Swansea University
Prifysgol Abertawe

Loss of Dynamic Stability in a Host-Parasitoid System is Related to the Magnitude and Temporal Scale of Trend in Environmental change.

Brett Petersen

Swansea University

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Abstract

Climate change is driving changes to populations leading to biodiversity crises. Knowledge is increasing on how populations are changing with research predicting how future population dynamics may predict population dynamics. Mathematical models have been an important tool to predict how biodiversity may change as the climate changes. Much research has concentrated on a 'step change' of the environment, but research on the effects of a gradual increase in the environmental parameters, whereby these parameters gradually increase or decrease over time, has been underexplored.

To address this gap, I used a version of the Nicholson-Bailey model that has been modified to include an environmental trend, whereby, over time, the environment increases the response of the host and parasitoids intrinsic growth rate across each time step over a temporal scale, to show how this could affect population dynamics within a discrete-time host-parasitoid system and how this differs to a constant environment. I further change the magnitude and temporal scale of the trend of the environment to establish their effects on population dynamics and try to analyse the dynamics.

The constant environment became unstable after an initial transient phase, when the environmental effect on the system caused the host population growth rate to reach 115% of the current population size, showing cyclic/chaotic dynamics. The trend in the environment contrasted this by almost always having stability after the initial transient phase, sometimes becoming cyclic/chaotic at a certain environmental value within the trend when population growth rate became higher than 115% of the current population size. At smaller speeds of environmental change, the population started oscillating at lower environmental parameter values than for faster speeds. This was dependent on an increase in temporal scale, causing rate of increase from one environmental value to the next to become smaller, allowing for populations to track the environmental change and shift from stability to instability at an earlier stage, whereas larger rates of increase at smaller temporal scales rather abruptly shifted from stability to sudden amplified instability.

This research emphasises the need to study the effects of a trend in the environment with more intricacy and detail, to predict the future of population dynamics under different climate change scenarios.

Lay summary

Climate change is poised to cause changes to our natural world, potentially leading to a biodiversity crisis. By researching the effects of future climate conditions on future populations, we can try to gain an understanding of potential threats to our planet's plants and animals. Simulations of these effects can be applied to computational models that can predict the dynamics of populations, thus allowing us to predict future consequences of the changing climate and try to prepare for them. Studies observing an environmental value that has been fixed across time (a constant environment) demonstrate that an environment will affect population dynamics, but the question of how a trend in the environment affects population dynamics has been underexplored. The trend of the environment is increased at each time step of a time scale, and the rate of increase is affected by time scale and magnitude of environment. A host-parasitoid interaction is a system where a parasitoid lays eggs into a host egg and a single parasitoid larva outcompetes other parasitoid larvae, living as a parasite on the host, outcompeting the host it and emerging as an adult by living off the host.

My research aims to compare the constant environment with the trend in the environment whilst also observing how population dynamics of a host-parasitoid system are affected by different trend scenarios. Both the constant, and trend in the environment are applied to a simple host-parasitoid model, to compare between the two systems.

Results obtained within my research indicate that there is a difference between both the constant environment and the trend in the environment, with population dynamics in the constant environment becoming unstable when host population growth rate reached 115% of the current population size or more. Analysing the trend in the environment, there was always a period of stability prior to population dynamics becoming unstable, as host population growth rate must be greater than 115% of the current population size for populations to become unstable.

The period of stability was further altered by the size of rate of increase, which altered the distance between one environmental value and the next within the trend in the environment, which was affected by the length of time. Longer time periods within the trend in the environment can equate to slower rates of climate change, and shorter time periods of the trend in the environment (that run from the same minimum to maximum environmental value) equate to faster rates of climate change. Populations can track and adapt to slower climate change, whereby temperature is increased at a slower rate and instability occurs at an earlier stage (and thus, a smaller environmental value), with small oscillations that become

gradually larger across the trend as environmental value increase. Within a fast climate change, populations may not be able to track the sudden high temperature difference, thus stability suddenly becomes amplified instability that becomes highly unpredictable and increases extinction risks.

This research emphasises the need to study the effects of a trend in the environment with more intricacy and detail, to predict the future of population dynamics under different climate change scenarios.
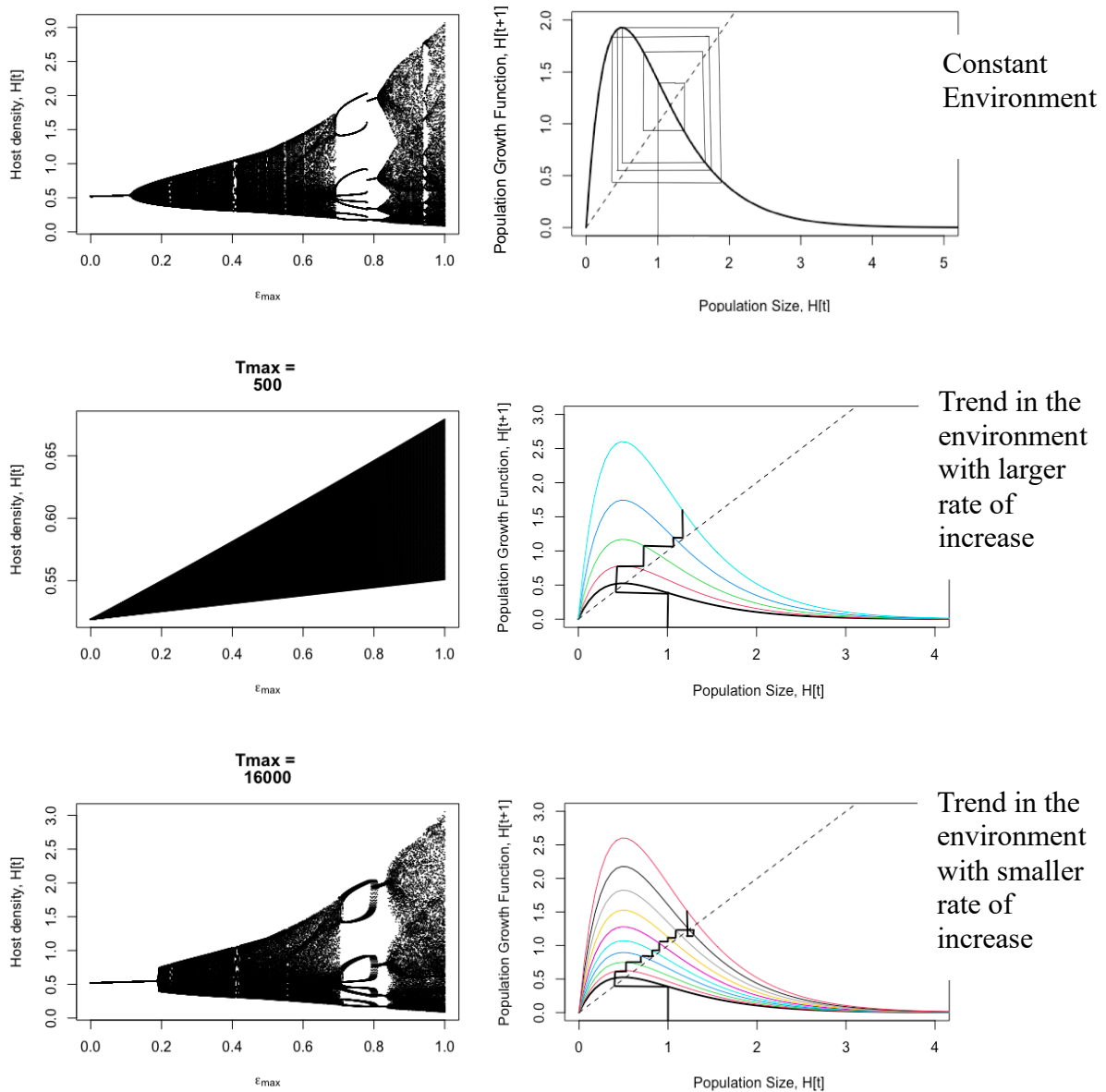
<u>Declarations</u>

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed.......... ████████████...

Date...09/04/2024...

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references.   A bibliography is appended.

Signed...... ████████████...

Date...09/04/2024..

I hereby give consent for my thesis, if accepted, to be available for electronic sharing

Signed....████████████...

Date...09/04/2024..

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

Signed....████████████..

Date...09/04/2024..

Statement of Expenditure

This thesis was curated without any expenditure. All relevant information, documents, training courses and software was freely accessible online or within Swansea University thus no costs were incurred.

Statement of Contributions

Brett Petersen = BP.

Professor Mike Fowler = MF.

Doctor Christophe Coste = CC.

Contributor role	Persons involved
Conceptualization	BP, MF, CC
Data Curation	BP, MF
Formal analysis	BP, MF, CC
Funding Acquisition	N/A
Investigation	BP
Methodology	BP, MF, CC
Project Administration	BP, MF
Resources	BP, MF, CC
Software	BP, MF
Supervision	MF, CC
Validation	N/A
Visualisation	BP
Writing – Original Draft and Preparation	BP
Writing – Review and editing	BP, MF, CC

Ethics Approval

Thank you for completing a research ethics application for ethical approval and submitting the required documentation via the online platform.

Project Title	gradual increase of temperature changes populations of host - parasitoid interactions across different time scales and increases of temperature
Applicant name	MR BRETT PETERSEN
Submitted by	MR BRETT PETERSEN /
Full application form link	https://swansea.forms.ethicalreviewmanager.com/Project/Index/9031

The Science and Engineering ethics committee has approved the ethics application, subject to the conditions outlined below:

Approval conditions

1. The approval is based on the information given within the application and the work will be conducted in line with this. It is the responsibility of the applicant to ensure all relevant external and internal regulations, policies and legislations are met.
2. This project may be subject to periodic review by the committee. The approval may be suspended or revoked at any time if there has been a breach of conditions.
3. Any substantial amendments to the approved proposal will be submitted to the ethics committee prior to implementing any such changes.

Specific conditions in respect of this application:

The application has been classified as Low risk to the University.

No additional conditions.

Statement of compliance

The Committee is constituted in accordance with the Governance Arrangements for Research Ethics Committees. It complies with the guidelines of UKRI and the concordat to support Research Integrity.

Science and Engineering Research and Ethics Chair

Swansea University.

If you have any query regarding this notification, then please contact your research ethics administrator for the faculty.

- For Science and Engineering contact FSE-Ethics@swansea.ac.uk
- For Medicine, Health and Life Science contact FMHLS-Ethics@swansea.ac.uk
- For Humanities and Social Sciences contact FHSS-Ethics@swansea.ac.uk

Health and Safety Risk Assessment

The health and safety risk assessment was undertaken by myself and Swansea University, and can be observed in Appendix 1. All precautions and safety measures were made clear and aware and followed by myself to complete my thesis safely.

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1   <u>Introduction</u>

Climate change caused by anthropogenic impacts are affecting biodiversity through different ways (Muluneh, 2021, Williams & Newbold, 2019, Lovejoy et al., 2019, Sintayehu, 2018). This is having a detrimental impact on many species, altering fitness and life history traits (Hill et al., 2021, Walker et al., 2019, Marshall et al., 2016), causing population declines and ultimately leading to potential extinctions (Raven & Wagner, 2021, Cox et al., 2020, Román-Palacios & Wiens, 2020).

Increasing temperature since the industrial revolution (Shivanna, 2022) is altering population dynamics throughout marine, terrestrial and freshwater ecosystems (Scheffers et al., 2016). Individuals are reacting by changing their behavioural patterns and responses to climate change (Buchholz et al., 2019). Specifically, individuals may react by shifting spatial distributions (Zylstra et al., 2022, McCain & Garfinkel, 2021, Pureswaran et al., 2018, Zhang et al., 2020, Hulme, 2016) and changing cues within nature, due to altering phenological times (Pardikes et al., 2022, Visser et al., 2021, Thackeray et al., 2016, Visser et al., 2005), therefore competition between organisms may change, causing stability to change within ecological interactions. This could result in population increases to species with capable adaptability (high phenotypic plasticity) to climate change, whereas species that cannot adapt to climate change quickly enough may decline (Scheiner et al., 2019), e.g specialist species (organisms that require unique resources).There is an increased importance to understand the impacts that a changing climate is having on biodiversity (Urban et al., 2016), with new research methods and techniques being discovered to predict future crises.

There is a particular interest to understand how insects are responding to climate change (Halsch et al., 2021). They are the most diverse taxa of all multicellular organisms (Stork, 2018) and play key roles in establishing how freshwater and terrestrial ecosystems function across the whole planet (Halsch et al., 2021). Most insects tend to have short generation times (Jactel et al., 2019), so can be used to study the effects of climate change across many generations. Other species could have longer generation times, for example, a bowhead whale (*Balaena mysticetus*) has a generation time of around 100 years (George et al., 1999). Bowhead whales would experience the same amount of climate change over 1 generation contrasted to the 100's of insect generations during this period. The mostly shorter generation times of insects can be a great indicator of how species may react over time to climate change

as they are widespread and sensitive to environmental changes (Parikh et al., 2020). They can also be used as indicators of climate status (Shrestha, 2019); therefore, it is vital to study their behaviour and population trends throughout the near future as climate changes.

Climate change can alter traits; thus, insects must respond to track and adapt to the changing climatic conditions. This can be seen through phenological (timings of cyclic/biological events) (Forrest, 2016, Thackeray et al., 2016, Visser et al., 2005), morphological (size, shape and structural features) (Dongmo et al., 2018, Lu et al., 2016), physiological (mechanisms and functions) (Zhu et al., 2021, Stange & Ayres, 2010, Régnière et al., 2010), or demographic (survival probability) changes (Ma et al., 2021, Chaves et al., 2014). Insect populations that cannot adapt to changing climate through expressing a change in traits (characteristics or attributes of an organism that are expressed by genes and/or influenced by the environment (Andrew et al., 2013)) due to having low epigenetic plasticity (the ability of neurons to change their physiological or structural properties in response to internal or external factors (Vogt, 2022)) face the possibility of extinction.

Warmer temperatures act as a stimulus for insects to oviposit (Cury et al., 2019). Higher temperatures increase insect metabolic rates, thus resulting in faster oviposition rates and higher egg loads (Francuski et al., 2020, Hans et al., 2018). An increase in temperature is also an important environmental factor for offspring that affects insect growth, development, generation time and body size (Cui et al., 2018). Adult insects respond to temperature increase by egg laying. Phenological changes may cause insects to oviposit at earlier or later times, to coincide with temperature to allow for greater offspring fitness (Visser et al., 2005). Voltinism (number of broods or generations of organism within a year) may also transition to differing numbers of broods a year within multivoltine species (univoltine species only produce 1 brood per year) (Zografou et al., 2021), thus possibly resulting in a changing demography within a species responding to climate change. Life history traits could cause trophic asynchrony between species (Damien & Tougeron, 2019) as climate change increases, therefore causing potential destabilization of trophic food web systems (Abarca & Spahn, 2021, Fussmann & Heber, 2002).

Parasitoids are described as animal in which the immature stage feeds on a single host individual, and the feeding activity normally results in the death of the host (Johnson, 2001). Parasitoids are well known to play significant roles in suppressing potential host pest species

across different environments (Prinsloo, 1997). For a given host-parasitoid system, estimated optimal temperatures for parasitoid survival are significantly lower than that for their host (Furlong & Zalucki, 2017, Hance et al., 2007). Other climate conditions can reduce the success of parasitoid effectiveness suppressing hosts such as elevated temperature in concert with drought (Romo & Tylianakis, 2013). This implies that host-parasitoid trophic asynchronies are expected to become more frequent under a warming and changing climate (Chidawanyika et al., 2019), highlighting the importance of studying host-parasitoid population dynamics.

Simple simulation modelling of population dynamics predict how population dynamics of both host and parasitoids may react under certain environmental conditions such as temperature, food availability and space (Garay et al., 2014), both in discrete and continuous time mathematical models (Bellows & Hassell, 1988). It should be mentioned that simulation models imitate and predict the time-evolution of a real-life system to a specific degree but may not be 100% accurate to what is observed in real-life (Durán, 2020, Chwif et al., 2000). Discrete-time models have also been used for predator-prey systems or to describe consumer-resource dynamics within its broadest sense and have thus become important predictors for ecosystem stability and mitigating potential problems (Marcinko, 2020). Though they have been successfully used throughout industry and academia, discrete-time models present constraints such as assuming equally spaced time-intervals (Loossens et al., 2021) and inability to deal with large numbers of variables (Stefansson et al., 2011), thus continuous-time models can be used to overcome this. Within host-parasitoid systems, discrete-time models are generally clear enough and traditionally used as insects follow distinct trends across time steps (Murdoch et al., 2013), and not many variables are needed within the model system, therefore it can be used to simplify systems to explain larger phenomena.

The logistic map can show how a population grows slowly, then rapidly, before tapering off as it reaches the carrying capacity, defined by mapping the population at any time step to its value at the next time step, first described by (May, 1976). Historically, logistic maps have been one of the most important tools to describe a shift from stability to instability (cycling/chaos) within a population time series using a deterministic approach, as its formal simplicity still exhibits an unexpected degree of complexity (May, 1976). Despite the simplicity of logistic maps, they still yield complex population dynamics (Erguler & Stumpf, 2008).

Population stability can transition into unstable oscillatory behaviour when initial conditions are slightly changed, such as the input of an environmental variable, or even within slight changes of parameters such as population growth rate. Oscillations and patterns within population dynamics have been heavily researched since the research of Charles. S Elton in 1924 (Jones, 2016), but most hypotheses are still lacking consensus for reasoning behind this occurrence (Lindström et al., 2001). Species may exhibit cyclic patterns (Lindström et al., 1996), but the understanding behind variation in amplitude and periodicity remains somewhat a mystery (Myers, 2018). Species may also exhibit chaotic dynamics, which is not rare in natural ecosystems (Rogers et al., 2022), whereby a system may be sensitive to small changes in initial conditions, and population dynamics become unpredictable (Oestreicher, 2007). Refining these initial conditions to change at every time-step could lead to differing dynamics that have not been previously seen.

Researchers have used constant 'step-change' environments to predict the consequences of increases in temperature (Cavigliasso et al., 2021, Iltis et al., 2020, Meisner et al., 2014, Olsson et al., 2013), whereby populations have changed due to different environemtnal factors acting on them. Changing the constant environment is a valuable way of highlighting responses to climate change, however it only portrays a narrow ecological scale (O'Connor & Bernhardt, 2018). The constant environment is limited as it stays the same across a period, or changes from one value to another without looking at values in-between. Comparisons can be made to other environmental values that may be higher or lower but could miss out key events that may occur at specific values. By using a gradual change (trend) in environment along with accurate predictive models (Urban et al., 2016), it will hopefully provide a more realistic outcome to understanding the effects of environment on population dynamics, whereby the environment changes at each time-step within a discrete-time system.

In this thesis, I use a modified Nicholson-Bailey discrete-time host-parasitoid model (Kendall, 2001) to explore how a simple host-parasitoid system may alter dynamics across different environmental values of a constant environment. The model from the Kendall paper attributes to a wide range of dynamics, exhibiting stable focus, cycling and chaotic dynamics with small changes to initial conditions, and uses a constant variable to show these dynamics. The Nicholson-Bailey model that I use has been modified to include trend in the environment and the trend will be used to compare to and constant environmental model, like that of the

(Kendall, 2001) model, with different environmental parameter values to compare with than that of the (Kendall 2001) model, without including any environmental variation. I then establish how a trend in the environment may affect the population dynamics of the simple, stable focus equilibrium of this host-parasitoid model and how this compares to the population dynamics within the constant environment. I next describe how the magnitude and temporal scale of the trend in environment affect the population dynamics. Finally, I determine why the dynamics of the model may change when explicitly considering how a trend in the environment affects this host-parasitoid model.

2 Methodology

2.1 Host-Parasitoid Model

To project population dynamics of an insect host and parasitoid system I extended on the Nicholson-Bailey discrete-time model (Nicholson and Bailey, 1935):

$$\begin{cases} H_{t+1} = H_t e^{r(1-H_t)-\alpha P_t+\varepsilon_t} \\ \quad P_{t+1} = H_t(1-e^{-\alpha P_t}) \end{cases} \tag{1}$$

Whereby H_t and P_t = host and parasitoid densities; e = exponential growth function; r = host intrinsic growth rate; α = attack rate of parasitoids on hosts and ε_t = (a time-varying in general) parameter that encompasses the effect of the environment on the change in the host population size, thus is included within the exponent. It is an addition onto the Nicholson-Bailey model. No stochastic term was used within the original model, so it is not implemented here.

2.2 Beddington, Free and Lawton Model

(Beddington et al., 1975) have used this system for $\varepsilon_t = 0$ and studied the deterministic trajectories associated with various values for r to highlight how the system shifts from stable to cyclic to chaos with an increasing r value. The model aims to explore how parasitoids regulate the host population and considers parameters that would affect this such as birth rate

of parasitoid, death rate of host due to predation from parasitoid and the death rate of parasitoid due to availability of hosts. Host carrying capacity (K) was set at 1 to analyse how much a parasitoid can suppress its host below carrying capacity through affecting r. Models would become chaotic and unpredictable in the absence of host-density dependence or other regulating factors (Nicholson & Bailey, 1935) thus the model includes host density-dependence.

2.3 Kendall Model

The (Kendall, 2001) model is an addition to this model, studying the consequences of added noise into the model by including ε_t, that was kept the same value across time, into a normal distribution of different parameter values that were used to simulate data from the associated attractors taken from the system in (Beddington et al., 1975) (stable focus: r = 2.0, α = 3.0; quasiperiodic: r = 1.8, α = 4.0; periodic (phase locked): r = 2.2. α = 4.5 and chaotic: r = 2.7, α = 5). Values of ε_t= 0, 0.01, 0.1 and 0.3 were used to represent amplifying noise and how an environment can affect the system. By understanding the different effects that an increasing noise value had within the (Kendall, 2001) paper, I could predict the stable or unstable patterns that may be seen when increasing the constant environmental value.

2.4 Incorporating a Trend in the Environment *vs* Constant Environment Model

I wanted to understand the consequences of trend in the environment on the host-parasitoid system by setting:

$$\varepsilon_t = -\varepsilon_{max} + (t - 1)\frac{(\varepsilon_{max}*2)}{(T_{max}-1)} \tag{2}$$

where the trend goes from - ε_{max} to ε_{max} across time-steps (T_{max} = 500, 1000, 2000, 4000, 8000, 16,000). The difference between ε_t and ε_{t+1} is also the rate of increase (v_t) from $-\varepsilon_{max}$ to ε_{max}, which is affected by a differing number of time-steps (T_{max}), at a rate of:

$$v_t = \varepsilon_{t+1} - \varepsilon_t \tag{3}$$

The model will be affected by the trend in the environment ε_t, that will increase by v_t at each individual timestep across the temporal scale. I wanted to compare these trajectories to that of constant environmental models for various $\varepsilon_t = \varepsilon_{max}$ values. In both systems, parameter values were $\varepsilon_{max} = 0$ to 1, r = 2 and a = 3. After running sensitivity analyses with other values from the (Kendall, 2001) paper, these values were selected as they showed stable population dynamics when no environmental value was added, and always began stable. Other parameter values, as mentioned within the (Kendall, 2001) paper and paragraph above, caused populations to become cyclic or chaotic when ran with no environmental effect, and thus I wanted to observe the effect of an environment with stable parameters and how it affected populations. I further ran parameters that showed cyclic or chaotic populations with the environmental value to understand what happened, with results showing that the trend suppressed oscillations at lower T_{max} values, but quickly populations became chaotic, and at r = 2.7, a = 5, parastioid populations became extinct. I believe this is something that should be studied in the future, but to allow for simplicity and to understand effect of environment in relation to stable dynamics, r = 2 and a = 3 were chosen. H_t and $P_t = 1$ always at the start of each simulation, to represent carrying capacity. Within all equations, 't' is the number of time steps that range from 1 to T_{max}. v_t is essentially the combination of the two main study parameters, ε_{max} and T_{max}, whereby for each simulation ran for the trend in the environment, parameter values of $\varepsilon_{max} = 0$ to 1 (501 values in bifurcation plots, 51 values in time series and cycle period analyses) and ($T_{max} = 500, 1000, 2000, 4000, 8000, 16,000$) are combined to create a v_t value. By executing a series of time series analyses, this allowed me to observe how v_t influenced population dynamics.

2.5 Time Series Analyses: Bifurcation Plots

To analyse the host densities (only hosts used as parasitoid followed a similar population dynamics), 501 values of ε_{max} were taken in a sequence from 0 to 1, to observe the point at which population dynamics changed with the ε_t value. Within the analysis, each ε_{max} value was run across the different values of T_{max}, whereby the last 200 attractor points of hosts within each system that had been affected by v_t were used to highlight the trend after transient dynamics had occurred. In the case of the constant environment, ε_{max} was fixed at each time step across the analysis. In the case of the trend in environment, that ran from -ε_{max} at $t = 1$, to ε_{max} at $t = T_{max}$, ε_t was a different value at each timestep. Therefore, I used

the last 200-time steps for the analysis on the trend of the environment also, as host attractors would be closer to the effects seen within the constant environment. As the constant environment is the same across time, it is already at the maximum value of the trend in the environment. Therefore, the trend in the environment never reaches ε_{max} until the final time step, thus population growth rate % within the trend will always remain lower than the constant environment up until the final time step. The last 200-time steps of the trend in the environment are therefore closer to the ε_{max} than at the start of T_{max}. This allowed me to observe how different sizes of T_{max} values and ε_{max} values affected H_t dynamics within the trend in the environment.

2.6 Time Series Analyses: Time series plots

To observe what was occurring at each environmental value within the bifurcation plot, I applied a time series analysis to observe the cyclic behaviour of both H_t and P_t. I selected ε_{max} = 0.0, 0.2, 0.4, 0.6, 0.8 and 1.0 and ran the values within the model for different lengths of T_{max} selected. This was applied to a deterministic model approach as I could track the full effect of number of time steps on the trend in the environment from -ε_{max} to ε_{max} (constant environment was fixed to ε_{max} value across time), so I could investigate the effect of different negative and positive ε_t values on the H_t and P_t dynamics. It was thought that T_{max} may influence population dynamics within the trend in the environment, thus by changing the number of time steps at the same ε_{max} value for each run, I could observe how the size of ν_t affected population dynamics.

2.7 Time Series Analyses: Cycle-Period Analysis

51 ε_{max} values were selected from 0 to 1 and all the T_{max} values were used so I could track the changes to the H_t and P_t cycle lengths and at which ε_t value cycling occurred with 0.02 increments at each T_{max} value. By applying the autocorrelation function, which observed the most likely cycle length corresponding to each individual value of T_{max} and ε_t, I could determine the cycling trend between H_t and P_t. If the variance of the last 200 attractor values of H_t or P_t was greater than 0, the autocorrelation function was applied, thus I could work out the most likely cycle period length for a specific ε_{max} value. If the values of H_t or P_t were 0,

it was said to be extinct. If stability occurred, the cycle period would have a non-applicable length (N/A) as no cycling happened. This is shown in appendix 3.

2.8 Schematic Cobweb Plot Analysis

To analyse the effect of v_t on the constant environment and the trend in the environment, I used the population growth function equation on H_t to analyse the growth from H_t to H_{t+1} at each timestep. v_t had no effect on the constant environment as the value was fixed throughout, however across ε_t within the trend in the environment (-ε_{max} to ε_{max}) number of time steps whilst reaching the same ε_{max} value would differ meaning v_t would change. I wanted to analyse why the population dynamics within the trend in the environment occurred, thus showed how a slight increase of the population growth function curve, at larger T_{max} values, and therefore shorter distances between ε_t and ε_{t+1} (rate of increase, v_t) could possibly cause the dynamics seen within the system.

All models were simulated in Rstudio Version 2023.09.0+463 (R Core Team, 2023) using the base packages that are automatically installed within Rstudio to keep figures simple but understandable. Parameter values were used from the (Kendall, 2001) paper and applied to my model to understand the comparability between the constant and trend in environment, as well as understanding the effects of the trend in environment. The full code to produce repeatable results is in appendix 2.

<u>**3 Results**</u>

3.1 Constant Environment

Figure 1 highlights the trend of the population dynamics for H_t in different constant environments over the last 200 time-steps (fixed over time). P_t follows a similar trend of stability to instability at a similar ε_{max} value, so was not included in figure 1, but is included in figure 2 to show the similarity of dynamics between them, as it relies on host populations. P_t does not reach such large oscillatory amplitudes but still shows similar oscillatory behaviour.
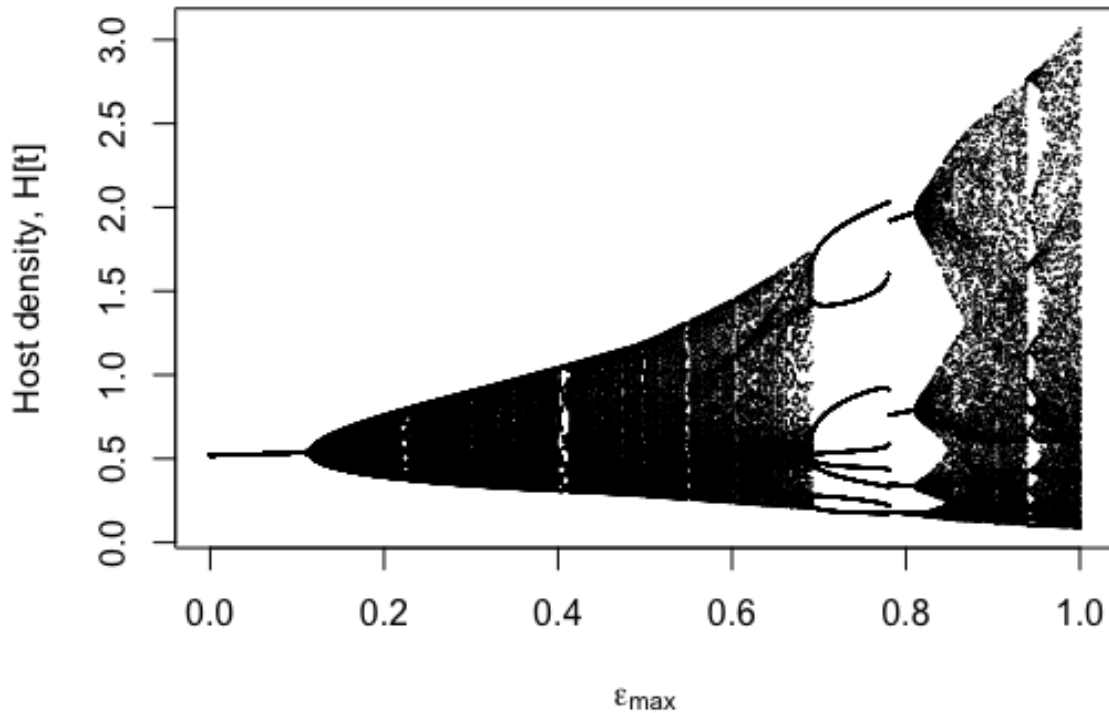
Figure 1: bifurcation plot of H_t with parameter values starting off at: r = 2, α = 3 and ε_{max} fixed over $T_{max} = 2000$, where 501 ε_{max} values from 0 to 1 were used to show the dynamics of the last 200-time steps (*t*) of H_t at ε_{max}.

From $\varepsilon_{max} = 0$ to $\varepsilon_{max} = 0.14$, the population density follows a stable attractor (straight line) at around $H_t = 0.51$ that is slowly increasing up until $\varepsilon_{max} = 0.14$, where oscillations start to appear at $\varepsilon_{max} > 0.14$. H_t oscillations become larger from $\varepsilon_{max} > 0.14$ to $\varepsilon_{max} = 1.0$, following a wider range of attractor values as amplitude of cycles increases, thus going from periodicity at lower ε_{max} values to chaos at the highest ε_{max} value (see figure 2). At $\varepsilon_{max} = 0.14$, the host population growth rate reaches 115% (exp(0.14) *100), meaning that any population growth rate above 115% of the current population size will cause the dynamics to shift to cycling or chaos. This can be seen by all following ε_{max} values > 0.14 (or greater than 115% host population growth rate from current population size). From $\varepsilon_{max} = 0.64$ to $\varepsilon_{max} = 0.83$, there is a window of periodic stability whereby the ε_{max} is causing the system to oscillate periodically, meaning at this stage the H_t is oscillating around the equilibrium

point at specific attractor values. There are other windows of periodic stability that appear too; however, they are not as profound as the window appearing at 0.64 to 0.83. The overall trend shows how in a constant environment, as the fixed value ε_{max} increases, and host population growth rate % of the current population size increases, the system will go from stable attractors, to oscillating periodic attractors to chaotic attractors (with the window occurring in between). Corresponding to figure 1, figure 2 plots A-F illustrate how dynamics change across different constant environmental values at T_{max} = 250, showing how an increase in environment and thus host population growth rate % from current size can cause a stable population to becoming cyclic populations and lead to chaotic populations at higher environmental values.

The time series analyses plots in figure 2 are an illustration of dynamics at specific values of ε_{max} across the bifurcation plot (figure 1), to observe the change in dynamical behaviour of H_t and P_t (which have been included here to show they follow a similar trend to hosts) when ε_{max} is increased (and fixed) at the start of each system. Plot A highlights the stability at ε_{max} = 0 whereby long term stable equilibrium occurs after a phase of transient oscillatory dynamics whereby the populations are reaching equilibrium, hence densities stay stable at attractor values H_t = 0.51 and P_t = 0.32. Plots B-F show the oscillatory behaviour of H_t and P_t and how an increasing ε_{max} causes oscillations to become more amplified, first becoming cyclic at lower ε_{max} values and then becoming chaotic at high ε_{max} values. The window at ε_{max} = 0.64 to 0.83 causes cyclic dynamics as seen in Plot E, but chaos ensues after this point (plot F). The increased ε_{max} values cause H_t and P_t to reach larger amplitudes (e.g Plot B, H_t = 0.78, whereas Plot E, H_t = 2.0), however as amplitudes have increased with increasing ε_{max} values, H_t and P_t have become much closer to hitting 0 (extinction). In Plot F, ε_{max} = 1, there is clear evidence that ε_{max} has caused chaos to ensue as periodicity becomes unpredictable, with H_t and P_t attractor values appearing almost randomly at each timestep.
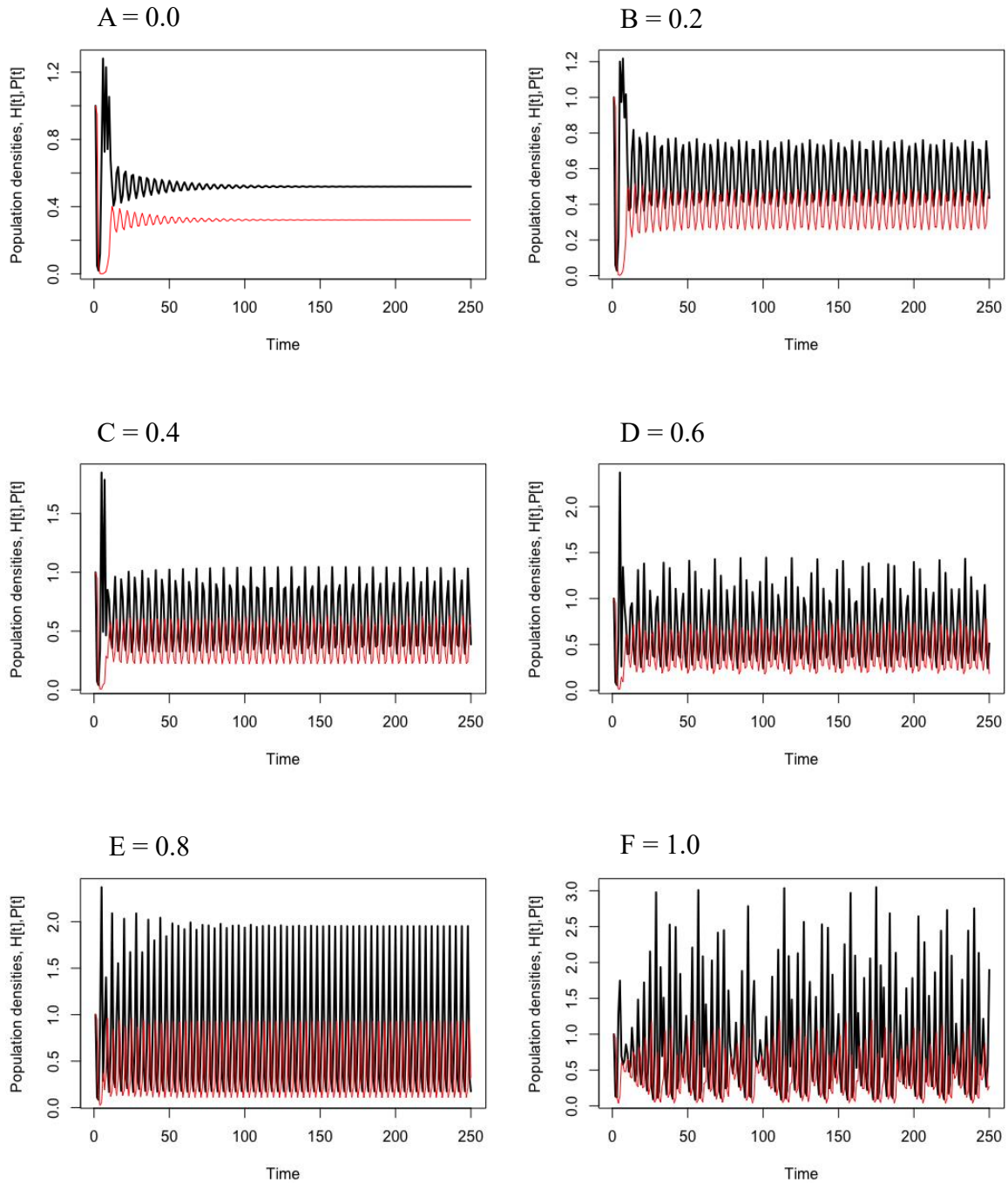
Figure 2: Population time series of H_t (black line) and P_t (red line) at parameter values ε_{max} = 0.0 (A), 0.2 (B), 0.4 (C), 0.6 (D), 0.8 (E) and 1.0 (F) fixed across T_{max} = 250, r = 2 and α = 3.

Figures 3 and 4 illustrate this in another way, showing the attractor values of the last 200 points of H_t and P_t of the 2000 time-steps. As the transient phase has long passed at 2000 time-steps, it does not affect the attractor values seen, and long-term dynamics stay the same

throughout the constant environment (same dynamics at 250 time-steps as 2000 time-steps).
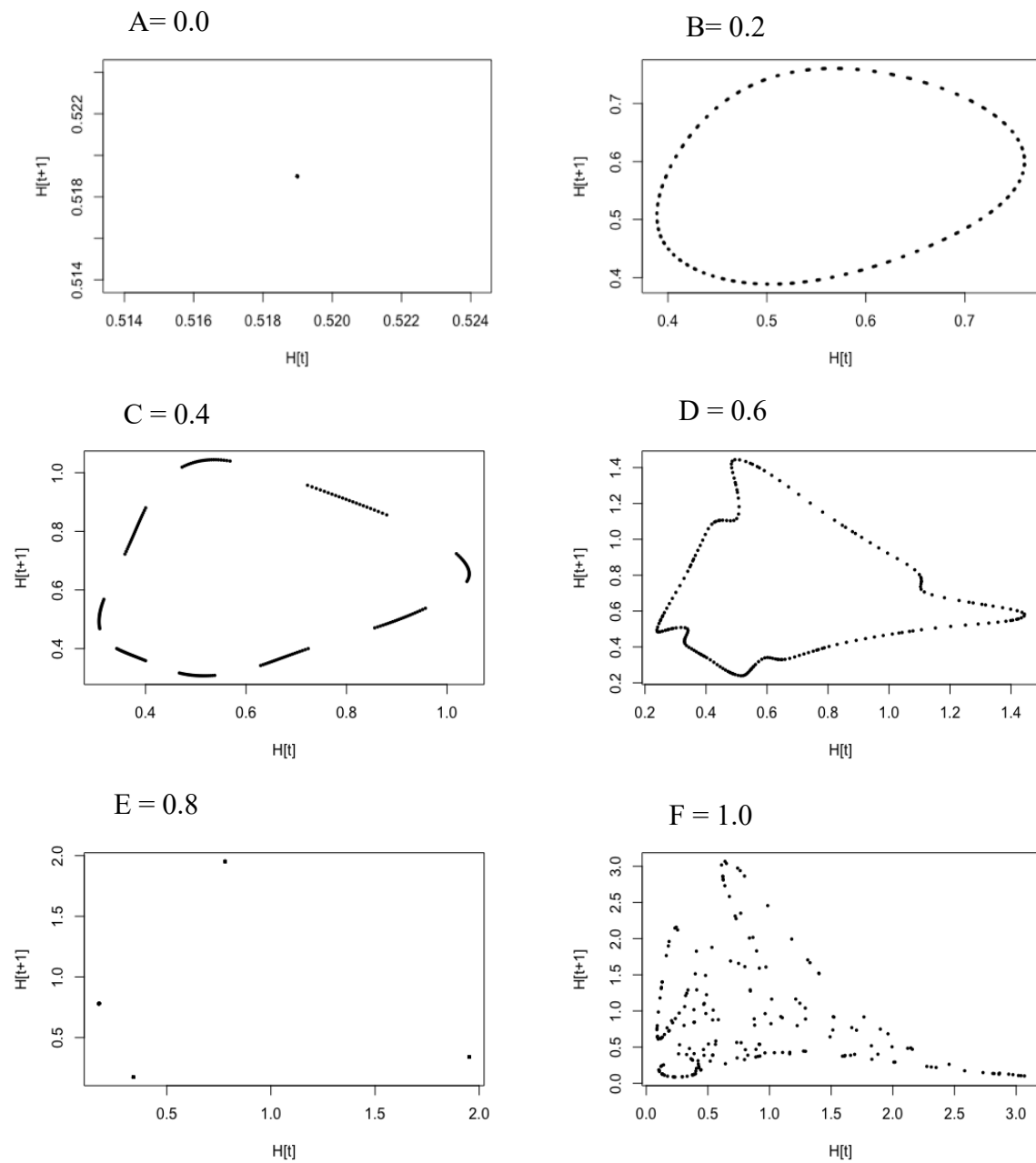
Figure 3: Phase plane plots of H_t and H_{t+1} attractor values at parameter values $\varepsilon_t = 0.0$ (A), 0.2 (B), 0.4 (C), 0.6 (D) and 0.8 (E) and 1.0 (F) (fixed across T_{max}), r = 2 and α = 3, showing the last 200 attractor values of T_{max} = 2000.

Attractor values expand away from the stable point seen in plot A (ε_{max} = 0) thus highlighting that the amplitude of the cycles is increasing. There also becomes less of a clear relationship between H_t and P_t oscillations as ε_{max} is increased from plot A-F (excluding E) in figures 3 and 4. This can be seen by the positions of the last 200 H_t and P_t values

becoming infrequently patterned, whereby H_t and P_t attractor values have become more chaotic and appear more randomly around the equilibrium point (seen in plot F).
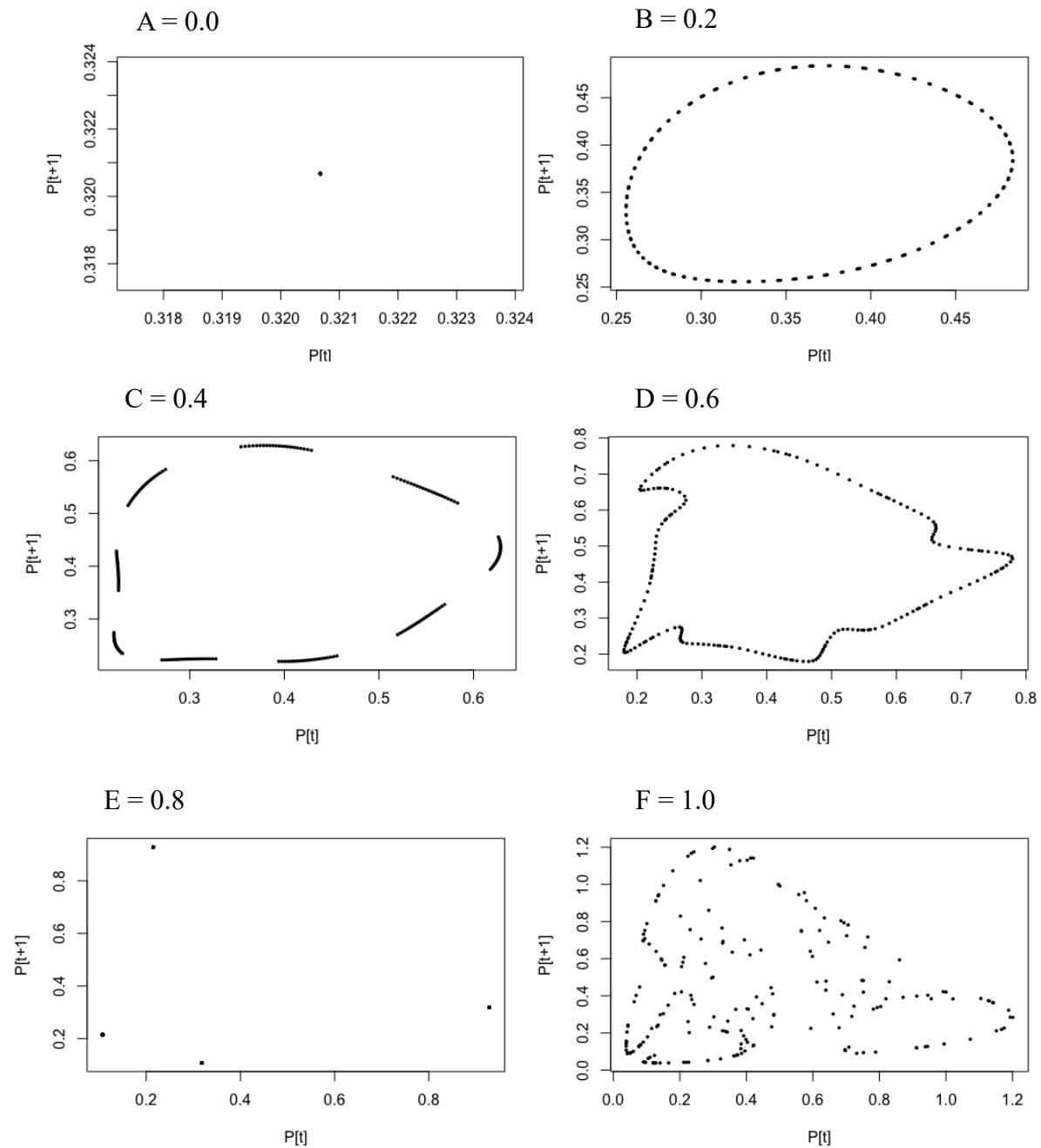
Figure 4: Phase plane plots of P_t and P_{t+1} attractor values at parameter values $\varepsilon_t = 0.0$ (A), 0.2 (B), 0.4 (C), 0.6 (D) and 0.8 (E) and 1.0 (F) (fixed across T_{max}), r = 2 and α = 3, showing the last 200 attractor values of $T_{max} = 2000$.

Plot E ($\varepsilon_{max} = 0.8$) in figures 3 and 4 appears to show oscillations around specific attractor values, which can be referred to figure 1 as it falls within the window of periodic stability,

whereby H_t and P_t are following a similar oscillatory trend around the equilibrium point, though amplitude of oscillations is increased. This is seen by the HT attractor values settling at large differences between one another in a 4-point cycle. In plot F of figures 3 and 4 (ε_{max} = 1), there is clear evidence to show chaos ensues as attractor values are following no pattern.

Oscillations always occur after ε_{max} = 0.14, when host population growth rate reaches 115% of the current population sizewithin H_t and P_t and though there are some slight changes between the cycle periods, both mostly follow a similar trend across T_{max} as the environmental value is kept the same over time. The full table of cycle periods can be seen in appendix 3 (Table S1).

The overall summary from the constant environment (ε_{max} fixed across time) indicates that as ε_{max} is increased, oscillatory attractors occur from a point of stable attractors (ε_{max} > 0.14, or host population growth rate of 115%) and increase in amplitude up to ε_{max} = 1, where chaos ensues as the r value is increased and the chance of instability between H_t and P_t to occur is increased. I now want to compare these results to understand what happens with a trend in the environment, to see if it has any effect on the dynamics of the population densities H_t and P_t.

3.2 Trend in the Environment

Figure 5 highlights the trend of the population dynamics in the host population at the last 200 time-steps of the different T_{max} values, thus the last 200 ε_t values up to ε_{max} were also being used. The parasitoid population follows a very similar trend of stability to instability so was not included. At T_{max} = 500, the attractor values become larger from ε_{max} = 0 to ε_{max} = 1, but never reach periodic/chaotic attractor dynamics and stay stable. The gradient of H_t at increasing ε_{max} values across T_{max} = 500 becomes steeper (see appendix 4) due to the last 200 ε_t values being larger at higher ε_{max} values (at ε_{max} = 0.4, last 200 ε_t values are smaller than at ε_{max} = 1.0), therefore causing H_t attractor values to also become larger, but not become unstable. This can be seen in figure 5, T_{max} = 500, by the increasing thickness of the stable attractors as ε_{max} is increased but unstable dynamics do not occur even at ε_{max} = 1, due to a large v_t.
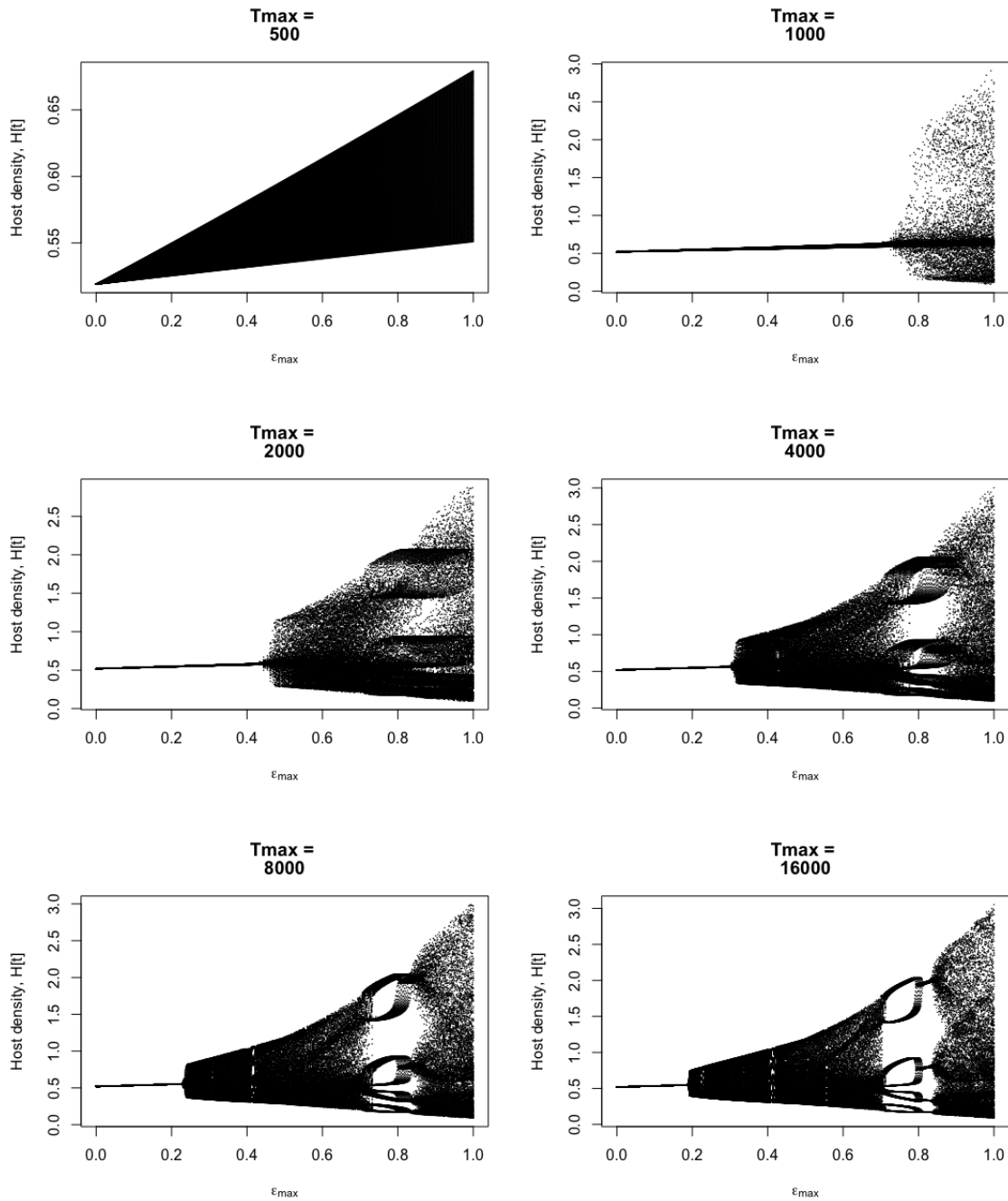
Figure 5: Bifurcation plots of H_t with parameter values starting off at: r = 2, α = 3 and differing T_{max} values (500, 1000, 2000, 4000, 8000, 16000). 501 ε_{max} values from 0 to 1 were used to show how ε_t affected the dynamics. The last 200 attractor values of H_t shown at each ε_{max} value correspond to the last 200 ε_t values.

As T_{max} is increased, the difference between consecutive ε_t and ε_{t+1} values are decreased. Therefore, v_t is larger between ε_t values at, for example, ε_{max} = 0.4 at T_{max} = 500, in

comparison to ε_{max} = 0.4, T_{max} = 4000, whereby ν_t is smaller. The ν_t between ε_t at each time step may explain why the system can stay stable across lower T_{max} values, as H_t does not shift over the carrying capacity and thus not over the population growth rate of 115% of the current population size, still causing attractor values to increase, but not shift into instability due to ν_t being larger (see figure 9).

It should also be mentioned that even at T_{max} = 1000, there are many stable attractor values within the instability seen within the last 200 time-steps when ε_{max} > 0.75 (see plots of T_{max} = 1000 in figure 6 or appendix 4), with ν_t still being large from one time step to next. Lower values of the trend such as within ε_{max} = 0.8 (e.g. ε_t = -0.8 + (800 - 1)*(0.8 * 2)/(1000 - 1) = 0.480), equate to stable attractor values thus do not shift the system into instability, until ε_t is increased to a higher increment (e.g. ε_t =-0.8 + (975 - 1)*(0.8 * 2)/(1000 - 1) = 0.760), where the H_t attractor value and the H_{t+1} attractor value have become close enough together to reach a point of instability (explained in figure 10).

Within the systems whereby T_{max} > 1000, oscillations at a certain ε_t value are seen. As T_{max} is increased, the point at which H_t switches from a stable attractor to unstable attractors shifts to the left, meaning the onset of oscillations happens at an earlier time when T_{max} is increased within the gradually increasing ε_t system. Further, the onset of oscillations does not seem to happen as smoothly within the ε_t system compared to the constant environment, whereby it more abruptly shifts from stable dynamics to sudden oscillatory attractors. For example, at T_{max} = 4000, stable attractors are seen in the last 200 time-steps at ε_{max} = 0.27, ranging from H_t = 0.572 to 0.578, but at ε_{max} = 0.32, the system quickly shifts to amplified oscillations with attractor values ranging from H_t = 0.300 to 0.995.

As T_{max} is increased, the trend in environment system seems to become more comparable to the constant environment with H_t. This is because ν_t is smaller, thus the last 200 ε_t values of higher T_{max} values are closer to the constant environment system seen in figure 1, for example the last 200 time-steps of ε_t = 0.8 at T_{max} = 16000 would be > 0.77, extremely close to the fixed value of 0.8. The window of periodicity can be seen to become more defined at higher T_{max} values also, thus backing the thought that ν_t is the reason behind closer attractor values to the constant environment.

The population time series graphs within figure 6 illustrate ε_t values from figure 5 to observe how H_t (and P_t) changes across an entire timescale (not just the last 200 time-steps), with ε_t changing at every time step. The full figure with T_{max} = 500, 1000, 2000, 4000, 8000 and 16,000 and ε_t = 0.2, 0.4, 0.6, 0.8 and 1.0 can be found in appendix 4 highlighting full time series trend across each of these values.

Figure 6 shows an illustration of specific points of the bifurcation plot (figure 5), showing the full trend of ε_t from -ε_{max} to ε_{max}, instead of the last 200-time steps when affected by T_{max}. As the magnitude of ε_t is increased (-0.2 to 0.2, -0.6 to 0.6 and -1.0 to 1.0), the chance for the system to move from stability to oscillations increases. This is comparable to the constant environment seen in figure 2, whereby larger ε_t values cause H_t to transition from stability to chaos. Larger ε_t values amplify the H_t and P_t chaotic attractor values, creating a higher chance for oscillatory behaviour.

v_t plays a key role in the reasoning behind oscillating attractors appearing earlier at larger T_{max} values. For example, at ε_t = 0.6, no oscillations are seen across every time step of 1000 time-steps. When T_{max} is increased, v_t is smaller meaning ε_t to ε_{t+1} distance is smaller, allowing for chaotic attractors of H_t and P_t to shift into instability. The difference between ε_t values at different T_{max} values can be seen by working out v_t, whereby, for example, v_t = -0.6 + (1000 - 1)*(0.6 *2)/(1000 - 1) – (-0.6 +(999 -1)*(0.6 * 2)/(1000 – 1)) = 0.0012, but when T_{max} is increased, v_t becomes smaller e.g. v_t = -0.6 + (4000 - 1)*(0.6 *2)/(4000 - 1) – (-0.6 +(3999 -1)*(0.6 * 2)/(4000 – 1)) = 0.0003. The v_t value, or difference between ε_t to ε_{t+1}, creates oscillatory population dynamics when it is smaller as it gives more of a chance for H_t and P_t to shift from stability to instability with smaller increments allowing for a more detailed system.
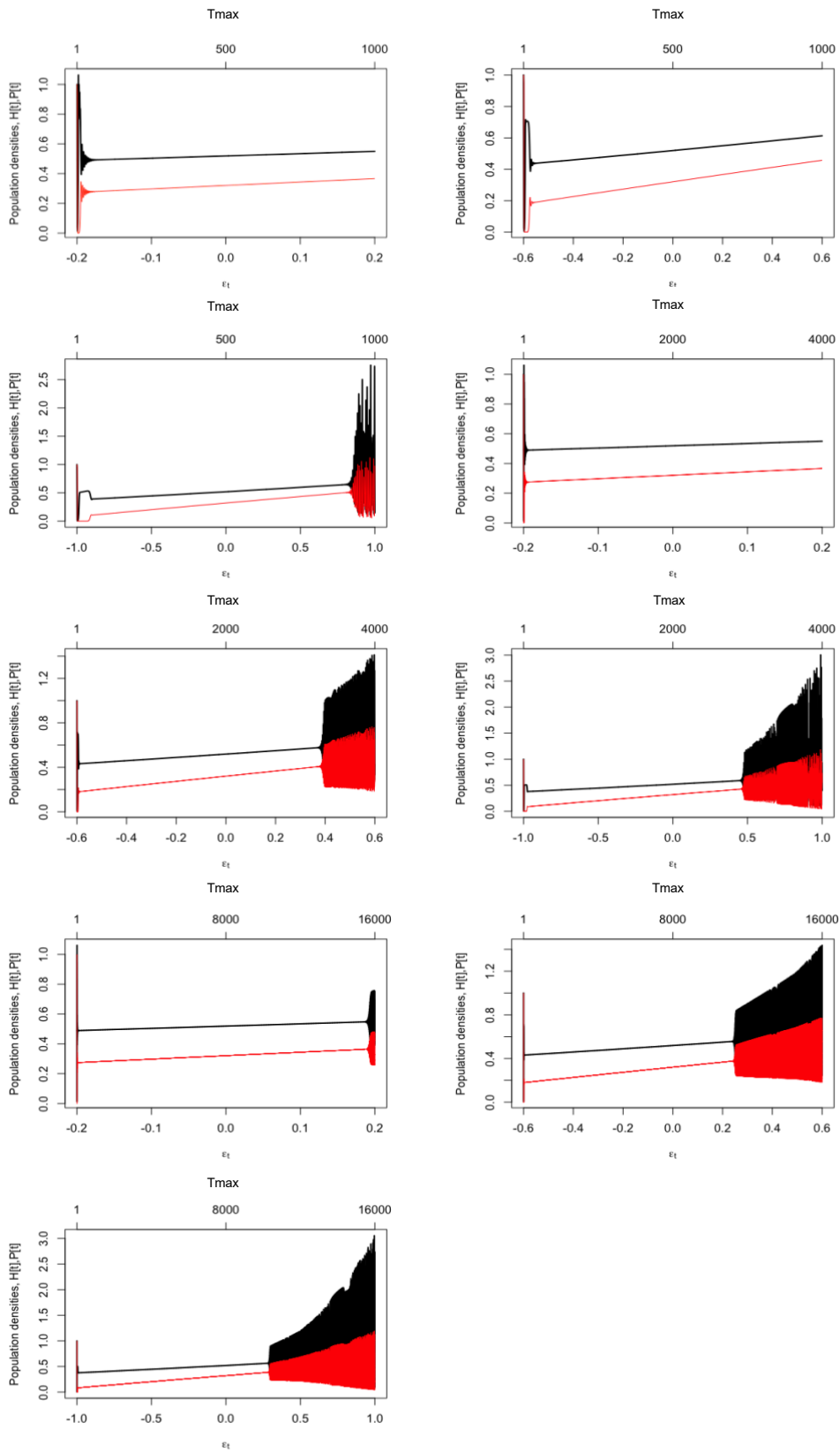
Figure 6: Population time series of H_t (black line) and P_t (red line) at parameter values $\varepsilon_{max} = 0.2$, 0.6 and 1.0 across different timestep values (T_{max} = 1000, 4000, 16,000), r = 2 and α = 3.

Within ε_{max} = 0.6 and T_{max} = 4000, oscillations ensue at around time step 3700, thus at ε_{max} = 0.6 and T_{max} = 16,000 you would expect oscillations to ensue at t = 3700 x 4 = 14,800, however chaos ensues at time step 11,500, which is 3300 time-steps out of when chaos is expected. This indicates that when T_{max} is smaller, larger v_t values clearly play a role in suppressing oscillatory dynamics.

Figure 6 differs from the constant environment (figure 2) as there is always stability before oscillations occur. Amplified chaos is still seen as ε_t reaches higher values for example at ε_{max} = 0.6, H_t = 1.4, at ε_{max} = 1.0, H_t = 3.0, indicating that chaos follows a similar trend to the constant environment system (figure 2) when the ε_t value is closer to the ε_{max} value. This coincides with the T_{max} value, as smaller v_t values cause ε_t values to be closer to the ε_{max} value for a longer period, resulting in similar oscillatory patterns to the constant environment. The larger E values further cause larger host population growth rate percentages, meaning that the system is trying to become cyclic when above 115% of the current population size, and even at higher host population growth rate percentages, however the size of v_t prevents this from occurring.

Within appendix 3 (Table S2), there are clear differences when oscillations occur across different values in both H_t and P_t. At the same ε_{max} value, e.g., at ε_{max} = 0.4, there are no oscillations occurring at 500-, 1000- and 2000-time steps, but oscillations occur at 4000-, 8000-, and 16,000- time steps, due to v_t. It should be noted that though there are key differences between the constant environment and trend in the environment, the results of appendix 3 were not significant enough to rely on as it is an assumption of the most likely cycle period, but still provide valuable insight to differences between the two systems.

The phase plane plots in figure 7 of the last 200 values of H_t follow the trends of stability and chaos seen in figure 6. At T_{max} = 1000 and ε_{max} = 0.2, H_t attractor values gradually increase, but never reach oscillations, representing the stable attractor values seen. At T_{max} = 1000 and ε_{max} = 1.0, at around a value of H_t = 0.61, there is stability from the time series seen. Then, the attractor values amplify quickly to a point at which large amplitudes of chaotic oscillations ensue over a short period of time. This is due to the large v_t value; thus, the value does not spend long close to ε_{max} = 1.0, resulting in stable attractors of H_t at lower ε_t values,

before chaos is seen at higher ε_t values closer to $\varepsilon_{max} = 1.0$, representing the chaotic attractors. In contrast to this, at $T_{max} = 16{,}000$ and $\varepsilon_{max} = 1.0$, ν_t is decreased, thus ε_t is closer to ε_{max} for longer, and the H_t attractor values are similar to the chaotic attractor values seen in figure 3 of the constant environment.
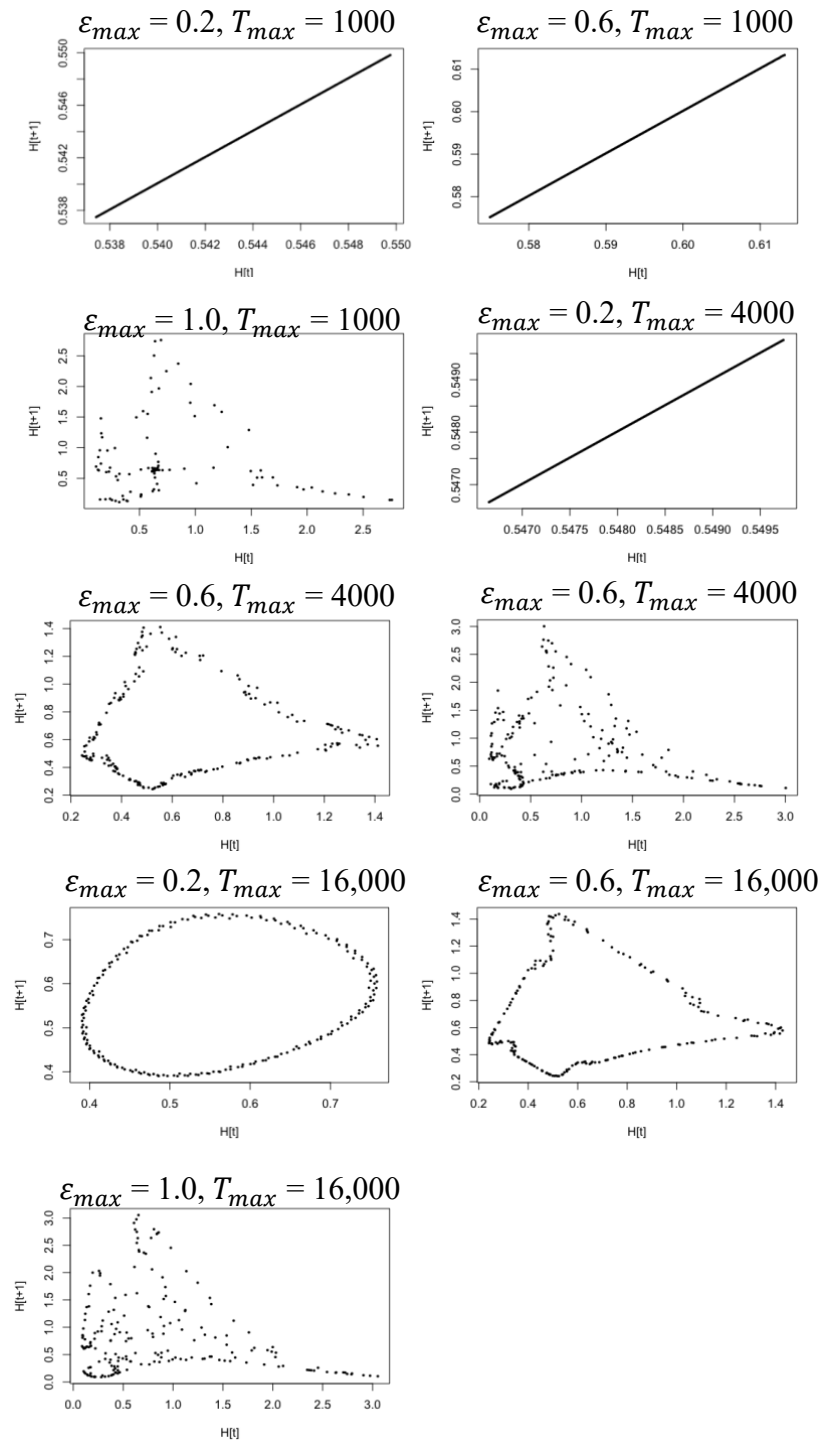

Figure 7: Phase plane plots of H_t and H_{t+1} attractor values at parameter values $\varepsilon_{max} = 0.2$, 0.6 and 1.0 across different timestep values ($T_{max} = 1000$, 4000, 16,000), r = 2 α = 3 showing the last 200 timestep of the T_{max} value (P_t not included as it follows similar trend to H_t).

Within the trend in the environment, stable attractors occur whilst ε_t includes values at which periodic/chaotic attractors have been seen in the constant environment. This indicates that differing sizes of v_t play a part in keeping H_t stable across the trend. To highlight why this is happening, schematic cobweb plots have been plotted on population growth function curves, to indicate why stability may be seen at larger v_t values and instability may be seen at smaller v_t values within the trend, and how the trend in environment compares to the constant environment.

3.3 Schematic Cobweb Analysis of Population Growth Curves

The schematic cobweb diagram on the population growth function curve (figure 8) features how oscillations occur within the constant environment, whereby populations expand and increase in an oscillatory manner. Within figure 8, cycling dynamics are expected as the cobweb fixes to a point where cycling occurs. v_t has no effect on ε_{max} as it is a fixed value, thus the populations oscillate around the equilibrium for a lengthy amount of time steps until finally over a magnitude of time it may settle on a cycling/chaotic attractor. Oscillatory dynamics are seen when the growth curve comes back on itself and shows a spiral like pattern as dynamics increase then proceed to decrease. This can relate to periodic or chaotic dynamics, with chaotic dynamics continuing to grow outwards, whereas periodicity tends to hit the same attractor values. In this case, stable dynamics are seen when the growth curve keeps on growing at a steady pace.

Figure 8 is only altered by the size of ε_{max}, with larger ε_{max} values causing increasingly amplified oscillating population dynamics. $\varepsilon_{max} = 0.8$ falls within the window of periodic stability, thus within this scenario in figure 8, that is why it is expected to follow a highly amplified periodic attractor.

The trend across the environment creates different values of ε_t across different T_{max} values. v_t becomes smaller when T_{max} increases, therefore at higher T_{max} values, ε_t and ε_{t+1} is closer, thus oscillations occur at a certain point in the system. When T_{max} is smaller, there are less time steps, meaning v_t is larger, thus the distance from ε_t to ε_{t+1} is larger, therefore

stability occurs as there is less of a chance for H_t to H_{t+1} to hit oscillatory values before hitting the last value of H_t. This is explained by figures 9 and 10.
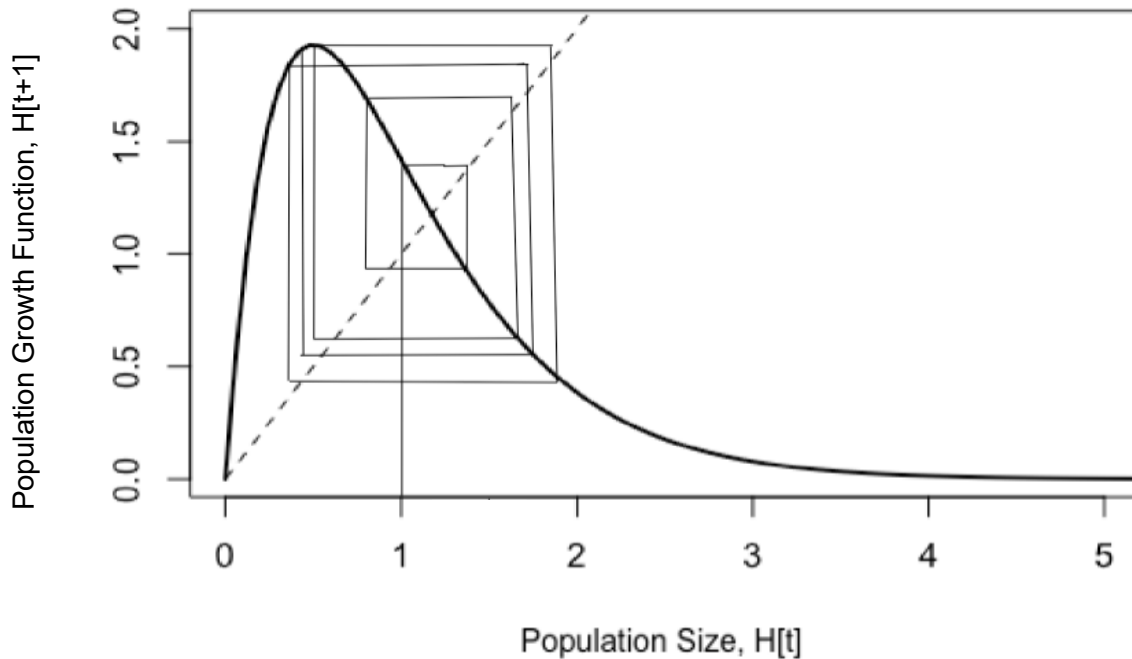
Figure 8: schematic cobweb diagram on a population growth function curve showing a constant environment where $\varepsilon_{max} = 0.8$ fixed throughout time. r = 2, α = 3, $H_1 = 1$ and $P_t =$ 0.05. Black curve corresponds to the growth of H_t across time, drawn black line represents dynamics of H_t from H_1 to H_{t+1} (until T_{max} is reached).

Figure 9 represents a larger v_t value, whereby the distance between ε_t and ε_{t+1} is larger, causing the distance between growth of H_t and growth of H_{t+1} to be larger between each growth curve. This larger v_t value keeps the dynamics of H_t stable. As the distances between each coloured line are so large, due to v_t, H_{t+1} never shifts into unstable dynamics and continually increases up until it reaches T_{max}, as seen by the drawn black line. In comparison to figure 8, where only one intrinsic growth curve is seen and unstable dynamics occur, multiple lines are seen here as the ε_t value shifts the population growth curve to become larger by v_t, keeping the dynamics stable as there is no shift and there is a continual increase of H_t values.

Figure 9: Schematic population growth function curve showing trend in the environment whereby $\varepsilon_{max} = 0.8$, $P_t = 0.05$, H1 = 1, $T_{max} = 5$, r = 2 and α = 3. Black curve corresponds to first population growth of H_t affected by ε_t, and every curve afterwards is population growth of H_{t+1} affected by ε_{t+1} until ε_{max}/the final time-step is reached (light blue line). Drawn black line represents the dynamics of H_t from H_1 to H_{t+1} (until $\varepsilon_{max}/T_{max}$ is reached).

Figure 10 represents a smaller v_t value, whereby growth of H_t and growth of H_{t+1} distances are shorter, as distance between ε_t and ε_{t+1} is smaller. As H_t, starting at $H_1 = 1$, moves to H_{t+1} up to H_{10}, there is an increased opportunity for dynamics to become unstable because of the smaller increment increase from ε_t to ε_{t+1}.

At time-step 8 to 9 (grey curve and second black curve), there is a shift in the dynamics, where the increasing H_t line stops increasing and comes back on itself as the population has overshot its population growth rate. This means that at time step 9, the unstable oscillatory dynamics can be observed by the black line following oscillatory dynamics, caused by possible cyclic/chaotic attractors changing with ε_{t+1}. As seen in Figure 1, any environmental value > 0.14 should cause population instability, as host population growth rate reaches 115% or higher. This is not seen in the trend in the environment due to the ε_t value constantly increasing, thus making it harder for H_t populations to overshoot into instability. The chance of an overshoot, and thus instability, increases when v_t is decreased, as the slower increments allow the H_t dynamics to overshoot and become oscillatory due to ε_t and ε_{t+1} being closer to one another over a long period.
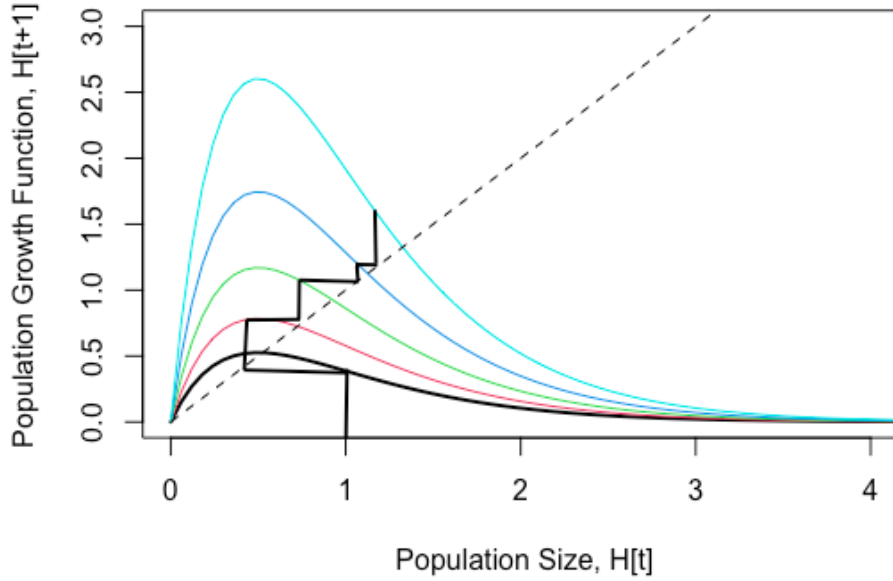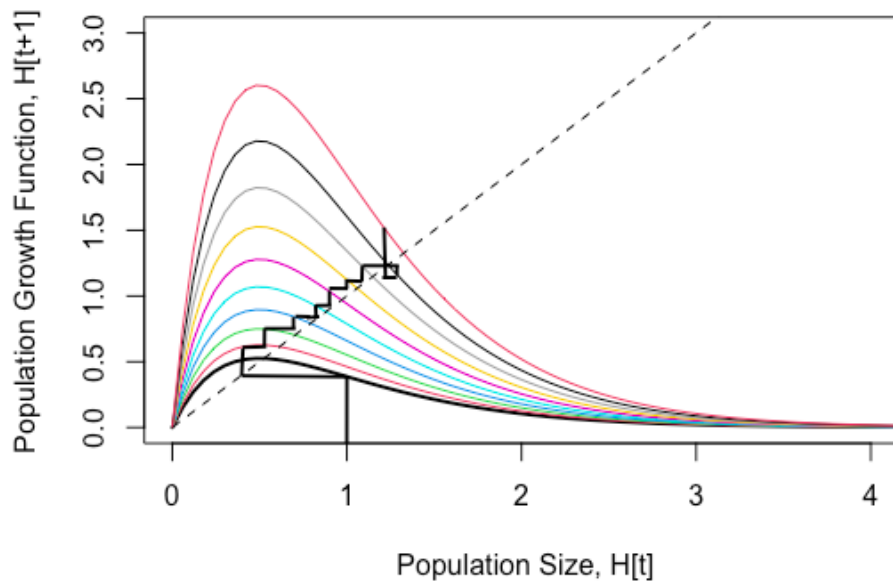
Figure 10: Schematic population growth function curve showing trend in the environment, whereby $\varepsilon_{max} = 0.8$, $P_t = 0.05$, $H_1 = 1$, $T_{max} = 10$, r = 2 and α = 3. Black curve corresponds to first population growth of H_t affected by ε_t, and every curve afterwards is population growth of H_{t+1} affected by ε_{t+1} until ε_{max}/the final time-step is reached (second red line). Thick black line represents the dynamics of H_t from H_1 to H_{t+1} (until $\varepsilon_{max}/T_{max}$ is reached).

Had ε_{max} been increased for both figure 9 and 10, unstable dynamics may have been seen for both. As there are more time-steps and thus ε_t values within a $T_{max} = 10$ system, there is a higher chance that the system overshoots and becomes unstable at an earlier point, with less amplified oscillations. With less time-steps occurring in the $T_{max} = 5$ system and thus a smaller number of ε_t values, with a larger ν_t, the point at which instability occurs may be missed and populations cannot overshoot. However, if ε_{max} is increased to a high value, The $T_{max} = 5$ system may be exposed to a higher ε_{t+1} value from ε_t, causing amplified oscillations to occur more abruptly. Within the $T_{max} = 10$ system, the shift to unstable dynamics would occur earlier giving H_t and P_t more of a chance to track and adapt to environmental change.

4 Discussion

Using a trend within an environment across a host-parasitoid model has been underexplored. Much research has revolved around a constant environment or variation within an environment and how this affects the population dynamics of the system (Thierry et al., 2022, Moore et al., 2021, Moore et al., 2019, Echaubard et al., 2017, Wetherington et al., 2017, Kendall, 2001). By observing how a trend within an environment can affect the population dynamics, I have demonstrated that magnitude and temporal scale can greatly alter host population dynamics in comparison to a constant environment, and how rate of increase of trend is the main cause behind the dynamics seen within a simple host-parasitoid model that is being affected by a trend in the environment.

4.1 Constant Environment Dynamics

By first researching the dynamics of the hosts and parasitoid densities observed within the constant environment, it allowed me to understand the differing impacts of an increased environmental value that is fixed across temporal scale. At any environmental value greater than 0.14, and thus a host population growth rate of 115% of the current population size, oscillatory dynamics occurred. In accordance with past research, increasing the constant environmental value will cause the population dynamics of the system to become more unpredictable, with amplitude increasing, a higher chance of chaos ensuing, and dynamics of host and parasitoids having increased possibility of becoming destabilized (Meisner et al., 2014, Bannerman & Roitberg, 2013, Bonsall et al., 2007), with extinction risks further increasing. These effects on the system may lead to increased chance of phenological asynchrony between host and parasitoid as the environment is increased (Pardikes et al., 2022, Chidawanyika et al., 2019, Wetherington et al., 2017, Hance et al., 2007), causing the potential for trophic desynchronisation and ecosystem failure (Thackeray et al., 2010).

My model implied that anything below a constant environmental value of 0.14 showed stable dynamics, but anything above this value became cyclic/chaotic. This is line with the host population growth rate reaching 115%, due to the environment, which causes the system to turn cyclic/chaotic. The host population growth rate reaching 115% of the current population size and tipping into cyclic characteristics could be due to the increase in competition for resources (Roques & Chekroun, 2011) causing host populations to suddenly start fluctuating

dynamics, therefore leading to parasitoid dynamics fluctuating. The dynamics that lead from stability to periodicity to chaos by increasing the constant environmental value underline the sensitivity of the system to the initial conditions and how small changes to an environmental value can have significant effects on the long-term dynamics on the host-parasitoid system (Wang et al., 2019). This highlights the need of studying trend in the environment as the environmental value changes at every time step from a minimum to a maximum environmental value, causing dynamics to also change at every time step of a temporal scale.

4.2 Comparison Between the Constant and Trend in the Environment

By comparing the constant environment and trend in the environment systems, this accentuates the advantages that future research using a trend in the environment can explore. Whilst the constant environment is important to show how dynamics can occur across fixed, closed systems, they portray a narrow ecological scale (O'Connor & Bernhardt, 2018) where the system is concentrated on a fixed environmental value. The trend in the environment can be used to observe changes to population dynamics across an increasing environment over time, and by changing the magnitude and temporal scale of the trend, we can understand the consequences of slower or faster climate change on population dynamics to reduce climatic unpredictability on these dynamics (Jeffs & Lewis, 2013).

The magnitude of the environmental value caused oscillations to occur with increased amplitudes in both systems, which is expected (Meisner et al., 2014, Bannerman & Roitberg, 2013, Bonsall et al., 2007). However, temporal scale had an influence on the trend in the environment, whereas it had no influence on the constant environment. There were large differences between when the shift from stability to instability occurred, when temporal scale was changed within the trend in the environment. As temporal scale was increased, dynamics in the trend in the environment became more alike the dynamics seen within the constant environment, as the environment spent more time closer to the maximum value, which equated to the constant environment.

4.3 Effect of Rate of Increase on the Trend in the Environment Dynamics

Current research suggests that long-term monitoring of population trends can allow for a better understanding of population dynamics and short time-series can be misleading (White,

2018). My findings suggest that within a trend in the environment, understanding shorter temporal scales in comparison to larger temporal scales is significant due to the different effects it has on population dynamics. Explicitly, it is important to understand changes across a timescale of an environment (Hastings, 2010) as it can summarise differences between a quick climate change increase or a slower climate change increase. Within my findings, the rate of increase could be attributed to the rate of climate change occurring. At larger rates of increase between one environmental value and the next, climate change would occur faster, and populations could struggle to track and adapt to the rapidly changing environment. This can be seen when species exhibit low plasticity, thus struggle to track changing climate variables (Bellard et al., 2012, Berteaux, 2004,). At larger rates of increase, population stability was either kept stable throughout, or it shifted to amplified population instability whereby oscillations of population dynamics were suddenly very large. This could cause consequences to host and parastioid populations as the extremity of climate change occurring so quickly would force them into large cycling/chaotic population dynamics (Mugabo et al., 2019).

If climate is increased at a smaller rate of increase, across larger temporal scales, it gives the populations of host and parasitoids a chance to track the changing climatic conditions at earlier intervals of time. Therefore, species with epigenetic plasticity can adapt to the changing climate with across time (Canale & Henry, 2010). When rate of increase was small, oscillations occurred in a less volatile state, starting off small, but ultimately increasing to larger oscillations seen at later time-steps as the environmental value became larger. As the environmental value becomes larger within the trend in the environment, as does the host population growth rate percentage above the current population size, this is why oscillations become more amplified and chaotic. Species can track and adapt to climate change if rate of increase is slower, however the maximum value of the environment is also a factor to unpredictable population dynamics and whether they possibly become extinct (Maclean & Wilson, 2011). This coincides with research where larger environmental input values to a system cause more unpredictability within population dynamics (Dee et al., 2020, Sekerci, 2020, Meisner et al., 2014, Kendall, 2001), as seen by the increased amplitudes of oscillations that become chaotic at higher environmental values within my findings. With climate change becoming an increasing threat, it may cause stable populations to suddenly tip into

unpredictable oscillatory dynamics thus increasing their chance of extinction if temperature is increased quickly and to higher temperatures.

On a wider scale, the dynamics seen within the trend in the environment due to differences in the rate of increase could attribute to altered development rates (Erguler et al., 2022, Moore et al., 2021), phenologic asynchrony (Pardikes et al., 2022, Chidawanyika et al., 2019, Wetherington et al., 2017, Hance et al., 2007,) and competitive interactions and relationships (Thierry et al., 2020, Jeffs & Lewis, 2013) between hosts and parasitoids. It is important to note that in real life situations, specific effects can vary depending on species involved, ecological characteristics, plasticity to change and the overall environmental context.

4.4 Future Research Using a Trend in the Environment

My research used minimum to maximum trend difference that equated to 2 (-1 to 1) which is somewhat arbitrary, as there was little reason other than studying the effect of trend as to why I chose the values. Future research should consider looking into more concrete biological changes/mechanisms or climate change scenarios (IPCC, 2023, Urban et al., 2016,), as a trend in the environment may alter population dynamics in other ways. Researching how different parameter values (intrinsic growth rate and attack rate) may affect population dynamics with a trend in the environment is also scientific importance. By using the different parameter values stated within the (Kendall, 2001) paper for periodicity, quasi-periodicity, and chaos, this can bring about different dynamical responses to climate change. I have already seen this within my sensitivity analyses and would be beneficial to study the impacts of trends in the environment on these parameter values further, with dynamics becoming stable due to v_t being in place from ε_{max} and T_{max}, when we know with no environmental impact that there are oscillations happening. Starting host and parasitoid densities at different values may also give rise to differing dynamics. The number of time-steps could also be reintroduced to the model as number of generations, and an in-depth analysis of multigenerational population dynamics could be undertaken instead of thinking about the system as a temporal scale.

More advanced models which include other parameter values (specific traits) could allow for a more realistic simulation of what may happen within real life dynamics, as the intricacy and

detail of the model is increased. Many traits have been specifically studied with climate change over time, but as mentioned, looking at the effects that a trend on the environment has on them has been underexplored. Temperature causes life-history traits like body size (Wonglersak et al., 2021, Wonglersak et al., 2020, Tseng et al., 2018), insect development (Régnière et al., 2012, Ratte, 1984) and many other significant traits to change (see research by (Harvey et al., 2022, Laughton & Knell, 2019). This could lead to new population dynamics seen within the trend in the environment within a host-parasitoid model and could further improve knowledge of understanding species responses to climate.

5 Conclusions

I have demonstrated that a trend in the environment shows different population dynamics in comparison to a constant environment depending on the temporal scale and magnitude of environmental values, and how changing the temporal scale and magnitude of the trend causes differences in population dynamics within a simple discrete-time host-parasitoid model. The research highlights that as the rate of increase of the trend in the environment is decreased, there is an increased chance for stability to become unstable at smaller environmental values. This is somewhat beneficial as it allows the populations of hosts and parasitoids to track and adapt to climate change at earlier time-steps. At larger rates of increase of the trend in the environment, the dynamics rather more abruptly shift from stable dynamics to amplified oscillations at later time-steps and thus larger environmental values, resulting in increased unpredictability and potential of extinction for host and parastioid populations. This highlights the need for future study into trends within an environment on population dynamics, as they can greatly shift dynamics from points of stability to cycling/chaos. With climate change increasing, it is best to start tracking population dynamics with regards to future climate projections as soon as possible. By applying trends in the environment to simulation models, it can help us predict and prevent potential biodiversity crises at different predicted rates of increase of climate change.

6. Appendix

6.1 Appendix 1: H&S and Risk Assessment Form

HEALTH & SAFETY
IECHYD A DIOGELWCH

Office Risk Assessment			
BRETT PETERSEN, 980892.			
College/ PSU	**Biosciences**	**Assessment Date**	22/02/23
Location	**Wallace building, room 121**	**Assessor**	**Professor Mike Fowler**
Activity	**Mres research project**	**Review Date (if applicable)**	24/02/2023
Associated documents:	• **Sitting at a computer**		

This is a generic risk assessment for an office. There should be **one** of these documents for each office and followed by all office users. Check boxes are used to guide you, please tick the controls used. This generic office risk assessment should also be amended to identify any additional hazards and controls required for **your office**. Line managers/ supervisors are responsible for ensuring that controls are implemented and communicated to staff/ students and safe working practices are monitored. The university should have already carried out and completed an office risk assessment for Wallace room 121, thus the majority of safety procedures for this space should already have been assessed.

Part 1: Risk Assessment

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/ No
Slips and trips.	Staff and visitors may be injured if they trip over objects or slip on spillages.	All areas well lit. The flooring is well maintained. General good housekeeping is carried out. Staff/ students keep work areas clear, e.g. no boxes are left in walkways. Trailing leads or cables are moved or protected. Staff/ students mop up or report spillages.	Make sure personal area is clear of any bags/ clothing that could cause a trip. Make sure any laptop cable is tidily placed away from walking area.	Staff. Me. Other students.	Date of starting	yes

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HEALTH & SAFETY
IECHYD A DIOGELWCH

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/ No
Display screen equipment e.g. computers, laptops.	Staff risk posture problems and pain, discomfort or injuries e.g. to their hands/ arms, from overuse or improper use or from poorly designed workstations or work environments. Headaches or sore eyes can also occur, e.g. if the lighting is poor.	All **staff** have received mandatory DSE training as part of their induction. All DSE users self-assess their workstation; issues identified are raised with their line manager/ supervisor and risks are reduced. Review assessment upon change to user, equipment or the location of the workstation. Work is planned to include regular breaks or change of activity: • Employer pays for eye tests for display screen "users". • Employer pays a fixed amount to cover the cost of basic spectacles prescribed for DSE use only; or to contribute to a more expensive pair. Laptop users trained to carry out own DSE assessment for use away from office. When used at office, laptop should be used with docking station, screen, keyboard and mouse.	Make sure to take regular breaks away from the screen. Clean area of work	Me.		yes
Working at height e.g. filing on top shelves, etc.	Falls from any height can cause bruising and fractures.	Where possible the storage of items at height is avoided. A step ladder is available if staff need to access items on high shelves, etc. Step ladders are inspected, to ensure they remain safe to use.	No.	Staff.		Yes.
Health of	All staff could	Staff/ students have management/	Look out for others in case	Staff.		Yes.

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What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/ No
workers in the office environment.	be affected by factors such as, lack of job control, bullying, not knowing their role, etc.	supervisory help to understand what their duties and responsibilities are. Staff/ student can speak confidentially to a manager or supervisor if they are feeling unwell or uneasy about things at work. Change is managed and communicated effectively. Systems are in place to ensure demands are reasonable. Signpost staff to mental health assistance and professional mental health services should they require them (see University Guidance - Health and Wellbeing).	they do not seem okay.

Make sure to look after oneself and take breaks when needed. | Me. | | |
| Electrical | Staff could get electrical shocks or burns from using faulty electrical equipment.

Electrical faults can also lead to fires. | Staff/ students are trained to spot and report any defective plugs, discoloured sockets or damaged cable/ equipment. Defective equipment taken out of use safely and promptly replaced. Staff/ students are told not to bring in their own appliances, toasters, fans, etc.

Electrical appliances are PAT tested. | Make sure own electrical items brought in are safe to use as university appliances should be up to health and safety standards. | Staff. Me. Other students. | | yes |
| Fire | If trapped, staff could suffer fatal injuries from smoke inhalation/ burns. | • A Fire risk assessment has been completed and adequate fire safety measures are in place.
• Evacuation plan has been implemented and tested.
• Fire alarm tested regularly. | No. | Staff. | | Yes. |

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/ No
		• Fire drills carried out at least once a year. **All staff** have received mandatory fire awareness training as part of their induction. Regular checks made to ensure escape routes and fire exit doors are not obstructed. Combustible materials are stored safely. Waste is removed regularly.				
Work equipment including, photocopier, printers, paper shredders, guillotines, etc.	Staff could get electrical shocks or burns from using faulty electrical equipment.

Staff may also suffer injury from moving parts of equipment or unbalanced equipment. | All new equipment checked before first use to ensure there are no obvious accessible dangerous moving parts, or siting of the equipment does not cause additional hazards. Staff/ students trained in use of equipment where necessary. Checks in place to ensure new staff/ students are trained to use equipment. Staff encouraged to spot and report any defects. Defective equipment is taken out of use safely and promptly replaced. | Be careful when using said equipment and not get distracted by other tasks when doing so. | | | |
| Cleaning | Staff risk skin irritation or eye damage from direct contact with cleaning | Offices are cleaned by trained cleaning staff.

If cleaning is carried out by office users: | No. | | | Yes |

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What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
	chemicals. Vapour from cleaning chemicals may cause breathing problems.	Cleaning products marked 'irritant' have been replaced by milder alternatives where available. Mops, brushes and protective gloves are provided and used, if required. Staff are shown how to use cleaning products safely. Cleaning materials are stored in a safe location.				
Asbestos	When materials that contain asbestos are disturbed or damaged, fibres are released into the air. When these fibres are inhaled they can cause serious diseases (e.g. mesothelioma, asbestosis, lung cancer and pleural thickening).	• An asbestos survey has been carried out. • Office users must not carry out building maintenance activities, these are to be arranged through the Estates Helpdesk • If asbestos is considered present, planned measures are in place to manage asbestos and warn visiting workers etc.	No.			Yes

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
No actions required – all safety hazards have been thought of and taken care of by university staff that may lead to serious injury or any problem regarding technical fault etc.	Swansea biosciences department	ASAP.	Yes/

Further information can be found on the Health & Safety intranet page: https://staff.swansea.ac.uk/healthsafety/

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6.2 Appendix 2: R Code

#Bifurcation plots:

```
#set parameter values (intrinsic growth rate, attack rate,
Tmax, Emax, matrix for iteration of env value over tmax)
r <- 2
a <- 3
Tmax <- 2000
e.r.values <- seq(0, 1, length.out = 501)
P.Y <- matrix(0, nrow = length(e.r.values), ncol = Tmax) ->
H.Y -> H.X -> P.X -> H.Z -> P.Z -> H.er -> P.er

#change Tmax <- 500,1000,4000,8000,16000 for other tmax values

#for loop to run each env value across tmax (in the trend, env
goes from -e.r to e.r)

for (i in 1:length(e.r.values)){
  e.r <- e.r.values[i]

#set the trend in environment (-emax to emax across tmax)
  z <- seq(-e.r, e.r, length = Tmax)

#set initial desnities to 1
 1 -> H.Z[,1] -> P.Z[,1] -> H.er[,1] -> P.er[,1]




    for(t in 1: (Tmax - 1)){
    H.Z[i,t+1] <- H.Z[i,t] * exp(r * (1-H.Z[i,t])-
a*P.Z[i,t]+z[t])
    P.Z[i,t+1] <- H.Z[i,t]*(1-exp(-a * P.Z[i,t]))
```

```
    H.er[i,t+1] <- H.er[i,t] * exp(r * (1-H.er[i,t])-
a*P.er[i,t]+e.r)
    P.er[i,t+1] <- H.er[i,t]*(1-exp(-a * P.er[i,t]))
      }
}


#bifurcation plot of constant environment
matplot(e.r.values, tail(H.er, c(length(e.r.values), 200)),
pch = 16, cex = 0.2, col = "black", xlab =
expression(paste(epsilon[max])), ylab = 'Host density, H[t]')


#bifurcation plot of trend in the environment
matplot(e.r.values, tail(H.Z, c(length(e.r.values), 250)), pch
= 16, cex = 0.2, col = "black", xlab =
expression(paste(epsilon[max])), ylab = 'Host density, H[t]',
main = c('Tmax = ', Tmax))


#can also be done for parasitoid using P.Z/P.er if wanting to
check bifurcation of parasitoid




#Time series plots:
#set parameter values (intrinsic growth rate, attack rate,
Tmax, Emax)
# within the constant environment, plot Tmax = 250 to show
clearer dynamics. Makes no difference to dynamics.
r <- 2
a <- 3
Tmax <- 2000
e.r.values <- seq(0, 1, length.out = 51)


#change Tmax <- 500,1000,4000,8000,16000 for other tmax values
```

```
#set specific emax value (e.r.values[1] = 0.0, [11] = 0.2,
[21] = 0.4, [31] = 0.6, [41] = 0.8, e.r.values[51] = 1.0.
e.r <- e.r.values[21]


#e.r.values[21] would = 0.4


#set trend in environment
z <- seq(-e.r, e.r, length = Tmax)


#set up the matrix and the densities
  P.Z <- matrix(0, nrow = Tmax, ncol = 1) -> H.Z -> H.er ->
P.er
  H.Z[1] <- 1 -> P.Z[1] -> H.er[1] -> P.er[1]


#for loop to look at the fixed constant environment and trend
in the environment (-emax to plus emax) across time

for(t in 1: (Tmax - 1)){
 H.Z[t+1] <- H.Z[t] * exp(r * (1-H.Z[t])-a*P.Z[t]+z[t])
 P.Z[t+1] <- H.Z[t]*(1-exp(-a * P.Z[t]))


 H.er[t+1] <- H.er[t] * exp(r * (1-H.er[t])-a*P.er[t]+e.r)
 P.er[t+1] <- H.er[t]*(1-exp(-a * P.er[t]))


 }


#Constant environment time series plot
plot(H.er, type = "l", lwd = 2, xlab = 'Time', ylab =
"Population densities, H[t],P[t]")
#add parasitoid
 lines(P.er, col = "red" )


#trend in the environment time series plot
```

```r
plot(z, H.Z, type = "l", lwd = 2, xlab =
expression(paste(epsilon[t])), ylab = "Population densities,
H[t],P[t]")
 axis(3, at = seq(z[1],z[Tmax], length.out = 3), labels = c(1,
Tmax/2, Tmax), xlab = "Time")
#add parasitoid
 lines(z, P.Z, col = "red")


#phase plane plots
#constant env
plot(H.er[1800:2000],H.er[1801:2001], type = 'p', pch = 16,
cex = 0.5, xlab = 'H[t]', ylab = 'H[t+1]')
 plot(P.er[1800:2000],P.er[1801:2001], type = 'p', pch = 16,
cex = 0.5, xlab = 'P[t]', ylab = 'P[t+1]')


#trend in environment
plot(H.Z[1800:2000],H.Z[1801:2001], type = 'p', pch = 16, cex
= 0.5, xlab = 'H[t]', ylab = 'H[t+1]')
 plot(P.Z[1800:2000],P.Z[1801:2001], type = 'p', pch = 16, cex
= 0.5, xlab = 'P[t]', ylab = 'P[t+1]')


#change value of H.Z & H.Z+1 to correspond with last 200 time-
steps of set Tmax e.g if Tmax = 4000, H.Z = 3800:4000, H.Z+1 =
3801:4001. Same with P.er.


#cycle period tables

#set parameter values
r <- 2
a <- 3
e.r.values <- seq(0, 1, length.out = 51)
Tmax.values <- c(500, 1000, 2000, 4000, 8000, 16000)
```

```r
#set for loop matrix for most likely cycle period of host or
parasitoid and if any values become extinct
cycle.period.H.Z.B <- matrix(NA, length(e.r.values),
length(Tmax.values)) -> cycle.period.P.Z.B  ->
cycle.period.H.er -> cycle.period.P.er
extinct.H.Z.B <- matrix(0, length(e.r.values),
length(Tmax.values)) -> extinct.P.Z.B  ->extinct.H.er ->
extinct.P.er

for (i in 1:length(e.r.values)) {
  e.r <- e.r.values[i]

  for (j in 1:length(Tmax.values)) {
    Tmax <- Tmax.values[j]

    z <- seq(-e.r, e.r, length = Tmax)
    y <- replicate(its, sample(z, Tmax))

    H.Z.B <- 1 -> P.Z.B -> H.er -> P.er


    for (t in 1:(Tmax - 1)) {
      H.Z.B[t + 1] <- H.Z.B[t] * exp(r * (1 - H.Z.B[t]) - a *
P.Z.B[t] + z[t])
      P.Z.B[t + 1] <- H.Z.B[t] * (1 - exp(-a * P.Z.B[t])

      H.er[t + 1] <- H.er[t] * exp(r * (1 - H.er[t]) - a *
P.er[t] + e.r)
      P.er[t + 1] <- H.er[t] * (1 - exp(-a * P.er[t]))
    }

    if (var(tail(diff(H.Z.B), 200)) > 0.01) {
      co.H.Z.B <- acf(tail(H.Z.B, 200), lag.max = 20, plot =
FALSE)
```

```
      cycle.period.H.Z.B[i, j] <-
        which.max(co.H.Z.B$acf[2:21]) *
(max(co.H.Z.B$acf[2:21]) > 0.15)
    }
    if (tail(H.Z.B, 1) == 0) {
      extinct.H.Z.B[i, j] <- 1
    }


    if (var(tail(diff(P.Z.B), 200)) > 0.01) {
      co.P.Z.B <- acf(tail(P.Z.B, 200), lag.max = 20, plot =
FALSE)
      cycle.period.P.Z.B[i, j] <-
        which.max(co.P.Z.B$acf[2:21]) *
(max(co.P.Z.B$acf[2:21]) > 0.15)
    }
    if (tail(P.Z.B, 1) == 0) {
      extinct.P.Z.B[i, j] <- 1
    }


    if (var(tail(diff(H.er), 200)) > 0.01) {
      co.H.er <- acf(tail(H.er, 200), lag.max = 20, plot =
FALSE)
      cycle.period.H.er[i, j] <-
        which.max(co.H.er$acf[2:21]) * (max(co.H.er$acf[2:21])
> 0.15)
    }
    if (tail(H.er, 1) == 0) {
      extinct.H.er[i, j] <- 1
    }


    if (var(tail(diff(P.er), 200)) > 0.01) {
      co.P.er <- acf(tail(P.er, 200), lag.max = 20, plot =
FALSE)
      cycle.period.P.er[i, j] <-
```

```
        which.max(co.P.er$acf[2:21]) * (max(co.P.er$acf[2:21])
> 0.15)
    }
    if (tail(P.er, 1) == 0) {
      extinct.P.er[i, j] <- 1
    }
  }
}


# tables
cycle.period.H.Z.B
cycle.period.P.Z.B
cycle.period.H.er
cycle.period.P.er


#population growth functions:
# set parameter values
r <- 2
a <- 3
n <- seq(0, r*a, length.out =101) # host
n.p <- 0.05 #parasitoid


#constant environment
n.er <- 0.8 # constant environmental value
f.n.er <- exp(r * (1-n)-a*n.p + n.er[1])
plot(n, n*f.n.er, type = 'l', lwd = 2, xlab = ' population
size, H[t]', ylab = 'population growth function, H[t+1]', ylim
= c(0,2), xlim = c(0,5))
lines(n, n, lty = 2) #equilibirum line


#trend in environment
n.z <- seq(-0.8,0.8, length.out = 10)


f.n.1 <- exp(r * (1-n)-a*n.p + n.z[1])
```

```
f.n.2 <- exp(r * (1-n)-a*n.p + n.z[2])
f.n.3 <- exp(r * (1-n)-a*n.p + n.z[3])
f.n.4 <- exp(r * (1-n)-a*n.p + n.z[4])
f.n.5 <- exp(r * (1-n)-a*n.p + n.z[5])
f.n.6 <- exp(r * (1-n)-a*n.p + n.z[6])
f.n.7 <- exp(r * (1-n)-a*n.p + n.z[7])
f.n.8 <- exp(r * (1-n)-a*n.p + n.z[8])
f.n.9 <- exp(r * (1-n)-a*n.p + n.z[9])
f.n.10 <- exp(r * (1-n)-a*n.p + n.z[10])

plot(n, n*f.n.1, type = 'l', lwd = 2, xlab = ' population
size, H[t]', ylab = 'population growth function, H[t+1]', ylim
= c(0,2), xlim = c(0,4))
lines(n, n*f.n.2, col = 2)
lines(n, n*f.n.3, col = 3)
lines(n, n*f.n.4, col = 4)
lines(n, n*f.n.5, col =5)
lines(n, n*f.n.6, col =6)
lines(n, n*f.n.7, col = 7)
lines(n, n*f.n.8, col = 8)
lines(n, n*f.n.9, col = 9)
lines(n, n*f.n.10, col = 10)
lines(n, n, lty = 2) #equilibirum line
```

6.3 Appendix 3: Cycle Period Tables

Table S1: most likely cycle period of host and parasitoid densities in the constant environment, ε_{max} = 51 values from 0 to 1, across T_{max} = 500, 1000, 2000, 4000, 8000 and 16,000, r = 2, α = 3. NA = no cycling seen therefore stability is occurring. Autocorrelation function was used to select most likely cycle lengths (H_t cycle length = blue, Pt cycle length = red, if H_t and Pt were same cycle lengths = black).

	Most likely cycle length (Ht/Pt)					
Tmax value **Emax**	500	1000	2000	4000	8000	16,000
0.00	NA	NA	NA	NA	NA	NA
0.02	NA	NA	NA	NA	NA	NA
0.04	NA	NA	NA	NA	NA	NA
0.06	NA	NA	NA	NA	NA	NA
0.08	NA	NA	NA	NA	NA	NA
0.10	NA	NA	NA	NA	NA	NA
0.12	NA	NA	NA	NA	NA	NA
0.14	NA	NA	NA	NA	NA	NA
0.16	14 NA	14 NA	14 NA	14 NA	14 NA	14 NA
0.18	14 NA	14 NA	14 NA	14 NA	14 NA	14 NA
0.20	14	14	14	14	14	14
0.22	14	14	14	14	14	14
0.24	14	14	14	14	14	14
0.26	14	14	14	14	14	14
0.28	14	14	14	14	14	14
0.30	9	9	9	9	9	9
0.32	9	9	9	9	9	9
0.34	9	9	9	9	9	9
0.36	9	9	9	9	9	9
0.38	9	9	9	9	9	9
0.40	9	9	9	9	9	9
0.42	9	9	9	9	9	9

0.44	9	9	9	9	9	9
0.46	9	9	9	9	9	9
0.48	9	9	9	9	9	9
0.50	9	9	9	9	9	9
0.52	13	13	13	13	13	13
0.54	13	13	13	13	13	13
0.56	13	13	13	13	13	13
0.58	13	13	13	13	13	13
0.60	17	17	17	17	17	17
0.62	17	17	17	17	17	17
0.64	4	4	4	4	4	4
0.66	4	4	4	4	4	4
0.68	4	4	4	4	4	4
0.70	8	8	8	8	8	8
0.72	8	8	8	8	8	8
0.74	8	8	8	8	8	8
0.76	8	8	8	8	8	8
0.78	8	8	8	8	8	8
0.80	4	4	4	4	4	4
0.82	4	4	4	4	4	4
0.84	4	4	4	4	4	4
0.86	12	4	4	4	4	4
0.88	4	4	4	4	4	4
0.90	4	4	4	4	4	4
0.92	4	4	4	4	4	4
0.94	13	13	13	13	13	13
0.96	13 4	13 4	13	13	4	13
0.98	4	4	4	4	4	4
1.00	4	4	4	4	4	4

Table S2: most likely cycle period of host and parasitoid densities across the trend in the environment, ε_{max} = 51 values from 0 to 1, across T_{max} = 500, 1000, 2000, 4000, 8000 and 16,000, r = 2, α = 3. NA = no cycling seen therefore stability is occurring. Autocorrelation function was used to select most likely cycle lengths (Ht cycle length = blue, Pt cycle length = red, if Ht and Pt were same cycle lengths = black).

Tmax value / Emax	Most likely cycle length (Ht/Pt)					
	500	1000	2000	4000	8000	16,000
0.00	NA	NA	NA	NA	NA	NA
0.02	NA	NA	NA	NA	NA	NA
0.04	NA	NA	NA	NA	NA	NA
0.06	NA	NA	NA	NA	NA	NA
0.08	NA	NA	NA	NA	NA	NA
0.10	NA	NA	NA	NA	NA	NA
0.12	NA	NA	NA	NA	NA	NA
0.14	NA	NA	NA	NA	NA	NA
0.16	NA	NA	NA	NA	NA	NA
0.18	NA	NA	NA	NA	NA	NA
0.20	NA	NA	NA	NA	NA	14 NA
0.22	NA	NA	NA	NA	NA	14
0.24	NA	NA	NA	NA	14 NA	14
0.26	NA	NA	NA	NA	14	14
0.28	NA	NA	NA	NA	14	14
0.30	NA	NA	NA	NA	9	9
0.32	NA	NA	NA	9 NA	9	9
0.34	NA	NA	NA	9	9	9
0.36	NA	NA	NA	9	9	9
0.38	NA	NA	NA	9	9	9
0.40	NA	NA	NA	9	9	9
0.42	NA	NA	NA	9	9	9
0.44	NA	NA	NA	9	9	9

0.46	NA	NA	NA	9	9	9
0.48	NA	NA	4 NA	9	9	9
0.50	NA	NA	9	9	9	9
0.52	NA	NA	9	9	13	13
0.54	NA	NA	13	13	13	13
0.56	NA	NA	13	13	13	13
0.58	NA	NA	13	13	13	13
0.60	NA	NA	13	13	17 13	17
0.62	NA	NA	13	17	17	17
0.64	NA	NA	13	17	17 4	4
0.66	NA	NA	4	4	4	4
0.68	NA	NA	4	4	4	4
0.70	NA	NA	4	4	4	4
0.72	NA	NA	4	4	8	8
0.74	NA	NA	4	4	8	8
0.76	NA	NA	4	8	8	8
0.78	NA	NA	8 4	8	8	8
0.80	NA	NA	8	8	8	8 4
0.82	NA	4	8	8	8 4	4
0.84	NA	4	8	8	4	4
0.86	NA	4	8	8 4	4	4
0.88	NA	4	8	4	12 4	4
0.90	NA	4	8	4	4	4
0.92	NA	4	8 4	4	4	4
0.94	NA	4	8 4	4	4	4
0.96	NA	4	4	4	4	4
0.98	NA	4	4	4	4	13 4
1.00	NA	4	4	4	4	4

6.4 Appendix 4: Time Series Analysis of Host and Parasitoid Densities in the Trend in the Environment
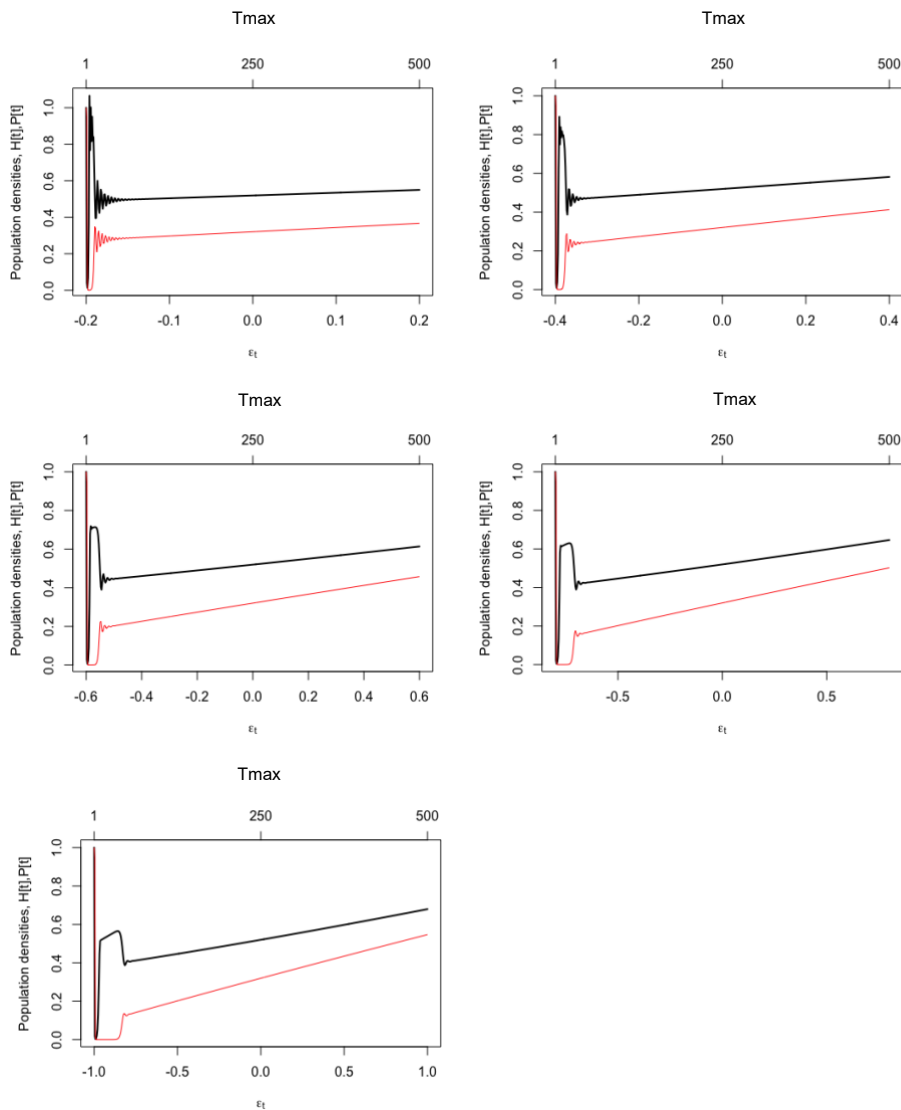

Figure S11: Population time series of H_t (black line) and P_t (red line) at parameter values ε_{max} = 0.2, 0.4, 0.6, 0.8 and 1.0 across T_{max} = 500, r = 2 and α = 3.
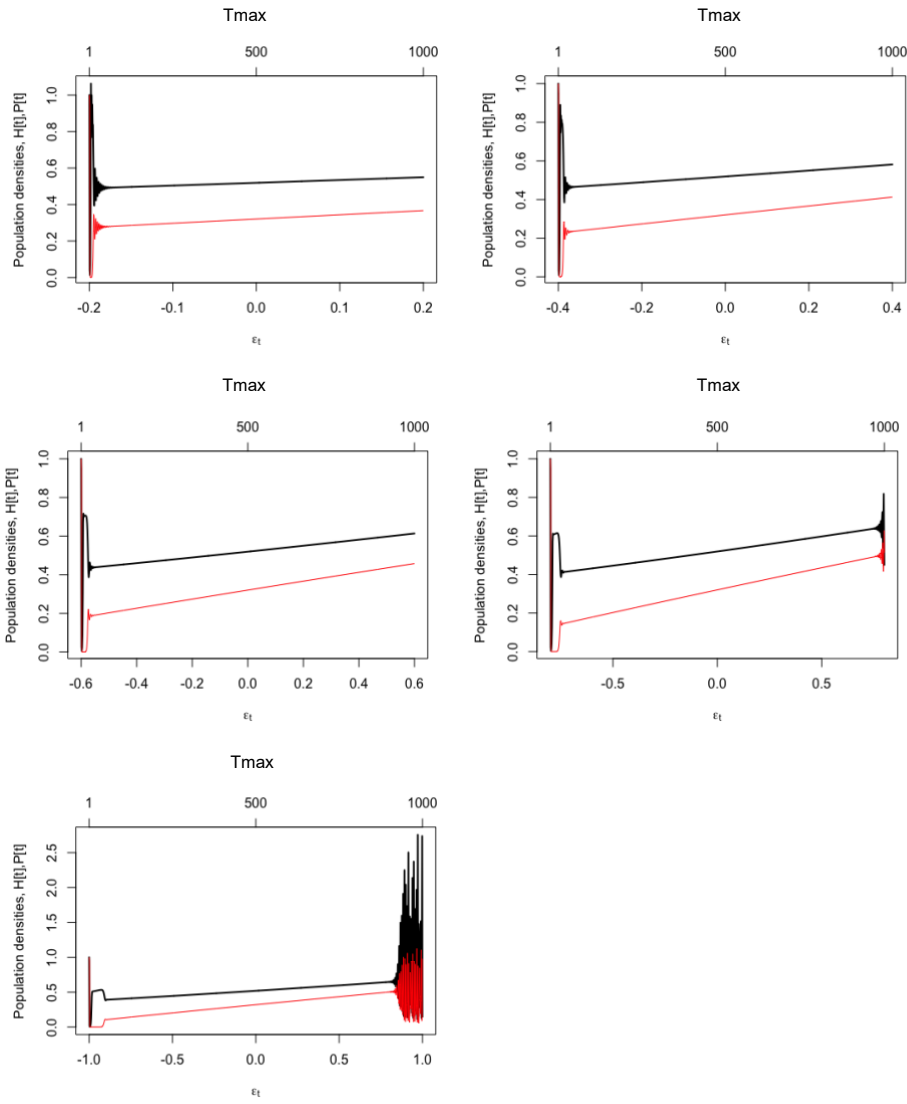
Figure S12: Population time series of H_t (black line) and P_t (red line) at parameter values ε_{max} = 0.2, 0.4, 0.6, 0.8 and 1.0 across T_{max} = 1000, r = 2 and α = 3.
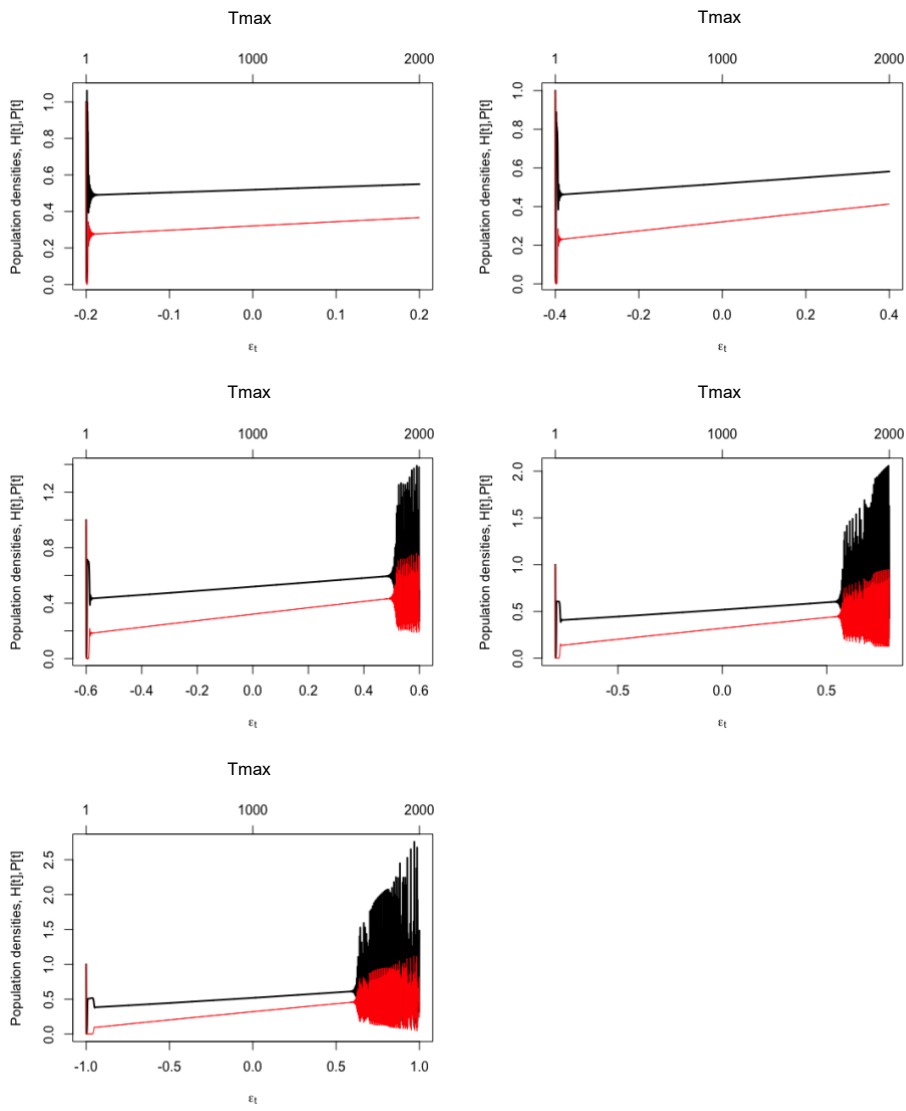
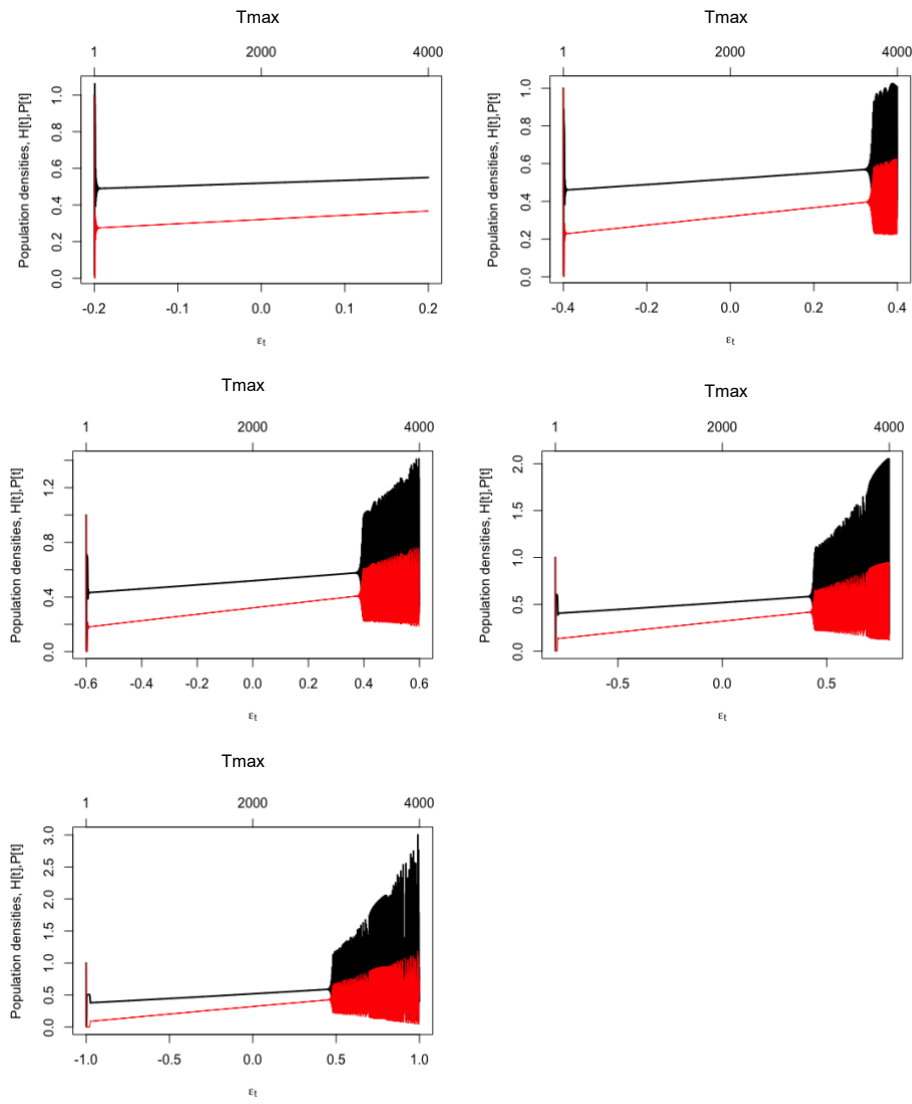Figure S13: Population time series of H_t (black line) and P_t (red line) at parameter values ε_{max} = 0.2, 0.4, 0.6, 0.8 and 1.0 across T_{max} = 2000, r = 2 and α = 3.

Figure S14: Population time series of H_t (black line) and P_t (red line) at parameter values $\varepsilon_{max} = 0.2, 0.4, 0.6, 0.8$ and 1.0 across $T_{max} = 4000$, $r = 2$ and $\alpha = 3$.
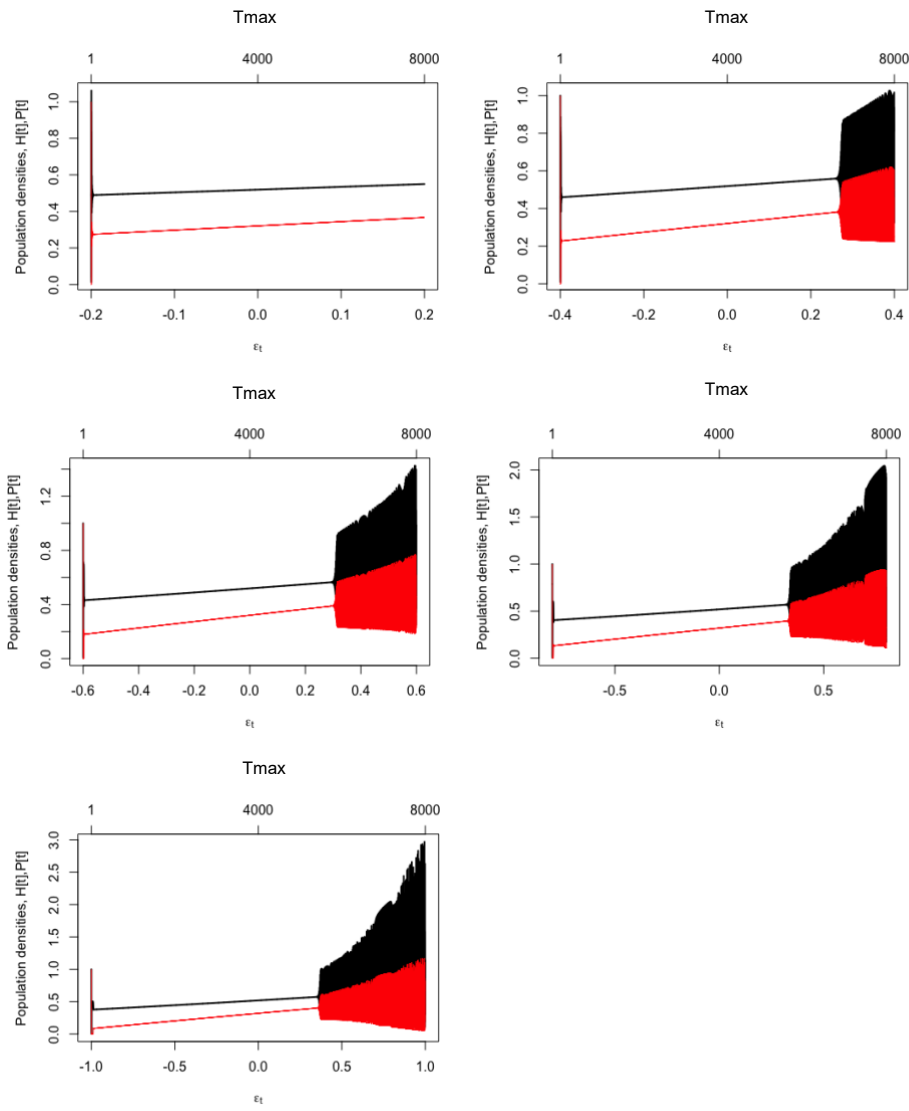
Figure S15: Population time series of H_t (black line) and P_t (red line) at parameter values ε_{max} = 0.2, 0.4, 0.6, 0.8 and 1.0 across T_{max} = 8000, r = 2 and α = 3.
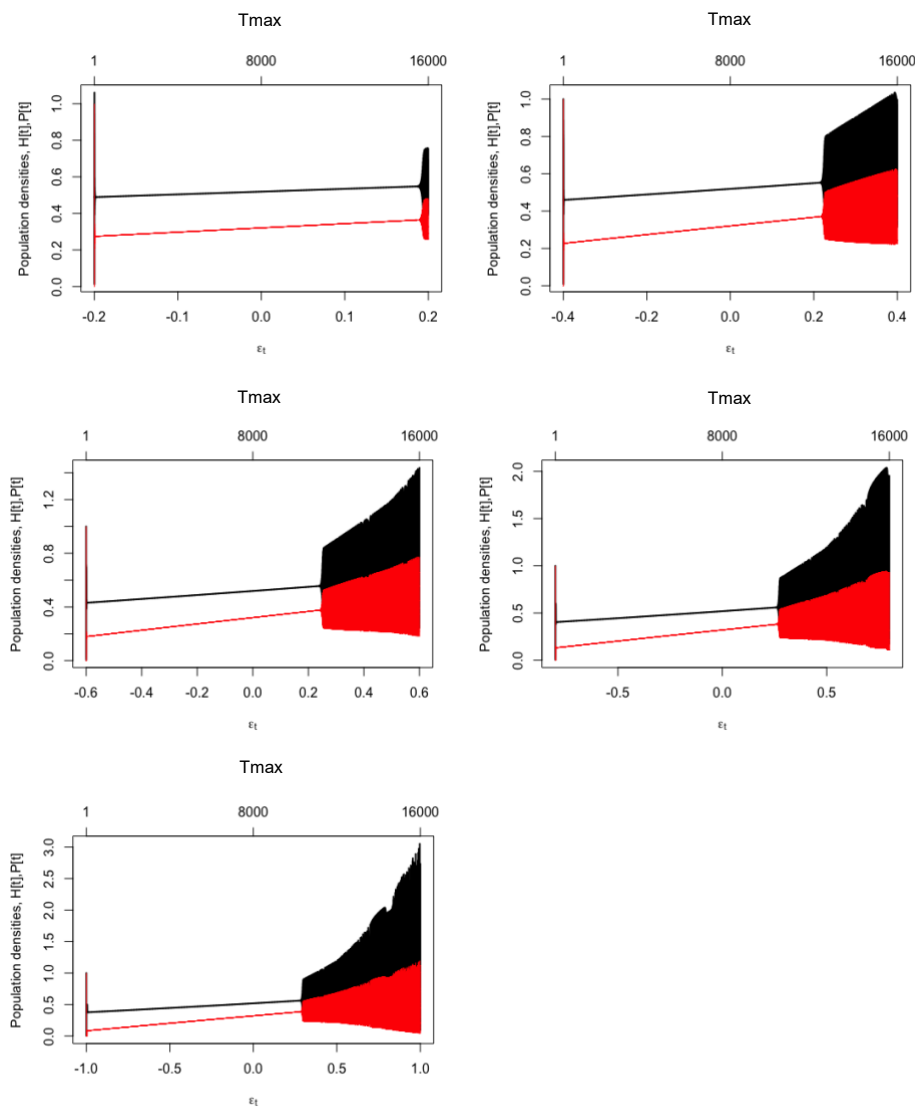
Figure S16: Population time series of H_t (black line) and P_t (red line) at parameter values $\varepsilon_{max} = 0.2, 0.4, 0.6, 0.8$ and 1.0 across $T_{max} = 16{,}000$, r = 2 and a = 3.

7 References

Abarca, M., & Spahn, R. (2021). Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. *Current Opinion in Insect Science*. https://doi.org/10.1016/j.cois.2021.04.008

Andrew, N. R., Hill, S. J., Binns, M., Bahar, M. H., Ridley, E. V., Jung, M.-P., Fyfe, C., Yates, M., & Khusro, M. (2013). Assessing insect responses to climate change: What are we testing for? Where should we be heading? *PeerJ*, *1*, e11. https://doi.org/10.7717/peerj.11

Bannerman, J. A., & Roitberg, B. D. (2013). Impact of extreme and fluctuating temperatures on aphid-parasitoid dynamics. *Oikos*, *123*(1), 89–98. https://doi.org/10.1111/j.1600-0706.2013.00686.x

Beddington, J. R., Free, C. A., & Lawton, J. H. (1975). Dynamic complexity in predator-prey models framed in difference equations. *Nature*, *255*(5503), 58–60. https://doi.org/10.1038/255058a0

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bellows, T. S., & Hassell, M. P. (1988). The Dynamics of Age-Structured Host--Parasitoid Interactions. *The Journal of Animal Ecology*, *57*(1), 259. https://doi.org/10.2307/4777

Berteaux, D. (2004). Keeping Pace with Fast Climate Change: Can Arctic Life Count on Evolution? *Integrative and Comparative Biology*, *44*(2), 140–151. https://doi.org/10.1093/icb/44.2.140

Bonsall, M. B., Hasan, N., & Nakamura, K. (2007). Density dependence and noise determine the long-term dynamics of two species of lady beetle (Coleoptera: Coccinellidae:

Epilachninae) in the Indonesian tropics. *Ecological Entomology*, *32*(1), 28–37.

https://doi.org/10.1111/j.1365-2311.2006.00832.x

Buchholz, R., Banusiewicz, J. D., Burgess, S., Crocker-Buta, S., Eveland, L., & Fuller, L.
(2019). Behavioural research priorities for the study of animal response to climate
change. *Animal Behaviour*, *150*, 127–137.

https://doi.org/10.1016/j.anbehav.2019.02.005

Canale, C., & Henry, P. (2010). Adaptive phenotypic plasticity and resilience of vertebrates to
increasing climatic unpredictability. *Climate Research*, *43*(1), 135–147.

https://doi.org/10.3354/cr00897

Cavigliasso, F., Gatti, J.-L., Colinet, D., & Poirié, M. (2021). Impact of Temperature on the
Immune Interaction between a Parasitoid Wasp and Drosophila Host Species. *Insects*,
12(7), 647. https://doi.org/10.3390/insects12070647

Chaves, L. F., Scott, T. W., Morrison, A. C., & Takada, T. (2014). Hot temperatures can force
delayed mosquito outbreaks via sequential changes in Aedes aegypti demographic
parameters in autocorrelated environments. *Acta Tropica*, *129*, 15–24.

https://doi.org/10.1016/j.actatropica.2013.02.025

Chwif, L., Barretto, M. R. P., & Paul, R. J. (2000). On simulation model complexity. *2000
Winter Simulation Conference Proceedings (Cat. No.00CH37165)*, *1*.

https://doi.org/10.1109/wsc.2000.899751

Cox, A. R., Robertson, R. J., Rendell, W. B., & Bonier, F. (2020). Population decline in tree
swallows (Tachycineta bicolor) linked to climate change and inclement weather on
the breeding ground. *Oecologia*, *192*(3), 713–722. https://doi.org/10.1007/s00442-
020-04618-8

Cui, J., Zhu, S., Bi, R., Xu, W., Gao, Y., & Shi, S. (2018). Effect of Temperature on the
Development, Survival, and Fecundity of Heliothis viriplaca (Lepidoptera:

Noctuidae). *Journal of Economic Entomology*, *111*(4), 1940–1946.

https://doi.org/10.1093/jee/toy151

Cury, K. M., Prud'homme, B., & Gompel, N. (2019). A short guide to insect oviposition:

when, where and how to lay an egg. *Journal of Neurogenetics*, *33*(2), 75–89.

https://doi.org/10.1080/01677063.2019.1586898

Damien, M., & Tougeron, K. (2019). Prey–predator phenological mismatch under climate

change. *Current Opinion in Insect Science*, *35*, 60–68.

https://doi.org/10.1016/j.cois.2019.07.002

Dee, L. E., Okamtoto, D., Gårdmark, A., Montoya, J. M., & Miller, S. J. (2020). Temperature

variability alters the stability and thresholds for collapse of interacting species.

Philosophical Transactions of the Royal Society B: Biological Sciences, *375*(1814),

20190457. https://doi.org/10.1098/rstb.2019.0457

Dongmo, M. A. K., Bonebrake, T. C., Hanna, R., & Fomena, A. (2018). Seasonal

Polyphenism in Bicyclus dorothea (Lepidoptera: Nymphalidae) Across Different

Habitats in Cameroon. *Environmental Entomology*. https://doi.org/10.1093/ee/nvy135

Durán, J. M. (2020). What is a Simulation Model? *Minds and Machines*.

https://doi.org/10.1007/s11023-020-09520-z

Echaubard, P., León, T., Suwanatrai, K., Chaiyos, J., Kim, C. S., Mallory, F. F., Kaewkes, S.,

Spear, R. C., & Sripa, B. (2017). Experimental and modelling investigations of

Opisthorchis viverrini miracidia transmission over time and across temperatures:

implications for control. *International Journal for Parasitology*, *47*(5), 257–270.

https://doi.org/10.1016/j.ijpara.2016.10.007

Erguler, K., Mendel, J., Petrić, D. V., Petrić, M., Kavran, M., Demirok, M. C., Gunay, F.,

Georgiades, P., Alten, B., & Lelieveld, J. (2022). A dynamically structured matrix

population model for insect life histories observed under variable environmental

conditions. *Scientific Reports*, *12*(1). https://doi.org/10.1038/s41598-022-15806-2

Erguler, K., & Stumpf, M. P. H. (2008). Statistical interpretation of the interplay between

noise and chaos in the stochastic logistic map. *Mathematical Biosciences*, *216*(1), 90–

99. https://doi.org/10.1016/j.mbs.2008.08.012

Forrest, J. R. (2016). Complex responses of insect phenology to climate change. *Current*

Opinion in Insect Science, *17*, 49–54.

https://doi.org/10.1016/j.cois.2016.07.002

Francuski, L., Jansen, W., & Beukeboom, L. W. (2020). Effect of temperature on egg

production in the common housefly. *Entomologia Experimentalis et Applicata*, *168*(6-

7), 513–522. https://doi.org/10.1111/eea.12912

Furlong, M. J., & Zalucki, M. P. (2017). Climate change and biological control: the

consequences of increasing temperatures on host–parasitoid interactions. *Current*

Opinion in Insect Science, *20*, 39–44. https://doi.org/10.1016/j.cois.2017.03.006

Fussmann, G. F., & Heber, G. (2002). Food web complexity and chaotic population

dynamics. *Ecology Letters*, *5*(3), 394–401. https://doi.org/10.1046/j.1461-

0248.2002.00329.x

Garay, J., Zoltán Sebestyén, Varga, Z., Gámez, M., A. Cracknell Torres, Belda, J. E., &

Cabello, T. (2014). A new multistage dynamic model for biological control

exemplified by the host–parasitoid system Spodoptera exigua–Chelonus oculator.

Journal of Pest Science, *88*(2), 343–358. https://doi.org/10.1007/s10340-014-0609-z

George, J. C., Bada, J., Zeh, J., Scott, L., Brown, S. E., O'Hara, T., & Suydam, R. (1999).

Age and growth estimates of bowhead whales (Balaena mysticetus) via aspartic acid

racemization. *Canadian Journal of Zoology*, *77*(4), 571–580.

https://doi.org/10.1139/z99-015

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences*, *118*(2), e2002543117. https://doi.org/10.1073/pnas.2002543117

Hance, T., van Baaren, J., Vernon, P., & Boivin, G. (2007). Impact of Extreme Temperatures on Parasitoids in a Climate Change Perspective. *Annual Review of Entomology*, *52*(1), 107–126. https://doi.org/10.1146/annurev.ento.52.110405.091333

Hans, K. R., LeBouthillier, R., & VanLaerhoven, S. L. (2018). Effect of Temperature on Oviposition Behavior and Egg Load of Blow Flies (Diptera: Calliphoridae). *Journal of Medical Entomology*, *56*(2), 441–447. https://doi.org/10.1093/jme/tjy173

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., de Boer, J. G., De Snoo, G. R., Deacon, C., Dell, J. E., Desneux, N., Dillon, M. E., Duffy, G. A., Dyer, L. A., & Ellers, J. (2022). Scientists' warning on climate change and insects. *Ecological Monographs*, *93*(1). https://doi.org/10.1002/ecm.1553

Hastings, A. (2010). Timescales, dynamics, and ecological understanding. *Ecology*, *91*(12), 3471–3480. https://doi.org/10.1890/10-0776.1

Hill, G. M., Kawahara, A. Y., Daniels, J. C., Bateman, C. C., & Scheffers, B. R. (2021). Climate Change Effects on Animal ecology: Butterflies and Moths as a Case Study. *Biological Reviews*, *96*(5). https://doi.org/10.1111/brv.12746

Hulme, P. E. (2016). Climate change and biological invasions: evidence, expectations, and response options. *Biological Reviews*, *92*(3), 1297–1313. https://doi.org/10.1111/brv.12282

Iltis, C., Moreau, J., Manière, C., Thiéry, D., Delbac, L., & Louâpre, P. (2020). Where you come from matters: temperature influences host–parasitoid interaction through

parental effects. *Oecologia*, *192*(3), 853–863. https://doi.org/10.1007/s00442-020-04613-z

Intergovernmental Panel on Climate Change (IPCC). (2023). Future Global Climate: Scenario-based Projections and Near-term Information. *Climate Change 2021 – the Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.*, 553–672. https://doi.org/10.1017/9781009157896.006

Jactel, H., Koricheva, J., & Castagneyrol, B. (2019). Responses of forest insect pests to climate change: not so simple. *Current Opinion in Insect Science*, *35*, 103–108. https://doi.org/10.1016/j.cois.2019.07.010

Jeffs, C. T., & Lewis, O. T. (2013). Effects of climate warming on host-parasitoid interactions. *Ecological Entomology*, *38*(3), 209–218. https://doi.org/10.1111/een.12026

Johnson, N. F. (2001). Hymenoptera. *Elsevier EBooks*, 417–426. https://doi.org/10.1016/b0-12-226865-2/00154-1

Jones, S. D. (2016). Population Cycles, Disease, and Networks of Ecological Knowledge. *Journal of the History of Biology*, *50*(2), 357–391. https://doi.org/10.1007/s10739-016-9441-z

Kendall, B. E. (2001). Cycles, chaos, and noise in predator–prey dynamics. *Chaos, Solitons & Fractals*, *12*(2), 321–332. https://doi.org/10.1016/s0960-0779(00)00180-6

Laughton, A. M., & Knell, R. J. (2019). Warming at the population level: Effects on age structure, density, and generation cycles. *Ecology and Evolution*, *9*(8), 4403–4420. https://doi.org/10.1002/ece3.4972

Lindström, J., Ranta, E., Kokko, H., Lundberg, P., & Kaitala, V. (2001). From arctic lemmings to adaptive dynamics: Charles Elton's legacy in population ecology.

Biological Reviews of the Cambridge Philosophical Society, *76*(1), 129–158.

https://doi.org/10.1017/s1464793100005637

Lindström, J., Ranta, E., Lindén, H., Lindstrom, J., & Linden, H. (1996). Large-Scale

Synchrony in the Dynamics of Capercaillie, Black Grouse and Hazel Grouse

Populations in Finland. *Oikos*, *76*(2), 221. https://doi.org/10.2307/3546193

Loossens, T., Tuerlinckx, F., & Verdonck, S. (2021). A comparison of continuous and discrete

time modeling of affective processes in terms of predictive accuracy. *Scientific*

Reports, *11*(1). https://doi.org/10.1038/s41598-021-85320-4

Lovejoy, T. E., Lee Jay Hannah, & Wilson, E. O. (2019). *Biodiversity and climate change :*

transforming the biosphere. Yale University Press.

Lu, K., Chen, X., Liu, W., & Zhou, Q. (2016). Characterization of heat shock cognate protein

70 gene and its differential expression in response to thermal stress between two wing

morphs of Nilaparvata lugens (Stål). *Comparative Biochemistry and Physiology Part*

A: Molecular & Integrative Physiology, *199*, 47–53.

https://doi.org/10.1016/j.cbpa.2016.05.009

Ma, G., & Ma, C.-S. (2021). Potential distribution of invasive crop pests under climate

change: incorporating mitigation responses of insects into prediction models. *Current*

Opinion in Insect Science. https://doi.org/10.1016/j.cois.2021.10.006

Maclean, I. M. D., & Wilson, R. J. (2011). Recent ecological responses to climate change

support predictions of high extinction risk. *Proceedings of the National Academy of*

Sciences, *108*(30), 12337–12342. https://doi.org/10.1073/pnas.1017352108

Marcinko, K. (2020). *Mathematical Analysis of Host–Parasitoid Dynamics*.

Digital.lib.washington.edu; University of Washington.

http://hdl.handle.net/1773/46369

Marshall, D. J., Burgess, S. C., & Connallon, T. (2016). Global change, life-history complexity and the potential for evolutionary rescue. *Evolutionary Applications*, *9*(9), 1189–1201. https://doi.org/10.1111/eva.12396

May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature*, *261*(5560), 459–467. https://doi.org/10.1038/261459a0

McCain, C. M., & Garfinkel, C. F. (2021). Climate change and elevational range shifts in insects. *Current Opinion in Insect Science*. https://doi.org/10.1016/j.cois.2021.06.003

Meisner, M. H., Harmon, J. P., & Ives, A. R. (2014). Temperature effects on long-term population dynamics in a parasitoid–host system. *Ecological Monographs*, *84*(3), 457–476. https://doi.org/10.1890/13-1933.1

Moore, M. E., Hill, C. A., & Kingsolver, J. G. (2021). Differing thermal sensitivities in a host–parasitoid interaction: High, fluctuating developmental temperatures produce dead wasps and giant caterpillars. *Functional Ecology*, *35*(3), 675–685. https://doi.org/10.1111/1365-2435.13748

Moore, M. E., Kester, K. M., & Kingsolver, J. G. (2019). Rearing temperature and parasitoid load determine host and parasitoid performance in Manduca sexta and Cotesia congregata. *Ecological Entomology*, *45*(1), 79–89. https://doi.org/10.1111/een.12776

Mugabo, M., Gilljam, D., Petteway, L., Yuan, C., Fowler, M. S., & Sait, S. M. (2019). Environmental degradation amplifies species' responses to temperature variation in a trophic interaction. *Journal of Animal Ecology*, *88*(11), 1657–1669. https://doi.org/10.1111/1365-2656.13069

Muluneh, M. G. (2021). Impact of climate change on biodiversity and food security: a global perspective—a review article. *Agriculture & Food Security*, *10*(1). https://doi.org/10.1186/s40066-021-00318-5

Murdoch, W. W., Briggs, C. J., & Nisbet, R. M. (2013). Consumer-Resource Dynamics

(MPB-36). In *Princeton University Press eBooks*. Princeton University Press.

https://doi.org/10.1515/9781400847259

Myers, J. H. (2018). Population cycles: generalities, exceptions and remaining mysteries.

Proceedings of the Royal Society B: Biological Sciences, *285*(1875), 20172841.

https://doi.org/10.1098/rspb.2017.2841

Nicholson, A. J., & Bailey, V. A. (1935). The Balance of Animal Populations.-Part I.

Proceedings of the Zoological Society of London, *105*(3), 551–598.

https://doi.org/10.1111/j.1096-3642.1935.tb01680.x

O'Connor, M. I., & Bernhardt, J. R. (2018). The metabolic theory of ecology and the cost of

parasitism. *PLOS Biology*, *16*(4), e2005628.

https://doi.org/10.1371/journal.pbio.2005628

Oestreicher, C. (2007). A history of chaos theory. *Chronobiology in Psychiatry*, *9*(3), 279–

289. https://doi.org/10.31887/dcns.2007.9.3/coestreicher

Olsson, C., Bolmgren, K., Lindström, J., & Jönsson, A. M. (2013). Performance of tree

phenology models along a bioclimatic gradient in Sweden. *Ecological Modelling*,

266, 103–117. https://doi.org/10.1016/j.ecolmodel.2013.06.026

Pardikes, N. A., Revilla, T. A., Lue, C., Thierry, M., Souto-Vilarós, D., & Hrcek, J. (2022).

Effects of phenological mismatch under warming are modified by community

context. *Global Change Biology*, *28*(13), 4013–4026.

https://doi.org/10.1111/gcb.16195

Parikh, G., Rawtani, D., & Khatri, N. (2020). "Insects as an Indicator for Environmental

Pollution." *Environmental Claims Journal*, 1–21.

https://doi.org/10.1080/10406026.2020.1780698

Prinsloo, G. L. (1997). Parasitoids. *World Crop Pests*, 69–109. https://doi.org/10.1016/s1572-4379(97)80078-4

Pureswaran, D. S., Roques, A., & Battisti, A. (2018). Forest Insects and Climate Change. *Current Forestry Reports*, *4*(2), 35–50. https://doi.org/10.1007/s40725-018-0075-6

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Ratte, H. T. (1984). Temperature and Insect Development. *Environmental Physiology and Biochemistry of Insects*, 33–66. https://doi.org/10.1007/978-3-642-70020-0_2

Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, *118*(2). https://doi.org/10.1073/pnas.2002548117

Régnière, J., Powell, J., Bentz, B., & Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. *Journal of Insect Physiology*, *58*(5), 634–647. https://doi.org/10.1016/j.jinsphys.2012.01.010

Régnière, J., St-Amant, R., & Duval, P. (2010). Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. *Biological Invasions*, *14*(8), 1571–1586. https://doi.org/10.1007/s10530-010-9918-1

Rogers, T. L., Johnson, B. J., & Munch, S. B. (2022). Chaos is not rare in natural ecosystems. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01787-y

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, *117*(8), 4211–4217. https://doi.org/10.1073/pnas.1913007117

Romo, C. M., & Tylianakis, J. M. (2013). Elevated Temperature and Drought Interact to Reduce Parasitoid Effectiveness in Suppressing Hosts. *PLoS ONE*, *8*(3), e58136. https://doi.org/10.1371/journal.pone.0058136

Roques, L., & Chekroun, M. D. (2011). Probing chaos and biodiversity in a simple competition model. *Ecological Complexity*, *8*(1), 98–104. https://doi.org/10.1016/j.ecocom.2010.08.004

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313), aaf7671. https://doi.org/10.1126/science.aaf7671

Scheiner, S. M., Barfield, M., & Holt, R. D. (2019). The genetics of phenotypic plasticity. XVII. Response to climate change. *Evolutionary Applications*, *13*(2), 388–399. https://doi.org/10.1111/eva.12876

Sekerci, Y. (2020). Climate change effects on fractional order prey-predator model. *Chaos, Solitons & Fractals*, *134*, 109690. https://doi.org/10.1016/j.chaos.2020.109690

Shivanna, K. R. (2022). Climate change and its impact on biodiversity and human welfare. *Proceedings of the Indian National Science Academy*, *88*(2). https://doi.org/10.1007/s43538-022-00073-6

Shrestha, S. (2019). Effects of Climate Change in Agricultural Insect Pest. *Acta Scientific Agriculture*, *3*(12), 74–80. https://doi.org/10.31080/asag.2019.03.0727

Sintayehu, D. W. (2018). Impact of climate change on biodiversity and associated key ecosystem services in Africa: a systematic review. *Ecosystem Health and Sustainability*, *4*(9), 225–239. https://doi.org/10.1080/20964129.2018.1530054

Stange, E. E., & Ayres, M. P. (2010). Climate Change Impacts: Insects. *Encyclopedia of Life Sciences*. https://doi.org/10.1002/9780470015902.a0022555

Stefansson, H., Sigmarsdottir, S., Jensson, P., & Shah, N. (2011). Discrete and continuous time representations and mathematical models for large production scheduling problems: A case study from the pharmaceutical industry. *European Journal of Operational Research*, *215*(2), 383–392. https://doi.org/10.1016/j.ejor.2011.06.021

Stork, N. E. (2018). How Many Species of Insects and Other Terrestrial Arthropods Are

    There on Earth? *Annual Review of Entomology*, *63*(1), 31–45.

    https://doi.org/10.1146/annurev-ento-020117-043348

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S.,

    Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D.,

    Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck,

    C., Edwards, M., & Elliott, J. M. (2016). Phenological sensitivity to climate across

    taxa and trophic levels. *Nature*, *535*(7611), 241–245.

    https://doi.org/10.1038/nature18608

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham,

    M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A.,

    Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech,

    D. I., & Roy, D. B. (2010). Trophic level asynchrony in rates of phenological change

    for marine, freshwater and terrestrial environments. *Global Change Biology*, *16*(12),

    3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

Thierry, M., Pardikes, N. A., Lue, C., Lewis, O. T., & Hrček, J. (2020). Experimental

    warming influences species abundances in a Drosophila host community through

    direct effects on species performance rather than altered competition and parasitism.

    BioRxiv (Cold Spring Harbor Laboratory).

    https://doi.org/10.1101/2020.12.22.423937

Thierry, M., Pardikes, N. A., Rosenbaum, B. P., Ximénez-Embún, M. G., & Hrcek, J. (2022).

    The presence of multiple parasitoids decreases host survival under warming, but

    parasitoid performance also decreases. *Proceedings of the Royal Society B Biological*

    Sciences, *289*(1971). https://doi.org/10.1098/rspb.2022.0121

Tseng, M., Kaur, K. M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., Toor, H. S., & Fograscher, K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, *87*(3), 647–659. https://doi.org/10.1111/1365-2656.12789

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. - B., Peer, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., & Schmitz, A. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), aad8466. https://doi.org/10.1126/science.aad8466

Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2005). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, *147*(1), 164–172. https://doi.org/10.1007/s00442-005-0299-6

Visser, M. E., Lindner, M., Gienapp, P., Long, M. C., & Jenouvrier, S. (2021). Recent natural variability in global warming weakened phenological mismatch and selection on seasonal timing in great tits (Parus major). *Proceedings of the Royal Society B: Biological Sciences*, *288*(1963). https://doi.org/10.1098/rspb.2021.1337

Vogt, G. (2022). Epigenetics and Phenotypic Plasticity in Animals. *Epigenetics, Development, Ecology and Evolution*, 35–108. https://doi.org/10.1007/978-3-031-13771-6_3

Walker, W. H., Meléndez-Fernández, O. H., Nelson, R. J., & Reiter, R. J. (2019). Global climate change and invariable photoperiods: A mismatch that jeopardizes animal fitness. *Ecology and Evolution*, *9*(17), 10044–10054. https://doi.org/10.1002/ece3.5537

Wang, P., Qin, W., & Tang, G. (2019). Modelling and Analysis of a Host-Parasitoid Impulsive Ecosystem under Resource Limitation. *Complexity*, *2019*, 1–12. https://doi.org/10.1155/2019/9365293

Wetherington, M. T., Jennings, D. E., Shrewsbury, P. M., & Duan, J. J. (2017). Climate variation alters the synchrony of host-parasitoid interactions. *Ecology and Evolution*, *7*(20), 8578–8587. https://doi.org/10.1002/ece3.3384

White, E. R. (2018). Minimum Time Required to Detect Population Trends: The Need for Long-Term Monitoring Programs. *BioScience*, *69*(1), 40–46. https://doi.org/10.1093/biosci/biy144

Williams, J. J., & Newbold, T. (2019). Local climatic changes affect biodiversity responses to land use: A review. *Diversity and Distributions*, *26*(1), 76–92. https://doi.org/10.1111/ddi.12999

Wonglersak, R., Fenberg, P. B., Langdon, P. G., Brooks, S. J., & Price, B. W. (2020). Temperature-body size responses in insects: a case study of British Odonata. *Ecological Entomology*, *45*(4), 795–805. https://doi.org/10.1111/een.12853

Wonglersak, R., Fenberg, P. B., Langdon, P. G., Brooks, S. J., & Price, B. W. (2021). Insect body size changes under future warming projections: a case study of Chironomidae (Insecta: Diptera). *Hydrobiologia*, *848*(11), 2785–2796. https://doi.org/10.1007/s10750-021-04597-8

Zhang, K., Liu, H., Pan, H., Shi, W., Zhao, Y., Li, S., Liu, J., & Tao, J. (2020). Shifts in potential geographical distribution of *Pterocarya stenoptera* under climate change scenarios in China. *Ecology and Evolution*, *10*(11), 4828–4837. https://doi.org/10.1002/ece3.6236

Zhu, L., Hoffmann, A. A., Li, S., & Ma, C. (2021). Extreme climate shifts pest dominance hierarchy through thermal evolution and transgenerational plasticity. *Functional Ecology*, *35*(7), 1524–1537. https://doi.org/10.1111/1365-2435.13774

Zografou, K., Swartz, M. T., Adamidis, G. C., Tilden, V. P., McKinney, E. N., & Sewall, B. J. (2021). Species traits affect phenological responses to climate change in a butterfly community. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-82723-1

Zylstra, E. R., Neupane, N., & Zipkin, E. F. (2022). Multi-season climate projections forecast declines in migratory monarch butterflies. *Global Change Biology*. https://doi.org/10.1111/gcb.16349