Math for Jon and Lauren for seasonality and synchrony paper

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2021 09 21

1 The model

We consider a 2-patch model using $i = 1, 2$ to index the patches, which are considered identical. The model is

$$N_i(t) = (1 - d)N_1(t - 1)f[N_1(t - 1), \epsilon_{B,1}(t)]s[N_1(t - 1)f[N_1(t - 1), \epsilon_{B,1}(t)], \epsilon_{W,1}(t)] \tag{1}$$
$$+ dN_2(t - 1)f[N_2(t - 1), \epsilon_{B,2}(t)]s[N_2(t - 1)f[N_2(t - 1), \epsilon_{B,2}(t)], \epsilon_{W,2}(t)] \tag{2}$$
$$N_2(t) = (1 - d)N_2(t - 1)f[N_2(t - 1), \epsilon_{B,2}(t)]s[N_2(t - 1)f[N_2(t - 1), \epsilon_{B,2}(t)], \epsilon_{W,2}(t)] \tag{3}$$
$$+ dN_1(t - 1)f[N_1(t - 1), \epsilon_{B,1}(t)]s[N_1(t - 1)f[N_1(t - 1), \epsilon_{B,1}(t)], \epsilon_{W,1}(t)], \tag{4}$$

where $N_i(t)$ is population density in patch i at time t, $0 \leq d < 0.5$ is a dispersal parameter, the function $f(N, \epsilon_B)$ is a breeding season multiplier, the function $s(B, \epsilon_W)$ is a winter survival rate, $\epsilon_{B,i}(t)$ is the environment during the breeding season in patch i at time t, and $\epsilon_{W,i}(t)$ is the environment during the winter in patch i at time t. We assume $f > 0$ and $\frac{\partial f}{\partial N} < 0$, so that more pre-breeding density is always bad for per-capita population growth during the breeding season. We do not assume $f > 1$, so net death during the breeding season may occur. We assume $\frac{\partial f}{\partial \epsilon_B} > 0$, so that higher values of the breeding-season environmental variable are good for breeding and breeding-season survival. We assume $0 < s < 1$, and $\frac{\partial s}{\partial B} < 0$, so that more pre-winter, post-breeding-season individuals are always bad for winter survival. We assume $\frac{\partial s}{\partial \epsilon_W} > 0$, so that higher values of the winter environmental variable are always good for winter survival. We adopted the convention that larger values of environmental variables are always "good" for the population. This convention is arbitrary, but is also adopted without loss of generality, since one could always replace an environmental variable for which larger values are "bad" for the population with its negative. For simplicity, we assume the four-dimensional random variables $(\epsilon_{B,1}(t), \epsilon_{B,2}(t), \epsilon_{W,1}(t), \epsilon_{W,2}(t))$ are independent and identically distributed (iid) across time (so the t argument can usually be dropped); and that $(\epsilon_{B,1}, \epsilon_{W,1})$ and $(\epsilon_{B,2}, \epsilon_{W,2})$ are identically distributed and $(\epsilon_{B,1}, \epsilon_{W,2})$ and $(\epsilon_{B,2}, \epsilon_{W,1})$ are identically distributed. The first of these assumptions is a kind of stationarity and white-noise assumption, and the second and third assumptions help make our model spatially homogeneous.

2 Linearization

For this section, we assume $d = 0$, for simplicity. We also assume the one-patch, deterministic version of the model has a positive stable equilibrium, N^*, i.e.,

$$N^* = N^* f[N^*, \bar{\epsilon}_B]s[N^* f[N^*, \bar{\epsilon}_B], \bar{\epsilon}_W]. \tag{5}$$

Here, an overline denotes expected value of a random variable. The expected values $\bar{\epsilon}_B$ and $\bar{\epsilon}_W$ need no patch index because of assumptions made about identically distributed environments across patches.

We let $B^* = N^* f[N^*, \bar{\epsilon}_B]$, so that $N^* = B^* s[B^*, \bar{\epsilon}_W]$. This is the post-breeding, pre-winter equilibrium density of the one-patch deterministic model. We have $\frac{B^*}{N^*} = f[N^*, \bar{\epsilon}_B]$, $\frac{N^*}{B^*} = s[B^*, \bar{\epsilon}_W]$ and $f[N^*, \bar{\epsilon}_B] = \frac{1}{s[B^*, \bar{\epsilon}_W]}$. Thus, at average environmental values and at equilibrium, fecundity and survival balance each other out, as expected.

We now linearize the no-dispersal model at the equilibrium. Defining

$$g(N, \epsilon_B, \epsilon_W) = N f[N, \epsilon_B] s[N f[N, \epsilon_B], \epsilon_W], \tag{6}$$
$$n_i(t) = N_i(t) - N^*, \tag{7}$$
$$e_{B,i}(t) = \epsilon_{B,i}(t) - \bar{\epsilon}_B, \tag{8}$$
$$e_{W,i}(t) = \epsilon_{W,i}(t) - \bar{\epsilon}_W, \tag{9}$$

linearizing gives

$$n_i(t) \approx P_A n_i(t-1) + P_B e_{B,i}(t) + P_W e_{W,i}(t) \tag{10}$$

for $i = 1, 2$, where

$$P_A = \left[\frac{\partial g}{\partial N} \Big|_{(N^*, \bar{\epsilon}_B, \bar{\epsilon}_W)} \right] \tag{11}$$

$$P_B = \left[\frac{\partial g}{\partial \epsilon_B} \Big|_{(N^*, \bar{\epsilon}_B, \bar{\epsilon}_W)} \right] \tag{12}$$

$$P_W = \left[\frac{\partial g}{\partial \epsilon_W} \Big|_{(N^*, \bar{\epsilon}_B, \bar{\epsilon}_W)} \right]. \tag{13}$$

This is an autoregressive moving average-type model, which can be subjected to a wide range of mathematical analyses. The stability assumption, above, is the same as assuming $|P_A| < 1$. It is straightforward to show

$$P_A = P_{A,B} P_{A,W}, \tag{14}$$

where

$$P_{A,B} = \frac{\partial}{\partial N} [N f(N, \epsilon_B)|_{(N^*, \bar{\epsilon}_B)} \tag{15}$$

is the marginal benefit, at equilibrium and at average environment, to the post-breeding population of a single additional pre-breeding individual, and

$$P_{A,W} = \frac{\partial}{\partial B} [B s(B, \epsilon_W)|_{(B^*, \bar{\epsilon}_W)} \tag{16}$$

is the marginal benefit, at equilibrium and at average environment, to the post-winter population of a single additional pre-winter individual. The condition $|P_A| < 1$ is then equivalent to the condition $|P_{A,B}| \times |P_{A,W}| < 1$.

3   Analysis of the linearized model

To compute synchrony of the model (10), we compute $\text{cor}(n_i, n_j)$ for $i \neq j$ by computing $\text{cov}(n_i, n_j)$, $\text{var}(n_i)$ and $\text{var}(n_j)$. We have

$$\text{cov}(n_i(t), n_j(t)) = \text{cov}(P_A n_i(t-1) + P_B e_{B,i}(t) + P_W e_{W,i}(t), P_A n_j(t-1) + P_B e_{B,j}(t) + P_W e_{W,j}(t)) \tag{17}$$

$$= P_A^2 \, \text{cov}(n_i(t-1), n_j(t-1)) \tag{18}$$
$$+ P_B^2 \, \text{cov}(\epsilon_{B,i}(t), \epsilon_{B,j}(t)) \tag{19}$$
$$+ P_W^2 \, \text{cov}(\epsilon_{W,i}(t), \epsilon_{W,j}(t)) \tag{20}$$
$$+ 2 P_B P_W \, \text{cov}(\epsilon_{B,i}(t), \epsilon_{W,j}(t)). \tag{21}$$

We here used some of the assumptions about the environmental noise random variables listed at the end of section 1. We then have

$$(1 - P_A^2) \operatorname{cov}(n_i, n_j) = P_B^2 \operatorname{cov}(\epsilon_{B,i}, \epsilon_{B,j}) + P_W^2 \operatorname{cov}(\epsilon_{W,i}, \epsilon_{W,j}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,j}). \tag{22}$$

Furthermore,

$$\operatorname{var}(n_i(t)) = P_A^2 \operatorname{var}(n_i(t-1)) + P_B^2 \operatorname{var}(\epsilon_{B,i}(t)) + P_W^2 \operatorname{var}(\epsilon_{W,i}(t)) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}(t), \epsilon_{W,i}(t)), \tag{23}$$

and therefore

$$(1 - P_A^2) \operatorname{var}(n_i) = P_B^2 \operatorname{var}(\epsilon_{B,i}) + P_W^2 \operatorname{var}(\epsilon_{W,i}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,i}), \tag{24}$$

which holds independently of the value of i. Therefore,

$$\operatorname{cor}(n_i, n_j) = \frac{P_B^2 \operatorname{cov}(\epsilon_{B,i}, \epsilon_{B,j}) + P_W^2 \operatorname{cov}(\epsilon_{W,i}, \epsilon_{W,j}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,j})}{P_B^2 \operatorname{var}(\epsilon_{B,i}) + P_W^2 \operatorname{var}(\epsilon_{W,i}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,i})}. \tag{25}$$

The correlation $\operatorname{cor}(n_i, n_j)$ approximately equals the correlation $\operatorname{cor}(N_i, N_j)$ of the original (un-linearized) model, so the main text should probably show this result:

$$\operatorname{cor}(N_i, N_j) \approx \frac{P_B^2 \operatorname{cov}(\epsilon_{B,i}, \epsilon_{B,j}) + P_W^2 \operatorname{cov}(\epsilon_{W,i}, \epsilon_{W,j}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,j})}{P_B^2 \operatorname{var}(\epsilon_{B,i}) + P_W^2 \operatorname{var}(\epsilon_{W,i}) + 2 P_B P_W \operatorname{cov}(\epsilon_{B,i}, \epsilon_{W,i})}. \tag{26}$$

Note that the first two terms in the numerator relate to traditional measures of spatial synchrony of environmental variables, but "cross-variable" synchrony, both between and within locations (in the numerator and denominator, respectively), also contribute.

There are some interpretations available for the coefficients P_A, P_B, P_W, but they may or may not be all that interesting, so I'll maybe save those for another time. Likewise it may (or may not) be interesting to try to develop interpretations of how cross-site, cross-variable synchrony versus same-site, cross-variable synchrony may influence population synchrony under different circumstances corresponding to different values of P_B and P_W. Also note that the value of P_A does not matter in the end for population synchrony.

4 The simulation model

I think the simulation model should be a special case of the model from (1)-(4), so it suffices to specify f and s. I think $f(N, \epsilon_B) = \exp(f_0) \exp(-N/K_B) \exp(\epsilon_B)$ is probably a good choice. This is similar to what was used in the version of the manuscript that I read. I think $s(B, \epsilon_W) = \min(\exp(s_0) \exp(-B/K_W) \exp(\epsilon_W), 1)$ is probably a reasonable choice. It might be possible to think of a better choice for s, one that does not involve that pesky min function, but probably not worth worrying too much about it. Ricker-like formulations were used previously, but interpretations of parameters of such models, in this context, as growth rates and carrying capacities, are not appropriate. Instead we have $\exp(f_0)$ and $\exp(s_0)$ the fecundity and survival, respectively, at 0 density in an average environment, and K_B and K_W which control how quickly fecundity and survival decrease with increasing density. We must require $\exp(s_0) \leq 1$. There are other constraints on the parameters required for the model to have a stable equilibrium, it's probably best to just test using simulations whether the model has a stable equilibrium for whatever parameters you choose, and if it does not, choose others. If you end up really needing an analytic statement of what parameter constraints have to be imposed to get a stable equilibrium for this model, let me know. Note that you should also ensure that the random variables in your simulations satisfy the assumptions about the random variables listed at the end of section 1. Let me know if those are unclear. Your first set of simulations should use $d = 0$ and should agree with what can be computed from the analytic results above. For that comparison, you'll need the values of P_B and P_W. Let me know if you need help with that.