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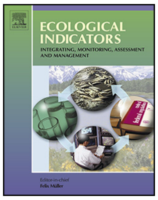

To aggregate or not? Capturing the spatio-temporal complexity of the thermal regime

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ABSTRACT

Freshwater stream systems are under immense pressure from various anthropogenic impacts, including climate change. Stream systems are increasingly being altered by changes to the magnitude, timing, frequency, and duration of their thermal regimes, which will have profound impacts on the life-history dynamics of resident biota within their home range. Although temperature regimes have a significant influence on the biology of instream fauna, large spatio-temporal temperature datasets are often reduced to a single metric at discrete locations and used to describe the thermal regime of a system; potentially leading to a significant loss of information crucial to stream management. Models are often used to extrapolate these metrics to unsampled locations, but it is unclear whether predicting actual daily temperatures or an aggregated metric of the temperature regime best describes the complexity of the thermal regime. We fit spatial statistical stream-network models (SSNMs), random forest and non-spatial linear models to stream temperature data from the Upper Condamine River in QLD, Australia and used them to semi-continuously predict metrics describing the magnitude, duration, and frequency of the thermal regime through space and time. We compared both daily and aggregated temperature metrics and found that SSNMs always had more predictive ability than the random forest models, but both models outperformed the non-spatial linear model. For metrics describing thermal magnitude and duration, aggregated predictions were most accurate, while metrics describing the frequency of heating events were better represented by metrics based on daily predictions generated using a SSNM. A more comprehensive representation of the spatio-temporal thermal regime allows researchers to explore new spatio-temporally explicit questions about the thermal regime. It also provides the information needed to generate a suite of ecologically meaningful metrics capturing multiple aspects of the thermal regime, which will increase our scientific understanding of how organisms respond to thermal cues and provide much-needed information for more effective management actions.

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1. Introduction

Spatio-temporal variation in water temperature is one of the most important factors influencing the dynamics of freshwater populations and communities (Jackson et al., 2001). Climate change impacts on temperature are predicted to be particularly profound for aquatic ecosystems. Warming air temperatures, increased thermal variability and changing precipitation are likely to result in increased water temperatures, altered stream hydrology, and changes in the frequency, magnitude, and extent of extreme climate events including floods and droughts (Jentsch et al., 2007; Rieman and Isaak, 2010; Cahill et al., 2013). The biological implications of climate change are expected to be significant as physiological tolerances are exceeded, leading to fundamental changes in physiology and behaviour (Ebersole et al., 2003).

Temperature affects aquatic populations both directly and indirectly across local and broad geographic scales. Thermal tolerances of species help describe broad geographic patterns of occurrence, while thermal preferences acting at finer scales are often reflective of conditions that are optimal for growth, feeding and reproduction (Pankhurst and Munday, 2011). Given the current climate and

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expected rate of temperature increase, it is likely that the thermal regimes of streams will shift upwards and increase in variability. Altered thermal regimes are likely to exceed physiological thresholds and reduce the amount of thermally suitable habitat available to many aquatic species, having population and ecosystem wide consequences (Parmesan and Yohe, 2003; Pörtner and Farrell, 2008; Rieman and Isaak, 2010). As well as the direct physiological impact of increased temperature, higher water temperatures reduce oxygen availability which can have a direct impact on individuals. The combination of warmer temperatures and reduced oxygen can indirectly impact organisms through reduced fitness (Ficklin et al., 2013).

It is commonly accepted that the spatio-temporal variability of both physical and biological components within ecological systems is important for ecosystem integrity (Gomi et al., 2002; Thorp et al., 2006). Historically, limitations on the spatial and temporal density of stream temperature datasets may have limited our ability to capture the full spatio-temporal complexity of the thermal regime. However, advancements in in-stream sensor technology, along with reduced prices, have increased the number and rate at which data loggers have been deployed across large catchments globally. For example, the NorWeST database in the Pacific North-Western USA has over 15,000 unique locations collecting temperature readings across over 25,000 km^2 of fish bearing streams (Isaak et al., 2011). Such technological developments have led to the proliferation of data available to stream ecologists. Unfortunately, these 'big data' are often aggregated over time and reduced to a single temperature metric (e.g. weekly, monthly, seasonal means or maximums or instantaneous maxima or minima) at discrete locations. When semi-continuous data are reduced to aggregated metrics, information about specific aspects of the thermal regime (e.g. magnitude, frequency, duration, timing, or variability) may be lost, which are important for management decisions as key drivers of ecological processes (Mohseni et al., 1998; Moore et al., 2013). Aggregated metrics are likely an oversimplification of the underlying thermal processes occurring in stream ecosystems and potentially lack biological and ecological significance (Arismendi et al., 2013; Butryn et al., 2013). Various methods have been used to predict stream temperature from measured locations to unsampled locations including spatial stream-network models (SSNMs) (Isaak et al., 2010; Ruesch et al., 2012; A. Steel, personal communication), non-spatial regression-based models (Mohseni et al., 1998) and machine learning methods (Chenard and Caissie, 2008), but it is unclear whether a loss of information occurs when data are aggregated through time and single metrics are subsequently extrapolated through space. An alternate approach would be to use the full spatio-temporal dataset to make daily predictions at unsampled locations throughout a network. These daily predictions could then be used to generate a semi-continuous coverage of ecologically and biologically relevant temperature metrics throughout the network. However, to our knowledge this approach has not been implemented in stream systems. Given that anthropogenic stressors related to land-use and climate change are likely to synergistically alter the temporal regime in important headwater habitats (Piggott et al., 2012), there is an urgent need to make full use of the 'big data' being collected by new sensor technologies.

Our goal was to compare a suite of methods used to generate stream temperature metrics to determine whether spatially and temporally dense stream temperature data can be used to better describe the magnitude, frequency, and duration of the thermal regime throughout a stream network. We used SSNMs, random forest and non-spatial linear models to predict five temperature metrics throughout the Upper Condamine River catchment, Queensland (QLD), Australia. Temperature metrics at unsampled locations were generated using two different approaches; first, we fit models to maximum daily temperature at sampled locations and predicted maximum daily temperature at unsampled locations. These daily predictions were then used to generate metrics at unsampled locations (i.e. daily metrics). Then, models were fit to metrics generated from daily maximum temperature measurements at sampled locations and used to predict metrics, rather than daily temperatures at unsampled locations (i.e. aggregated metrics) (Fig. 1). The three models and two metric-based generation approaches were compared to determine whether (1) models based on daily or aggregated metrics had greater predictive ability; (2) the predictive ability of the metric-generation approach differed depending on the type of stream temperature metric (magnitude, frequency, or duration); and (3) one model type had more predictive ability than the others, depending on the metric type and metric-generation approach.

2. Methods

2.1. Study area

The Condamine River catchment in southern QLD spans an area of approximately 29,150 km^2. The study area is located in the upper Condamine River and Spring Creek tributaries, QLD, Australia, with the elevation ranging between 507 m at Killarney up to 900 m above

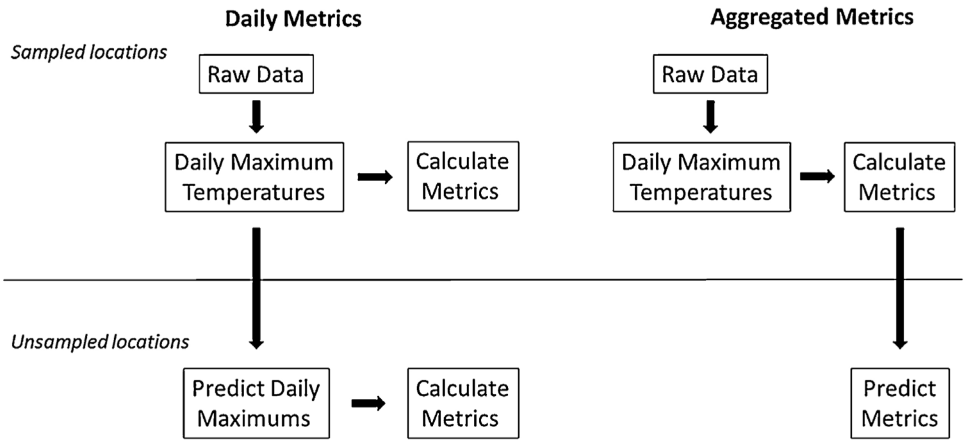

Fig. 1. Conceptual flowchart visualising the process of calculating daily (left) and aggregated (right) temperature metrics. Daily metrics were generated from daily maximum stream-temperature observations and predictions, at sampled and unsampled locations respectively. In contrast, aggregated metrics were generated using maximum stream-temperature observations at sampled locations and then the temperature metric was predicted at unsampled locations.

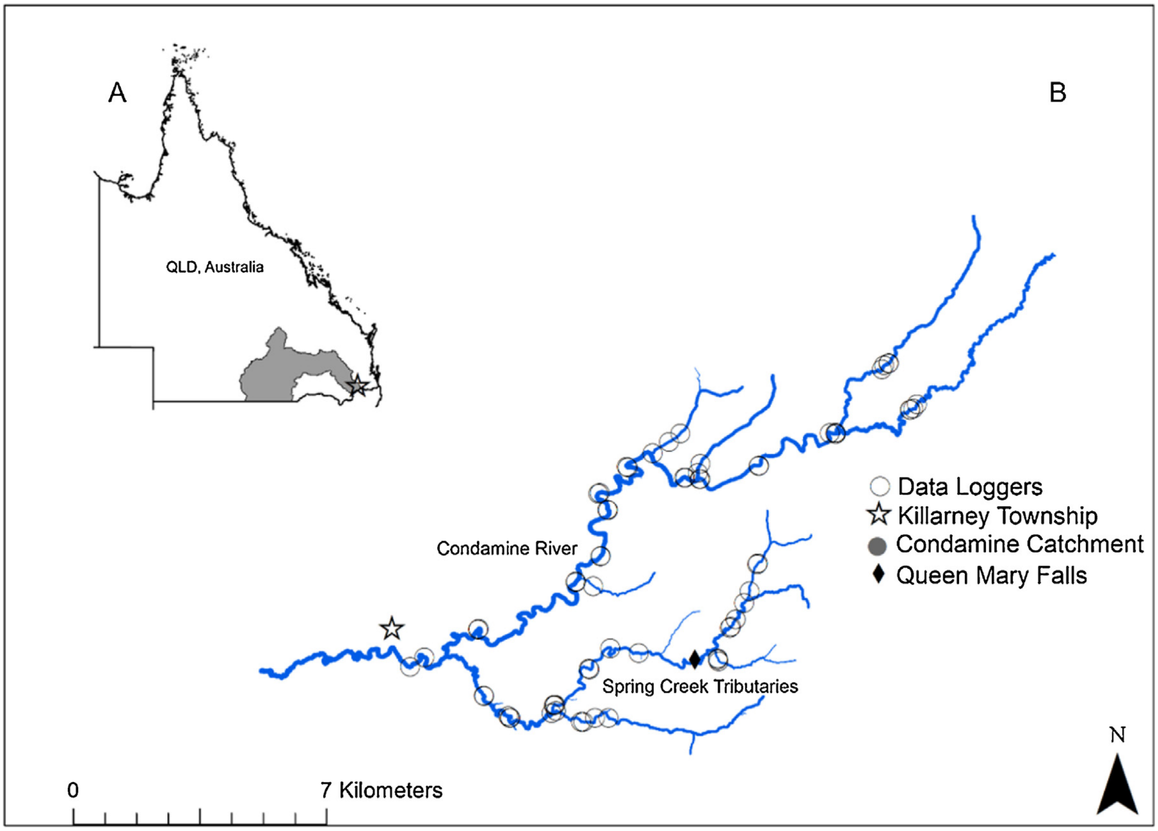

Fig. 2. The study site lies within the Condamine catchment, Queensland, Australia (A). Temperature data loggers were installed throughout the upper Condamine River and Spring Creek sub-catchments during the summer of 2013 (B). Streamlines are drawn in proportion to their catchment area.

Queen Mary Falls (Fig. 2). It ranges from Killarney in the southeast to past Chinchilla in the northwest; with the Great Dividing Range bordering the northern and eastern boundary and Herries Ridge forming the southern and western boundary. Much of the region is used for agriculture (cropping and grazing) due to the highly fertile soils, while the regional climate is typified by dry, cold winters with an average minimum temperature of 5 °C. Summer days are hot with temperatures often exceeding 35 °C. Most rainfall occurs over the austral summer period between November and March and the mean annual rainfall for Killarney is around 750 mm per year (Bureau of Meteorology, 2014).

2.2. Field methods

A total of 60 stream temperature data loggers (UTBI-001 Tidbit V2 Data loggers, Onset Computer Corporation, Massachusetts, USA; accuracy = ±0.2 °C) were deployed during the first week of December, 2013 (Fig. 2) and were pre-programmed to record stream temperature on an hourly basis. The stream bed was rocky in many places and so steel fencing stakes were driven into the substrate and used as attachment sites for loggers. Sensors were held in place between 15 and 30 cm below the water surface with galvanised 3 mm wire and zip ties. Data loggers were housed in a white PVC housing made up of 50 mm PVC pipe with push on caps (Isaak and Horan, 2011). A minimum of 8 mm × 6 mm holes were drilled into the pipe and end-caps to ensure adequate water flow to the sensor as recommended by the US Forest Service (D. Isaak, personal communication). Data were downloaded from loggers throughout March of 2014, which provided a minimum of 80 full days of temperature recordings throughout the austral summer period. All temperature data were manually screened to identify dewatering events and logger malfunctions as recommended by Sowder and Steel (2012) and Dunham et al. (2005).

2.3. Temperature metrics

We selected five temperature metrics that are often considered biologically relevant for this study. Maximum summer temperatures are most likely to affect species in headwater systems and so we included the following metrics: (1) highest instantaneous summer temperature (Max); (2) the maximum weekly maximum temperature (MWMT), which is the highest seven-day moving average of the daily maximum temperature; (3) mean-summer maximum temperature (Mean Max); (4) thermal event days (Event Days), which describes the longest duration of consecutive days exceeding a threshold of 26 °C; and (5) the total number of days where the maximum daily temperature exceeded a threshold of 26 °C (Frequency Days). A threshold value of 26 °C was chosen to represent an approximate thermal suitability for multiple species within the region (Balcombe et al., 2011). These metrics of thermal magnitude, frequency, and duration of heating events within the thermal regime (Table 1) provide an indicator of the general thermal suitability of the streams throughout summer, as well as the degree of thermal stress exerted on species inhabiting these headwater streams throughout summer extremes. We used two different methods to calculate the five metrics. "Daily metrics" were generated from daily maximum stream-temperature observations and predictions, at sampled and unsampled locations respectively. In contrast, "aggregated metrics" were generated using maximum stream-temperature observations at sampled locations and then the temperature metric was predicted at unsampled locations. All metrics were calculated using customised scripts in R statistical software (R Development Core Team, 2014).

Table 1
Stream temperature metrics describing aspects of the thermal regime including magnitude, duration and frequency.

Metric	Aspect of thermal regime	Description
Max	Magnitude	Highest instantaneous summer temperature
MWMT	Magnitude	Maximum weekly maximum temperature. The highest 7 day moving average of daily maximum temperatures
Mean Max	Magnitude	The mean summer maximum temperature
Event Days	Duration	The number of successive days stream temperature exceeds a pre-defined threshold of 26 °C
Frequency Days	Frequency	The total number of days throughout the study period in which temperature exceeded a pre-defined threshold of 26 °C

2.4. GIS methods

Digital streams data (1:25,000) were provided by the Department of Natural Resources and Mines (2010). The spatial coordinates for temperature logger sites were imported into a geographic information system (GIS) and manually “snapped” to the stream layer to ensure that the sample site coincided with the stream lines. A 10 m Digital Elevation Model (DEM) raster was derived from 1:25,000 contour data using the Topo to Raster tool in the ArcGIS 3D Analyst toolbox (ESRI, 2012). Note that, all other raster datasets used in this study were resampled to match the spatial resolution of the DEM. Streams were converted to raster format and ‘burned in’ to the DEM to ensure that DEM-delineated flow paths coincided with stream lines (e.g. Peterson et al., 2011). All GIS analyses were performed in ArcGIS version 10.1 (ESRI, 2012).

A total of 195,040 prediction sites were also created at daily time steps and 50 m intervals along the stream network using ETGeowizards (Tchoukanski, 2009). These sites represented 2438 unique locations, with 80 repeated measures, which provided a semi-continuous spatio-temporal coverage of unsampled locations throughout the entire Upper Condamine River and Spring Creek tributaries. Additional spatial data needed to fit a SSNM (e.g. pairwise in-stream distances and spatial weights) were generated using the Spatial Tools for the Analysis of Rivers Systems (STARS) custom ArcGIS toolset (Peterson and Ver Hoef, 2014).

2.5. Predictor variables

Site-scale elevation (Isaak and Hubert, 2001) and air temperature (Stefan and Preud’Homme, 1993; Mohseni et al., 1998; Caissie et al., 2005) have been found to be strongly correlated with water temperature in previous studies. Elevation was extracted from the DEM at each observed logger site and unobserved prediction site throughout the stream network. We obtained site-scale maximum air temperature estimates from the Scientific Information for Land Owners (SILO) Data Drill (Jeffrey et al., 2001). We chose to include air temperature even though it had a relatively coarse spatial resolution (5 km^2) because our primary goal was to explain temporal variability in daily maximum temperatures, rather than spatial variability.

Shade cover moderates stream temperature and is arguably one of the most important ecological services that riparian vegetation provides (Beschta, 1997; Johnson, 2004). Foliage Projective Cover (FPC) was obtained from the 2010 Statewide Landcover and Tree Study (SLATS) (Kuhnell et al., 1998) and used to derive rasters representing riparian cover and shading. A moving-average function was used to generate the mean FPC cover for each cell based on the four nearest raster cells. Site-scale canopy cover was then extracted at both observed and prediction sites. Research has suggested that shaded patches in the riparian zone must be approximately 500–1000 m in length upstream from a site for headwater streams systems in Australia to reach temperature equilibrium (Rutherford et al., 2004). Therefore, we calculated an upstream shading variable, which represented the mean FPC within a 10 m riparian buffer, extending 1 km upstream from each observed and prediction site (for further details see Appendix).

Grazing of native and introduced pastures is the primary land use throughout the upper Condamine (BRS, 2002) and grazing has been shown to contribute to riparian degradation, reductions in stream shading and an overall increase in stream temperatures (Beschta, 1997; Isaak and Hubert, 2001). We reclassed the 2006 Queensland Land Use Mapping Programme (QLUMP) dataset to generate a raster dataset of grazed land. Grazed land use included native, introduced and modified pastures as categorised by the Australian Land Use and Management (ALUM) Classification Version 7 (BRS, 2002). The grazing raster was used to generate a hydrologically active, inverse-distance weighted (IDW-HA) land-use metric for each observed and prediction site (Peterson et al., 2011):

$$\%\mathrm{LU} = \frac{\sum_{i=1}^{n} I(k) W_i(\mathrm{FA}_i + 1)}{\sum_{i=1}^{n} W_i(\mathrm{FA}_i + 1)} \times 100, \tag{1}$$

where $\%LU$ represents the percent grazed land use in the catchment. Here, $I(k)$ is an indicator equal to 1 if cell i contains grazed land and 0 for other land uses and n is the number of cells in the catchment. W_i is the distance-based weighting function, $(d+1)^{-0.75}$, where distance, d, is represented using flow length to the stream and FA_i represents the flow accumulation value at each cell plus 1, so that all $\mathrm{FA}_i \geq 1$. We chose to use IDW-HA metrics rather than non-spatial, lumped catchment metrics because IDW-HA metrics account for the greater influence of grazed areas in close proximity to the stream or areas prone to higher overland flows (Peterson et al., 2011; Sheldon et al., 2012). In addition, we chose a $(d+1)^{-0.75}$ inverse-distance weighting scheme because it creates a smooth transition in weights near the stream, where both land use and riparian vegetation are known to significantly influence instream condition and temperature in small upland systems (Gregory et al., 1991).

Direct solar radiation is generally recognised as one of the major factors controlling stream temperatures (Stefan and Preud’Homme, 1993; Johnson, 2003; Caissie, 2006). A 10 m raster of solar radiation was generated in ArcGIS 10.1 (ESRI, 2012) for the summer period in which our stream temperature loggers were deployed and site-scale solar radiation values (kWh/m^2) were extracted for all observed and prediction sites. Stream aspect has also been used as a surrogate for direct solar radiation and has been shown to influence stream temperature (Bourque and Pomeroy, 2001; Isaak and Hubert, 2001). Therefore, we generated a categorical stream aspect variable for streams bearing North-South (0–45°, 135–225°, and 315–360°), and East-West (45–135° and 225–315°).

2.6. Statistical methods

We fit SSNMs to five temperature metrics (Table 1), which were generated using two different approaches. First, we fit SSNMs models to daily maximum stream temperatures at observed sites and used the predictions to generate temperature metrics (daily metrics). We then used the daily maximum stream temperatures at observed sites to generate temperature metrics (aggregated metrics) and fit models to the metrics themselves. This allowed us to determine whether a loss of information occurred when the aggregated metrics were directly modelled and predicted rather than calculated them from daily predictions at unsampled locations. Furthermore, we compared the predictive performance and accuracy of SSNM predictions to aggregated and daily temperature metrics generated using random forest and non-spatial linear models for both daily and aggregated metrics, which allowed us to determine whether accounting for spatial autocorrelation in the temperature data improved the predictive ability of our models, and whether this differed depending on the metric generation approach and the type of temperature metric (e.g. duration, frequency, or magnitude). In total, we fit 30 models (three methods × five temperature metrics × two metric types) and all statistical analyses were implemented using R statistical software version 3.1.3 (R Development Core Team, 2014).

2.6.1. Spatial statistical stream-network models

Temperature data collected throughout stream networks are often spatially correlated (Peterson et al., 2006; Isaak et al., 2010; Ruesch et al., 2012). Spatial statistical stream-network models can be used to describe patterns of spatial autocorrelation across these dendritic, complex networks (Ver Hoef et al., 2006; Ver Hoef and Peterson, 2010). These methods are different than traditional spatial-statistical methods because they are based on hydrological (i.e. in-stream distance) rather than Euclidean distance and allow for discontinuities at confluences; as such, they account for the spatial configuration of the network, longitudinal connectivity, and directionality of streams. Spatial statistical methods are also useful because they can be used to make predictions at un-sampled locations, with site-specific estimates of uncertainty, and can be used to model a variety of stream data including water quality, biological data and habitat conditions (Isaak et al., 2014).

The "tail-up" and "tail-down" autocovariance models were developed to account for two types of spatial relationships based on hydrologic distance: flow-connected and flow-unconnected (Ver Hoef and Peterson, 2010). A pair of locations is considered flow-connected if water flows from an upstream site to a downstream site. In contrast, a pair of locations is flow-unconnected if they reside on the same network, but do not share flow. However, the way that the two autocovariance models represent these relationships is different. Tail-up autocovariance models restrict spatial autocorrelation to flow-connected sites, and are allocated spatial weights to account for the disproportionate influence that converging tributaries may have on downstream reaches. Tail-down autocovariance models allow spatial autocorrelation between both flow-connected and flow-unconnected locations, given they share a common downstream outlet (Peterson and Ver Hoef, 2010).

Spatial statistical models are simply an extension of the basic linear model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon} \tag{2}$$

where $\mathbf{y}$ is a vector of the response variable (e.g. maximum temperature), $\mathbf{X}$ is a matrix containing predictor variables, $\boldsymbol{\beta}$ is a vector of regression coefficients and $\boldsymbol{\varepsilon}$ is a vector of independent random errors. However, streams data often exhibit multiple patterns of spatial autocorrelation due to a variety of terrestrial and aquatic processes operating at multiple scales (Peterson et al., 2006). As such, autocovariance models for streams are often combined with Euclidean autocovariance models using a variance component approach. This is accomplished by decomposing $\boldsymbol{\varepsilon}$ into multiple random effects, $\mathbf{z}$:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{z}_{\mathrm{EUC}} + \mathbf{z}_{\mathrm{TD}} + \mathbf{z}_{\mathrm{TU}} + \mathbf{z}_{\mathrm{NUG}}. \tag{3}$$

Here, $\mathbf{z}_{\mathrm{EUC}}$, $\mathbf{z}_{\mathrm{TD}}$, and $\mathbf{z}_{\mathrm{TU}}$, are vectors of zero-mean random variables with an autocovariance structure based on the Euclidean, tail-down, and tail-up autocovariance models, respectively, and $\mathbf{z}_{\mathrm{NUG}}$ is a vector of independent random errors. Thus, a mixed covariance structure (TU, TD, EUC) provides a flexible way to model multiple patterns of spatial autocorrelation within a single model (Peterson and Ver Hoef, 2010).

2.6.2. SSNM model fitting and selection

Prior to fitting SSNMs, all predictors were checked for collinearity. No predictor variables had a Spearman's rank correlation coefficient greater than 0.6 and thus all predictors were kept for further analyses. Three potential global outliers were identified and removed from all models and further analyses. In addition, 4 outliers were removed for Event Days and 3 for Frequency Days in the aggregated metric models. The sites identified as outliers in the aggregated models were also removed from the daily prediction models to ensure comparability between daily and aggregated prediction results.

SSNMs were fitted to a total of 4800 maximum daily measurements (60 sites × 80 daily measures) and potential predictor variables. All SSNMs were fitted with the following mixed covariance structure: Mariah tail-up, linear-with-sill tail-down and the exponential Euclidean models. A unique location identifier (locID) was also included as a random effect to account for repeated (i.e. daily) measurements at observed sites. We chose to use a backwards stepwise-model selection strategy so that we could assess model residuals for normality at each step. The parameter estimates were calculated using maximum likelihood (ML) rather than restricted maximum likelihood (REML) during the predictor selection process because we wanted to use Akaike's information criterion (AIC) (Akaike, 1974) for model selection and REML cannot be used with information criteria when fixed effects are changing (Verbeke and Molenberghs, 2009). We compared the model fit and predictive ability of the models based on the AIC score and the root-mean-squared prediction error (RMSPE) for the daily temperature observations and a set of leave-one-out cross-validation (LOOCV) predictions. We did not use a model selection process to select the individual components in the covariance mixture because previous research has shown that representing the correct components (e.g. TU, TD, and EUC) was more important than choosing a particular covariance model within a component (Frieden et al., 2014). All SSNMs were fit in R statistical software version 3.1.3 (R Development Core Team, 2014), using the SSN package (Ver Hoef et al., 2014).

Once we identified the best set of predictor variables based on AIC and RMSPE, the final model was refit using REML for parameter estimation, before making predictions. We then used spatial and temporal cross validation to gain insight into the predictive ability of the final SSNM in both space and time. First, we evaluated the SSNMs ability to make maximum daily temperature predictions at unobserved locations (i.e. spatial cross-validation) by iteratively removing all measurements at each observed site ($n = 80$ daily measurements at a site) refitting the model to the remaining data, and making daily predictions at the missing location (60 sites = 60 models). Next, we evaluated the SSNMs ability to predict at unobserved times steps using a similar approach (i.e. temporal cross-validation); we iteratively removed all measurements at each time step ($n = 60$ sites at each time step), refitted the model to the remaining data, and made a daily prediction at all sites within a time step (80 time steps = 80 models). Pearson's squared-correlation coefficient was calculated based on the observations and the cross validation predictions (predictive r^2), as well as the RMSPE for the observations and the cross-validation predictions. Daily maximum stream-temperature predictions were then used to generate the five daily metrics (Table 1) at each observed site.

Fitting a SSNM model to a large spatio-temporal stream temperature dataset requires a significant amount of GIS processing and can be computationally intensive (Rushworth et al., 2015). All of the models described here were fit on a high performance computing (HPC) cluster due to the large number of observations and models fit during the cross-validation procedures. However, it is unclear whether fitting models to daily temperature observations, making predictions at unobserved locations, and then using those predictions to generate metrics of the thermal regime increases the predictive performance of the models. Therefore, we also fit SSNMs to five aggregated temperature metrics which were generated from the daily maximum temperature observations at each logger site. Models were fit to each of the five metrics, using the same predictor variables as the final SSNM used to predict daily maximum temperatures. We used spatial cross-validation to evaluate the predictive ability of the five models (60 sites = 60 models × 5 metrics = 300 models) based on the predictive r^2, while the RMSPE was calculated from the observations and the cross-validation predictions. Note that the Event and Frequency Days metrics were based on counts, and so these SSNMs were fitted using the Poisson distribution, with a log-link function.

2.6.3. *Random forest and non-spatial model fitting*

To compare the predictive performance of the SSNMs, we fit a suite of random forest and non-spatial linear models to the (1) daily maximum temperatures and (2) five aggregated temperature metrics.

Random forest models were fit to daily maximum stream-temperature using the same predictor variables as the final SSNM for daily maximum temperature. The models included 1000 trees, 1 variable randomly sampled at each split, and sampling with replacement. Note, that error plots of the random forest model showed significant error stabilisation after only 300 trees and thus tree numbers were kept at 1000. All random forest models were fit using the randomForest package (Liaw and Wiener, 2002) in R (R Development Core Team, 2014).

Non-spatial linear models were also fit to daily maximum stream-temperature using the same set of predictor variables as the final SSNM. The predictive r^2 and the RMSPE were generated from spatial and temporal LOOCV and were used to assess the predictive ability of the daily maximum stream temperature models. The spatial LOOCV predictions were then used to generate estimates of the five daily temperature metrics (Table 1) at each logger site for non-spatial linear models, random forest and SSNMs. The predictive r^2 and the RMSPE were calculated for the daily metric predictions and the observed metrics.

Random forest and non-spatial linear models were also fit to the five aggregated temperature metrics generated from observed data at the logger sites. Non-spatial linear models for Event and Frequency Days metrics were fit using the Poisson distribution, with a log-link function. A spatial LOOCV was performed on the aggregated metric models and the predictive r^2 and RMSPE were calculated from the observations and the spatial LOOCV predictions.

3. Results

3.1. *Daily maximum stream temperature models*

Four predictors were included in the final SSNM for daily maximum stream-temperature: maximum daily air-temperature, elevation, upstream shading, and direct foliage cover at a site (Table 2). All of the statistical relationships in the model made ecological sense; air temperature had a positive relationship with stream temperature, while increases in elevation, upstream shading, and direct foliage cover had a negative influence on temperature.

Table 2
Model summary for the final spatial stream-network model, including predictor variables, parameter estimates, standard errors, *t*-values, and *p*-values. Airmax, maximum air temperature (°C); UpBuff, mean riparian shading1 km upstream within a10 m riparian buffer; Elev, elevation (m); FPC, Foliage Projective Cover (%).

	Estimate	Std. Error	*t* value	*Pr*(>|*t*|)
Intercept	20.147	2.804	7.185	<0.001*
Airmax	0.375	0.004	87.687	<0.001*
UpBuff	−0.038	0.015	−2.560	0.011*
Elev	−0.008	0.003	−2.111	0.035*
FPC	−0.018	0.006	−2.690	0.007*

* Significance at $p < 0.05$.

Table 3
A comparison of the predictive ability of the spatial stream-network (SSNM), random forest and non-spatial linear models ($n = 4800$). The predictive r^2 and root-mean-square prediction errors (RMSPE) for both spatial and temporal cross validation (CV) of daily maximum temperatures were based on the observations and the predictions from both the spatial and temporal cross validation (CV).

	Spatial CV		Temporal CV	
	Predictive r^2	RMSPE	Predictive r^2	RMSPE
SSNM	0.775	1.273	0.825	1.122
Random forest	0.631	1.643	0.810	1.177
Non-spatial	0.446	2.005	0.824	1.123

The residual error structure of the final daily maximum stream-temperature model showed that the tail-up proportion of the covariance structure explained the majority of the residual variation (49%), as expected for passive stream features (Isaak et al., 2010). The tail-down and Euclidean components represented relatively little of the variation (1.6% and 27.6%, respectively), while around 21% of the residual variation was attributed to the nugget effect, which describes spatial variance observed at a finer scale than the closest measurements and measurement error (Peterson and Ver Hoef, 2010). The random effect for site described 0.8% of the total residual variation.

There were clear differences in the predictive ability of the SSNM, random forest, and non-spatial linear models fit to daily maximum stream-temperature based on the spatial and temporal cross validation (Table 3). Spatial stream-network models significantly outperformed both the random forest and non-spatial models based on the spatial CV, with a higher predictive r^2 and lower RMSPE (Table 3). However, this was not the case for the temporal CV. The predictive ability of the SSNM and non-spatial model were almost identical, while both models had more predictive ability than the random forest model (Table 3). In addition, the results indicated that the predictive ability of all three models was lower when a spatial CV was used compared to the same models assessed in the temporal CV.

3.2. *Daily vs aggregated temperature metrics*

Aggregated SSNMs always had the best predictive ability comparative to both random forest and non-spatial linear models. In the case of Frequency Days metrics, the daily SSNM outperformed all of the other models, including the aggregated SSNM as indicated by a higher predictive r^2 and lower RMSPE values (Table 4). Random forest models outperformed non-spatial models when predicting the three metrics describing thermal magnitude (Max, MWMT, Mean Max), as well as Frequency Days in both daily and aggregated metrics. However, non-spatial models had improved predictive performance for Event Days metrics compared to random forest models (Table 4).

Aggregated metrics describing thermal magnitude (Max, MWMT, Mean Max) and duration (Event Days) had more predictive ability than models of daily temperature metrics for all models (Table 4). For metrics describing the frequency of heating events (Frequency Days), daily predictions generated using a SSNM improved the model's predictive performance and

Table 4
The root-mean-square prediction error and predictive r^2 (shown in parentheses) for the spatial stream-network models (SSNMs), random forest (RF) models, and non-spatial linear models, for both daily and aggregated temperature metrics. These values were based on the observations and the spatial cross-validation predictions. Metrics represent the highest instantaneous summer temperature (Max); the maximum weekly maximum temperature, the highest 7-day moving average of daily maximum temperatures (MWMT); the number of successive days stream temperature exceeded a pre-defined threshold of 26 °C (Event Days); and the total number of days throughout the study period in which temperature exceeded a pre-defined threshold of 26 °C (Frequency Days).

Model type	Model	Max	MWMT	Mean Max	Event Days	Frequency Days
Daily	SSNM	1.18 (0.81)	0.9 (0.87)	0.62 (0.9)	1.61 (0.75)	**7.82 (0.65)**
	RF	2.3 (0.59)	1.56 (0.61)	1.24 (0.61)	2.80 (0.26)	12.10 (0.25)
	Non-spatial	2.32 (0.15)	1.93 (0.27)	1.67 (0.32)	2.55 (0.29)	12.19 (0.14)
Aggregated	SSNM	**0.90 (0.86)**	**0.73 (0.89)**	**0.56 (0.92)**	**1.02 (0.89)**	10.64 (0.62)
	RF	1.72 (0.53)	1.46 (0.61)	1.29 (0.63)	2.03 (0.54)	8.21(0.58)
	Non-spatial	2.04 (0.29)	1.66 (0.44)	1.44 (0.48)	1.66 (0.69)	8.30 (0.58)

Bold indicates the best performing model for each temperature metric.

accuracy compared to aggregated metrics. In addition, the daily SSNM model outperformed random forest and non-spatial models based on the RMSPE and predictive r^2 (Table 4). Overall, daily SSNMs were second-best in terms of predictive performance after the aggregated SSNMs for all metrics besides Frequency Days, for which they were best (Table 4).

Significant difference in the predictive performance of the models was also found for the different metrics. For example, metrics describing magnitude (Max, MWMT, Mean Max) had the greatest predictive performance, followed by the duration metric (Event Days). The frequency of heating events (Frequency Days) had less predictive capacity based on the RMSPE and predictive r^2 values compared to all other metric types (Table 4). Note that, within the magnitude metrics, Mean Max was most accurately predicted based on the RMSPE, followed by MWMT and Max.

4. Discussion

Temperature data are often summarised into relatively simple aggregated metrics to describe the maximum, minimum and mean temperature of a system over a given time period (e.g. weekly, monthly, yearly, or seasonal). However, it is unlikely that any single metric alone will capture multiple aspects of the thermal regime related to the magnitude, frequency, duration and timing of thermal events (Dunham et al., 2005; Arismendi et al., 2013; Butryn et al., 2013). To our knowledge, this is the first comparative assessment of temperature metrics produced from daily predictions, compared to aggregating data through space and time to predict single temperature metrics that describe thermal behaviour of a stream system.

4.1. Models

As expected, SSNMs consistently outperformed RF and non-spatial models in spatial cross-validations of daily predictions, while results of the temporal cross-validation for the three methods were almost identical. This strongly suggests that there is more spatial than temporal variability in stream temperature across the summer period in this river system. Thus, the model's ability to accurately predict through space should be taken into consideration when the goal is to make temperature predictions at unsampled locations across a network. Accurate spatial predictions are important as stream temperature metrics are often used to base stream management decisions as well as being associated with aquatic organismal life history and phenology (Moore et al., 2013). Furthermore, SSNMs provide automatic estimates of uncertainty with each prediction, providing more information about the system than either random forest or non-spatial linear models. However, the results of this study also indicate that the dataset and research question should be considered when making the decision to spend the time implementing SSNMs to predict daily temperatures and metrics; as aggregated metrics outperformed daily models for all but one metric. The benefits and caveats of each method are discussed below.

4.2. Dataset

Data collected over stream networks often exhibit spatial dependence (Isaak et al., 2010; Peterson et al., 2006). Spatially correlated data present problems for many traditional statistical approaches because the assumption of independence is violated, leading to biased parameter estimates due to the spatial clustering of measurements, and artificially small standard error estimates (Legendre, 1993). Hence, if data exhibit spatial dependence, then SSNMs fitted to either aggregated data or daily measurements must be used to avoid violating model assumptions. However, if stream data are not spatially dependent, then machine learning methods such as random forests will likely provide relatively accurate predictions for most temperature metrics. In such cases, however, care must be taken because spatial autocorrelation has been found in stream data at broad spatial scales and between sites that are not connected by flow (Peterson et al., 2006; Peterson and Ver Hoef, 2010). Spatial stream-network models account for spatial dependence in the data, but require more measurements than traditional non-spatial models to estimate the additional model parameters (Isaak et al., 2014). Given the general rule-of-thumb of 10 measurements for each parameter estimate, a minimum of 50–100 measurements are required to fit SSNMs (Isaak et al., 2014). Thus, in cases where spatial autocorrelation is present in the data and the number of observed sites is relatively small, we recommend fitting models to all of the daily temperature measurements, rather than reducing the data based on the number of locations. In fact, daily SSNMs were either second best, or the best models (Frequency Days metric) in terms of predictive ability compared to SSNM models for the aggregated metrics. Conversely, when the spatio-temporal dataset is large, it may be less technologically challenging and time consuming to fit a model to aggregated temperature metrics.

4.3. Metrics: daily vs aggregated

If the overall goal of a study is to calculate metrics describing thermal magnitude (Maximum, MWMT and Mean Max) or duration (Event Days) and the number of sites is large, then our results suggest that fitting SSNMs to daily temperature data provides no benefit. Models of aggregated metrics had better predictive ability compared to daily metrics (Table 4), with the exception of the Frequency Days model. Furthermore, the model fitting process is more computationally efficient for aggregated metrics. For example, it took approximately 6 h on a HPC cluster for daily models compared to approximately 9 min for aggregated models; though as previously mentioned, the reader must consider the potential consequences of reducing the sample size (Isaak et al., 2014).

However, we found that the predictions were more accurate for the daily SSNM Frequency Days model. That said, the Frequency Days models had the poorest predictive performance of all the metrics for both daily and aggregated models. The large RMSPE associated with the aggregated Frequency Days metric compared to other metrics is most likely due the reduced strength of spatial autocorrelation for this particular metric. When maximum temperatures were aggregated into a Frequency Days metric, we potentially reduced and masked spatial correlation, reducing the predictive performance of SSNMs. Our results suggest strong spatial correlation remained in the other four metrics after aggregation, though not for the Frequency Days metric. The reader must be aware that this may potentially also occur for other metrics that were not generated in the present study.

4.4. The complexity of thermal regimes

Traditional views of thermal regimes suggest longitudinal, asymptotic warming along streams until thermal convergence is reached between water and the atmospheric conditions (Vannote et al., 1980; Fullerton et al., 2015). As river research has progressed, the complexity of thermal regimes has been hinted at, and recent research by Fullerton et al. (2015) and Maheu et al. (2015) has attempted to quantify and classify this complexity. These studies suggest that thermal regimes are complex across broad spatial scales and display an extremely diverse array of warming patterns. Furthermore, the drivers of each of these different warming patterns are river dependent, making it difficult to apply research outcomes from a particular system across an entire catchment for management purposes (*sensu* Balcombe et al., 2014). These studies suggest that a single aggregated metric cannot be used to describe complex spatio-temporal thermal regimes. Rather, SSNMs with strategically placed sensors across a network (Som et al., 2014), could be used to predict and accurately characterise a combination of both daily and aggregated metrics describing different characteristics of the thermal regime in streams. It is crucial to understand the unique spatio-temporal context of thermal habitat in stream systems before we can predict climate warming and effects on stream biota (Fullerton et al., 2015), particularly for thermally restricted and threatened species.

4.5. Thermal regimes and aquatic species

A deeper understanding of the physical drivers of species distributions in streams is vitally important for aquatic species with restricted distributions. In many areas, species are predicted to be pushed towards their physiological boundaries, with no option for migration due to the presence of downstream thermal barriers (Chu et al., 2005; Pörtner and Farrell, 2008; Rieman and Isaak, 2010). Thermal data have often been categorised and studied in either a spatial or temporal mindset, but studies examining the two in conjunction are rare (Steel et al., 2012). The advent of relatively inexpensive in situ temperature sensors and spatial stream-network models provide researchers with the tools to create relatively rapid, accurate spatio-temporal information that can be used to ask a variety of ecological questions across both of these scales simultaneously. For example, by predicting a combination of both daily as well as aggregated metrics describing spatio-temporal data, researchers have the flexibility to look at a range of metrics that may link aspects of phenology, physiology and biology to aspects of the thermal regime (Arismendi et al., 2013). Further, by having full, year round daily temperature predictions, researchers can investigate how thermal variability changes throughout the year and how the timing of heating events may shift under warming scenarios, as early onset spawning caused by earlier spring warming has become evident in freshwater systems (Crozier et al., 2008; Isaak et al., 2012).

A large body of stream research literature has focussed on understanding the spatial heterogeneity of temperatures, where temporal data are simplified and summarised across spatial locations to predict how climate induced changes affect organismal distribution and likely population persistence (Torgersen et al., 1999; Rieman et al., 2007; Isaak et al., 2010; Wenger et al., 2011; Ruesch et al., 2012). However, research must include both the temporal shifts in the thermal regime and spatial heterogeneity over a stream network to gain a more holistic understanding of thermal requirements for aquatic organisms. The effect of thermal temporal variation has been explored by Steel et al. (2012), who demonstrated experimentally that temporal heterogeneity in thermal regimes led to significant changes in phenology, inducing changes in emergence timing and development in Chinook salmon (*Oncorhynchus tshawytscha*). Early onset spawning and altered timing of emergence are critical components of a species life-history that can have wide ranging implications, not only at the individual level, but also at population and even species levels (Crozier et al., 2008; Isaak et al., 2012). Early emergence can also significantly alter survival by exposing juveniles to unfavourable environmental conditions including altered flow regimes, or through resource limitations (Brannon, 1987; Crozier et al., 2008).

Temperature increases are expected to alter life history strategies and reproduction in fish, from shifted spawning times to the complete physiological inhibition of reproduction itself, depending on the nature of warming (Morrongiello et al., 2011; Pankhurst and Munday, 2011). For instance, many fish species rely on certain changes in water temperatures to trigger seasonal spawning migration or even the physiological event of spawning itself (Jeppesen et al., 2010; Pankhurst and Munday, 2011). Various aquatic organisms including invertebrates, other fish species, and algae also have life history patterns triggered by changes in the thermal regime, and are thus expected to experience phenological shifts under climate warming (Steel et al., 2012). However, expected changes in optimal spawning and resource emergence are unlikely to occur at the same rate, potentially leading to a mismatch in resource availability and a reduction in juvenile survival (Humphries et al., 1999; Durant et al., 2007; Crozier et al., 2008; Wenger et al., 2011; Otero et al., 2014). This mismatch has been identified as one of the likely causes of severe reductions in threatened species throughout Australia's Murray-Darling Basin (Koehn, 2001; Astles, 2003). Studies focussing on the complexity of the thermal regime are important because stream systems may show no significant differences in common metrics such as mean and maximum temperatures, while the duration and frequency of thermal variability may differ greatly (Arismendi et al., 2013).

4.6. Future directions

Currently, many management decisions focussed on stream systems are made without knowledge about the drivers that shape important instream processes that ultimately determine ecosystem function (Rieman and Isaak, 2010). Thus, it is vitally important to make full and efficient use of the available data, especially given the context of the global changes ecosystems are facing. We are currently shifting into the age of 'big data', and the progression of biological and ecological fields requires a fundamental shift in thinking to identify solutions to complex ecological problems. As Fisher (1997) discussed the need for a paradigm shift from a linear to network-based structure to better understand the complex, dynamic processes occurring within stream systems, a similar change is needed concerning the use of large spatio-temporal datasets. There is a need to change the way we think about spatio-temporally variable in-stream habitat and the subsequent effects on aquatic species life-history processes, and ultimately distributions and abundances. Most of the large body of research focusing on the thermal regime was developed when data were sparse and studies focused on single sites, but research is now moving into a new age where predictions can be obtained for full thermal regimes in a cost-effective manner. Thus, the methods used to analyse such data and extract additional information need to evolve to match the rate of data acquisition. This will in turn allow us to ask more ecologically relevant questions, and provide the critical information needed to make evidence-based management decisions now and into the future.

5. Conclusions

We have demonstrated that for thermal metrics describing the magnitude, duration and frequency of heating events, SSNMs provide more accurate predictions compared to random forest and non-spatial linear models when data are spatially correlated. Furthermore, we have shown that models fit to temporally aggregated temperature data can provide more accurate predictions for metrics describing thermal magnitude and duration, while frequency metrics are improved by using SSNMs of daily predictions over a network; highlighting the need to integrate and adapt the methods currently used to assess thermal regimes. When thermal data are spatially correlated, SSNMs must be used to derive reliable parameter estimates and standard errors. In addition, we demonstrated that they provide accurate predictions of both daily and aggregated metrics, with estimates of uncertainty. However, if the dataset has less than 50 locations, we strongly recommend using SSNMs to create daily predictions of temperature at unobserved locations which can then be used to calculate temperature metrics. For larger datasets (>100 locations), aggregated metrics are recommended with the exception of Frequency Days metrics, which were more accurately predicted by daily predictions. For intermediate datasets (50–100 locations) that exhibit spatial dependence, then SSNMs fitted to either aggregated data or daily measurements are recommended so as to avoid violating model assumptions. The use of SSNMs in conjunction with temporal metrics describing different components of the thermal regime allow researchers to explore new spatio-temporally explicit questions about the thermal regime in stream systems. Furthermore, with a greater understanding on the effects of temperature on ecosystems and their biota, we can begin to explore the interactions between flow, temperature, water quality, land use, and climate effects in an effort to gain a more holistic understanding of freshwater ecosystems. This knowledge will assist in the conservation of species threatened by anthropogenic changes to climate and land use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.02.014.

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