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Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study

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Abstract

• *Key message* Climate factors affect seed biomass production which in turn influences autumn wild boar spatial behaviour. Adaptive management strategies require an understanding of both masting and its influence on the behaviour of pulsed resource consumers like wild boar.

• *Context* Pulsed resources ecosystem could be strongly affected by climate. Disantangling the role of climate on mast seeding allow to understand a seed consumer spatial behaviour to design proper wildlife and forest management strategies.

• *Aims* We investigated the relationship between mast seeding and climatic variables and we evaluated the influence of mast seeding on wild boar home range dynamics.

• *Methods* We analysed mast seeding as seed biomass production of three broadleaf tree species (*Fagus sylvatica* L., *Quercus cerris* L., *Castanea sativa* Mill.) in the northern Apennines. Next, we explored which climatic variables affected tree masting patterns and finally we tested the effect of both climate and seed biomass production on wild boar home range size.

• *Results* Seed biomass production is partially regulated by climate; high precipitation in spring of the current year positively affects seed biomass production while summer precipitation of previous year has an opposite effect. Wild boar home range size is negatively correlated to seed biomass production, and the climate only partially contributes to determine wild boar spatial behaviour.

• *Conclusion* Climate factors influence mast seeding, and the negative correlation between wild boar home range and mast seeding should be taken into account for designing integrated, proactive hunting management.

Keywords Masting · Mast seeding · Seed consumer · Deciduous forests · Hunting management · Apennine forests

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1 Introduction

The understanding of species responses to climate variation is essential for designing proactive management strategies (Heller and Zavaleta 2009). Changes in climate and land use affect distribution, phenology and population dynamics of several organisms (Bellard et al. 2012; Pagel and Shurr 2012). Changes can affect inner ecosystem processes and functioning at various scales and both flora and fauna have to cope with or adapt to these phenomena (Walther et al. 2002; Parmesan 2007). However, making predictions about the particular response of a species to climate change is difficult because the predictions hinge on knowing how climate influences them directly and indirectly. This implies that an integrated approach is required to properly understand the exact nature and direction of emergent effects because they are the net result of multiple species responding to multiple changes in their environment.

Several studies have demonstrated that plant physiology and phenology are often driven and altered by climatic variables (Michelot et al. 2012; Reyer et al., 2013) and this can create phenological mismatches between different trophic levels within ecosystems (DeLucia et al. 2012; Jamieson et al. 2012; Reed et al. 2013). These effects, in turn, are expected to alter trophic interaction within food chains. Therefore, understanding climatic constraints on plant species is crucial as plants represent the base of ecological food chains (Voight et al. 2003; Barton et al. 2009).

Mast seeding (or masting) is a natural process where pulsed resources create lagged responses in successive trophic levels of ecological communities. Numerous studies have demonstrated that mast seeding in many plant species is driven by external factors such as variations in climate (Williamson and Ickes 2002; Lusk et al. 2007; Drobyshev et al. 2010; Cutini et al. 2015). For example, this was the case of beech masting, which typically occurs after a year characterised by high summer temperature and low precipitation (Piovesan and Adams 2001; Övergaard et al. 2007; Drobyshev et al. 2014). Such strong interplay between plant masting and climate is in line with the environmental prediction hypothesis namely, "large reproductive episodes are timed to anticipate favourable conditions for establishment" (Kelly 1994). In this context, plant reproduction become extremely important in shaping forest ecosystem response to global climate change as the vulnerability or ability of plants to adapt will affect all of the food chain. This relationship between producer and consumer is more evident in pulsed resource ecosystems, where the equilibrium between mast seeding plants and vertebrates heavily relies on their synchronisation (Kelly and Sork 2002; Clotfelter et al., 2007; Boutin et al. 2006; Wauters et al. 2008; Cutini et al. 2013).

In the next century, the Mediterranean basin will be one of the regions most affected by climate change (Giorgi and Lionello 2008) and this could have severe consequences on forest productivity (Boisvenue and Running 2006) including mast seeding. Indeed, masting is a typical feature of the Fagaceae (Hiroki and Matsubara 1995; Hilton and Packham 2003; Espelta et al. 2008; Montserrat-Martì et al. 2009), a tree and shrub family that includes the prevailing species of the Mediterranean region, i.e. beech (Fagus sylvatica L.), chestnut (Castanea sativa Mill.) and various evergreen and deciduous oak (Quercus spp.) species (Skjøth et al. 2008). Nonetheless, the interaction between mast seeding, climate and seed-consumers in the Mediterranean region have received limited attention, particularly regarding ungulate species that are of economic interest from a forest management perspective (Bieber and Ruf 2005; Cutini et al. 2013; Canu et al. 2015; Vetter et al. 2015). Therefore, a comprehensive understanding of the mechanisms involved between climate, forest and ungulate dynamics and behaviour represents an important issue for an effective management of forest and wildlife resources (Chianucci et al. 2015; Cutini et al. 2013).

Among ungulates, the wild boar (Sus scrofa L.) exhibits strong responses to food pulses (Groot Bruinderink et al. 1994; Cutini et al. 2013). The increasing wild boar densities observed in Europe during the last five decades (Apollonio et al. 2010) have led to recent increase in human-wildlife conflicts. As a consequence, ecologists have only relatively recently paid attention to the role of pulsed resources and climate-induced variations in wild boar population dynamics (e.g. Cutini et al. 2013) and life-history traits (e.g. Servanty et al. 2009; Canu et al. 2015). On the other hand, the understanding of climatic effects on direct and indirect trophic interactions requires a long-term perspective and a temporal sequence of information including climate, forest and fauna data.
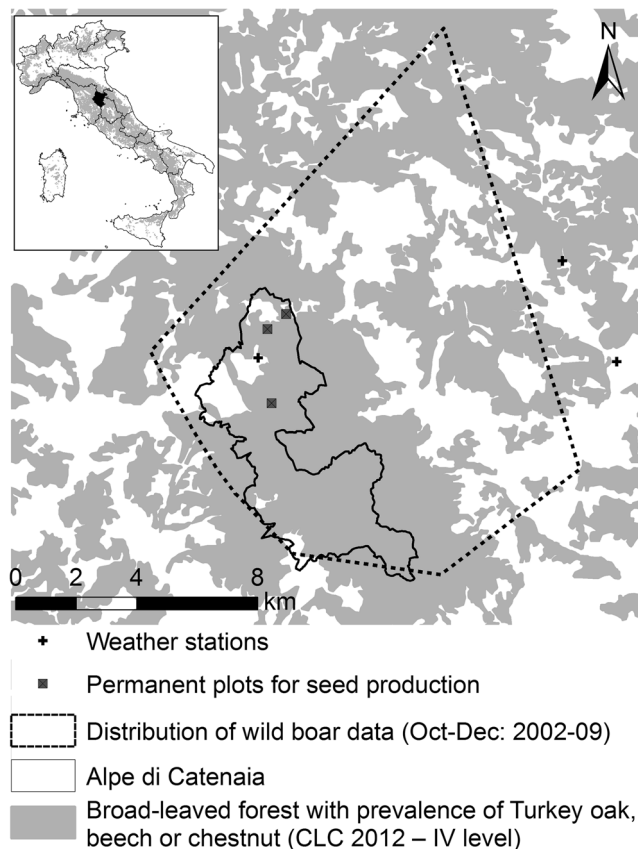
Several factors could influence both wild boar spatial behaviour and plant reproduction but to better understand their interaction and the role of climate as a first contributor, we decided to analyse 23 years masting data in three most common broadleaved tree species in the Apennines (Fagus sylvatica L., Quercus cerris L., Castanea sativa Mill.) and 8 years wild boar spatial behaviour to assess: (1) if climatic variables trigger masting patterns, identifying weather cues that better explain seed biomass production; and (2), by controlling the direct effect of climate experienced by each individual, if a relation exists between wild boar spatial behaviour, i.e. its home range, and mast seeding. This was motivated because wild boar diet in the Apennines heavily relies on acorns, chestnuts and beech nuts (Massei et al. 1996, 1997). Hence, according to the 'food-exploitation hypothesis' of Larter and Gates (1994), home range size of a species is inversely related to food availability. Hence, we hypothesised

that wild boar home range extension should increase when food availability decrease.

2 Methods

2.1 Study area

This study was conducted in a mountainous area in the Central Apennines (Alpe di Catenaia, 4579 ha, 43° 48′ N, 11° 49′ E, Fig. 1). The climate is temperate, with warm, dry summers and cold, rainy winters. The mean annual rainfall is 1224 mm, and the mean annual temperature 9.5 °C. Approximately 87% of the area was covered with forests, mainly broadleaved forests (about 90% of the total forested area). The most diffuse tree species in the area are Turkey oak (*Quercus cerris* L.), beech (*Fagus sylvatica* L.) and chestnut (*Castanea sativa* Mill), which cover respectively 14.9, 22.1 and 7.8% of the forest area. These species are mainly represented by even-aged, pure stands, which are currently managed as coppice

+ Weather stations

■ Permanent plots for seed production

⬚ Distribution of wild boar data (Oct-Dec: 2002-09)

▢ Alpe di Catenaia

▨ Broad-leaved forest with prevalence of Turkey oak, beech or chestnut (CLC 2012 – IV level)

Fig. 1 Mountainous study area in the province of Arezzo, Central Italy. Wild boar distribution based on the Minimum Convex Polygon of all locations of individual animals (October–December period from 2002 to 2009). Forested areas with prevalence of Turkey oak, beech or chestnut (grey colour) in the Alpe di Catenaia (Arezzo Province) (main panel) and in the whole of Italy (left top panel; land use data available from CORINE Land Cover—level IV—Commission of the European Communities, 2012)

in transition to high forest (Cutini et al. 2015). These stands are mainly spread between 700 and 1100 m a.s.l and are mainly aged between 50 and 70 years old.

2.2 Seed biomass production

Three 1-ha permanent plots in beech, chestnut and Turkey oak stands were selected in the study area, in which masting data were collected since the 90s. Annual masting were estimated using the 'littertrap' method, following the protocol by Chianucci and Cutini (2013) as described below. Nine 0.25-m^2 litter traps were positioned in each stand 1 m above ground level using a systematic grid sampling. Litterfall was collected every 2 weeks during fall and winter and monthly during the rest of the year. The collected litter was separated in laboratory into main components (leaves, twigs, seeds, husks) and then oven-dried at 85° ± 2 °C until constant weight. The obtained seed biomass production was converted as Mg ha^{-1} year^{-1}.

2.3 Observed climate data

Temperature and precipitation data were collected at three weather stations located inside and around the study area at different elevations (i.e. 420, 500 and 900 m a.s.l.; Fig. 1) by the National Forestry Service (UTB 2015). Daily data were available since 1989 (26 years). We calculated the daily average temperature (°C) and the cumulated daily precipitation for the following periods as predictor variables that potentially influence mast seed production (points 1 and 2; Piovesan and Adams 2001) and eventually wild boar spatial behaviour directly (point 3; Keuling et al. 2008; Thurfjell et al. 2014):

1. Daily average temperature (°C) and cumulated daily precipitation (mm) during spring (March–May—considering the current year, year$_{-1}$ and year$_{-2}$ for each mast season);
2. Daily average temperature (°C) and cumulated daily precipitation (mm) during summer (June–August, considering the current year, year$_{-1}$ and year$_{-2}$ for each mast season);
3. Daily average temperature (°C) and cumulated daily precipitation (mm) during autumn (October–December, considering the current year for each wild boar home range size).

2.4 Wild boar spatial behaviour data

Radio-tracking location data were collected from April 2002 to August 2010 by triangulation using bearings obtained from three different points (White and Garrott 1990) using the 'loudest signal' method. Bearings were marked out on a 1:10000 scale map (Kenward 1987) of the study area keeping into account that the error box should be smaller than 1 ha.

The telemetry data were uniformly distributed over the 24 h (discontinuous telemetry; Swihart and Slade 1985) with 8–12 locations recorded for each boar each month, and considering at least 12 h between consecutive locations to exclude data autocorrelation (Van Winkle 1975). Wild boars were tracked using Wildlife Materials TRX-1000S receivers and a three-element hand-held Yagi antenna. A total of 230 individuals were equipped with VHF tags (collar or VHF-ear tag, with mortality sensor) (Televilt, Sweden, 150-151 MHz wavebands). Location data (minimum 20 locations) were available for 62 adults and subadults wild boars in October–December period. Seasonal home ranges (October–December) were calculated with the R package HRTools (Preatoni and Bisi 2013) and adehabitat (Calenge 2006) using the 95% fixed kernel density estimator (KDE).

2.5 Statistical analyses

The masting time series for each tree species was tested for autocorrelation using an autoregressive model to assess whether there was a pattern in masting behaviour in the different species. To test for possible trend in seed biomass production, we calculate Sen's slope (Sen 1968; McLeao 2011) and used Mann-Kendall trend test (Mann 1945; Pohlert 2016).

The climate independent variables were standardised as follows:

$$\frac{\left(WF_{d,s} - \overline{WF_s}\right)}{\sigma_s}$$

where WF = climate variable, d = day, s = meteo station, σ = standard deviation.

As proposed by Bisi et al. (2016), we did not focus on single species models because we are not interested in identifying the climatic triggers for each species but we were interested in the overall seed biomass production. As we observed a great difference in seed biomass production between species (see "Mast seeding" paragraph) and we were interested in evaluating mast seeding, we transformed each tree species' masting series using the formula (Bisi et al. 2016):

$$SP = \frac{SP_i}{\overline{SP_{sp}}}$$

where SP = transformed seed biomass production in a given year, $\overline{SP_{sp}}$ = mean seed biomass production of species sp over entire study period, SP_i = seed of species sp in the given year.

The complete standardised dataset of seed biomass production and climate indicators was then analysed using linear mixed effect models (LMEM), with seed biomass production (Mg ha^{-1}) per species and year as dependent variables. Because seed biomass production was not normally distributed (Shapiro-Wilk's test $W = 0.654$), it was

log-transformed. The log-transformed values met the assumptions of normality (Shapiro-Wilk's test $W = 0.924$). We compared a full model with all 12 weather variables and log-transformed seed biomass production of the previous year as predictors.

To reduce the number of predictors, as well as to identify the most effective ones as determinants of the variations in seed biomass production, we performed evaluation of a set of models with all possible combinations (subsets) of terms in the global model, ranking them with AICc (Burnham and Anderson 2002). We estimated goodness of fit as reported in Magee (1990). Since the AICc information criterion penalty for every term is equal to 2, we averaged all the models under delta AICc = 2, weighted by AICc weights.

Finally, correlations between wild boar home range size, annual seed biomass production (not standardised) and climatic variables (autumn temperature and precipitation) were tested by a mixed effects model including sampled boar individual as a random factor. We applied both methods to the complete dataset and to a subsample including only adults (> 24 months old) and subadults (12–24 months old).

All statistical analysis were performed using R software (R Core team 2015) and in particular the packages 'nlme' (Pinheiro et al. 2015) and 'MuMIn' (Barton 2015).

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

3 Results

3.1 Mast seeding

The autocorrelation function did not show masting patterns for any of the three surveyed tree species, even though a more pronounced autocorrelation was observed in Turkey oak and chestnut; beech showed a weak masting pattern (Online Resource 1). This indicates that reproductive investment each year was not strictly related to the seed produced in the previous year. For all three species, Sen's slopes are positive (beech 0.012; chestnut 0.035; Turkey oak 0.026), but not statistically significant (beech: tau = 0.111, $p = 0.475$; chestnut: tau = 0.238, $p = 0.139$; Turkey oak: tau = 0.169, $p = 0.284$).

Seed biomass production differed in amount and timing between the tree species (Fig. 2). Annual seed biomass was similar between Turkey oak (mean ± SE = 0.72 ± 0.15 Mg ha^{-1}) and chestnut (mean ± SE = 0.68 ± 0.08 Mg ha^{-1}; Tukey's HSD $p = 0.964$), but was significantly lower in beech (mean ± SE = 0.12 ± 0.04 Mg ha^{-1}; Tukey's HSD, $p < 0.001$) compared to the other two species.
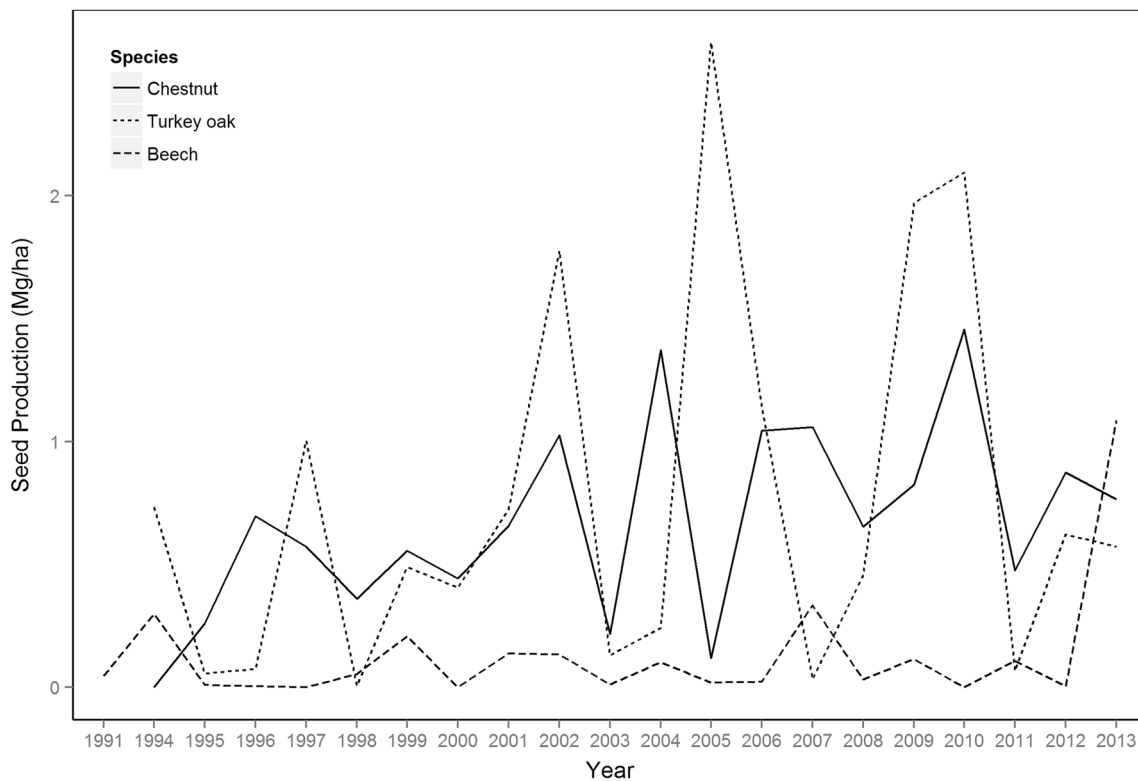
Fig. 2 Seed biomass production for the three broadleaved species over the entire study period

3.2 Effects of climatic variables on mast seeding

According to the model testing for climate effect on masting, Online Resource 2 reports the first 20 models selected based on the AICc information. Only the first two models had a delta AICc < 2; goodness of fit of the two models are respectively 0.153 for model 1 0.162 for model 2. The average model includes climate variable of year t_{-1} and specifically 'Temperature of Spring t_{-1}' and 'Precipitation of Summer t_{-1}', both exhibiting a negative effect on seed biomass production, and 'Spring Precipitation of year t' with a positive effect (Table 1).

3.3 Mast seeding and wild boar home range

Models with and without random effects have been run on the same dataset; we only showed results of the model without random effect as AICc value was lower (924 vs 1557); in this model seed biomass production was negatively significantly correlated with wild boar home range size (seed biomass production = -85.37, SE = 12.12, $t = -7.045$, $p < 0.001$),

precipitation was positively correlated (autumn precipitation = 436.87, SE = 126.61, $t = 3.45$, p < 0.001) and temperature was negatively correlated (-125.14, SE = 38.96, $t = -3.12$). All terms were statistically significant and seed biomass production accounted for the 38% of the total deviance, while temperature accounted for 4.8% and precipitation only for 4%. R^2 was 0.47 and model residuals were normally distributed (Shapiro-Wilk normality test = 0.930).

Only one synchronous null masting event was observed (2003); during this year, wild boar home range size (adults and subadults) averaged 779 ha (SE = 113 ha), compared to a total average of 407 ha (SE = 29 ha).

4 Discussion

4.1 Mast seeding

We did not find a clear masting patterns for any of the surveyed tree species; this lack of cyclic pattern, along with the

Table 1 Averaged model

	Estimate	Standard error	Z value	P
Intercept	0.368	0.187	1.940	0.052
Temperature of spring year t_{-1}	-0.084	0.231	0.358	0.720
Precipitation of spring year t	1.621	0.671	2.365	0.018
Precipitation of summer of year t_{-1}	-1.7362	0.566	3.005	0.003

absence of synchronisation reported using the same dataset (Cutini et al. 2013) and in other study areas (Nussbaumer et al. 2016), may partly explain the limited influence of climate on seed biomass production, at least at small scale (i.e. stand level), since the different species most likely exhibit different strategies in allocating resources (Genet et al. 2009) and thus different species-specific responses to climatic inputs.

4.2 Masting patterns and climate drivers

Although many studies have already investigated climate-beech mast seeding relation at broad scale, a limited number of studies have analysed such relationships for chestnut and Turkey oak, i.e. two dominant species with important implication for wild boar management in Mediterranean environments. We found that the mast seeding was only slightly influenced by climatic variables, which explained about 16% of the variance. This is probably due to the fact that tree species masting was not synchronous and that these three species in Central Italy are in the *optimum* of their distributional range (Cutini et al. 2015), implying that climate conditions are not as limiting as in the extremes of species distribution. However, precipitation during spring (positive influence) and summer (negative influence) in the previous year were the most significantly predictors of mast seeding, in accordance with previous studies conducted on beech and oak species (Piovesan and Adams 2001; Övergaard et al. 2007; Espelta et al. 2008; Scharnweber et al. 2011; Drobyshev et al. 2014). Some authors have interpreted a link between climate and masting under the so-called environmental prediction hypothesis (Kelly 1994), which states that masting strategy has evolved to promote natural regeneration after disturbances, since limiting climate conditions like summer drought may reduce competitor pressure due to canopy trees mortality. This leads to favourable light conditions at the forest floor for seedling establishment (Williamson and Ickes 2002). Although the observed negative correlation between summer temperature and masting does not invalidate this hypothesis, we believe that this mechanism may not be prominent in the Apennines and therefore climate conditions are not as limiting as in the extremes of species distribution. Instead, the regular occurrence of mast years in these species supports the predator satiation hypothesis in accordance with previous findings (Kon et al. 2005) as the change between high and low seed biomass production has a strong impact on animal populations like wild boar, as demonstrated in a previous study (Cutini et al. 2013).

There has been widespread interest in how increase in local mean temperature might affects masting (e.g. Rees et al. 2002; Övergaard et al. 2007). A recent study indicated that mast seeding may be unaffected by gradual increases in mean temperature, since masting is more sensitive to year-to-year variation in summer temperature rather than mean temperature

(Kelly et al. 2013). Such hypothesis is interesting as it can be applied to other environmental cues like precipitation, which is often overlooked in modelling mast seeding under environmental change. In our study, we observed that precipitation was more correlated than temperature to seed biomass production, for which we conclude that precipitation can be considered a relevant cue at the local scale. Oak can tolerate drier condition than beech (Breda et al. 2006) particularly when water becomes a limiting factor. In many Mediterranean environments, the process of acorn maturation occurs under water-limited conditions, and oaks usually exhibit high abortion rates during this period (Espelta et al. 2008), which may reflect the influence of both direct (increasing respiratory costs) and indirect effects (increasing water stress) on the internal storage of carbohydrates of the tree. In areas with sufficient water availability, like in Apennines, the seed production is likely mainly driven by light availability, which have direct influence on either the light-use efficiency of the trees, which is related to the photosynthetic performance and thus the ability of trees to accumulate resources to produce seed, and either the length of pollen season, which is a more limiting factor in oak than beech (Bogdziewicz et al. 2017); in this line, the higher shade tolerance of beech can favour this species over less tolerant oak species in non-water-limiting conditions (Scharnweber et al. 2011). The consequences of these trade-offs can influence both growth and seed biomass production and therefore all the components of the consumers community relying on tree masting in Apennines.

4.3 Influence of mast seeding on wild boar spatial behaviour

Schley and Roper (2003) reported that wild boar diet is strongly influenced by food availability and they rely strongly on acorns, beech and chestnuts during mast years (e.g. Fournier-Chambrillon et al. 1995; Massei et al. 1996). Thus, the asynchronous patterns among tree species could contribute to support consumer populations through time (Cannon et al. 2007). Furthermore, previous studies demonstrated that the large forage availability is one of the most important factors shaping wild boar food habits (e.g. Groot Bruinderink et al. 1994).

A previous study by Cutini et al. (2013) conducted in the same wild boar population showed that mast seeding influences the population density; the current study also revealed that mast seeding influences the spatial behaviour of wild boar, in agreement with previous reports on other mammal species (Anderson et al. 2005; Kozakai et al. 2011; Morellet et al. 2013). These population features are linked to two different biological processes: on one hand, the increase of wild boar density after a mast year can be attributed to an increase in reproductive performance of sows, because wild boar females need to reach a threshold body mass (27–33 kg) before

breeding (Servanty et al. 2009). On the other hand, increase of home range extension are linked to seasonal food availability, and are particularly driven by the research of alternative food during limiting condition (fall-winter period), consistently with the 'food-exploitation hypothesis'. However, this species shows a high behavioural plasticity (e.g. Podgórski et al. 2013) and studies testing this hypothesis over a shorter period (3 years) reached contrasting conclusions (Massei et al. 1997) underling the importance of using long time series to understand mammal spatial behaviour. This aspect stresses the fact that the expansion of wild boar populations and their growth may be partially attributed to the behavioural plasticity of the species and its response to different ecological contexts (hunting management, predator presence, forest composition) at population (Podgórski et al. 2013) and individual (Keuling et al. 2008) level. During the wild boar space use monitoring, there has been only one synchronous, null masting event that involved all the sampled species in 2003 and during this year, home range size strongly increased compared to the total average. This emphasises the importance of broadleaf forests for wild boar movement ecology, because alternative food patches require long movements far from wild boar's usual home ranges when the tree masting was not sufficient. This aspect also demonstrated the plasticity of this species and the importance to collect multiple and long time series dataset to completely understand the ecological role of the different species in the forest ecosystem. The ecological role of wild boar in forest ecosystems should be further investigated because of its complex impact on the plant community, that is in fact not only negative (Genov and Massei 2004; Gomez and Holdar 2008; Wirthner et al. 2012) and can also affect tree masting as reported by Wirthner et al. (2012).

4.4 Management implications

It has been demonstrated that large tree seed availability, particularly during mast years, may reduce wild boar pressure on agricultural crops (e.g. Groot Bruinderink et al. 1994), while low tree seed availability could cause severe damage to agricultural crops (Jezierski and Myrcha 1975; Andrzejewski and Jezierski 1978). Together with increased food availability, the reduced home range of wild boar during mast years offers a clear interpretation of the causal mechanism behind this finding. Therefore, predicting masting pattern of the dominant species can allow to take an adaptive approach when planning proper damage prevention measures and hunting plans. Use of local weather station data can support the prediction of masting patterns in the most dominant species. In addition, forest managers should consider the value of mast produced by the secondary most dominant species as alternative forage for wild boar.

5 Conclusions

This study indicates that climate factors may shape forest dynamics through their influence on mast seeding, but also that the negative correlation between mast seeding and wild boar home range size is an important mechanism whose consequences should be taken into account. Adaptive management strategies require both an understanding of masting and their influence on the behaviour of pulsed resource consumers like wild boar, supporting an integrated wildlife-forest management approach.

Compliance with ethical standards

Following the Italian law 157/92 on wildlife management, the authors acquired the permission of catching wild boars in 2002 and 2005 from the Regional Government of Tuscany.

Conflict of interest   There are no conflicts of interest and research integrity and ethical standards are maintained.

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