Temperature dynamics in Klamath River off-channel floodplain restoration sites depend on location within the watershed

Jessie Moravek[1], Toz Soto[2], Justin Brashares[1], Albert Ruhi[1]

[1]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA
[2]Karuk Tribe Fisheries Program

Corresponding Author: jessie_moravek@berkeley.edu

Keywords: Klamath River, *Oncorhynchus kisutch*, floodplain, off-channel, restoration

Summary

The mid-Klamath River is heavily impacted by altered streamflow and warm water temperatures, which contribute to the decline of native salmonids. In an effort to restore critical salmonid habitat, the Karuk Tribe, National Forest Service, and Mid-Klamath Watershed Council have created a variety of off-channel floodplain ponds that provide habitat for juvenile Coho Salmon (*Oncorhynchus kisutch*) and other juvenile salmonids such as Steelhead (*O. mykiss)*. One purpose of these ponds is to provide cool water refuges for juvenile salmonids during high summer water temperatures. However, no studies have quantified how these ponds vary in temperature regimes across the river floodplain. Characterizing alternative temperature regimes in the Klamath floodplain can help us better understand why these habitats are important for salmonid populations in the Klamath.

In July 2020, we placed 30 temperature sensors in 9 off-channel ponds and 2 creeks (Seiad Creek and Horse Creek) in the mid-Klamath floodplain. For this analysis we only used data recorded in the last 3 weeks of July 2020, but sensors will continue recording data until August 2021. We placed 1-4 sensors in each pond and creek. We used a multivariate auto-regressive state space (MARSS) models to determine the number and spatial arrangement of distinct thermal regimes (hereafter, "temperature states") in floodplain ponds and tributaries.

We found that pond temperatures have lower daily maximums and fluctuate less than tributary temperatures. We also found that Seiad Creek, Seiad Creek ponds, Horse Creek, and Horse Creek ponds all have different patterns of temperature change throughout the summer. The temperature diversity introduced by off-channel ponds likely creates a "portfolio effect" that may allow fish to access a variety of water temperatures at any given time. The benefits of cool water temperature refuges for salmonids in the Klamath River watershed has been demonstrated by previous studies in the mainstem and tributary mouths but has never been specifically studied in off-channel ponds.

Historical data (2010-2019) for Alexander and Stender Ponds showed that over time, daily fluctuations in pond water temperature became less drastic. This pattern was also observed by MKWC in their reports on Alexander and Stender Ponds (MKWC 2020; Wickman et al. 2020), and our analysis provides a quantification of this pattern. This pattern is likely due to an increase in canopy cover and riparian vegetation as the ponds age and move to later successional stages post-construction. More stable water temperatures in the ponds contrast to creek temperatures, which continue to fluctuate widely on a daily basis during summer. Fish monitoring data from MKWC show that Coho Salmon growth rates are higher in these two ponds, which suggests that Coho Salmon may experience a metabolic benefit from more stable water temperatures (MKWC 2020; Wickman et al. 2020).

The temperature sensors used to complete this analysis are still recording data, and we will re-do our analysis in fall 2021 after a full year of data is available. Overall, our analysis provides deeper insight into the thermal benefits of floodplain habitats and off-channel ponds on the mid-Klamath River, and informs the future collection of fish population and movement data that will reveal more precise information about how floodplains benefit salmonids.

Contents

List of Tables:

List of Figures:

Supplementary Materials:

Introduction

Flow alteration impacts river ecosystems worldwide, and one major effect of flow alteration is the disruption of lateral hydrologic connectivity between rivers and their floodplains (Ward and Stanford 1995; Winemiller et al. 2016). In recent decades, many efforts to mitigate the effects of altered flow on native fish have focused on restoring floodplain habitats (Bellmore et al. 2013). Re-establishing the physical and biological connections between river and floodplain habitats has been shown to benefit fish growth, but it is unclear exactly how the physical characteristics of floodplains support fish populations (Jeffres et al. 2020). To better understand why connecting rivers and floodplains is an effective method for fish conservation, it is critical to understand how the physical characteristics of floodplain habitats differ and complement other parts of the watershed, such as river and tributary habitats. In particular, floodplain habitats often have groundwater inputs, aquatic vegetation, and deeper water compared to tributaries, which may create temperature heterogeneity that allows fish to take refuge from particularly cold or warm temperatures in rivers and tributaries (Tonolla et al. 2010). Characterizing alternative temperature regimes in floodplains can help us better understand how and why these habitats are important for conserving critical fish populations within watersheds.

To answer these questions, we studied floodplain restoration projects along the mid-Klamath River in northern California, USA. Hydropower dams have altered natural streamflow in the Klamath, severely impacting native fish populations. Over the last ten years, restoration activities by the Karuk Tribe, National Forest Service, and the Mid-Klamath Watershed Council have created a variety of off-channel ponds within the Klamath floodplain that provide habitat for juvenile Coho Salmon (*Oncorhynchus kisutch*) and other juvenile salmonids such as Steelhead (*O. mykiss*). These ponds vary in location and temperature regime, creating a unique experimental system in which to study how pond temperatures differ from tributary temperatures. Characterizing temperature regimes across a river-tributary floodplain will help us understand the roles these habitats play in creating habitat diversity and providing temperature refuges for juvenile salmonids.

This study seeks to understand temperature diversity in restored floodplain habitats in the Klamath River watershed using multivariate auto-regressive state space models, or MARSS models (temperature "states" are often referred to as temperature or thermal "regimes", and we use the two terms interchangeably in this report). Our objectives are to 1) identify the number of temperature states that exist among nine restored floodplain ponds on two different tributaries of the Klamath River; 2) understand how air temperature influences temperature dynamics in ponds and tributaries; 3) consider how temperature states contribute to the diversity of temperature regimes available to juvenile salmonids in the watershed; and 4) explore how seasonal and daily temperature fluctuations in ponds have changed over time.

To address these objectives, we developed four hypotheses to test how temperature regimes differ across the watershed in ponds and tributaries, specifically focusing on how many temperature states exist and how they are distributed throughout the watershed. These hypotheses were developed based on the spatial distribution of floodplain ponds along two different tributaries (Horse Creek and Seiad Creek) to the Klamath River.

H1: Eleven temperature states exist, one for each pond (9) and one for each tributary (2).

H2: Two temperature states exist, one that describes all ponds and one that describes all tributaries.

H3: Four temperature states exist, two for pond and tributary habitats on the first tributary, and two for pond and tributary habitats on the second tributary.

H4: One temperature state exists and all ponds and tributaries have the same state.

To address our last objective of exploring changes in seasonal and daily temperature fluctuations over time, we used wavelet analysis to visualize and quantify temperature fluctuations between 2010 and 2019 in two of the oldest ponds. These unique analysis tools allow us to understand patterns in temperature data, and help us characterize how these patterns become more or less important as pond ecosystems develop and move into later successional stages.

Methods

Study Sites

For this study, we focused on nine man-made floodplain restoration ponds constructed between 2010 and 2019 in the mid-Klamath watershed. The ponds are located on Horse Creek and Seiad Creek (Table 1, Figure 1). One pond (Goodman Pond) is located on Middle Creek which is a tributary of Horse Creek. Ponds are fed mainly by groundwater inputs and flow into the creek. Pond banks are stabilized with native plants including alder, blackberry, and horsetail. Ponds range between 0.7m and 1.1m average water depth during the summer dry period, but sustain much higher water levels during the wet season (MKWC 2020; Wickman et al. 2020).

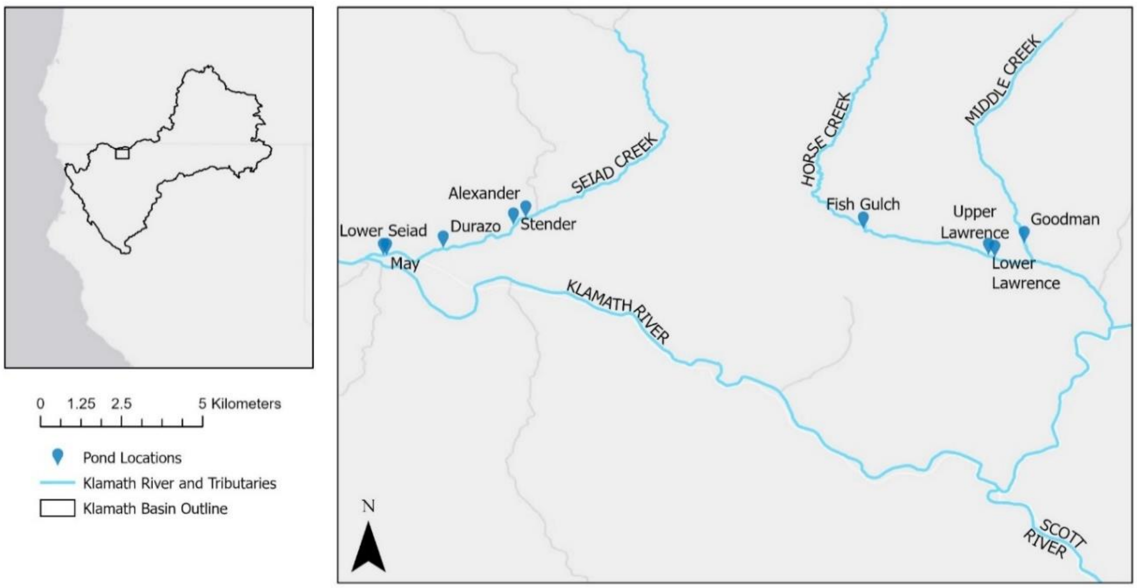


Figure 1: *A map of the Klamath River watershed and the specific tributaries and floodplain ponds used in this study.*

Table 1: *Tributaries included in this study and the ponds on each tributary. Ponds are listed upstream to downstream on the tributary. *Goodman Pond is on Middle Creek, which is a small tributary to Horse Creek.*

Seiad Creek	**Horse Creek**
Alexander Pond	Fish Gulch Pond
Stender Pond	Goodman Pond*
Durazo Pond	Upper Lawrence Pond
Lower Seiad pond	Lower Lawrence Pond
May Pond	

Data Collection

In July 2020, we deployed 30 temperature sensors (HOBO MX2021, Onset Corporation, Massachusetts) programmed to measure temperature every 15 minutes in off-channel ponds and creeks. We distributed sensors between ponds on two tributaries. We placed 1-4 sensors in each pond to capture local-scale temperature variation in the pond. We also placed 1 sensor in the tributary upstream of the outlet of each pond. We placed sensors between 7 and 13 July 2020, and read them out between 27 and 28 July 2020. All sensors will continue collecting data until July 2021, and after that a longer time series will be available to analyze. Daily temperature means were calculated for each sensor. Data from all sensors was log transformed and z-scored to control for outliers.

Historical temperature data from temperature sensors in Alexander and Stender Ponds were provided by MKWC. These are two of the oldest ponds in the study and were constructed in 2010, and temperature data were collected hourly in these ponds from 2010-2019. In Alexander Pond, data collection ended in January 2019, but in Stender Pond it continued until November 2019, so Stender Pond has an extra summer of data. Data from all sensors was log transformed and z-scored to control outliers.

We obtained air temperature data from the National Oceanic and Atmospheric Administration's Climate Data Online database for Siskiyou County, CA (NOAA 2020). Of the multiple air temperature sensors located in the county, we only used data from the Slater Butte sensor. This sensor was close geographically to our study sites and was located at a more similar elevation than other sensors.

MARSS

We used a set of multivariate auto-regressive state space (MARSS) models to test our hypotheses about the number of temperature regimes present in the ponds and tributaries. MARSS models take advantage of temporal correlation to estimate how a driver affects a biological or environmental response, or process (Holmes, Ward, and Wills 2014). In our case, MARSS models incorporate air temperature data, which allowed us to estimate water temperature sensitivity to air temperature. We tested for different lags and introduced a 4-day lag in our air temperature data, in agreement with water temperature buffering variation in air temperature. We used the 'MARSS' R package to fit the different set of models, and compare support for each of our four hypotheses sing multi-model inference (R Development Core Team 2020; Holmes, Ward, and Wills 2014; for more details on MARSS see Appendix I). In particular, we evaluated relative support for each model using Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002).

ARIMA and Wavelet Analysis

To prepare temperature data for our wavelet analysis, we first used an autoregressive integrated moving average model (ARIMA) to interpolate sporadic missing data in historical temperature datasets (Knape and de Valpine 2012; for more details on ARIMA see Appendix I). We used the 'wavelets' package in R with historical datasets (2010-2019) for Alexander Pond and Stender Pond to visualize and quantify how seasonal and daily water temperature fluctuations changed over the 9-year period (R Development Core Team 2020; Roesch 2018).

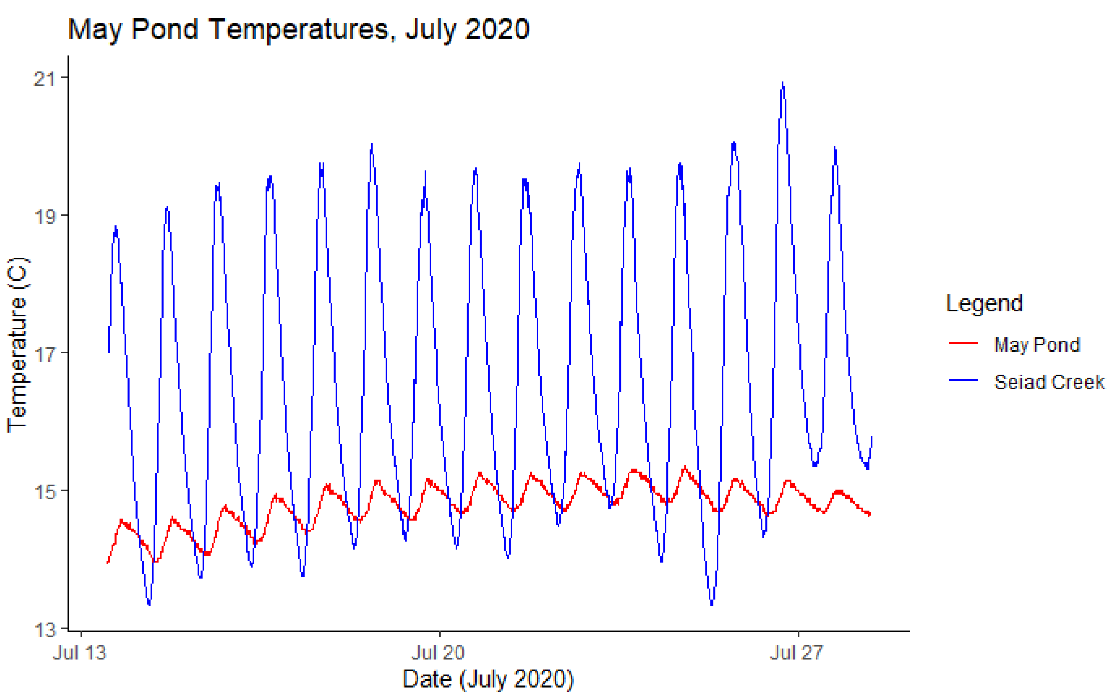


Figure 2: *Example of temperature sensor readings in May Pond (red time series) and Seiad Creek (blue time series) just upstream of the pond's outlet. 1-4 individual temperature sensors were placed in each pond and creek. When a pond or creek had more than one sensor, each was treated as a replicate in the MARSS model (May Pond only had one sensor).*

Results

Temperatures in ponds in the month of July 2020 were generally cooler and more stable than temperatures in tributary habitats (e.g. May Pond, Figure 2). Compared to tributaries, ponds had lower daily temperature maximums, and lower daily amplitudes (i.e. the difference in daily maximum and minimum daily temperatures). Within the same pond or tributary, different sensors generally recorded similar water temperatures. Air temperature peaked on 20 July, and pond and tributary water temperatures peaked around 24 or 25 July, indicating an approximately 4-day lag in water temperature response, which we accounted for by incorporating a 4-day lag into the covariate matrix data.

The best supported model was Model 3 (AICc 877.8), supporting that four temperature states (or thermal regimes) exist for each creek and set of ponds (Table 2). The four separate temperature states are specifically Seiad Creek ponds, Seiad Creek, Horse Creek ponds, and Horse Creek. The next best model was Model 1 (AICc 880.7), which modeled 11 different temperature states for each pond and tributary separately.

Table 2: *Brief descriptions of hypotheses, model ID (numbers), and AICc values for the four Multivariate Autoregressive State-Space (MARSS) models considered. Model 3 (temperature state depends on tributary) has the lowest AICc value and is therefore considered the best supported model. Mean daily temperature was used as a variate (response) in this analysis.*

Hypothesis	Model Number	AICc
Eleven temperature states exist, one for each pond (9) and one for each tributary (2)	Model 1	880.7
Two temperature states exist, one that describes all ponds and one that describes all tributaries.	Model 2	906.5
Four temperature states exist, two for pond and tributary habitats on the first tributary, and two for pond and tributary habitats on the second tributary.	Model 3	877.8*
One temperature state exists and all ponds and tributaries have the same state.	Model 4	940.8

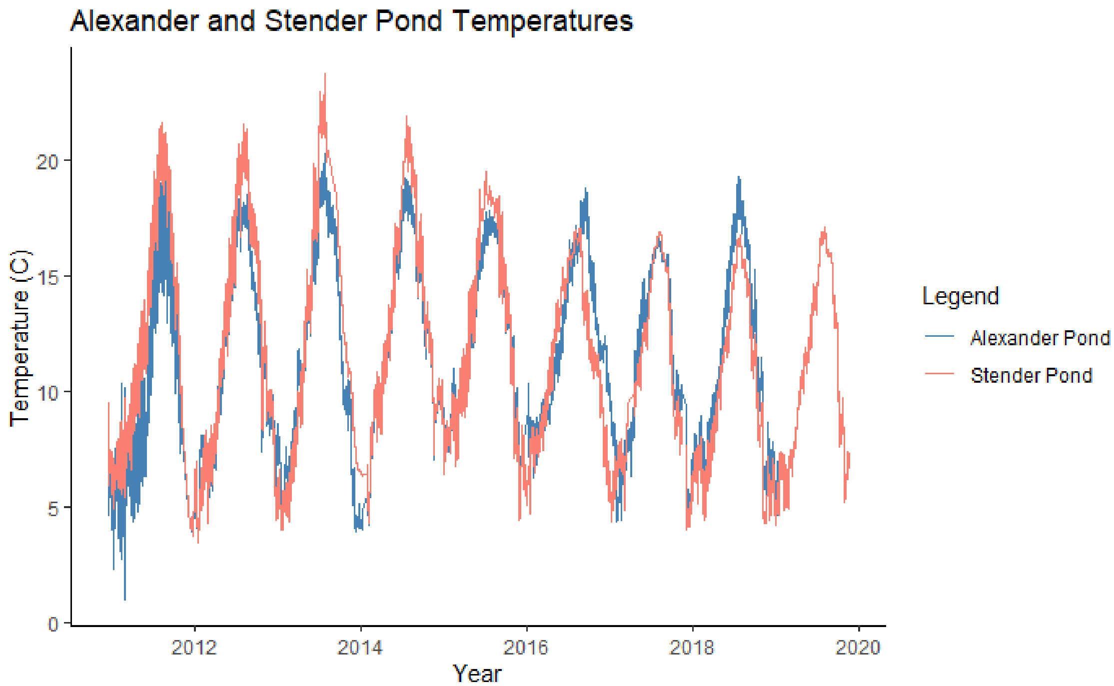


Figure 3*: Historical hourly temperature data for Alexander and Stender Ponds, 2010- 2019. Data collection started on the same day, but recording stopped in Alexander Pond in January 2019, while recording continued in Stender Pond until November 2019.*

Using the best-fit Model 3, we evaluated the effects of air temperature on each of the four temperature states. We did not find that air temperature was a significant predictor of water temperature in any of the four states (Appendix II, Figure i). We also found that pond and creek temperatures do covary significantly, but the covariance is weak, indicating that pond and creek temperatures are mostly decoupled (Appendix II, Figure ii).

Finally, the wavelet analysis of Alexander and Stender Pond historical data indicated that both ponds had strong seasonal and daily temperature fluctuations and were highly correlated in in these fluctuations (Figure 3). However, in both ponds the strength of diel fluctuations (i.e., 24-h period, or day *vs.* night) decreased over the 9-year period of record (Figure 4).

Discussion

The MARSS model comparison supported hypothesis 3, which suggests that there are four temperature states or 'thermal regimes' in the mid-Klamath floodplain area: Seiad Creek ponds, Seiad Creek, Horse Creek ponds, and Horse Creek. According to the best-fit model, air temperature did not have a significant effect on water temperature, but we did identify significant covariance between the four states—meaning that some coordinated fluctuations exist. Overall, our results indicate that off-channel floodplain ponds do indeed add temperature diversity to the mid- Klamath River floodplain habitat. Wavelet analysis for the two oldest ponds also suggest that summer pond temperatures become more stable and fluctuated less over 9 years, likely representing stabilizing effects of ecosystem succession and the development of vegetation.

The different temperature patterns that we identified in Seiad Creek ponds, Seiad Creek, Horse Creek ponds, and Horse Creek illustrate how the ponds add to temperature diversity in the floodplain habitat. First, different tributaries (Seiad Creek and Horse Creek) have different temperature patterns. Seiad Creek is in a more densely populated area than Horse Creek and experiences more water abstractions. As a result, surface water on Seiad Creek disappeared for at least 2 km downstream of Stender Pond during the study period, while Horse Creek remained wetted throughout the length of the study area. The differences in water usage and surface water presence between the two tributaries likely contribute to differences in temperature patterns. Second, temperature patterns in ponds and tributaries covary slightly, but the significance of the relationship between in the two habitats is weak (Figure ii). This weak relationship indicates that although pond creek temperatures are connected, there is also some level of dissociation between temperatures in the two habitats. All ponds are partially fed by groundwater and are also much deeper than creeks, which may contribute to the decoupling of pond and creek temperatures.

Surprisingly, air temperature did not significantly influence water temperature in any of the ponds or creeks (Figure i). Although it is conceivable that pond temperatures are primarily driven by groundwater inputs, it was unexpected that the temperatures of shallow creeks are not significantly influenced by air temperature. It is possible that the location of the air temperature recording station did not accurately reflect the air temperature in the tributary valleys, and future data collection should include on-location air temperature measurements.

The diversity of temperature regimes identified in our analysis likely provides critical temperature refuges for juvenile salmonids. The existence of separate pond and creek temperature states shows that the ponds create an alternate temperature regime within the tributary watershed. This allows juvenile salmonids to access optimal water temperatures by moving between the pond and creek habitats, and creates a portfolio effect that buffers the salmonid population against temperature extremes (Schindler et al. 2010). Furthermore, although we did not place temperature sensors deeper than 1.5m, most of the ponds had a maximum depth of 2-3m, and water temperatures at that depth are likely cool and stable and further add to the temperature portfolio.

The importance of Klamath tributaries as cool-water refuges has already been established. A study that investigated juvenile salmonid foraging activity in the mainstem Klamath River and several tributaries found that while juvenile salmonids obtained most of their food from the mainstem, they spent most of their non-foraging time in the cool water refuge of tributary mouths (Brewitt, Danner, and Moore 2017). This indicates that a variety of temperature regimes and foraging opportunities are essential to healthy juvenile salmonid populations in this watershed. We suspect that the cool, stable temperatures of the off-channel ponds may function similarly to cool tributary mouths on the mainstem by providing a diversity of temperature and foraging options. Additionally, a more detailed study on juvenile salmonid movement between the mainstem Klamath River and the Beaver Creek tributary mouth indicated that juvenile salmonids moved into cooler water when mainstem temperatures exceeded about 22^{o}C (Sutton et al. 2007). While tributary temperatures recorded during our study period rarely exceeded the

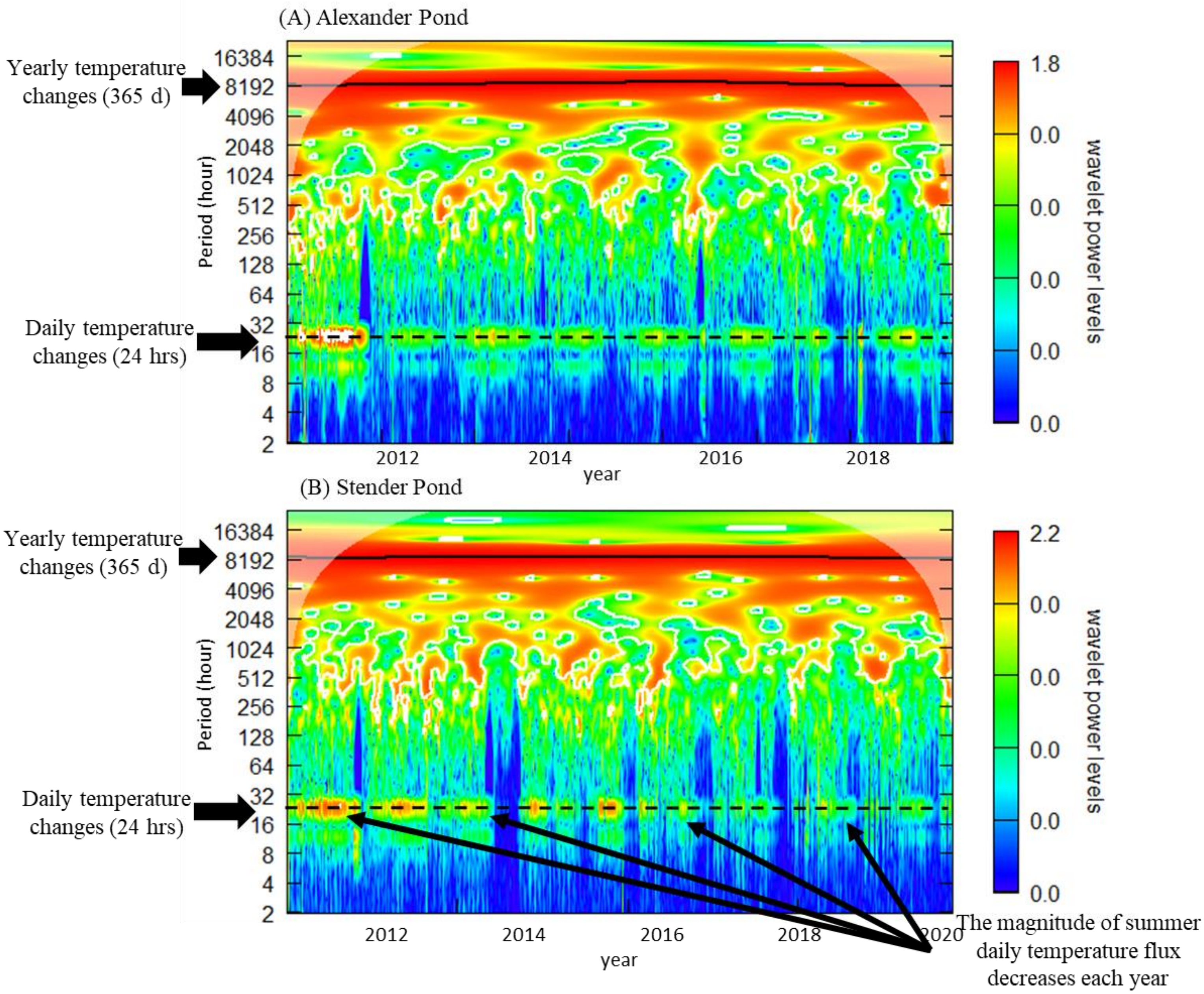


***Figure 4**: Diel fluctuations in temperature in (A) Alexander Pond and (B) Stender Pond decreased over 9 years, especially in the summer, likely as a result of increased canopy cover. This wavelet diagram shows the amplitude of these fluctuations on an hourly scale. In this diagram, the y-axis represents "frequency", or periodicity, in hours (for example, there are significant temperature changes in a 24-hour period), and the x-axis represents "location", or time, in years. Colors represent the strength of a recurring temperature fluctuation, against a background of red noise (positive temporal autocorrelation): red represents strong positive autocorrelation at a given period and time (for example, the strongest temperature fluctuation occurs at a 1-year period, or every ~8,760 hours).*

22°C threshold, it is conceivable that some juvenile salmonids in the tributary would seek cooler water and more stable temperatures in the off-channel ponds. Additionally, mainstem temperatures exceeded 24°C during our study period (data not presented), and it is likely that at least some salmonids taking refuge in tributary mouths would move upstream to the ponds. Cool, stable water temperatures are also critical to fish trapped in the ponds if outflow channels dry up in the summer (Lower Seiad, Durazo, and Stender outflows were dry in July 2020).

The two oldest off-channel ponds developed more stable summer temperatures over time. This is somewhat evident in Figure 3, where the "fuzziness" of the lines (caused by diel fluctuations in temperature) decrease over the years. We examined this trend with wavelet analysis of hourly temperature data from 2010-2019 in Alexander and Stender Ponds, which showed that the diel amplitude in the summer decreased over the 9-year period (Figure 4). The downward trend in daily temperature fluctuations was also observed by MKWC in their off-channel habitat case study monitoring reports for Alexander and Stender ponds (MKWC 2020; Wickman et al. 2020), and our wavelet analysis confirms this pattern. As suggested by the MKWC reports, we suspect the growth of riparian vegetation and development of a well-shaded canopy after pond construction contributed to this stabilizing pattern.

Adequate canopy cover is often considered beneficial for salmonids, but some studies in the lower Klamath have shown that the biomass of adult trout increases when canopy cover decreases (Wilzbach et al. 2005). However, this pattern was only observed for mature trout, and most of the salmonids using the off-channel ponds in our study are young of the year Coho Salmon that do not usually stay in the system longer than one year (Toz Soto, personal communication). Although we did not analyze data to substantiate this relationship, we suspect that a modest increase in canopy cover may be beneficial in this case because it creates cooler and more stable water temperatures in the summer, when creek temperatures tend to be most stressful.

Future Monitoring

Our study supports the notion that constructed, off-channel floodplain ponds can increase the diversity of thermal regimes in the Klamath watershed. As warm water temperatures and dam-altered flows continue to impact fish movement and fitness, and plans for dam removal move slowly, the construction of off-channel ponds may be a valuable restoration technique for creating much-needed salmonid habitat. Additionally, our analysis highlights how thermal regimes change over time, with canopy cover likely contributing to stabilize pond water temperatures. As new ponds are constructed in other areas of the watershed, planting of native riparian vegetation after construction may accelerate the restoration of thermal refugia.

Future studies should focus on connecting temperature patterns in the ponds and creeks with fish population and movement data. Extensive fish population monitoring by the Karuk Tribe has generated a rich dataset of salmon population, diversity, and age structure in these ponds and creeks. Although we did not analyze the Tribal fish dataset in this study, we acknowledge that such information could be combined with temperature data to provide valuable insights to how and why salmonids use the ponds.

Detailed foraging and movement studies would also contribute to our understanding of how the ponds benefit fish. As suggested in the MKWC monitoring report for Alexander Pond (Wickman et al. 2020), the reduction in daily temperature fluctuations in the pond allows for metabolic savings for Coho Salmon, but the details of fish movement between pond and creek habitats and the impact on metabolism is not fully understood. Fish movement and foraging studies have been conducted in the mainstem Klamath and tributary mouths that show fish tend to feed in the mainstem Klamath but spent most of their time in the cooler tributary mouths, and we suspect similar patterns may occur between tributaries and off-channel ponds (e.g. Brewitt et al 2017; Sutton et al. 2007). One way to examine the mechanisms at play would be to install PIT arrays at the outflow of the ponds year-round, which would substantiate fish movement and behavior during the summer, when cool ponds become important refuges.

Conclusions

We found different temperature patterns or 'thermal regimes' in Seiad Creek, Seiad Creek ponds, Horse Creek, and Horse Creek ponds, which indicates that off-channel ponds contribute significant temperature diversity to the mid-Klamath floodplain habitat. We also found that daily fluctuations in water temperature in ponds decreased over time, likely due to ecosystem succession and an associated increase in canopy cover in the years following pond construction. Further studies should connect temperature patterns with fish population and movement data and examine the mechanisms that may stimulate fish to use constructed, off-channel ponds as refugia. Overall, this preliminary analysis characterizes the thermal benefits of off-channel floodplain ponds in the mid-Klamath river. We hope it will support and inform future construction of additional ponds and the collection of fish population and movement data.

Acknowledgements

Data for this project was collected on Karuk ancestral land, and the initial report was prepared for the Karuk Tribe Fisheries Program. We are grateful to Susan Fricke with the Karuk Tribe and the Klamath Basin Monitoring Program for providing essential background information and logistical support. We are also grateful to Will Harling, James Peterson, Charles Wickman, and Mitzi Wickman at MKWC for providing historical temperature data. Grant Johnson with the Karuk Tribe assisted with data acquisition and freezer space. Laurel Genzoli at the University of Montana and Kyle Leathers at UC Berkeley assisted in data collection. This project was funded in part by the UC Berkeley ESPM Starter Grant. The author is funded by the National Science Foundation GRFP and the Berkeley Fellowship. Cover photo by J. Moravek.

References

Bellmore, J Ryan, Colden V Baxter, Kyle Martens, and Patrick J Connolly. 2013. “The Floodplain Food Web Mosaic: A Study of Its Importance to Salmon and Steelhead with Implications for Their Recovery.” *Ecological Applications* 23 (1): 189–207.

Brewitt, Kimberly S, Eric M Danner, and Jonathan W Moore. 2017. “Hot Eats and Cool Creeks: Juvenile Pacific Salmonids Use Mainstem Prey While in Thermal Refuges.” *Canadian Journal of Fisheries and Aquatic Sciences* 74 (10): 1588–1602.

Burnham, Kenneth P, and David R Anderson. 2002. “A Practical Information-Theoretic Approach.” *Model Selection and Multimodel Inference, 2nd Ed. Springer, New York* 2.

Holmes, Eli, Eric Ward, and K Wills. 2014. “MARSS: Multivariate Autoregressive State-Space Modeling.” *R Package Version 3.9*. http://cran.r–project.org/web/ package/MARSS.

Ives, Anthony R, B Dennis, K L Cottingham, and S R Carpenter. 2003. “Estimating Community Stability and Ecological Interactions from Time-series Data.” *Ecological Monographs* 73 (2): 301–30.

Jeffres, Carson A, Eric J Holmes, Ted R Sommer, and Jacob V E Katz. 2020. “Detrital Food Web Contributes to Aquatic Ecosystem Productivity and Rapid Salmon Growth in a Managed Floodplain.” *Plos One* 15 (9): e0216019.

Knape, Jonas, and Perry de Valpine. 2012. “Are Patterns of Density Dependence in the Global Population Dynamics Database Driven by Uncertainty about Population Abundance?” *Ecology Letters* 15 (1): 17–23.

MKWC. 2020. “Stender Pond Monitoring Report.” *Off Channel Habitat Case Study*.

NOAA (National Oceanic and Atmospheric Administration). 2020. “Climate Data Online. Siskiyou County, CA. Slater Butte Station.” National Oceanic and Atmospheric Administration, United States Department Commerce. https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/locations/FIPS:06093/detail.

R Development Core Team. 2020. “R: A Language and Environment for Statistical Computing.” R Foundation for Statistical Computing, Vienna, Austria.

Roesch, Angi. 2018. “WaveletComp.” R package version 1.1. https://cran.r-project.org/web/packages/WaveletComp/WaveletComp.pdf.

Ruhí, Albert, Elizabeth E Holmes, John N Rinne, and John L Sabo. 2015. “Anomalous Droughts, Not Invasion, Decrease Persistence of Native Fishes in a Desert River.” *Global Change Biology* 21 (4): 1482–96.

Schindler, Daniel E, Ray Hilborn, Brandon Chasco, Christopher P Boatright, Thomas P Quinn, Lauren A Rogers, and Michael S Webster. 2010. “Population Diversity and the Portfolio Effect in an Exploited Species.” *Nature* 465 (7298): 609–12.

Sutton, Ronald J, Michael L Deas, Stacy K Tanaka, Toz Soto, and R Alex Corum. 2007. “Salmonid Observations at a Klamath River Thermal Refuge under Various Hydrological and Meteorological Conditions.” *River Research and Applications* 23 (7): 775–85.

Tonkin, Jonathan D, Michael T Bogan, Núria Bonada, Blanca Rios-Touma, and David A Lytle. 2017. “Seasonality and Predictability Shape Temporal Species Diversity.” *Ecology* 98 (5): 1201–16.

Tonolla, Diego, Vicenc Acuna, Urs Uehlinger, Thomas Frank, and Klement Tockner. 2010. “Thermal Heterogeneity in River Floodplains.” *Ecosystems* 13 (5): 727–40.

Torrence, Christopher, and Gilbert P Compo. 1998. “A Practical Guide to Wavelet Analysis.” *Bulletin of the American Meteorological Society* 79 (1): 61–78.

Ward, J V, and J A Stanford. 1995. “The Serial Discontinuity Concept: Extending the Model to Floodplain Rivers.” *Regulated Rivers: Research & Management* 10 (2-4): 159–68.

Wickman, Mitzi, Charles Wickman, and Will Harling. 2020. “Alexander Pond Monitoring Report.” *White Paper- Off Channel Habitat*.

Wilzbach, Margaret A, Bret C Harvey, Jason L White, and Rodney J Nakamoto. 2005. “Effects of Riparian Canopy Opening and Salmon Carcass Addition on the Abundance and Growth of Resident Salmonids.” *Canadian Journal of Fisheries and Aquatic Sciences* 62 (1): 58–67.

Winemiller, Kirk O, P B McIntyre, L Castello, E Fluet-Chouinard, T Giarrizzo, S Nam, I G Baird, W Darwall, N K Lujan, and I Harrison. 2016. “Balancing Hydropower and Biodiversity in the Amazon, Congo, and Mekong.” *Science* 351 (6269): 128–29.

Appendix I: MARSS and ARIMA

MARSS

The multivariate auto-regressive state space model (MARSS) is ideal for investigating environmental time series data because it takes advantage of temporal correlation in environmental variables to estimate how a particular driver affects environmental processes (Holmes, Ward, and Wills 2014)(Ives et al. 2003; Ruhí et al. 2015). The MARSS model also incorporates observation error, which may include sampling error, measurement error, and any other variability in the measurement of an environmental variable. Accounting for observation error is critical because it can drastically change our interpretation of the underlying environmental process (Knape and de Valpine 2012). The MARSS model is able to separate observation error from true process variability because observation error does not influence current or future temperatures, it only affects our measurements (Holmes, Ward, and Wills 2014). MARSS models can also incorporate environmental covariate data, which allows us to quantify the effects of external drivers on the process of interest (Ruhí et al. 2015). In our case, this allowed us to correct for variation in daily temperatures. We used the MARSS R-package (R Development Core Team 2020; Holmes, Ward, and Wills 2014). The MARSS model can be expressed as follows:

(Eqn 1) $X_t = BX_{t-1} + U + Cc_{t-4} + w_t$, where $w_t \sim MVN(0, Q)$ *(Process model)*

(Eqn 2) $Y_t = ZX_t + A + v_t$, where $v_t \sim MVN(0, R)$ *(Observation model)*

Most of these variables are expressed as matrices, which allows the model to handle multivariate data. X_t represents true process values over time (in this case, true water temperature), and Y_t represents temperature measurements over time as a function of X_t and c_{t-4}, which are environmental covariates (i.e. air temperature) that are lagged by four days (i.e. air temperature data from 3-24 July 2020). C is a matrix that describes the effects of the covariate on each state. B is an interaction matrix that models the effect of states on each other. U is a matrix of trends in true process values. w is a matrix of process error (i.e. white noise), and the process error at time t is a multivariate normal with mean 0 and covariance matrix Q. In the observation model (Eqn 2), Z is a matrix that defines the distribution of states in the dataset. A is a vector of trends or biases between sensors. v is a vector of observation errors, and the observation error at time t is a multivariate normal with mean 0 and covariance matrix R.

Process Model

Air temperature values from 3-24 July 2020 were used to populate the c matrix. The C matrix was set to “unequal”, since we expected the effects of air temperature on each sensor to depend on its location in the floodplain (i.e. state). We set the B matrix to “identity” because there were no density-dependent interactions between sensors or states. We set the U matrix to “zero” because the data was demeaned before being used in the MARSS model, thus removing any trends from the data. The Q matrix was set to “unconstrained” because we expected some covariance between sensors, especially those located in the same pond or tributary.

Observation Model

We set A to “zero” because our data was demeaned, so there were no biases in any particular sensor. We made the R matrix “diagonal and equal” because all the sensors were the same make and model, so we expected observation error to be the same across all sensors.

We manipulated the Z matrix to test our hypotheses. To test hypothesis 1 (eleven temperature states), we used a Z matrix (30x11) to group sensors by pond or creek. To test hypothesis 2 (two temperature states), the Z matrix (30x2) grouped ponds together and creeks together. For hypothesis 3 (four temperature states), the Z matrix (30x4) grouped ponds and creeks by tributary. To test hypothesis 4 (one temperature state), the Z matrix grouped all sensors together (30x1). We evaluated relative support for each model using Akaike’s Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002). We analyzed the effect of air temperature using 95% confidence intervals with 3000 bootstrap iterations.

ARIMA and Wavelets

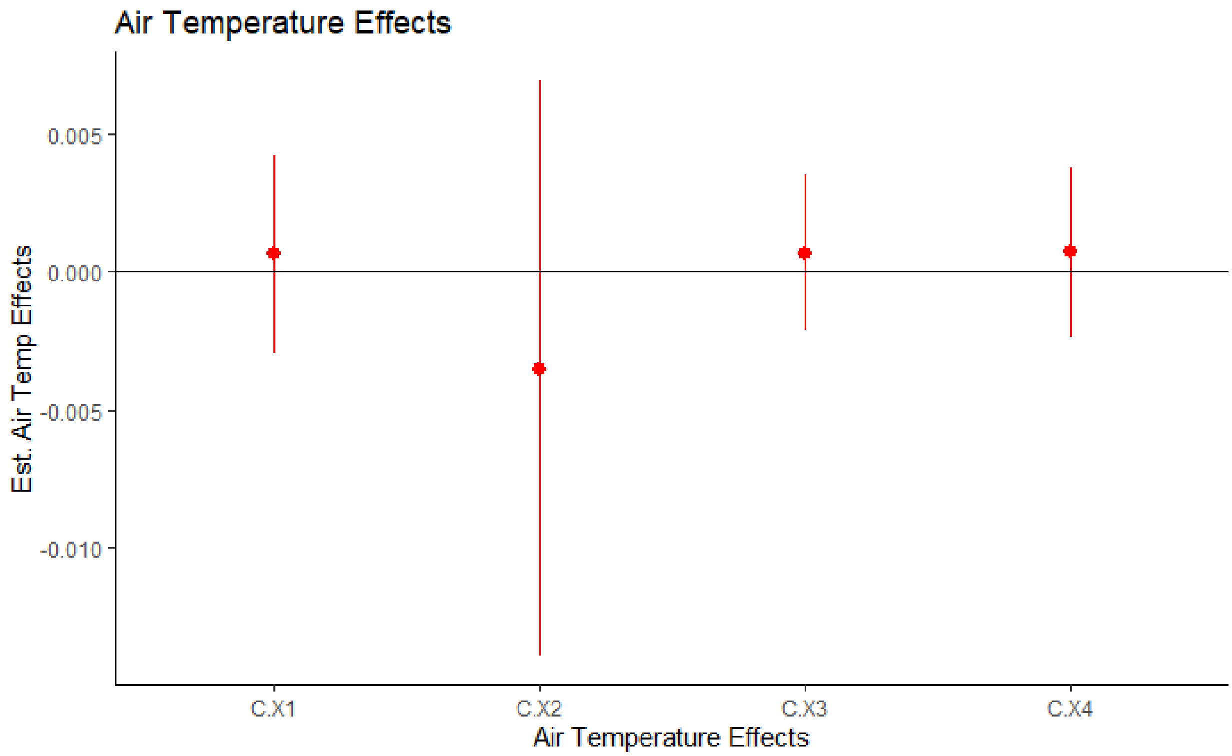
We used an autoregressive integrated moving average model (ARIMA) to interpolate missing data in historical temperature datasets. This model is generally expressed as ARIMA(p, d, q), where p is the order of the autoregressive model, i.e. the dependence of the model on prior values; d is the order of non-seasonal differences, i.e. degree of differencing of raw observations; and q is the order of the moving average, i.e. the model’s dependence on longer term values. After identifying the best-fit ARIMA model, we used the Kalman filter to interpolate missing data (Knape and de Valpine 2012), which was used in wavelet analyses.

Wavelet analysis allows us to identify the contribution to each frequency to the power of an environmental regime or pattern (Tonkin et al. 2017). This allows us to see how the power of a particular variable (for example, season) to influence an environmental regime (for example, water temperature) (Torrence and Compo 1998).

Appendix II: MARSS Covariates and Variance/Covariance

Air Temperature

Figure i: Maximum likelihood (ML) effect of air temperature on each state (Seiad Creek ponds, Seiad Creek, Horse Creek ponds, and Horse Creek, red dot) and 95% confidence intervals (lines). Air temperature did not have a significant effect on any of the ponds or creeks.



Variance and Covariance

For the best-fit model (Model 3), we found that variance and covariance (Q) were significant in all cases. "Diagonal" values (i.e. Q(1,1), Q(2,2), etc.) represent stochastic variation within a site, or variation that cannot be explained by covariates like air temperature (Figure iiA). "Off-diagonal" values (i.e. Q(1,2), etc.) represent spatial synchrony in stochastic variation between two sites (Figure iiB). For example, the covariance between state 3 (Horse Creek ponds) and state 1 (Seiad Creek ponds) is significant but weak. The covariance between state 2 (Horse Creek) and state 1 (Horse Creek ponds) is more strongly significant (Figure iiB).

Figure ii: (A) ML effect of stochastic variance (diagonals) in each site (red dot) and 95% confidence intervals (lines). (B) ML effect of stochastic covariance (off-diagonals) between sites (red dot) and 95% confidence intervals (lines). The black line in each figure is zero, and if the confidence intervals cross zero, the ML estimate is insignificant.