**How do population cycle frequency and dispersal interact to shape population genetic structure of Mountain pine bettle?**

Xiao Ju, Jeremy Larroque, Julian Wittische, Patrick M. A. James

JamesLab

Département Science Biologique

Université de Montréal

**Introduction:**

In this study, we are interested in a pest has cyclic population, the mountain pine beetle (*Dendroctonus ponderosae.* MPB in the following text). MPB is a native insect that attacks pines in western North American forests (Harvey, Donato, and Turner 2014). The current MPB outbreak started in British Columbia in the early 1990s. The insect has since killed about 50% of the total volume of commercial lodgepole pine (Pinus contorta) in the province which cause a huge damage in the forestry (Duncan et al. 2015). Although there are a lot of researches about MPB, but no one has ever studied the impact of the cyclic frequency of this insect.

A cyclic population rises and falls over a predictable period over time (Myers 2018). The phenomena of cyclic population of many organisms have been observed by biologists for very long time (Howell 1923). Several organisms including both insects (forest Lepidoptera, spruce budworm, Tent Caterpillars) (Myers 2018; Boulanger and Arseneault 2004; Franklin, Myers, and Cory 2014). and mammals (voles, lemmings, snowshoe hares) (Rikalainen et al. 2012; Ims, Yoccoz, and Killengreen 2011; Krebs, Boonstra, and Boutin 2018) piqued scientific interest and hence have been studied. Figure1 demonstrates the change in one cycle of an ideal cyclic population and defines the different terms will be used in this study.

The population change in one cycle of a 40-year-frequency cyclic population.

Demographic processes and dispersal of the population determine the geographic structure and its genetic differentiation (Slatkin 1987). The genetic structure of a cyclic population supposed to be varied overtime, because the continuous valleys will cause bottleneck effect and founder effect after which make population lose its genetic diversity. Recent researches show dispersal may overcome effects of the bottleneck during the cycling (Row, Wilson, and Murray 2016, Franklin, Myers, and Cory 2014). Dispersal helps the population to disperse geographically over the landscape. With favorable condition, this process will favor the expansion, increase population and eventually lead to a population peak. It also favors the genetic exchange among populations and inside a population. Genetic similarity among populations and inside a population therefore increase as population grows. So in this study, we would like to see how frequency and dispersal would affect the diversity loss and how it maintains the genetic structure of a cyclic population.

The study of a cyclic population can be difficult. For largely dispersed species, it is difficult to sample the population from the entire landscape. The processes of the population changes during the time can be invaluable to study a cyclic specie. However, this asks for a long period of work and samples during years even decades. As a result, these tempo-spatial difficulties always trouble researchers and slow down the researches and causes no research about the cyclic frequency. That is why in this study we use the simulation program CDmetaPOP to simulate the cyclic population of MPB.

CDmetaPOP is an individual-based, eco-evolutionary model for spatially-explicit simulation of population viability in landscape demogenetic . The advantage of CDmetaPOP is that it can model complex demographic and genetic processes for a system of hundreds of thousands of individuals, it can simulate the movement between patches and the dispersal of the population over time to track the spatial pattern, the population demography, and the genetic flow. With the help of the different simulation scenarios, we would like to study how do population cycle frequency and dispersal impact population genetic structure? Is there interaction between them and if yes, how do they interact to shape population genetic structure of MPB?

**Method:**

Nine different scenarios of cyclic MPB population were created by combining three different cyclic frequencies (10 year, 20 year, 40 year) with three different dispersal capacities (low, medium, high). For each scenario, we built a grid to represent the landscape. Then we controlled the population change by using sinusoidal carrying capacity (K) with different frequencies. In the gird, the change of carrying capacity of all the cells are synchronised except for the refuges. The total K over the grid will then lead the population to rise and fall.

***Landscape grid:***

We used different size of homogeneous grid as our virtual landscape for different scenario. Dispersal capacity is defined by the max distance an individual can move in one year. We have tested the maximum distance the population can reach in each scenario. Then we used a grid slightly bigger than their maximum needed for each scenario to ensure no individual will reach the edge and to simulate less empty cells during the simulation.

|  |  |  |
| --- | --- | --- |
| Frequency | dispersal (pixel) | grid size (pixel\*pixel) |
| 10 year | 1.99 | 21\*21 |
| 10 year | 2.99 | 21\*21 |
| 10 year | 8.99 | 41\*41 |
| 20 year | 1.99 | 21\*21 |
| 20 year | 2.99 | 31\*31 |
| 20 year | 8.99 | 61\*61 |
| 40 year | 1.99 | 41\*41 |
| 40 year | 2.99 | 51\*51 |
| 40 year | 8.99 | 81\*81 |

**Table 1**, Landscape grid size used in different simulation scenario. Frequency is described by the wave length between two continuous population peaks; dispersal is the maximal distance that an individual may reach in one year.

***Refuges:***

Refuges are the cells in which individuals can survive during crash at population valleys. In our simulation scenarios, we set a 3x3 refuge in the centre of the grids. Individuals survived the crash will be the founders who rebuild the population after.

***Carrying capacity model:***

We need a small carrying capacity that need less computer memory and less simulation time, but big enough to have a bottleneck strong enough during population valley. After several tests, we finally chose 30 as our max carry capacity, it is the smallest carrying capacity which can cause different allelic lost after 10 cycles in different scenarios. We synchronized the carrying capacity of all the cells of the landscape grid, except for the centre refuge where it stays at 30. To build a cyclic population, we made the value of K follows a sinusoidal curve. As showed in Figure2, the peaks and the valleys represent the highest and the lowest carry capacity in each cell. The gird will have the same cycle frequency as it is the sum of the synchronized cells.

A close up of a map

Description generated with very high confidence

**Figure2**: Carrying capacity (K) in each cell of the landscape grid for different frequencies.

***Dispersal:***

Dispersal determines the distributing speed of the population over the landscape grid. In order to test its impact and its interaction with frequency, we combined three levels of dispersal with three levels of frequency. Dispersal is simulated by using a simple dispersal kernel in which the probability of dispersal declines exponentially as a function of the Euclidean distance between cells and which allows long-distance dispersal events:

Where *dij* is the distance between two cells *i* and *j* in the landscape grid. is set to 100, and is set to 0.3 to reach a compromise where most dispersal events are short-distance (i.e., close to the focal cell) while allowing the presence of long-distance dispersal events. The final dispersal model is showed in Figure1.

A close up of a map

Description generated with very high confidence

**Figure3:** Dispersal model: Probability of dispersal function and distribution of probabilities

Three levels of dispersal capacity have been used, which are 1.99 cells, 2.99cells and 8.99 cells. During the simulation, CDmetaPOP rescales automatically the probability of different disperse distance by using the minimum distance and the dispersal capacity. The movement of the individuals in the simulations will then be set according to the probabilities.

***MPB genetic:***

In all the simulations in CDmetaPOP, all input parameters are based on the characteristics of MPB, including the sex ratio, offspring numbers, reproduction mode, etc.. (Annexe B). To have enough genetic structure data, individuals have been set with a genotype of 100 neutral biallelic SNP loci and no adaptive locus.

***Input data:***

CDMetaPOP needs three input files to specific information and corresponding parameters for the simulation, including patch level control file “PatchVars.csv”, class level control file “ClassVars.csv”, run parameters and output control file “PopVars.csv”. Another file used in our simulations is the file “Cdmatrix.csv”, this file contains the cost distance matrix among cells in the grid. A R script was coded to generate Cdmatrix.csv PatchVars.csv and “cdclimgentime” (this vector controls the changing timesteps of K) in the PopVars.csv. Other parameters in PopVars.csv and ClassVars.csv files are created by using MPB as simulation specie model. All the input parameters are showed in Table S.1 (Annexe). To study the genetic structure of each generation, in ClassVars.csv file, MPB age level has been set into three stages: 0,1,2. Age0 level is the larvae stage, Age1 is the adult stage, only Age1 individuals can disperse into other cells before reproducing. In the end, Age2 is the dead stage, individuals have 100% mortality at the beginning of this stage. In our simulations, at timestep 0, we begin with 270 Age0 individuals in the centre refuge. In timestep 1 these individuals become Age1 and begin to reproduce and disperse. Then in timestep 3, all these individuals become Age2 and dead will no longer contribute, at the same time, their descendants: new Age0 individuals hatched. Thus every 2 timesteps represent a generation (one-year time). Because of this setting, Age0 at every 2 timestep gives us the population genetic information of every generation before dispersal.

***Output:***

We simulated ten cycles for each scenario with ten replicates. The outputs of CDmetaPOP give us the genetic information for every generation at individual level. We also used the expected heterozygosity and egg laying information provided by CDmetaPOP in our analysis to study the genetic diversity change and the reproducing process in the population. CDmetaPOP provid the total number of breeding females (N\_BreedFemales) and the number of breeding events for females (EggLayEvents) at every timestep, as each MPB female lay only one clutch of eggs , we obtained the reproducing rate of female by: EggLayEvents/ N\_BreedFemales

***Sampling:***

We first find out population peaks and valleys according to the numbers of the individuals in the generation. Peaks are when population are the biggest in a cycle and valleys are the generations that have minimum populations. Population peaks are used as our sampling timesteps. Then we sampled 10% of the individuals from the output information at the timestep to study their genetic structure.

***Test and analysis:***

The output of each replicate has been analysed in R. Samples were converted into genind object using function df2genind of the “adegenet” package. We extracted expected heterozygosity provided by CDmetaPOP outputs at peaks. Pairwise Fst values between peaks from the same replicate have been calculated by the function pairwise.fstat() of the “hierfstat” package. We also used mantel.randtest() function of “ade4” package to perform the Mantel test between pairwise Fst and cycle numbers between two peaks, which can be considered as an isolation by numbers of outbreak cycles. In the end, we tested the significance of the dispersal and frequency and their interaction by aov().

***ComputeCanada:***

Because of the large amount of data and the large number of generations to simulate, the simulation and the calculation of the pairwise Fst have been done on the supercomputer Cedar of Compute Canada in distance.

**Result:**

***Outbreak cycle:***

Our scenarios successfully simulated cyclic populations. Figure 4 shows an example of the demographic changes in one cycle of a 10-years frequency cyclic MPB population at medium dispersal level. At valleys, MPB population is limited in the centre refuge of the landscape. K rises after the crash, MPB disperses continuously from the refuge over the landscape. As the rise continues, population eventually reaches a peak ( Figure4 d). Then, due to the decline of the K (except for the refuges), the population in each cell begins to decrease and eventually dropped to 0 again.

A screenshot of text

Description generated with high confidence

**Figure 4:** Simulated population dynamics and spatial patterns for a 10-year cycle with medium dispersal. At peaks, cells contain a maximum of K=30 individuals. During population crashes all cells go to K=0, except a centre refuge cell that remains at K=30.

***Expected heterozygosity***

CDmetaPOP provides expected heterozygosity (He) at each timestep. Figure 5 shows the mean He value at peaks in ten cycles of the 10 replicates for all scenarios.

A close up of a map

Description generated with very high confidence







**Figure5:** Expected heterozygosity at each population peak.

\*Please notice that for different frequencies, time between peaks is different

To study the impact of dispersal over the diversity, we also illustrate figures with the time scale as showed in Figure 6:

A close up of a map

Description generated with high confidenceA close up of a map

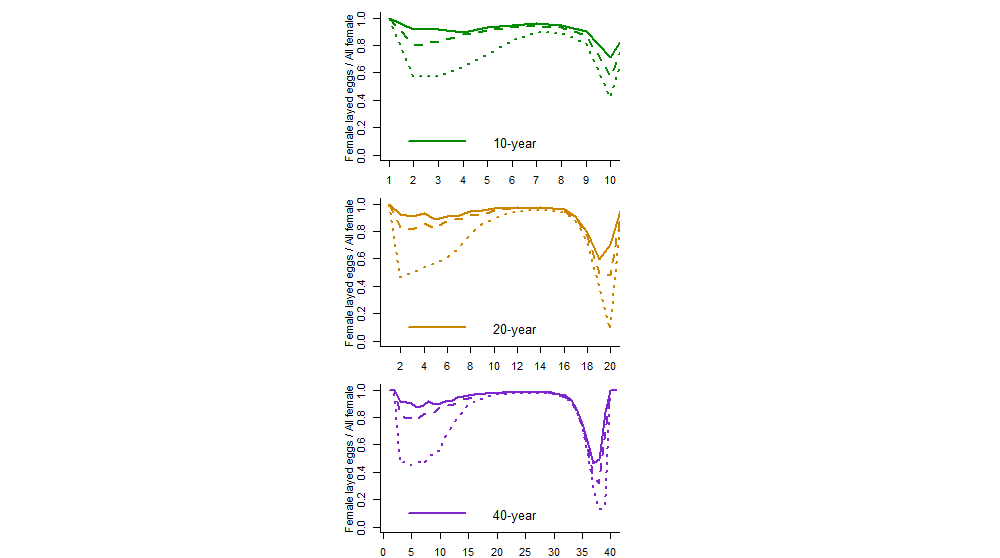
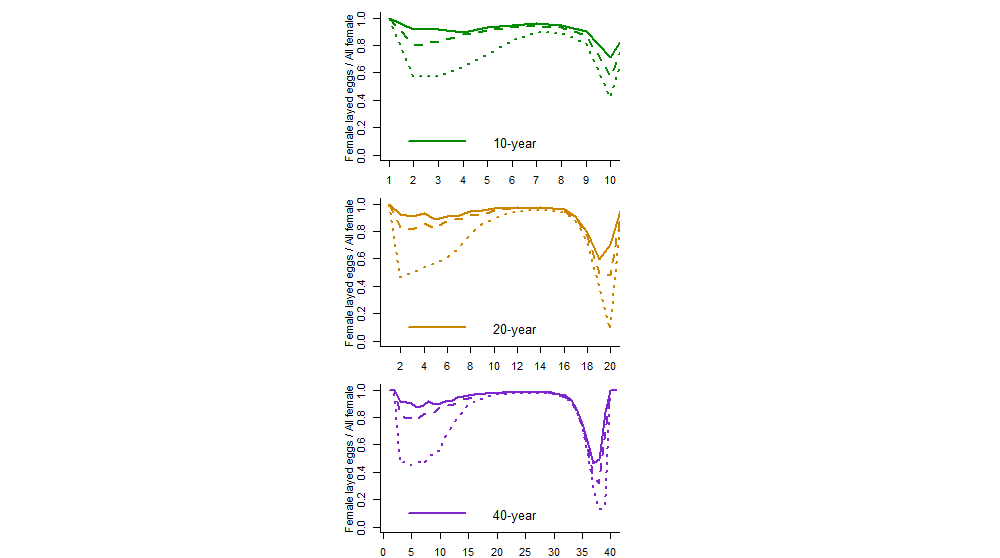
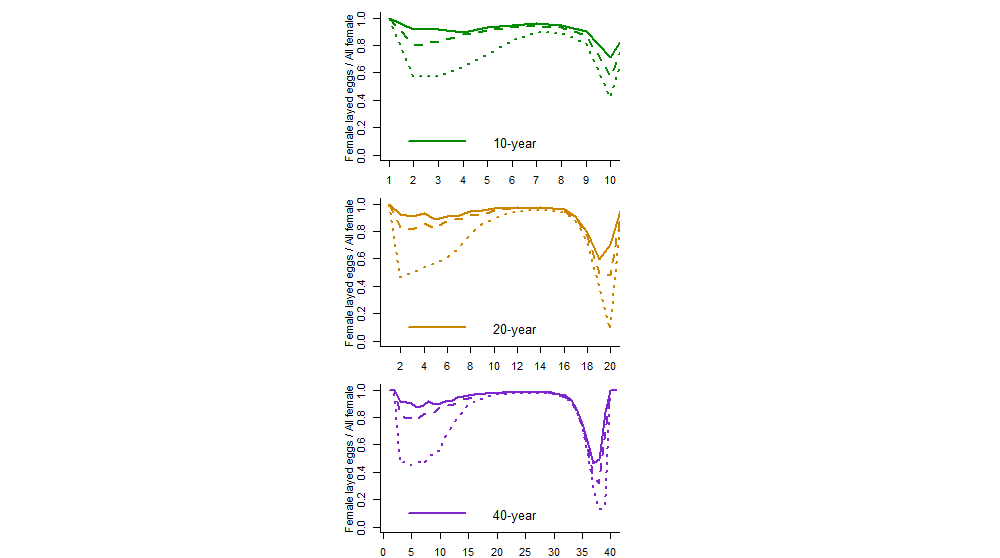
Description generated with high confidenceA close up of a map

Description generated with high confidence

**Figure.6**- Expected heterozygosity over time.

**Female reproducing rate**

To understand the impact of dispersal over the reproducing process, we sampled one cycle from each scenario to print out the reproducing rate in Figure.



**Figure.7**- The change of female reproducing rate in one outbreak cycle. High dispersal: solid line, medium dispersal: dashed line, low dispersal: dotted line.



***Pairwise Fst***

For each simulation, we calculated pairwise Fst between each pair of population peaks. Figure7 shows the mean Fst by the numbers of the outbreak cycles for all scenarios.

A close up of a map

Description generated with high confidence







**Figure8**. Genetic differentiation (Fst) by numbers of outbreak cycles.

Please notice that for different frequencies, time between peaks is different.

**Discussion:**

In this research we used CDmetaPOP to simulate cyclic MPB populations with different frequencies and dispersal capacities. Although simulation programme has been used to study population genetic (Row, Wilson, and Murray 2016) (Landguth et al. 2016), this is first research that uses this method to simulate cyclic population to study the impact of the frequency.

As we use carrying capacity K to lead the population change during cycling, a time lag between K and the population size has been observed. Figure 4 is an example of the demographic process in a cycle of the 10-years frequency with medium dispersal scenario, it demonstrates the lag between the population peak (Figure4 d) and the max K (Figure4 c) . While K cycling follow a sinusoidal variation, because the landscape grid is set to be bigger than the population peak, there are always empty cells surround the population. This makes population can continuous spread even after K reaches it maximum. As we can see in Figure4.d, population will reach its biggest value when the K\*(numbers of the cell occupied) is the highest in the cycle. Even though population will still spread spatially, population size will then decrease due to the lower K value.

Besides the lag, population (blue line) shows an asymmetric pattern in Figure4. After a crash (Figure 4.a), population rebuilds from the refuges and begin to disperse. This progress is controlled by K and the dispersal capacity. As we discussed earlier, population continues to grow after K reaches its max value. However, the decreasing process does not follow the same pattern. Population will not shrink from the edge of the population back to the refuge. Instead, K in each case goes down simultaneously and makes the population size decrease all over the landscape until K return to 0. For K is kept to 30 all time in the refuges, during this crash process, individuals in the refuge will survive and will rebuild the population for the next cycle. Although the real reason of this asymmetric is still unknow and may different from our model, it has been observed in many cyclic populations’ species (3. Myers 2018).

The mean expected heterozygosity at peaks for all scenarios is showed in Figure5 to study the change of the genetic diversity. From the figure, we saw that genetic diversity always decreases as the number of outbreak cycles increases. The crash of population leads to population valley, only very small number of individuals from a larger population will survive in the refuge, then the population will regrow base on the survivors. This dynamic process makes population affected by bottleneck effect and founder effect which cause directly the loss of genetic variation in each cycle. Another information given by Figure 5 is that with the same dispersal capacity, lower outbreak frequency favors diversity loss in each cycle. In the figure, same type of lines present same dispersal capacity, and same color means same cycle frequency. If we consider only the frequency (color), we notice that with the same dispersal level (line type), the He decrease faster with a lower frequency. If we consider only the dispersal (line type) and look at only the frequency (color), we notice that the dotted yellow line is lower than two of the purple lines. This means with 20-year frequency and high dispersal, genetic diversity loss is higher than 40-year frequency with low or medium dispersal. This indicate that genetic loss is not only determined by frequency, the dispersal also have strong effect over genetic structure.

To study more about the effect of dispersal, we grouped He over time by dispersal capacity in Figure 6. Comparing the three levels of dispersals, we notice that with the same frequency (color). Genetic diversity decreases as dispersal capacity increases. Although for the three different dispersal capacities used we didn’t find a regular pattern, more heterozygosity changes are observed when dispersal is higher, and we see more zigzag form of the line with higher dispersal. This phenomenon then explained by the reproducing rate change in Figure7. The reproducing rate changes in a cycle follows a “W” pattern. It is high at the population valley and around the peak. The rate is lower during the growing phase and has the lowest value during the decreasing phase. To understand these changes, we need the help of the demographic figures in Figure 4. During the valley (Figure4 a), although the population just went through a severe bottleneck, the density in the refuge is high. It ensures that most of the females can find mate and lay eggs. In the growing phase (Figure4 b c), as K begins to increase in all the cells, population disperse from the refuge into the cells around. At the beginning, due to the low population and the low K in the cells outside the refuge, females moved into these cells may have difficulty meeting males and will not lay eggs. This causes a strong Allee effect (Courchamp, Berec, and Gascoigne 2008 ) at the first one or two years right after the valley. As both the population and K increase with time, Allee effect declines and reproducing rate will go back to a high level till population reaches its peak (Figure4 d). Then comes the decreasing phase in which population goes down again. At this time, population will not stop spreading over the landscape and will invade into new cells, but the density in the cells gets lower and lower. The low density then causes again the Allee effect lead to another period of low reproducing rate because females have lower and lower chance to find a mate in their cells. When K drops to 0 outside the refuge, population goes back to a valley but reproducing rate goes back to high level and reproduction is only limited in the refuge. After understood the change of the reproducing rate, Figure 7 shows that higher dispersal produces stronger Allee effect during low-density phases. For example, in Figure7.b with 20-year frequency, during the decreasing phase, reproducing rate is 58% with low dispersal, 42% with medium dispersal and only 5% for high dispersal. Indeed, higher dispersal makes population covers more cells on the grid. When K goes down, these cells contains larger percentage of the population and lead to more females without partners. On the other hand, lower cyclic frequency means longer cycle, and longer period in each phase. If we compare the decreasing phase in Figure7, it is 2 years for 10-year frequency, 4 years for 20-year frequency and 10 years for 40-year frequency. Higher frequency cycles shorten the duration of dispersal-induced Allee effects, that is why we saw the lines are smoother in Figure6. But it will create more bottlenecks through time, which cause the order of lines differ in Figure7.

Due to different cycle, it is hard to compare the differentiation of genetic structure in different scenarios. Instead, we use the numbers of cycles between peaks as our temporal index and the result is showed in Figure8. we see that mean genetic differentiation (*Fst*) (Nei,1973) between outbreak peaks increases with the number of cycles between them. To test the significance of this observation, we created a test that similar to isolation by time (Hendry and Day 2005). Due to different cycle length in the scenarios, we tested the isolation by numbers of cycles (IBC) instead of time. The IBC test demonstrates that all *r* >0.9 and all *pvalue* >0.05 indicate that the isolation by numbers of cycles is significant. Beside the IBC, the frequency (color) and dispersal (line type) are presented by color and line type. The combination of frequency and dispersal gives different slope indicate differentiation is affected by both dispersal and outbreak frequency. More specifically, we saw that higher dispersal (line type) and lower cycle frequency (color) favours genetic differentiation between peaks, which gives a bigger slope in the figure. This result

is consistent with the analysis of He in Figure6, because larger diversity loss will certainly because population differs more during cycling.

We saw that both genetic diversity and differentiation are impacted by cyclic frequency and dispersal capacity. Furthermore, the influence over the reproducing rate indicate frequency and dispersal may interact during cycling. We did a two-way ANOVA test to verify the interaction, and all F-values > 0.05 prove that frequency and dispersal are statistically significant, as well as their interaction.

**Conclusion:**

In this research, we successfully simulated cyclic MPB populations with different cyclic frequencies and dispersal capacities. Our result shows that lower frequency and higher dispersal can lead to more genetic diversity loss and more differentiation during a population cycle. The interaction of these two factors is also significant and have impact over the genetic structure.

**Reference:**

Boulanger, Yan, and Dominique Arseneault. 2004. “Spruce Budworm Outbreaks in Eastern Quebec over the Last 450 Years.” Canadian Journal of Forest Research 34 (5): 1035–43.

Courchamp, Franck, Ludek Berec, and Joanna Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.

Duncan, Jacob P., James A. Powell, Luis F. Gordillo, and Joseph Eason. 2015. “A Model for Mountain Pine Beetle Outbreaks in an Age-Structured Forest: Predicting Severity and Outbreak-Recovery Cycle Period.” *Bulletin of Mathematical Biology* 77 (7): 1256–84.

Howell, A. Brazier. 1923. “Periodic Fluctuations in the Numbers of Small Mammals.” Journal of Mammalogy 4 (3): 149–55.

Ims, Rolf A., Nigel G. Yoccoz, and Siw T. Killengreen. 2011. “Determinants of Lemming Outbreaks.” Proceedings of the National Academy of Sciences of the United States of America 108 (5): 1970–74.

Landguth, Erin L, Andrew Bearlin, Casey Day, and Jason B. Dunham. 2016. “CDMetaPOP: An Individual-Based, Eco-Evolutionary Model for Spatially Explicit Simulation of Landscape Demogenetics.” Methods in Ecology and Evolution 8 (1): 411.

Landguth, Erin L., Andrew Bearlin, Casey C. Day, and Jason Dunham. 2017. “CDMetaPOP: An Individual-Based, Eco-Evolutionary Model for Spatially Explicit Simulation of Landscape Demogenetics.” *Methods in Ecology and Evolution* 8 (1): 4–11.

Myers, Judith H. 2018. “Population Cycles: Generalities, Exceptions and Remaining Mysteries.” Proceedings of the Royal Society B: Biological Sciences 285 (1875). https://doi.org/10.1098/rspb.2017.2841.

Row, Jeffrey R., Paul J. Wilson, and Dennis L. Murray. 2016. “The Genetic Underpinnings of Population Cyclicity: Establishing Expectations for the Genetic Anatomy of Cycling Populations.” Oikos 125 (11): 1617–26. https://doi.org/10.1111/oik.02736.

Slatkin, M. 1987. “Gene Flow and the Geographic Structure of Natural Populations.” *Science (New York, N.Y.)* 236 (4803): 787–92.

**Annexes:**

**Table S.1**: Simulation parameters summary. Parameters not mentioned are either set to default value or unused.

1. *PatchVars* input file: with a total of 1804 rows, one for each cell.

|  |  |  |
| --- | --- | --- |
| Parameters | Value | Justification |
| K | 30 | Cell carrying capacity |
| N0 | 20 in the refuges; 0 for the rest of them | Initial population in the centre of the 4% of the grid |
| Natal.Grounds | 1 | Individuals can occupy a natal cell |
| Genes.Initialize | random | Random initial assignment of alleles |
| Mortality.Back | 100 for border cells; N for the rest of them | Mortality associates with individuals at the border cells: they can’t disperse out of those cells (they die) |
| Migration | 0 | Individuals can’t disperse during simulator’s emigration phase |
| Straying | 1 | Individuals disperse during simulator’s immigration phase |
| Fitness\_AA | 0 | No selection in genetic level |
| Fitness\_Aa | 0 |
| Fitness\_aa | 0 |

1. *ClassVars* input file: with 3 rows, one for each age class.

|  |  |  |
| --- | --- | --- |
| Parameters | Value | Justification |
| Age class | 0, 1 and 2 | Three age classes in order to produce a univoltin species model in CDmetaPOP |
| Distribution | 1 for Age 0 | Simulations begin with only Age 0 individuals |
| Percent Female | 66 for all age classes | Sex ratio for MPB is about 1 male for 2 females, although it can change according to climatic conditions and epidemic stages (Les Safranyik & Wilson, 2006) |
| Age Mortality Out % | 100 for Age 3 | All Age 2 individuals are discarded each generation during the simulation process (they don’t contribute to dispersal or reproduction) |
| Age Mortality Back % | 100 for Age 3 |
| Migration | 0 for all age classes | Age 1 individuals are dispersing during the immigration phase, before reproducing |
| Straying | 1 for Age 1 |
| Male Maturation | 1 for Age 1 | Age 1 individuals become sexually mature right before the simulator’s reproduction process |
| Female Maturation | 1 for Age 1 |
| Fecundity\_mu | 60 for Age 1 | MPB females lay on average 60 eggs per mating event (Les Safranyik & Wilson, 2006) |

1. *PopVars* input file

|  |  |  |
| --- | --- | --- |
| Parameters | Value | Justification |
| runtime | 200 (10 years cycle)  400 (20 years cycle)  800 (40 years cyce) | For every scenario, simulate 10 cycles |
| output\_years | 2 | Extract genetic data at the beginning of every generation |
| cdclimgentime | 0|2|4|…….. | Carrying capacity K changes every 2 timestep (correspond a generation) following a sinusoidal curve |
| cdmat (mate, dispout, dispback and stray) | Cdmatrix.csv |
| StrayBackno | 5 |  |
| StrayBackparA | 1 |  |
| StrayBackparB | 0.3 |  |
| StrayBackparC | 1 |  |
| StrayBackthresh | see Table1 dispersal | The maximal dispersal distance |
| Freplace | N | Males MPB sometimes reproduce with more than one female (Les Safranyik & Wilson, 2006) |
| Mreplace | Y |
| offno | 2 | The number of offspring in a clutch follows a Poisson distribution law |
| eggFrequency | 1 | Fertilized MPB females always lay eggs |
| Egg\_Mortality | 0 | Even there is different mortality for different life stages of MPB, from larvae to adulthood (Amman & Cole, 1983; L. Safranyik, Barclay, Thomson, & Riel, 1999; L. Safranyik et al., 2010; Les Safranyik & Wilson, 2006). We set mortality to 0 to compromise the small population in the simulation. |
| Egg\_FemalePercent | 66 | Sex ratio for MPB is about 1 male for 2 females, although it can change according to climatic conditions and epidemic stages (Les Safranyik & Wilson, 2006) |
| loci | 100 | 100 neutral loci and no adaptive locus |
| alleles | 2 | 2 alleles for each locus (bi-allelic) |
| muterate | 0,00000001 | Although no direct reference of the mutation rate of MPB, we use 10-8, which is a little higher than insects mentioned in similar researches. (Liu et al. 2017) |
| mutationtype | random |
| cdevolveans | 1 | Selection model (1 adaptive locus) |