Ecology Article  
Mechanistic population matrix model for ectothermic organisms in disturbance prone seasonal environments  
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Abstract (350 words)

Introduction

In ecological contexts, experimentation in the field can be prohibitive, due to replication issues, timescales beyond the lives of humans, and the inability to reasonably control the experimental treatments. Mathematical modeling has long been viewed as a method evaluate hypotheses which cannot or should not be tested *in situ*, and can help researchers organize thinking and identify uncertainty in current ecological research(Ecological Detective, Power, 1996).

Process-based models, which link species’ underlying biological mechanisms, like survival and fecundity, to environmental conditions, such as disturbance regime and temperature, offer a method to analyzing and understanding disturbance-ecology relationships. Previous mechanistic models that link populations to disturbance regimes have been successful in simulating observed population dynamics, and with increasing access to high performance computers, can be used to predict population changes under a variety of future scenarios (McMullen 2017, Tonkin 2019). Analysis of model outputs can provide important conservation insights related to life stage bottlenecks, keystone species identification, and vital rates, such as survivorship and fecundity, that drive ecosystem-level responses to disturbance regime (Tonkin 2019).

Invertebrates form the food base of many ecosystems, both aquatic, marine, and terrestrial. Their ecology is marked by characteristic features, like the interplay between growth and development in response to temperatures, population-level responses to disturbances, and density dependence (Vannote 1980, Grimm 1989). Vannote and Sweeney (1980) developed the Thermal Equilibrium Hypothesis which posits that biological characteristics, like growth, metabolism, and reproductive potential, are mediated by temperature. For insects in cooler regimes, time spent in larval or sub-adult stages increases, while organisms in warmer regions have a shorter time to maturation (Vannote and Sweeney 1980). This is related to fecundity through body size, as longer time spent maturing results in a larger body size, which in turn leads to higher fecundity (Vannote 1980).

Disturbances, like fire, flood, drought, disease, to name a few, are naturally occurring phenomena in ecosystems. Local populations’ lifecycles are likely adapted to either persist through disturbances, called resistance, or quickly regenerate after disturbances, called resilience (Lytle and Poff, 2004 Lytle (2004)). Variation in disturbance type can impact the population response. Short-term pulse disturbances like floods often cause immediate mortality but may have a rejuvenating effect on the ecosystem. On the other hand, press disturbances often arise slowly and then reach a constant level that is maintained, like sedimentation processes (Lake 2000). Changes in the timing, frequency, and magnitude of disturbances impact population regulation and community structure (Lytle et al 2007). As human activity alters disturbance regimes and novel environments are projected for the future, models can forecast how these changes will impact local populations.

In addition, density dependence is a common ecological phenomenon within populations, especially insects and invertebrates (Brook 2006). As populations density increases, the per capita population growth rate decreases, allowing populations to stabilize at an equilibrium density, known as carrying capacity. This process is caused by limitations in food availability, predation, competition, and disease (Sibly 2002).

We introduce a population matrix model that integrates the unifying themes of thermal equilibrium hypothesis, disturbance response, and density dependence in population ecology for organisms of interest. Applying a population matrix model that can accommodate seasonality, disturbance, and density dependence is a novel approach to link the fields of theoretical ecology to applied ecology. This framework can be used to give a better understanding of how populations respond to variety of interacting environmental forces, and forecast how large-scale shifts in seasonality and disturbance due to climate change or anthropogenic management can impact populations. We hypothesize that we can recreate observable trends in population responses related to the Thermal Equilibrium Hypothesis, disturbance ecology, and density dependence using this approach that incorporates species’ responses to environmental changes.

Methods

Model Structure

Stage-structured population models use matrix multiplication to incrementally step populations forward in time using the notation

in which ***n****i(t)*, the stage-class abundances for species *i* at time *t* are multiplied by ***Ai****(t)*, the transition matrix for that species under certain environmental conditions over time *t*, which results in ***n****i(t+1)*, the stage-class abundances for species *i* in the next timestep (Caswell 2001).

The transition matrix ***Ai****(t)* includes vital rate information for species j with stages classes *i* = 1, 2, 3 is noted below:

in which species-stage specific fecundity rates *Fji*, species-stage specific transition probabilities from stage *i* to stage *i+1*, *Gji*, and the probability of remaining in a specific stage, *Pji* are represented (Table 1). In our model, we limit our matrices to three stages for the sake of simplicity.

*Vital Rate Estimation*

In this model, vital rates are modified in response to temperatures. In insects, the rate of development, or the rate at which an organism reaches maturity, can be represented by *Gji*, as cohorts move from stage to stage towards sexual maturity. Meanwhile, *Pji*, remaining within a stage, can be a proxy for growth via the accumulation of biomass the longer a cohort remains in its larval stage. These rates can vary depending on temperature thresholds, as demonstrated by Vannote (1980, Table S1). Insect cohort emergence is linked to the total number of days above a critical temperature threshold accumulated over the life cycle, using the equation

in which *TempMean* represents the mean temperature in ˚C of the timestep, and *TempCrit* represents the critical temperature threshold, usually 0˚C. Degree days and critical temperature thresholds are determined from the literature. We can estimate how long cohorts remained in their larval stages by a back-looking accounting method. We assume the number of back-looking timesteps it takes to accumulate the threshold number of degree days for new Stage 3 individuals at any timestep is how long that cohort has been in Stage 1 or Stage 2. Based on these numbers, we can calculate body size using growth rates from the literature. Observations have shown that cohorts that remain in larval stages longer have larger body sizes, while cohorts that develop quickly have smaller body sizes (Vannote 1980). Female fecundity of insects is closely linked to body size, we can also use body size estimates to predict cohort-specific fecundity (Roff 1986). Invertebrates with less complex lifecycles do not require such accounting. Instead, stage-specific fecundity is assigned based on assumed size at each stage.

To demonstrate the model ability to recover elements of the thermal equilibrium hypothesis, we recreated parameterized the model for an *Ephemerella subvaria* population in West Branch Brandywine Creek, PA, close to where Vannote (1980) did their primary studies on the thermal equilibrium hypothesis (Table TBD). Biweekly temperatures were summarized from USGS water temperature data between October, 1, 2007 and October 1, 2022 (USGS). We assumed that no disturbance events (flood events) occurred during this time. We scaled larval and pupal stages to minimum and maximum sizes of *E. subvaria* (Sweeney 1981). The data points from Vannote (1980) Figure 7 were calculated using GraphGrabber2.0.

*Disturbance Response*

This model also incorporates disturbance response to pulse and press disturbance events. Pulse disturbances are assumed to cause immediate mortality within the timestep following a negative exponential function

Where *h* and k are shape modifiers for the negative exponential function and *Q* is disturbance magnitude (McMullen 2017, Figure 1, Table 1). Disturbance-adapted ecosystems also often see a brief increase in carrying capacity in response to disturbances, which can be represented by increasing K in proportion to the disturbance magnitude post-disturbance accordingly

In which *K0* represents post-disturbance carrying capacity in individuals at time *t*, *Kpre* represents the pre-disturbance carrying capacity, *Kd* represents maximum carrying capacity after a large disturbance (McMullen 2017). *Qf* is a modifier that describes the relationship between disturbance magnitude and carrying capacity, which is determined by the equation

in which Qmin is the minimum disturbance magnitude to influence *K* and *a* is the half-saturation constant for that relationship (McMullen 2017, Table 1). We also allow *K* to return to *Kb*, which represents baseline *K* in the absence of disturbances following

in which g is a shape parameter that determines the rate at which *K* returns to *Kb* and τ is the number of timesteps since the disturbance (McMullen 2017. Figure 2). *Kb*, although a constant in this model for the sake of simplicity, could fluctuate as a function of varying productivity in the system.

We parameterized the model for a Baetid mayfly in Sycamore Creek, AZ after a large flood events on March 17, 1986, as referenced in Grimm (1989, Table S1). This flood event had an instantaneous maximum discharge of 1080.0 cfs and a biweekly mean maximum discharge of 209.9 cfs, since flows dropped down to 35 cfs during that two-week timestep (USGS). Discharge (cfs) was summarized for a biweekly period and the model was run between October 1, 1982 and September 30, 1987, although results are only shown for the 130 days post-disturbance. We scaled the discharge data by dividing the biweekly discharge by the Sycamore Creek bankfull discharge to get disturbance magnitude.

Press disturbances was incorporated into the model as a continuously suppression of population growth. In the example of tail water hydropeaking intensity, we calculated percent eggs surviving hydropeaking as

in which r represents location of oviposition along a cross section of the river, which 0 being the river edge and 1 being the center of the river, and c = 2 (Kennedy et al. 2016). We modify that equation to be a modifier of survival related to hydropeaking index, where a higher hydropeaking index represents a more intense hydropeaking regime (Dibble, 2015). We multiplied *whydro* by (1 – hydropeaking index) to scale for different intensities.

*Density Dependence*

Density dependence is incorporated into the model via fecundity following a logistic relationship

in which stage-specific fecundity is modified by the relationship between total *N* at time *t* and carrying capacity at time *t* (Rogosch 2019).

*Study Organisms*

Invertebrates are a diverse group of organisms representing a wide variety of life history strategies and organismal traits. This model allows us to incorporate the distinct biology of an organism into its population dynamics. We have chosen to investigate aquatic invertebrates that represent well-defined trait-groups within the Colorado River ecosystem. These invertebrates represent primary aquatic consumers that are the basis of both aquatic and terrestrial foodwebs within the system (Kennedy 2016). Baetid mayfly species (Ephemeroptera: Baetidae) are considered to have a fast-life cycle and are often multivoltine in warm conditions. Many species are flood-adapted, and populations can recover quickly post-flood disturbance. They have three life-stages: an aquatic nymphal stage, a short subimago stage, and their adult stage. In our model, we have divided the life cycles so that Stage 1 represents small nymphs, Stage 2 represents large nymphs, and Stage 3 represents adults. Because the subimago stage is so short, it is lumped in with the adult stage (Figure 1A). *Hydropsyche* species (Trichoptera: Hydropsychidae) are a genus of net-spinning caddisflies that represent a slower-life cycle species that are typically univoltine (is a ref needed here?). They are observed to recovery quickly post-flood (Kimura 2011)Figure 1B). New Zealand Mudsnails are indeterminate growth species without specific life stage, so we have divided their life history by size, instead of stage (Figure 1, B). Hydropsyche species have three life stages: a larval stage (Stage 1), a pupal stage (Stage 2), and an adult stage (Stage 3, Figure 1, C). New Zealand Mudsnails (*Potamopyrgus antipodarum*) are a prolific aquatic snail, invasive in the United States. They are not flood-adapted, but are resistant to desiccation and reproduce quickly, since they are primarily parthenogenic. In the United States, New Zealand Mudsnails do not have natural predators or parasites that control populations, and they are not bioenergetically available for aquatic or terrestrial consumers (Cross 2011). To test the generality of the model to another system, we chose to model a marine intertidal species that also experiences seasonality and disturbance. The California mussel (*Mytilus californianus*) is a dominant rocky intertidal invertebrate, meaning that in its niche it will out-compete and overgrowth any other species of invertebrate (does this need a reference? In the marine lit it doesn’t). Like the New Zealand Mudsnail, it has indeterminate growth and thus is divided into size classes.

Table 1: Summary of model parameters

|  |  |
| --- | --- |
| Parameter | Description |
| t | Timestep |
| Nt | Population abundance at timestep t |
| K | Carrying capacity |
| Kpre | Pre-disturbance K at time t |
| Kd | Maximum post-disturbance K |
| K0 | Post-disturbance K at time t |
| Kb | Baseline K (in the absence of disturbance) |
| Q | Disturbance magnitude |
| Qf | Disturbance magnitude carrying capacity relationship |
| Qmin | Minimum Disturbance magnitude |
| a | Half-saturation constant |
| b | Scaling modifier for disturbance-mortality relationship |
| h | Modifier for disturbance-mortality relationship |
| g | Rate that K returns to baseline K post-disturbance |
| τ | Timesteps post minimum disturbance |
| m | immediate post disturbance mortality |
| Pi | Probability of remaining in Stage *i* |
| Gji | Probability of transitioning from Stage *i* to Stage *j* |
| Fi | Stage *i* Fecundity |
|  |  |
|  |  |
|  |  |
|  |  |

Graphical user interface, application

Description automatically generated

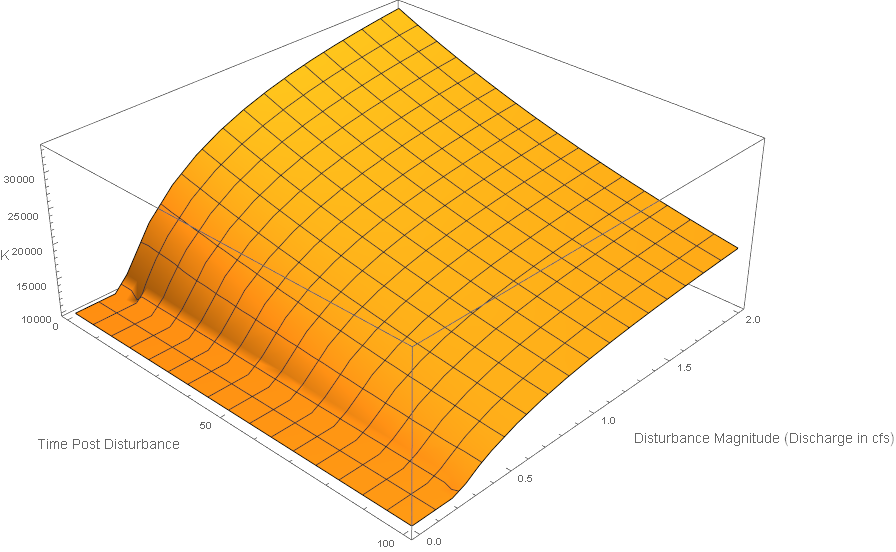
Figure 1: Comparison of different life histories of modeled organisms. A represents a modeled Baetid mayfly. B represents a modeled P. antipodarum, C represents a modeled Hydropsyche species. Other abbreviations listed in Table 1.

Figure 2: Graphical relationship between disturbance magnitude, Q (discharge in cfs) and K (carrying capacity) and time post-disturbance (t) for a Baetid mayfly following Equations 5, 6, and 7. Discharge is scaled to represent flows possible in the Colorado River.

Results

Chart, line chart

Description automatically generated

Figure 4: Recreation of Vannote (1980) decreasing size over the course of emergence as temperature in the system increases for E. subvaria. Temperature data is mean biweekly temperature of White Clay Creek between October 1, 2007 and October 1, 2022 (USGS Gauge 01480617). No flood disturbances were included. Data points for Vannote (1980) from GraphGrabber2.0.

Chart

Description automatically generated

Figure 5: Recreation of Grimm (1989) data for Ephemeroptera in Sycamore Creek after a large flood disturbance. A Baetid mayfly population was modelled. Temperature-related growth and development rates were ignored in this example. Biweekly discharge (cfs) was calculated from USGS gauge 09510200.

* Figure 6: Comparison of

population trajectory for a mayfly and a caddis/NZMS with differences in temperature and discharge (maybe use Diamond Creek as an example?)

* Rocky Intertidal Example to show usefulness to a broader context
  + Want to model M. californianus in some useful context (compare ENSO years?) BUT because mussels are space limited, assumed to be close to K pretty much either way – the question would then be about total biomass or productivity – how to ask and answer these questions and how to model?

Discussion:

* This will hopefully add evidence of mechanistic models recovering general ecological hypotheses
* Theoretical v management applications
  + Difference in density dependence assumptions (a theoretical application)
  + Forecasting population response under different novel environments in the face of climate change (a management application)
* Future Steps
  + Using this to test hypotheses about the Natural Flow Regime
  + Using model to looking at how climate change could impact populations
  + Optimization of dam releases
  + Make multispecies

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Supplemental Material

Table S1: Parameter values of species of interest.

To calculate flood mortality relationship, we fit a negative exponential equation (Eq 4) to data from the literature. Using shell-length and fecundity data, we created a linear model to describe fecundity at each size class. Using a growth rate function from Cross et al. (2010), we then calculated how many 2-week timesteps it takes to reach each size class. We assumed the individuals above 3.95mm remain in that size class for about 7 timesteps, thus limiting the lifespan of a modeled snail to 1 year. How accurate this assumption is is unclear, since the longest that a cohort of NZ mudsnails has been tracked is around 12 months (Dybdahl and Kane, 2005 *Ecological Archives* E086-087-A3). Cross et al. 2010 suggested a lifetime survivorship of between 80 – 100% . Using Caswell (2001) fixed time stage duration equation, we can calculate *Pi* and *Gi* using the equation

In which *σi* represents stage *i* survival and where *T*is number of timesteps it takes to complete stage *i* (Caswell 2001, pg 160-161).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Parameter | Values | Baetid Mayfly | *Hydropsyche* spp. | New Zealand Mudsnail | *M. californianus* |
| t | 2 weeks |  |  |  |  |
| Kd | 40000 |  |  |  |  |
| Kb | 10000 |  |  |  |  |
| Qmin | 40000 |  |  |  |  |
| a | 3000 |  |  |  |  |
| h | 0.02 |  |  |  |  |
| b | 1 |  |  |  |  |
| g | 0.1 |  |  |  |  |
| P1 |  |  | 0.7c | 0.4d |  |
| G1 |  |  | 0.1c | 0.1d |  |
| P2 |  |  | 0 | 0.5d |  |
| G2 |  |  | 0.445c | 0.1d |  |
| P3 |  | 0 | 0 | 0.8d |  |
| F1 |  | 0 | 0 | 0 | 0 |
| F2 |  | 0 | 0 |  |  |
| F3 |  |  |  |  |  |

Notes: a (Sweeney 2018), based on data regarding maximum and minimum temperatures for growth

b (Vannote 1980 )

c (Willis 1992), based on data about survival over time and scaling fecundity to time spent in larval and pupal stages

d (Cross 2011), estimates calculated from data regarding growth and survival rates

e (McKenzie 2013)

f (Carson 2011)

g (McPeek 1998), based on daily mortality rates

h (Degrange 1960), model parameter pulled form normal distribution

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Values | Vannote and Sweeney Recreation | Grimm & Fisher (1998) Recreation |  |
| t | 2 weeks |  |  |  |
|  |  |  |  |  |
| Kd | 40000 |  |  |  |
| Kb | 10000 |  | 150 |  |
| Qmin | 40000 |  | 11.25 |  |
| a | 3000 |  | 0.0075 |  |
| h |  |  |  |  |
| b | 1.221403 |  | 0.23g |  |
| g | 0.1 |  | 0.25g |  |
| P1 |  |  | 0.23g |  |
| G1 |  |  | 0.25g |  |
| P2 |  |  | 0 |  |
| G2 |  |  | 0 |  |
| P3 |  | 0 | 0 |  |
| F1 |  | 0 | 1104.5h |  |
| F2 |  | 0 |  |  |
| F3 |  | (59 \* size) + 143b |  |  |

Notess:

a Temperature relationship was assumed to be the same as a Baetid mayfly.

b Sweeney 1981