

# GUIDANCE DOCUMENT

## Web Tools for Riparian and Aquatic Population Modeling

SERDP Project RC-2511

JANUARY 2020

Dr. David A. Lytle  
**Oregon State University**

Dr. Jonathan Tonkin  
**University of Canterbury**

Dr. Julian D. Olden  
**University of Washington**

Dr. David M. Merritt  
**US Forest Service, Watershed, Fish,  
Wildlife, Air and Rare Plants**

Dr. Laura McMullen  
**ICF International**

Jane Rogosch  
**University of Washington**

*Distribution Statement A*

*This document has been cleared for public release*

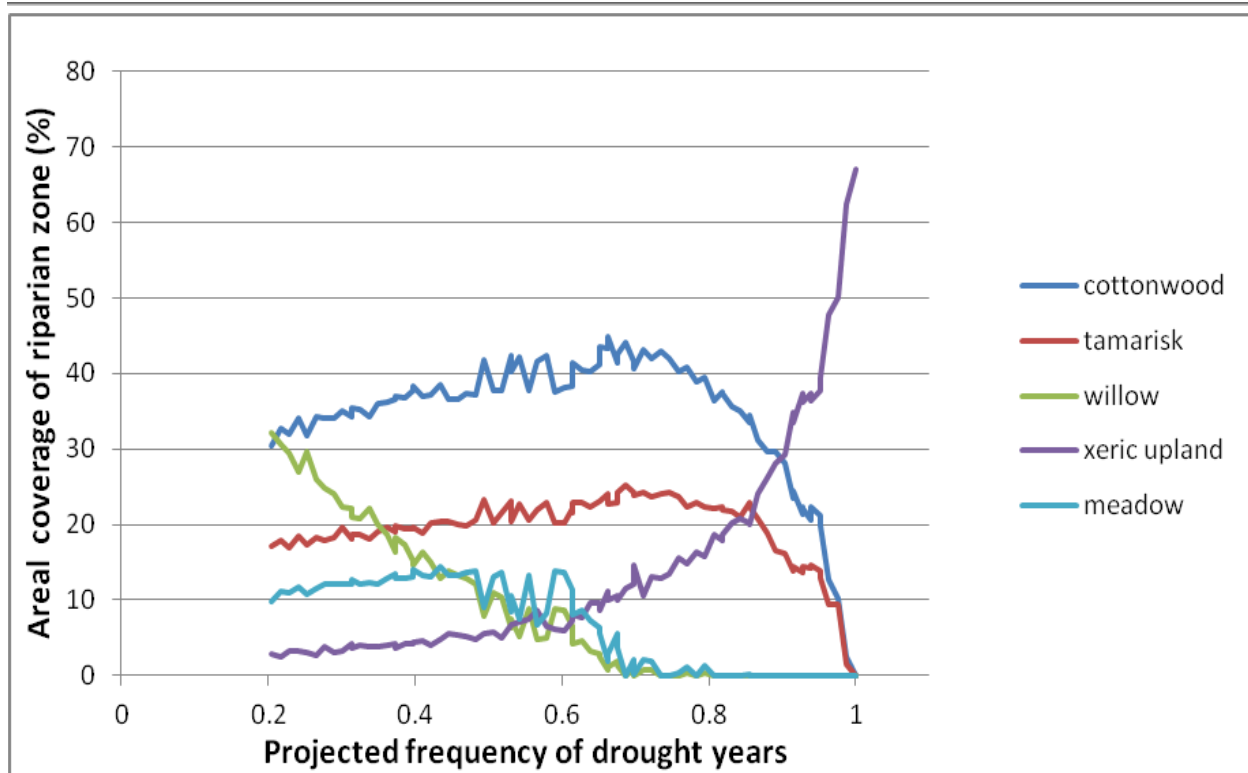


This report was prepared under contract to the Department of Defense Strategic Environmental Research and Development Program (SERDP). The publication of this report does not indicate endorsement by the Department of Defense, nor should the contents be construed as reflecting the official policy or position of the Department of Defense. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the Department of Defense.

REPORT DOCUMENTATION PAGE					Form Approved OMB No. 0704-0188	
<p>The public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing the burden, to Department of Defense, Washington Headquarters Services, Directorate for Information Operations and Reports (0704-0188), 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.</p> <p><b>PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.</b></p>						
1. REPORT DATE (DD-MM-YYYY) 25/01/2020		2. REPORT TYPE SERDP Guidance Document		3. DATES COVERED (From - To) 5/12/2015 - 5/12/2020		
4. TITLE AND SUBTITLE  Web Tools for Riparian and Aquatic Population Modeling				5a. CONTRACT NUMBER 15-C-0009		
				5b. GRANT NUMBER		
				5c. PROGRAM ELEMENT NUMBER		
6. AUTHOR(S) Dr. David A. Lytle, Oregon State University Dr. Jonathan Tonkin, University of Canterbury Dr. Julian D. Olden, University of Washington Dr. David M. Merritt, US Forest Service, Watershed, Fish, Wildlife, Air and Rare Plants Dr. Laura McMullen, ICF International Jane Rogosch, University of Washington				5d. PROJECT NUMBER RC-2511		
				5e. TASK NUMBER		
				5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Oregon State University OSU Zoology 3029 Cordley Hall Corvallis, OR 97331				8. PERFORMING ORGANIZATION REPORT NUMBER  RC-2511		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) Strategic Environmental Research and Development Program (SERDP) 4800 Mark Center Drive, Suite 16F16 Alexandria, VA 22350-3605				10. SPONSOR/MONITOR'S ACRONYM(S) SERDP		
				11. SPONSOR/MONITOR'S REPORT NUMBER(S) RC-2511		
12. DISTRIBUTION/AVAILABILITY STATEMENT DISTRIBUTION STATEMENT A. Approved for public release: distribution unlimited.						
13. SUPPLEMENTARY NOTES						
14. ABSTRACT This document assembles computer code, supporting data, and supplementary materials necessary to implement the flow-population models developed as part of RC-2511, Flow - population models for tracking non - stationary changes in riparian and aquatic ecosystems. Materials are presented separately for the three modeling structures pertaining to riparian vegetation, fish, and aquatic invertebrates. All materials are available free to the public online at the URLs below. The first section of this document presents and abbreviated summary of the materials with only brief descriptions and direct web links. The second section adds detailed descriptions of linked content.						
15. SUBJECT TERMS Web Tools, Riparian and Aquatic Population Modeling, Flow-population Models, Non-stationary Changes, Riparian and Aquatic Ecosystems						
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON	
a. REPORT	b. ABSTRACT	c. THIS PAGE			David Lytle	
UNCLASS	UNCLASS	UNCLASS	UNCLASS	96	19b. TELEPHONE NUMBER (Include area code) 541-737-1068	

# WEB TOOLS FOR RIPARIAN AND AQUATIC POPULATION MODELING

RC-2511



Date: January 25, 2020

## Authors

Dr. David A. Lytle, Department of Integrative Biology, Oregon State University

Dr. Jonathan Tonkin, University of Canterbury

Dr. Julian D. Olden, School of Aquatic and Fishery Sciences, University of Washington

Dr. David M. Merritt, US Forest Service, Watershed, Fish, Wildlife, Air and Rare Plants

Dr. Laura McMullen, ICF International

Jane Rogosch, PhD student, University of Washington

**Abstract:** This document assembles computer code, supporting data, and supplementary materials necessary to implement the flow-population models developed as part of RC-2511, *Flow-population models for tracking non-stationary changes in riparian and aquatic ecosystems*. Materials are presented separately for the three modeling structures pertaining to riparian vegetation, fish, and aquatic invertebrates. All materials are available free to the public online at the URLs below. The first section of this document presents an abbreviated summary of the materials with only brief descriptions and direct web links. The second section adds detailed descriptions of linked content.

## Section 1: Summary of Web Tools and Data URLs

### Riparian vegetation model



#### Main publications describing the methodology:

Lytle, D.A., Merritt, D.M., Tonkin, J.D., Olden, J.D. and Reynolds, L.V., 2017. Linking river flow regimes to riparian plant guilds: A community-wide modeling approach. *Ecological Applications*, 27(4), pp.1338-1350.

<https://doi.org/10.1002/eap.1528>

Tonkin, J.D., Merritt, D.M., Olden, J.D., Reynolds, L.V. and Lytle, D.A., 2018. Flow regime alteration degrades ecological networks in riparian ecosystems. *Nature Ecology & Evolution*, 2(1), pp.86-93.

<https://www.nature.com/articles/s41559-017-0379-0>

#### ShinyApp demo:

<https://jdonkin.shinyapps.io/CotTam/>

This is a simplified version of the riparian model that allows the user to directly adjust the drought frequency and project the model forward in time.

**Vital rate estimation for xeroriparian shrub and hydroriparian tree:**

<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecap.1528&file=eap1528-sup-0001-AppendixS1.docx>

An illustrative example of the process of obtaining species vital rates from the literature.

**R code for implementing the riparian model:**

[https://figshare.com/articles/5-guild\\_riparian\\_flow-population\\_model/4652608](https://figshare.com/articles/5-guild_riparian_flow-population_model/4652608)

**Sample hydrograph input data for riparian model (Maybell.csv):**

[https://figshare.com/articles/5-guild\\_riparian\\_flow-population\\_model/4652608](https://figshare.com/articles/5-guild_riparian_flow-population_model/4652608)

### Fish population model



**Primary publication describing the fish model methodology:**

Rogosch, J.S., Tonkin, J.D., Lytle, D.A., Merritt, D.M., Reynolds, L.V. and Olden, J.D., 2019. Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere*, 10(4), p.e02681.

<https://doi.org/10.1002/ecs2.2681>

**Fish model vital rate estimation:**

<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecs2.2681&file=ecs22681-sup-0001-AppendixS1.pdf>

**R code for fish model:**

<https://doi.org/10.5281/zenodo.1309024>

**Test dataset for fish model:**

<https://zenodo.org/record/1309024#.XitmFhPYrVo>

## Invertebrate population model



### **Primary publication describing the methodology:**

McMullen, L.E., De Leenheer, P., Tonkin, J.D. and Lytle, D.A., 2017. High mortality and enhanced recovery: modelling the countervailing effects of disturbance on population dynamics. *Ecology Letters*, 20(12), pp.1566-1575.

<https://doi.org/10.1111/ele.12866>

### **Mathematical proof of the time-varying logistic model:**

<https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fele.12866&file=ele12866-sup-0001-SupInfo.docx>

### **Methodology for obtaining vital rates for the invertebrate model:**

<https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fele.12866&file=ele12866-sup-0001-SupInfo.docx>

### **R code for implementing the invertebrate model:**

<https://doi.org/10.6084/m9.figshare.5476993>

## Section 2: Detailed resource descriptions

### Riparian vegetation model

#### Main publications describing the methodology:

Lytle, D.A., Merritt, D.M., Tonkin, J.D., Olden, J.D. and Reynolds, L.V., 2017. Linking river flow regimes to riparian plant guilds: A community-wide modeling approach. *Ecological Applications*, 27(4), pp.1338-1350.

<https://doi.org/10.1002/eap.1528>

Tonkin, J.D., Merritt, D.M., Olden, J.D., Reynolds, L.V. and Lytle, D.A., 2018. Flow regime alteration degrades ecological networks in riparian ecosystems. *Nature Ecology & Evolution*, 2(1), pp.86-93.

<https://www.nature.com/articles/s41559-017-0379-0>

#### ShinyApp demo:

<https://jdtonkin.shinyapps.io/CotTam/>

This is a simplified version of the riparian model that allows the user to directly adjust the drought frequency and project the model forward in time.

#### Vital rate estimation for xeroriparian shrub and hydroriparian tree:

<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Feap.1528&file=eap1528-sup-0001-AppendixS1.docx>

An illustrative example of the process of obtaining species vital rates from the literature.

Xeroriparian shrub and hydroriparian tree possess similar vital rates in terms of response to flooding, timing of seedset, and other vital rates. We review the literature pertaining to these two guilds and present the relevant data here. For xeroriparian shrub we used chronosequence studies along the upper and lower Colorado River, where stem thinning rate averaged 2,317 ( $\pm 394$ ) stems ha<sup>-1</sup> yr<sup>-1</sup> along the upper Colorado





River and 3,257 ( $\pm 937$ ) stems  $\text{ha}^{-1} \text{yr}^{-1}$  along the lower Colorado River (Merritt and Shafroth 2012). Self-thinning relations were:  $S = 130,790 - 2,317(\text{age})$  and  $S = 167,781 - 3,257(\text{age})$ . Stands older than 50 years had average stem densities of 12,300 and 16,800 stems  $\text{ha}^{-1}$  along the upper and lower Colorado River, respectively. There was no significant difference in the thinning rate between the upper and lower Colorado River ( $P = 0.1$ ), and the overall thinning rate of xeroriparian shrub was  $2,455 \pm 312$  stems  $\text{ha}^{-1} \text{yr}^{-1}$  over the 70 years modeled. The relationship between stand age and xeroriparian shrub stem density (ST) along both upper and lower Colorado River sites was  $ST = 135,478 - 2,455(\text{age})$  ( $r^2 = 0.27$ ;  $P < 0.0001$ ). Using data from Horton and Clark (2001) and Shafroth et al. (1998) we estimated the relationship between stage decline and seedling recruitment for xeroriparian shrub as  $g(h) = 0.92 \cdot \exp[-0.5 \cdot ((h - 1.8)/3.4)^2]$  for  $h \geq 0$ ; 0 otherwise. The shape of this function is similar to that of hydriparian tree (Lytle and Merritt 2004), but reflects the fact that xeroriparian shrub seedlings are more tolerant of static water levels and rapid water declines than hydriparian tree seedlings.

Hydriparian tree and xeroriparian shrub have several similarities in terms of life history attributes and regeneration niche, as well as some important differences. Species in both guilds (e.g., *Populus deltoides* and *Tamarix ramosissima*, respectively) require bare, moist freshly exposed substrate for short-lived aerial or water dispersed seeds to germinate and become established (Merkel and Hopkins 1957, Warren and Turner 1975, Fenner et al. 1984). Flood-created bare patches and areas of fresh sediment deposition are common sites for recruitment; neither guild typically recruit into heavily vegetated or shaded areas (Braatne et al. 1996, Scott et al. 1996, Cooper et al. 1999). Typically, plant establishment occurs as part of the processes of channel narrowing, point bar development due to channel meandering, or overbank deposition of sediment (Scott et al. 1996, Cooper et al. 2003). If viable seeds reach such sites, hydrologic conditions are conducive to seedling survival, and subsequent disturbance does not remove or bury individuals, establishment may occur.

Timing of flowering and seed dispersal phenology differ significantly for the hydriparian tree and xeroriparian shrub guilds in the climate of the Colorado Plateau and in much of the western U.S. (Warren and Turner 1975, Cooper et al. 1999). In



warm climates, xeroriparian shrub may flower as early as its second year of growth and flowering may occur multiple times during the growing season (Merkel and Hopkins 1957, Horton et al. 1960). Older, larger individuals may produce several hundred thousand seeds during a single season (Merkel and Hopkins 1957). Hydroriparian tree reaches reproductive stage later (5-10 years) and flowers only once per growing season, yet females may produce tens of thousands of seeds per growing season (Karrenberg and Suter 2003). Furthermore, xeroriparian shrub has bisexual flowers, so each individual produces seeds in contrast to dioecious hydroriparian tree, which has a lower ratio of seed producing individuals to individual plants (Warren and Turner 1975).

Our representative species for the hydroriparian guild, *Populus fremontii*, was found to release seeds over a six week period beginning in late-June along the Yampa River (Cooper et al. 1999). By contrast, our representative for xeroriparian shrub, *Tamarix*, began releasing seed in mid-July, seed rain peaked in mid-August, and seeds were still being dispersed in mid-September during the years measured (Cooper et al. 1999). Warren and Turner (1975) found that *Populus* dispersal occurred earlier than *Tamarix*, was of a shorter duration, and had almost ceased by the time the flowering season for *Tamarix* began along two rivers in Arizona, U.S.A.

*Tamarix* seed density in areas of establishment has been shown to be as high as ~5000 seedlings m<sup>-2</sup> (Cooper et al. 1999) to 170,000 seedlings m<sup>-2</sup> in dense *Tamarix* stands (Warren and Turner 1975). In germination trials, *Tamarix* seed viability ranged from 76% at the time of harvest to 40% after four months of cold storage (Merkel and Hopkins 1957), but seed viability in the field lasts only a few weeks (Horton et al. 1960). Laboratory trials indicate that viability ranges from 75% (Moss 1938) to greater than 90% (Van Splunder et al. 1995, Karrenberg and Suter 2003) for various species of *Populus*.

The combination of limited seed viability and differences in the separation in seed release timing of seed release may result in spatial separation in hydroriparian tree and xeroriparian invasive shrub recruitment sites, though mixed stands are not uncommon may occur due to dispersal overlap during the middle of some growing seasons. Hypocotyl extension and primary root growth occur in moist soils and at this stage



seedlings are very vulnerable to desiccation. *Populus* seedling root growth rates have been shown to average 0.6-1.3 cm/day, resulting in 72-162 cm of root growth by the end of their first season (Fenner et al. 1984, Mahoney and Rood 1998, Horton and Clark 2001), however, it has been reported that *Populus* seedlings can survive ground water decline rates of 2-4 cm day<sup>-1</sup> (Mahoney and Rood 1991, Segelquist et al. 1993). These values may more than double in finer soils with higher water-holding retention capacity soils (Cooper et al. 1999). *Populus* root growth and leaf area were found to be highest with steady shallow water tables and declined as a function of water table drawdown rate in rhizopod experiments (Mahoney and Rood 1991). *Tamarix* root growth rates were 1.1 cm d<sup>-1</sup> in field studies in Arizona, U.S.A. (Merkel and Hopkins 1957). *Tamarix* survival was 86-92% across treatments involving lowering water tables 0, 1, 2, and 4 cm/d, though biomass declined with increasing rates of decline (Horton and Clark 2001). *Tamarix* root growth rate was highest in 1 cm d<sup>-1</sup> water table drawdowns and *Tamarix* root length averaged 160 cm after 42 days of growth (about double that for *Salix gooddingii*) (Horton and Clark 2001). *Tamarix* seedlings are more tolerant of groundwater declines than are *S. gooddingii* and *Populus*, because it is known to utilize water from both phreatic sources and unsaturated soils (Everitt 1980, Busch and Smith 1995). Higher drought tolerance may enable *Tamarix* seedlings to persist in dry soils where *Salix* and *Populus* seedlings are unable (Cooper et al. 1999, Horton and Clark 2001).

Seedlings in both guilds are vulnerable to flow-related scour and deposition as well as wind abrasion and dune-burial during the first several months of growth. Due to *Tamarix* seedlings' prostrate growth form in the seedling stage, it may render it be more susceptible than *Populus* to burial (Levine and Stromberg 2001), but may be more resistant to scour due to the high tensile strength of the roots (De Baets et al. 2008). *Tamarix* is more vulnerable to inundation and anoxia in seedling and sapling stages than *Populus* (Bhattacharjee et al. 2006). Sher et al. (2000) and Sher and Marshall (2003) found that *Tamarix* was competitively suppressed by *Populus* mixed stand experiments, suggest that flooding puts native *Populus* at a competitive advantage over *Tamarix*. Degree of shade had no effect on survival of *Populus* seedlings under well-



watered conditions, but dramatically effected survival under drought conditions (43% survival in full sun; 0.03% survival in 4% sun) (Cooper et al. 1999). Interspecific competition contributed significantly to mortality over a range of light levels in field experimentation (Cooper et al.1999). Because *Tamarix* maximum aboveground height is less than *Populus*, competition for light and the negative effects of shading remain inhibitive for older age-classes of *Tamarix* (Dewine and Cooper 2008).

## References

- Bhattacharjee, J., J. P. Taylor and L. M. Smith. 2006. Controlled flooding and staged drawdown for restoration of native cottonwoods in the middle Rio Grande Valley, New Mexico, USA. *Wetlands* 26: 691-702.
- Braatne, J. H., S. B. Rood and P. E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *Biology of Populus*. R. F. Stettler, H. D. Bradshaw Jr., P. E. Heilman and T. M. Hinckley. Ottawa, ON, Canada, NRC Research Press, National Research Council of Canada: 57-85.
- Busch, D. E. and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 65: 347-370.
- Cooper, D. J., D. C. Andersen and R. A. Chimner. 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *Journal of Ecology* 91: 182-196.
- Cooper, D. J., D. M. Merritt, D. C. Andersen and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, U.S.A. *Regulated Rivers: Research and Management* 15: 419-440.
- De Baets, S., J. Poesen, B. Reubens, K. Wemans, J. De Baerdemaeker and B. Muys. 2008. Root tensile strength and root distribution of typical Mediterranean plant species and their contribution to soil shear strength. *Plant and Soil* 305: 207-226.
- Dewine, J. M. and D. J. Cooper. 2008. Canopy shade and the successional replacement of tamarisk by native box elder. *Journal of Applied Ecology* 45: 505-514.



- Everitt, B. L. 1980. Ecology of saltcedar- a plea for research. *Environmental Geology* 3: 77-84.
- Fenner, P., W. W. Brady, and D. R. Patton. 1984. Observations on seeds and seedlings of Fremont Cottonwood. *Desert Plants* 6: 55-58.
- Horton, J. L. and J. L. Clark. 2001. Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecology and Management* 140: 239-247.
- Horton, J. S., F. C. Mounts and J. M. Kraft. 1960. Seed germination and seedling establishment of phreatophyte species. Research Note 50. Fort Collins, CO., U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station.
- Karrenberg, S. and M. Suter. 2003. Phenotypic trade-offs in the sexual reproduction of Salicaceae from flood plains. *American Journal of Botany* 90: 749-754.
- Levine, C. M. and J. C. Stromberg. 2001. Effects of flooding on native and exotic plant seedlings: implications for restoring southwestern riparian forests by manipulating water and sediment flows. *Journal of Arid Environments* 49: 111-131.
- Lytle, D. A. and D. M. Merritt. 2004. Hydrologic regimes and riparian forests: a structured population model for cottonwood. *Ecology* 85: 2493-2503.
- Mahoney, J. and S. Rood. 1991. A device for studying the influence of declining water-table on poplar growth and survival. 8: 305-314.
- Mahoney, J. M. and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment-an integrative model. *Wetlands* 18: 634-645.
- Merkel, D. L. and H. H. Hopkins. 1957. Life History of Salt Cedar (*Tamarix gallica* L.). *Transactions of the Kansas Academy of Science* 60: 360-369.
- Merritt, D. M. and P. B. Shafroth. 2012. Edaphic, salinity, and stand structural trends in chronosequences of native and non-native dominated riparian forests along the Colorado River, USA. *Biological Invasions* 14: 2665-2685.
- Moss, E. H. 1938. Longevity of seed and establishment of seedlings in species of *Populus*. *Botanical Gazette* 99: 529-542.



- Scott, M. L., J. M. Friedman and G. T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology* 14: 327-339.
- Segelquist, C. A., M. L. Scott and G. T. Auble. 1993. Establishment of *Populus deltoides* under simulated alluvial groundwater declines. *American Midland Naturalist* 130: 274-285.
- Shafroth, P. B., G. T. Auble, J. C. Stromberg and D. T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18: 577-590
- Sher, A. A. and D. L. Marshall. 2003. Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamaricaceae) across water regimes and substrate types. *American Journal of Botany* 90: 413-422.
- Sher, A. A., D. L. Marshall and S. A. Gilbert. 2000. Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conservation Biology* 14: 1744-1754.
- Van Splunder, I., H. Coops, L. Voeselek and C. Blom. 1995. Establishment of alluvial forest species in floodplains - the role of dispersal timing, germination characteristics and water-level fluctuations. *Acta Botanica Neerlandica* 44: 269-278.
- Warren, D. K. and R. M. Turner. 1975. Saltcedar (*Tamarix chinensis*) seed production, seedling establishment, and response to inundation. *Journal of the Arizona Academy of Science* 10: 135-144.

#### R code for implementing the riparian model:

[https://figshare.com/articles/5-guild\\_riparian\\_flow-population\\_model/4652608](https://figshare.com/articles/5-guild_riparian_flow-population_model/4652608)

For code to run, it requires the accompanied 'Maybell.csv' file in the same directory.

```
# -----  
# -----  
# 5-guild riparian plant flow-population model  
# Date: Feb 2017  
# Authors: Jonathan Tonkin, David Lytle  
# Emails: jdtonkin@gmail.com, lytle@oregonstate.edu
```



```

# Core model associated with Lytle, D. A., Merritt, D. M., Tonkin, J.
  D., Olden, J. D. &
# Reynolds, L. V. (2017) Linking river flow regimes to riparian plant
  guilds: a community-
# wide modeling approach. Ecological Applications.

# Running the code as is produces a 250 year projection of the five
  guilds at the current
# natural flow regime. To alter the flow regime, change 'outerreps' to
  however severe you
# want flow alteration to be and change the settings inside the ' FLOW
  ALTERATIONS'
# section. Changing 'outerreps' to 84 alters flood or droughts from
  natural flow to 100%
# modified.

# Note: In the paper, we refer to five guilds: HT (Hydroriparian
  Tree), XS (Xeroriparian
# Shrub), HS (Hydroriparian Shrub), MM (Mesoriparian Meadow), and DS
  (Desert Shrub).
# Here, we use different names, with local examples as follows:
# HT: Cottonwood. Includes anything with 'C' or 'Cot'. e.g. 'Cgraph',
  'Crep', 'DomC'
# XS: Tamarisk. Includes anything with 'T' or 'Tam'. e.g. 'Tgraph',
  'Trep', 'DomT'
# HS: Willow. Includes anything with 'W'. e.g. 'Wgraph', 'Wrep'
# MM: Meadow. Includes anything with 'M'. e.g. 'Mgraph', 'Mrep'
# DS: Sagebrush. Includes anything with 'S'. e.g. 'Sgraph', 'Srep'
# -----
  -----

# Required libraries
library(ggplot2)
library(tidyr)
library(dplyr)

# SETUP -----
  -----

rm(list = ls()) # clearing the workspace
count <- 250 # number of years to project simulations (inner loop)

```



```

burnin = 100 # number of years to discard as burn in during long term
mean estimation
outerreps <- 1 # number of iterations for outer loop that alters
drought/flood frequency
replicates <- 100 # number of replicate projections to run (mid loop)

# FLOW -----
-----

# Maybell flow data 1916-1998, 83 years continuous
flowdata <- read.csv("maybell.csv")
str(flowdata)
head(flowdata)
# flooddates is peak dates of all floods (Oct 1 = 1)
# basedates is baseflow dates

# FLOOD REGIME DEFINITIONS -----
-----

# CALCULATION OF p<j> and p<tam> -----
-----

# Prop. of possible recruitment days that occur between Q and return
to baseflow at 700cfs
cseedfirst = 260 # COT: first date of seedset, June 17th or 260
cseedlast = 298 # COT: last date of seedset, 298 or July 25.
tseedfirst = 280 # TAM: first date of seedset, which is July 7th or
280
tseedlast = 336 # TAM: last date of seedset, 336 or 1 Sept.

# FUNCTIONS FOR INCLUDING INSIDE LOOPS -----
-----

# Assign either the first date of cottonwood seedset or the first date
of flooding
# Cottonwood
csf_func <- function(x) {
  ifelse(cseedfirst > x, cseedfirst, x)
}
cfirstdate <- csf_func(flowdata$flooddates)

# Assign either the last date of cottonwood seedset or the date that
baseflow occurs

```





```

csl_func <- function(x) {
  ifelse(cseedlast > x, x, cseedlast)
}
clastdate <- csl_func(flowdata$basedates)

# Calculate the number of days in the seedset period
cdifference <- clastdate - cfirstdate

# Check to make sure value is positive, assigns 0 otherwise
gzero_func <- function(x) {
  ifelse(x > 0, x, 0)
}

# Length of season for seedset - with negative values removed
cseasonlength <- gzero_func(cdifference)

# Proportion of season available
cproportion <- cseasonlength/(cseedlast - cseedfirst)

# Now repeat all this to get p<tam>
tsf_func <- function(x) {
  ifelse(tseedfirst > x, tseedfirst, x)
}
tfirstdate <- tsf_func(flowdata$flooddates)
tsl_func <- function(x) {
  ifelse(tseedlast > x, x, tseedlast)
}
tlastdate <- tsl_func(flowdata$basedates)
tdifference <- tlastdate - tfirstdate
tseasonlength <- gzero_func(tdifference)
tproportion <- tseasonlength/(tseedlast - tseedfirst)

# FLOOD THRESHOLD FUNCTIONS -----
-----
# Currently these are the same for cot and tam
# flowdata$floodmag - vector containing peak flood magnitude

# Magnitude of peak flow over which is considered a mortality causing
  flood event
mortcutoff = 9888 # This is in CFS, as are the Maybell data points
# Floods above 280 cms 9888 cfs cause mortality, below cause none

```



```

# Same for drought (threshold below rather than above)
droughtcutoff = 7416 # floods above 210 cms / 7416cfs do not cause
drought mortality

# Convert peak discharge values into a vector of floods/no floods,
# 1 = an above threshold flood (some scouring), 0 = below threshold
(no scouring)
bigflood_func <- function(x) {
  ifelse(x > mortcutoff, 1, 0)
}

# Another similar vector for droughts
# Both of these appear in the functions for vital rates and fecundity,
below
drought_func <- function(x) {
  ifelse(x < droughtcutoff, 1, 0)
}

# Vector containing 1's for years that do not have a flood, e.g.
normal and drought years
nonflood_func <- function(x) {
  ifelse(x > mortcutoff, 0, 1)
}

# ITERATION PARAMETERS -----
-----
# Setting up arrays/vectors to fill with data from loops

# Inner loop details -----
-----
# 'count' - number of years to project simulations (inner loop)

# Output of no. ind. for each age class for each year projected into
the future
# An array with 6 columns (each age class) and however many rows there
are years projected
Coutput <- array(0, dim = c(count, 6)) # Cottonwood
Toutput <- array(0, dim = c(count, 6)) # Tamarisk
Woutput <- array(0, dim = c(count, 6)) # Willow
Soutput <- array(0, dim = c(count, 6)) # Sagebrush
Moutput <- array(0, dim = c(count, 6)) # Meadow

```



```

# Total cottonwood pop. size as % of K
# This is the total space occupied by this species in cottonwood
  seedling units
Cspaceoutput <- numeric(length = count) # Cottonwood
Tspaceoutput <- numeric(length = count) # Tamarisk
Wspaceoutput <- numeric(length = count) # Willow
Sspaceoutput <- numeric(length = count) # Sagebrush
Mspaceoutput <- numeric(length = count) # Meadow

# Flood and drought settings for each year projected into the future
  (i.e. 0 or 1)
floodoutput <- numeric(length = count) # flood
droughtoutput <- numeric(length = count) # drought
nonfloodoutput <- numeric(length = count) # nonflood
normaloutput <- numeric(length = count) # normal

# Total pop. size as % of K WITHOUT SEEDLINGS for each year projected
  into future
# contains %K of each guild except for seedlings for each year of
  projection
Cnonseedling <- numeric(length = count)
Tnonseedling <- numeric(length = count)
Wnonseedling <- numeric(length = count)
Snonseedling <- numeric(length = count)
Mnonseedling <- numeric(length = count)

# No. ind. at stages as per Merritt and Poff 2010
# Vector of cot age class 5 for each year projected
DomC <- numeric(length = count) # these will record the NUMBER of
  individuals in stg 5,
# which are 5-10 year olds
DomT <- numeric(length = count) # same, for stages 4, although this is
  7-15 year olds

# Mid loop details -----
  -----
# 'replicates' - number of replicate projections to run (mid loop)

# Mean values for each rep. run over the period specified from burnin
  to end of projection
# Mean density of each guild WITHOUT seedlings included - each
  replicate run

```



```

Crep <- numeric(length = replicates)
Trep <- numeric(length = replicates)
Wrep <- numeric(length = replicates)
Srep <- numeric(length = replicates)
Mrep <- numeric(length = replicates)

# Mean density of each guild WITH seedlings included
Crep_all <- numeric(length = replicates)
Trep_all <- numeric(length = replicates)
Wrep_all <- numeric(length = replicates)
Srep_all <- numeric(length = replicates)
Mrep_all <- numeric(length = replicates)

# Mean of DomC for each of the replicate runs
DomCrep <- numeric(length = replicates) # to record output of DomC
from flow scenarios
DomTrep <- numeric(length = replicates)

# Outer loop details -----
-----
# 'outerreps' - number of iterations for outer loop that alters
drought/flood frequency
# Results of flow mod scenarios. Not useful unless simulating changes
to flow regime
# This is the mean of each flow mod. setting for the full burnin->end
of projection period

# No seedlings for each of the flow mod settings
Cgraph <- numeric(length = outerreps)
Tgraph <- numeric(length = outerreps)
Mgraph <- numeric(length = outerreps)
Wgraph <- numeric(length = outerreps)
Sgraph <- numeric(length = outerreps)

# All incl. seedlings for each of the flow mod settings
Cgraph_all <- numeric(length = outerreps)
Tgraph_all <- numeric(length = outerreps)
Mgraph_all <- numeric(length = outerreps)
Wgraph_all <- numeric(length = outerreps)
Sgraph_all <- numeric(length = outerreps)

# Mean of DomC for each of the flow mod settings

```



```

DomCrep_graph <- numeric(length = outerreps)
DomTrep_graph <- numeric(length = outerreps)

# Proportion of flow years in each flow mod setting
droughtgraph <- numeric(length = outerreps) # droughts
floodgraph <- numeric(length = outerreps) # floods
nonfloodgraph <- numeric(length = outerreps) # nonfloods
normalgraph <- numeric(length = outerreps) # normal years

# Setting flow scenario change to none to begin with
# The outer loop iterates these one step at a time until it reaches
'outerreps'
droughtchanged = floodchanged = 0

# RECRUITMENT AS FUNCTION OF FLOOD DECLINE RATE -----
-----

# COT: vector containing the NEGATIVE VALUE OF slopes of all declining
limbs of floods
flooddecline <- -flowdata$slopecot
# COT: drawdown survival, a lognormal FUNCTION.
# Positive values of h indicate receding water
cdds_func <- function(x) {
  .944 * exp(-.5 * ((log(x/1.279))/0.987)^2)
}
decline <- cdds_func(flooddecline) # flood decline is the h value from
paper

# TAM: vector containing NEGATIVE VALUE OF slopes of all declining
limbs of floods
tflooddecline <- -flowdata$slopetam
# TAM: drawdown survival, a lognormal FUNCTION
tdds_func <- function(x) {
  0.917 * exp(-.5 * ((x - 1.8)/3.4)^2)
}
tdecline <- tdds_func(tflooddecline)

# Checks to see if at least one adult is present
adult_func <- function(x) {
  ifelse(x > .99999, 1, 0)
}

```



```

# Keeps FC6 from dividing by zero by substituting an arbitrary nonzero
# number that will get
# multiplied by zero later anyway during matrix multiplication
nonind <- function(x) {
  ifelse(x == 0, 666, x)
}

# checkpos makes sure that the K-occupied term is positive, assigns 0
# if not
checkpos <- function(x) {
  ifelse(x < 0, 0, x)
}

# Quasi extinction threshold of 1, keeps pop from asymptoting
# infinitely to zero
quasi <- function(x) {
  ifelse(x < 1, 0, x)
}

# Quasi rescue function that keeps species from disappearing,
# e.g. sagebrush that can encroach from uplands
quasiten <- function(x) {
  ifelse(x < 10, 10, x)
}

# OUTER LOOP
#####
#####
# DAMMING & DROUGHT SIMULATION

for(zim in 1:outerreps) {

bigflood <- bigflood_func(flowdata$floodmag)
drought <- drought_func(flowdata$floodmag)
nonflood <- nonflood_func(flowdata$floodmag)

# -----
# ----- #
# FLOW ALTERATIONS start
#####
# -----
# ----- #

```



```

# IMPORTANT: For modifying bigflood/drought/normal - you need to be
# careful to modify them
# simultaneously, otherwise you can get simultaneous drought and flood
# years
# e.g. #1 incr. floods: add 1s to bigflood, but also add 0s to both
# drought and nonflood.
# e.g. #2 homogenizing flows: add 0s to bigflood and drought and add
# 1s to nonflood.
# e.g. #3 increasing drought: add 1s to drought and nonflood and add
# 0s to bigflood.

# Comment/uncomment the following to set up these scenarios

# ifelse(floodchanged == 0, bigflood, bigflood[1:floodchanged] <- 0)
# '0' eliminates floods in Maybell vector going from year 1 to
# floodchanged
# Floodchanged is how many flood years to remove
# To CREATE floods use = 1

# ifelse(droughtchanged == 0, drought, drought[1:droughtchanged] <- 0)
# '0' eliminates droughts in Maybell vector going from year 1 to
# droughtchanged
# To CREATE droughts use = 1

# ifelse(floodchanged == 0, nonflood, nonflood[1:floodchanged] <- 1)

# -----
# ----- #
# FLOW ALTERATIONS end
#####
# -----
# ----- #

# MIDDLE LOOP
#####
#####
# Middle loop uses iterator "rep" to get "replicates" number of runs
# for averaging
for(rep in 1:replicates) {

```



```

# VITAL RATES -----
-----

# K is total area available to cottonwood or tamarisk initially
  calculated as total area
# occupied by cottonwood.

# VITAL RATES - cottonwood -----
-----

# Stage specific densities
denC1 <- 350
denC2 <- 10
denC3 <- 1
denC4 <- .91
denC5 <- .6
denC6 <- .12

# "Self thinning" rates, or equivalency rules, for stage transitions
bC1 <- denC2/denC1
bC2 <- denC3/denC2
bC3 <- denC4/denC3
bC4 <- denC5/denC4
bC5 <- denC6/denC5

# Baseline maturation probabiliity, aC6 (adult senescence rate)
aC1 <- 1
aC2 <- 1
aC3 <- 1
aC4 <- 1
aC5 <- .167
aC6 <- .03

# Flood mortality in a flood year
SC1 <- .97
SC2 <- .33
SC3 <- .224
SC4 <- .19
SC5 <- .073
SC6 <- .02

# Drought mortality in a drought year

```





```

DC1 <- .49
DC2 <- .16
DC3 <- .083
DC4 <- .05
DC5 <- .05
DC6 <- .05

# Initial area in m2. Here, it is calculated based ONLY on cottonwood.
areaC1 <- 11816
areaC2 <- 11816
areaC3 <- 11144
areaC4 <- 11144
areaC5 <- 13819
areaC6 <- 59605

K <- (areaC1 + areaC2 + areaC3 + areaC4 + areaC5 + areaC6) * denC1

# VITAL RATES - TAMARISK -----
-----

# K is common to both cot and tam

# Stage specific densities, number per m2
denT1 <- 400
denT2 <- 29
denT3 <- 4.5
denT4 <- 1.4
denT5 <- 1.3
denT6 <- 1.3

# "Self thinning" rates, or equivalency rules, for stage transitions
bT1 <- denT2/denT1
bT2 <- denT3/denT2
bT3 <- denT4/denT3
bT4 <- denT5/denT4
bT5 <- denT6/denT5

# Baseline maturation probability, aT6 (adult senescence rate)
aT1 <- 1
aT2 <- 1
aT3 <- .25
aT4 <- .11

```



```

aT5 <- .07
aT6 <- .05

# Flood mortality in a flood year
ST1 <- .9
ST2 <- .55
ST3 <- .25
ST4 <- .05
ST5 <- .01
ST6 <- .01

# Drought mortality in a drought year
DT1 <- .5
DT2 <- .15
DT3 <- .05
DT4 <- .025
DT5 <- .025
DT6 <- .025

# Initial area in m2. Not included in initial K calculation
areaT1 <- 1000
areaT2 <- 0
areaT3 <- 0
areaT4 <- 0
areaT5 <- 0
areaT6 <- 0

# VITAL RATES - willow -----
-----

# Stage specific densities, number per m2
# THESE NUMBERS ARE ARBITRARY, but reflect a final adult size/spacing
# of 1 m2 per plant
denW1 <- 350
denW2 <- 35
denW3 <- 1
denW4 <- 1
denW5 <- 1
denW6 <- 1

# "Self thinning" rates, or equivalency rules, for stage transitions
bw1 <- denW2/denW1

```



```

bW2 <- denW3/denW2
bW3 <- denW4/denW3
bW4 <- denW5/denW4
bW5 <- denW6/denW5

# Baseline maturation probability, aW6 is adult senescence rate
# Only aW6 is different from cottonwood (faster)
aW1 <- 1
aW2 <- 1
aW3 <- 1
aW4 <- 1
aW5 <- .167
aW6 <- .01

# Flood mortality in a flood year. HALF THAT OF COTTONWOOD
SW1 <- .49
SW2 <- .17
SW3 <- .11
SW4 <- .10
SW5 <- .04
SW6 <- .01

# Drought mortality in a drought year
# Basically, SURVIVORSHIP rate is half that of cottonwood: convert
  mortality to
# survivorship, divide by two, convert back to mortality
DW1 <- .75
DW2 <- .58
DW3 <- .54
DW4 <- .53
DW5 <- .51
DW6 <- .51

# Initial area in m2. Not included in initial K calculation
areaW1 <- 100
areaW2 <- 100
areaW3 <- 100
areaW4 <- 100
areaW5 <- 100
areaW6 <- 100

```



```

# VITAL RATES - sagebrush -----
-----

# Stage specific densities, number per m2
# THESE NUMBERS ARE ARBITRARY, but reflect an adult size/spacing of 1
  m2
denS1 <- 350
denS2 <- 35
denS3 <- 1
denS4 <- 1
denS5 <- 1
denS6 <- 1

# "Self thinning" rates, or equivalency rules, for stage transitions
bS1 <- denS2/denS1
bS2 <- denS3/denS2
bS3 <- denS4/denS3
bS4 <- denS5/denS4
bS5 <- denS6/denS5

# Baseline maturation probabiliity, aS6 is adult senescence rate.
# SAME AS COTTONWOOD
aS1 <- 1
aS2 <- 1
aS3 <- 1
aS4 <- 1
aS5 <- .167
aS6 <- .03

# Flood mortality in a flood year
# Taken by taking survivorship of cot (1-S), dividing by 2, and
  coverting back to mort.
# So, flood SURVIVORSHIP is 1/2 that of cottonwood
SS1 <- .99
SS2 <- .67
SS3 <- .61
SS4 <- .60
SS5 <- .54
SS6 <- .51

# Drought MORTALITY in a drought year. ONE HALF COTTONWOOD RATES
DS1 <- .24

```



```

DS2 <- .08
DS3 <- .042
DS4 <- .025
DS5 <- .005
DS6 <- .005

# Initial area in m2. Not included in initial K calculation
areaS1 <- 100
areaS2 <- 100
areaS3 <- 100
areaS4 <- 100
areaS5 <- 100
areaS6 <- 100

# VITAL RATES - Meadow -----
-----

# Stage specific densities, number per m2
# THESE NUMBERS ARE ARBITRARY, but reflect an adult size/spacing of 1
m2
denM1 <- 350
denM2 <- 35
denM3 <- 1
denM4 <- 1
denM5 <- 1
denM6 <- 1

# "Self thinning" rates, or equivalency rules, for stage transitions
bM1 <- denM2/denM1
bM2 <- denM3/denM2
bM3 <- denM4/denM3
bM4 <- denM5/denM4
bM5 <- denM6/denM5

# Baseline maturation probabiliity, aM6 is adult senescence rate. SAME
AS COTTONWOOD
aM1 <- 1
aM2 <- 1
aM3 <- 1
aM4 <- 1
aM5 <- .167
aM6 <- .03

```



```

# Flood mortality in a flood year
# Taken by taking survivorship of cot (1-S), dividing by 2, and
  coverting back to mort.
# FOR STAGES 1-3 ONLY
# So, flood SURVIVORSHIP is 1/2 that of cottonwood for those stages,
  reflecting instability
# of meadow habitats in highly flood-prone situations.
SM1 <- .99
SM2 <- .67
SM3 <- .61
SM4 <- .19
SM5 <- .073
SM6 <- .02

```

```

# Drought MORTALITY in a drought year
# ONE HALF COTTONWOOD RATES in stages 4-6 only, reflecting greater
  drought tolerance in
# established meadows and less groundwater dependence
DM1 <- .49
DM2 <- .16
DM3 <- .083
DM4 <- .025
DM5 <- .005
DM6 <- .005

```

```

# Initial area in m2. Not included in initial K calculation
areaM1 <- 100
areaM2 <- 100
areaM3 <- 100
areaM4 <- 100
areaM5 <- 100
areaM6 <- 100

```

```

# Maybell area in m2, as established from initial cottonwood occupancy
# K is the total area available for cot OR tam expressed in cottonwood
  seedlings per m2
NC <- c(areaC1 * denC1,
        areaC2 * denC2,
        areaC3 * denC3,
        areaC4 * denC4,
        areaC5 * denC5,

```



```

        areaC6 * denC6)
# NC gives the total number of individuals for each age class.
# Initially here, this is found by multiplying the number of m2
  occupied by a given class
# by the the density per m2

NT <- c(areaT1 * denT1,
        areaT2 * denT2,
        areaT3 * denT3,
        areaT4 * denT4,
        areaT5 * denT5,
        areaT6 * denT6)

NW <- c(areaW1 * denW1,
        areaW2 * denW2,
        areaW3 * denW3,
        areaW4 * denW4,
        areaW5 * denW5,
        areaW6 * denW6)

NS <- c(areaS1 * denS1,
        areaS2 * denS2,
        areaS3 * denS3,
        areaS4 * denS4,
        areaS5 * denS5,
        areaS6 * denS6)

NM <- c(areaM1 * denM1,
        areaM2 * denM2,
        areaM3 * denM3,
        areaM4 * denM4,
        areaM5 * denM5,
        areaM6 * denM6)

# Inner loop
#####
#####
for(i in 1:count) {

y = sample(nrow(flowdata), 1)
# y is a random number within the length of the flow data to randomly
  select a year from

```



```

# the 'bigflood' and 'drought' vector
# in this case anything between 1 and 83 in the maybell data

# VITAL RATE DEFINITIONS: cottonwood -----
-----
# G is prob. of transition to next stage
# P is prob. of remaining in that stage
GC1 <- aC1 * bC1 * (1 - bigflood[y] * SC1) * (1 - drought[y] * DC1)
GC2 <- aC2 * bC2 * (1 - bigflood[y] * SC2) * (1 - drought[y] * DC2)
GC3 <- aC3 * bC3 * (1 - bigflood[y] * SC3) * (1 - drought[y] * DC3)
GC4 <- aC4 * bC4 * (1 - bigflood[y] * SC4) * (1 - drought[y] * DC4)
GC5 <- aC5 * bC5 * (1 - bigflood[y] * SC5) * (1 - drought[y] * DC5)
PC5 <- (1 - aC5) * (1 - bigflood[y] * SC5) * (1 - drought[y] * DC5)
PC6 <- (1 - aC6) * (1 - bigflood[y] * SC6) * (1 - drought[y] * DC6)

# VITAL RATE DEFINITIONS: tamarisk -----
-----
GT1 <- aT1 * bT1 * (1 - bigflood[y] * ST1) * (1 - drought[y] * DT1)
GT2 <- aT2 * bT2 * (1 - bigflood[y] * ST2) * (1 - drought[y] * DT2)
GT3 <- aT3 * bT3 * (1 - bigflood[y] * ST3) * (1 - drought[y] * DT3)
GT4 <- aT4 * bT4 * (1 - bigflood[y] * ST4) * (1 - drought[y] * DT4)
GT5 <- aT5 * bT5 * (1 - bigflood[y] * ST5) * (1 - drought[y] * DT5)
PT3 <- (1 - aT3) * (1 - bigflood[y] * ST3) * (1 - drought[y] * DT3)
PT4 <- (1 - aT4) * (1 - bigflood[y] * ST4) * (1 - drought[y] * DT4)
PT5 <- (1 - aT5) * (1 - bigflood[y] * ST5) * (1 - drought[y] * DT5)
PT6 <- (1 - aT6) * (1 - bigflood[y] * ST6) * (1 - drought[y] * DT6)

# VITAL RATE DEFINITIONS: willow -----
-----
GW1 <- aW1 * bW1 * (1 - bigflood[y] * SW1) * (1 - drought[y] * DW1)
GW2 <- aW2 * bW2 * (1 - bigflood[y] * SW2) * (1 - drought[y] * DW2)
GW3 <- aW3 * bW3 * (1 - bigflood[y] * SW3) * (1 - drought[y] * DW3)
GW4 <- aW4 * bW4 * (1 - bigflood[y] * SW4) * (1 - drought[y] * DW4)
GW5 <- aW5 * bW5 * (1 - bigflood[y] * SW5) * (1 - drought[y] * DW5)
PW5 <- (1 - aW5) * (1 - bigflood[y] * SW5) * (1 - drought[y] * DW5)
PW6 <- (1 - aW6) * (1 - bigflood[y] * SW6) * (1 - drought[y] * DW6)

# VITAL RATE DEFINITIONS: sagebrush -----
-----
GS1 <- aS1 * bS1 * (1 - bigflood[y] * SS1) * (1 - drought[y] * DS1)
GS2 <- aS2 * bS2 * (1 - bigflood[y] * SS2) * (1 - drought[y] * DS2)
GS3 <- aS3 * bS3 * (1 - bigflood[y] * SS3) * (1 - drought[y] * DS3)

```





```

GS4 <- aS4 * bS4 * (1 - bigflood[y] * SS4) * (1 - drought[y] * DS4)
GS5 <- aS5 * bS5 * (1 - bigflood[y] * SS5) * (1 - drought[y] * DS5)
PS5 <- (1 - aS5) * (1 - bigflood[y] * SS5) * (1 - drought[y] * DS5)
PS6 <- (1 - aS6) * (1 - bigflood[y] * SS6) * (1 - drought[y] * DS6)

# VITAL RATE DEFINITIONS: meadow -----
-----
GM1 <- aM1 * bM1 * (1 - bigflood[y] * SM1) * (1 - drought[y] * DM1)
GM2 <- aM2 * bM2 * (1 - bigflood[y] * SM2) * (1 - drought[y] * DM2)
GM3 <- aM3 * bM3 * (1 - bigflood[y] * SM3) * (1 - drought[y] * DM3)
GM4 <- aM4 * bM4 * (1 - bigflood[y] * SM4) * (1 - drought[y] * DM4)
GM5 <- aM5 * bM5 * (1 - bigflood[y] * SM5) * (1 - drought[y] * DM5)
PM5 <- (1 - aM5) * (1 - bigflood[y] * SM5) * (1 - drought[y] * DM5)
PM6 <- (1 - aM6) * (1 - bigflood[y] * SM6) * (1 - drought[y] * DM6)

# FECUNDITY -----
-----
# Assumes that if any breeding tam or cot is present, they will seed
# all recently-scoured
# substrates, although success is scaled by the lognormal hydrograph
# drawdown functions.
# If cot and tam seedlings behave entirely independently as modeled
# here, this means that
# under the right conditions there can be overseeding such that if (K-
# occupied) is the
# total amount of scoured habitat remaining, then up to 2*(K-occupied)
# could be colonized
# by seedlings, half tam and half cot. One consequence of this is if
# an extended drought
# is followed by a good flood and then many growth years, populations
# could exceed K for
# many years, and when pop > K, recruitment will not occur (although
# flood-related
# mortality will keep lowering population sizes).

# Post flood space occupied -----
-----
# postfloodC gives the amount of space occupied by cottonwood after
# the flood (AND
# ACTUALLY AFTER DROUGHT OR NORMAL YEARS AS WELL!!!) IN COTTONWOOD
# SEEDLING UNITS
postfloodC <-

```



```

NC[1] * GC1/bC1 +
NC[2] * GC2/(bC2 * bC1) +
NC[3] * GC3/(bC3 * bC2 * bC1) +
NC[4] * GC4/(bC4 * bC3 * bC2 * bC1) +
NC[5] * PC5/(bC4 * bC3 * bC2 * bC1) +
NC[5] * GC5/(bC5 * bC4 * bC3 * bC2 * bC1) +
NC[6] * PC6/(bC5 * bC4 * bC3 * bC2 * bC1)

```

# postfloodT gives the amount of space occupied by tamarisk after the flood

# IN TAMARISK SEEDLING UNITS

```

postfloodT <-
  NT[1] * GT1/bT1 +
  NT[2] * GT2/(bT2 * bT1) +
  NT[3] * GT3/(bT3 * bT2 * bT1) +
  NT[3] * PT3/(bT2 * bT1) +
  NT[4] * GT4/(bT4 * bT3 * bT2 * bT1) +
  NT[4] * PT4/(bT3 * bT2 * bT1) +
  NT[5] * GT5/(bT5 * bT4 * bT3 * bT2 * bT1) +
  NT[5] * PT5/(bT4 * bT3 * bT2 * bT1) +
  NT[6] * PT6/(bT5 * bT4 * bT3 * bT2 * bT1)

```

# postfloodW gives the amount of space occupied by willow after the flood

# IN WILLOW SEEDLING UNITS

```

postfloodW <-
  NW[1] * GW1/bW1 +
  NW[2] * GW2/(bW2 * bW1) +
  NW[3] * GW3/(bW3 * bW2 * bW1) +
  NW[4] * GW4/(bW4 * bW3 * bW2 * bW1) +
  NW[5] * PW5/(bW4 * bW3 * bW2 * bW1) +
  NW[5] * GW5/(bW5 * bW4 * bW3 * bW2 * bW1) +
  NW[6] * PW6/(bW5 * bW4 * bW3 * bW2 * bW1)

```

# postfloodS gives the amount of space occupied by SAGEBRUSH after the flood

# IN SAGEBRUSH SEEDLING UNITS

```

postfloodS <-
  NS[1] * GS1/bS1 +
  NS[2] * GS2/(bS2 * bS1) +
  NS[3] * GS3/(bS3 * bS2 * bS1) +
  NS[4] * GS4/(bS4 * bS3 * bS2 * bS1) +

```



```

NS[5] * PS5/(bS4 * bS3 * bS2 * bS1) +
NS[5] * GS5/(bS5 * bS4 * bS3 * bS2 * bS1) +
NS[6] * PS6/(bS5 * bS4 * bS3 * bS2 * bS1)

# postfloodM gives the amount of space occupied by meadow after the
# flood
# IN MEADOW SEEDLING UNITS
postfloodM <-
  NM[1] * GM1/bM1 +
  NM[2] * GM2/(bM2 * bM1) +
  NM[3] * GM3/(bM3 * bM2 * bM1) +
  NM[4] * GM4/(bM4 * bM3 * bM2 * bM1) +
  NM[5] * PM5/(bM4 * bM3 * bM2 * bM1) +
  NM[5] * GM5/(bM5 * bM4 * bM3 * bM2 * bM1) +
  NM[6] * PM6/(bM5 * bM4 * bM3 * bM2 * bM1)

# POTENTIAL COTTONWOOD FECUNDITY -----
-----
FC6 <- checkpos((adult_func(NC[6])) * # checks to see if at least 1
  adult is present
    (1/nonind(NC[6])) *
    bigflood[y] *
    cproportion[y] *
    decline[y] *
    (K - (postfloodC +
      postfloodT * (denC1/denT1) +
      postfloodW * (denC1/denW1) +
      postfloodS * (denC1/denS1) +
      postfloodM * (denC1/denM1))))

# '(1/nonind(NC[6]))' keeps FC6 from dividing by zero by substituting
# an arbitrary non-0
# number that will be multiplied by 0 later anyway during matrix
# multiplication

# This gives POTENTIAL MAX fecundity based on amount of bare substrate
# available AFTER
# that year's flood.
# Reproduction is conditional on:
# 1. at least one reproductive cottonwood being present
# 2. a big flood occurring
# 3. flood during seedset window.

```



```

# It is independent of # of repro adults, but it is scaled by the rate
# of flooddecline AND
# BY THE PROPORTION OF SEEDSET DAYS.
# Number of new seedlings is determined by the total amount of bare
# substrates;
# i.e. whatever is not occupied by surviving cottonwood OR OTHER
# SPECIES.
# The denC1/denT1 term converts tam to cot seedling units and likewise
# for other 3 guilds.
# The 1/nonind[NC[6]] term will cancel out with NC[6] during matrix
# projection.
# i.e. number of seedlings is independent of number of mature trees.

# POTENTIAL TAMARISK FECUNDITY -----
-----
FT <- checkpos((adult_func(NT[3] + NT[4] + NT[5] + NT[6])) *
  bigflood[y] *
  tproportion[y] *
  tdecline[y] *
  (denT1/denC1) *
  (K - (postfloodC +
    postfloodT * (denC1/denT1) +
    postfloodW * (denC1/denW1) +
    postfloodS * (denC1/denS1) +
    postfloodM * (denC1/denM1))))))

# This gives fecundities of TAMARISK seedlings based on amount of bare
# substrates
# available AFTER that year's flood.
# Note that units are cot seedlings in the (K-occupied) term, but are
# then converted back
# to tam seedlings.
# Repro is conditional on
# 1. at least one repro tamarisk being present,
# 2. a big flood occurring
# 3. during seedset.
# It is independent of # of repro adults, but it is scaled by the rate
# of flooddecline and
# by prop of seedset days.
# Note that the independence of FT from breeding pop size is achieved
# differently here
# than for cot, it is "forced" during matrix iteration, below.

```



```

# WILLOW FECUNDITY -----
-----
FW <- checkpos((adult_func(NW[3] + NW[4] + NW[5] + NW[6])) *
  bigflood[y] *
  (denW1/denC1) *
  (K - (postfloodC +
    postfloodT * (denC1/denT1) +
    postfloodW * (denC1/denW1) +
    postfloodS * (denC1/denS1) +
    postfloodM * (denC1/denM1))))))
# checks to make sure at least one stage 3 to 6 age individual is
# present, and that a
# flood occurs. No dependence on drawdown or seedset timing.

# SAGEBRUSH FECUNDITY -----
-----
FS <- checkpos((adult_func(NS[2] + NS[3] + NS[4] + NS[5] + NS[6])) *
  nonflood[y] *
  (denS1/denC1) *
  (K - (postfloodC +
    postfloodT * (denC1/denT1) +
    postfloodW * (denC1/denW1) +
    postfloodS * (denC1/denS1) +
    postfloodM * (denC1/denM1))))))
# Sagebrush fecundity in # of sagebrush seedlings, to be added using
# "placeholder" to NS1
# during iteration.
# Here, sagebrush can colonize any empty portion of K, but only during
# NONFLOOD years.

# MEADOW FECUNDITY -----
-----
FM <- checkpos((adult_func(NM[2] + NM[3] + NM[4] + NM[5] + NM[6])) *
  bigflood[y] *
  (denM1/denC1) *
  (K - (postfloodC +
    postfloodT * (denC1/denT1) +
    postfloodW * (denC1/denW1) +
    postfloodS * (denC1/denS1) +
    postfloodM * (denC1/denM1))))))

```



```
# Meadow fecundity in # of seedlings, to be added using "placeholder"
# to NM1 during iter.
# Here, meadow can colonize any empty portion of K.
```

```
# K -----
-----
```

```
# Cottonwood
# gives total cottonwood population size as a percentage of K;
# this is the total space occupied by this species in cottonwood
# seedling units
```

```
KC <- 100 * (NC[1] +
             NC[2]/(bC1) +
             NC[3]/(bC2 * bC1) +
             NC[4]/(bC3 * bC2 * bC1) +
             NC[5]/(bC4 * bC3 * bC2 * bC1) +
             NC[6]/(bC5 * bC4 * bC3 * bC2 * bC1))/K
```

```
# same as above, but without seedlings
```

```
CnonseedK <- 100 * (NC[2]/(bC1) +
                   NC[3]/(bC2 * bC1) +
                   NC[4]/(bC3 * bC2 * bC1) +
                   NC[5]/(bC4 * bC3 * bC2 * bC1) +
                   NC[6]/(bC5 * bC4 * bC3 * bC2 * bC1))/K
```

```
# Tamarisk
```

```
KT <- 100 * (denC1/denT1) * (NT[1] +
                             NT[2]/(bT1) +
                             NT[3]/(bT2 * bT1) +
                             NT[4]/(bT3 * bT2 * bT1) +
                             NT[5]/(bT4 * bT3 * bT2 * bT1) +
                             NT[6]/(bT5 * bT4 * bT3 * bT2 * bT1))/K
```

```
TnonseedK <- 100 * (denC1/denT1) * (NT[2]/(bT1) +
                                     NT[3]/(bT2 * bT1) +
                                     NT[4]/(bT3 * bT2 * bT1) +
                                     NT[5]/(bT4 * bT3 * bT2 * bT1) +
                                     NT[6]/(bT5 * bT4 * bT3 * bT2 *
                                     bT1))/K
```

```
# Willow
```

```
KW <- 100 * (NW[1] +
             NW[2]/(bW1) +
             NW[3]/(bW2 * bW1) +
             NW[4]/(bW3 * bW2 * bW1) +
```



```

NW[5]/(bW4 * bW3 * bW2 * bW1) +
NW[6]/(bW5 * bW4 * bW3 * bW2 * bW1))/K

WnonseedK <- 100 * (NW[2]/(bW1) +
                    NW[3]/(bW2 * bW1) +
                    NW[4]/(bW3 * bW2 * bW1) +
                    NW[5]/(bW4 * bW3 * bW2 * bW1) +
                    NW[6]/(bW5 * bW4 * bW3 * bW2 * bW1))/K

# Sagebrush
KS <- 100 * (NS[1] +
             NS[2]/(bS1) +
             NS[3]/(bS2 * bS1) +
             NS[4]/(bS3 * bS2 * bS1) +
             NS[5]/(bS4 * bS3 * bS2 * bS1) +
             NS[6]/(bS5 * bS4 * bS3 * bS2 * bS1))/K

SnonseedK <- 100 * (NS[2]/(bS1) +
                    NS[3]/(bS2 * bS1) +
                    NS[4]/(bS3 * bS2 * bS1) +
                    NS[5]/(bS4 * bS3 * bS2 * bS1) +
                    NS[6]/(bS5 * bS4 * bS3 * bS2 * bS1))/K

# Meadow
KM <- 100 * (NM[1] +
             NM[2]/(bM1) +
             NM[3]/(bM2 * bM1) +
             NM[4]/(bM3 * bM2 * bM1) +
             NM[5]/(bM4 * bM3 * bM2 * bM1) +
             NM[6]/(bM5 * bM4 * bM3 * bM2 * bM1))/K

MnonseedK <- 100 * (NM[2]/(bM1) +
                    NM[3]/(bM2 * bM1) +
                    NM[4]/(bM3 * bM2 * bM1) +
                    NM[5]/(bM4 * bM3 * bM2 * bM1) +
                    NM[6]/(bM5 * bM4 * bM3 * bM2 * bM1))/K

# TRANSITION MATRICES -----
-----

# TRANSITION MATRIX FOR cottonwood -----
-----
AC1 <- c(0, 0, 0, 0, 0, FC6)
AC2 <- c(GC1, 0, 0, 0, 0, 0)

```



```

AC3 <- c(0, GC2, 0, 0, 0, 0)
AC4 <- c(0, 0, GC3, 0, 0, 0)
AC5 <- c(0, 0, 0, GC4, PC5, 0)
AC6 <- c(0, 0, 0, 0, GC5, PC6)
# Matrix
AC <- rbind(AC1, AC2, AC3, AC4, AC5, AC6)

# TRANSITION MATRIX FOR tamarisk -----
-----
# Note: fecundity is not included here, since it is assigned directly
  during iteration
AT1 <- c(0, 0, 0, 0, 0, 0)
AT2 <- c(GT1, 0, 0, 0, 0, 0)
AT3 <- c(0, GT2, PT3, 0, 0, 0)
AT4 <- c(0, 0, GT3, PT4, 0, 0)
AT5 <- c(0, 0, 0, GT4, PT5, 0)
AT6 <- c(0, 0, 0, 0, GT5, PT6)
# Matrix
AT <- rbind(AT1, AT2, AT3, AT4, AT5, AT6)

# TRANSITION MATRIX FOR dynamic riverbank specialist, willow -----
-----
# Similar stage structure to cot, except that reproduction can occur
  in all but 1st yr
AW1 <- c(0, 0, 0, 0, 0, 0)
AW2 <- c(GW1, 0, 0, 0, 0, 0)
AW3 <- c(0, GW2, 0, 0, 0, 0)
AW4 <- c(0, 0, GW3, 0, 0, 0)
AW5 <- c(0, 0, 0, GW4, PW5, 0)
AW6 <- c(0, 0, 0, 0, GW5, PW6)
# Matrix
AW <- rbind(AW1, AW2, AW3, AW4, AW5, AW6)

# TRANSITION MATRIX FOR sagebrush -----
-----
# Arid shrubland indicator big sagebrush.
# Similar stage structure to cottonwood, fecundity is assigned
  directly as with tamarisk
# during iteration.
AS1 <- c(0, 0, 0, 0, 0, 0)
AS2 <- c(GS1, 0, 0, 0, 0, 0)
AS3 <- c(0, GS2, 0, 0, 0, 0)

```





```

AS4 <- c(0, 0, GS3, 0, 0, 0)
AS5 <- c(0, 0, 0, GS4, 0, 0)
AS6 <- c(0, 0, 0, 0, GS5, PS6)
# Matrix
AS <- rbind(AS1, AS2, AS3, AS4, AS5, AS6)

# TRANSITION MATRIX FOR 5th species, xeric meadow -----
-----
# Includes grasses such as wheatgrass.
# Similar stage structure to cottonwood, fecundity is assigned
  directly as with tamarisk
# during iteration.
AM1 <- c(0, 0, 0, 0, 0, 0)
AM2 <- c(GM1, 0, 0, 0, 0, 0)
AM3 <- c(0, GM2, 0, 0, 0, 0)
AM4 <- c(0, 0, GM3, 0, 0, 0)
AM5 <- c(0, 0, 0, GM4, 0, 0)
AM6 <- c(0, 0, 0, 0, GM5, PM6)
# Matrix
AM <- rbind(AM1, AM2, AM3, AM4, AM5, AM6)

# COMPILING OUTPUTS -----
-----
# Cottonwood
Coutput[i,1:6] <- log(NC + 1) # array of no. ind. of each age class
  for each yr
# projected. NC = total no. ind. for each age class
DomC[i] <- NC[5] # vector of cot age class 5 for each year projected
Cnonseedling[i] <- CnonseedK # total cottonwood pop. size as % of K
  WITHOUT SEEDLINGS for
# each projected year
Cspaceoutput[i] <- KC # total cottonwood pop. size as % of K; this is
  the total space
# occupied by this species in cottonwood seedling units

# Tamarisk - same as cottonwood
Toutput[i,1:6] <- log(NT + 1)
DomT[i] <- NT[4]
Tnonseedling[i] <- TnonseedK
Tspaceoutput[i] <- KT

# Willow

```



```

Woutput[i,1:6] <- log(NW + 1)
Wnonseedling[i] <- WnonseedK
Wspaceoutput[i] <- KW

# Sagebrush
Soutput[i,1:6] <- log(NS + 1)
Snonseedling[i] <- SnonseedK
Sspaceoutput[i] <- KS

# Meadow
Moutput[i,1:6] <- log(NM + 1)
Mnonseedling[i] <- MnonseedK
Mspaceoutput[i] <- KM

# Records flood settings of each particular projected year (0 for
  nonflood, 1 for flood)
floodoutput[i] <- bigflood[y]

# Same for drought
droughtoutput[i] <- drought[y]

# Same for nonflood
nonfloodoutput[i] <- nonflood[y]

# Same for normal
normaloutput[i] <- ifelse(bigflood[y] == 0 & drought[y] == 0 &
  nonflood[y] == 1, 1, 0)

# Fecundity of all but cottonwood to put into matrix projection.
# Cottonwood is already in matrix
Tplaceholder <- FT
Splaceholder <- FS
Wplaceholder <- FW
Mplaceholder <- FW

# MATRIX MULTIPLICATION -----
-----
# Cottonwood
NC <- AC %*% NC # AC is transition matrix, NC = total no. ind. for
  each age class
NC <- quasi(NC) # quasi extinction threshold of 1: below 1 go to 0

```



```

# Tamarisk
# Note the use of 'placeholders' for fecundity in the following guilds
NT <- AT %*% NT
NT[1] <- Tplaceholder
NT <- quasi(NT)

# Willow
NW <- AW %*% NW
NW[1] <- Wplaceholder
NW <- quasi(NW)

# Sagebrush
NS <- AS %*% NS
NS[1] <- Splplaceholder
NS <- quasiten(NS)

# Meadow
NM <- AM %*% NM
NM[1] <- Mplaceholder
NM <- quasi(NM)
} # End of inner loop
#####

# Mean vals for each replicate run over period specified from burning
to end of projection
# No seedlings
Crep[rep] <- mean(Cnonseedling[seq(burnin + 1, count)])
Trep[rep] <- mean(Tnonseedling[seq(burnin + 1, count)])
Wrep[rep] <- mean(Wnonseedling[seq(burnin + 1, count)])
Srep[rep] <- mean(Snonseedling[seq(burnin + 1, count)])
Mrep[rep] <- mean(Mnonseedling[seq(burnin + 1, count)])

# All incl. seedlings
Crep_all[rep] <- mean(Cspaceoutput[seq(burnin + 1, count)])
Trep_all[rep] <- mean(Tspaceoutput[seq(burnin + 1, count)])
Wrep_all[rep] <- mean(Wspaceoutput[seq(burnin + 1, count)])
Srep_all[rep] <- mean(Sspaceoutput[seq(burnin + 1, count)])
Mrep_all[rep] <- mean(Mspaceoutput[seq(burnin + 1, count)])

# Stage 5 cot, stage 4 tam - as per Merritt and Poff 2010
DomCrep[rep] <- mean(DomC[seq(burnin + 1, count)])
DomTrep[rep] <- mean(DomT[seq(burnin + 1, count)])

```



```

} # End of mid loop
#####

# Outer loop compilation - results of flow mod scenarios. Not useful
  unless simulating
# changes to flow regime
# Adults - mean of Crep (Mean values for each replicate run over the
  period specified from
# burnin to end of projection)
# This is then the mean of each flow modification setting for the full
  burnin -> end of
# projection period.

# No seedlings
Cgraph[zim] <- mean(Crep)
Tgraph[zim] <- mean(Trep)
Wgraph[zim] <- mean(Wrep)
Sgraph[zim] <- mean(Srep)
Mgraph[zim] <- mean(Mrep)

# All incl. seedlings
Cgraph_all[zim] <- mean(Crep_all)
Tgraph_all[zim] <- mean(Trep_all)
Wgraph_all[zim] <- mean(Wrep_all)
Sgraph_all[zim] <- mean(Srep_all)
Mgraph_all[zim] <- mean(Mrep_all)

# Stage 5 cot, stage 4 tam - as per Merritt and Poff 2010
DomCrep_graph[zim] <- mean(DomCrep)
DomTrep_graph[zim] <- mean(DomTrep)

# Proportion of drought years in model run
droughtgraph[zim] <- sum(drought)/length(bigflood)

# Proportion of flood years in model run
floodgraph[zim] <- sum(bigflood)/length(bigflood)

# Proportion of nonflood years in model run
nonfloodgraph[zim] <- sum(nonflood)/length(bigflood)

```



```

# Proportion of normal years in model run (not floods and not
droughts)
normalgraph[zim] <-
  sum(ifelse(bigflood == 0 & drought == 0 & nonflood == 1, 1,
0))/length(bigflood)

# Adding 1 to droughtchanged and floodchanged - this keeps going until
reaching the number
# specified in outerreps (i.e. 84 mods all years)
droughtchanged = floodchanged = droughtchanged + 1

} # End outer loop
#####
#

#
#####
#####
# OUTPUT -----
-----
#
#####
#####

# This will change depending on what simulations we are running
# Showing a couple of example outputs below. One for flow mod scenario
and one just
# showing the core results for the projection period

# Flow mod graph -----
-----
# only relevant if OUTER LOOP is run with flow modification scenarios
# Showing here just the graph of how drought scenarios affect the 5
guilds including all
# stages, incl. seedlings.

# Compiling all results from flow mods into a dataframe
graph_df <- as.data.frame(cbind(Cgraph, Tgraph, Wgraph, Sgraph,
Mgraph, droughtgraph,
                                floodgraph, nonfloodgraph,
normalgraph, Cgraph_all,

```



```

                                Tgraph_all, Wgraph_all, Sgraph_all,
Mgraph_all))

# Adding a column of replicate number
graph_df$replicate <- as.numeric(as.character(row.names(graph_df)))

# Gathering dataframe for plotting
graph_df_g <- gather(graph_df, key, value, Cgraph:Mgraph) # WITHOUT
seedlings
graph_df_g_all <- gather(graph_df, key, value, Cgraph_all:Mgraph_all)
# WITH seedlings

# 5 guilds mean percent of K over full drought mod settings during the
burnin to full
# projection period (incl. seedlings)
# uncomment if running flow mod scenario
# droughtplot_all <- ggplot(graph_df_g_all,
#                             aes(droughtgraph, value, colour = key,
linetype = key)) +
#   geom_path() +
#   theme_classic() +
#   scale_colour_brewer(type = 'qual', palette = 6)
# droughtplot_all

# Space occupied in each year over full projection -----
-----
# Results from MIDDLE LOOP - replications of each setting

# All incl. seedlings
space_df <- as.data.frame(cbind(Cspaceoutput, Tspaceoutput,
Wspaceoutput, Sspaceoutput,
                                Mspaceoutput))

# Adding a year column
space_df$year <- as.numeric(as.character(row.names(space_df)))

# Gathering into long form for plotting
space_df_g <- gather(space_df, key, value, Cspaceoutput:Mspaceoutput)

# Plotting
space_plot <- ggplot(space_df_g, aes(year, value, colour = key)) +
  geom_path()
space_plot

```



```

# OVERVIEW OF PROCESS -----
-----

# 1. draw a year at random from hydrograph
# 2. log the current values of the five guilds, store these in a
  vector for output
# 3. calculate space occupied by each guild as a percentage of K
# 4. keep track of whether a drought or flood year
# 6. store non-cottonwood guild fecundities in placeholder. At this
  point FT/FW/FS/FM look
# ahead and calculate how much space will be left after cot and tam
  flood mortality
# occurs. Had to be done before matrix projection because FT/FW/FS/FM
  depend on current
# matrix values of all guilds.
# 7. Project populations. The quasi function turns numbers less than
  one to zero. quasiten
# is used for sagebrush (<10 = 0).

# VARIOUS CHECKS OF FINAL RUN -----
-----

floodfreq <- sum(bigflood)/length(bigflood)
droughtfreq <- sum(drought)/length(bigflood)
normalfreq <- (length(bigflood) - (sum(drought) +
  sum(bigflood)))/length(bigflood)
sum(floodfreq + droughtfreq + normalfreq)

floodchanged
floodfreq
droughtfreq
normalfreq

# END -----
-----

```

**Sample hydrograph input data for riparian model (Maybell.csv):**

[https://figshare.com/articles/5-guild\\_riparian\\_flow-population\\_model/4652608](https://figshare.com/articles/5-guild_riparian_flow-population_model/4652608)

year	floodmag	flooddates	slopecot	slopetam	basedates
------	----------	------------	----------	----------	-----------



1916	11700	223	-2.93	-1.28	295
1917	17900	231	-2.33	-3.42	315
1918	10500	258	-1.88	-2.4	306
1919	7670	233	-3.18	-0.68	279
1920	16000	239	-4.62	-1.95	307
1921	17700	259	-4.39	-1.71	318
1922	10800	240	-3.14	-1.33	293
1923	10900	240	-2.92	-1.62	310
1924	7810	259	-2.29	-1.16	294
1925	6640	235	-2.03	-0.82	291
1926	9090	242	-3	-0.68	292
1927	11800	231	-2.16	-1.89	294
1928	13700	225	-4.26	-1.45	300
1929	14400	226	-2.34	-2.21	319
1930	7980	244	-3.53	-0.57	279
1931	6500	231	-2.15	-0.81	279
1932	12100	236	-1.97	-1.94	316
1933	11200	246	-4.12	-1.35	288
1934	4080	223	-2.36	-0.05	253
1935	9870	259	-2.87	-1.73	291
1936	10600	230	-3.36	-1.14	283
1937	10000	229	-1.86	-0.97	297
1938	12100	231	-3.69	-1.57	295
1939	7860	219	-3.28	-0.92	280
1940	9170	226	-3.48	-0.72	280
1941	11700	227	-2.76	-1	285
1942	9930	239	-3.67	-1.21	288
1943	9280	246	-2.92	-1.93	290
1944	9080	237	-3.6	-1.7	289
1945	10900	225	-1.81	-1.68	328
1946	6850	211	-1.62	-0.92	286
1947	12400	222	-1.89	-1.77	303
1948	11300	234	-3.3	-1.12	287
1949	9730	262	-2.8	-1.96	303
1950	8210	237	-2.62	-1.57	292
1951	8870	242	-3.02	-1.74	305
1952	13800	249	-3.39	-1.24	293
1953	10100	258	-3.34	-1.11	295
1954	5480	235	-1.96	-0.72	275





1955	7000	228	-2.38	-0.98	281
1956	9870	237	-3.64	-0.68	281
1957	15700	252	-1.44	-3.46	331
1958	12200	242	-4.7	-1.04	283
1959	6690	253	-2.45	-1.49	286
1960	8000	227	-2.76	-1	284
1961	6350	243	-3.28	-0.77	277
1962	11500	226	-1.42	-2.31	300
1963	6290	224	-2.29	-0.35	273
1964	9990	234	-2.36	-1.82	293
1965	11800	258	-1.9	-1.78	314
1966	6900	167	-2.61	-0.7	273
1967	8890	239	-2.51	-1.85	301
1968	11400	250	-3.34	-1.72	296
1969	8290	208	-2.44	-1.4	299
1970	12700	235	-3.17	-2.3	305
1971	10300	244	-3.32	-2.14	303
1972	8890	253	-3.15	-1	283
1973	12100	234	-1.41	-2.09	308
1974	15400	223	-3.48	-1.68	302
1975	11700	252	-1.05	-2.38	309
1976	7450	235	-2.27	-1.31	290
1977	3620	248	-1.98	0.12	263
1978	11570	256	-2.28	-2.62	309
1979	13600	242	-3.11	-2.06	304
1980	11700	236	-3.05	-1.6	292
1981	6490	252	-2.7	-0.94	270
1982	10700	217	-1.99	-2.48	312
1983	13400	242	-2.82	-2.8	329
1984	25100	229	-3.57	-2.41	319
1985	13600	219	-3.16	-1.22	311
1986	11000	251	-2.92	-1.86	309
1987	6140	230	-1.29	-0.44	269
1988	10200	231	-2.79	-1.41	284
1989	4940	225	-2.44	-0.69	273
1990	7020	256	-2.23	-1.23	286
1991	8560	235	-2.75	-0.81	280
1992	5900	240	-1.59	-0.52	273
1993	12800	234	-3.03	-2.17	303



1994	5880	231	-3.16	-0.62	271
1995	13300	260	-0.88	-2.63	316
1996	15000	231	-2.69	-1.84	296
1997	18800	247	-4.33	-1.69	326
1998	10700	234	-2.71	-1.97	312



## Fish population model

### **Primary publication describing the fish model methodology:**

Rogosch, J.S., Tonkin, J.D., Lytle, D.A., Merritt, D.M., Reynolds, L.V. and Olden, J.D., 2019. Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere*, 10(4), p.e02681.

<https://doi.org/10.1002/ecs2.2681>

### **Fish model vital rate estimation:**

<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecs2.2681&file=ecs22681-sup-0001-AppendixS1.pdf>

#### **Desert sucker**

- Reproductive timing/temperature, clutch size, lengths at life stages (Minckley 1973, Ivanyi 1989, Ivanyi et al. 1995)
- Average adult length, length-weight (Gibson et al. 2015 unpublished data using 143 individuals)
- Longevity (for congeners; Klein et al. 2017)
- GSI, ages and lengths at life stages (for congeners; Carothers and Minckley 1980, McCall 1980, McAda and Wydoski 1983, Propst et al. 2001)

#### **Sonora sucker**

- Reproductive timing/temperature, lengths (Minckley 1973, Minckley and Marsh 2009)
- Age at maturity (Frimpong and Angermeier 2009)
- Length-weight (Gibson et al. 2015, unpublished data using 109 individuals)
- Longevity (for congener; Klein et al. 2017)
- Clutch size, GSI (for congeners; Kennedy and Kucera 1978, Hinck et al. 2007, Bowron 2008, Mendoza 2016, Begley et al. 2017)

#### **Roundtail chub**

- Reproductive timing/temperature, clutch size, GSI, ages and lengths at life stages, longevity (Brouder et al. 2000, Brouder 2005, Brouder et al. 2006)
- Effects of floods on recruitment (Brouder 2001)



### Yellow bullhead

- Reproductive timing/temperature, GSI, lengths and ages at life stages (for congener; Copp et al. 2016)
- Length-weight (Gibson et al. 2015, unpublished data using 22 individuals)
- Age, length, and longevity (Murie et al. 2009)

### Green sunfish

- Reproductive timing/temperature, GSI (Kaya and Hasler 1972)
- Clutch size (Carlander 1977)
- Length-weight (Mannes and Jester 1980)
- Age at maturity (Moyle 2002, Wang 1986)
- Lengths at life stages, longevity (Delp et al. 2000, Quist and Guy 2001)
- Resilience to drought (Bêche et al. 2009)

### Smallmouth bass

- Reproductive timing/temperature, clutch sizes, GSI (Minckley 1973, Moyle 2002, Dauwalter and Fisher 2007, Blazer et al. 2012)
- Longevity (Smith et al. 2005)
- Length-weight relationship (Lawrence et al. 2015)
- Lengths and ages at life stages (Knotek and Orth 1998, Robertson and Winemiller 2001, Dauwalter and Fisher 2007, Jackson et al. 2008, Humston et al. 2015)

### Red shiner

- Reproductive timing/temperature, GSI, clutch sizes (Gale 1986, Marsh-Matthews et al. 2002, Brewer et al. 2008, Herrington and DeVries 2008)
- Longevity (Matthews et al. 2001, Quist and Guy 2001, Yildirim and Peters 2006)
- Length-weight (Franssen et al. 2007)
- Length and ages at life stages (Marsh-Matthews et al. 2002, Brewer et al. 2006, Yildirim and Peters 2006, Herrington and DeVries 2008)



## Information tables about vital rates and references for vital rates

### Appendix Tables

Table S1. Flow modifiers derived from flow-ecology relationships in literature (see also Table 2 and main text for references and details). Flow modifiers ( $Y_{ijk}$ ) act on baseline mortality rates ( $M_{ij}$ ; Table A3) specific for stage  $i$ , species  $j$  and flow-event year  $k$ . Values greater than 1 increase mortality, values less than 1 decrease mortality. Abbreviations for flow event year (SP\_HF = spring high flood, SU\_HF = summer high flood, SP\_MF = spring medium flood, NE = non-event, DR = drought). S1 = post-larval young-of-year fishes, S2 = size at first maturity, S3 = average adult size in population.

Stage	Flow Event	Desert sucker	Sonora sucker	Roundtail chub	Yellow bullhead	Red shiner	Green sunfish	Smallmouth bass
S1	SP_HF	0.1	0.1	0.1	1	1	1	1
S1	SU_HF	1	1	1	2	1.5	2	2
S1	SP_MF	0.2	0.2	0.2	1	1	1	1
S1	NE	1	1	1	0.1	0.3	0.1	0.1
S1	DR	2	2	2	0.2	0.2	0.2	0.2
S2, S3	SP_HF	1	1	1	1	1	1	1
S2, S3	SU_HF	1	1	1	1	1.5	1	1
S2, S3	SP_MF	1	1	1	1	1	1	1
S2, S3	NE	1	1	1	0.1	0.3	0.2	1
S2, S3	DR	3	3	3	1	0.2	1	1.5



Table S2. Length-weight relationships. Length-weight relationships used to calculate biomass for individuals at all three life stages based on their lengths at the end of their first year ( $L_1$ ), length at maturity ( $L_2$ ) and average adult length ( $L_3$ ; see also "References for vital rates" above).

	Length-Weight ( $W = aL^b$ )		$L_1$	$L_2$	$L_3$
	$a$	$b$			
Desert sucker	9.76E-06	3.038	68	92	180
Sonora sucker	9.61E-06	3.022	152	282	360
Roundtail chub	7.89E-06	3.022	101	181	237
Yellow bullhead	7.03E-06	2.92	99	200	218
Red shiner	5.75E-06	3.16	25	30	53
Green sunfish	3.31E-05	3.356	45	65	87
Smallmouth bass	1.16E-06	3.02	70	200	222

## Literature Cited

- Bêche, L. A., P. G. Connors, V. H. Resh, and A. M. Merenlender. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography* 32:778–788.
- Begley, M., S. M. C. Jr, and J. Zydlewski. 2017. A Comparison of age, size, and fecundity of harvested and reference white sucker populations. *North American Journal of Fisheries Management* 37:510–523.
- Blazer, V. S., L. R. Iwanowicz, H. Henderson, P. M. Mazik, J. A. Jenkins, D. A. Alvarez, and J. A. Young. 2012. Reproductive endocrine disruption in smallmouth bass (*Micropterus dolomieu*) in the Potomac River basin: spatial and temporal comparisons of biological effects. *Environmental Monitoring and Assessment*; Dordrecht 184:4309–4334.
- Bowron, L. 2008. Responses of white sucker (*Catostomus commersoni*) populations to changes in pulp mill effluent discharges. Thesis. University of New Brunswick, Canada.



Brouder, M. J., D. D. Rogers, and L. D. Avenetti. 2000. Life history and ecology of the roundtail chub *Gila robusta*, from two streams in the Verde River Basin. Technical guidance bulletin No. 3. Federal aid in sportfish restoration. Project F-14-R. Arizona Game and Fish Department, Phoenix, Arizona, USA.

Brewer, S. K., D. M. Papoulias, and C. F. Rabeni. 2006. Spawning habitat associations and selection by fishes in a flow-regulated prairie river. Transactions of the American Fisheries Society 135:763–778.

Brewer, S. K., C. F. Rabeni, and D. M. Papoulias. 2008. Comparing histology and gonadosomatic index for determining spawning condition of small-bodied riverine fishes. Ecology of Freshwater Fish 17:54–58.

Brouder, M. J. 2001. Effects of flooding on recruitment of roundtail chub, *Gila robusta*, in a southwestern river. The Southwestern Naturalist 46:302–310.

Brouder, M. J. 2005. Age and growth of roundtail chub in the Upper Verde River, Arizona. Transactions of the American Fisheries Society 134:866–871.

Brouder, M. J., D. D. Rogers, and L. D. Avenetti. 2006. Observations on the reproductive biology of roundtail chub, *Gila robusta*, in the Upper Verde River, Arizona. Western North American Naturalist 66:260–262.

Carlander, K. D., 1977. Handbook of freshwater fishery biology. Volume two: life history data on Centrarchid fishes of the United States and Canada. Ames, Iowa, USA: Iowa State University Press.

Carothers, S. W. and C. O. Minckley. 1981. A survey of the fishes, aquatic invertebrates and aquatic plants of the Colorado River and selected tributaries from Lee Ferry to Separation Rapids. Report. Submitted to Water and Power Resources Service (Bureau of Reclamation). Contract No.: 7-07-30-X0026. Department of Biology – Museum of Northern Arizona.

Dauwalter, D. C., and W. L. Fisher. 2007. Spawning chronology, nest site selection and nest success of smallmouth bass during benign streamflow conditions. The American Midland Naturalist 158:60–78.

Delp, J. G., J. S. Tillma, M. C. Quist, and C. S. Guy. 2000. Age and growth of four centrarchid species in southeastern Kansas streams. Journal of Freshwater Ecology 15:475–478.



- Franssen, N. R., K. B. Gido, and D. L. Propst. 2007. Flow regime affects availability of native and nonnative prey of an endangered predator. *Biological Conservation* 138:330–340.
- Frimpong, E. A., and P. L. Angermeier. 2009. Fish traits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries* 34:487–495.
- Gale, W. F. 1986. Indeterminate fecundity and spawning behavior of captive red shiners—fractional, crevice spawners. *Transactions of the American Fisheries Society* 115:429–437.
- Herrington, S. J., and D. R. DeVries. 2008. Reproductive and early life history of nonindigenous red shiner in the Chattahoochee River drainage, Georgia. *Southeastern Naturalist* 7:413–428.
- Hinck, J. E., V. S. Blazer, N. D. Denslow, K. R. Echols, T. S. Gross, T. W. May, P. J. Anderson, J. J. Coyle, and D. E. Tillitt. 2007. Chemical contaminants, health indicators, and reproductive biomarker responses in fish from the Colorado River and its tributaries. *Science of the Total Environment* 378:376–402.
- Humston, R., M. Moore, C. Wass, D. Dennis, and S. Doss. 2015. Correlations between body length and otolith size in smallmouth bass *Micropterus dolomieu* Lacépède, 1802 with implications for retrospective growth analyses. *Journal of Applied Ichthyology* 31:883–887.
- Ivanyi, C. S. 1989. Selected aspects of the natural history of the desert sucker [*Catostomus (Pantosteus) clarkii*]. Thesis. University of Arizona, Tucson, Arizona, United States of America.
- Ivanyi, C. S., J. P. Hill, and W. J. Matter. 1995. Time of spawning by desert sucker. *The Southwestern Naturalist* 40:425–426.
- Jackson, Z. J., M. C. Quist, and J. G. Larscheid. 2008. Growth standards for nine North American fish species. *Fisheries Management and Ecology* 15:107–118.
- Kaya, C. M., and A. D. Hasler. 1972. Photoperiod and temperature effects on the gonads of green sunfish, *Lepomis cyanellus* (Rafinesque), during the quiescent, winter phase of its annual sexual cycle. *Transactions of the American Fisheries Society* 101:270–275.
- Kennedy, J., and P. Kucera. 1978. The reproductive ecology of the Tahoe sucker, *Catostomus tahoensis*, in Pyramid Lake, Nevada. *Great Basin Naturalist* 38.
- Klein, Z. B., M. J. Breen, and M. C. Quist. 2017. Population characteristics and the influence of discharge on bluehead sucker and flannelmouth sucker. *Copeia* 105:375–388.





- Knotek, W. L., and D. J. Orth. 1998. Survival for specific life intervals of smallmouth bass, *Micropterus dolomieu*, during parental care. *Environmental Biology of Fishes*; Dordrecht 51:285–296.
- Lawrence, D. J., D. A. Beauchamp, and J. D. Olden. 2015. Life-stage-specific physiology defines invasion extent of a riverine fish. *Journal of Animal Ecology* 84:879–888.
- Mannes, J. C., and D. B. Jester. 1980. Age and growth, abundance, and biomass production of green sunfish, *Lepomis cyanellus* (Centrarchidae), in a eutrophic desert pond. *The Southwestern Naturalist* 25:297–311.
- Marsh-Matthews, E., W. J. Matthews, K. B. Gido, and R. L. Marsh. 2002. Reproduction by young-of-year red shiner (*Cyprinella lutrensis*) and its implications for invasion success. *The Southwestern Naturalist* 47:605–610.
- Matthews, W. J., K. B. Gido, and E. Marsh-Matthews. 2001. Density-dependent overwinter survival and growth of red shiners from a southwestern river. *Transactions of the American Fisheries Society* 130:478–488.
- McCall, T. C. 1980. Fishery investigation of Lake Mead, Arizona-Nevada, from Separation Rapids to Boulder Canyon 1978-1979. Report. Submitted to Water and Power Resources Service (Bureau of Reclamation). Contract No.: 8-07-30-X0025. Arizona Game and Fish Department – Region III.
- McAda, C. W., and R. S. Wydoski. 1983. Maturity and fecundity of the bluehead sucker, *Catostomus discobolus* (Catostomidae), in the Upper Colorado River Basin, 1975-76. *The Southwestern Naturalist* 28:120–123.
- Mendoza, J. 2016. Stable isotope analyses ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) as a tool to define exposure of white sucker (*Catostomus commersonii*) to pulp mill effluent in Jackfish Bay, Lake Superior. Thesis. University of Waterloo, Waterloo, Ontario, Canada.
- Minckley, W. L. A. 1973. *Fishes of Arizona*. First paperback edition. Arizona Game and Fish Department.
- Minckley, W. L., and P. C. Marsh. 2009. *Inland fishes of the greater Southwest: Chronicle of a vanishing biota*. University of Arizona Press.



- Moyle P. B., 2002. Inland fishes of California. Berkeley, USA: University of California Press.
- Propst, D. L., A. L. Hobbes, and T. L. Stroh. 2001. Distribution and notes on the biology of Zuni bluehead sucker, *Catostomus discobolus yarrowi*, in New Mexico. The Southwestern Naturalist 46:158–170.
- Quist, M. C., and C. S. Guy. 2001. Growth and mortality of prairie stream fishes: relations with fish community and instream habitat characteristics. Ecology of Freshwater Fish 10:88–96.
- Robertson, M. S., and K. O. Winemiller. 2001. Diet and growth of smallmouth bass in the Devils River, Texas. The Southwestern Naturalist 46:216–221.
- Smith, S. M., J. S. Odenkirk, and S. J. Reeser. 2005. Smallmouth bass recruitment variability and its relation to stream discharge in three Virginia Rivers. North American Journal of Fisheries Management 25:1112–1121.
- U.S. Fish and Wildlife Service. 2015. Species status assessment report for the headwater chub and the lower Colorado River distinct population segment of roundtail chub. Version 1.0, September 2015. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, NM.
- Wang, J. C. S., 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Berkeley, USA: Digital Library Project. Interagency Ecological Program Technical Report No. 9.
- Yildirim, A., and E. J. Peters. 2006. Life history characteristics of red shiner, *Cyprinella lutrensis*, in the Lower Platte River, Nebraska, USA. Journal of Freshwater Ecology 21:307–314.



## R code for fish model:

<https://doi.org/10.5281/zenodo.1309024>

```
## -----  
-----  
## Verde Fish Model  
## Jane Rogosch, Jono Tonkin, et al.  
## July 2018  
## Community-wide stochastic matrix population model that links  
  population  
## dynamics with river flow regimes.  
## This is the bare model used in the Rogosch et al. ms.  
## -----  
-----  
  
## Required libraries  
library(ggplot2)  
library(plyr)  
library(tidyverse)  
library(popbio)  
  
## * SETUP -----  
-----  
  
#rm(list = ls()) # clearing the workspace  
  
## Bringing in flow data  
all.scenarios.list <- readRDS('data/all_scenarios_list.rds')  
  
## When using natural flow data, just pull it out from the list here  
flowdata <- all.scenarios.list$natural.flow  
  
count <- 54 # 54 years in flow record, if count = 45 goes to 2008  
iterations <- 10 # number of replicate projections to run (mid loop)  
  
## Modifiers  
modifiers <- read.csv('data/modifiers-all-spp.csv')  
  
## adding 'Modifier' value from csv to 'Code' in csv  
for(j in 1:length(modifiers[,1])) {  
  nam <- paste(modifiers[j,4])  
  assign(nam, modifiers[j,5])  
}
```



```

## Vital rates
## Baseline maturation probability, aACL3 (adult senescence rate)
## Background mortality
## Initial volume in grams in 100-m reach
## Fecundity based on year type and GSI
## Stage specific densities (ind./g)

vitalrates <- read.csv('data/vital-rates.csv')

## assigning vital rate values from column 3 to 'code' in column 2
for(k in 1:length(vitalrates[,1])) {
  nam <- paste(vitalrates[k,2])
  assign(nam, vitalrates[k,3])
}

## * Key -----
-----
## CACL (Catostomus clarki) – desert sucker
## GIRO (Gila robusta) – roundtail chub
## LECY (Lepomis cyanellus) – green sunfish
## CAIN (Catostomus insignis) – sonora sucker
## MIDO (Micropterus dolomieu) – smallmouth bass
## CYLU (Cyprinella lutrensis) – red shiner
## AMNA (Ameiurus natalis) – yellow bullhead

## Average total volume of water per 100 m reach in m3: 307
## Average total fish biomass per 100 m reach in g: 4766
## Average total biomass Bonar 2004 in g/100m2: 606
## Max for a 100 m rech in Gibson samples (excluding GAAF): 6996

## vector of species names
sppnames <- c('CACL', 'GIRO', 'LECY', 'CAIN', 'MIDO', 'CYLU', 'AMNA')

K = 47660 # mean for 1-km reach across 6 replicate reaches

## Loading functions from functions.R file -----
-----
source('code/functions.R')

## * ITERATION PARAMETERS -----
-----
## Setting up arrays/vectors to fill with data from loops

```



```

## Mid loop details -----
-----
## 'iterations' - number of replicate flow sequences to run for
averaging

years <- flowdata$year
stages <- as.character(c("S1", "S2", "S3"))

## Total. N of stages 2 and 3 each year -----
-----
## Takes all stages 2 and 3 and sums them for each year and iteration
Total.N <- array(0,
                 dim = c(54, iterations),
                 dimnames = list(years, 1:iterations)
                 )

## replist. List of arrays w/ abundance data for each spp -----
-----
## Creating a list of 7 arrays to fill in. One for each spp.
## Create an array to be repeated
repparray <- array(0,
                  dim = c(54, 3, iterations),
                  dimnames = list(years, stages, 1:iterations)
                  )

## Repeating the array 7 times
replist <- rep(list(repparray), 7)

## Assigning names to each array from sppnames vector
names(replist) <- sppnames

## Inner loop details -----
-----
## 'count' - number of years to project simulations (inner loop)

## N -----
-----
## Output of biomass and no. ind. for each age class for each year
projected
## Array w/ 3 cols (stage classes) and however many rows there are yrs
projected
## Creating a list of 7 arrays to fill in. One for each spp.
## Create an array to be repeated
output.N.array <- array(0, dim = c(count, 3))

```



```

## Repeating the array 7 times
output.N.list <- rep(list(output.N.array), 7)

## Assigning names to each array from sppnames vector
names(output.N.list) <- sppnames

## Create a df to fill in w/ lambda values -----
-----
lambda.df <- data.frame(matrix(ncol = 7, nrow = count))
names(lambda.df) <- sppnames

## Biomass -----
-----
## Creating a list of 7 arrays to fill in. One for each spp.
## Create an array to be repeated
output.biom.array <- array(0, dim = c(count, 3))

## Repeating the array 7 times
output.biom.list <- rep(list(output.biom.array), 7)

## Assigning names to each array from sppnames vector
names(output.biom.list) <- sppnames

## Total biomass as % of K -----
-----
## Creating a list of 7 vectors to fill in. One for each spp.
## Create a vector to be repeated
biomoutput.vector <- numeric(length = count)

## Repeating the vector 7 times
biomoutput.list <- rep(list(biomoutput.vector), 7)

## Assigning names to each vector from sppnames vector
names(biomoutput.list) <- sppnames

## Flow results -----
-----
## Flood and drought settings for each yr projected into future (i.e.
  0 or 1)
## Create data frame with 5 cols and 'count' rows to fill in with flow
  results
flowresults <- data.frame(matrix(ncol = 5, nrow = count))
names(flowresults) <- c('SPhighflood',

```



```

        'SUhighflood',
        'medflood',
        'drought',
        'nonevent')

## Fecundities -----
-----
## Creating a list of 7 vectors to fill in. One for each spp.
## Create a vector to be repeated
fec.vector <- numeric(length = count)

## Repeating the vector 7 times
fec.list <- rep(list(fec.vector), 7)

## Assigning names to each vector from sppnames vector
names(fec.list) <- sppnames

### -----
-----
## * Mid loop
#####
### -----
-----
## Middle loop uses iterator "iter" to get "iterations" for suming S2
and S3
## No 'outer' loop under normal runs.

for(iter in 1:iterations) {

    ## USE THIS to examine different flow year types
    ++++++
    ##
    ++++++
    +++

    # # All 2010 SPflood +
    SUflood years

    # z <- rep(47, 84)

    # # All SPflood 1993
    # z <- rep(30, 84)

    # # All drought Y2K
    # z <- rep(37, 84)

```



```

# # Nonevent 1985
# z <- rep(22, 84)

# # SUflood
# z <- rep(21, 84)

# # Medflood
# z <- rep(25, 84)

## Need to read in initial biom every time so starting biomass is
reset each
## iteration
## N gives the total number of individuals for each age class.
## Initially here, this is found by multiplying the number of g
occupied by
## a given class by the density per g
## biom = g/m3
## den = indiv/g

## To have different initial starting population sizes for each
iteration,
## taking biom of stage 3 from negative binomial distribution,
where the
## parameter (lambda = mean) and K (dispersion) is calculated from
mean and
## variance in abundance across seven sites in Verde River from
94-08, and
## scaled to biomass from Gibson 2012 survey in file:
## "Rinne Verde River Data 1994-2008-.xlsx"

biomCACL <- c(biomCACL1,
              biomCACL2,
              rlnbinom(1, size = 1.52, mu = 5284))

biomGIRO <- c(biomGIRO1,
              biomGIRO2,
              rlnbinom(1, 0.44, mu = 2376))

biomLECY <- c(biomLECY1,
              biomLECY2,
              rlnbinom(1, 0.34, mu = 164))

biomCAIN <- c(biomCAIN1,

```





```

        biomCAIN2,
        rnbinom(1, 1.33, mu = 34068))

biomMIDO <- c(biomMIDO1,
             biomMIDO2,
             rnbinom(1, 0.66, mu = 4202))

biomCYLU <- c(biomCYLU1,
             biomCYLU2,
             rnbinom(1, 1.78, mu = 238))

biomAMNA <- c(biomAMNA1,
             biomAMNA2,
             rnbinom(1, 0.36, mu = 1306))

### -----
-----
## * Inner loop
#####
### -----
-----
    for(i in 1:count) {

        ## CHANGE WHAT 'y' IS TO SIMULATE DIFFERENT FLOW REGIMES
ACROSS THE 54 Y
        ## y is directly taken from flow vector.
        y = i # follow flow record sequence

        ## Sampling randomly from the flow record
        y = sample(nrow(flowdata), 1)

        ## Transition probabilities -----
        -----
        ## G is prob. of transition to next stage
        ## P is prob. of remaining in that stage
        ## Baseline mortality vital rate (from file object: 'vital-
rates.csv')
        ## 'STmort...' is multiplied by modifier (from file object:
        ## 'modifiers-all-species.csv') based on yeartype as specified
above
        ## So we have SP_highflood, SU_highflood, medflood, nonevent,
drought
        ## and '..._J/2/3_SUHF/SPHF/MF/NE/DR'

```



```

## Stage 1 - G
for(nm in sppnames) {
  assign(paste0('G', nm, '1'),

        get(paste0('a', nm, '1')) *
        get(paste0('den', nm, 'J')) *
        (1 /
         get(paste0('den', nm, '2'))
        ) *
        (1 -
         (flowdata$SU_highflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_J_SUHF'))))
        ) *
        (1 -
         (flowdata$SP_highflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_J_SPHF'))))
        ) *
        (1 -
         (flowdata$medflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_J_MF'))))
        ) *
        (1 -
         (flowdata$nonevent[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_J_NE'))))
        ) *
        (1 -
         (flowdata$drought[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_J_DR'))))
        )
  )
}

```

```

## Stage 2 - G
for(nm in sppnames) {
  assign(paste0('G', nm, '2'),

        get(paste0('a', nm, '2')) *
        get(paste0('den', nm, '2')) *
        (1 /

```



```

        get(paste0('den', nm, '3'))
      ) *
      (1 -
        (flowdata$SU_highflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_A_SUHF'))))
      ) *
      (1 -
        (flowdata$SP_highflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_A_SPHF'))))
      ) *
      (1 -
        (flowdata$medflood[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_A_MF'))))
      ) *
      (1 -
        (flowdata$nonevent[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_A_NE'))))
      ) *
      (1 -
        (flowdata$drought[y] *
          get(paste0('STMort', nm)) *
          get(paste0(nm, '_A_DR'))))
      )
    )
  }

```

```

## Stage 3 - P
for(nm in sppnames) {
  assign(paste0('P', nm, '3'),

    (1 -
      get(paste0('a', nm, '3'))
    ) *
    (1 -
      (flowdata$SU_highflood[y] *
        get(paste0('STMort', nm)) *
        get(paste0(nm, '_A_SUHF'))))
    ) *
    (1 -
      (flowdata$SP_highflood[y] *

```



```

        get(paste0('STMort', nm)) *
        get(paste0(nm, '_A_SPHF'))))
    ) *
    (1 -
    (flowdata$medflood[y] *
    get(paste0('STMort', nm)) *
    get(paste0(nm, '_A_MF'))))
    ) *
    (1 -
    (flowdata$nonevent[y] *
    get(paste0('STMort', nm)) *
    get(paste0(nm, '_A_NE'))))
    ) *
    (1 -
    (flowdata$drought[y] *
    get(paste0('STMort', nm)) *
    get(paste0(nm, '_A_DR'))))
    )
  )
}

```

## POTENTIAL FECUNDITY -----

-----

```

## 1st calculate total grams occupied after year
totbiom <- ldply(sppnames, function(x)
  get(paste0('biom', x))[1] +
  get(paste0('biom', x))[2] +
  get(paste0('biom', x))[3]) %>%
  sum

```

## Carrying capacity (K) is limiting spawning of all species based on

## the total biomass occupied at the end of the previous year.  
i.e. if

## above K, no spp spawn in that year. If spawning occurs, they all do.

## Some slight differences in fecund btwn spp so can't loop/lapply

```

## CACL stage 2
FCACL2 <- ((0.5 * GSI.CACL * (1 - S0MortCACL)) *
  checkpos((K - totbiom)/K)) *
denCACL1 *

```



(1/denCACLJ)

## CACL stage 3

```
FCACL3 <- ((0.5 * GSI.CACL * (1 - S0MortCACL)) *  
           checkpos((K - totbiom)/K)) *  
denCACL1 *  
(1/denCACLJ)
```

## GIRO stage 2

```
FGIRO2 <- ((0.5 * GSI.GIRO * (1 - S0MortGIRO)) *  
           checkpos((K - totbiom)/K)) *  
denGIRO1 *  
(1/denGIROJ)
```

## GIRO stage 3

```
FGIRO3 <- ((0.5 * GSI.GIRO * (1 - S0MortGIRO)) *  
           checkpos((K - totbiom)/K)) *  
denGIRO1 *  
(1/denGIROJ)
```

## CAIN stage 3

```
FCAIN3 <- ((0.5 * GSI.CAIN * (1 - S0MortCAIN)) *  
           checkpos((K - totbiom)/K)) *  
denCAIN1 *  
(1/denCAINJ)
```

## LECY stage 2

```
FLECY2 <- ((0.5 * GSI.LECY * (1 - S0MortLECY)) *  
           checkpos((K - totbiom)/K)) *  
denLECY1 *  
(1/denLECYJ)
```

## LECY stage 3

```
FLECY3 <- ((0.5 * GSI.LECY * (1 - S0MortLECY)) *  
           checkpos((K - totbiom)/K)) *  
denLECY1 *  
(1/denLECYJ)
```

## MIDO stage 3

```
FMIDO3 <- ((0.5 * GSI.MIDO * (1 - S0MortMIDO)) *  
           checkpos((K - totbiom)/K)) *  
denMIDO1 *  
(1/denMIDOJ)
```



```

## CYLU
## because they are serial spawners, they are allowed to spawn
twice a
## season in stage 2 and 3
## CYLU stage 1
FCYLUJ <- ((0.5 * GSI.CYLU * (1 - S0MortCYLU)) *
            checkpos((K - totbiom)/K)) *
            denCYLU1 *
            (1/denCYLUJ)

## CYLU stage 2
FCYLU2 <- ((0.5 * 2 * GSI.CYLU * (1 - S0MortCYLU)) *
            checkpos((K - totbiom)/K)) *
            denCYLU1 *
            (1/denCYLUJ)

## CYLU stage 3
FCYLU3 <- ((0.5 * 2 * GSI.CYLU * (1 - S0MortCYLU)) *
            checkpos((K - totbiom)/K)) *
            denCYLU1 *
            (1/denCYLUJ)

## AMNA
FAMNA3 <- ((0.5 * GSI.AMNA * (1 - S0MortAMNA)) *
            checkpos((K - totbiom)/K)) *
            denAMNA1 *
            (1/denAMNAJ)

## K -----
-----
## Calculating the percentage of K occupied and adding to
KCACL etc
for(nm in sppnames) {
  assign(paste0('K', nm), 100 * (
    get(paste0('biom', nm))[1] +
    get(paste0('biom', nm))[2] +
    get(paste0('biom', nm))[3])/K)
}

## TRANSITION MATRICES -----
-----

## CACL
ACACL1 <- c(0, FCACL2, FCACL3)

```



```

ACACL2 <- c(GCACL1, 0, 0)
ACACL3 <- c(0, GCACL2, PCACL3)

## GIRO
AGIRO1 <- c(0, FGIRO2, FGIRO3)
AGIRO2 <- c(GGIRO1, 0, 0)
AGIRO3 <- c(0, GGIRO2, PGIRO3)

## LECY
ALECY1 <- c(0, FLECY2, FLECY3)
ALECY2 <- c(GLECY1, 0, 0)
ALECY3 <- c(0, GLECY2, PLECY3)

## CAIN
ACAIN1 <- c(0, 0, FCAIN3)
ACAIN2 <- c(GCAIN1, 0, 0)
ACAIN3 <- c(0, GCAIN2, PCAIN3)

## MIDO
AMIDO1 <- c(0, 0, FMIDO3)
AMIDO2 <- c(GMIDO1, 0, 0)
AMIDO3 <- c(0, GMIDO2, PMIDO3)

## CYLU
ACYLU1 <- c(FCYLUJ, FCYLU2, FCYLU3)
ACYLU2 <- c(GCYLU1, 0, 0)
ACYLU3 <- c(0, GCYLU2, PCYLU3)

## AMNA
AAMNA1 <- c(0, 0, FAMNA3)
AAMNA2 <- c(GAMNA1, 0, 0)
AAMNA3 <- c(0, GAMNA2, PAMNA3)

## rbinding the vectors from above into transition matrices
## Makes ACACL, AGIRO etc.
for(nm in sppnames) {
  assign(paste0('A', nm), rbind(
    get(paste0('A', nm, '1')),
    get(paste0('A', nm, '2')),
    get(paste0('A', nm, '3'))
  ))
}

```



```

## COMPILING OUTPUTS -----
-----

## Lambda values
## Filling in the df with lambda values for each species and
each year
## Species as columns, years as rows
## This applies 'lambda(ACACL)' etc and adds to correct column
each
## 'i' value (year)
lambda.df[i,] <- sapply(mget(paste0('A', names(lambda.df))),
lambda)

## Fecundity values
## Cant loop or anything as different for diff spp
fec.list$CACL[i] <- FCACL3 + FCACL2
fec.list$GIRO[i] <- FGIRO3 + FGIRO2
fec.list$LECY[i] <- FLECY3 + FLECY2
fec.list$CAIN[i] <- FCAIN3
fec.list$MIDO[i] <- FMIDO3
fec.list$CYLU[i] <- FCYLU3 + FCYLU2 + FCYLUJ
fec.list$AMNA[i] <- FAMNA3

## biomass values into each df/array in the list
for(nm in sppnames) {
  output.biom.list[[nm]][i,1:3] <- get(paste0('biom', nm))
}

## N values into each df/array in the list
for(nm in sppnames) {
  output.N.list[[nm]][i,1:3] <- c(get(paste0('biom', nm))[1]
*
                                     get(paste0('den', nm, 'J')
                                     ),
*
                                     get(paste0('biom', nm))[2]
                                     get(paste0('den', nm, '2')
                                     ),
*
                                     get(paste0('biom', nm))[3]
                                     get(paste0('den', nm, '3')
                                     ))
}

```





```

## Flow results -----
-----
## Records flood settings of each particular projected year
## (1 = yes, 0 = no)
flowresults$SPhighflood[i] <- flowdata$SP_highflood[y]
flowresults$SUhighflood[i] <- flowdata$SU_highflood[y]
flowresults$medflood[i] <- flowdata$medflood[y]
flowresults$nonevent[i] <- flowdata$nonevent[y]
flowresults$drought[i] <- flowdata$drought[y]

## MATRIX MULTIPLICATION -----
-----
## can include rescue function for each with 0.5 chance of
reach being
## colonized by 2 individuals
## Loop essentially == biomAMNA <- AAMNA %*% biomAMNA
## AAMNA is transit. matrix, biomAMNA = total biomass for each
age class
  for(nm in sppnames) {
    assign(paste0('biom', nm),
           get(paste0('A', nm)) %*% get(paste0('biom', nm)))
  }
}
### -----
-----
### End of inner loop
#####
### -----
-----

## Mean values for each iteration run over each sequence of years
-----
  for(nm in sppnames) {
    replist[[nm]][,iter] <- output.N.list[[nm]]
  }

## Total.N -----
-----
## Caculating Total.N for each year, and adding it to total.N data
frame
## with however many iterations run.
## Total does not incl. juveniles.

```



```

    ## map is purrr version of lapply. Can pass fn using ~ and .x
    instead of
    ## function(x) x
    ## Gets list output of stages 2:3 for ea spp, then cbinds them all
    together,
    ## then calcs sum.
    Total.N[,iter] <- map(output.N.list, ~ .x[,2:3]) %>%
      do.call('cbind', .) %>%
      apply(1, sum)

}
### -----
-----
### End of mid loop
#####
### -----
-----

## Saving image here - pre compiling results
save.image()

## * OUTPUTS -----
-----
#####
#####

## FINAL iteration data to examine plots -----
-----
## Compiling abundance and biomass outputs into single dfs

## Biomass
## Compiling df from output.biom.list, renaming cols to stages, adding
a
## replicate col and gathering into long form
ALLoutput.biom.DF <- ldply(output.biom.list, function(x) {
  as.data.frame(x) %>%
    rename(S1 = V1, S2 = V2, S3 = V3) %>%
    mutate(rep = row.names(.)) %>%
    gather(stage, val, -rep)
}) %>%
  rename(spp = `.id`, g = val)

## Abundance
ALLoutput.N.DF <- ldply(output.N.list, function(x) {

```



```

as.data.frame(x) %>%
  rename(S1 = V1, S2 = V2, S3 = V3) %>%
  mutate(rep = row.names(.)) %>%
  gather(stage, val, -rep)
}) %>%
  rename(spp = `.id`, N = val)

## Graph biomass
ggplot(ALLoutput.biom.DF, aes(as.numeric(rep), g, colour = stage)) +
  geom_point() +
  geom_path() +
  facet_grid(stage~spp, scales = "free")

## Graph abundance
ggplot(ALLoutput.N.DF, aes(as.numeric(rep), N, colour = stage)) +
  geom_point() +
  geom_path() +
  facet_grid(stage~spp, scales = "free")

## Graph all species together
ggplot(ALLoutput.biom.DF, aes(as.numeric(rep), g, colour = stage)) +
  geom_point() +
  geom_path() +
  facet_grid(~spp)

ggplot(ALLoutput.N.DF, aes(as.numeric(rep), N, colour = stage)) +
  geom_point() +
  geom_path() +
  facet_grid(~spp)

## Graph flows
flowresults.l <- flowresults %>%
  mutate(rep = as.numeric(row.names(.))) %>%
  gather(metric, value, -rep)

ggplot(flowresults.l, aes(rep, value)) +
  geom_point() + geom_path() +
  facet_wrap(~metric)

## Checking to see if flows used in actual model runs match those
input.
## This current run uses natural flow only.
flowtest <- data.frame(cbind(flowdata$SP_highflood,
                             flowdata$SU_highflood,

```



```

                                flowdata$medflood,
                                flowdata$drought,
                                flowdata$nonevent))

flowtest

apply(flowtest, 1, sum)

flowresults
flowtest[,1]-flowresults[,1]
flowtest[,2]-flowresults[,2]
flowtest[,3]-flowresults[,3]
flowtest[,4]-flowresults[,4]
flowtest[,5]-flowresults[,5]

## -----
##
## Plot summary from all iterations of model run and compare to
  relative
## abundance from observed surveys
## -----
##
## Reading in observed field data
Verde <- read.csv("data/Rel_Abu_Verde_94-08.csv", header = T)

## renaming as observed, removing tot abund, and renaming cols
observed <- Verde %>%
  select(year = Year,
         species = SppCode,
         obs.mean.rel.abund = MeanRelAbu,
         obs.se.rel.abund = SERelAbu)
observed$year <- as.numeric(as.character(observed$year))

## turning replist into a df
repdf <- ldply(repllist, function(x) {
  adply(x, c(1,2,3))
})

names(repdf) <- c('species', 'year', 'stage', 'rep', 'abund')
repdf <- filter(repdf, stage != 'S1')
repdf$year <- as.numeric(as.character(repdf$year))

totn <- adply(Total.N, c(1,2))
names(totn) <- c('year', 'rep', 'tot.abund')

```



```

totn$year <- as.numeric(as.character(totn$year))

## joining totn and repdf together
repdf <- left_join(totn, repdf)

## calculating relative abundance
repdf <- mutate(repdf, rel.abund = abund/tot.abund)

## Taking mean results to cf w/ observed data
means <- repdf %>%
  select(-tot.abund) %>%
  group_by(year, rep, species) %>% # combining stages
  summarise(abund = sum(abund),
            rel.abund = sum(rel.abund)) %>%
  ungroup() %>%
  group_by(species, year) %>%
  summarise(mean.abund = mean(abund),
            sd.abund = sd(abund),
            se.abund = sd(abund)/sqrt(iterations),
            mean.rel.abund = mean(rel.abund),
            sd.rel.abund = sd(rel.abund),
            se.rel.abund = sd(rel.abund)/sqrt(iterations)) %>%
  ungroup()
means

## Taking the end period to compare with observed data
mean_end <- filter(means, year >= 1994)

## Joining w/ observed data
mean_end <- left_join(mean_end, observed)

## Plotting model vs. observed for 1994-2017
rel.abund.trends <- ggplot(mean_end, aes(year,
                                          mean.rel.abund,
                                          colour = species,
                                          fill = species)) +
  geom_ribbon(aes(ymin = mean.rel.abund - 1.96 * se.rel.abund,
                  ymax = mean.rel.abund + 1.96 * se.rel.abund),
            colour = 'transparent',
            alpha = .5,
            show.legend = FALSE) +
  geom_line(show.legend = FALSE) +
  facet_wrap(~species, ncol = 2) +
  theme_classic_facet() +

```



```

    coord_cartesian(ylim = c(0,1)) +
    ylab('Relative abundance') +
    xlab('Year')
## adding observed data
rel.abund.trends +
  geom_pointrange(aes(y = obs.mean.rel.abund,
                      ymin = obs.mean.rel.abund - 1.96 *
obs.se.rel.abund,
                      ymax = obs.mean.rel.abund + 1.96 *
obs.se.rel.abund),
                  size = .1,
                  show.legend = FALSE)

ggsave('export/multi-spp2.pdf', width = 4, height = 6)

## -----
## * Correlation tests -----
## -----

## Create a df w/ model and observed relative abundances from 1994-
2008 to test
## correlation between them
spearman.results <- mean_end %>%
  filter(year >= 1994, year <= 2008) %>%
  group_by(year) %>%
  summarise(rho = cor.test(mean.rel.abund,
                          obs.mean.rel.abund,
                          method = 'spearman')$estimate,
            pval = cor.test(mean.rel.abund,
                          obs.mean.rel.abund,
                          method = 'spearman')$p.value
  )

spearman.results

## Overall correlation between mean observed and modeled relative
abund -----
mod.obs.mean.by.spp <- mean_end %>%
  filter(year >= 1994, year <= 2008) %>%
  group_by(species) %>%
  summarise(model = mean(mean.rel.abund),

```



```

        obs = mean(obs.mean.rel.abund))

mod.obs.mean.by.spp %>%
  summarise(rho = cor.test(model,
                           obs,
                           method = 'spearman')$estimate,
            pval = cor.test(model,
                           obs,
                           method = 'spearman')$p.value
  )

## Species level correlations -----
-----

## Spearmans
mean_end %>%
  filter(year >= 1994, year <= 2008) %>%
  select(species, year, mean.rel.abund, obs.mean.rel.abund) %>%
  group_by(species) %>%
  summarise(spear.rho = cor.test(mean.rel.abund,
                                obs.mean.rel.abund,
                                method = 'spearman')$estimate,
            spear.pval = cor.test(mean.rel.abund,
                                obs.mean.rel.abund,
                                method = 'spearman')$p.value
  )

## Pearsons
mean_end %>%
  filter(year >= 1994, year <= 2008) %>%
  select(species, year, mean.rel.abund, obs.mean.rel.abund) %>%
  group_by(species) %>%
  summarise(pear.r = cor.test(mean.rel.abund,
                              obs.mean.rel.abund,
                              method = 'pearson')$estimate,
            pear.pval = cor.test(mean.rel.abund,
                              obs.mean.rel.abund,
                              method = 'pearson')$p.value
  )

## Saving current state
save.image()

### Local Variables:
### eval: (orgstruct-mode 1)

```



```
### orgstruct-heading-prefix-regexp: "## "  
### End:
```

### Test dataset for fish model:

<https://zenodo.org/record/1309024#.XitmFhPYrVo>

Year	SppCode	MeanRelAbu	SERelAbu
1994	AMNA	0.00474129	0.0015367
1995	AMNA	0.02369851	0.00659485
1996	AMNA	0.01542454	0.00484929
1997	AMNA	0.01782863	0.00909657
1998	AMNA	0.04751465	0.01304762
1999	AMNA	0.02869334	0.00733422
2000	AMNA	0.01625465	0.00667679
2001	AMNA	0.02373947	0.00765028
2002	AMNA	0.02755906	0.0194872
2003	AMNA	0.01556787	0.00542145
2004	AMNA	0.01701088	0.00582928
2005	AMNA	0.06875478	0.04801822
2006	AMNA	0.01820826	0.00520848
2007	AMNA	0.03008951	0.00462392
2008	AMNA	0.01882535	0.00562542
1994	CACL	0.36355263	0.02473104
1995	CACL	0.31718884	0.04181266
1996	CACL	0.3083794	0.02946542
1997	CACL	0.20041592	0.05741031
1998	CACL	0.15306896	0.03719239
1999	CACL	0.19768335	0.034577
2000	CACL	0.05151472	0.01629347
2001	CACL	0.17419184	0.05427227
2002	CACL	0.09934383	0.04667647
2003	CACL	0.09034051	0.04579828
2004	CACL	0.06695886	0.02289526
2005	CACL	0.1527301	0.06418209
2006	CACL	0.34151287	0.04582022
2007	CACL	0.32437406	0.10218552
2008	CACL	0.21786307	0.07327176
1994	CAIN	0.33618776	0.05901669
1995	CAIN	0.31572465	0.04577041





1996	CAIN	0.33950901	0.03753834
1997	CAIN	0.14186852	0.04088214
1998	CAIN	0.1539453	0.03651483
1999	CAIN	0.13942865	0.0397454
2000	CAIN	0.11702555	0.05773223
2001	CAIN	0.06639228	0.02344621
2002	CAIN	0.07362205	0.01865203
2003	CAIN	0.05831369	0.02539519
2004	CAIN	0.06853656	0.0206245
2005	CAIN	0.08974169	0.03180243
2006	CAIN	0.22810135	0.03261757
2007	CAIN	0.246846	0.06974082
2008	CAIN	0.30335155	0.08384131
1994	CYLU	0.19513838	0.05095858
1995	CYLU	0.10965148	0.04324903
1996	CYLU	0.11786913	0.02877738
1997	CYLU	0.52653933	0.13207607
1998	CYLU	0.46119419	0.10330325
1999	CYLU	0.43415439	0.09697001
2000	CYLU	0.72122078	0.0786306
2001	CYLU	0.47704808	0.13264191
2002	CYLU	0.26692913	0.09409531
2003	CYLU	0.56485803	0.03661946
2004	CYLU	0.71210731	0.04081048
2005	CYLU	0.57879833	0.11942473
2006	CYLU	0.28684651	0.07329326
2007	CYLU	0.28979869	0.10017037
2008	CYLU	0.22581426	0.08361998
1994	GIRO	0.09705336	0.02366
1995	GIRO	0.19873357	0.04229313
1996	GIRO	0.17723518	0.03449633
1997	GIRO	0.0375248	0.01620933
1998	GIRO	0.05669829	0.01805462
1999	GIRO	0.03922614	0.0147227
2000	GIRO	0.01400304	0.00665164
2001	GIRO	0.04192696	0.02243223
2002	GIRO	0	0
2003	GIRO	0.0030888	0.00285968
2004	GIRO	0.00354541	0.00262117
2005	GIRO	0	0



2006	GIRO	0.06814602	0.02737813
2007	GIRO	0.03393931	0.02908034
2008	GIRO	0.01450861	0.01066999
1994	LECY	0.0002471	0.00022557
1995	LECY	0.02661457	0.00983772
1996	LECY	0.00566725	0.00243058
1997	LECY	0.0277769	0.01576466
1998	LECY	0.03324574	0.01702813
1999	LECY	0.02936869	0.01970524
2000	LECY	0.04948392	0.02375537
2001	LECY	0.09059527	0.05744906
2002	LECY	0.11463255	0.06927234
2003	LECY	0.08863909	0.03731152
2004	LECY	0.02951	0.01300644
2005	LECY	0.05923339	0.01494385
2006	LECY	0.00457825	0.00219272
2007	LECY	0.03035992	0.01601996
2008	LECY	0.0885592	0.03250162
1994	MIDO	0.00307949	0.00094557
1995	MIDO	0.00838838	0.00348347
1996	MIDO	0.03591548	0.01434669
1997	MIDO	0.04804591	0.03089934
1998	MIDO	0.09433287	0.02663666
1999	MIDO	0.13144544	0.0305531
2000	MIDO	0.03049735	0.00944073
2001	MIDO	0.1261061	0.0469021
2002	MIDO	0.41791339	0.02268866
2003	MIDO	0.17919201	0.02800196
2004	MIDO	0.10233099	0.03465866
2005	MIDO	0.05074172	0.03476232
2006	MIDO	0.05260674	0.01876522
2007	MIDO	0.04459252	0.01427386
2008	MIDO	0.13107796	0.03760383



## Invertebrate population model

### Primary publication describing the methodology:

McMullen, L.E., De Leenheer, P., Tonkin, J.D. and Lytle, D.A., 2017. High mortality and enhanced recovery: modelling the countervailing effects of disturbance on population dynamics. *Ecology letters*, 20(12), pp.1566-1575.

<https://doi.org/10.1111/ele.12866>

### Mathematical proof of the time-varying logistic model:

<https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fele.12866&file=ele12866-sup-0001-SupInfo.docx>

Logistic equation solution that allows time-varying growth rate and carrying capacity

Consider the logistic equation with time-varying maximal per capita growth rate  $r(t)$ , and time-varying carrying capacity  $K(t)$ :

$$\frac{dN}{dt}(t) = r(t)N(t) \left(1 - \frac{N(t)}{K(t)}\right), N(t_0) = N_0 \quad (4)$$

Here  $t_0$  is a given initial time, and  $N_0 > 0$  is the initial population size. We assume that  $r(t)$  and  $K(t)$  are positive, bounded, piecewise continuous functions, defined on the interval  $[t_0, +\infty)$ . (A function  $f(t)$ , defined on the interval  $[t_0, +\infty)$  is said to be piecewise continuous, if for each  $t > t_0$ , the restriction of  $f(t)$ , to the interval  $[t_0, t]$ , has at most finitely many points of discontinuity, and with finite right and left limits). We also assume that  $K(t)$  is bounded below by  $K_{\min} > 0$  on the interval  $[t_0, +\infty)$ . These are fairly general mathematical assumptions that are satisfied in most biological contexts, and they are satisfied in all the scenarios investigated in this paper.

We claim that the solution of Eq. (4) is given by:

$$N(t) = \frac{\left(e^{\int_{t_0}^t r(\tau) d\tau}\right) N_0}{\left(\int_{t_0}^t \frac{r(\tau)}{K(\tau)} e^{\int_{t_0}^{\tau} r(s) ds} d\tau\right) N_0 + 1} \quad (5)$$



Notice that the assumptions made on  $r(t)$  and  $K(t)$  ensure that all the integrals appearing in Eq. (5) are well-defined. The variables  $\tau$  and  $s$  are dummy variables for integration.

To prove the validity of Eq. (5), we first introduce a new variable  $n(t)$ , which is a particular scaled version of the original population size  $N(t)$ :

$$n(t) = N(t)e^{-\int_{t_0}^t r(\tau)d\tau} \quad (6)$$

Taking derivatives with respect to time, using the product rule for differentiation, using Eq. (4) for  $dN/dt$ , and expressing the resulting equation in terms of  $n(t)$  rather than  $N(t)$  by using Eq. (6), shows that  $n(t)$  must satisfy the following differential equation:

$$\frac{dn}{dt}(t) = -\frac{r(t)}{K(t)}e^{+\int_{t_0}^t r(\tau)d\tau}n^2(t), n(t_0) = N_0 \quad (7)$$

The key point is that the latter equation is a separable differential equation, which can be solved by a standard solution method:

$$n(t) = \frac{N_0}{\left(\int_{t_0}^t \frac{r(\tau)}{K(\tau)}e^{\int_{t_0}^{\tau} r(s)ds}\right)N_0 + 1} \quad (8)$$

Eq. (6) implies that  $N(t) = n(t)e^{\int_{t_0}^t r(\tau)d\tau}$ , and substituting the above expression for  $n(t)$ , shows that  $N(t)$  is indeed given by Eq. (5), as claimed.

### Methodology for obtaining vital rates for the invertebrate model:

<https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fele.12866&file=ele12866-sup-0001-SupInfo.docx>

Estimating intrinsic rates of population increase.

Intrinsic rates of population increase ( $r$ ) for the three target taxa were tabulated from age-specific fecundity and survival rates from published values using the method of Birch (1948).  $r$  was defined as the number of offspring produced by one individual per day, thus measuring the per capita rate of increase over a short time (Gotelli 1998). The parameter values used for this



approach, and the resulting estimated intrinsic rates of population increase, are given in Table B1. When information could not be found on the exact taxon of interest, information from a closely related taxon was used. When a range of values were reported, the average was used in the estimation.

#### *Example Calculation of Intrinsic Rate of Increase*

In order to calculate the estimated intrinsic rate of population increase, total average lifespan, number of eggs laid, and survivorship of life stages or overall survivorship were necessary (Table B1). Calculations began at the egg stage, and number of individuals were successively reduced by survivorship values until  $r$  was estimated. For example, for *Fallceon quilleri*, calculations began with eggs laid per individual (1850). The value of survivorship of eggs used was 80%, so 1850 was reduced to 1480. This was assumed to be the average number of offspring that survive to larval stage per individual. The value of survivorship of larvae used was 8.9%, so 1480 was reduced to 131.72. This was assumed to be the average number of offspring that survive to the adult stage per individual. The value of survivorship of pre-reproductive adults used was 5%, so 131.72 was reduced to 6.57. This value was divided by the mean duration of lifecycle, 28.5 days, to arrive at an estimated intrinsic rate of population increase of 0.23.

**Table B1.** Parameter values used for life-table calculations and resulting estimated intrinsic rates of population increase.

	Mayfly ( <i>Fallceon quilleri</i> )	Dragonfly ( <i>Progomphus borealis</i> )	Ostracod (Ostracoda)
Egg stage duration (d)	3-34 (18.5)	13 to 56 (34.5)	9 to 86 (47.5)
Egg stage survivorship (%)	70-90 (80)	77.4	-



Larval stage duration (d)	6- 12 (9)	30-180 (105)	21-365 (193)
Larval survivorship (%)	8.9	2.53	-
Adult stage duration (d)	1	30	28-180 (104)
Adult survivorship (pre-reproductive) (%)	1.2-8.8 ( 5)	78.2	-
Overall survivorship (%)	-	-	40-80 (60)
Mean life cycle duration (d)	28.5	181.5	344.5
Eggs laid per individual	1200-2500 (1850)	1000	8-180 (94)
Estimated intrinsic rate of population increase ( <i>r</i> )	0.23	0.08	0.16

---

SOURCES: Information used for parameter values were found in Ferguson 1944, Gray 1981,

Corbet 1999, Braune et al. 2008, Dole-Olivier et al. 2000, Gandolfi et al. 2001, Werneke and

Zwick 2006, and Merritt et al. 2008.

NOTE: Mean values used in the analyses shown in parentheses.



*Literature Cited Only in Appendix B*

- Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* 17: 15-26.
- Braune, E., Richter, O., Sondgerath, D., and F. Suhling. 2008. Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology* 14: 470-482.
- Corbet, P.S. 1999. *Dragonflies: Behavior and Ecology of Odonata*. Cornell University Press.
- Ferguson, E. 1944. Studies on the seasonal life history of three species of freshwater ostracoda. *American Midland Naturalist* 32: 713-727.
- Gandolfi, A., Todeschi, E.B.A., Rossi, V. and Monozzi, P. 2001. Life history in *Darwinula stevensoni* (Crustacea: Ostracoda) from Southern European populations under controlled conditions and their relationship with genetic features. *Journal of Limnology* 60: 1-10.
- Gotelli, N.J. 1998. *A Primer of Ecology*, 2nd ed. Sinauer Associates, Inc.
- Merritt, R.W., Cummins, K.W., and Berg, M.B. 2008. *An Introduction to the Aquatic Insects of North America*. Kendall Hunt Publishing Company.
- Werneke, U. and Zwick, P. 1992. Mortality of the terrestrial adult and aquatic nymphal life stages of *Baetis vernus* and *Baetis rhodani* in the Breitenbach, Germany (Insecta: Ephemeroptera). *Freshwater Biology* 28: 249-255.

**R code for implementing the invertebrate model:**

<https://doi.org/10.6084/m9.figshare.5476993>

##

=====

=====



```
## Code to run time-varying logistic population growth model for 3
  aquatic invertebrates
## Date: October 2017
## Authors: Jonathan Tonkin, David Lytle, Laura McMullen, Patrick
  DeLeenheer
## Emails: jdtonkin@gmail.com, lytle@oregonstate.edu,
  laurabethmcm@gmail.com,
## deleenhp@science.oregonstate.edu
## Accompanies paper: McMullen, LE, DeLeenheer, P, Tonkin JD, and
  Lytle, DA. (2017) High mortality
## and enhanced recovery: modelling the countervailing effects of
  disturbance on population
## dynamics. Ecology Letters. doi: 10.1111/ele.12866.
## The following uses the logistic model to create flood-population
  response surfaces for three taxa
## with contrasting life histories after a single-flood event (Figure
  1 in the paper).
```

```
##
```

```
=====
=====
```

```
## Setup -----
-----
```

```
## Required libraries
```

```
library(tidyverse)
library(ggplot2)
library(lattice)
library(RColorBrewer)
```

```
## Plot setup
```

```
clrs <- colorRampPalette(brewer.pal(9, "YlOrRd"))
trellis.par.set("axis.line", list(col = NA, lty = 1, lwd = 1))
theme.novpadding <- list(
  layout.heights = list(top.padding = 0, bottom.padding = 0),
  layout.widths = list(left.padding = 0, right.padding = 0)
)
```

```
## General settings -----
-----
```

```
## Minimum threshold of what is considered a flood
```

```
Qmin = 5
```

```
## Half saturation constant
```





```

a = 100

## Maximum flood size to run model to
Qmax = 1000

## Time to run model out to - days
t = 200

## Time zero. Can also set this in the MainLogisticSolution function
instead
t0 = 0

## Main function -----
## Function to calculate N at time t in relation to flood intensity
MainLogisticSolution <- function(r, t0, t, Q) {

  n0 = initialpopsize(Q)

  intfunc <- function(y) {
    (r / kfunc(y, Q)) * (exp(r * (y - t0)))
  }

  (exp(r * (t - t0)) * n0) / (integrate(intfunc, lower = t0, upper =
t)$value * n0 + 1)

}

## Species settings -----
-----
## Note that species-specific values keep the same notation with
different values further down
## e.g. g, h, r, Kd, and Kb. So it's important to run through in
sequence

## Progomphus -----
-----

## Values

## Rate that K returns to pre-disturbance level
g = 0.01

## Strength of disturbance-mortality relationship
h = 0.01

```



```

## Intrinsic rate of population increase
r = .08

## Kd is the carrying capacity limit following strong disturbance
Kd = 100

## Kb is the carrying capacity baseline when disturbances are absent
Kb = 40

## Functions -----
## Some of these differ between species depending on their
  relationship to disturbance

## Function to calculate the initial population size "N0" after a
  disturbance
initialpopsize = function(x) Kb * exp(-h * x)

## Function to calculate the disturbance magnitude-K relationship.
  Sets to 0 if below the Qmin
QFunction <- function(x)
  ifelse(x < Qmin, 0, (x - Qmin)/(a + (x - Qmin)))

## Function to determine K0. Carrying capacity immediately following
  the disturbance
K0func <- function(x) {Kb + (Kd - Kb) * QFunction(x)}

## Function to calc. K as a function of time post-disturbance at a
  particular disturbance intensity
kfunc <- function(tau, Q){
  Kb + (K0func(Q) - Kb) * exp(-g * tau)
}

## Checking the relationship between Q (disturbance intensity) and K0
  (K post-disturbance)
dfK <- data.frame(Q = seq(0, Qmax))
dfK <- dfK %>%
  mutate(K0 = K0func(Q))
ggplot(dfK, aes(Q, K0)) + geom_line()

## Creating a df for storing and examining K as a function of Q and t
KQT <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

## Filling in Q

```



```

KQT$Q <- rep(seq(0, Qmax), each = t + 1)

## Calculating K0
KQT$K0 <- K0func(KQT$Q)

## Filling in t
KQT$t <- rep(seq(0, t), Qmax + 1)

## Calculating K
KQT$K <- Kb + (KQT$K0 - Kb) * exp(-g * KQT$t)

## Plotting K
wireframe(K ~ t + Q, data = KQT,
          aspect = c(1, .4),
          drape = TRUE,
          shade = FALSE,
          colorkey = FALSE,
          col = alpha('#ffeda0', 0.08),
          scales = list(arrows = FALSE, col = 'black'),
          screen = list(z = -40, x = -70),
          par.settings = theme.novpadding,
          col.regions = clr(1000),
          main = 'Progompheus K')

## Creating a df to fill in with results
flowdf <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

## Filling in Q
flowdf$Q <- rep(seq(0, Qmax), each = t + 1)

## Filling in t
flowdf$t <- rep(seq(0, t), Qmax + 1)

## Calculating N at t
flowdf$Nt <- apply(flowdf, 1, function(x) MainLogisticSolution(r = r,
  t0 = t0, t = x[2], Q = x[1]))

## Plotting Nt as a function of Q and t
wireframe(Nt ~ Q + t, data = flowdf,
          ylab = 'Time\n(days)',
          aspect = c(1, .4),
          drape = TRUE,
          shade = FALSE,
          colorkey = FALSE,

```



```

col = alpha('#ffeda0', 0.08),
scales = list(arrows = FALSE, col = 'black'),
screen = list(z = -40, x = -70),
par.settings = theme.novpadding,
col.regions = clrs(1000),
main = 'Progomphus Nt')

### Fallceon -----
-----
## Note that Fallceon has the same model as Progomphus but different
rates

## Values

## Rate that K returns to pre-disturbance level
g = 0.01

## Strength of disturbance-mortality relationship
h = 0.02

## Intrinsic rate of population increase
r = .23

## Kd is the carrying capacity limit following strong disturbance
Kd = 100

## Kb is the carrying capacity baseline when disturbances are absent
Kb = 40

## Functions -----
## Same as Progomphus

## Function to calculate the initial population size "N0" after a
disturbance
initialpopsize = function(x) Kb * exp(-h * x)

## Function to calculate the disturbance magnitude-K relationship
## Sets to 0 if below the Qmin
QFunction <- function(x)
  ifelse(x < Qmin, 0, (x - Qmin)/(a + (x - Qmin)))

## Function to determine K0. Carrying capacity immediately following
the disturbance
K0func <- function(x) {Kb + (Kd - Kb) * QFunction(x)}

```



```

## Fn to calculate K as a function of time post-disturbance at a
  particular disturbance intensity
kfunc <- function(tau, Q){
  Kb + (K0func(Q) - Kb) * exp(-g * tau)
}

## Checking the relationship between Q (disturbance intensity) and K0
  (K post-disturbance)
dfK <- data.frame(Q = seq(0, Qmax))
dfK <- dfK %>%
  mutate(K0 = K0func(Q))
ggplot(dfK, aes(Q, K0)) + geom_line()

## Creating a df for storing and examining K as a function of Q and t
KQT <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

## Filling in Q
KQT$Q <- rep(seq(0, Qmax), each = t + 1)

## Calculating K0
KQT$K0 <- K0func(KQT$Q)

## Filling in t
KQT$t <- rep(seq(0, t), Qmax + 1)

## Calculating K
KQT$K <- Kb + (KQT$K0 - Kb) * exp(-g * KQT$t)

## Plotting K
wireframe(K ~ t + Q, data = KQT,
  aspect = c(1, .4),
  drape = TRUE,
  shade = FALSE,
  colorkey = FALSE,
  col = alpha('#ffeda0', 0.08),
  scales = list(arrows = FALSE, col = 'black'),
  screen = list(z = -40, x = -70),
  par.settings = theme.novpadding,
  col.regions = clr(1000),
  main = 'Fallceon K')

## Creating a df to fill in with results
flowdf <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

```



```

## Filling in Q
flowdf$Q <- rep(seq(0, Qmax), each = t + 1)

## Filling in t
flowdf$t <- rep(seq(0, t), Qmax + 1)

## Calculating N at t
flowdf$Nt <- apply(flowdf, 1, function(x) MainLogisticSolution(r = r,
  t0 = t0, t = x[2], Q = x[1]))

## Plotting Nt as a function of Q and t
wireframe(Nt ~ Q + t, data = flowdf,
  ylab = '      Time\n      (days)',
  aspect = c(1, .4),
  drape = TRUE,
  shade = FALSE,
  colorkey = FALSE,
  col = alpha('#ffeda0', 0.08),
  scales = list(arrows = FALSE, col = 'black'),
  screen = list(z = -40, x = -70),
  par.settings = theme.novpadding,
  col.regions = clrs(1000),
  main = 'Fallceon Nt')

```

```

### Ostracod -----
-----

```

## Note that Ostracod has a different model to the previous two

## Values

## Rate that K returns to pre-disturbance level

g = 0.01

## Strength of disturbance-mortality relationship

h = 0.05

## Intrinsic rate of population increase

r = .16

## Kd is the carrying capacity limit following strong disturbance

## Note difference to other two spp

Kd = 40



```

## Kb is the carrying capacity baseline when disturbances are absent
Kb = 100

## Functions -----
## Different from two previous spp

## Function to determine K0. Carrying capacity immediately following
the disturbance
K0func <- function(x) {Kb - (Kb - Kd) * QFunction(x)}

## Fn to calculate K as a function of time post-disturbance at a
particular disturbance intensity
kfunc <- function(tau, Q){
  Kb - (Kb - K0func(Q)) * exp(-g * tau)
}

## Checking the relationship between Q (disturbance intensity) and K0
(K post-disturbance)
dfK <- data.frame(Q = seq(0, Qmax))
dfK <- dfK %>%
  mutate(K0 = K0func(Q))
ggplot(dfK, aes(Q, K0)) + geom_line()

## Creating a df for storing and examining K as a function of Q and t
KQT <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

## Filling in Q
KQT$Q <- rep(seq(0, Qmax), each = t + 1)

## Calculating K0
KQT$K0 <- K0func(KQT$Q)

## Filling in t
KQT$t <- rep(seq(0, t), Qmax + 1)

## Calculating K
KQT$K <- Kb + (KQT$K0 - Kb) * exp(-g * KQT$t)

## Plotting K
wireframe(K ~ t + Q, data = KQT,
  aspect = c(1, .4),
  drape = TRUE,
  shade = FALSE,
  colorkey = FALSE,

```



```

col = alpha('#ffeda0', 0.08),
scales = list(arrows = FALSE, col = 'black'),
screen = list(z = -40, x = -70),
par.settings = theme.novpadding,
col.regions = clr(1000),
main = 'Ostracod K')

## Creating a df to fill in with results
flowdf <- data.frame(Q = numeric((Qmax + 1) * (t + 1)))

## Filling in Q
flowdf$Q <- rep(seq(0, Qmax), each = t + 1)

## Filling in t
flowdf$t <- rep(seq(0, t), Qmax + 1)

## Calculating N at t
flowdf$Nt <- apply(flowdf, 1, function(x) MainLogisticSolution(r = r,
  t0 = t0, t = x[2], Q = x[1]))

## Plotting Nt as a function of Q and t
wireframe(Nt ~ Q + t, data = flowdf,
  ylab = 'Time\n (days)',
  aspect = c(1, .4),
  drape = TRUE,
  shade = FALSE,
  colorkey = FALSE,
  col = alpha('#ffeda0', 0.08),
  scales = list(arrows = FALSE, col = 'black'),
  screen = list(z = -40, x = -70),
  par.settings = theme.novpadding,
  col.regions = clr(1000),
  main = 'Ostracod Nt')

## end

```

