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ABSTRACT

Temporal autocorrelation in environmental conditions influences population dynamics through its effects on vital rates. However, a comprehensive understanding of how and to what extent temporal autocorrelation shapes population dynamics is still lacking because most empirical studies have unrealistically assumed that environmental conditions are temporally independent. Mast seeding is a biological event characterized by highly fluctuating and synchronized seed production at the tree population scale, as well as a marked negative temporal autocorrelation. In the current context of global change, mast seeding events are expected to become more frequent, leading to strengthened negative temporal autocorrelations and thereby amplified cyclicality in mast seeding dynamics. Theory predicts that population growth rates are maximized when the environmental cyclicality of consumer resources and their generation times are closely matched. To test this prediction, we took advantage of the long-term monitoring of a wild boar population, a widespread seed consumer species characterized by a short generation time (ca. 2 years). As expected, simulations indicated that its stochastic population growth rate increased as mast seeding dynamics became more negatively autocorrelated. Our findings demonstrate that accounting for temporal autocorrelations in environmental conditions relative to generation time of the focal population is required, especially under global warming where the cyclicality in resource dynamics is likely to change.

Keywords: oak mast seeding, wild boar, temporal autocorrelation, cyclicality, stochastic population growth rate, generation time.

Introduction

Populations in the wild are consistently challenged by environmental variation that induces temporal variation in vital rates (e.g. survival) affecting, in turn, population dynamics (Tuljapurkar 1990; Lande et al. 2003; Boyce et al. 2006). Temporal variation in the environment can be decomposed into several conspicuous patterns that occur on different time scales (Wolkovich et al. 2014). Long-term trends reveal the intensity and direction of global change. However, temporal autocorrelation (i.e. the tendency for observations close to each other to be related; Legendre 1993; Vasseur and Yodis 2004), which is detected over shorter time scales, can also be influenced by global change and in turn affect vital rates in the wild. Accordingly, Steele (1985) introduced the idea of colored – i.e. time correlated – noise to ecology. He proposed that fluctuations in environmental conditions over time could be ranked along a spectrum to describe their patterning: from random fluctuations with no autocorrelation (i.e. white noise) to ones with either positive (i.e. red noise) or negative (i.e. blue noise) correlations across a time series (see Fig. 1). In these latter cases, individual observations at any point depend on each other by being either more similar (red noise) or more different (blue noise) than expected by chance (Vasseur and Yodis 2004; Schwager et al. 2006). More specifically, a strongly negative temporal autocorrelation indicates that the probability for similar individual observations to succeed each other in time is very low, leading to cyclical patterns of environmental conditions (see Fig. 1, left panel). An absence of temporal autocorrelation indicates that individual observations succeed each other in time randomly (see Fig. 1, middle panel). A strongly positive temporal autocorrelation indicates that the probability for similar individual observations to succeed each other in time is very high, ultimately leading to a single type of observations (see Fig. 1, right panel). Altogether, these different levels of environmental variation occur on time scales relevant to ecology (Wolkovich et

al. 2014), and are important drivers of population fluctuations and life history trait evolution. Despite the awareness regarding the color of environmental noise, most empirical studies conducted so far on population dynamics have assumed white noise, i.e. independent and identically distributed (IDD) environmental conditions over time (but see Tuljapurkar and Wiener 2000, Metcalf and Koons 2007, or more recently Tuljapurkar et al. 2020 and Schreiber 2021 for notable exceptions). Similarly, theoretical work has investigated evolutionary and demographic responses in stable vs. stochastic (i.e. IDD environmental conditions) environments (e.g. Vindenes et al. 2008; Koons et al. 2016; Lande et al. 2017; Engen et al. 2020).

To date, the few empirical studies of the influence of temporal autocorrelations in environmental conditions on population dynamics have reported fairly contrasting results. Some studies have revealed only a weak effect of temporal autocorrelation on population dynamics (Van de Pol et al. 2011; Engen et al. 2013), while others have detected a strong effect which seems to depend on the position of the species along the slow-fast continuum of life history variation – i.e. the species life history strategy (Paniw et al. 2018; Smallegange et al. 2019). Slow-living species typically have longer generation time, longer lifespan, reproduce later in life and produce less offspring than fast-living species (Gaillard et al. 2005). Lastly, some studies reported an effect of temporal autocorrelation on population dynamics that depended on the direction of the autocorrelation (Smallegange et al. 2020). These conflicting results point out the need to deepen our understanding of the effects of temporal autocorrelations in environmental conditions on population dynamics. In the current context of global change that involves changes in the patterning of environmental states (Turner et al. 2010; García Carreras and Reuman 2011; Lenton et al. 2017; IPCC 2018), better understanding the influence of temporal autocorrelation on population dynamics is urgently needed.

Remarkably, temporal autocorrelation is not only characterized by the probability for similar observations to succeed each other, but also by the time elapsed between two identical observations. MacArthur (1968) first recognized that environmental or climatic fluctuations occurring in a cyclical – or periodic – fashion have implications for population growth. Later on, Tuljapurkar (1985) showed theoretically that the response of age-structured populations to cyclical variations in environmental conditions is explicitly related to the length of the cycle period relative to the transient properties of the population's average vital rates. Then, if the cycle period is similar to the mean generation time of the population experiencing this periodicity, its growth rate should increase. Consequently, an increase in population growth rate should occur in organisms with short generation times because negative temporal autocorrelation in resources increases cyclicality, thus leading to matching generation time and environmental periodicity. On the other hand, cycle periods either shorter or longer than generation time should lead to decrease population growth rate. These theoretical findings highlight the significance of considering the match between generation time, which characterizes the organism's life history strategy (i.e. fast vs. slow), and the periodicity in environmental conditions. Only including the life history strategy to explain populations' response to environmental autocorrelation, as commonly done, might explain the contrasting results reported in the literature (i.e. Paniw et al. 2018; Smallegange and Berg 2019; Smallegange et al. 2020).

From seasons or tides to prey population outbreaks, there is a great diversity of cyclical environmental fluctuations in nature. However, to the best of our knowledge, Tuljapurkar's theoretical prediction positing that a close match between the cycle period in environmental conditions and generation time should increase population growth has not been yet tested empirically in any natural system. For instance, while Henden et al. (2008) did not find any

evidence for an effect of the matching between the cycle period of the abundance of small rodents (prey) and generation time of Arctic fox (*Vulpes lagopus*) (predator), Hörnfeldt (2004) found that declining mean and variance of rodent spring densities over time strongly dampened the potential effect of prey cyclicality on Arctic fox population dynamics. Likewise, Park and Wootton (2021) showed that manipulating the periodicity in environmental conditions strongly influenced population growth rate. However, in none of these studies the changes in periodicity have been scaled to generation time.

We took advantage of the oak mast seeding – wild boar study system to empirically assess whether and how the match between environmental cyclicality (i.e. mast seeding) and wild boar (*Sus scrofa*) generation time increases the stochastic population growth rate, as predicted by the theory (Tuljapurkar 1985). A mast seeding event corresponds to the short-term availability of extremely high seed productions that are synchronized within a tree population (Silvertown 1980; Kelly 1994; Pearse et al. 2016). Dramatic among-year fluctuations in seed production involved in mast seeding typically display marked negative temporal autocorrelations (i.e. blue noise), which prevent the occurrence of two successive mast seeding events (Kelly and Sork 2002; Schermer et al. 2019). Positively autocorrelated environmental conditions, unlike negative ones, are the rule in both terrestrial and marine systems (e.g. minimum and maximum temperatures recorded at a monthly scale, Vasseur and Yodzis, 2004). Therefore, mast seeding not only constitutes one of the most widespread examples of negative temporal autocorrelations in resource availability (Ostfeld and Keesing 2000), but also a fairly unique system to assess the importance of negatively autocorrelated resources on consumer dynamics. The succession of years with good and poor acorn production in oak mast seeding dynamics results from two components. The combination of synchronized internal resource dynamics and depletion among trees generates fluctuations in

pollen production, and the amount of airborne pollen available for oak reproduction depends on spring weather conditions (Schermer et al. 2019). Under global warming, higher spring temperatures should increase the frequency of mast seeding events and thereby strengthen the negative temporal autocorrelation characterizing this reproductive tactic (Schermer et al. 2020; Touzot et al. 2020). We thus expect a cyclical patterning in the way good and poor years of acorn production succeed each other, with the occurrence of one good year every two years (Schermer et al. 2020, Touzot et al. 2020).

Wild boar is a widespread species worldwide (Lowe et al., 2000; Tabak et al. 2018), which preferentially feeds on acorns when available (Brandt et al. 2006). This fast-living species has a short generation time of about two years (Servanty et al. 2009 and 2011; Gamelon et al. 2012 and 2021). Taking advantage of long-term capture-mark-recapture data collected in a wild boar population and information on annual acorn production, we previously showed that increasing acorn availability positively influenced the probability for a female to reproduce and, hence, increased population growth rate (Touzot et al. 2020; Gamelon et al. 2021a). However, whether a good match between wild boar generation time and cyclicality of mast seeding events positively influences population growth rate has never been tested. The oak mast seeding – wild boar study system provides an ideal and particularly relevant system to investigate whether Tuljapurkar's theoretical prediction is empirically supported and examine its biological implications in the current context of global change.

We first assessed the impact of good vs. poor years of acorn production on all stage-specific vital rates to build two stage-structured matrix population models, one for each environmental state (i.e. good vs. poor acorn production years, see Touzot et al. 2020). However, we relaxed the Touzot et al. (2020)'s assumption of a perfectly negative temporal autocorrelation with a coefficient of -

1.0 and assessed the influence of time series of mast seeding events differing in their patterning on wild boar dynamics. Thus, we simulated sequences of mast seeding events under various scenarios of autocorrelation and cyclicality and examined the resulting effects on wild boar population trajectories. This allowed us to disentangle the influence of more frequent events of high resource availability from the potential effect of an amplified cyclicality on wild boar population growth rate. Long-term simulations (100,000 years) were conducted to test Tuljapurkar (1985)'s prediction. Shorter-term simulations (150 years) allowed us to bring a more applied perspective to our results with outcomes for management strategies in a global warming context.

Materials and Methods

Study area and data collection

The study was conducted in the 11,000 ha forest of Châteauvillain-Arc-en-Barrois (North-eastern part of France; 48°02N, 4°56E). In this study, a year was defined according to the period of acorn availability (i.e. from October 1st to September 30th). From 1983 to 2016, a capture-mark-recapture-recovery (CMRR) program on wild boar has been running in this broad-leaved deciduous forest, thus providing us with detailed and accurate annual estimates of vital rates. These data were collected during two periods each year. From March to September, females were captured, marked (or identified for females already marked) and weighed (in kg) before being released, which provided information on growth and survival for 1,474 females over the course of the study. Next, information on the reproductive status of 4,244 females shot between 1983 and 2016 (i.e. either previously marked or not) were collected during the hunting season that took place yearly from October to February. Body mass (in kg), reproductive status (i.e. defined as reproductive or not based on the presence of fetuses in the uterus or of Graafian follicles and/or

corpora lutea in the ovaries; see Gamelon et al. 2017 for further details), and litter size were recorded on all shot females. Last but not least, stomach contents of shot individuals were analyzed over the course of the study (i.e. 3,090 stomach contents throughout the study period) to assess acorn production. As the main period of acorn crop commonly overlaps the beginning of the hunting season in French oak forests (see. Touzot et al. 2018; Appendix 11 for an analysis of the seasonal dynamics of acorn production in French oak forests), we indirectly assessed acorn production using acorn consumption by wild boars as a proxy (see Servanty et al. 2009; Gamelon et al. 2017 and Touzot et al. 2020 for a similar approach). Based on the amount of seeds found annually in the stomachs throughout the hunting season, we defined two environmental states: "good years" corresponding to years when acorns represented at least 50% of stomach contents vs. "poor years" of acorn production otherwise (see Touzot et al. 2020 for a similar approach).

Building state-dependent stage-structured population projection matrices

Vital rates were estimated from demographic data collected during (re)captures and hunting bag analyses, for three stages corresponding to the following body mass classes: small (< 30kg) (*S*), medium (30 kg < body mass < 50 kg) (*M*) and large (> 50kg) (*L*), and for the two defined environmental states: good vs. poor years of acorn production. The annual survival probability of females of body class *i* S_i was estimated as the probability of not dying from natural causes (1 – Mn_i) multiplied by the probability of not being shot (1 – h_i) (Eq. 1).

$$(1)\ S_i = (1 - Mn_i) \times (1 - h_i)$$

Surviving females either remained in the same body mass class until the next year (*pSS* for the probability of small females to remain small and (1 – *pML)* for the probability of medium females to remain medium) or moved upward the following class (*pSM* for small females becoming

medium, *pSL* for small females becoming large and *pML* for medium females becoming large). Large females remain in that state from one year to the next. Females from all body mass classes produced offspring. The fecundity R_i was estimated as the product of breeding proportion (BP_i), litter size (LS_i), postnatal survival (*Spn*) and sex ratio (assumed to be balanced, see Servanty et al. 2007 for supporting empirical evidence) (Eq. 2).

$$(2)\ R_i = BP \times LS_i \times 0.5 \times Spn$$

Offspring produced either remained in the small body mass class (*piOs*) or moved upward the following class (1-*piOs*). We refer the readers to Touzot et al. (2020) for a more thorough description of the analytical steps for estimating vital rates. The only vital rate responding to acorn production was the probability for a female to participate to reproduction (BP_i). Thus, the probability for a female to breed was higher during good than poor years of acorn production for both medium and large-sized females (see Table 1 for state- and stage-specific vital rates).

Note that *piOs* (i.e. the probability of juvenile females to enter the small body mass class within the year) and *Spn* (postnatal survival) were set to values previously reported in Touzot et al. (2020).

Stage and state-dependent vital rates were then included in two stage-structured matrix population models $\boldsymbol{A_z}$, with *z* corresponding to the environmental state. The stage-structured matrix $\boldsymbol{A}$ was then:

$$\begin{array}{c} S \\ M \\ L \end{array}\begin{bmatrix} R_S \times piOs \times Ss + pSS \times Ss & R_M \times piOs \times Ss & R_L \times piOs \times Ss \\ R_S \times (1 - piOs) \times Sm + pSM \times Sm & R_M \times (1 - piOs) \times Sm + (1 - pML) \times Sm & R_L \times (1 - piOs) \times Sm \\ pSL \times Sl & pML \times Sl & Sl \end{bmatrix}$$

These state-dependent matrices allowed stage-specific population sizes at year t+1 to be estimated from stage-specific population sizes at year t.

Simulating sequences of good vs. poor years of acorn production

Stochastic time series of environmental conditions were generated by defining a discrete Markov chain that included the two environmental states (i.e. good vs. poor years of acorn production). To do so, we used the following transition matrix ***P***:

$$\boldsymbol{P} = \begin{pmatrix} p & q \\ 1-p & 1-q \end{pmatrix}$$

where p and q represent the probabilities of transitioning to a good year of acorn production at time t+1 when acorn production was good or poor at time t, respectively (Tuljapurkar and Haridas 2006). These transition probabilities can be derived from the frequency of years of good environmental conditions (f) incorporated into the simulations and the autocorrelation coefficient v_1; in other words, the temporal autocorrelation determining the succession of good and poor years of acorn production that corresponds to $(p - q)$ such as $q = f\,(1 - v_1)$ and $p = v_1 + q$ (Tuljapurkar and Haridas 2006). We used v_1 between -0.50 and 0.50 to implement the transition matrix ***P*** to move along a continuum of environmental noises ranging from blue (i.e. high negative values of v_1) to red (i.e. high positive values of v_1) noise. Note that when the autocorrelation coefficient was negative, the frequency of good years of acorn production in the simulations was constrained within the interval $[|v_1|/(1 + |v_1|), 1/(1 + |v_1|)]$. Thus, only frequencies between 0.35 and 0.65 were used in the simulations. This wide continuum of v_1, ranging from -0.50 to +0.50, allowed us to investigate the effects of temporal autocorrelation on wild boar population dynamics, without neglecting the effects of the frequency of good years. By doing so, we considered temporal autocorrelations that led to cycle periods in environmental conditions either longer than (i.e. red noise) or closely similar to (i.e. blue noise) the mean generation time of our population (i.e. 2.46 years and 2.50 years for good and poor years of acorn production, respectively; see Gamelon et al. 2021a).

Performing stochastic simulations of wild boar population dynamics

For each combination of autocorrelation coefficient and long-term frequency of years of good acorn production (i.e. acorn mast years), we ran 500 stochastic simulations of 100,000 time steps. Thus, based on the transition matrix $\boldsymbol{P}$, an environmental state was randomly selected at each time step, and the corresponding stage-structured matrix $\boldsymbol{A_z}$ model was implemented. To account for demographic variation in the simulations, all vital rates were randomly drawn from a normal distribution based on their means and variances (see Fig. 2 for a graphical display). Additionally, to be consistent in our comparisons across combinations of autocorrelation coefficient and long-term frequency of years of good acorn production, the initial population vector (n_0) considered an equally distributed population between body mass classes (i.e. $n_s = n_m = n_l$) and the simulated sequences of environmental conditions systematically started with a good year of acorn production. Finally, the initial 1,000 iterations were discarded from the simulations to minimize the influence of initial conditions. The stochastic population growth rate ($\log \lambda_s$) was estimated for each simulation within each combination of autocorrelation coefficient and long-term frequency of years of good acorn production as $\log(\lambda_S) = \lim_{t \to \infty} (1 / t) \, . \log\left[N_{(t)}/N_{(0)}\right]$, where $N_{(0)}$ and $N_{(t)}$ represent the total population size at the first time step of the simulation (i.e. corresponding to the first population size estimated after discarding the 1,000 first iterations) and at time t, respectively (Tuljapurkar et al. 2003).

We conducted perturbation analyses by calculating the elasticity of $\log(\lambda_s)$ to each entry of the stage-structured matrix $\boldsymbol{A}$. These prospective demographic analyses allowed us to identify which stages of the wild boar life cycle were the most influential to the stochastic population growth rate according to the different regimes of temporal autocorrelations and frequencies of

good years of acorn production that were accounted for in the simulations. To do so, we assessed the influence of a 1% change of the mean and the standard deviation of all vital rates of the stage-structured matrix $\boldsymbol{A}$ on $\log(\lambda_s)$.

Performing short-term simulations of wild boar population dynamics

Using the same approach as described in section 2.4, we projected wild boar population size over a shorter time period. We ran 500 simulations of 150-time steps and discarded the initial 50 iterations resulting in 100-time step simulations. Additionally, for each simulated population trajectory, we computed the coefficient of variation (CV) of the wild boar population size.

All analyses were performed using R version 4.0.3 (R Development Core Team 2017). Data underlying all analyses described above are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.pnvx0k6pt (Touzot et al. 2022).

Results

Wild boar stochastic growth rate across different scenarios of mast seeding dynamics

The wild boar stochastic population growth rate ($\log(\lambda_s)$) was influenced by both the long-term frequency of years of good acorn production (f) and the intensity of temporal autocorrelation (v_1) among those years. Specifically, the higher the frequency of good years, the higher $\log(\lambda_s)$, regardless of the temporal autocorrelation considered in mast seeding dynamics (Fig. 3A). Thus, across our simulations, for a 0.1 increase in the frequency of good years, $\log(\lambda_s)$ increased on average by 0.012 (Fig. 3A). This increase of $\log(\lambda_s)$ in response to increasing frequencies of good years also translated into a decrease of the doubling time (DT) of the wild boar population (i.e. mean amount of time required for the population to double in size over the simulated sequence of

environmental conditions; see Supplementary Materials Fig. S1). While DT was on average 15.64 years [15.51 – 15.79] across the different amount of temporal autocorrelation included in the simulations (i.e. from -0.50 to +0.50) for a frequency of 0.35 during good years, it was of only 8.54 years [8.51 – 8.59] for a frequency of 0.65 (see Supplementary Materials, Fig. S1).

As expected from Tuljapurkar's theoretical results (1985), $\log(\lambda_s)$ decreased when v_1 shifted from blue noise (i.e. negative values of temporal autocorrelation in years of good acorn production) to red noise (i.e. positive values of temporal autocorrelation in years of good acorn production), irrespective of the frequencies of good years (Fig. 3A). In other words, the higher the mismatch between mast seeding cyclicality and wild boar generation time, the smaller $\log(\lambda_s)$ (Fig. 3A).

Then, we compared the magnitude of this decrease across the frequencies of good years. We calculated for each frequency of good years the proportional percentage of decrease in stochastic population growth rate between the highest value of $\log(\lambda_s)$ observed across the continuum of environmental noise (i.e. between v_1 = -0.50 and v_1 = +0.50) and the value of $\log(\lambda_s)$ obtained with the autocorrelation coefficient considered as $(\max(\log(\lambda_S) - \log(\lambda_S)) * 100 / (\max(|\log(\lambda_S)|))$. The response of $\log(\lambda_s)$ to shifting environmental noise (i.e. from blue (i.e. negative autocorrelation) to red (i.e. positive autocorrelation noise)) was similar regardless of the frequency of good years (Fig. 3B). $\text{Log}(\lambda_s)$ decreased along the continuum of autocorrelation coefficients, reaching 3.11% [2.66 – 3.69] and 5.87% [4.97 – 6.75] of decrease between v_1 = -0.50 and v_1 = +0.50 for frequencies of good years of 0.65 and 0.35, respectively (Fig. 3B).

The wild boar population displayed lower log(λs) when temporal autocorrelation in mast seeding dynamics was highly positive, corresponding to a time elapsed between two years of acorn production longer than wild boar generation time. Conversely, a positive response of the

population to highly negative temporal autocorrelation occurred when the time elapsed between two years of acorn production was close to wild boar generation time, regardless of the frequency of good years of acorn production.

Elasticity of the stochastic growth rate to perturbations in the stage-structured matrix A

The perturbation analyses revealed that large females, through their survival and reproductive abilities (i.e. participation to reproduction and number of offspring produced; see description of the stage-structured population model $\boldsymbol{A_z}$), contributed the most to the changes observed in $\log(\lambda_s)$, regardless of the frequency of good years of acorn production and/or temporal autocorrelation (Fig. 4A to D). However, while the elasticity at mean vital rates was similar under the different dynamics of mast seeding (Fig. 4A and 4B), marked variations occurred in the way perturbing the variance of the vital rates of large individuals affected $\log(\lambda_s)$ according to the chosen autocorrelation coefficient. As such, the more positive the autocorrelation coefficient was, the more negative the effects of perturbations in the variance of vital rates of large individuals on $\log(\lambda_s)$ were, regardless of the frequency of good years of acorn production (Fig. 4C and 4D). In other words, a negative coefficient of autocorrelation in the simulations led to decrease the effects of perturbations in the variance of vital rates of large individuals on $\log(\lambda_s)$ (Fig. 4C and 4D).

Wild boar population size across different scenarios of mast seeding dynamics

Change to short-term simulations indicated that wild boar population size responded to both the frequency of good years (f) and the temporal autocorrelation (v_1). Not surprisingly, population size increased with frequencies of good years. For an autocorrelation of -0.50 (i.e. blue noise), wild boar population size was 37,867 [17,843 - 77,884] (median [± 95% confidence interval])

individuals at the end of the simulated scenarios for a frequency of good years of 0.35 (Fig. 5A), while it was 1,435,544 [695,104 – 2,876,269] individuals for a frequency of 0.65 (Fig. 5B). This increase corresponds to a 38-fold difference in population size. Similarly, when the autocorrelation coefficient was positive in the simulations (0.50 to be specific), population size reached 31,912 [5,492 – 268,399] individuals and 1,318,312 [171,037 – 8,357,917] individuals for frequencies of good years of acorn production of 0.35 (Fig. 5A) and 0.65 (Fig. 5B), respectively.

In accordance, population sizes at the end of the short-term simulations (i.e. 100 years) increased when temporal autocorrelation in mast seeding dynamics shifted from positive to negative, regardless of the frequency of good years of acorn production (Fig. 5A and 5B). For instance, for a frequency of good years of 0.35, population sizes were of 37,867 [17,843 – 77,884] and 31,912 [5,492 – 268,398] individuals for v_1 = -0.50 and +0.50, respectively (Fig. 5A).

Additionally, a marked increase of the temporal variation in wild boar population size occurred when v_1 shifted from blue noise (for f = 0.35: CV = 0.28 [0.09 – 0.38]; for f = 0.65: CV = 0.26 [0.09 – 0.35]; expressed as median [± 95% confidence interval]) to red noise (for f = 0.35: CV = 0.87 [0.13 – 1.69]; for f = 0.65: CV = 0.74 [0.12 – 1.10]), irrespective of the frequencies of good years (Fig. 5A and 5B, top left corners, see also differences obtained in the width of 95% CIs in main panels). As such, fluctuations in wild boar population size over time were on average 3.11 and 2.85 times higher in the scenarios considering a positive temporal autocorrelation in mast seeding dynamics (i.e. v_1 = +0.50) than in the ones considering a negative temporal autocorrelation (i.e. v_1 = -0.50), for frequencies of good years of 0.35 and 0.65, respectively (Fig. 5A and 5B).

Discussion

Temporal autocorrelation in environmental conditions is affected by the rapid and directional global change we currently face. Therefore, assessing its effects on population dynamics of species with contrasted life history strategies is crucial if we aim to accurately project their future trajectories and deploy sustainable protection and/or management strategies. In this context, we tested Tuljapurkar's theoretical prediction (1985) by empirically investigating the importance of the match between the length of the cycle period characterizing time series of resource availability and generation time in the wild. We focused on the biological event of mast seeding, a tree reproductive tactic characterized by a strong negative temporal autocorrelation, and on wild boar, a seed consumer species characterized by a short generation time close to the expected period in seeding dynamics (Schermer et al. 2020; Touzot et al. 2020). With simulations over long and short periods of time (i.e. 100,000 and 100 years), we demonstrated that wild boar stochastic population growth rate increased as temporal autocorrelation in mast seeding dynamics became more negative (Fig. 3A and 3B), and that fluctuations in population size were buffered (Fig. 5A and 5B).

Although most often overlooked, temporal autocorrelation in environmental conditions might be the rule rather than the exception (Vasseur and Yodis 2004; Park 2019). As expected on the basis of Tuljapurkar's seminal work (1985), wild boar stochastic population growth rate increased with both increasing frequencies of good years of acorn production (Fig. 3A), and when environmental noise shifted from red (i.e. positive temporal autocorrelation) to blue (i.e. negative temporal autocorrelation) (Fig. 3B). Furthermore, amplified cyclicality in mast seeding dynamics dampened the influence of changing the variance of vital rates displayed within all life stages on the stochastic population growth rate (Fig. 4C and 4D). Lastly, results from long-term simulations were in line with those obtained from short-term simulations. A dramatic decrease of the

magnitude of fluctuations over time in wild boar population size occurred in response to a shift from positive to negative temporal autocorrelation in mast seeding dynamics (Fig. 5A and 5B). Thus, temporal autocorrelation shapes population dynamics by either triggering dramatic fluctuations within a population, which leads to increase extinction rates (Lande et al. 2003), or dampening these fluctuations. The closer the time elapsed between two good years of acorn production was to generation time, the higher was the stochastic population growth rate (Fig. 3A and 3B) and the lower were the fluctuations in population size over time (Fig. 5A and 5B), regardless of the frequency of good years. Our findings provide the first empirical support for Tuljapurkar's theoretical prediction (1985): the effect of temporal autocorrelations in environmental conditions does not only depend on species' life history strategy in itself, but rather on the match between the species' generation time and the cyclicality period in environmental conditions.

A correspondence between generation time and environmental cyclicality minimizes the negative effects of environmental fluctuations on population dynamics, clearly highlighting the significance of considering both environmental patterning and life history strategy when studying population dynamics. Warm spring temperatures, known to favor pollen dispersion and thereby acorn production in oak trees (Schermer et al. 2020), are expected to become more frequent (IPCC 2018) and could lead to amplified cyclicality in the patterning of occurrence of mast seeding events (Touzot et al. 2020). We demonstrated that the highly negatively autocorrelated pattern of acorn production expected under global warming should be beneficial to wild boar population dynamics, through a closer match between wild boar generation time and cyclicality in acorn production dynamics. In addition to life-history-dependent responses of population dynamics to increased environmental cyclicality (Stott et al. 2010; Gamelon et al. 2014), our findings suggest population-

dependent responses of population dynamics for a given species. Indeed, marked among-population differences in generation times are commonly observed in the wild (e.g. 2.25 to 11.12 years in wild boar, Gamelon et al. 2021a; 3.9 to 6.8 years in roe deer (*Capreolus capreolus*), Nilsen et al. 2009; 5.0 to 8.3 years in Pyrenean chamois (*Rupicapra pyrenaica*), Crampe et al. 2006). Therefore, an autocorrelation coefficient equal to -0.50 (i.e. corresponding to a cycle period of about 2 years) that boosts our heavily hunted wild boar population may negatively influence wild boar population growth rate under weak hunting pressure with a longer generation time. We call for an intraspecific comparative analysis with populations of different generation times to provide a thorough empirical test of Tuljapurkar's theoretical prediction. Our results thus offer promising avenue of research.

In our work, we did not explicitly include density-dependent response of vital rates. This was a reasonable assumption given the intense hunting that takes place in the studied population for management purposes (Toïgo et al. 2008, Gamelon et al. 2011, 2012). More precisely, the proportion of individuals killed by hunting within each sex and body mass class was set to 0.425 in our modelling. Associated with a rich environment in terms of food resources (Veylit et al. 2020), it is unlikely that the carrying capacity was reached. However, and as suggested by the unrealistically high population sizes projected by simulation models (Fig. 5A and 5B), the assumption of no density dependence might not hold in the future, potentially translating into reduced body mass, reproductive and survival rates (see Bonenfant et al. 2009 for a review). It is noteworthy that in our modelling, breeding probabilities were lower during years of poor acorn production (Table 1). Therefore, by projecting the population trajectories under global warming, with scenarios of stronger negative autocorrelation and thus higher cyclicality in mast seeding, we can consider that, to some extent, density-dependent reproduction was accounted for. Indeed,

following a year of high acorn production, a year of low acorn production will be characterized by a combination of high population density and low food resources, leading to reduced breeding probabilities. Nevertheless, density dependence remains to be carefully explored to be integrated into population models.

To conclude, mast seeding events are not limited to oak tree species but occur widely among perennial and wind-pollinated plant species (Janzen 1976; Kelly and Sork 2002). As revealed here, the expected increase of negative temporal autocorrelation could potentially benefit fast-living consumers with generation times close to 2 years. On the other hand, species with a slow life history strategy might be negatively affected by changes in the patterning of environmental conditions. Indeed, the mismatch between the rapid cyclicality in mast seeding events and the long generation time of slow species may translate into a high temporal variation in population size, thus potentially increasing extinction risk (Lande et al. 2003). Moreover, a memory effect of past perturbations in slow-living species may generate an accumulated variation in vital rates over time (Tuljapurkar and Haridas 2006). Together with a low turn-over of individuals in populations of slow-living species associated with a reduced maximum growth rate, this might amplify the negative effects of increasing negative temporal autocorrelation in food resource availability. For instance, the slow-living edible mouse (*Glis Glis*) may skip reproduction during poor years of seed production but during good years of seed production, they invest a lot in reproduction at the expense of a lower survival the subsequent year (Ruf et al. 2006). Therefore, an increase of the negative temporal autocorrelation in seeding dynamics would negatively affect population dynamics of this species as it would increase the mismatch between generation time and the cycle period in these environmental conditions. These contrasting responses to mast

seeding events reinforce the idea that understanding the effects of temporal autocorrelation on population dynamics is of high importance.

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Statement of authorship

Laura Touzot: Conceptualization; Data analysis; Model analysis; Coding simulation; Writing – original draft; Writing – review & editing.

Samuel Venner: Conceptualization; Funding acquisition; Supervision; Writing – review & editing.

Éric Baubet: Conceptualization; Funding acquisition; Data collection; Data validation; Supervision; Writing – review & editing.

Cyril Rousset: Data collection; Data validation.

Jean-Michel Gaillard: Conceptualization; Funding acquisition; Methods development; Supervision; Writing – review & editing.

Marlène Gamelon: Conceptualization; Funding acquisition; Methods development; Supervision; Writing – review & editing.

Data and code accessibility

Data supporting the results are available online in the following permanent and publicly accessible data repository: https://doi.org/10.5061/dryad.pnvx0k6pt (Touzot et al. 2022). Code for estimating demographic parameters and running all simulations are available on GitHub: https://github.com/LauraTouzot/Environmental-cyclicality-.

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Table

Table 1. Mean vital rates ± standard deviations used in the body mass-structured matrix $\boldsymbol{A_z}$, one matrix for each environmental state (i.e. "good" vs. "poor" years of acorn production). Cells in boldface correspond to vital rates that varied both among body mass classes (small (*s*), medium (*m*), and large (*l*)) and among environmental states.

Vital rate	Biological meaning	Good acorn production	Poor acorn production
Mns	Natural mortality of small females	0.022 ± 0.002	
Mnm	Natural mortality of medium-sized females	0.080 ± 0.007	
Mnl	Natural mortality of large females	0.083 ± 0.006	
BPs	**Proportion of small reproductive females**	**0.178 ± 0.016**	**0.155 ± 0.012**
BPm	**Proportion of reproductive medium-sized females**	**0.680 ± 0.018**	**0.501 ± 0.016**
BPl	**Proportion of large reproductive females**	**0.842 ± 0.019**	**0.602 ± 0.019**
LSs	Mean number of juveniles produced by small females	3.917 ± 0.250	
LSm	Mean number of juveniles produced by medium-sized females	4.708 ± 0.105	
LSl	Mean number of juveniles produced by large females	6.095 ± 0.121	
pSS	Probability of small females remaining in the same class during the year	0.137 ± 0.014	
pSM	Probability of small females entering the medium-sized class during the year	0.284 ± 0.025	
pSL	Probability of small females entering the large class during the year	0.555 ± 0.028	
pML	Probability of medium-sized females entering the large class during the year	0.490 ± 0.036	
h	Proportion of individuals killed by hunting within each sex and body mass class	0.425	
Spn	Postnatal survival	0.750	
piOs	Probability of juvenile females entering the small class during the year	0.600	

Figure legends

Figure 1. Schematic representation of colored environmental noise, also referred to as temporal autocorrelation. Temporal autocorrelation is characterized by its magnitude (from 0 to 1) and direction (positive vs. negative). The interplay between both components leads to an autocorrelation coefficient v_1 that ranges from -1.0 (i.e. blue noise) to +1.0 (i.e. red noise) and ultimately to dynamics of environmental conditions that are either cyclical (left panel) or composed of a single type of observations over long periods of time (right panel). Note also that similar frequencies of good and poor environmental conditions have been considered here (i.e. $f_{good} = f_{poor} = 0.5$).

Figure 2. Schedule of simulations conducted to assess the effects of the frequency of years of good acorn production (f) and of the magnitude and direction of temporal autocorrelations (v_1) in acorn production on the wild boar stochastic population growth rate ($\log(\lambda_s)$) and population size (n_t), respectively.

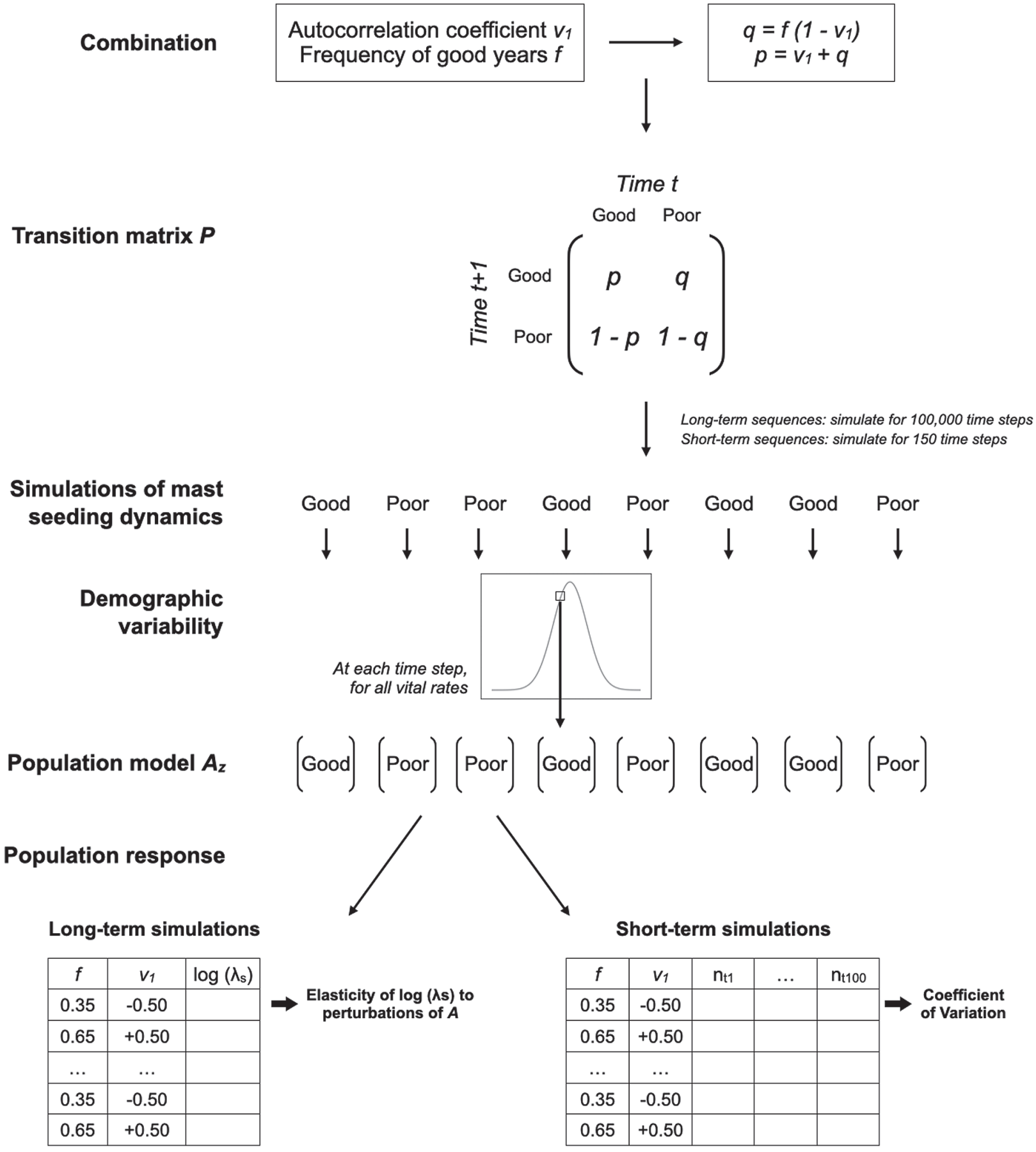
Figure 3. A) Stochastic population growth rate ($\log(\lambda_s)$ ± 95% confidence interval (CI)) obtained for each combination of long-term frequency of years of good acorn production (f) and temporal autocorrelation (v_1) incorporated into the simulations and **B)** proportional decrease in stochastic population growth (± 95% CI) observed between the two extreme values of temporal autocorrelation considered (i.e. from -0.50 to +0.50). Frequencies of good years from the lowest (0.35) to the highest (0.65) are represented by a green gradient, from the lightest to the darkest, respectively.

Figure 4. Effect of a change in the mean (A) or variance (B) of each matrix entry ***A***(i,j) on the stochastic population growth rate, for contrasting temporal autocorrelation and long-term frequency of years of good acorn production. Negative (v_1 = -0.50) and positive (v_1 = 0.50) temporal autocorrelations are represented in blue and red, respectively. For each type of temporal autocorrelation, low (f = 0.35) and high frequencies (f = 0.65) are represented in light and dark, respectively. Capital letters S, M, and L correspond to Small, Medium, and Large females, respectively.

Figure 5. Projected wild boar population size expressed as median (solid lines) ± 95% confidence interval (CI) (dotted lines) according to the frequency of years of good acorn production (f) and sign and magnitude of temporal autocorrelation (v_1) (**A and B**). Cumulative frequency distribution of the coefficients of variation in population size obtained from the 500 scenarios simulated are presented in the top left corner of each panel. In panels A and B are represented the trajectories obtained for frequencies of 0.35 and 0.65, respectively. Trajectories obtained for temporal autocorrelations of -0.50 and +0.50 are represented in blue and red, respectively.

Figure 1

Figure 2



f	v_1	log (λ_s)
0.35	-0.50	
0.65	+0.50	
…	…	
0.35	-0.50	
0.65	+0.50	

f	v_1	n_{t1}	…	n_{t100}
0.35	-0.50			
0.65	+0.50			
…	…			
0.35	-0.50			
0.65	+0.50			

Figure 3

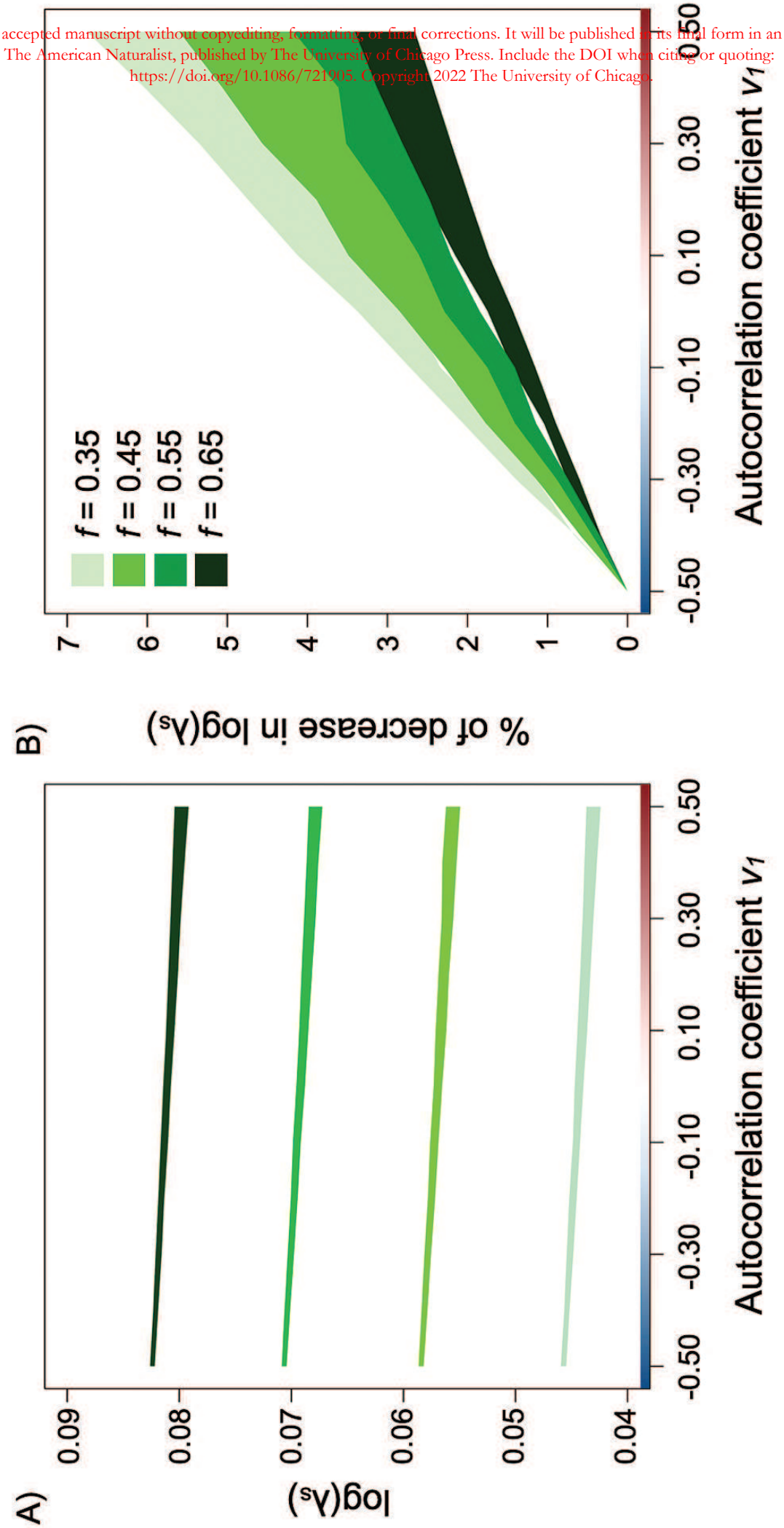
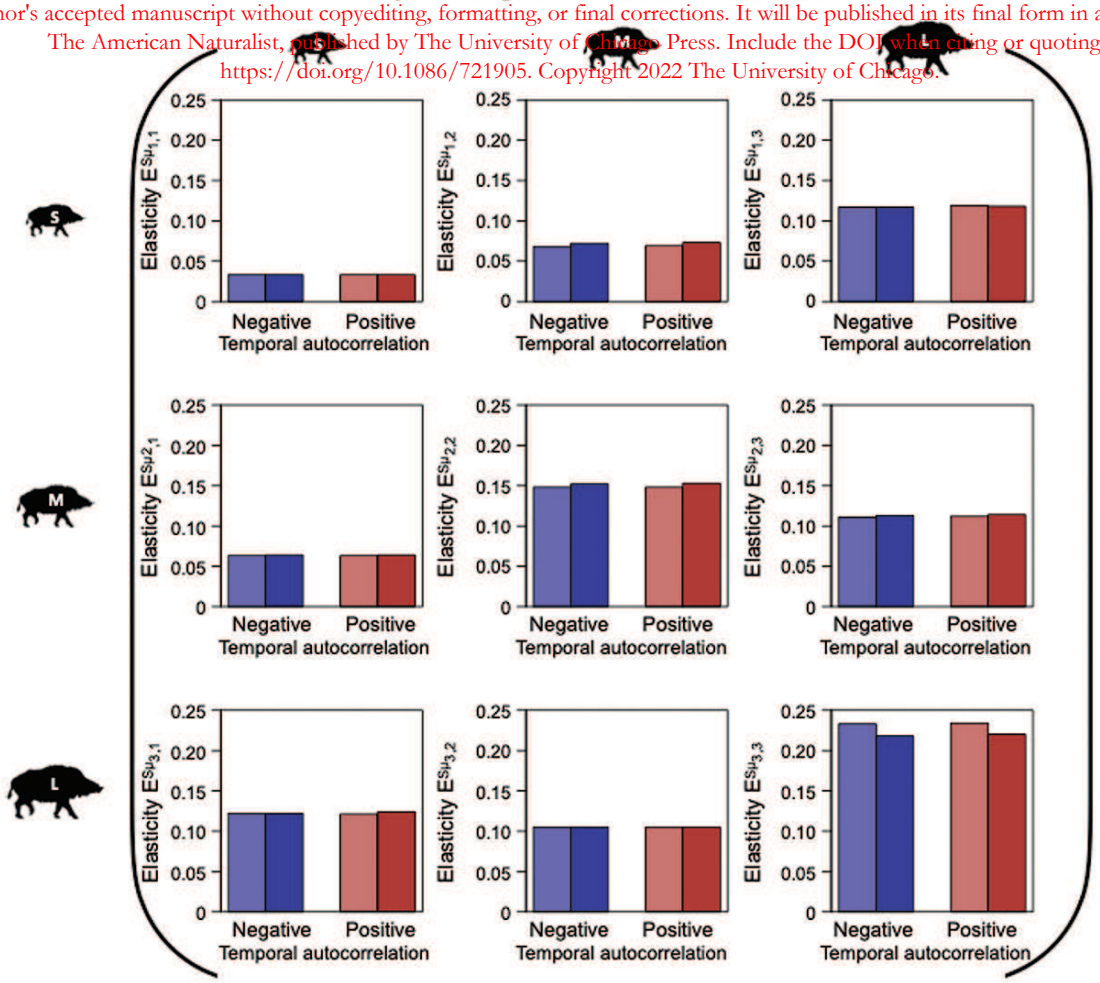


Figure 4



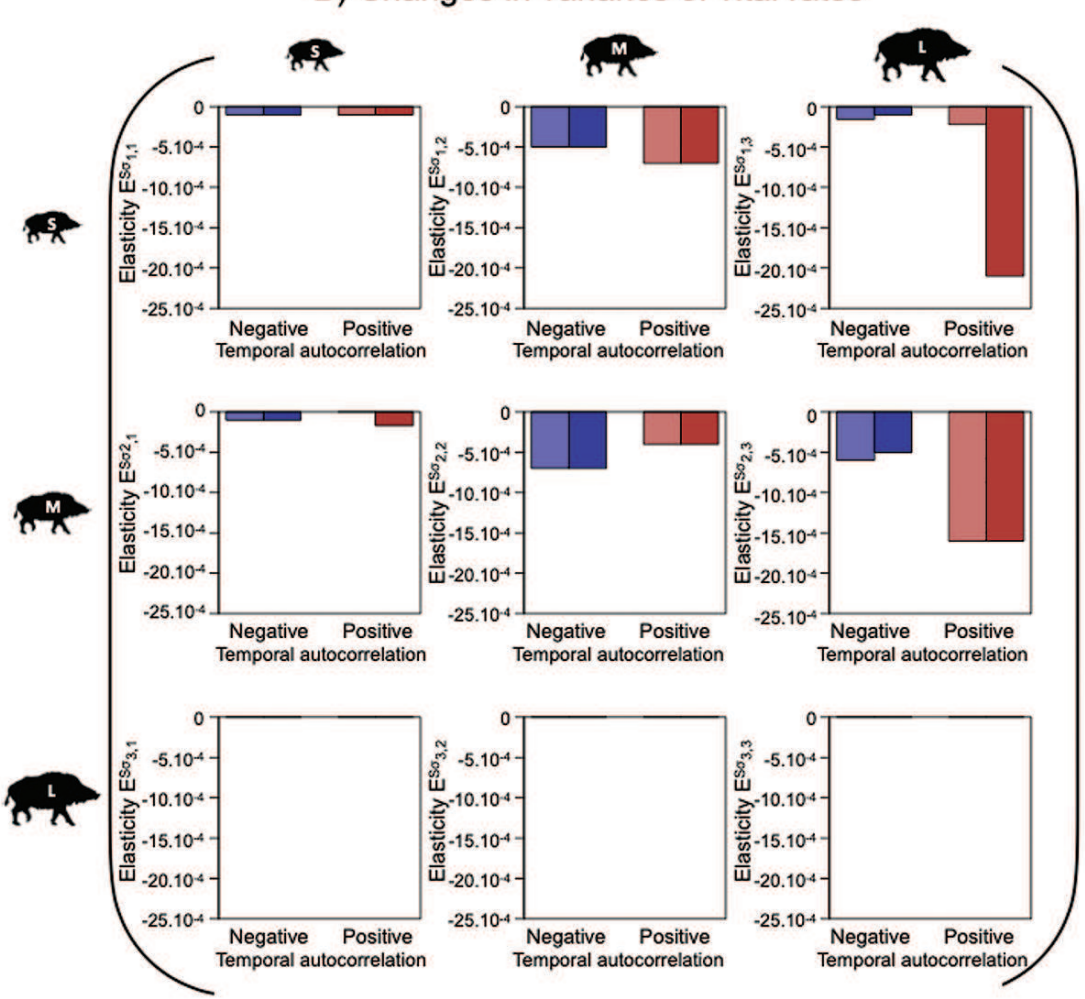
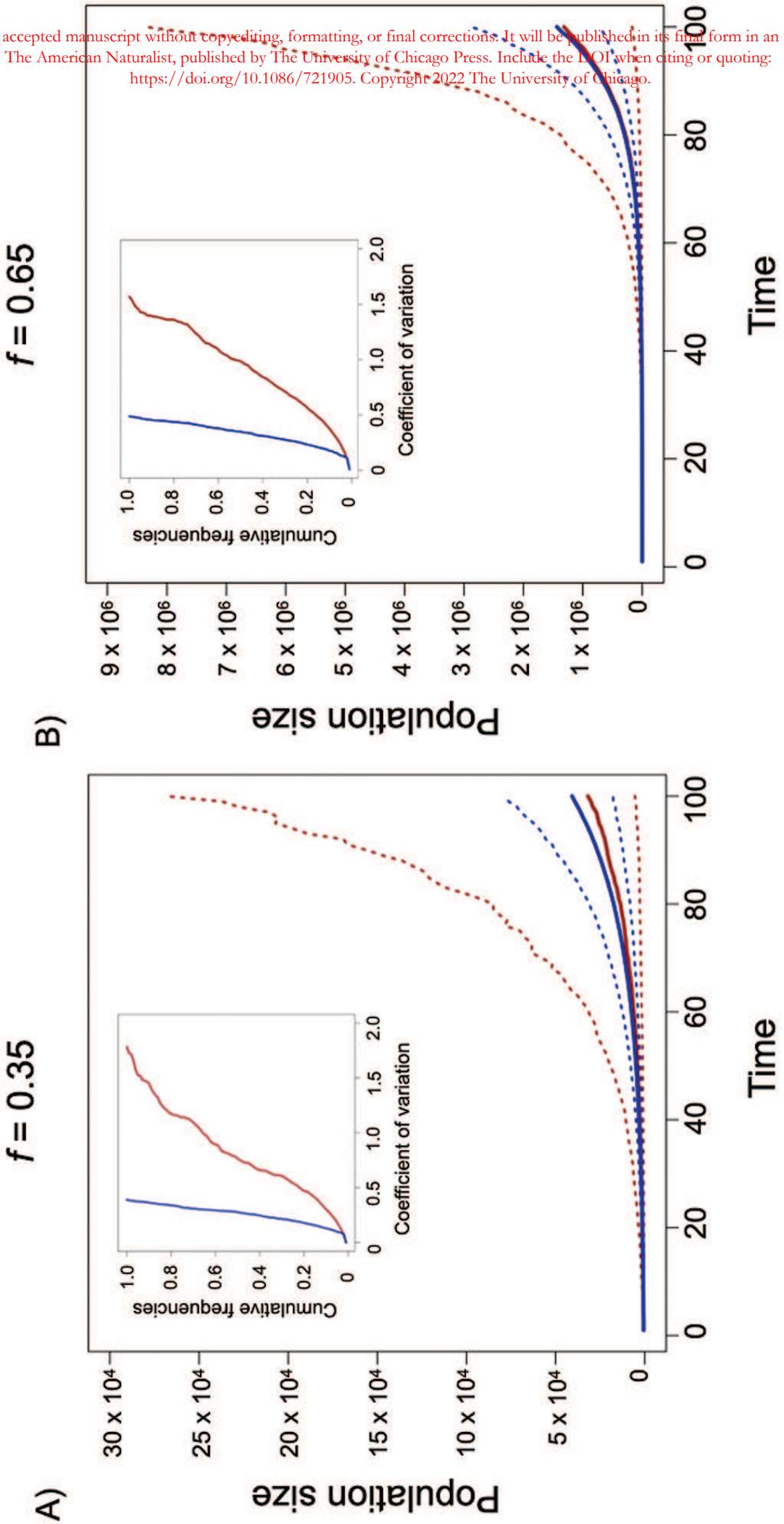


Figure 5



Amplified cyclicality in mast seeding dynamics positively influences the dynamics of a seed consumer species

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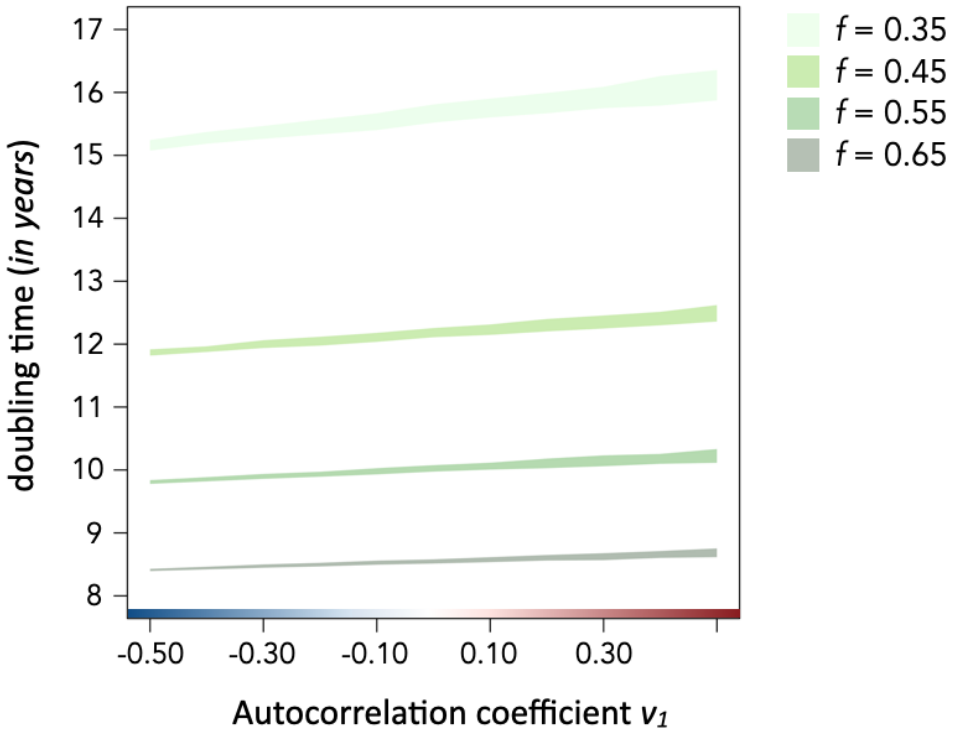

Figure S1 Doubling team ± 95% confidence interval (CI)) obtained for each combination of long-term frequency of years of good acorn production (f) and temporal autocorrelation (v_1) incorporated into the simulations.