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What drives wild boar density and population growth in Mediterranean environments?

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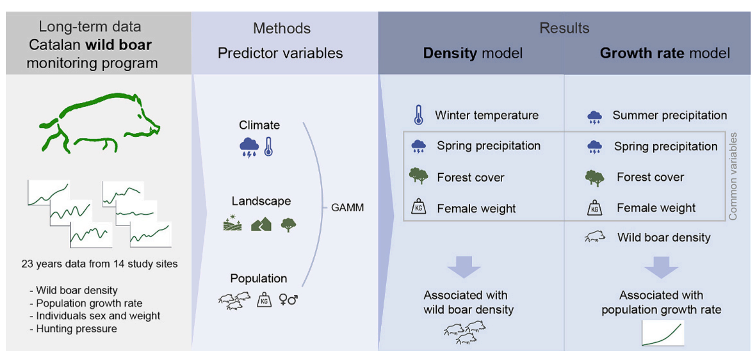
HIGHLIGHTS

- Effective wildlife management requires accurate predictions of population fluctuations.
- Two models explored factors affecting wild boar density and population growth rate.
- Spring precipitation, forest cover and female weight positively affect wild boar density and population growth.
- Density dependent processes affect wild boar population dynamics.

GRAPHICAL ABSTRACT



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ABSTRACT

Accurate prediction of fluctuations of wildlife local number of individuals is crucial for effective population management to minimise human-wildlife conflicts. Climate, habitat, food availability, and density dependence are among the main factors influencing mammalian population dynamics. In southern Europe, precipitation and temperature, particularly during summer have been suggested as key factors affecting wild boar (*Sus scrofa* L.). However, there is uncertainty regarding the role of these factors and the mechanisms driving population fluctuations. This study utilized long-term data of wild boar populations from 14 study sites collected for 23 years in Catalonia, Spain, to analyse the factors that drive population density and growth rate. Generalized Additive Mixed Models (GAMM) explained respectively, 94 % and 65 % of the density and growth rate variability. Spring precipitation in both current and previous year, female weight, and forest cover (particularly above 60 %) were directly associated with higher wild boar densities and population growth rates. The interaction between crop cover and total annual precipitation also played a significant role in determining population density. Higher densities were linked to lower population growth in the following year, likely due to a density-dependent process. These results suggest that the expected decrease in rainfall linked with global warming may limit the

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availability of natural resources and potentially slow wild boar population growth. Nevertheless, wild boar can exploit alternative anthropogenic food sources, potentially leading to an increase of human-wildlife conflicts. Therefore, incorporating management policies aimed at restricting wild boar access to human food sources is key for controlling their reproductive output. Additionally, landscape management strategies targeted at diminishing refuge and resource availability in regions experiencing high wild boar impact are essential for contributing to sustainable coexistence between wild boars and human populations.

1. Introduction

Wildlife population dynamics is affected by birth, death, immigration, and emigration, which are in turn influenced by many factors including climate, habitat, food availability, population density and age structure (Krebs, 2002; Moss et al., 1982).

Understanding how these factors influence wild boar (*Sus scrofa* L.) population dynamics is crucial for reliable population forecast and effective management strategies. For instance, the EFSA Panel on Animal Health and Welfare (AHAW) (ENETWILD - consortium et al., 2022) highlighted the need for comprehensive collection and analysis of data on wild boar population dynamics to identify the key demographic drivers associated with this species and improve wild boar management.

The economic impacts of wild boar include crop and infrastructure damage, transmission of diseases to people, livestock and other wildlife, and traffic accidents. Moreover, high densities of wild boar can pose significant threats to biodiversity conservation in sensitive areas (Ballari and Barrios-García, 2014). Generating accurate population dynamics predictions is key to inform decisions about the timing, scale and type of management interventions to prevent or mitigate the negative impacts of this species. This is particularly important in Europe, where wild boar numbers and range have steadily increased in the last decades (Massei et al., 2015).

Compared to other ungulates, wild boar are particularly difficult to manage because of their ecological plasticity and relatively high reproductive rates (Cutini et al., 2013; Fernández-Llario and Carranza, 2000; Fonseca et al., 2011; Giménez-Anaya et al., 2008; Sáez-Royuela and Telleria, 1987). Boar are omnivorous and adapt their diet to locally available resources, with 86 %–96 % of plant (mostly tree seeds, bulbs and crops) and 10 %–20 % of animal and fungi matter (Ballari and Barrios-García, 2014; Giménez-Anaya et al., 2008; Herrero et al., 2006; Massei et al., 1996; Schley and Roper, 2003).

Wild boar prefer dense forest habitats, particularly those formed by masting tree species (Abaigar et al., 1994). However, they occur in almost any type of habitat, including agricultural areas, and more recently in urban environments, where they have access to highly nutritional anthropogenic food (Cahill et al., 2012; Castillo-Contreras et al., 2021; Meriggi and Sacchi, 2001).

Precipitation and temperature, particularly in spring and summer, have been described as key factors affecting wild boar population dynamics in southern Europe. Nevertheless, studies are not unanimous on the role of climate, and factors reported as significant include spring and summer precipitation, (Bisi et al., 2018; Frauendorf et al., 2016), summer temperatures (Focardi et al., 2008; Uzal Fernandez and Nores, 2004) and winter temperatures in colder regions (Borowik et al., 2013).

Climate can impact wild boar dynamics in several ways. For instance, drought can directly affect piglet survival, as piglets have high water requirements during early development (England, 1986; Fernández-Llario and Carranza, 2000; Fraser and Phillips, 1989; Phillips et al., 1990) and dry conditions that harden the soil can make rooting more difficult for all ages, thus reducing food accessibility (Massei et al., 1997).

Weather conditions can also indirectly affect female fecundity. Studies undertaken in Italy and Spain found that spring and summer drought lead to a decrease in the percentage of breeding females (Fernández-Llario and Carranza, 2000; Massei et al., 1996; Sáez-Royuela and Tellería, 1986). Additionally, the effect of climate on the availability of food, such as acorns, affects directly female body weight and litter size (Fonseca et al., 2011; Gamelon et al., 2013; Massei et al., 1996; Mauget, 1972; Rosell et al., 2012). In northern regions (with cooler summers, and barely limited water availability), spring and winter temperatures, snow cover, forest cover and acorn availability appear to have the most pronounced impacts on wild boar dynamics (Borowik et al., 2013; Geisser and Reyer, 2005; Heptner et al., 1988; Jędrzejewska et al., 1997; Melis et al., 2006; Oloff, 1951). Gethöffer et al., 2007, 2023 also showed that precipitation during May and July, together with the number of frost days in February affect wild boar female weight, which is directly related with the reproductive output.

Masting events are another factor adding complexity to food availability and wild boar dynamics. Masting events are the highly synchronous production of seeds by various tree species (mostly oak, *Quercus* sp. and beech, *Fagus* sp. in southern Europe) that result in a sudden increase in the availability of high-energy food which directly influence female body weight, especially in forest habitats (Gethöffer et al., 2023). These resources affect the population dynamics of many ungulate species and of wild boar in particular as this species, unlike other ungulates, is a monogastric and depends on consuming high-energy food for its survival (Barrere et al., 2020; Bieber and Ruf, 2005; Gamelon et al., 2021).

In Mediterranean landscapes the spatial habitat distribution plays a key role for wild boar occurrence (Bosch et al., 2012; Markina-Lamonja, 1998). Wild boar occur more frequently in areas with forest fragments adjacent to large forests and near mountains or riparian woodlands (Giménez-Anaya et al., 2008; Herrero et al., 2006; Virgós, 2002; Acevedo et al., 2006). However, the availability of farmland provide an alternative food source when food is scarce (Abaigar, 1992; Herrero et al., 2006; Sáenz de Buruaga, 1995).

Studies on the effect and extent of density-dependent processes on wild boar population dynamics have reached different conclusions. Some studies suggested that density can influence female body weight, reproductive success and thus population growth (Bruinderink and Hazebroek, 1995; Imperio et al., 2012; Vetter et al., 2015), while other have not found any density-dependence effect on wild boar population growth, fertility or litter size (Choquenot, 1998; Frauendorf et al., 2016; Ditchkoff et al., 2012). Other studies argued that food availability is not regulated by wild boar consumption, as in classic herbivore-plant systems, but it depends on external factors with stochastic variations, hence for this species this density-independent variability would be more prominent than density-dependent processes (Choquenot, 1998; Uzal Fernandez and Nores, 2004).

Most studies on wild boar dynamics have relied on short time series of a single site or on-site comparisons within a single year. However, long-term studies would be ideal for assessing the role of multiple factors on wild boar population dynamics.

The main aim of this study was to investigate the drivers of wild boar demography (population density and growth rate) in 14 sites in a Mediterranean region, where 23 years of wild boar density data are available. This enabled a more robust analysis of wild boar population dynamics with covariates that vary in both time and space and encompass diverse habitats and climate conditions.

Based on the previous studies and knowledge of the populations we formulated four main hypotheses:

1. Wild boar population densities are positively associated with forest cover and habitat diversity.
2. Increased precipitation during spring and summer may lead to higher availability of food resources and survival, resulting in higher population density and growth rate.
3. Female wild boar with higher body weight have better reproductive success, higher survival rates, and higher recruitment rates, leading to higher population density and growth rate.
4. As wild boar densities are still growing, density-dependent processes are unlikely to be a key factor in affecting wild boar population dynamics.

2. Materials and methods

2.1. Study area

The study was conducted in 14 sites spread throughout Catalonia (NE Spain) (Fig. 1). These sites represent a variety of climatic and habitat typologies in the region (Table 1).

2.2. Data collection

2.2.1. Wild boar population data

The wild boar population data used in this study were provided by the Catalan Wild Boar Monitoring Program. Data on wild boar densities were obtained from driven hunts from 1998–1999 to 2020–2021 (23 years), for this study, data from 14 study sites across the Catalan territory with long series (a minimum of 15 years) on wild boar density was used. In total there were 290 yearly estimates of wild boar density across 14 sites (Fig. 2).

Density estimations were derived from driven hunts data which include date, number of hunters and dogs, number of wild boar culled, and number of wild boar observed but not culled. Wild boar density (*d*) was calculated following the method by (Sáez-Royuela and Tellería, 1988), using the equation:

$$d_{i,t} = \frac{\left(\frac{B_{i,t}}{E_{i,t}}\right)}{A_i}$$

where $d_{i,t}$ is the derived density for location i in year t. B is the number of boar hunted in the location in each study period. E is the hunting effectiveness (calculated as the probability of a wild boar to be culled by: $E_{i,t} = \frac{\sum_{y=1}^{n} B_{y,t}/O_{y,t}}{n}$); where B is the is number of wild boar hunted and O the number of boar observed (including hunted and the scaped) for each drive hunt y in year t, and n is the number of observations. A is the surface area (km^2) of the given hunting location.

A total of 290 yearly density estimates were included in the analysis. Density estimates based on hunting bags are often used for monitoring wild boar population trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). The density calculation used in this paper, is also based on hunting bags, but includes a correction for the hunting efficiency (wild boar hunted/wild boar observed). (Acevedo et al., 2009; Segura et al., 2014) showed that hunting effectiveness is highly dependent on local landscape structure parameters and hunters experience among others; thus correcting for hunting efficiency is key to obtaining more precise population estimates particularly when comparing different areas where the conditions can vary (Acevedo et al., 2009;

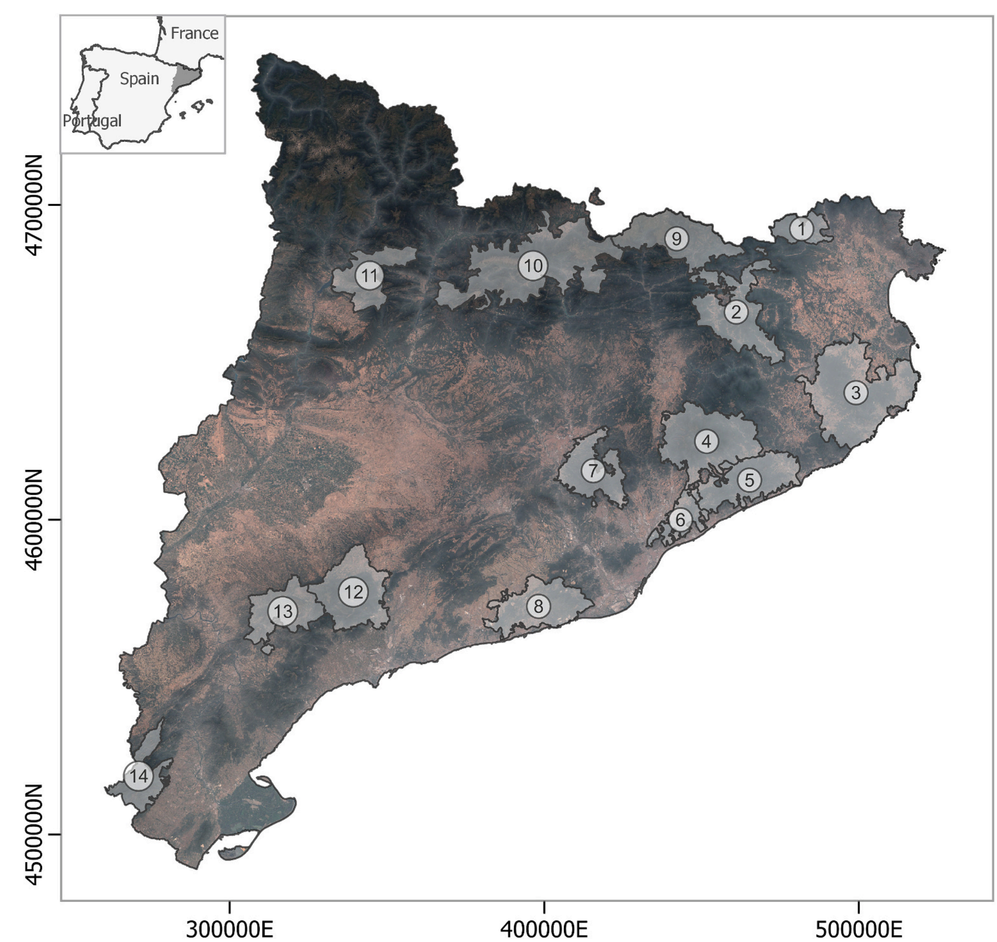

Fig. 1. Location of the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis.

Table 1
Characteristics of the 14 study sites included in the analysis. Yearly rainfall and monthly temperatures correspond to the mean of the last 10 years recorded in the nearest meteorological station (data from the Servei Meteorològic de Catalunya).

Sites	Area (ha)	Altitude range (m.a.s.l)	Yearly rainfall (ml)	Mean temp. cooler month (°C)	Mean temp. warmer month (°C)	Wild boar density first monitoring season (wild boar/km^2)	Wild boar density 2021–2022 (wild boar/km^2)
1. Alt Empordà	13.0	53–1.451	647.6	7.7	24.0	16.4	17.5
2. Zona Volcànica de la Garrotxa	41.7	136–1.513	866.1	5.4	22.7	6.4	15.9
3. Gavarres	70.6	0–532	516.5	7.3	24.1	4.5	12.9
4. Montseny	40.7	61–1.706	912.8	1.2	20.6	4.1	14.9
5. Montnegre-Corredor	33.6	0–760	580.6	8.2	23.9	3.0	15.1
6. Serralades Litoral i de Marina	12.9	11–536	581.2	7.5	24.8	3.3	10.5
7. St. Lloren del Munt	23.8	148–1.103	586.8	6.6	24.0	1.7	7.2
8. Garraf-Olèrdola-Foix	30.2	0–657	635.9	7.3	23.7	2.9	5.9
9. Freser-Setcases	21.5	404–2.909	1031.9	2.2	18.9	3.8	6.1
10. Cadí	26.8	603–2.648	569.4	0.3	18.4	1.0	2.6
11. Boumort	10.8	501–2.077	527,7	2.6	24.7	2.0	4.6
12. Muntanyes de Prades	33.9	118–1.200	485.8	6.0	23.4	2.4	5.8
13. Montsant	29.6	79–1.163	426.6	5.2	24.6	1.2	4.2
14. Ports de Tortosa i Beseit	28.8	163–1.441	648.8	9.4	24.9	1.8	2.2

Segura et al., 2014).

Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Chauvenet et al., 2017; Rowcliffe et al., 2008) carried out in the Montseny Natural Park, provided similar density estimates (Minuartia, 2020), strengthening the reliability of the method based on culling and hunting efficiency.

Population growth rate (r_t) was calculated in this study as the log difference in densities of two consecutive years (Roos et al., 2022; Royama, 1992), using the equation:

$$r_{t,i} = ln\left(d_{t,i}\right) - ln\left(d_{t-1,i}\right)$$

where $r_{t,i}$ is the proportional growth rate in densities from year $t-1$ to year t in hunting area i.

2.2.2. Meteorological data

For each of the 14 study sites, meteorological data were obtained from the closest available meteorological station (11 were located within the sites, 2 were within 5 km and the furthest station from a site was 11.6 km). Daily data on precipitation, mean, maximum and minimum temperature, solar radiation and relative humidity were provided by the Catalan Meteorological Service, for the period 01/01/1998–31/12/2021. Variables included in the analysis were seasonal, for easier interpretation, with seasons defined as winter (January, February and March); spring (April, May and June); summer (July, August and September) and autumn (October, November and December).

2.2.3. Landscape data

Landscape variables included in the model (Percentage of forest cover and crop cover) were obtained from the land use and cover cartography elaborated by the Cartography and Geology Institute of Catalonia [ICGC] (1987 a 2002) and the Teledetection and Geographical information system research group [Grumets, CREAF-UAB (2007 a 2017)] using the R package 'Landscapemetrics' (Hesselbarth et al., 2019).

2.3. Conceptual framework

Prior to data analysis, we established a conceptual framework, or Directed Acyclic Graph (DAG) (Digitale et al., 2022; Ethier and Nudds, 2017) for an initial consideration of the potential relationship between the different factors affecting wild boar population dynamics. In the conceptual framework we included climate (temperature and precipitation) and landscape (such as altitude, forest cover, crop cover, and habitat diversity) factors that may have an indirect effect mainly through resource availability that in turn may influence population reproduction and mortality. Immigration, emigration, and density dependence processes were also included (Fig. 3).

2.4. Data analysis

Statistical analysis was performed using Generalized Additive Mixed Models (GAMM) to explore the associations of weather conditions, landscape characteristics, and density-dependent processes on wild boar density and population growth rate. A GAMM is a flexible and non-linear regression technique for modelling complex relationships without relying on a predefined functional form, as it allows the estimation both linear and non-linear relationships by using non-parametric smoothing (Murase et al., 2009; Schimek, 2000).

Before running the models, we used Pearson correlation coefficient to measure the linear dependence between two variables. The threshold coefficient was set to $\geq$0.6 but none pair of variables exceeded this value (Zuur et al., 2010).

Two models were run, each using different response variables. The first included derived wild boar population density (wild boar/km^2) as the response variable and was modelled as a log-Gaussian distribution (whereby densities were assumed to be strictly positive). We included weather conditions (seasonal precipitation from current and previous year and temperature from previous year), landscape characteristics (forest cover, crop cover), and population variables (female weight previous year) as fixed effects in the model. The model included both site and year as random effects. The model included the following 15 predictor variables (See Supplementary Materials, Tables S1 and S2): current year winter precipitation $\left(WP_{i,t}\right)$, previous year winter precipitation $\left(WP_{i,t-1}\right)$, current year spring precipitation $\left(SP_{i,t}\right)$, previous year spring

Fig. 2. Wild boar density series for the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis. Shadowed in blue are the trends fitted with *Generalized Additive Mixed Models* with 95 % Confidence Intervals for visual aid, the assumptions of the models had not been checked.

precipitation ($SP_{i,t-1}$), previous year autumn precipitation $\left(AP_{i,t-1}\right)$, current year summer precipitation ($UP_{i,t}$), previous year summer precipitation $\left(UP_{i,t-1}\right)$, current year total precipitation ($YP_{i,t}$), previous year winter temperature ($WT_{i,t-1}$), previous year spring temperature ($ST_{i,t-1}$), previous year summer temperature ($UT_{i,t-1}$), previous year autumn temperature ($AT_{i,t-1}$), percentage crop surface ($CS_{i,t}$), percentage forest surface ($FS_{i,t}$), previous year female weight ($FW_{i,t-1}$). The model also included 2 random factors (site; $Z_i s$ and year; $Z_i y$) and was based on a sample of 228 observations. Autumn precipitation of the current year was not included as the density is estimated in autumn and there is no time for the autumn precipitation to have any effect. The model was fit using the form:

$$d_{i,t} \sim Normal(\mu_i, \sigma)$$

$$\begin{aligned} log(\mu_i) = \beta_0 &+ f\left(WP_{i,t}\right) + f\left(SP_{i,t}\right) + f\left(UP_{i,t}\right) + f\left(WP_{i,t-1}\right) + f\left(SP_{i,t-1}\right) \\ &+ f\left(UP_{i,t-1}\right) + f\left(AP_{i,t-1}\right) + \left(AP_{i,t-1}\right) + f\left(YP_{i,t}\right) + f\left(WT_{i,t-1}\right) \\ &+ f\left(ST_{i,t-1}\right) + f\left(UT_{i,t-1}\right) + f\left(AT_{i,t-1}\right) + f\left(CS_{i,t}\right) + f\left(FS_{i,t}\right) \\ &+ f\left(FW_{i,t-1}\right) + f\left(YP_{i,t}, CS_{i,t}\right) + Z_i s + Z_i y \end{aligned}$$

In the second model, the response variable was population growth rate ($r_{t,i}$), modelled as a Gaussian distribution. The same variables used in the first model were included in this model, except for wild boar density at time $t-1$ that was included as a covariate to assess the association with growth rate at time t, to account for 1st order density-

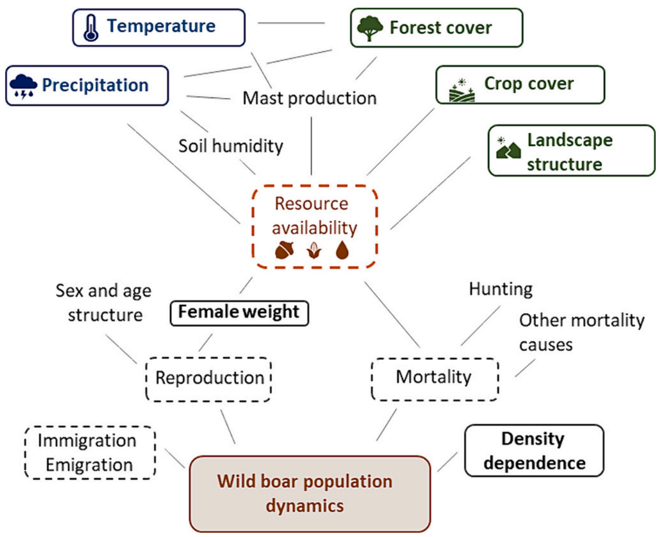

Fig. 3. Simplified conceptual framework, depicting possible associations of the different drivers of wild boar population dynamics. Bold font indicates factors which we had data for and were included in the analysis.

dependent processes. The model included 15 predictor variables, 2 random factors (site and year) and was based on a sample of 201 observations. The variables were the same as in the density model except for the inclusion of previous year density and the dropping of yearly precipitation.

Within both GAMMs, for variable selection we included a penalty on the null space of the basic functions (via the 'select = true' argument in the GAMM function in R) to shrink the terms towards zero, if valid, to prevent overfitting and reduce the complexity of the smooth terms (Marra & Wood, 2011). By setting select = true model selection method, we utilized likelihood-based procedures conceptually, similar to variable selection with Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) to identify the most suitable model that balances goodness of fit with model complexity. This model selection process is essential for ensuring that the chosen GLMM accurately captures the relationships within the data, particularly in the context of ecological research where the selection of predictors is a critical aspect of model development. Relevant variables were selected through visual inspection of the smooth plots, further enhancing the model's validity and interpretability. Model assumptions, such as overdispersion and residual plots, were checked to ensure the validity of the model. For both models assumptions were considered to be met (see Supplementary materials, Figs. S1 and S2). Restricted Maximum Likelihood (REML) was used to estimate the variance components in the mixed model, ensuring unbiased estimates of the parameters. Cubic regression splines were used for constructing smooth terms. Maximum number of knots were set to 10. To assess autocorrelation of population growth rate, we employed the autocorrelation function (ACF). In our analysis, no significant autocorrelation in the ACF plot (Supplementary materials Fig. S3) was detected, indicating that the population growth at a given time point is not strongly correlated with its immediate historical values. All GAMM analyses were carried out in R 4.51.1 (R Core Team, 2022) 'mgcv' version 1.8–33 (Wood, 2023).

3. Results

The wild boar density GAMM model had a good fit with the data, with 94.1 % of the deviance explained. Spring precipitation and previous year spring precipitation had both a clear positive, linear effect on wild boar density, with higher wild boar densities associated with higher precipitation during the spring months (March, April and May) of current and previous year. Mean winter temperature of previous year had a significant non-linear effect, with a positive effect until a threshold around 7 °C; beyond this, the effect transitions into a slightly negative trend. Mean female weight of the previous year showed a significant positive effect, with a stronger effect at the lower weight range, from 33 to 43 kg. The percentage of forest cover also showed a significant association, with a notable positive relationship above 60 % of forest cover (Fig. 4, and supplementary materials Fig. S4).

The population growth GAMM model had a lower fit with the data, with 65.8 % of the deviance explained. The four variables significant for the density model (spring precipitation, previous year spring precipitation, previous year female weigh and forest cover), were also significant in the growth model, with similar patterns. Moreover, density had a significant negative effect and previous year summer precipitation was also found as a relevant factor with a non-linear effect with a positive trend above 200 mm of total rainfall (Fig. 5, and supplementary materials Fig. S5).

4. Discussion

By evaluating the main drivers of wild boar density and population dynamics, this research offers an in-depth understanding of the associations between meteorological, habitat and population factors on wild boar populations density and growth in Mediterranean ecosystems.

The results of the analyses indicate that spring precipitation (both from current and previous year), forest cover and female body weight are strongly associated with both wild boar densities and population growth. Summer precipitation and density of the previous year also appear to play a role in population growth. Moreover, density-dependance was detected and it may also play a relevant role in population dynamics.

In particular, spring precipitation and previous year spring precipitation were detected to be positively associated with both response variables (density and population growth) suggesting that drought conditions during the spring months may be a key limiting factor for wild boar, as hypothesized. This relationship could be attributed to increase of food and water availably, leading to higher reproductive output, in terms of proportion of females reproducing and litter size, and higher piglet survival. The positive influence of previous year spring precipitation on wild boar density may be attributed to the heightened availability of food resources. Increased spring precipitation leads to a greater of mast and plant biomass production (Cutini et al., 2013; Espelta et al., 2008), which contributes to higher female body weight, and an increase of the reproductive output. These findings align with prior research conducted in southern Europe, which established that the number of rainy days during spring is a limiting factor for wild boar populations (Uzal Fernandez and Nores, 2004). This is also supported by the fact that our results show the association between mean female body weight from the previous year with both density and population growth, as hypothesized. The positive relationship between female body weight an reproductive output (and thus, population grow potential) has been described in previous papers on wild boar (Aumaitre et al., 1982; Cellina, 2008; Frauendorf et al., 2016; Lombardini et al., 2014; Mauget, 1972; Rosell et al., 2012). Moreover, changes in food availability can also affect on the timing of mating, the age of puberty and the sex ratio of the offspring, which in turn affect population dynamics (Cachelou et al., 2022; Drimaj et al., 2020; Malmsten et al., 2017; Malmsten and Dalin, 2016).

Conversely, the positive association of spring precipitation in the current year on population density could be explained through effects on survival, especially of younger individuals. Given that the majority of wild boar birth occur during March and April, (Fonseca et al., 2011; Rosell et al., 2012), moisture content of soil during spring plays a crucial role in facilitating piglet foraging and access subterranean food resources once they are weaned. Low rainfall can prevent access to these food resources and subsequently negatively affect piglet survival (England, 1986; Fernández-Llario and Carranza, 2000; Fraser and Phillips,

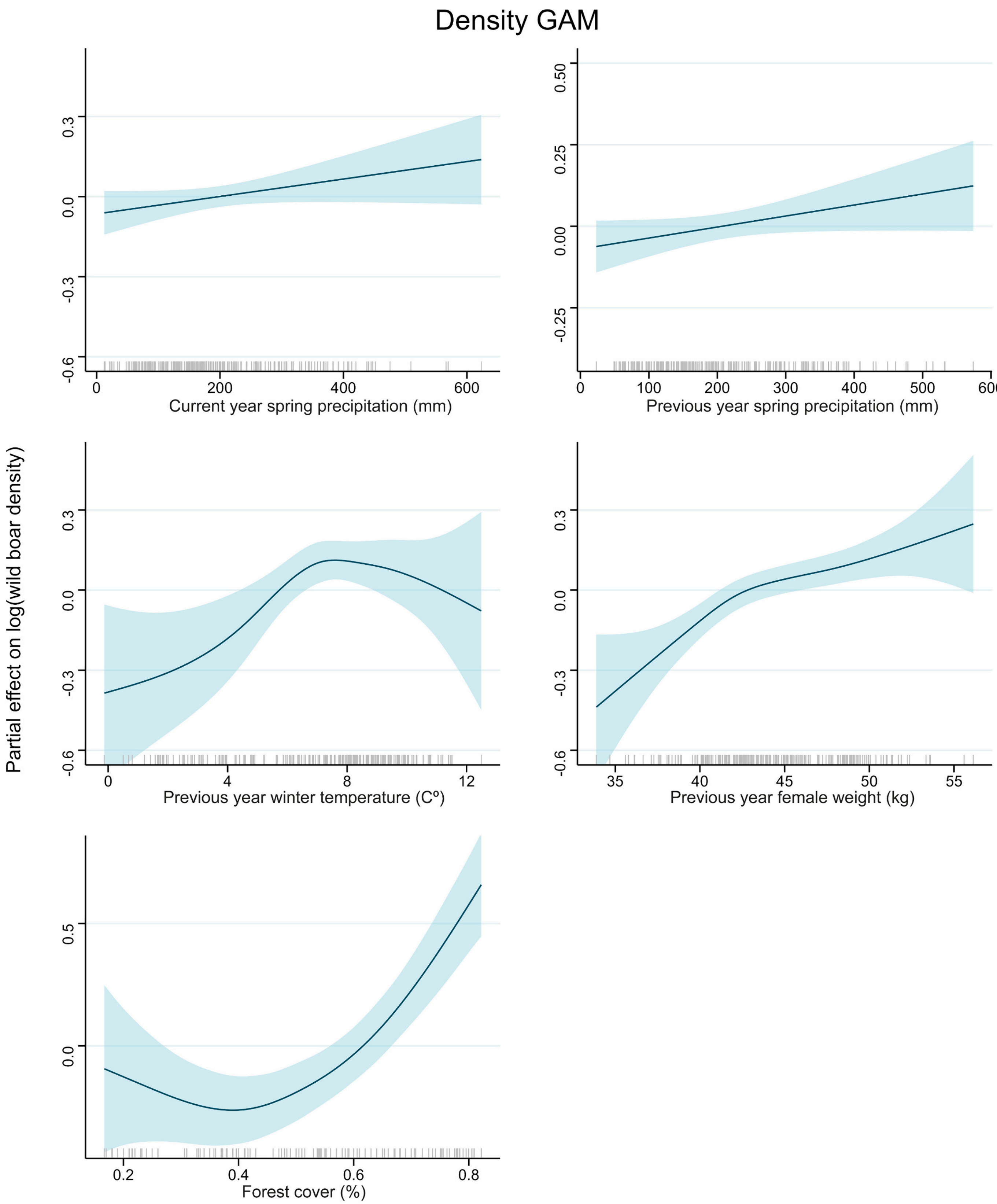

Fig. 4. Effects of selected factors on wild boar density (expressed as the partial effect on log10 density) in Catalonia derived from the results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95 % confidence intervals.

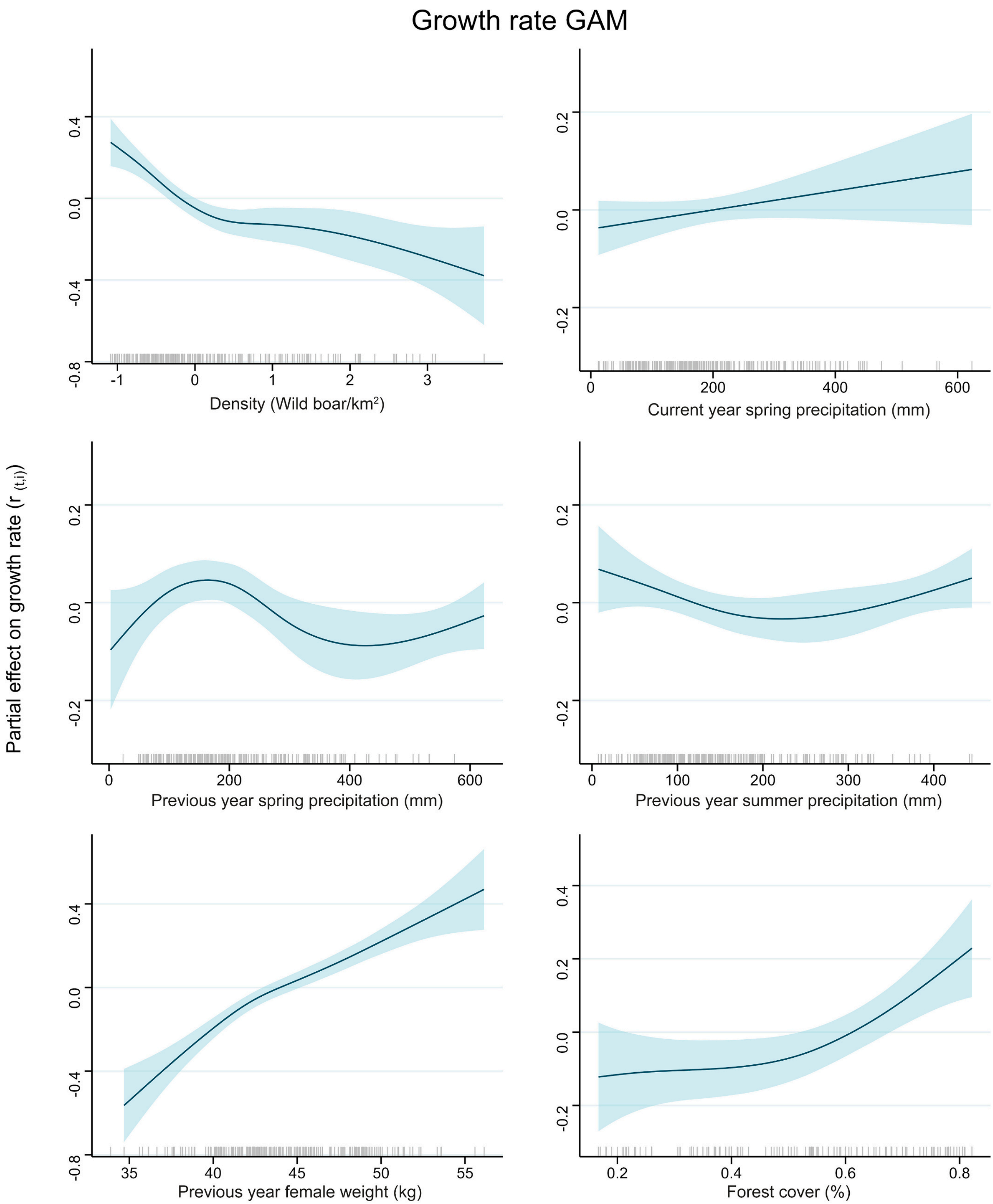

Fig. 5. Effects of selected factors on wild boar population growth rate ($r_{t,i}$, expressed as the partial effect on growth rate), in Catalonia derived from the results of generalized additive mixed models (GAMM). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95 % confidence intervals.

1989; Phillips et al., 1990). Additionally, water shortages could reduce female milk production, thereby reducing piglet survival during the initial weeks of life, as demonstrated in other ungulates (Cain III et al., 2006).

These results imply that spring precipitation plays a key role in wild boar population dynamics in Mediterranean areas. Given the predicted decrease in precipitation levels in these regions over the next decades (Zittis et al., 2019) due to global warming, this may limit wild boar populations in drier areas and cause a shift of populations to higher and wetter areas within the region. However, wild boar residing in the proximity of agricultural and urban areas may increasingly rely on anthropogenic food (such crop and urban waste), thus making their energy requirements independent of weather conditions. This, in turn, will lead to an escalation of human-wild boar conflicts.

In terms of habitat composition, our study identified forest cover as an important variable associated wild boar density, while crop cover showed no clear relationship. However, the proportion of crop and forest cover are partially mutually exclusive, which might explain why only one of these variables (forest cover) was associated with wild boar density. These results may suggest that forest habitats remain the most favorable for wild boar populations in Catalonia, with a relationship showing a sharp increase in wild boar density when forest cover exceeded 60 %. Similar results were found in previous studies but in more continental climate; for example, Borowik et al., 2013 reports higher wild boar densities in woodland cover above 40–50 %. On the other hand, another study in Poland reported that the number of harvested wild boars was correlated positively to the increasing of maize crops surface (Kopij and Panek, 2016). In Catalonia, the highest densities of wild boar have historically been recorded in large, continuous forests, although it is likely that crops provide an alternative food source, particularly during drought periods or in years of low production of forest fruits.

The population growth model shows a negative relationship between wild boar density of previous year and population growth. This finding implies Catalonian boar have negative density-dependence, where higher densities can limit but not suppress population growth, likely due to intraspecific competition for resources. Negative density-dependent processes have been widely described in other ungulates, such as moose, chamois or deer (Brown, 2011; Capurro et al., 1997; Coulson et al., 2000), and for wild boar (Imperio et al., 2012; Kapota and Saltz, 2018; Vetter et al., 2015). Other studies investigating wild boar dynamics found only weak density dependence, suggesting that this factor is unlikely to limit wild boar population growth (Bieber and Ruf, 2005; Choquenot, 1998; Frauendorf et al., 2016; Vetter et al., 2020), especially at the current stage of wild boar populations in Catalonia, which are assumed to be far from carrying capacity. Uzal Fernandez and Nores (2004) highlighted the apparent contradiction of assuming intraspecific competition for resources in populations that are still increasing in numbers, particularly in species like wild boar, with highly varied diet. Nevertheless, the variability in environmental factors could produce rapid changes in resource availability from one year to another in certain areas, resulting in increased or decreased intraspecific in-situ competition and subsequent density-dependence (Choquenot, 1998; Massei et al., 1997). In temperate climates with high population densities, intraspecific competition increases winter mortality and reduces fecundity rate in ungulates like chamois (*Rupicapra rupicapra*) and roe deer (*Capreolus capreolus*) (Capurro et al., 1997; Coulson et al., 2000). Density dependence can also affect sex ratio when food resources are limited (Frauendorf et al., 2016) and influence the age of sexual maturity and pregnancy rate among ungulates such as red deer (*Cervus elaphus*) (Clutton-Brock et al., 1986; Kruuk et al., 1999), or affect daily activity patterns for red deer, roe deer and wild boar (Ramirez et al., 2021).

One of the limitations of this study was the lack of data on the availably of natural food resources, as there are no consistent records on forest fruit production or other food sources. The second limitation was the impossibility to use the number of wild boar hunted as an indicator for mortality, as the number of individuals hunted is one of the parameters employed for calculating density and thus could not be included as an explanatory variable. Finally, the complex nature of our models, combined with the relatively limited sample size and number of factors potentially affecting population density and growth poses a risk of overfitting, implying that the models may excessively capture noise of training data, and its performance in new scenarios should be interpreted carefully. So that, our work should be seen as an exploration of the relevant variables for our study area and conditions which may also be relevant in other situations and are worth to be further studied.

In conclusion, our results provide key insights into the effects of climate, landscape and population factors on wild boar population dynamics in Catalonia, with significant implications for wild boar population management. While meteorological factors cannot be directly controlled, our findings will contribute to elaborate more accurate population predictions based on the interaction of different climate variables for local populations in global change scenarios. Accurate predictions are essential for anticipating and planning management strategies, such as adjusting hunting efforts, implementing alternative methods to culling in conflict areas, or identifying key areas for habitat management and conservation.

Moreover, the limitation by spring precipitation shown by our results, which is likely to affect natural resources availability, is predicted to be more important during the next decades as precipitation is predicted to decrease in Mediterranean areas. Due to the high adaptability of this species, the reliance of wild boar on human-related food (such crop, urban waste or domestic animals food) is likely to increase. Anthropogenic food provide wild boar with highly nutritious resources that improve female fitness (Castillo-Contreras et al., 2021) and the reproductive output of the populations (Rosell et al., 2012). Additionally, crops and urban food resources provide a more stable food supply, independent of weather conditions, that may be particularly relevant for populations residing near agricultural and urban areas, thereby increasing the likelihood of wild boar-human conflicts.

Therefore, effective management measures to reduce anthropogenic food availability are crucial for mitigating conflicts and controlling population growth. These measures can include preventing access to anthropogenic trough crop field fencing or other exclusion measures, securing garbage bins and prevent access of wild boar to domestic animal food, contributing to limit reproductive output, which is directly related to female body weight. Habitat management and reducing refuge areas for wild boar in urban areas might also contribute to mitigate potential conflicts. One of the main findings is the density-dependence processes detected, as population density appeared as relevant factor affecting population growth rate in the study area. Finally, further research is needed to investigate the underlying mechanisms which influence these processes, including the potential impact of factors such as predation, diseases, and climate change. This information may help to design proactive and adaptive management strategies to ensure the sustainable coexistence of wild boars and human populations.

CRediT authorship contribution statement

J. Colomer: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **G. Massei:** Writing – review & editing, Supervision, Conceptualization. **D. Roos:** Writing – review & editing, Validation, Methodology, Formal analysis. **C. Rosell:** Writing – review & editing, Funding acquisition, Conceptualization. **J.D. Rodríguez-Teijeiro:** Writing – review & editing, Supervision, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

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