system, for instance, by adjusting energy content of prey to consumed arthropods, or tailoring activity patterns to each predator. However, such refinements would introduce minimal variation in the results while requiring generation of currently unavailable data.

In contrast, the impact predicted for biased or insufficient data is considerably larger. Hence, the framework incorporates an iterative approach to account for the level of uncertainty of the data. For instance, despite the large effort for characterising diet using DNA metabarcoding (over 350 individuals, seven species, 40 locations, 8 countries), relative pest prey consumption measurements in our case study are clearly insufficient to cover the entire complexity of dietary variation across space, predator species and time. However, our framework addresses such a shortcoming by assigning error ranges to relative pest consumption estimates using a

bootstrapping approach.

Bat population estimates are also uncertain, due to the inherent complications of estimating densities of elusive and nocturnal animals. To accommodate this, as well as the natural variation of the biological system under study, our framework implements an iterative approach whereby the analysed data are randomly sampled from value distributions. This approach enables quantifying the amount of variation of the estimates, which for the overall pest predation pressure is relatively large ( $CV = 0.22$ ) compared to other large-scale estimations (Nyffeler *et al.* 2018), yet variable across species (e.g.  $CV_{Mda} = 0.40$ ,  $CV_{Msc} = 0.21$ ). These differences are mainly driven by the uncertainty of population size estimations for different species, which in the case of bats, largely depends on the roosting behaviour and echolocation properties of the species. *M. schreibersii* roosts almost exclusively in underground cavities, in which large aggregations usually hang from the ceiling (Ramos Pereira *et al.* 2009). This makes it relatively easy to count the number of animals (Brown *et al.* 2008; Battersby 2010), and thus rather accurate estimates can be obtained. In contrast, *M. daubentonii* creates smaller aggregations, uses a wider range of roosting resources and often shelters in small cavities (Ngamprasertwong *et al.* 2014). This prevents accurate roost count-based estimations, which coupled with the difficulties to accurately identify *Myotis* species using ultrasound detectors, complicates population size estimates of *M. daubentonii* (Battersby 2010), hence increasing the uncertainty. In addition, our framework refines the density distributions of predators across space by using species distribution models. We are aware that a continental level spatial model that relies on climatic variables and broad habitat features cannot accurately capture local-scale variation that depends on many other ecological variables. Within these limitations though, we believe this is the best available tool to refine predator densities across space in a continental scale.

Unlike measurement uncertainty, the part of the dispersion derived from the natural variability of the data cannot be reduced. This is largely due to predators consuming multiple types of arthropods and different-sized prey with varying energetic content, and body mass varying across predator individuals. Critically though, our framework accommodates such data dispersion by not relying on specific values to represent each element, but again using value distributions.

Showcasing system: bat predation on pest insects in Europe

We use our newly developed methodological framework to estimate the predation pressure of an assemblage of natural predators, namely bats, on crop-damaging arthropods at the European scale. The widespread consumption of pest arthropods by European insectivorous bats we report expands the taxonomic and geographic breadth of similar previous observations (Aizpurua *et al.* 2018; Cohen *et al.* 2020). Crop-damaging arthropods are not only consumed by species that mainly forage in open areas, but pest consumption is widespread across bats with different ecological features. The combination of the relative dietary weight of pest arthropods with the energy budget of each predator estimates the consumption of pest arthropods to be highest (between 6-7 g/day) in *M. schreibersii*, *R. euryale* and *R. ferrumequinum*. The first two species have similar body mass and exhibit narrow dietary niches limited to moths (Alberdi *et al.* 2020), the taxon that encompasses some of the most important flying arthropod pests (Bebber *et al.* 2014). In contrast, the dietary niche of *R. ferrumequinum* is broader, with a lower incidence of pest arthropods, yet its larger body size predicts a similar level of pest arthropod consumption as the other two. *M. daubentonii*, *M. capaccinii* and *M. myotis* are the species with the broadest dietary niches, in part because they are able to gaff prey either from the water surface, foliage or ground (Denzinger & Schnitzler 2013), which seems to be the cause under the reduction on the relative incidence of crop-damaging arthropods in their diet.

However, the overall pest predation impact of each predator changes drastically when predator species' population densities and distribution ranges are accounted for. For instance, despite its low relative predation on pest arthropods, *M. daubentonii* is the species exerting the largest overall pressure due to its large distribution area and population densities. In contrast, both *Rhinolophus* species exhibit poor overall and per-grid-cell pest predation pressure, although they are two of the species with the highest estimated pest consumption per individual bat. Such results highlight the complexity of the pest predation pressure exerted by different predators, and show that the relevance of different predators on pest predation might differ

across geographic scales. For instance, despite *Rhinolophus* bats being almost irrelevant at a European scale, they might be important assets for pest suppression at local scales, when agricultural fields are located close to colonies of these species.

The fine-scale maps of pest predation our framework generates enable conducting spatial analyses and geographical comparisons of the intensity of the predation pressure. Pest predation pressure varies considerably across predator taxa and space. The contribution of different species to the overall pressure differs drastically, as the pressure estimated for *M. daubentonii* is ten times larger than that of *R. euryale*. However, these patterns vary across space, as exemplified by the larger predation pressure of *R. euryale* in the Balkan area compared to *M. daubentonii*, due to differences in their respective population densities. The Ecosystem Service Evenness (ESE) index maps show that in some areas the pest predation pressure is dominated by one or a few predators, while in other cases the pressure is evenly distributed across the species that comprise the community. In fact, our data show that similar overall predation pressure on pest arthropods can be achieved with a different number of predator species. The ESE index could therefore be used to guide managers and policy makers on measures to be taken to enhance pest predation pressure by natural predators like bats in different areas. If pest predation is mainly executed by a single species (i.e. ESE index close to 0), species-specific measures might be taken, e.g. provision of bat boxes suited for the species. On the contrary, in areas with higher ESE index values there is a multi-predator effect on pest predation produced by functionally distinct species. This scenario will require more integral management strategies to conserve and enhance the population status of an entire community (Gunnell *et al.* 2012).

Overlaying pest predation pressure estimates with agricultural intensity maps shows that the highest pressure is achieved when the intensity of agricultural activities is lowest, and pressure steadily decreases as the intensity increases. This is probably due to the advantage structurally complex heterogeneous landscapes provide to bats. Bat activity is known to increase with farmland heterogeneity (Heim *et al.* 2015; Monck-Whipp *et al.* 2018), since heterogeneous landscapes typically provide commuting landmarks and increased resources for sheltering and foraging. Besides, heterogeneous landscapes provide a more stable supply of food through time, while intensive croplands are characterised for a higher level of insect density fluctuation (Djaman *et al.* 2019; Yang *et al.* 2020). This is the most probable reason for the high overall pest predation pressure estimated for the Balkan peninsula, where the landscape is more heterogeneous, compared to other areas in Europe. The small rebound observed at very high cropland intensity areas might be due to small sample size, as only a few patches exhibit >90% of cropland cover.

Our framework does not provide information about suppression of pest arthropod populations by the analysed predators, as it does not incorporate biomass estimations of crop-damaging arthropods. Such estimations are largely absent in the literature and the large temporal fluctuations further complicates incorporating them into such modelling approaches. As a first approximation to identify areas with high ecosystem service potential, our framework provides the ESP index, which identifies areas where high agricultural intensity and pest predation pressure coincide. The ESP index map (Fig. 4e) shows that the highest potential is achieved in small patches of intense agriculture surrounded by other types of landscape (Fig. 4f-g), or edges of large agriculturally intense patches (Fig. 4h). In contrast, large agriculturally intensive areas show small ESP (Fig. 4i), probably because the landscape offers no resources beyond large occasional prey availability for bats. These observations are in line with previously reported results in which the heterogeneity of surrounding landscapes shape the abundance and diversity of natural pest predators (Gurr *et al.* 2017; Karp *et al.* 2018).

The overall pest predation pressure of the analysed predators across the whole continent sums up to a daily consumption of  $63.3 \pm 13.9$  metric tonnes of pest arthropods. This number is lower than arthropod consumption estimates performed previously for bats and other taxa (Nyffeler *et al.* 2018), which probably responds to three factors. First, we employ conservative demographic estimates to avoid inflating pest predation pressure. Second, we use a stringent taxonomic identification to ensure maximum DNA sequence reliability and species-level identification (Alberdi *et al.* 2018). Lastly, we only consider a subset (7 species out of 51) of the European bat community with continent-wide dietary and density information available. As we exclude species that also exert predation pressure on pest arthropods (e.g. Puig-Montserrat *et al.* 2015; Baroja *et*

*al.* 2019; Cohen *et al.* 2020), the total predation pressure of bats on crop-damaging arthropods in Europe is certainly larger than the numbers we report.

#### Applicability of P3Mapper in other systems

The framework can be implemented in other taxa that enable gathering similar biological information, such as birds or invertebrates. The main advantage of birds compared to bats is that population density estimations are more reliable due to the higher detectability and better population monitoring infrastructure (du Feu *et al.* 2016). However, pest arthropod intake estimations through DNA metabarcoding are more complicated because most arthropod-eating species are omnivorous (Brandl *et al.* 1994), which complicates food intake relative pest consumption calculations. In the case of insects, one of the main issues is the difficulty to find DNA metabarcoding primers with broad taxonomic range and little taxonomic bias that exclude the predator from being amplified; an issue that might require a considerable increase of sequencing effort (Alberdi *et al.* 2018). The framework could also incorporate the temporal axis, which is important for going deeper into the relationship between natural predators and pest population dynamics, as insect biomass (Hallmann *et al.* 2017), bat activity (Korine *et al.* 2020), pest arthropod consumption (Baroja *et al.* 2019) and energy requirements (Encarnação & Dietz 2006) fluctuate throughout the year. We do not report temporal variability, because i) no reliable information about bat activity variation through time is available – hence a fixed foraging time of 4h was assumed following (Kurta *et al.* 1989), and ii) the samples size of relative pest consumption measures generated through DNA metabarcoding was too limited to implement a temporal perspective – hence obtained averages are assumed to represent typical diets.

## Conclusions

We introduce a methodological framework that enables estimating pest predation pressure at different scales, as well as scrutinising the complex features that determine it and identifying the limitations of the currently available data. It thus provides insights into the type of information that should be generated in order to increase the accuracy and reduce the uncertainty of the estimations. Hence, we believe our framework can be highly valuable as a baseline for more precise modelling approaches that rely on more abundant and accurate data, as well as to generate initial approximations of the impact of natural enemies of pest arthropods, identifying priority taxa and areas, and identifying potentially relevant relationships between pest control and environmental features. Finally, our analyses provide a quantitative approximation to the dimension of the ecosystem service bats provide, which serves to recognise the importance of bats not only for the functioning of natural ecosystems but also for direct human interests. Now that bats are at the spotlight due to their relationship with the covid19 outbreak, such a recognition is more necessary than ever.

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## Supporting Information

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library ([www.ecologyletters.com](http://www.ecologyletters.com)).

**Appendix S1** : full code employed to generate the pest predation pressure estimations.

**Table S1** : bat population density estimations per country and species.

**Table S2** : energy content estimations of prey arthropods.

**Table S3** : list of bibliographical sources to identify crop-damaging arthropods.

**Table S4** : list of crop-damaging arthropods identified in the DNA metabarcoding data in this study.

**Table S5** : body mass data of predators.

## Figures

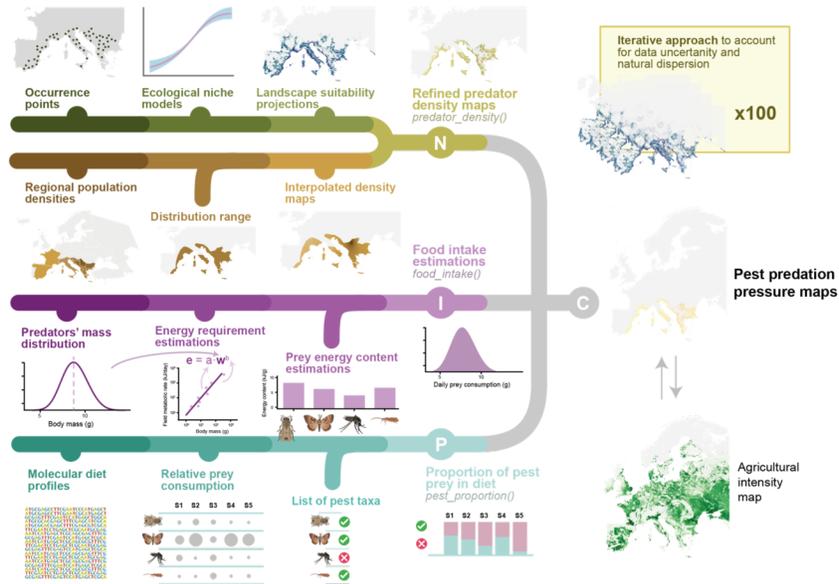
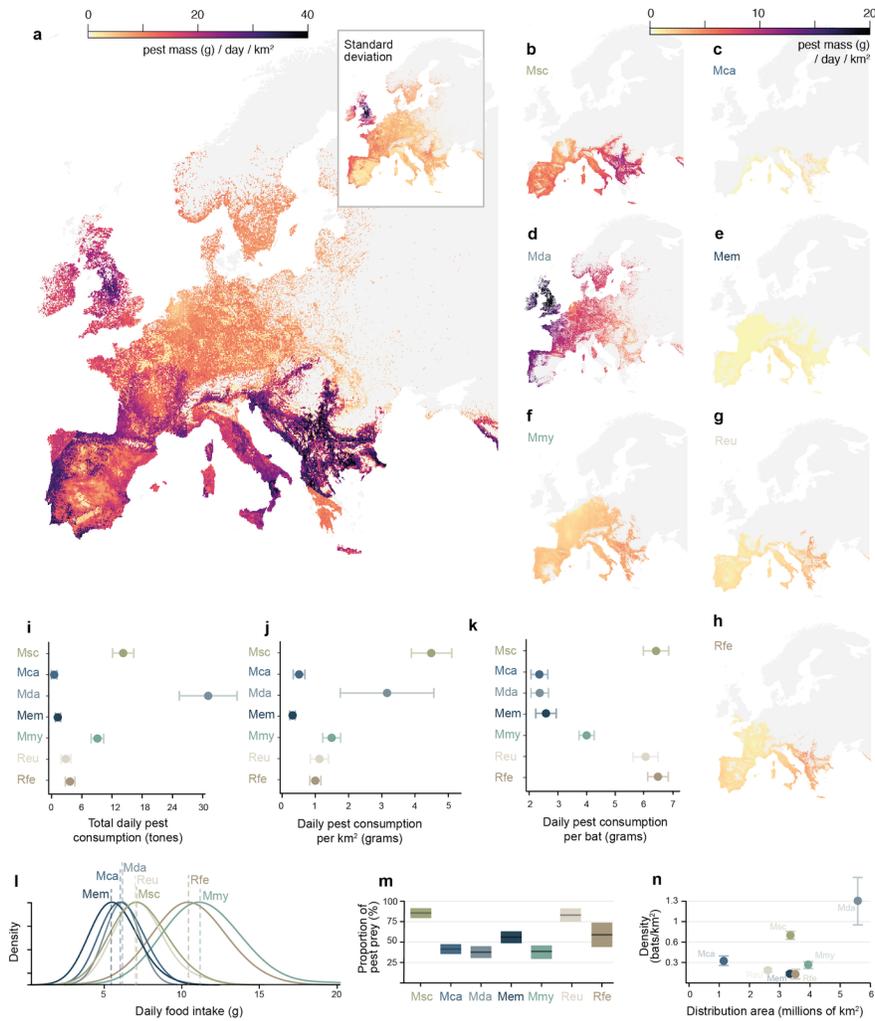


Figure 1. **Methodological workflow to generate pest predation pressure maps** . The letters N, I, P and C refer to the elements in Equation 1. N) Predator density maps are generated by combining ecological niche or species distribution models with regional species density estimations. I) Food intake estimations are performed by combining predator species' energetic requirements with the energetic value of consumed prey. P) Proportion of pest prey in the diet is calculated from DNA metabarcoding data, after annotating each detected prey as a pest or innocuous arthropod. C) The combination of all these data yields the pest arthropod consumption estimate maps, which when overlaid with other spatial data (e.g. agricultural intensity map) enable extracting geospatial information on pest predation pressure. The entire process is iterated (e.g. repeated 100 times) sampling from value distributions to also measure the dispersion of the employed data.



**Figure 2. Pest predation pressure maps and species-specific model parameter statistics .** (a) Map of the overall pest predation pressure estimated for the seven studied bat species. (b-h) Species-specific pest predation pressure maps. Larger images with their respective standard deviation maps are shown in the Supplementary files. Note the different colour scale of the main map and the species-specific maps, which was altered to improve the visual comparison of species-specific maps. (i) Total daily pest consumption estimated for each of the analysed bats. (j) Daily pest consumption estimated for each of the analysed bats per km<sup>2</sup>. (k) Daily pest consumption estimated for individual animals from each of the analysed bat species. (l) Daily food intake, (m) proportion of pest prey, and (n) density and geographic range estimated for each of the analysed bats.

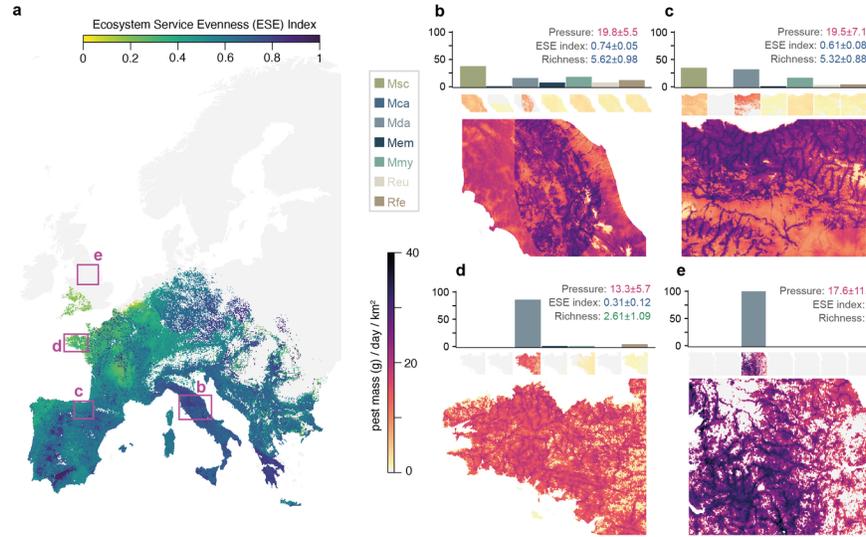


Figure 3. **Ecosystem Service Evenness (ESE) index and relative contribution of each studied species to the overall predation pressure.** (a) ESE index distribution across the study area and location of the analysed regions. Note the index is meaningful only when more than one predator is present. (b-e) Total predation pressure, relative contribution of each species and ESE index in (b) Central Italy, (c) Basque Country, (d) Brittany and (e) Northern England. Note that the combinations between predation pressure, ESE index and predator richness (number of predators present) varies across the four regions.

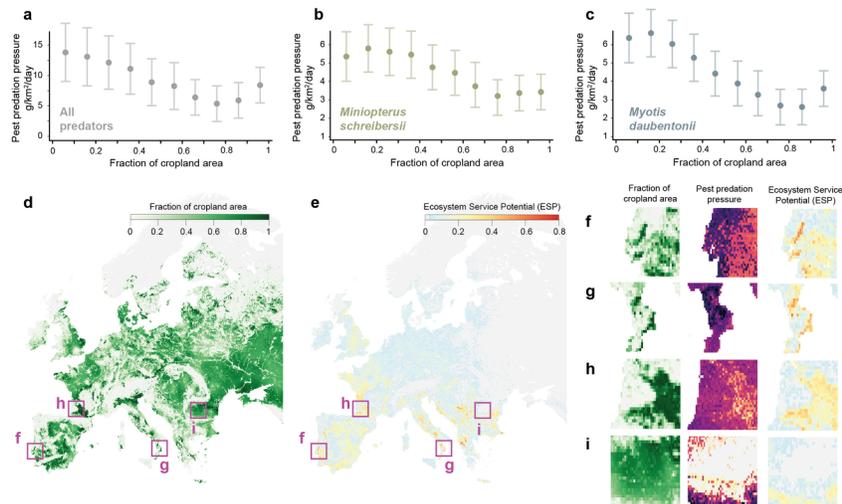


Figure 4. **Relationship between pest predation pressure and agricultural intensity .** (a) Pest predation pressure is largest in heterogeneous areas without croplands, and gradually decreases with increasing fraction of cropland area. (b-c) The pattern is similar for all analysed predators, although the intensity of the variation varies. Overlying pest predation pressure maps (Fig. 2a-h) with an agricultural intensity map (d), enabled calculating the Ecosystem Service Potential (ESP) index (e), which is shown to be highest when a small agriculturally intense patch is surrounded by heterogeneous landscape (f-h), and lowest on large patches dominated by cropland (i).