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The hidden side of the Allee effect: correlated demographic traits and extinction risk in experimental populations

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INTRODUCTION

Allee effects are a small population phenomenon in which individual or population performance increases with population density (Dennis 1989; Courchamp et al. 2008). As the presence of an Allee effect is often considered a major risk factor for extinction (Lande 1988; Boukal and Berec 2002), Allee effects are commonly included in population models for the management of small populations, either for conservation or management purposes (Tobin et al. 2011; Molnár et al. 2014; Hutchings 2015; Wittmann et al. 2018). One of the most common heuristic population model accounting for an Allee effect is a modified version of the logistic model (Lewis and Kareiva 1993; Amarasekare 1998; Boukal and Berec 2002, with analogous models existing in discrete time, Liebhold and Bascompte 2003; Tobin et al. 2007) as follows:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \left(\frac{x - A}{K}\right)$$

where A is the Allee threshold (weak Allee effect for $A \leq 0$; strong Allee effect for $A > 0$), r is the maximum per capita population growth rate in absence of the Allee effect, and K the carrying capacity.

However, this modified structure impacts several key population parameters, with potential significant consequences beyond the mere presence of positive density-dependence. For instance, when theoretical parameters r and K are held constant, the maximum per capita growth rate is lower in populations subject to an Allee effect than in populations affected by negative density-dependence only (Courchamp et al. 2008; Drake and Kramer 2011). A direct consequence of this lower growth rate is that the establishment or growth phase of an initially

small population, in which the population is most vulnerable to stochastic influences, lasts longer in presence of an Allee effect (Veit and Lewis 1996; Dennis 2002; Drake 2004; Sinclair and Arnott 2016). Both these parameters (maximum per capita growth rate and duration of establishment phase) have been shown theoretically and empirically to influence extinction risk (Lande 1993; Liebhold and Bascompte 2003; Drake et al. 2011; Cassey et al. 2014) and could have amplified the impact of Allee effects in population models.

It is not clear at this point whether this indirect impact of Allee effects on population performance is a theoretical artifact related to the non-independence between demographic parameters in most common population models, or a significant ecological property of natural populations. Indeed, as an Allee effect reveals specific processes internal to the population, it is likely to be correlated with other components of population dynamics, thus affecting the probability of population extinction beyond its direct effect on density dependence.

A major difficulty in addressing this issue is to find independent populations subject to an Allee effect or not, whose life histories are close enough to allow quantitative comparisons of demographic parameters. In this study, we analyzed the dynamics of 20 populations parasitoid wasps of the genus *Trichogramma* raised under similar conditions, and detected the presence of an Allee effect in 3 of these populations. This privileged experimental system allowed us to investigate how components of population dynamics correlate with the presence of an Allee effect, and their consequence on extinction probability.

METHODS

Biological model

We used parasitoid wasps of the genus *Trichogramma* as biological models. Our study populations were provided by the Biological Resource Center EP-Coll (INRA, France), specialized in egg parasitoids. 30 populations were initially chosen from a set of 70 populations collected in the field 2015 to evaluate the diversity of *Trichogramma* in France (D. Muru, pers. com). Detailed information on each population is available in Supplementary Material (Table S1). A “population” was defined as individuals sampled on the same plant in a given locality, so that several populations could have been collected from the same locality. At the time of the experiment, genetic information about the different populations was not available, so we selected populations to form a representative subset of the geographic diversity from the

2015 field sampling. Seven species were included in the 30 selected populations: *T. brassicae* (2 populations), *T. cacoeciae* (16), *T. cordubensis* (3), *T. euproctidis* (2), *T. evanescens* (2), *T. principium* (1), *T. semblidis* (4). Once the genetic information was available, we removed from the analysis the populations from the same species sampled in the same locality to avoid pseudo-replication. We also removed the data from one *T. cordubensis* population, for which all replicates went extinct at the first generation. The final dataset included 20 populations: *T. brassicae* (1 population), *T. cacoeciae* (10), *T. cordubensis* (2), *T. euproctidis* (1), *T. evanescens* (2), *T. principium* (1), *T. semblidis* (3).

Monitoring of population dynamics

Trichogramma are minute solitary parasitoids of Lepidopteran eggs that can be reared in small volumes. Experimental population units were housed in plastic tubes (diameter 50 mm, length 100 mm). Food for adults was provided ad libitum as drops of honey placed on the tube walls. Hosts for reproduction were provided as 3 mm-diameter patches of *Ephestia kuehniella* eggs glued on paper strips (10 egg patches at each generation; average number of eggs on a patch and 95% confidence interval: 458 [445–471]). Eggs of *E. kuehniella* were irradiated earlier, which prevented host development while allowing parasitoid development. For this experiment, temperature and light conditions were set on a cycle of 16 h daylight (22 °C)/8 h dark (20 °C) with constant 70% humidity. Under these conditions, generation time was 14 days for all populations.

Initial populations were founded by introducing between 10 and 30 parasitized eggs into a tube (8 replicates for each population with 10-12-14-16-18-20-25-30 parasitized eggs, randomized over 6 experimental blocks). At emergence, fresh host eggs were introduced in the tubes and exposed 48h to parasitism, then put aside for parasitoid development until the emergence of the next generation. Population size at the next generation was estimated by counting the total number of parasitized eggs before emergence. Parasitized eggs turn black when the parasitoid reaches the nymphal stage and the number of black eggs directly reflects adult population size at emergence. At the beginning of emergence, fresh host patches were introduced in the tubes and similarly exposed during 48 h to obtain the next parasitoid generation. Parasitoid population dynamics were monitored during three generations after introduction between January and March 2016. Time series of population dynamics are provided as Supplementary Material (Figure S1).

Detection of Allee effects

The presence of an Allee effect is indicated by a positive correlation between population size and per capita growth rate. However, this positive correlation may be present for small population sizes only and sometimes difficult to evidence due to strong stochastic effects and limited amount of data. We applied two different methods to try and detect this correlation: (i) linear regression on a subsample of small populations sizes and (ii) non-linear fit over the whole range of population sizes. In both cases, we analyzed the relationship between population size and the "modified per capita growth rate" $\lambda_{m(i,t)}$ calculated at each generation t and for each experimental replicate i as follows:

$$\lambda_{m(i,t)} = \ln\left(\frac{N_{i,t+1}}{N_{i,t}} + 1\right)$$

For the regression approach, we selected a sub-sample of population sizes $N_{i,t}$ either inferior to 50 or to 100 individuals, and we fitted a non-parametric Spearman correlation between population size and $\lambda_{m(i,t)}$. For the non-linear approach, we fitted a smooth (thin-plate regression spline) relationship between population size and $\lambda_{m(i,t)}$ using general additive models (package 'mgcv', Wood 2018) in R (R Core Team 2017). We allowed different values (3, 5, 8 or 10) for the dimension parameter k , which gives the maximum possible degrees of freedom allowed for the smooth term.

We acknowledged the presence of an Allee effect for the population if the fitted function was non-monotonic with a maximum λ_m for an intermediate value of population size.

Depending on the method used, different populations were identified as subject to an Allee effect. In what follows, we focused on the non-linear fit with parameter $k=8$, which managed to intersect all of the populations identified with the other methods and thus seemed the most conservative approach for the identification of Allee effects.

Estimation of demographic parameters and statistical analyses

Population dynamics were characterized in each replicate by the maximum modified per capita growth rate (λ_{max}), the maximum population size (N_{max}) and the mean population size across generations for non-extinct populations (N_{mean}). These three variables followed Normal distributions and were analyzed using linear mixed models with the presence of an

Allee effect as a fixed factor, and population as a random effect. Extinction probability followed a binomial distribution, and was analyzed using generalized linear mixed models with the presence of an Allee effect as a fixed factor, and population as a random effect. Both linear mixed models and generalized linear mixed models were fitted using the R package 'glmmADMB' (Skaug et al. 2018). Models including the presence of an Allee effect were compared with null models including only the random population effect using AIC ($\Delta AIC = AIC_{\text{null model}} - AIC_{\text{Allee model}}$), and if relevant (i.e. $\Delta AIC > 2$), the impact of an Allee effect was interpreted using the p-value of the fixed factor.

We quantified the stability of population dynamics using a repeatability index RI. The RI was calculated for each population as the mean of the sum of squares between the time series of each pair of replicates (excluding the founding generation where population size was assigned to each replicate).

$$RI = \frac{1}{C_8^2} \sum_{i,j} \sum_{t=1}^3 (n_{i,t} - n_{j,t})^2$$

The RI did not follow any classical distribution, and it was compared among Allee and non-Allee populations using a Kruskal-Wallis test.

RESULTS

Out of the 20 populations analyzed, 3 displayed an Allee effect (1 population from *T. cacoeciae*, 1 population from *T. principium*, 1 population from *T. semblidis*, Figure 1). Population dynamics were found to be markedly different between Allee and non-Allee populations (Figure 2). Allee populations were characterized by lower maximum modified per capita growth rate ($\Delta AIC = 5.4$, $p = 2.6 \times 10^{-3}$), lower maximum population size ($\Delta AIC = 2.2$, $p = 0.028$), lower average population size ($\Delta AIC = 4.6$, $p = 5.0 \times 10^{-3}$), and higher extinction rate ($\Delta AIC = 9.2$, $p = 8.4 \times 10^{-4}$). Their trajectories also tended to be less repeatable ($p = 0.081$) than for non-Allee populations.

DISCUSSION

Our analysis demonstrated the presence of an Allee effect in some, but not all, *Trichogramma* populations raised in laboratory conditions. This finding further confirms that Allee effects can

operate in small volumes and affect population persistence even in favourable, controlled conditions (Gertzen et al. 2011; Kaul et al. 2016). Unlike most classical experimental microcosm systems (e.g., *Tribolium*, *Daphnia*, *Tetrahymena*), our collection of *Trichogramma* populations allows us to compare populations with similar life-histories and raised under the same conditions, in order to single out the impact of the presence or absence of an Allee effect. We found that *Trichogramma* populations where an Allee effect was detected were characterized by qualitatively different dynamics from populations with no Allee effect. Interestingly, parameters related to equilibrium dynamics (i.e., carrying capacity and maximum population size) tended to be more similar than parameters related to transitory dynamics (i.e., maximum per capita growth rate and average population size, Figure 2). This confirms that the influence of the Allee effect on population dynamics is mostly restricted to small densities, and that the ecological mechanisms implicated in the Allee effect do not affect the demographic strategy once equilibrium is reached.

In our case, the mechanism responsible for the presence of positive density-dependence in some populations only has not been identified. Of the 3 populations subject to an Allee effect, the population of *T. cacoeciae* is strictly parthenogenous, so mate limitation is unlikely to be the major factor impairing population performance at small density, although it can still play a role in the two other populations. Alternatively, strong demographic stochasticity could act as a generic mechanism inducing positive density-dependence, even in parthenogenous populations. Classical ecology theory predicts that, if individual variance in reproductive success is high (e.g., because of random differences in fecundity and survival), the realized per capita growth rate will be reduced (May 1973; Melbourne 2012), especially at low density (Lande 1993), which can generate an Allee-like effect (Lande 1998). However, such a purely stochastic process has been argued to be qualitatively different from a deterministic Allee effect, the latter being characterized by an inflection point in the relationship between initial population size and extinction probability (Dennis 2002). Yet, the presence of such an inflection point is a characteristic of strong Allee effects only, while the detection of positive density-dependence in the per capita growth rate can be considered as a generic evidence for the presence of an Allee effect (Johnson et al. 2006; Kramer et al. 2009; Gregory et al. 2010), including stochastic Allee-like effects that are more similar to weak Allee effects.

Although the weak or strong nature of an Allee effect induces major qualitative differences in dynamics in theoretical models related to the existence of an unstable equilibrium in the case of a strong Allee effect (Dennis 19089; Lewis and Kareiva 1993; Wang and Kot 2001), the same ecological mechanisms are expected to be involved in both cases (e.g., mate limitation, cooperation, predation, Courchamp et al. 2008). In practice, the distinction between weak and strong Allee effect in empirical data thus relies only on the quantitative estimation of the per capita growth rate at small density, where stochastic variance is the highest and therefore the estimation is least precise (Kramer et al. 2009). In our three Allee populations, two have an estimated negative growth rate at low density, all three confidence intervals are large enough to include both positive (i.e., weak Allee effect) and negative (i.e., strong Allee effect) values. Furthermore, estimations of Allee effects in nature have demonstrated that the intensity of the Allee effect can vary geographically (Tobin et al. 2007), and results from stochastic models have demonstrated that weak Allee effects can be amplified by stochasticity (demographic or environmental) so as to induce a lower unstable equilibrium, similar to an Allee threshold (Roth and Schreiber 2014; Dennis et al. 2015). This converging evidence suggests that the dichotomous distinction of weak and strong Allee effect, though essential in deterministic theoretical approaches, might be less relevant in stochastic modelling or in nature where the “strength” or “intensity” of an Allee effect could be quantified continuously.

In all cases, regardless of the intensity of an Allee effect, the demographic parameters associated with its presence have direct consequences on short-term extinction risk. Indeed, low per capita growth rate and low population size interact to maintain the population in a defavourable demographic zone, where it is most vulnerable to extinction through the influence of demographic stochasticity (Dennis et al. 2015). This increased stochastic regime is noticeable in our data, as populations subject to an Allee effect show greater variability among replicates, and a higher extinction rate. In addition, this prolonged demographic bottleneck in presence of an Allee effect might increase genetic drift and inbreeding, so that even populations that manage to grow enough to reach carrying capacity will suffer from higher long-term extinction risk (Fauvergue et al. 2012). This special case of genetic extinction debt was previously reported in laboratory populations of a different species of *Trichogramma* (Vercken et al. 2013).

These results provide the first empirical demonstration of a correlation between the presence of positive density-dependence and impaired demographic performance during establishment phase. If the presence of an Allee effect is correlated with other demographic parameters, in particular the maximum per capita growth rate, then it remains a major risk factor for population extinction, even in the case of a weak Allee effect, or if the population introduced is superior to the theoretical Allee threshold for a strong Allee effect. The non-independence between these demographic parameters is thus likely to be of critical importance for the prediction of the establishment success of introduced species.

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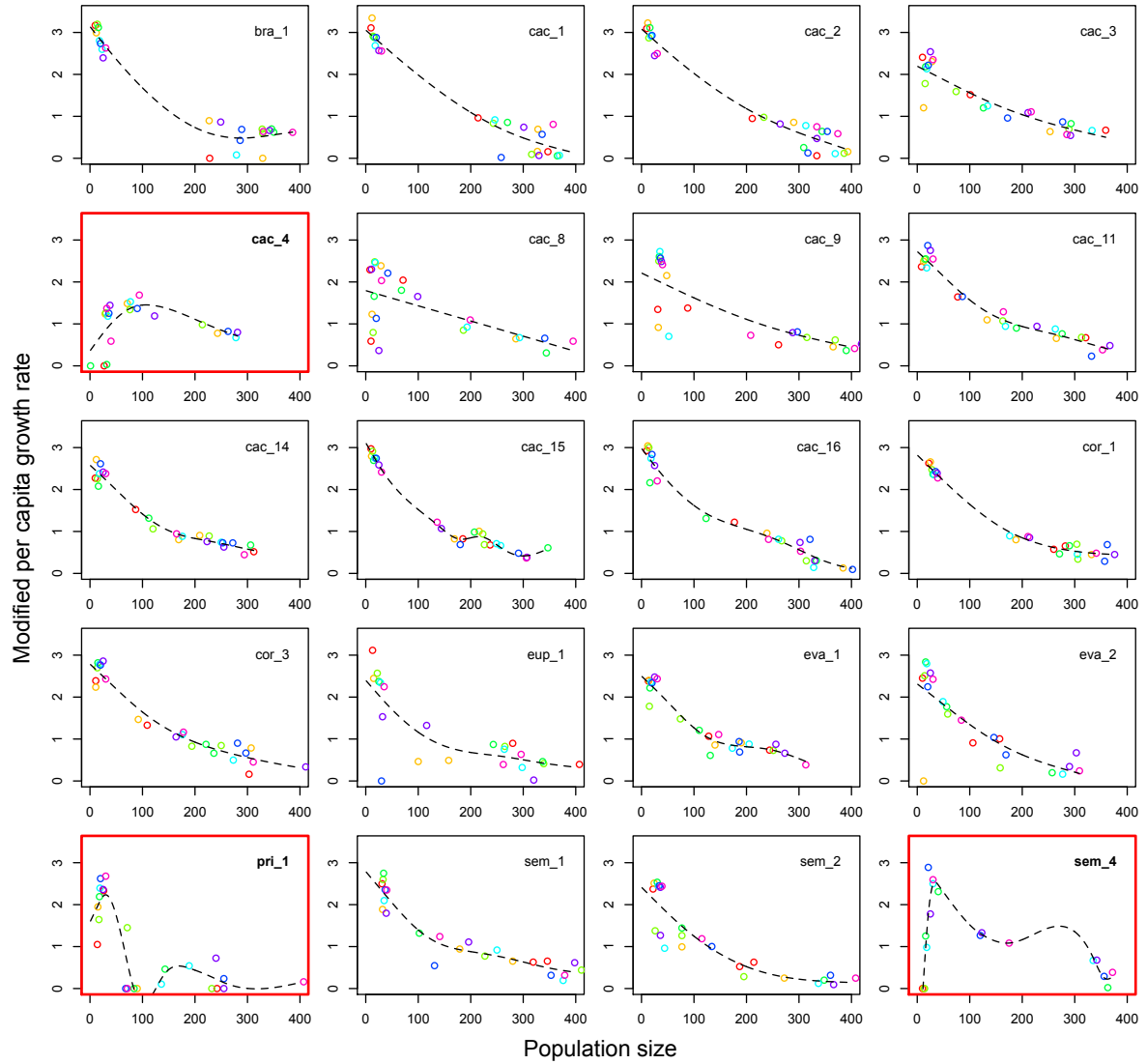


Figure 1: Raw data and GAM fits ($k=8$) for the relationship between population size and modified per capita growth rate λ_m . Red boxes: populations characterized by an Allee effect.

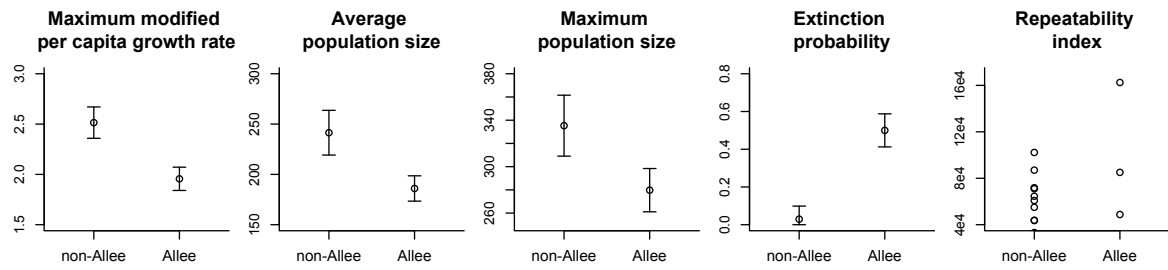


Figure 2: Comparison of demographic parameters between populations with or without an Allee effect. All graphs represent mean \pm 2 SE, except the repeatability index for which raw data are plotted because of the low number of replicates.

SUPPLEMENTARY MATERIAL

Pop_ID	Trichogramma species	Reproduction	Sampling date	Sampling location	Latitude	Longitude	Allee effect					
							Spearman N<50	Spearman N<100	GAM k=3	GAM k=5	GAM k=8	GAM k=10
bra_1	brassicae	sexual	13/07/2015	Aix en Provence	43.5917	5.4253						
<i>bra_2</i>	<i>brassicae</i>	<i>sexual</i>	<i>13/07/2015</i>	<i>Aix en Provence</i>	<i>43.5917</i>	<i>5.4253</i>						
cac_1	cacoeciae	asexual	20/05/2015	Banyuls sur mer	42.453894	3.087794						
cac_2	cacoeciae	asexual	21/06/2015	Grasse	43.660153	6.926492						
cac_3	cacoeciae	asexual	20/08/2015	Andon	43.77941	6.84057						
cac_4	cacoeciae	asexual	27/07/2015	Aime	45.548561	6.629682		X	X	X	X	X
<i>cac_5</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>27/07/2015</i>	<i>Aime</i>	<i>45.548561</i>	<i>6.629682</i>	X	X		X	X	X
<i>cac_6</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>27/07/2015</i>	<i>Aime</i>	<i>45.548561</i>	<i>6.629682</i>						
<i>cac_7</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>27/07/2015</i>	<i>Aime</i>	<i>45.548561</i>	<i>6.629682</i>			X	X	X	X
cac_8	cacoeciae	asexual	27/07/2015	Tours sur Meymont	45.670778	3.577523						
cac_9	cacoeciae	asexual	13/08/2015	Courmes	45.832313	4.976422						
<i>cac_10</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>30/04/2015</i>	<i>Beynost</i>	<i>45.832313</i>	<i>4.976422</i>						
cac_11	cacoeciae	asexual	22/06/2015	Rancé	45.951937	4.883082						
<i>cac_12</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>22/06/2015</i>	<i>Rancé</i>	<i>45.951937</i>	<i>4.883082</i>						
<i>cac_13</i>	<i>cacoeciae</i>	<i>asexual</i>	<i>30/04/2015</i>	<i>Rancé</i>	<i>45.951937</i>	<i>4.883082</i>						
cac_14	cacoeciae	asexual	23/04/2015	Joué les Tours	47.351861	0.6613099						
cac_15	cacoeciae	asexual	14/06/2015	Dannemois	48.45733	2.486348						
cac_16	cacoeciae	asexual	14/06/2015	Moret sur Loing	48.35066	2.809645						
cor_1	cordubensis	asexual	20/05/2015	Banyuls sur mer	42.453894	3.087794						
<i>cor_2</i>	<i>cordubensis</i>	<i>asexual</i>	<i>09/07/2015</i>	<i>La Pugère</i>	<i>43.74282</i>	<i>5.12722</i>						
cor_3	cordubensis	asexual	20/08/2015	La Pugère	43.7471	5.12456						
eup_1	euproctidis	sexual	13/07/2015	Aix en Provence	43.5917	5.4253						
<i>eup_2</i>	<i>euproctidis</i>	<i>sexual</i>	<i>13/07/2015</i>	<i>Aix en Provence</i>	<i>43.5917</i>	<i>5.4253</i>						
eva_1	evanescens	sexual	13/08/2015	Castellaras	43.78393	6.83258						
<i>eva_2</i>	<i>evanescens</i>	<i>sexual</i>	<i>20/07/2015</i>	<i>Estrablin</i>	<i>45.516941</i>	<i>4.962637</i>						
pri_1	principium	sexual	13/08/2015	Gréolières	43.82627	6.90479	X				X	X
sem_1	semblidis	sexual	13/07/2015	Aix en Provence	43.5917	5.4253						
sem_2	semblidis	sexual	22/06/2015	Rancé	45.951937	4.883082						
<i>sem_3</i>	<i>semblidis</i>	<i>sexual</i>	<i>22/06/2015</i>	<i>Rancé</i>	<i>45.951937</i>	<i>4.883082</i>						
sem_4	semblidis	sexual	14/06/2015	Dannemois	48.45733	2.486348	X	X			X	X

Table S1 : Sampling information and characterization of Allee effects for the 30 populations initially included in the study. In grey : extinct population. In bold: populations retained for the final analysis, after removing geographical duplicates.

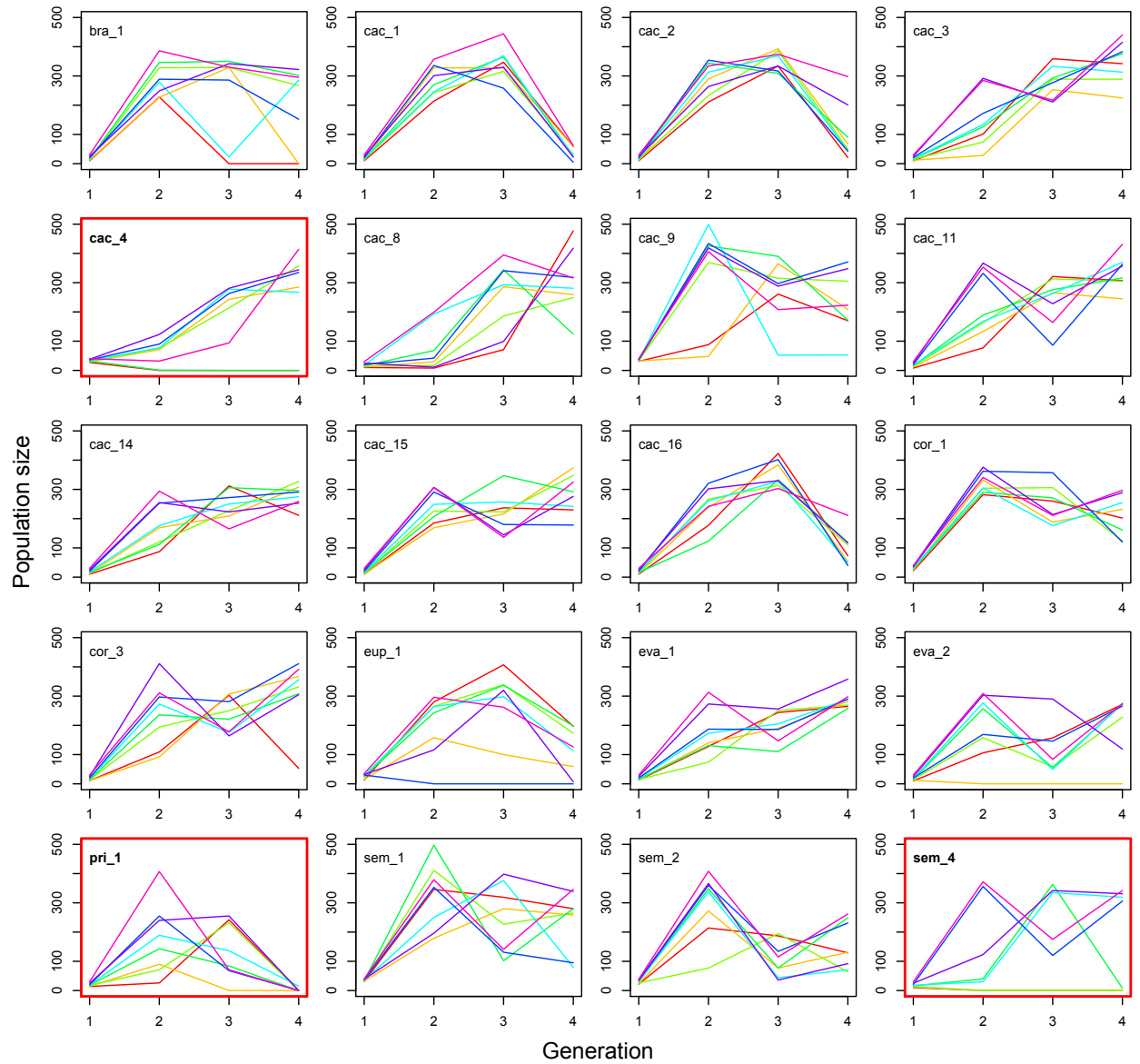


Figure S1: Time series of the 8 replicates for each of the 20 populations retained in the final analysis. Red boxes: populations characterized with an Allee effect.